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Nicholas P. Jones

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August 2022

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HALMOS COLLEGE OF ARTS AND SCIENCES

BENTHIC COMMUNITY DYNAMICS AND STONY CORAL DEMOGRAPHICS IN FLORIDA IN RELATION TO ACUTE DISTURBANCES AND CHRONIC PRESSURES

Nicholas P. Jones

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy with a specialty in:

Oceanography and Marine Biology

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General Abstract

The persistence of coral reef communities is threatened by a suite of pressures operating at varying spatial and temporal scales. In general, acute disturbances (short term stochastic events such as marine heatwaves or hurricanes) and chronic pressures, such as ocean warming, have caused the most significant changes to stony coral assemblages (order Scleractinia) and continue to impair recovery potential. Additionally, many coral reefs are subject to local chronic anthropogenic pressures resulting in poor water quality or sedimentation, which further impact stony corals and shape benthic community structure, particularly near urbanized coastlines. For the viability of communities on coral reefs, a balance must be struck between loss following disturbance and recovery (i.e., resilience). The current scientific consensus is that under moderate disturbance regimes, locations subject to less local chronic anthropogenic pressure will be more resilient and the community will recover during inter-disturbance periods. However, given observed and predicted increases in the frequency and severity of acute disturbances under global climate change, resilience may be undermined regardless of contemporary differences in local chronic pressure. Florida's Coral Reef (FCR), stretching 595km from St Lucie Inlet to the Dry Tortugas, exists along a gradient of chronic anthropogenic pressure and was impacted by multiple acute disturbances over the past two decades. This study explored benthic community dynamics and stony coral demographic processes, such as recruitment, growth and mortality, to assess the influence of acute disturbances and chronic pressures on FCR.

Spatiotemporal changes in the benthic community from 2004 to 2018 and stony coral resilience were assessed in relation to acute disturbances, in the three distinct coral reef regions on the FCR: the high-latitude, heavily urbanized Southeast Florida Coral Reef Ecosystem Conservation Area (ECA), the governmentally protected, but historically exploited Florida Keys and the comparatively remote, least exploited Dry Tortugas (Chapter 1). In the ECA, spatiotemporal variations in net growth rates and partial mortality were quantitively analyzed in the three most abundant coral species, *Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea* from 2000 to 2020 (Chapter 2). The influence of water quality and temperature on benthic community composition and interannual changes in stony coral abundance, recruitment, mortality and diversity were analyzed in the ECA from 2018 to 2021, a period with no known acute disturbances (Chapter 3). Finally, spatiotemporal variations in recruitment, density and size structure of the contemporary stony coral assemblage were assessed in the ECA from 2018 to 2022 (Chapter 4)

Overall, stony coral resilience was found to be low across the FCR, regardless of differences in chronic pressure, with significant declines in cover during periods with acute disturbances, limited recovery during inter-disturbance periods and corresponding proliferation of macroalgae. High partial and whole colony mortality, predominately related to acute disturbances and stony coral tissue loss disease, constrained net growth rates in *M. cavernosa*, *P. astreoides* and *S. siderea*, such that colonies reached just a third of their potential size. Recruitment was generally low in the ECA, averaging 0.95 ±0.2 recruits m^{-2} (± SE). *Siderastrea siderea* recruitment was high at some inshore sites (~7 recruits m^{-2}), but there was limited evidence these survived or grew into larger size classes. Spatial decoupling between recruitment, size structure and survival likely maintains a preponderance of small colonies in the ECA. Higher water temperature, particularly when annual mean water temperature was above 27 °C, was positively associated with stony coral recruitment, abundance and health, until threshold maximum temperatures were exceeded (>31 °C). The benefits associated with warmer temperatures were negated by poor water quality, as nutrient enrichment was related to increased macroalgae cover, reduced coral recruitment and higher partial mortality. At present the future for stony corals in Florida is bleak. High acute disturbance frequency, from a multitude of different stressors, and chronic environmental pressures were related to consistent declines in cover, high partial colony mortality which constrains growth and a degraded coral community composed of small colonies, primarily of weedy or resistant species. However, the data suggests reducing local chronic pressures in the ECA may limit increases in macroalgae cover and enhance stony coral recovery potential during inter-disturbance periods, particularly when temperatures are optimal. Urgent action to tackle global climate change and local anthropogenic pressures is therefore required for these coral communities to have any realistic prospect of recovery.

Keywords: Florida Reef Tract, Florida's Coral Reef, southeast Florida, resilience, recovery, growth, recruitment, temperature, water quality, *Montastraea cavernosa*, *Porites astreoides*, *Siderastrea siderea*

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Completing this dissertation has required immense support from many wonderful family members, friends and colleagues. First and foremost, huge thanks to my advisor Dr. Dave Gilliam for his incredible guidance and friendship during my master's and PhD. You've given me the support and flexibility to design and complete the project, as well as taken me to some fantastic places and shared some much-needed drinks, cheers! Thanks to my committee members, Drs. Zan Milligan, Matt Johnston and Morgan Pratchett for discussions, advice and critiques of my research that have vastly improved me as a scientist and writer. I thank the past and present members of the NSU Coral Reef Restoration, Assessment and Monitoring Lab, the Fish & Wildlife Research Institute and the NSU Water Quality Monitoring Team for the thousands of monitoring dives and boat hours spent collecting the data used in this dissertation. Within the FWRI team, special thanks to Rob Ruzicka and Mike Colella at FWC for extensive help, particularly designing and editing chapter 1. I further thank my friends and colleagues in the CRRAM lab and at Nova Southeastern University that have kept me sane and laughing during some challenging times in the office, working from home and in the field.

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Chapter 1. Frequent disturbances and chronic pressures constrain stony coral recovery on Florida’s Coral Reef

Abstract

Acute disturbances and chronic pressures have an important and increasing influence on the structure of coral reef communities. For the viability of benthic taxa such as stony corals, a balance between loss following disturbance and recovery is vital. Coral reefs with lower exposure to chronic pressures are often presumed to have increased recovery potential and hence resilience, but decades of anthropogenic stress and degradation may undermine systematic resilience in benthic communities. This study explored spatiotemporal changes in benthic community structure over a 15-year period at three distinct coral reef regions with a gradient of chronic pressures in Florida, USA, (southeast Florida, the Florida Keys and the Dry Tortugas). I specifically assessed the spatial scale, potential drivers of change and resilience in stony coral, octocoral, sponge and macroalgae cover. Spatiotemporal changes were assessed at four different scales: among regions, habitats, sub-regions, and habitat types within regions. Cover of stony corals remained very low or declined in every region from 2004 to 2018, with corresponding increases in macroalgae cover. Stony coral recovery was limited regardless of regional differences in chronic pressure. Octocorals exhibited greater resilience and generally had greater cover than stony corals on Florida’s Coral Reef, while cover of sponges was very stable over the study period. Acute disturbances, which affected sites on average once every three years, negatively impacted stony coral and/or octocoral cover in every region and habitat, contributing to the regionwide proliferation of macroalgae. This study determined that high disturbance frequency and chronic anthropogenic pressures on Florida’s Coral Reef have led to sustained declines in stony corals and corresponding proliferation of macroalgae. Stony corals were expected to recover during inter-disturbance periods, but on degraded reefs, even in locations with lower chronic pressure, recovery is severely limited. Further efforts to minimize anthropogenic pressures are urgently needed for these reefs to have any prospects for recovery.

Keywords: Florida Reef Tract; long-term monitoring; octocoral; sponges; macroalgae; benthic community

Introduction

Coral reefs are threatened by diverse and increasing pressures, operating at varying spatial and temporal scales (Hughes and Connell 1999; Porter et al. 1999; Hoegh-Guldberg et al. 2007; Hughes et al. 2018a; Lapointe et al. 2019). On many coral reefs, acute disturbances (short term stochastic events such as hurricanes and acute thermal stress) and chronic pressures (longer-term underlying factors, such as ocean warming, poor water quality and overfishing) have resulted in significant losses of stony (order Scleractinia) corals (Jackson et al. 2001; Knowlton and Jackson 2008; Graham et al. 2013; Hoegh-Guldberg et al. 2017; Lapointe et al. 2019). The ability to resist or recover from disturbance (i.e., resilience) fundamentally influences the contemporary state and trends in the composition of benthic communities. Under moderate disturbance regimes, stony coral cover on resilient coral reefs is expected to recover (Wilkinson 1999; Graham et al. 2015; Pratchett et al. 2020), however on degraded reefs, which have experienced sustained or repeated coral loss, resilience may be undermined, limiting stony coral recovery and facilitating community change (Bellwood et al. 2004; Hughes et al. 2013; De Bakker et al. 2017). Given observed and projected increases in the frequency and severity of major disturbances on coral reefs under global climate change, it is important to understand how chronic pressures influence the susceptibility or resilience of coral communities to contemporary and changing disturbance regimes (Graham et al. 2013; MacNeil et al. 2019; Pratchett et al. 2020).

Whether a coral reef community exhibits resilience, reflecting its ability to absorb a disturbance and recover (e.g., the rate at which community cover returns to its pre-disturbance level) is likely to vary across habitats or locations. These spatiotemporal variations reflect the community composition, the presence of chronic pressures and the type, frequency and severity of disturbance events (Bruno et al. 2009; Johns et al. 2014; Graham et al. 2015; Pratchett et al. 2020). Thermal stress and hurricane impacts are known to be heterogenous on coral reefs over time and space with variable impacts on benthic taxa and community dynamics (Hughes 1994; Gardner et al. 2005; van Woesik et al. 2011; Hughes et al. 2018b; Muñiz-Castillo et al. 2019; Jones et al. 2020). Chronic pressure may vary based on governmental protection, historic exploitation, isolation from human population centers, local stressors and latitude and can additionally influence the resilience of stony corals and other benthic fauna, magnifying the impact of acute disturbances and limiting recovery capacity (Knowlton and Jackson 2008; Carilli et al. 2009; Beger et al. 2014; Vergés et al. 2014). In particular, reefs with comparatively low chronic pressures, e.g., remote reefs further from human habitation, those subject to less eutrophication, or those with active local protection, are expected to be most resilient (Graham et al. 2015; De Bakker et al. 2016; Weijerman et al. 2018). On severely degraded reefs with depauperate coral communities, if disturbance frequency is too high or on reefs with persistent chronic pressures systematic resilience may be undermined, leading to sustained stony coral loss (Riegl et al. 2017; Donovan et al. 2018; Ortiz et al. 2018; Pratchett et al. 2020). Because many factors determine coral reef resilience, there is an increased need to explore spatiotemporal variation in benthic community dynamics in response to acute disturbances across a variety of reef locations that vary in exposure to chronic environmental pressures and are in different stages of reef degradation.

Florida's coral reefs have endured a long history of anthropogenic degradation (Pandolfi et al. 2005; Ruzicka et al. 2013; Lapointe et al. 2019). Acute disturbances, particularly thermal stress, disease outbreaks and hurricanes have contributed to substantial declines in cover of the two major framework builders, *Orbicella* spp. and *Acropora* spp., since at least the 1970s (Gladfelter 1982; Porter and Meier 1992; Precht and Miller 2007; Toth et al. 2019). In recent decades, stony coral cover and abundance has declined throughout much of the Florida Keys and in the Dry Tortugas following disease outbreaks and thermal stress, with the 1997/98 bleaching event particularly severe (Santavy et al. 2011; Ruzicka et al. 2013). Shallow forereefs in the Florida Keys, which had the majority of their cover comprised of *Acropora palmata* and *Millepora complanata* demonstrated limited stony coral recovery from these acute disturbances, which precipitated the transition to octocorals becoming the predominant benthic taxa in this habitat (Ruzicka et al. 2013). Meanwhile, stony coral abundance recovered within a few years in the comparatively remote Dry Tortugas (Santavy et al. 2011). While the Florida Keys is widely studied, long-term changes in the benthic community across all of Florida's Coral Reef (FCR) have not been investigated and the disturbance history of the benthic communities in the southeast Florida and Dry Tortugas regions are poorly documented.

The purpose of this study was to explore temporal changes in benthic community structure on Florida's Coral Reef (2004 to 2018), explicitly testing variability in the resilience of benthic communities at a range of spatial scales. To do this, I analyzed variation in stony coral, octocoral, sponge and macroalgae cover using long-term monitoring data collected annually at permanent sites in the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA), Florida Keys and in the Dry Tortugas as part of the Southeast Coral Reef Evaluation and Monitoring Project (SECREMP) and the Coral Reef Evaluation and Monitoring Project (CREMP). The specific questions motivating this research were: 1. Does variability in chronic pressure and protection status influence the response of stony coral, octocoral, sponge and macroalgae to acute disturbances, thereby influencing the community trajectory? 2. Is there apparent recovery in stony coral cover during inter-disturbance periods? The high-latitude ECA is a largely degraded system offshore of a heavily developed and populated coastline, with three major ports and limited government protection (Finkl and Charlier 2003). The Florida Keys have been formally protected since 1990 as part of the Florida Keys National Marine Sanctuary, but were heavily exploited historically and impacted by terrestrial runoff and water flow from Florida Bay (Ginsburg and Shinn 1995; Ruzicka et al. 2013). The Dry Tortugas National Park is furthest from human habitation at the remote western edge of the Florida Keys National Marine Sanctuary and considered the least exploited of the three regions. I hypothesize these regional differences predispose them to variations in resilience and benthic community recovery trajectories, with comparatively low coral cover reefs in the high-latitude, heavily urbanized, ECA having low stony coral resilience, and more developed coral reefs with low chronic pressure and active management designed to minimize localized anthropogenic pressures in the comparatively remote Dry Tortugas, demonstrating greater resilience and increased stony coral cover recovery between disturbances (Ortiz et al. 2018; Mellin et al. 2019).

Methods

Florida's Coral Reef

Florida's Coral Reef (FCR; previously referred to as the Florida Reef Tract) spans 595 km from Martin County to the Dry Tortugas (Fig. 1). It is generally split into three regions based on coastal geomorphology and hydrology: the high-latitude coral communities of southeast Florida, the Florida Keys and the comparatively remote Dry Tortugas (Hoffmeister and Multer 1968; Shinn and Jaap 2005; Banks et al. 2008; Finkl and Andrews 2008; Walker and Gilliam 2013). Coral reefs within the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) are towards the northern limit of coral distribution in the western Atlantic and extend from St Lucie Inlet to Biscayne Bay offshore mainland southeast Florida and the major international ports, Port

Everglades and Port of Miami. The Florida Keys National Marine Sanctuary protects over 9,900 km^2 of water surrounding the Florida Keys and Dry Tortugas. The ~260 km^2 Dry Tortugas National Park (113 km west of Key West), is furthest from human habitation, includes an exclusion zone where fishing and anchoring is prohibited and is considered the least exploited of the three regions. In each region, there are multiple reef habitats found on an inshore to offshore gradient.

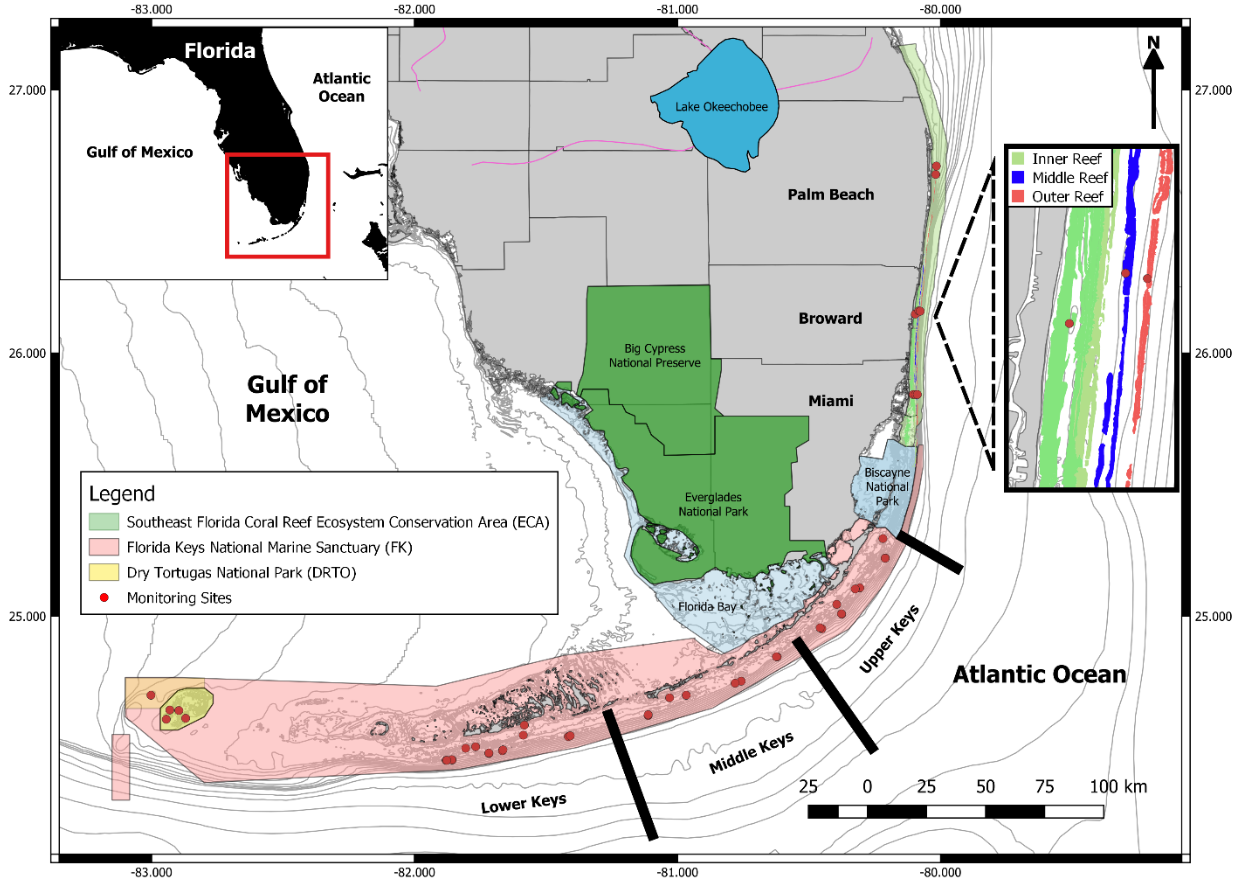

Figure 1. Florida’s Coral Reef with the three regions (Southeast Florida Coral Reef Ecosystem Conservation Area, Florida Keys and Dry Tortugas), sub-regions (Palm Beach, Broward, Miami, Upper Keys, Middle Keys, Lower Keys, Dry Tortugas) and monitoring sites. Note: DRTO sites are within the Dry Tortugas National Park and North Tortugas Ecological Reserve. Site depths ranged from 2m to 22m. Inset top left: Florida, with south Florida highlighted. Inset middle right: Habitats in the ECA (Inner, middle and outer reefs), for clarity of inshore to offshore spatial variability, only habitats within Broward are shown.

Spatial Designations

Changes in benthic community taxa were assessed at four scales on the FCR: Region, Sub-region, Habitat and Regional Habitat (Habitat within region). Each region (ECA, Florida Keys and Dry Tortugas) contains multiple reef habitats (e.g., patch reef or forereef). The ECA, divided north to south into the Palm Beach, Broward and Miami sub-regions, comprises three parallel linear reef habitats (inner: 6-8 m depth, middle: 12-14 m and outer: 18 m; Fig. 1 inset, Table S1) and a nearshore ridge complex with predominately low coral cover benthic communities. These all lie within 3 km of a heavily urbanized coastline (Banks et al. 2008; Jones et al. 2020). During analysis, sites on the nearshore ridge complex and inner reef which are at comparable depth and have higher relative stony coral cover in comparison to the middle and outer reefs were grouped to enhance replicates. The Palm Beach sub-region only contains outer reef habitats, the Broward and Miami sub-regions contain all three habitats. Southwest from the ECA, the Florida Keys National Marine Sanctuary covers the Florida Keys (FK) and offshore Dry Tortugas. Patch reef (2-10 m depth), shallow forereef (2-7 m) and deep forereef (11-16 m) habitats are found in the Florida Keys, which is divided east to west into the Upper Keys, Middle Keys and Lower Keys sub-regions (each contains all three habitats). The Dry Tortugas (DRTO) contains patch (5-10 m depth) and deep forereef (14-22 m) habitats and is not divided into sub-regions (Table S1).

Disturbances

The occurrence and spatial extent of major disturbances was determined through a comprehensive review of published literature during the study period (Lirman et al. 2011; Ruzicka et al. 2013; Walton et al. 2018; Kobelt et al. 2019; Muller et al. 2020). FCR wide heat stress was reported in 2005, 2014 and 2015, statewide hurricanes reported in 2005 and 2017 and a severe cold stress event reported on FK patch reefs in 2010 (Wilkinson and Souter 2008; Eakin et al. 2010; Lirman et al. 2011; Eakin et al. 2018). Heat stress and hurricane impacts were considered in relation to cover change the year after disturbance. Cold stress impact, which occurred in January/February prior to annual surveys, was considered in relation to 2010. Additionally, a disease outbreak, termed stony coral tissue loss disease (SCTLD; NOAA 2018) had a major effect on the ECA from 2014-2017, Upper Keys from 2016-2018 and Middle Keys from 2017-2018. The disease had not yet reached the Lower Keys or Dry Tortugas during the study period. Years with multiple disturbances were classified separately (e.g., 2015 in the ECA had both heat stress and disease) as both disturbances may have influenced the benthic community. Major disturbance frequency calculated as the average number of years an acute disturbance (cold stress, disease outbreak, heat stress or hurricane) was recorded to affect a site.

Data Collection

Data was compiled from annually repeated surveys conducted during summer months (May to August) at 45 permanent sites: eight sites along the ECA, 32 sites in the FK and five sites in the DRTO, four within the National Park boundary and one just outside in the North Tortugas Ecological Reserve (Fig. 1, Table S1). Each site comprised four 22 m long permanent transects marked with stakes at each end. Linearly along each transect ~60 abutting images, each 40 cm wide were taken at a fixed distance from the substrate covering ~8.8m^2 of hardbottom per transect. Images were analyzed using PointCount '99 to determine percent substrate coverage (Dustan et al. 1999); for each image, the benthic taxa were identified at 15 randomly placed points, for a total of 900-1000 points per transect. Benthic taxa were categorized as stony corals (Scleractinians and Milleporids), octocorals, sponges, macroalgae (grouped with cyanobacteria), zoanthids, turf algae/substrate, and other taxa (e.g., hydroids, anemones etc.). Broad taxonomic groups were used following other analyses for the region (e.g., Ruzicka et al. 2013). Stony corals were not analyzed at the species level due to very low stony coral species cover at numerous sites. Four benthic taxa categories are analyzed here (stony corals, octocorals, sponges and macroalgae). Methods used to collect images and estimate percent cover are described in more detail in Somerfield et al. (2008), Ruzicka et al. (2013) and Gilliam et al. (2019).

Statistical Analysis

Spatiotemporal Changes

Univariate analysis of spatiotemporal changes in percent cover of stony coral, macroalgae, octocoral, and sponge were conducted in R (R Core Team 2020). Binomial generalized linear mixed models (GLMMs) were created for each of the four benthic taxa categories using the "glmmTMB" function from the package of the same name (Brooks et al. 2017). For each taxon, a single model, with transects as replicates (n =2441), was used to assess how each response variable (stony coral, octocoral, sponge or macroalgae cover) changed temporally and the predominant spatial scale it was changing at over the FCR. A two-stage approach was used for model selection. First, the random effect structure was determined to account for the hierarchical structure of the data using Akaike Information Criterion (AIC), from the options, Site, Site nested within Habitat, Site nested within Sub-region or Site nested within region. Second, each response variable was assessed in relation to multiple factors: Year, Region, Sub-region, Habitat (patch reef, deep forereef etc.), Regional Habitat (habitat within a region) and Depth. A complete backwards stepwise approach was not possible; therefore, AIC was used to determine the fitted model from multiple candidate models containing temporal and/or spatial factors and their interaction (e.g., Equation 1). ‘Year’ was assessed as a categorical factor because temporal trends are unlikely to be linear, such that univariate trends were not skewed by the first or last survey years and so that changes within specific time periods could be examined during post-hoc analysis.

$$\text{Logit (Stony coral cover)} = \text{Year x Region} + \text{Depth} + (1|\text{ Habitat/Site}) \qquad \text{Equation 1}$$

Model validation was performed using the package “DHARMa”, with residual diagnostics, including overdispersion, heterogeneity and temporal autocorrelation, conducted on the fitted model (Hartig 2017). Temporal autocorrelation was found in sponge cover and a first order auto-regressive correlation structure fitted. Post-hoc, pairwise assessment of retained factors in the fitted models were conducted using the package “emmeans”, where differences in the response variable (e.g., stony coral cover) are analyzed between levels of a factor (e.g., Year) or interaction (e.g., Year x Habitat) based on model predictions (Lenth 2019). Between year differences in post-hoc analyses were considered significant at $p < 0.05$ (Table S2-5). The 2004 to 2018 time period was chosen specifically to maximize the number of sites surveyed in each region, allowing for consistent spatiotemporal comparisons within the time period.

Disturbances and Stony Coral Cover

I calculated relative and absolute annual rates of stony coral cover change each year at each site independently and then statistically analyzed the rate of stony coral cover change by disturbance type (cold stress, disease, heat stress, hurricane, multiple disturbances or non-disturbance) using Kruskal-Wallis non-parametric analysis of variance. I compared the rate of stony coral cover change between disturbance types and the rate of stony coral cover change for each disturbance type between regions, habitat and regional habitats. Kruskal-Wallis was used as data were non-normal even after transformation and validation of GLMMs suggested models were invalid. Both relative and absolute rate of change were assessed to enable comparisons with other studies and to contextualize the relative and absolute rates of change due to very low coral cover at some sites.

Benthic Community Structure

Multivariate assessment of benthic community cover composition (stony coral, octocoral, sponge, macroalgae, substrate/turf algae, zoanthids, other taxa) was conducted in Primer 7 (Clarke and Gorley 2006). Prior to generation of Bray-Curtis similarity coefficients, data were square root transformed. Transformation reduced the importance of abundant taxa and allowed mid-range and rarer taxa to influence the similarity calculation. Spatiotemporal variation in benthic community cover (2004-2018; n = 2441) was statistically analyzed using Permutation Analysis of Variance (PERMANOVA, Anderson 2001; McArdle and Anderson 2001). Type 3 PERMANOVA based on 9999 permutations of residuals under a reduced model was used to analyze benthic cover with transects as replicates. Similarity matrices were assessed by the fixed spatiotemporal factors: Year, Region, Sub-region and Regional Habitat. Site was included as a random factor. To account for the hierarchical structure of the data, site was nested within regional habitat, sub-region and region. Sub-region and regional habitat were each nested within region. Multivariate results were considered significant at $p < 0.05$. For visual assessment of similarity between regional habitats and years and between regions and years threshold metric multidimensional scaling (tmMDS) plots were created by calculating the distance among centroids from the Bray-Curtis resemblance matrix (Anderson 2017). Each sample in the tmMDS represents each regional habitat at one time point and the distance between samples depicts the similarity in community composition (i.e., the closer a sample, the more similar the community composition). Benthic community trajectories were plotted and the origin of differences between regional habitats visually assessed by plotting taxon vectors onto the tmMDS.

Results

Model selection and Spatial Scale of Temporal Change

Temporal variation in percentage cover for each of the four major categories of benthic organisms (stony corals, octocorals, sponges and macroalgae) occurred at multiple spatial scales (Table 1). Temporal changes in cover of stony coral, octocoral and sponge varied most strongly by regional habitat (i.e., habitat within region). Macroalgae cover varied most strongly by sub-region (Table 1). The minimum adequate model for stony coral cover contained depth, year and regional habitat, with a significant interaction between year and regional habitat and stony coral cover increasing with depth (GLMM, marginal R^2 = 0.244, conditional R^2 = 0.317, where the conditional R^2 accounts for fixed and random factors and the marginal R^2 accounts for fixed factors only; Supplementary Table 2). Octocoral cover varied by year and regional habitat, with a significant interaction between year and regional habitat (GLMM, marginal R^2 = 0.020, conditional R^2 = 0.156). Sponge cover increased with depth and varied by year and regional habitat, with a significant interaction between year and regional habitat (GLMM, marginal R^2 = 0.212, conditional R^2 = 0.281). Macroalgae cover varied by year and sub-region, with a significant interaction between year and sub-region (GLMM, marginal R^2 = 0.133, conditional R^2 = 0.241). The random effect site nested within habitat was chosen for stony coral and macroalgae cover models to account for the hierarchical structure of the data as it had the lowest AIC value of the random effect structures, with acceptable model residuals; the random effect site was used for octocoral and sponge cover.

Table 1. Candidate models for each benthic taxon. Fitted model, in bold, chosen as candidate model with the lowest AIC. If multiple models had AIC within two, the simplest model was chosen as the fitted model. Conditional R^2 calculated using fixed and random effects from fitted model, marginal R^2 based upon fixed effects only.

Taxon	**Candidate Model**	**AIC**	**Conditional R^2**	**Marginal R^2**
Stony Coral	Year + (1|Habitat/Site)	46915.0		
	Year x Region + (1|Habitat/Site)	46469.6		
	Year x Habitat + (1|Habitat/Site)	45789.8		
	Year x Regional Habitat + (1|Habitat/Site)	44849.8		
	Year x Sub-Region + (1|Habitat/Site)	45125.7		
	Year x Regional Habitat + Depth + (1|Habitat/Site)	**44847.2**	**0.317**	**0.244**
Macroalgae	Year + (1|Habitat/Site)	174437.9		
	Year x Region + (1|Habitat/Site)	146063.3		
	Year x Habitat + (1|Habitat/Site)	141892.2		
	Year x Regional Habitat + (1|Habitat/Site)	134350.8		
	Year x Sub-Region + (1|Habitat/Site)	**131462.6**	**0.241**	**0.133**
	Year x Sub-Region + Depth + (1|Habitat/Site)	131464.5		
Octocoral	Year + (1|/Site)	71834.1		
	Year x Region + (1|/Site)	69130.2		
	Year x Habitat + (1|/Site)	66844.8		
	Year x Regional Habitat + (1|/Site)	**64156.8**	**0.156**	**0.02**
	Year x Sub-Region + (1|/Site)	64412.0		
	Year x Regional Habitat + Depth + (1|/Site)	64158.6		
Sponge	Year + (1|/Site)	25879.0		
	Year x Region + (1| /Site)	25024.1		
	Year x Habitat + (1|/Site)	24230.5		
	Year x Regional Habitat + (1|/Site)	24153.0		
	Year x Sub-Region + (1|/Site)	24576.1		
	Year x Regional Habitat + Depth + (1|/Site)	**24136.4**	**0.284**	**0.212**

Benthic Taxa Cover Temporal Change

Univariate analysis revealed significant spatiotemporal variation for each of the four major categories of benthic organisms (stony corals, octocorals, sponges and macroalgae; Fig. 2). Stony coral cover significantly declined in six of eight regional habitats from 2004 to 2018: on the ECA inner and outer reefs, in all habitats in the FK and on deep forereefs in the DRTO (emmeans comparisons, $p < 0.01$; Table 2). Stony coral cover declined slightly, but not significantly on the ECA middle reef. Stony coral cover increased slightly, but not significantly from 2004 to 2018 on DRTO patch reefs. Octocoral cover significantly increased on the ECA inner reef ($p = 0.02$) and on DRTO patch and deep forereefs ($p < 0.01$) from 2004 to 2018. Octocoral cover declined on the ECA middle reef and outer reef, and on FK patch reefs and FK deep forereefs from 2004 to 2018 ($p < 0.001$). Sponge cover significantly increased on the ECA inner reef and FK and DRTO patch reefs from 2004 to 2018 ($p < 0.05$). Macroalgae cover fluctuated widely over the study period (Fig. 2, Table 2 & Fig. S1), but significantly increased in all seven sub-regions from 2004 to 2018 ($p < 0.001$), most noticeably in the Upper Keys (11.8 ±2.3% to 23.4 ±2.1%), Middle Keys (10.6 ±2.2% to 21.6 ±3.0%) and the DRTO (7.9 ±2.2% to 32.4 ±3.0%).

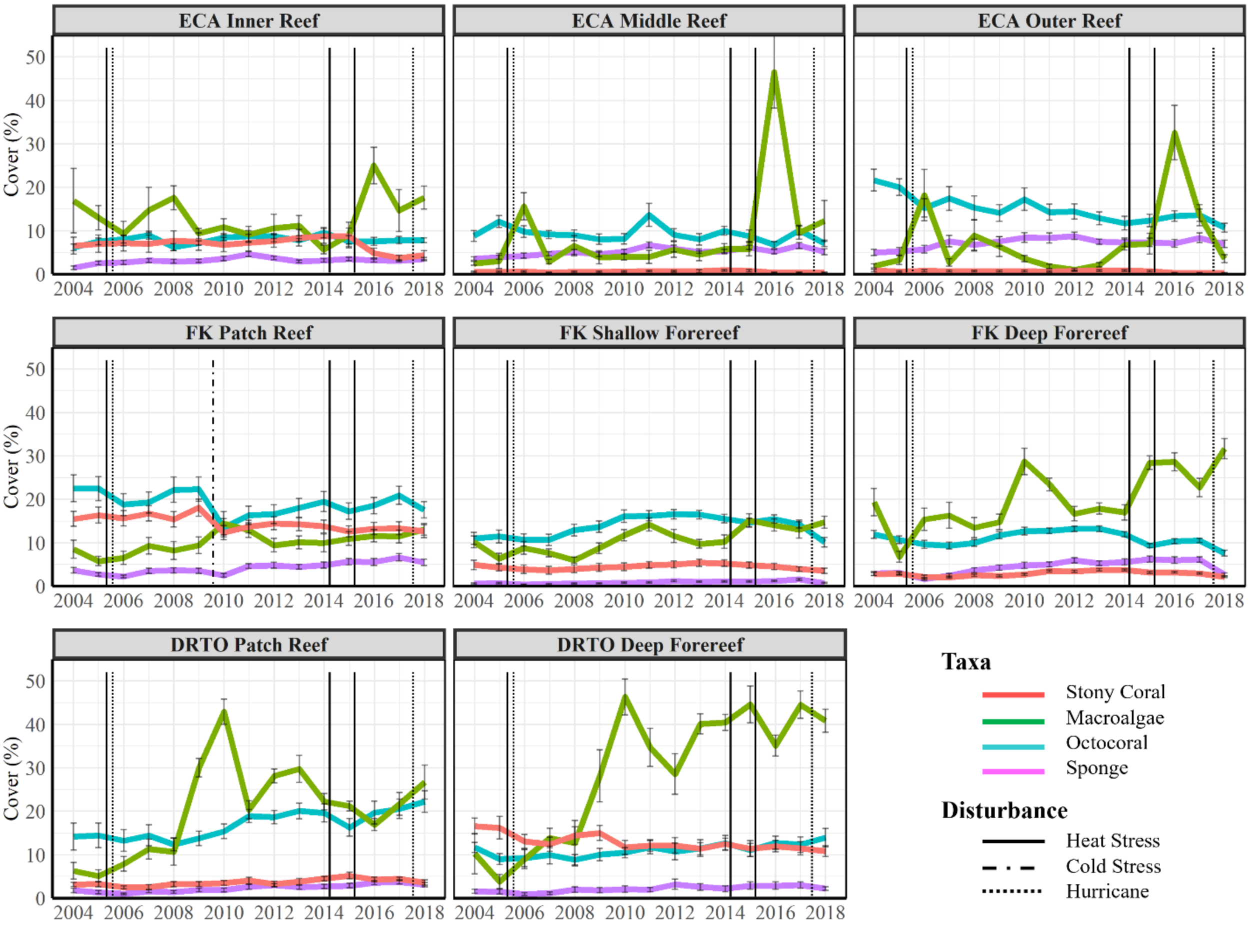

Figure 2. Mean percent cover (±SE) of stony coral, macroalgae, octocoral and sponge on Florida's Coral Reef. Top panel = ECA habitats, Middle Panel = FK habitats, Bottom Panel = DRTO habitats. Depth increases L – R. FK patch and shallow forereefs are at comparable depths. Interannual significant differences in cover of each taxon can be found in Tables S2-S5. Disturbance event indicated by vertical lines. Disturbance types are differentiated by line type. Disease, which was present in the ECA from late 2014 and progressed east to west in the Florida Keys from 2016 onwards, is not noted on the figure to avoid misinterpretation, as it was recorded on a site-by-site basis annually.

Spatiotemporal Changes in Benthic Cover

Interannual variation in cover of stony corals, octocorals, sponges and macroalgae were found throughout the study, especially between periods with acute disturbance: 2005 to 2006, 2009 to 2010, 2014 to 2015, 2015 to 2016, and 2017 to 2018 (Fig. 2; Tables S2-S5). Stony coral cover recovery was generally limited during inter-disturbance periods, and stony coral cover only significantly increased between years in the FK: from 2006 to 2007 and from 2008 to 2009 on FK patch reefs, from 2010 to 2011 on FK shallow and deep forereefs (statistical significance at $p < 0.01$ from emmeans comparisons of GLMMs unless stated; Table 2). In contrast, year to year declines in stony coral cover were often frequent, occurring in at least one regional habitat during eight of fourteen interannual periods, and generally following acute disturbance (Table S2). Stony coral cover declined at least once interannually in seven of eight regional habitats ($p < 0.05$), only not declining on the ECA middle reef where stony coral cover was already negligible. Octocoral cover declined at least once following disturbance in every regional habitat. Octocoral cover did recover after some disturbances, significantly increasing interannually in seven regional habitats ($p < 0.05$; Table S4). Sponge cover was relatively consistent throughout the study and positively changed three times in the FK: once on patch reefs (2010 to 2011; $p < 0.0001$), twice on deep forereefs (2006 to 2007, 2007 to 2008; $p < 0.05$) and only declining twice after hurricanes on both shallow and deep forereefs (2005 to 2006, 2017 to 2018; $p < 0.01$).

Macroalgae cover fluctuated widely in all sub-regions throughout the study, sometimes but not always in relation to acute disturbance (Fig. S1; Table S3). Macroalgae cover changed significantly in 12 of 14 years in the Dry Tortugas, the Middle and Upper Keys ($p < 0.001$; increasing eight, seven and seven times), in 13 of 14 years in Palm Beach and Miami ($p < 0.002$, increasing seven and five times) and in every year in the Lower Keys and Broward ($p < 0.01$, increasing eight and seven times).

Table 2. Sum of interannual statistically significant changes in stony coral, octocoral, sponge and macroalgae cover identified by emmeans post hoc comparisons of fitted GLMMs ($p < 0.05$); + indicates number of periods cover significantly increased, - indicates number of periods cover significantly decreased, = indicates number of periods taxa did not significantly change. Mean percentage cover of each taxon (% ±SE) at the start of the study period (2004) and at the end of the study period (2018). Asterisk in 2018 column indicates a significant change in taxon cover from 2004 to 2018 identified by emmeans post hoc comparisons of fitted GLMMs ($p < 0.05$). Note, although macroalgae cover varied most strongly by sub-region (Table 1 & Fig S2), cover change by regional habitat is included here for comparison.

Region	**Habitat**	**Stony Coral**					**Octocoral**					**Sponge**					**Macroalgae**				
		+	-	=	**2004**	**2018**	+	-	=	**2004**	**2018**	+	-	=	**2004**	**2018**	+	-	=	**2004**	**2018**
ECA	**Inner**	0	1	13	**6.6 ±2.0**	**4.4 ±1.0***	1	2	11	**6.2 ±0.7**	**7.8 ±0.6***	0	0	14	**1.5 ±0.4**	**3.5 ±0.4***	5	5	4	16.9 ±7.4	17.6 ±2.6
	Middle	0	0	14	0.6 ±0.2	0.4 ±0.1	4	4	6	**8.8 ±1.2**	**7.1 ±0.7***	0	0	14	3.6 ±0.4	5.2 ±0.7	6	4	4	**2.5 ±0.4**	**12.3 ±4.7***
	Outer	0	1	13	**0.8 ±0.3**	**0.3 ±0.1***	2	7	5	**21.6 ±2.5**	**10.7 ±1.0***	0	0	14	5.0 ±0.7	7.0 ±0.8	6	7	1	**1.9 ±0.5**	**3.6 ±2.4***
FK	**Patch**	2	3	9	**15.5 ±1.7**	**12.6 ±1.5***	6	4	4	**22.5 ±3.1**	**17.6 ±1.9***	1	0	13	3.7 ±0.6	5.5 ±0.7	5	4	5	**8.6 ±2.1**	**13.1 ±1.4***
	Shallow	1	2	11	**4.9 ±1.0**	**3.6 ±0.6***	2	4	8	11.0 ±1.3	10.2 ±1.1	0	2	12	0.6 ±0.1	0.7 ±0.1	6	7	1	**10.2 ±1.4**	**14.7 ±1.4***
	Deep	1	3	10	**2.8 ±0.3**	**2.2 ±0.2***	2	5	7	**12.0 ±0.9**	**7.6 ±0.6***	2	2	10	2.9 ±0.4	2.7 ±0.3	6	5	3	**19.4 ±3.2**	**31.7 ±2.3***
DRTO	**Patch**	0	1	13	3.2 ±0.5	3.6 ±0.6	3	2	9	**14.2 ±3.1**	**22.3 ±2.5***	0	0	14	**1.8 ±0.5**	**3.1 ±0.5***	7	3	4	**6.3 ±1.9**	**26.8 ±3.9***
	Deep	0	2	12	**16.6 ±1.9**	**10.8 ±1.2***	0	1	13	**11.7 ±0.1**	**13.9 ±2.1***	0	0	14	1.6 ±0.4	2.2 ±0.4	7	5	2	**10.2 ±5.7**	**40.9 ±2.6***

Disturbances and Stony Coral Cover

In years with heat stress or multiple disturbances (e.g., heat stress and hurricane) stony coral cover decline was greater than when no disturbance was reported (Fig. 3 and Fig. S2; Kruskal Wallis; $H = 58.274$, $df = 5$, $p < 0.0001$; $H = 46.137$, $df = 5$, $p < 0.0001$, respectively). There were no locations on the FCR where stony coral cover recovered significantly faster (measured as change in relative or absolute cover) during inter-disturbance periods or declined greater after heat stress or multiple disturbances at any broad spatial scale (region, habitat or regional habitat; Kruskal-Wallis; $p > 0.05$). In years with no disturbance, relative stony coral cover increased by an average 8.3% per year (± 1.53 SE), but this only accounted for an absolute increase of 0.15% per year (± 0.06 SE). In each region, habitats closest to shore had slightly, but not significantly higher increases in absolute stony coral cover during periods of no disturbance (ECA inner = 0.23 ±0.2% per year; FK patch reefs = 0.42 ±0.24 % per year; DRTO patch reefs = 0.23 ±0.15% per year). Stony coral cover significantly increased during the longest inter-disturbance period on ECA inner reefs (2006 to 2014; GLMM, $p < 0.05$), on FK patch reefs (2006 to 2009; GLMM, $p < 0.0001$), on FK shallow and deep forereefs (2006 to 2013; GLMM, $p < 0.0001$) and on DRTO patch reefs (2006 to 2013; GLMM, $p < 0.0001$). In contrast, following years with multiple disturbances, relative stony coral cover declined by an average 13.23% per year (±5.06 SE), corresponding to an absolute decline of 0.66% per year (±0.14 SE). Average relative decline following years with heat stress was 5.63% per year, corresponding to an absolute decline of 0.26% per year (±0.14 SE). The greatest absolute decline in cover occurred on FK patch reefs, following cold stress (4.3% ±3.46 SE).

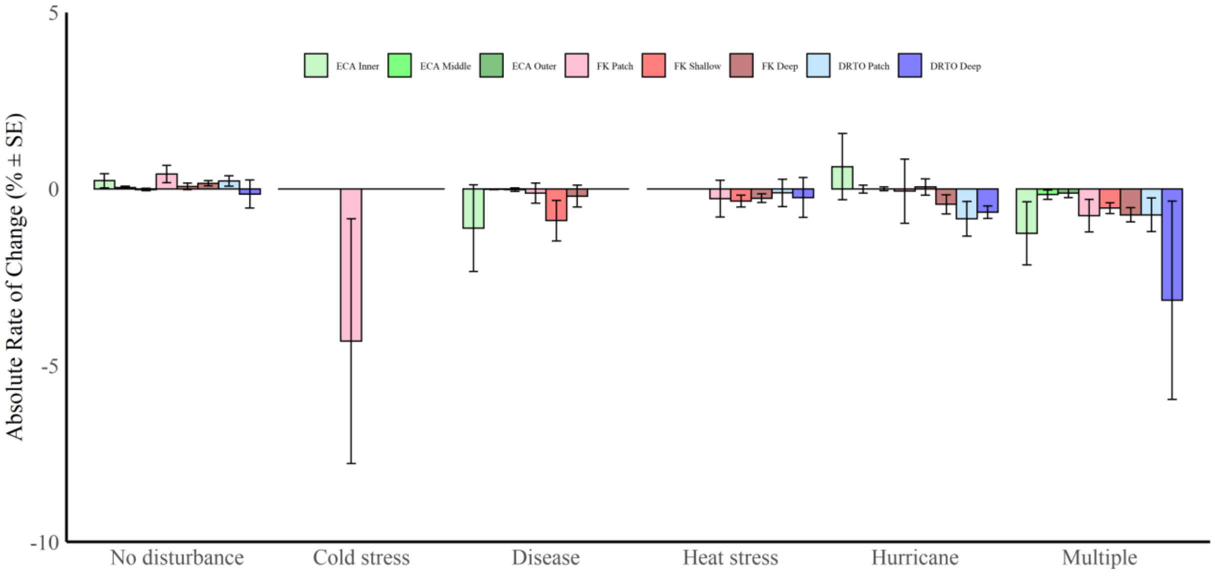

Figure 3. Stony coral cover absolute rate of change in each regional habitat following periods of no disturbance and major disturbances. The absence of bars indicate disturbance did not occur in the regional habitat over the course of the study. Note, the ECA did not experience heat stress alone, but heat stress in conjunction with hurricanes in 2005 and disease in 2014 and 2015.

Benthic Community Structure

Overall, benthic community structure significantly varied by Year (PERMANOVA, Pseudo-F = 40.011, p = 0.0001), Region (Pseudo-F = 4.9803, p = 0.0002), Regional Habitat (Pseudo-F = 6.988, p = 0.0001), and Site (Pseudo-F = 46.3, p = 0.0001). Significant interactions between Year and Region (Pseudo-F = 7.6343, p = 0.0001; Fig. S3), and between Year and Sub-region (Pseudo-F = 3.3101, p = 0.0001) were found. No significant interaction was found between Year and Regional Habitat ($p > 0.05$). Distance among centroids was calculated for regional habitat, as this term had the largest effect size and benthic community trends visually assessed using tmMDS (Fig. 4; Table S6). Stony coral cover was higher on FK patch reefs and DRTO deep forereefs relative to all other regional habitats. ECA middle and outer reefs had relatively higher turf algae/substrate and sponge cover. Benthic community structure trends followed similar patterns in many regional habitats despite 2004 baseline differences, most noticeably with similar benthic community trajectories in each habitat within each region (Fig. 4), as suggested by PERMANOVA. A trend of relative increase in macroalgae cover over time was seen in all regional habitats, with a relative decline in turf algae/substrate. Relative declines in stony coral cover over time were most evident on ECA inner reefs, FK patch reefs and DRTO deep forereefs. A trend of relative increase in stony coral cover was not evident in any regional habitat. The greatest change in dissimilarity from 2004 to 2018 was found on DRTO deep forereefs, followed by DRTO patch reefs (25.64% and 21.4% dissimilarity respectively), largely resulting from increased macroalgae cover.

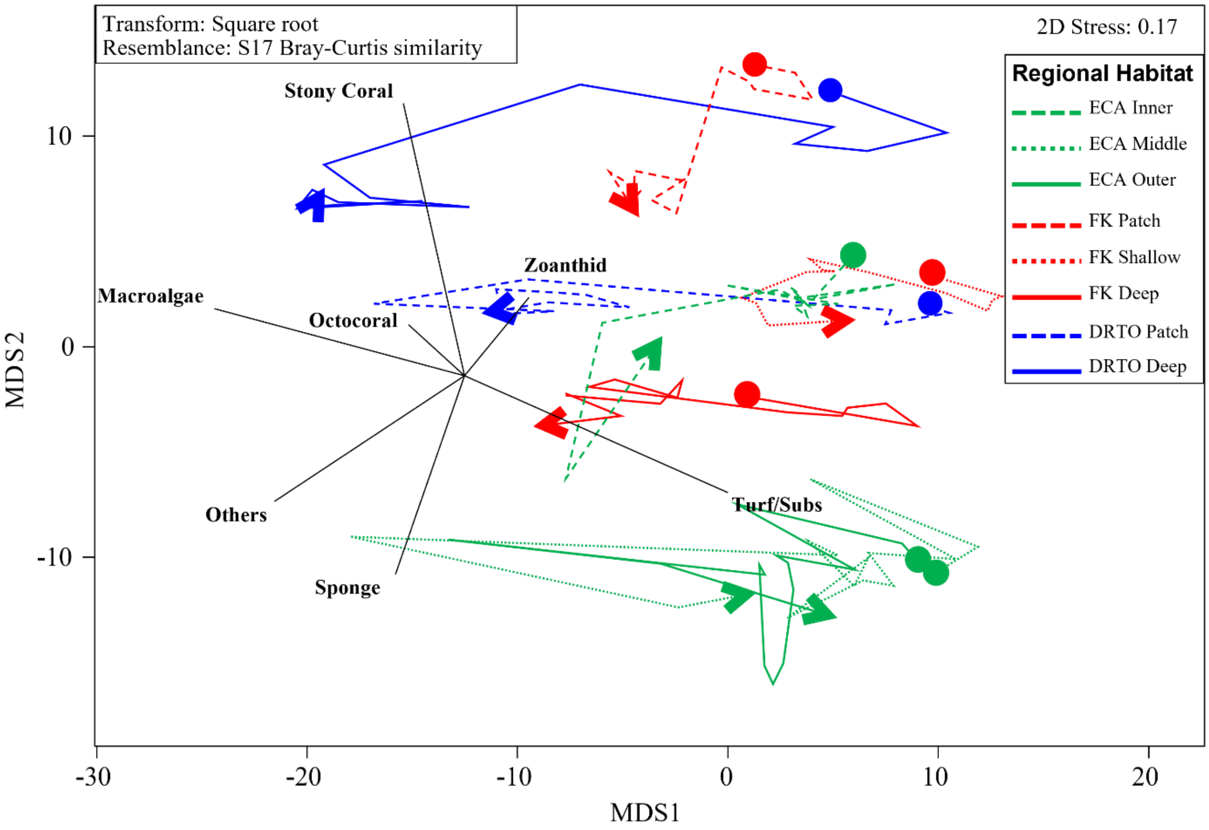

Figure 4. Threshold metric MDS plot showing benthic community trajectories from 2004 to 2018. Each line represents temporal trajectory in each regional habitat, based upon the distance among centroids calculation. Arrows represent direction of community change, from their start point in 2004 (circle) to end point in 2018 (arrow). Vectors represent relative importance of taxa in dissimilarity.

Discussion

From 2004 to 2018, stony corals demonstrated an inability to recover following frequent episodes of acute disturbance causing stony coral cover loss in every region on the FCR. Stony coral cover declined in six out of eight regional habitats, including the habitat with the highest stony coral cover at the start of the study in each region. Only the habitat with the lowest stony coral cover at the start of the study in the ECA and the DRTO did not decline significantly between 2004 and 2018. As a result, octocoral cover is now higher than stony coral cover in all habitats despite declining in four of the eight regional habitats. Sponge cover remained stable or gradually increased in each regional habitat, only significantly declining after hurricanes in 2005 and 2017. I expected community resilience to acute disturbances to vary regionally on Florida's Coral Reef. I determined that high acute disturbance frequency coupled with limited stony coral recovery during inter-disturbance periods continue to reshape the benthic community.

I hypothesized that benthic community dynamics on the FCR would vary regionally, with increased stony coral resilience in locations with comparatively low chronic pressure (i.e., those furthest from human habitation and with active management measures in place) or with higher initial stony coral cover (Ortiz et al. 2018; Mellin et al. 2019). Benthic community structure dynamics did vary most strongly by region, though there was limited evidence of marked regional differences in stony coral resilience, whereby rates of coral loss following major disturbances were generally comparable. Acute disturbances were also very prevalent across all regions, as predicted under global climate change (Pachauri et al. 2014; Hughes et al. 2017), with sites experiencing an average of 5.7 major disturbances in the 15-year period between 2004 and 2018. In particular, multiple thermal stress events (heat stress in 2005, 2014, 2015; cold stress in 2010), major hurricanes (multiple in 2005; Irma in 2017), and an unprecedented disease outbreak (Stony Coral Tissue Loss Disease (SCTLD); starting in 2014 through end of study period) were recorded on the FCR (Wilkinson and Souter 2008; Eakin et al. 2010; Lirman et al. 2011; Eakin et al. 2018; Kobelt et al. 2019; Muller et al. 2020).

Stony coral cover decline was significantly higher following thermal stress events and periods with multiple disturbances (i.e., heat stress and a hurricane) than during inter-disturbance periods. Likewise, octocoral cover frequently declined after thermal stress or a major hurricane. Severe heatwaves frequently result in coral bleaching, disease and high levels of mortality (Glynn

1991; Bruno et al. 2007; Prada et al. 2010; Hughes et al. 2018a), while hurricanes can detach and damage stony corals and octocorals (Woodley et al. 1981; Yoshioka and Yoshioka 1991; Wilkinson and Souter 2008). From 2005 to 2006, a period which included the 2005 El Niño and multiple hurricanes (Wilkinson and Souter 2008; Eakin et al. 2010), stony coral cover significantly declined on FK and DRTO deep forereefs and octocoral cover declined on ECA middle and outer reefs, FK patch reef and FK deep forereefs. Extreme cold stress caused the largest decline in absolute stony coral and octocoral cover, when water temperature dropped below 12 °C (Colella et al. 2012) on FK patch reefs in January 2010. Intense heat stress and coral bleaching was also experienced on the FCR during the 2014 and 2015 heat stress events (Gintert et al. 2018; Smith et al. 2019), with heat stress duration in the ECA particularly high in 2015 (Eakin et al. 2018; Jones et al. 2020). From 2014 to 2015, stony coral cover declined on FK deep forereefs and octocoral cover declined on FK and DRTO patch reefs. From 2015 to 2016, stony coral cover declined on the ECA inner and outer reefs and on DRTO patch reefs. In addition to and likely exacerbated by heat stress, Stony Coral Tissue Loss Disease (SCTLD), was recorded in the ECA from 2014 (Walton et al. 2018; Jones et al. 2021). SCTLD was not reported in the Florida Keys until 2016, where it spread east to west, and was first reported in the Lower Keys in 2018 and in the Dry Tortugas in May 2021 (Ruzicka, Pers comms, August 2021). Large declines in relative stony coral cover on ECA inner reefs from 2015 to 2016 (46%) and FK shallow forereefs from 2017 to 2018 (22%) were undoubtedly largely influenced by SCTLD. SCTLD remains endemic, the cause currently unknown and continues to contribute to stony coral cover decline throughout the FCR.

Stony coral cover did generally increase during inter-disturbance periods in all regional habitats except DRTO deep forereefs, though the average annual increase was very moderate (0.15% year^{-1}). The slow rate of recovery and limited disturbance-free periods meant that overall cover of stony corals was unchanged or declined from 2004 to 2018. Many of these communities were severely impacted in the 1970s, 1980s and 1990s (Dustan and Halas 1987; Porter and Meier 1992; Precht and Miller 2007; Somerfield et al. 2008), but the trend of declining stony coral cover has continued into the 2000s and 2010s. Stony coral recovery rate elsewhere has been shown to vary depending on disturbance type, disturbance history or chronic pressure (Ortiz et al. 2018; Mellin et al. 2019), but this was not evident from this study. Instead, I suspect chronic pressures suppress recovery rate across the FCR (Ortiz et al. 2018). As of 2018, only FK patch reefs and DRTO deep forereefs have stony coral cover above 10%, the level estimated to be the threshold for carbonate production, below which a reef moves from a net accretional to erosional state (Perry et al. 2013). Stony coral cover has declined in both habitats since 2004, suggesting low resilience across the reef tract and consistent with the wider Caribbean (Connell 1997; Roff and Mumby 2012). Whether this results from a lack of recruitment (Hoey et al. 2011; Holbrook et al. 2018), survival (McClanahan et al. 2012; Fourney and Figueiredo 2017), growth (De'ath et al. 2009; Hoegh-Guldberg et al. 2017) or community structure (Roff and Mumby 2012) likely varies spatially, but recovery rate is undoubtedly reduced by the absence of the comparatively fast growing *Acropora cervicornis*, *A. palmata* and *A. prolifera* at most study sites (Shinn 1966; Lirman 2000; Lirman et al. 2014) and replacement by smaller, encrusting species such as *Porites astreoides* (Jones et al. 2020).

Although, stony coral resilience was low throughout Florida, octocorals and sponges demonstrated greater resilience. As of 2018, octocoral cover is higher than stony coral cover in all habitats on the FCR, supporting previous suggestions of a shift in the dominant fauna (Ruzicka et al. 2013). Octocorals were not resistant to disturbance, but demonstrated resilience, generally increasing in cover following many disturbance events. While octocoral growth is fast and recruitment high (Lasker et al. 2020), the high frequency of disturbances still resulted in octocoral cover being lower in four of eight regional habitats during the study, including those where cover was highest in the ECA and FK at the start of the study. This is in part due to the study timeframe, concluding one year after Hurricane Irma when octocoral cover significantly declined in five of eight regional habitats, but does suggests that if disturbances continue to increase in frequency, then octocorals may be unable to sustain recovery.

Sponges exhibited resistance to thermal stress on the FCR, but were highly vulnerable to major hurricanes, declining from 2005 to 2006 and from 2017 to 2018. Sponge cover steadily increased in the habitat closest to shore in each region and contributes greatly to the benthic community on ECA middle and outer reefs, but cover was relatively low throughout the FK and DRTO. Stony coral cover decline has been associated with concomitant increases in sponge cover elsewhere (Jackson et al. 2001; De Bakker et al. 2016; Graham et al. 2018), but sponge cover has remained relatively low in much of the FCR.

The proliferation of macroalgae in multiple sub-regions followed most major disturbances and frequently occurred irrespective of stony coral cover decline. Benthic community trajectories suggest the increase in macroalgae cover primarily corresponds to a decrease in turf algae/substrate, which will likely further impact stony coral recruitment and juvenile survival (Hughes et al. 2007; Hoey et al. 2011; Dell et al. 2016). While in most locations macroalgae cover fluctuated widely, a sustained increase in macroalgae cover, which corresponded with a lack of recovery in stony coral cover (Fig. S4), was found on DRTO deep forereefs from 2008 onwards. DRTO deep forereefs, which started with the highest stony coral cover and were assumed to have the least chronic pressure, being farthest from shore and human habitation, were expected to be most resilient but macroalgae cover is now four times higher than stony coral cover. The data suggests increasing macroalgae cover, which averaged 13.3 ± 0.2% (± SE) across FCR, combined with high disturbance frequency, contributes to the continued degradation of the FCR under current conditions.

There was low resilience and limited stony coral recovery in all regions, suggesting current management protection levels designed to minimize chronic pressures are insufficient and that urgent action is needed to further minimize anthropogenic pressures. Regional habitats fall into three broad categories (least degraded, moderately degraded, most degraded), based upon their state of degradation and changes in benthic community structure. The least degraded reefs, FK patch reefs and DRTO deep forereefs, had the highest stony coral cover throughout the study, and traditionally have higher cover of large reef-building *Orbicella* spp. (Somerfield et al. 2008). FK patch reefs were least affected by the 1997/98 bleaching event (Ruzicka et al. 2013) and did show signs of stony coral recovery between periods of disturbance, with a significant increase between 2006 and 2009 and between 2010 and 2014. Manzello et al. (2015) found *Orbicella faveolata* growth rates recover faster on inshore patch reefs than offshore reefs in the Florida Keys and the evidence suggests FK patch reefs are still comparatively resilient. Models suggested stony coral cover increased slightly with depth, but the deepest reefs surveyed, DRTO deep forereefs, which were expected to be most resilient, also showed the greatest decline during the study and no substantial recovery. This habitat also had a significant increase in macroalgae cover since 2008. This suggests the erosion of coral resilience from increasing frequency and severity of disturbances throughout the FCR regardless of differences in chronic pressures. Moderately degraded reefs, ECA inner reefs, FK shallow forereefs, FK deep forereefs and DRTO patch reefs, have relatively moderate stony coral, octocoral and sponge cover. Stony coral cover significantly increased between disturbances from 2006 to 2014 on all moderately degraded reefs, but very slowly in comparison to increases in octocoral or macroalgae cover, indicative of the more common slow growing or weedy coral species found on these reefs. Both ECA inner reefs and DRTO patch reefs do have areas of high *Acropora* cover (Jaap and Sargent 1995; Vargas-Ángel et al. 2003), but these are isolated and spatially and temporally dynamic so not assessed here (Walker et al. 2012). The evidence suggests that following disturbances, these habitats currently support octocoral recovery or the proliferation of macroalgae which may depress stony coral recovery (Chong-Seng et al. 2014; Suchley and Alvarez-Filip 2017). Finally, the most degraded reefs, ECA middle and outer reefs have high sponge cover, limited stony coral accretion for the past few thousand years (Banks et al. 2007), and now have evidence of declining octocoral cover from increased disturbance frequency.

Overall, high acute disturbance frequency, from a multitude of different stressors, the predominance of macroalgae and slow stony coral recovery during periods without disturbance severely constrains recovery potential of stony corals on Florida's coral reefs. Under global climate change the frequency and intensity of acute disturbances is predicted to increase further (Pachauri et al. 2014; Hughes et al. 2017; Hughes et al. 2018b; Lough et al. 2018). My results suggest acute disturbance frequency is already too high for these degraded reefs to be resilient under current environmental conditions. Further, the lack of stony coral recovery during inter-disturbance periods suggests systematic chronic pressures throughout the FCR. Benthic community trajectories suggest continued increases in macroalgae cover and relative increases in octocoral and sponge cover, particularly in inshore habitats, which, without urgent action to tackle global climate change and local chronic pressures, will continue to reshape benthic community structure on Florida's Coral Reef.

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Supplementary Material

Table S1. Site designations and depths

Region	Site	Sub-Region	Habitat	Depth (m)
DRTO	Mayer's Peak	Dry Tortugas	Patch	9
DRTO	Temptation Rock	Dry Tortugas	Patch	7
DRTO	White Shoal	Dry Tortugas	Patch	9
DRTO	Bird Key Reef	Dry Tortugas	Deep Forereef	14
DRTO	Black Coral Rock	Dry Tortugas	Deep Forereef	22
FK	Admiral	Upper Keys	Patch	2
FK	Porter Patch	Upper Keys	Patch	5
FK	Turtle	Upper Keys	Patch	4
FK	Carysfort Shallow	Upper Keys	Shallow Forereef	2
FK	Conch Shallow	Upper Keys	Shallow Forereef	5
FK	Grecian Rocks	Upper Keys	Shallow Forereef	3
FK	Molasses Shallow	Upper Keys	Shallow Forereef	6
FK	Carysfort Deep	Upper Keys	Deep Forereef	16
FK	Conch Deep	Upper Keys	Deep Forereef	16
FK	Molasses Deep	Upper Keys	Deep Forereef	13
FK	Dustan Rocks	Middle Keys	Patch	4
FK	West Turtle Shoal	Middle Keys	Patch	7
FK	Alligator Shallow	Middle Keys	Shallow Forereef	5
FK	Sombrero Shallow	Middle Keys	Shallow Forereef	5
FK	Tennessee Shallow	Middle Keys	Shallow Forereef	6
FK	Alligator Deep	Middle Keys	Deep Forereef	11
FK	Sombrero Deep	Middle Keys	Deep Forereef	15
FK	Tennessee Deep	Middle Keys	Deep Forereef	13
FK	Cliff Green	Lower Keys	Patch	8
FK	Jaap Reef	Lower Keys	Patch	3
FK	West Washer Women	Lower Keys	Patch	7
FK	Western Head	Lower Keys	Patch	10
FK	Eastern Sambo Shallow	Lower Keys	Shallow Forereef	2
FK	Looe Key Shallow	Lower Keys	Shallow Forereef	7
FK	Rock Key Shallow	Lower Keys	Shallow Forereef	5
FK	Sand Key Shallow	Lower Keys	Shallow Forereef	6
FK	Western Sambo Shallow	Lower Keys	Shallow Forereef	4
FK	Eastern Sambo Deep	Lower Keys	Deep Forereef	15
FK	Looe Key Deep	Lower Keys	Deep Forereef	12
FK	Rock Key Deep	Lower Keys	Deep Forereef	13
FK	Sand Key Deep	Lower Keys	Deep Forereef	11
FK	Western Sambo Deep	Lower Keys	Deep Forereef	12
ECA	Broward County 1	Broward	Inner	8
ECA	Dade County 1	Miami	Inner	8
ECA	Broward County 2	Broward	Middle	12
ECA	Dade County 2	Miami	Middle	14
ECA	Broward County 3	Broward	Outer	17
ECA	Dade County 3	Miami	Outer	17
ECA	Palm Beach 2	Palm Beach	Outer	17
ECA	Palm Beach 3	Palm Beach	Outer	17

Table S2. Stony Coral Cover post-hoc between year and overall contrasts by regional habitat. Estimate represents the slope and are on the log odds scale, p value considered significant at $p < 0.05$. Overall change from 2004 to 2018 in bold.

Region	Habitat	Contrast	Estimate	SE	DF	T ratio	P value	Change
DRTO	Deep Forereef	2004-2005	0.034501	0.0548	2318	0.629	1	=
DRTO	Deep Forereef	2005-2006	0.242758	0.0578	2318	4.197	0.0026	-
DRTO	Deep Forereef	2006-2007	0.050348	0.0553	2318	0.911	0.9999	=
DRTO	Deep Forereef	2007-2008	-0.16496	0.0487	2318	-3.388	0.051	=
DRTO	Deep Forereef	2008-2009	-0.05198	0.045	2318	-1.156	0.9982	=
DRTO	Deep Forereef	2009-2010	0.298033	0.0444	2318	6.71	<0.0001	-
DRTO	Deep Forereef	2010-2011	-0.06618	0.049	2318	-1.352	0.991	=
DRTO	Deep Forereef	2011-2012	0.01293	0.0511	2318	0.253	1	=
DRTO	Deep Forereef	2012-2013	0.07126	0.0523	2318	1.361	0.9904	=
DRTO	Deep Forereef	2013-2014	-0.11477	0.0515	2318	-2.229	0.6441	=
DRTO	Deep Forereef	2014-2015	0.114445	0.0506	2318	2.26	0.621	=
DRTO	Deep Forereef	2015-2016	-0.06839	0.0517	2318	-1.323	0.9927	=
DRTO	Deep Forereef	2016-2017	0.051364	0.0521	2318	0.986	0.9997	=
DRTO	Deep Forereef	2017-2018	0.067027	0.0521	2318	1.287	0.9944	=
DRTO	**Deep Forereef**	**2004-2018**	**0.476386**	**0.0528**	**2318**	**9.014**	**<0.0001**	**-**
DRTO	Patch Reef	2004-2005	-0.00056	0.0887	2318	-0.006	1	=
DRTO	Patch Reef	2005-2006	0.242893	0.0954	2318	2.546	0.4074	=
DRTO	Patch Reef	2006-2007	-0.01401	0.0915	2318	-0.153	1	=
DRTO	Patch Reef	2007-2008	-0.24799	0.0769	2318	-3.225	0.0836	=
DRTO	Patch Reef	2008-2009	-0.03463	0.0687	2318	-0.504	1	=
DRTO	Patch Reef	2009-2010	-0.05553	0.0643	2318	-0.863	0.9999	=
DRTO	Patch Reef	2010-2011	-0.16474	0.0664	2318	-2.483	0.4535	=
DRTO	Patch Reef	2011-2012	0.228114	0.0723	2318	3.155	0.1018	=
DRTO	Patch Reef	2012-2013	-0.16108	0.0748	2318	-2.155	0.6974	=
DRTO	Patch Reef	2013-2014	-0.16133	0.0696	2318	-2.317	0.5777	=
DRTO	Patch Reef	2014-2015	-0.16873	0.0633	2318	-2.666	0.3267	=
DRTO	Patch Reef	2015-2016	0.219304	0.0642	2318	3.417	0.0466	-
DRTO	Patch Reef	2016-2017	-0.05061	0.0677	2318	-0.748	1	=
DRTO	Patch Reef	2017-2018	0.218691	0.0694	2318	3.151	0.1031	=
DRTO	**Patch Reef**	**2004-2018**	**-0.1502**	**0.0803**	**2318**	**-1.871**	**0.8674**	**=**
FK	Deep Forereef	2004-2005	-0.03875	0.0653	2318	-0.593	1	=
FK	Deep Forereef	2005-2006	0.291476	0.0699	2318	4.169	0.0029	-
FK	Deep Forereef	2006-2007	0.034115	0.068	2318	0.501	1	=
FK	Deep Forereef	2007-2008	-0.17695	0.0578	2318	-3.06	0.1319	=
FK	Deep Forereef	2008-2009	0.026911	0.0557	2318	0.483	1	=
FK	Deep Forereef	2009-2010	-0.12746	0.0548	2318	-2.325	0.5716	=
FK	Deep Forereef	2010-2011	-0.26591	0.0462	2318	-5.761	<0.0001	+
FK	Deep Forereef	2011-2012	0.036979	0.0381	2318	0.972	0.9997	=

FK	Deep Forereef	2012-2013	-0.09966	0.0377	2318	-2.645	0.34	=
FK	Deep Forereef	2013-2014	0.015322	0.0365	2318	0.42	1	=
FK	Deep Forereef	2014-2015	0.155386	0.0381	2318	4.083	0.0042	-
FK	Deep Forereef	2015-2016	0.000486	0.0395	2318	0.012	1	=
FK	Deep Forereef	2016-2017	0.067581	0.04	2318	1.689	0.9368	=
FK	Deep Forereef	2017-2018	0.327654	0.0452	2318	7.25	<0.0001	-
FK	**Deep Forereef**	**2004-2018**	**0.247182**	**0.0581**	**2318**	**4.252**	**0.0021**	**-**
FK	Shallow Forereef	2004-2005	0.159028	0.0429	2318	3.705	0.0176	-
FK	Shallow Forereef	2005-2006	0.113286	0.0458	2318	2.473	0.4606	=
FK	Shallow Forereef	2006-2007	0.06583	0.0434	2318	1.518	0.9737	=
FK	Shallow Forereef	2007-2008	-0.09069	0.0376	2318	-2.413	0.5052	=
FK	Shallow Forereef	2008-2009	-0.10109	0.0359	2318	-2.812	0.2406	=
FK	Shallow Forereef	2009-2010	-0.02381	0.0355	2318	-0.671	1	=
FK	Shallow Forereef	2010-2011	-0.13144	0.0335	2318	-3.928	0.0077	+
FK	Shallow Forereef	2011-2012	-0.03393	0.0312	2318	-1.089	0.9991	=
FK	Shallow Forereef	2012-2013	-0.07691	0.0304	2318	-2.533	0.4166	=
FK	Shallow Forereef	2013-2014	0.042144	0.0299	2318	1.411	0.9864	=
FK	Shallow Forereef	2014-2015	0.069798	0.0306	2318	2.281	0.6046	=
FK	Shallow Forereef	2015-2016	0.074254	0.0315	2318	2.361	0.5447	=
FK	Shallow Forereef	2016-2017	0.152056	0.0335	2318	4.542	0.0006	-
FK	Shallow Forereef	2017-2018	0.105726	0.0359	2318	2.944	0.177	=
FK	**Shallow Forereef**	**2004-2018**	**0.32425**	**0.0394**	**2318**	**8.239**	**<0.0001**	**-**
FK	Patch Reef	2004-2005	-0.05318	0.0299	2318	-1.777	0.9075	=
FK	Patch Reef	2005-2006	0.074294	0.0305	2318	2.438	0.4868	=
FK	Patch Reef	2006-2007	-0.11538	0.0275	2318	-4.195	0.0026	+
FK	Patch Reef	2007-2008	0.119934	0.0233	2318	5.147	<0.0001	-
FK	Patch Reef	2008-2009	-0.19389	0.0234	2318	-8.299	<0.0001	+
FK	Patch Reef	2009-2010	0.430243	0.0252	2318	17.083	<0.0001	-
FK	Patch Reef	2010-2011	-0.07943	0.025	2318	-3.182	0.0946	=
FK	Patch Reef	2011-2012	-0.0701	0.0225	2318	-3.11	0.1153	=
FK	Patch Reef	2012-2013	0.014931	0.0219	2318	0.682	1	=
FK	Patch Reef	2013-2014	0.048936	0.0218	2318	2.244	0.6328	=
FK	Patch Reef	2014-2015	0.129283	0.0227	2318	5.701	<0.0001	-
FK	Patch Reef	2015-2016	-0.07688	0.023	2318	-3.338	0.0597	=

FK	Patch Reef	2016-2017	-0.01253	0.023	2318	-0.545	1	=
FK	Patch Reef	2017-2018	0.066497	0.0233	2318	2.858	0.2173	=
FK	**Patch Reef**	**2004-2018**	**0.282723**	**0.0272**	**2318**	**10.406**	**<0.0001**	**-**
ECA	Inner	2004-2005	-0.087	0.081	2318	-1.074	0.9992	=
ECA	Inner	2005-2006	-0.01969	0.0799	2318	-0.246	1	=
ECA	Inner	2006-2007	0.014215	0.0733	2318	0.194	1	=
ECA	Inner	2007-2008	-0.11514	0.0613	2318	-1.877	0.8645	=
ECA	Inner	2008-2009	0.038375	0.0584	2318	0.657	1	=
ECA	Inner	2009-2010	0.114491	0.0614	2318	1.866	0.87	=
ECA	Inner	2010-2011	-0.06038	0.0627	2318	-0.963	0.9998	=
ECA	Inner	2011-2012	-0.06223	0.0593	2318	-1.05	0.9994	=
ECA	Inner	2012-2013	-0.11907	0.0572	2318	-2.08	0.7485	=
ECA	Inner	2013-2014	-0.04941	0.0559	2318	-0.883	0.9999	=
ECA	Inner	2014-2015	-0.0007	0.0555	2318	-0.013	1	=
ECA	Inner	2015-2016	0.64371	0.0639	2318	10.081	<0.0001	-
ECA	Inner	2016-2017	0.262526	0.0817	2318	3.213	0.0865	=
ECA	Inner	2017-2018	-0.16655	0.0868	2318	-1.918	0.8442	=
ECA	**Inner**	**2004-2018**	**0.39317**	**0.0831**	**2318**	**4.731**	**0.0002**	**-**
ECA	Middle	2004-2005	0.063047	0.2637	2318	0.239	1	=
ECA	Middle	2005-2006	-0.15396	0.2571	2318	-0.599	1	=
ECA	Middle	2006-2007	0.423797	0.2545	2318	1.665	0.9432	=
ECA	Middle	2007-2008	-0.31761	0.2348	2318	-1.353	0.9909	=
ECA	Middle	2008-2009	-0.00706	0.2102	2318	-0.034	1	=
ECA	Middle	2009-2010	-0.16627	0.2019	2318	-0.823	1	=
ECA	Middle	2010-2011	-0.10208	0.1902	2318	-0.537	1	=
ECA	Middle	2011-2012	0.100612	0.1856	2318	0.542	1	=
ECA	Middle	2012-2013	-0.05531	0.1888	2318	-0.293	1	=
ECA	Middle	2013-2014	-0.28124	0.1794	2318	-1.567	0.9654	=
ECA	Middle	2014-2015	0.170844	0.1725	2318	0.991	0.9997	=
ECA	Middle	2015-2016	0.71744	0.2163	2318	3.317	0.0635	=
ECA	Middle	2016-2017	0.012384	0.2616	2318	0.047	1	=
ECA	Middle	2017-2018	0.063872	0.268	2318	0.238	1	=
ECA	**Middle**	**2004-2018**	**0.46847**	**0.2656**	**2318**	**1.764**	**0.9122**	**=**
ECA	Outer	2004-2005	0.290824	0.164	2318	1.773	0.9087	=
ECA	Outer	2005-2006	-0.23583	0.1684	2318	-1.4	0.9874	=
ECA	Outer	2006-2007	0.066684	0.1438	2318	0.464	1	=
ECA	Outer	2007-2008	0.093864	0.1321	2318	0.711	1	=
ECA	Outer	2008-2009	-0.07305	0.132	2318	-0.553	1	=
ECA	Outer	2009-2010	-0.02317	0.1298	2318	-0.179	1	=
ECA	Outer	2010-2011	0.131788	0.1336	2318	0.986	0.9997	=
ECA	Outer	2011-2012	-0.17938	0.1298	2318	-1.382	0.9889	=

ECA	Outer	2012-2013	-0.12586	0.1227	2318	-1.026	0.9995	=
ECA	Outer	2013-2014	0.042594	0.1242	2318	0.343	1	=
ECA	Outer	2014-2015	0.127847	0.1268	2318	1.008	0.9996	=
ECA	Outer	2015-2016	0.867301	0.165	2318	5.257	<0.0001	-
ECA	Outer	2016-2017	0.072913	0.202	2318	0.361	1	=
ECA	Outer	2017-2018	-0.03933	0.2113	2318	-0.186	1	=
ECA	**Outer**	**2004-2018**	**1.017206**	**0.1836**	**2318**	**5.541**	**<0.0001**	**-**

Table S3. Macroalgae Cover post-hoc between year and overall contrasts by sub-region. Estimate represents the slope and are on the log odds scale, p value considered significant at $p < 0.05$. Overall change from 2004 to 2018 in bold.

Region	Habitat	Contrast	Estimate	SE	DF	T ratio	P value	Change
DRTO	DT	2004-2005	0.45764	0.0521	2334	8.783	<0.0001	-
DRTO	DT	2005-2006	-0.5564	0.0515	2334	-10.808	<0.0001	+
DRTO	DT	2006-2007	-0.45271	0.0386	2334	-11.726	<0.0001	+
DRTO	DT	2007-2008	0.0143	0.0308	2334	0.464	1	=
DRTO	DT	2008-2009	-1.10472	0.0263	2334	-41.977	<0.0001	+
DRTO	DT	2009-2010	-0.68406	0.0197	2334	-34.803	<0.0001	+
DRTO	DT	2010-2011	0.87707	0.0217	2334	40.413	<0.0001	-
DRTO	DT	2011-2012	-0.15044	0.0238	2334	-6.331	<0.0001	+
DRTO	DT	2012-2013	-0.25747	0.0232	2334	-11.113	<0.0001	+
DRTO	DT	2013-2014	0.1805	0.0229	2334	7.891	<0.0001	-
DRTO	DT	2014-2015	-0.01452	0.0228	2334	-0.637	1	=
DRTO	DT	2015-2016	0.32097	0.0238	2334	13.478	<0.0001	-
DRTO	DT	2016-2017	-0.34159	0.0241	2334	-14.195	<0.0001	+
DRTO	DT	2017-2018	-0.06977	0.0227	2334	-3.076	0.1265	+
DRTO	**DT**	**2004-2018**	**-1.78122**	**0.0365**	**2334**	**-48.79**	**<0.0001**	**+**
FK	LK	2004-2005	1.49149	0.0373	2334	40.031	<0.0001	-
FK	LK	2005-2006	-1.30999	0.0381	2334	-34.41	<0.0001	+
FK	LK	2006-2007	-0.13428	0.0245	2334	-5.478	<0.0001	+
FK	LK	2007-2008	0.58652	0.0232	2334	25.323	<0.0001	-
FK	LK	2008-2009	-0.24346	0.0246	2334	-9.893	<0.0001	+
FK	LK	2009-2010	-0.78422	0.0212	2334	-36.994	<0.0001	+
FK	LK	2010-2011	0.40883	0.0185	2334	22.115	<0.0001	-
FK	LK	2011-2012	0.60135	0.0209	2334	28.821	<0.0001	-
FK	LK	2012-2013	-0.45085	0.0211	2334	-21.324	<0.0001	+
FK	LK	2013-2014	0.36367	0.0204	2334	17.838	<0.0001	-
FK	LK	2014-2015	-0.80069	0.0195	2334	-41.116	<0.0001	+
FK	LK	2015-2016	-0.11889	0.0167	2334	-7.101	<0.0001	+
FK	LK	2016-2017	0.85292	0.0193	2334	44.157	<0.0001	-
FK	LK	2017-2018	-0.72726	0.0198	2334	-36.656	<0.0001	+

FK	**LK**	**2004-2018**	**-0.26488**	**0.022**	**2334**	**-12.045**	**<0.0001**	**+**
FK	MK	2004-2005	0.24764	0.0401	2334	6.171	<0.0001	-
FK	MK	2005-2006	-0.37364	0.0387	2334	-9.664	<0.0001	+
FK	MK	2006-2007	0.25015	0.0342	2334	7.311	<0.0001	-
FK	MK	2007-2008	-0.0022	0.032	2334	-0.069	1	=
FK	MK	2008-2009	-0.06545	0.0311	2334	-2.102	0.7339	=
FK	MK	2009-2010	-0.30158	0.0297	2334	-10.148	<0.0001	+
FK	MK	2010-2011	-0.57817	0.025	2334	-23.157	<0.0001	+
FK	MK	2011-2012	0.56636	0.0223	2334	25.384	<0.0001	-
FK	MK	2012-2013	0.20192	0.0251	2334	8.039	<0.0001	-
FK	MK	2013-2014	0.14145	0.0267	2334	5.302	<0.0001	-
FK	MK	2014-2015	-0.5833	0.0251	2334	-23.255	<0.0001	+
FK	MK	2015-2016	-0.17061	0.0218	2334	-7.82	<0.0001	+
FK	MK	2016-2017	0.15858	0.0218	2334	7.278	<0.0001	+
FK	MK	2017-2018	-0.28807	0.0218	2334	-13.215	<0.0001	+
FK	**MK**	**2004-2018**	**-0.79692**	**0.0314**	**2334**	**-25.374**	**<0.0001**	**+**
FK	UK	2004-2005	0.38974	0.0354	2334	11.012	<0.0001	-
FK	UK	2005-2006	0.38622	0.0419	2334	9.225	<0.0001	-
FK	UK	2006-2007	-0.37238	0.039	2334	-9.543	<0.0001	+
FK	UK	2007-2008	-0.15151	0.0299	2334	-5.07	<0.0001	+
FK	UK	2008-2009	-0.28315	0.0276	2334	-10.274	<0.0001	+
FK	UK	2009-2010	-0.60176	0.0243	2334	-24.731	<0.0001	+
FK	UK	2010-2011	0.18543	0.0207	2334	8.957	<0.0001	-
FK	UK	2011-2012	-0.01706	0.0196	2334	-0.871	0.9999	=
FK	UK	2012-2013	0.28613	0.0204	2334	14.041	<0.0001	-
FK	UK	2013-2014	-0.38322	0.0197	2334	-19.432	<0.0001	+
FK	UK	2014-2015	-0.1374	0.0181	2334	-7.604	<0.0001	+
FK	UK	2015-2016	0.28096	0.0186	2334	15.069	<0.0001	-
FK	UK	2016-2017	-0.42707	0.0184	2334	-23.192	<0.0001	+
FK	UK	2017-2018	0.04587	0.0177	2334	2.589	0.3778	=
FK	**UK**	**2004-2018**	**-0.79921**	**0.0264**	**2334**	**-30.251**	**<0.0001**	**+**
ECA	Broward	2004-2005	-1.49232	0.0925	2334	-16.132	<0.0001	+
ECA	Broward	2005-2006	-1.01911	0.0508	2334	-20.078	<0.0001	+
ECA	Broward	2006-2007	1.74578	0.0549	2334	31.818	<0.0001	-
ECA	Broward	2007-2008	-0.91554	0.0553	2334	-16.548	<0.0001	+
ECA	Broward	2008-2009	0.2058	0.0443	2334	4.643	0.0004	-
ECA	Broward	2009-2010	0.21113	0.0497	2334	4.252	0.0021	-
ECA	Broward	2010-2011	0.4976	0.0582	2334	8.547	<0.0001	-
ECA	Broward	2011-2012	-0.85584	0.0536	2334	-15.977	<0.0001	+
ECA	Broward	2012-2013	0.89136	0.0545	2334	16.356	<0.0001	-
ECA	Broward	2013-2014	-0.81075	0.0554	2334	-14.637	<0.0001	+

ECA	Broward	2014-2015	-0.29806	0.0424	2334	-7.023	<0.0001	+
ECA	Broward	2015-2016	-1.29388	0.0343	2334	-37.715	<0.0001	+
ECA	Broward	2016-2017	0.64084	0.0317	2334	20.232	<0.0001	-
ECA	Broward	2017-2018	1.46916	0.0492	2334	29.842	<0.0001	-
ECA	**Broward**	**2004-2018**	**-1.02385**	**0.093**	**2334**	**-11.004**	**<0.0001**	**+**
ECA	Miami	2004-2005	0.90698	0.0588	2334	15.416	<0.0001	-
ECA	Miami	2005-2006	-1.17559	0.057	2334	-20.615	<0.0001	+
ECA	Miami	2006-2007	0.49318	0.0432	2334	11.418	<0.0001	-
ECA	Miami	2007-2008	-0.45303	0.0397	2334	-11.405	<0.0001	+
ECA	Miami	2008-2009	0.61594	0.0399	2334	15.426	<0.0001	-
ECA	Miami	2009-2010	0.36817	0.047	2334	7.83	<0.0001	-
ECA	Miami	2010-2011	0.1723	0.0537	2334	3.21	0.0872	=
ECA	Miami	2011-2012	0.91319	0.0714	2334	12.784	<0.0001	-
ECA	Miami	2012-2013	-1.24315	0.0685	2334	-18.16	<0.0001	+
ECA	Miami	2013-2014	0.38847	0.0538	2334	7.218	<0.0001	-
ECA	Miami	2014-2015	0.38316	0.0642	2334	5.967	<0.0001	-
ECA	Miami	2015-2016	-3.35184	0.0526	2334	-63.742	<0.0001	+
ECA	Miami	2016-2017	2.39804	0.0392	2334	61.207	<0.0001	-
ECA	Miami	2017-2018	-0.7683	0.0431	2334	-17.831	<0.0001	+
ECA	**Miami**	**2004-2018**	**-0.35247**	**0.0427**	**2334**	**-8.256**	**<0.0001**	**+**
ECA	Palm	2004-2005	0.12188	0.1707	2334	0.714	1	=
ECA	Palm	2005-2006	-2.12279	0.1357	2334	-15.645	<0.0001	+
ECA	Palm	2006-2007	2.06684	0.109	2334	18.956	<0.0001	-
ECA	Palm	2007-2008	-1.03528	0.1145	2334	-9.041	<0.0001	+
ECA	Palm	2008-2009	1.30322	0.1242	2334	10.489	<0.0001	-
ECA	Palm	2009-2010	-0.86249	0.1313	2334	-6.571	<0.0001	+
ECA	Palm	2010-2011	-0.0145	0.1034	2334	-0.14	1	=
ECA	Palm	2011-2012	0.87072	0.1299	2334	6.705	<0.0001	-
ECA	Palm	2012-2013	-1.04814	0.1278	2334	-8.2	<0.0001	+
ECA	Palm	2013-2014	-0.39276	0.091	2334	-4.315	0.0016	+
ECA	Palm	2014-2015	-0.43962	0.0745	2334	-5.9	<0.0001	+
ECA	Palm	2015-2016	-0.81737	0.0564	2334	-14.488	<0.0001	+
ECA	Palm	2016-2017	0.49146	0.0526	2334	9.35	<0.0001	-
ECA	Palm	2017-2018	0.50434	0.0667	2334	7.563	<0.0001	-
ECA	**Palm**	**2004-2018**	**-1.37448**	**0.1257**	**2334**	**-10.933**	**<0.0001**	**+**

Table S4. Octocoral Cover post-hoc between year and overall contrasts by regional habitat. Estimate represents the slope and are on the log odds scale, p value considered significant at $p < 0.05$. Overall change from 2004 to 2018 in bold.

Region	Habitat	Contrast	Estimate	SE	DF	T ratio	P value	Change
DRTO	Deep Forereef	2004-2005	0.283081	0.066	2320	4.286	0.0018	-
DRTO	Deep Forereef	2005-2006	-0.0443	0.0688	2320	-0.644	1	=
DRTO	Deep Forereef	2006-2007	-0.06986	0.0612	2320	-1.142	0.9984	=
DRTO	Deep Forereef	2007-2008	0.17049	0.0561	2320	3.041	0.1388	=
DRTO	Deep Forereef	2008-2009	-0.18374	0.0544	2320	-3.38	0.0525	=
DRTO	Deep Forereef	2009-2010	-0.03134	0.049	2320	-0.64	1	=
DRTO	Deep Forereef	2010-2011	-0.12796	0.0495	2320	-2.583	0.3817	=
DRTO	Deep Forereef	2011-2012	0.077342	0.0517	2320	1.496	0.9768	=
DRTO	Deep Forereef	2012-2013	-0.07095	0.0522	2320	-1.358	0.9906	=
DRTO	Deep Forereef	2013-2014	-0.09585	0.05	2320	-1.918	0.8443	=
DRTO	Deep Forereef	2014-2015	0.136089	0.0497	2320	2.74	0.281	=
DRTO	Deep Forereef	2015-2016	-0.15626	0.0503	2320	-3.103	0.1174	=
DRTO	Deep Forereef	2016-2017	0.026301	0.0495	2320	0.531	1	=
DRTO	Deep Forereef	2017-2018	-0.13424	0.0477	2320	-2.817	0.2384	=
DRTO	**Deep Forereef**	**2004-2018**	**-0.22119**	**0.0544**	**2320**	**-4.066**	**0.0044**	**+**
DRTO	Patch Reef	2004-2005	0.007195	0.0446	2320	0.161	1	=
DRTO	Patch Reef	2005-2006	0.08441	0.0459	2320	1.841	0.8814	=
DRTO	Patch Reef	2006-2007	-0.13753	0.0418	2320	-3.288	0.0695	=
DRTO	Patch Reef	2007-2008	0.212348	0.0378	2320	5.62	<0.0001	-
DRTO	Patch Reef	2008-2009	-0.1204	0.0368	2320	-3.275	0.0722	=
DRTO	Patch Reef	2009-2010	-0.12551	0.0338	2320	-3.713	0.0171	+
DRTO	Patch Reef	2010-2011	-0.27062	0.0342	2320	-7.92	<0.0001	+
DRTO	Patch Reef	2011-2012	0.00684	0.035	2320	0.196	1	=
DRTO	Patch Reef	2012-2013	-0.09284	0.0352	2320	-2.634	0.3471	=
DRTO	Patch Reef	2013-2014	0.027643	0.0348	2320	0.794	1	=
DRTO	Patch Reef	2014-2015	0.239619	0.0357	2320	6.72	<0.0001	-
DRTO	Patch Reef	2015-2016	-0.24168	0.0358	2320	-6.759	<0.0001	+
DRTO	Patch Reef	2016-2017	-0.05235	0.0347	2320	-1.508	0.9752	=
DRTO	Patch Reef	2017-2018	-0.11005	0.0336	2320	-3.271	0.073	=
DRTO	**Patch Reef**	**2004-2018**	**-0.57293**	**0.0389**	**2320**	**-14.744**	**<0.0001**	**+**
FK	Deep Forereef	2004-2005	0.119386	0.0338	2320	3.528	0.0325	-
FK	Deep Forereef	2005-2006	0.122757	0.0357	2320	3.44	0.0434	-
FK	Deep Forereef	2006-2007	0.041737	0.0335	2320	1.248	0.996	=
FK	Deep Forereef	2007-2008	-0.08354	0.0291	2320	-2.87	0.2109	=
FK	Deep Forereef	2008-2009	-0.17217	0.0276	2320	-6.23	<0.0001	+
FK	Deep Forereef	2009-2010	-0.08194	0.0265	2320	-3.096	0.1197	=
FK	Deep Forereef	2010-2011	-0.02163	0.0236	2320	-0.916	0.9999	=

FK	Deep Forereef	2011-2012	-0.04393	0.0208	2320	-2.113	0.7262	=
FK	Deep Forereef	2012-2013	0.003145	0.0207	2320	0.152	1	=
FK	Deep Forereef	2013-2014	0.112823	0.0208	2320	5.42	<0.0001	-
FK	Deep Forereef	2014-2015	0.293129	0.0227	2320	12.926	<0.0001	-
FK	Deep Forereef	2015-2016	-0.1284	0.0234	2320	-5.48	<0.0001	+
FK	Deep Forereef	2016-2017	-0.01868	0.0227	2320	-0.822	1	=
FK	Deep Forereef	2017-2018	0.358148	0.025	2320	14.328	<0.0001	-
FK	**Deep Forereef**	**2004-2018**	**0.500829**	**0.0302**	**2320**	**16.6**	**<0.0001**	**-**
FK	Shallow Forereef	2004-2005	-0.06223	0.0279	2320	-2.231	0.6421	=
FK	Shallow Forereef	2005-2006	0.08531	0.028	2320	3.045	0.1372	=
FK	Shallow Forereef	2006-2007	0.013676	0.0261	2320	0.524	1	=
FK	Shallow Forereef	2007-2008	-0.24761	0.022	2320	-11.241	<0.0001	+
FK	Shallow Forereef	2008-2009	-0.04703	0.0208	2320	-2.263	0.6182	=
FK	Shallow Forereef	2009-2010	-0.18347	0.0202	2320	-9.103	<0.0001	+
FK	Shallow Forereef	2010-2011	-0.01884	0.0189	2320	-0.999	0.9996	=
FK	Shallow Forereef	2011-2012	-0.02498	0.0182	2320	-1.371	0.9897	=
FK	Shallow Forereef	2012-2013	0.006184	0.0181	2320	0.341	1	=
FK	Shallow Forereef	2013-2014	0.062839	0.0181	2320	3.465	0.0399	-
FK	Shallow Forereef	2014-2015	0.065995	0.0185	2320	3.561	0.0291	-
FK	Shallow Forereef	2015-2016	-0.05871	0.0185	2320	-3.169	0.0981	=
FK	Shallow Forereef	2016-2017	0.094127	0.0188	2320	5.001	0.0001	-
FK	Shallow Forereef	2017-2018	0.377621	0.021	2320	18.018	<0.0001	-
FK	**Shallow Forereef**	**2004-2018**	**0.062879**	**0.0256**	**2320**	**2.452**	**0.4763**	**=**
FK	Patch Reef	2004-2005	-0.00777	0.0269	2320	-0.289	1	=
FK	Patch Reef	2005-2006	0.251786	0.0281	2320	8.972	<0.0001	-
FK	Patch Reef	2006-2007	-0.02811	0.0262	2320	-1.073	0.9992	=
FK	Patch Reef	2007-2008	-0.19935	0.0218	2320	-9.155	<0.0001	+
FK	Patch Reef	2008-2009	-0.01363	0.0213	2320	-0.639	1	=
FK	Patch Reef	2009-2010	0.661056	0.0242	2320	27.272	<0.0001	-
FK	Patch Reef	2010-2011	-0.17433	0.024	2320	-7.249	<0.0001	+
FK	Patch Reef	2011-2012	-0.01625	0.0214	2320	-0.759	1	=
FK	Patch Reef	2012-2013	-0.11273	0.0207	2320	-5.438	<0.0001	+
FK	Patch Reef	2013-2014	-0.11962	0.0198	2320	-6.034	<0.0001	+
FK	Patch Reef	2014-2015	0.185938	0.0201	2320	9.238	<0.0001	-
FK	Patch Reef	2015-2016	-0.10618	0.0204	2320	-5.195	<0.0001	+
FK	Patch Reef	2016-2017	-0.15158	0.02	2320	-7.578	<0.0001	+
FK	Patch Reef	2017-2018	0.22686	0.0204	2320	11.138	<0.0001	-
FK	**Patch Reef**	**2004-2018**	**0.396092**	**0.0243**	**2320**	**16.327**	**<0.0001**	**-**
ECA	Inner	2004-2005	-0.23342	0.0789	2320	-2.96	0.1702	=
ECA	Inner	2005-2006	-0.05915	0.0745	2320	-0.794	1	=
ECA	Inner	2006-2007	-0.12506	0.0662	2320	-1.889	0.8591	=

ECA	Inner	2007-2008	0.405053	0.0611	2320	6.633	<0.0001	-
ECA	Inner	2008-2009	-0.16761	0.0622	2320	-2.695	0.3085	=
ECA	Inner	2009-2010	-0.14554	0.0578	2320	-2.517	0.4285	=
ECA	Inner	2010-2011	-0.063	0.056	2320	-1.125	0.9986	=
ECA	Inner	2011-2012	-0.00229	0.0543	2320	-0.042	1	=
ECA	Inner	2012-2013	0.120794	0.0557	2320	2.167	0.6884	=
ECA	Inner	2013-2014	-0.22156	0.0551	2320	-4.019	0.0054	+
ECA	Inner	2014-2015	0.257704	0.0559	2320	4.609	0.0004	-
ECA	Inner	2015-2016	0.026223	0.0596	2320	0.44	1	=
ECA	Inner	2016-2017	-0.06426	0.062	2320	-1.037	0.9995	=
ECA	Inner	2017-2018	-0.00498	0.0642	2320	-0.078	1	=
ECA	**Inner**	**2004-2018**	**-0.27708**	**0.0744**	**2320**	**-3.724**	**0.0164**	**+**
ECA	Middle	2004-2005	-0.32607	0.0645	2320	-5.059	<0.0001	+
ECA	Middle	2005-2006	0.217117	0.0626	2320	3.466	0.0399	-
ECA	Middle	2006-2007	0.075295	0.0617	2320	1.22	0.9968	=
ECA	Middle	2007-2008	0.023974	0.0558	2320	0.43	1	=
ECA	Middle	2008-2009	0.127103	0.0563	2320	2.256	0.6238	=
ECA	Middle	2009-2010	-0.02323	0.0574	2320	-0.405	1	=
ECA	Middle	2010-2011	-0.58191	0.052	2320	-11.187	<0.0001	+
ECA	Middle	2011-2012	0.465646	0.0494	2320	9.428	<0.0001	-
ECA	Middle	2012-2013	0.144916	0.0558	2320	2.596	0.373	=
ECA	Middle	2013-2014	-0.26316	0.0562	2320	-4.68	0.0003	+
ECA	Middle	2014-2015	0.150756	0.0542	2320	2.781	0.2579	=
ECA	Middle	2015-2016	0.283078	0.058	2320	4.879	0.0001	-
ECA	Middle	2016-2017	-0.4348	0.0584	2320	-7.446	<0.0001	+
ECA	Middle	2017-2018	0.443228	0.0586	2320	7.569	<0.0001	-
ECA	**Middle**	**2004-2018**	**0.301951**	**0.0661**	**2320**	**4.565**	**0.0005**	**-**
ECA	Outer	2004-2005	0.082973	0.0344	2320	2.412	0.506	=
ECA	Outer	2005-2006	0.346422	0.0372	2320	9.312	<0.0001	-
ECA	Outer	2006-2007	-0.17779	0.0346	2320	-5.144	<0.0001	+
ECA	Outer	2007-2008	0.17045	0.0304	2320	5.61	<0.0001	-
ECA	Outer	2008-2009	0.108527	0.0314	2320	3.458	0.0409	-
ECA	Outer	2009-2010	-0.24182	0.0307	2320	-7.873	<0.0001	+
ECA	Outer	2010-2011	0.225902	0.0309	2320	7.306	<0.0001	-
ECA	Outer	2011-2012	-0.02318	0.0314	2320	-0.737	1	=
ECA	Outer	2012-2013	0.122194	0.0325	2320	3.761	0.0144	-
ECA	Outer	2013-2014	0.123928	0.0348	2320	3.558	0.0293	-
ECA	Outer	2014-2015	-0.05119	0.0348	2320	-1.47	0.9802	=
ECA	Outer	2015-2016	-0.09153	0.0335	2320	-2.731	0.2864	=
ECA	Outer	2016-2017	-0.01332	0.0335	2320	-0.398	1	=
ECA	Outer	2017-2018	0.28039	0.0366	2320	7.666	<0.0001	-

ECA	**Outer**	**2004-2018**	**0.861963**	**0.0363**	**2320**	**23.74**	**<0.0001**	**-**

Table S5. Sponge Cover post-hoc between year and overall contrasts by regional habitat. Estimate represents the slope and are on the log odds scale, p value considered significant at $p < 0.05$. Overall change from 2004 to 2018 in bold.

Region	Habitat	Contrast	Estimate	SE	DF	T ratio	P value	Change
DRTO	Deep Forereef	2004-2005	0.031914	0.2533	2316	0.126	1	=
DRTO	Deep Forereef	2005-2006	0.402139	0.269	2316	1.495	0.9771	=
DRTO	Deep Forereef	2006-2007	-0.23473	0.2624	2316	-0.895	0.9999	=
DRTO	Deep Forereef	2007-2008	-0.38449	0.2321	2316	-1.657	0.9455	=
DRTO	Deep Forereef	2008-2009	0.188503	0.2249	2316	0.838	1	=
DRTO	Deep Forereef	2009-2010	-0.09175	0.223	2316	-0.412	1	=
DRTO	Deep Forereef	2010-2011	-0.16649	0.2215	2316	-0.751	1	=
DRTO	Deep Forereef	2011-2012	-0.31534	0.2172	2316	-1.452	0.9823	=
DRTO	Deep Forereef	2012-2013	0.104436	0.2141	2316	0.488	1	=
DRTO	Deep Forereef	2013-2014	0.218425	0.2181	2316	1.001	0.9996	=
DRTO	Deep Forereef	2014-2015	-0.32545	0.2156	2316	-1.509	0.975	=
DRTO	Deep Forereef	2015-2016	-0.01155	0.2108	2316	-0.055	1	=
DRTO	Deep Forereef	2016-2017	-0.12889	0.2089	2316	-0.617	1	=
DRTO	Deep Forereef	2017-2018	0.195928	0.2074	2316	0.944	0.9998	=
DRTO	**Deep Forereef**	**2004-2018**	**-0.51734**	**0.2901**	**2316**	**-1.784**	**0.9049**	**=**
DRTO	Patch Reef	2004-2005	0.218084	0.2	2316	1.09	0.999	=
DRTO	Patch Reef	2005-2006	0.200636	0.2107	2316	0.952	0.9998	=
DRTO	Patch Reef	2006-2007	-0.45743	0.1988	2316	-2.301	0.5901	=
DRTO	Patch Reef	2007-2008	0.098353	0.1802	2316	0.546	1	=
DRTO	Patch Reef	2008-2009	-0.23003	0.1769	2316	-1.3	0.9939	=
DRTO	Patch Reef	2009-2010	0.026721	0.1721	2316	0.155	1	=
DRTO	Patch Reef	2010-2011	-0.36649	0.1716	2316	-2.136	0.7107	=
DRTO	Patch Reef	2011-2012	-0.25108	0.1665	2316	-1.508	0.9752	=
DRTO	Patch Reef	2012-2013	0.240214	0.167	2316	1.438	0.9839	=
DRTO	Patch Reef	2013-2014	-0.10501	0.1686	2316	-0.623	1	=
DRTO	Patch Reef	2014-2015	-0.0945	0.1652	2316	-0.572	1	=
DRTO	Patch Reef	2015-2016	-0.27457	0.1614	2316	-1.701	0.933	=
DRTO	Patch Reef	2016-2017	-0.01816	0.1592	2316	-0.114	1	=
DRTO	Patch Reef	2017-2018	0.210088	0.1608	2316	1.306	0.9936	=
DRTO	**Patch Reef**	**2004-2018**	**-0.80318**	**0.2293**	**2316**	**-3.503**	**0.0353**	**+**
FK	Deep Forereef	2004-2005	-0.07725	0.0996	2316	-0.776	1	=
FK	Deep Forereef	2005-2006	0.67112	0.1077	2316	6.229	<.0001	-
FK	Deep Forereef	2006-2007	-0.38054	0.1065	2316	-3.573	0.0279	+
FK	Deep Forereef	2007-2008	-0.41045	0.0928	2316	-4.422	0.001	+
FK	Deep Forereef	2008-2009	-0.15022	0.0886	2316	-1.695	0.9348	=

FK	Deep Forereef	2009-2010	-0.1202	0.0872	2316	-1.378	0.9892	=
FK	Deep Forereef	2010-2011	-0.02005	0.0844	2316	-0.237	1	=
FK	Deep Forereef	2011-2012	-0.1723	0.0817	2316	-2.11	0.7286	=
FK	Deep Forereef	2012-2013	0.123606	0.0815	2316	1.516	0.974	=
FK	Deep Forereef	2013-2014	-0.01468	0.0818	2316	-0.18	1	=
FK	Deep Forereef	2014-2015	-0.1326	0.0814	2316	-1.629	0.9524	=
FK	Deep Forereef	2015-2016	0.083256	0.0814	2316	1.023	0.9995	=
FK	Deep Forereef	2016-2017	-0.13805	0.0811	2316	-1.703	0.9325	=
FK	Deep Forereef	2017-2018	0.837043	0.0843	2316	9.935	<0.0001	-
FK	**Deep Forereef**	**2004-2018**	**0.098686**	**0.1196**	**2316**	**0.825**	**1**	**=**
FK	Shallow Forereef	2004-2005	-0.12455	0.136	2316	-0.916	0.9999	=
FK	Shallow Forereef	2005-2006	0.596522	0.1486	2316	4.014	0.0055	-
FK	Shallow Forereef	2006-2007	-0.23288	0.1478	2316	-1.576	0.9638	=
FK	Shallow Forereef	2007-2008	-0.16394	0.1261	2316	-1.3	0.9939	=
FK	Shallow Forereef	2008-2009	-0.14035	0.1209	2316	-1.161	0.9981	=
FK	Shallow Forereef	2009-2010	-0.11372	0.1176	2316	-0.967	0.9998	=
FK	Shallow Forereef	2010-2011	-0.13178	0.1119	2316	-1.178	0.9978	=
FK	Shallow Forereef	2011-2012	-0.33586	0.1044	2316	-3.218	0.0853	=
FK	Shallow Forereef	2012-2013	0.162661	0.1021	2316	1.593	0.9603	=
FK	Shallow Forereef	2013-2014	-0.04443	0.103	2316	-0.431	1	=
FK	Shallow Forereef	2014-2015	-0.051	0.1019	2316	-0.5	1	=
FK	Shallow Forereef	2015-2016	-0.08388	0.1003	2316	-0.836	1	=
FK	Shallow Forereef	2016-2017	-0.28334	0.097	2316	-2.922	0.1866	=
FK	Shallow Forereef	2017-2018	0.68971	0.1034	2316	6.668	<0.0001	-
FK	**Shallow Forereef**	**2004-2018**	**-0.25684**	**0.147**	**2316**	**-1.747**	**0.9181**	**=**
FK	Patch Reef	2004-2005	0.227549	0.1088	2316	2.091	0.7413	=
FK	Patch Reef	2005-2006	0.226884	0.1141	2316	1.988	0.8056	=
FK	Patch Reef	2006-2007	-0.34981	0.1095	2316	-3.195	0.091	=
FK	Patch Reef	2007-2008	-0.06334	0.0996	2316	-0.636	1	=
FK	Patch Reef	2008-2009	0.058665	0.1001	2316	0.586	1	=
FK	Patch Reef	2009-2010	0.287187	0.1036	2316	2.771	0.2634	=
FK	Patch Reef	2010-2011	-0.64421	0.0998	2316	-6.452	<0.0001	+
FK	Patch Reef	2011-2012	0.08271	0.094	2316	0.88	0.9999	=
FK	Patch Reef	2012-2013	0.018389	0.0943	2316	0.195	1	=
FK	Patch Reef	2013-2014	-0.01507	0.0939	2316	-0.16	1	=
FK	Patch Reef	2014-2015	-0.19538	0.0932	2316	-2.097	0.7371	=
FK	Patch Reef	2015-2016	-0.00879	0.0922	2316	-0.095	1	=
FK	Patch Reef	2016-2017	-0.28849	0.091	2316	-3.169	0.0981	=
FK	Patch Reef	2017-2018	0.187599	0.0905	2316	2.073	0.7528	=
FK	**Patch Reef**	**2004-2018**	**-0.4761**	**0.1286**	**2316**	**-3.701**	**0.0178**	**+**
ECA	Inner	2004-2005	-0.58552	0.2293	2316	-2.554	0.402	=

ECA	Inner	2005-2006	-0.08463	0.2141	2316	-0.395	1	=
ECA	Inner	2006-2007	-0.17049	0.2048	2316	-0.832	1	=
ECA	Inner	2007-2008	0.080583	0.1956	2316	0.412	1	=
ECA	Inner	2008-2009	-0.03524	0.1949	2316	-0.181	1	=
ECA	Inner	2009-2010	-0.18864	0.1928	2316	-0.979	0.9997	=
ECA	Inner	2010-2011	-0.24419	0.1896	2316	-1.288	0.9944	=
ECA	Inner	2011-2012	0.195799	0.1884	2316	1.039	0.9994	=
ECA	Inner	2012-2013	0.266822	0.1924	2316	1.387	0.9885	=
ECA	Inner	2013-2014	-0.08458	0.1943	2316	-0.435	1	=
ECA	Inner	2014-2015	-0.11511	0.1926	2316	-0.598	1	=
ECA	Inner	2015-2016	0.115507	0.1928	2316	0.599	1	=
ECA	Inner	2016-2017	0.029536	0.1964	2316	0.15	1	=
ECA	Inner	2017-2018	-0.13675	0.1975	2316	-0.692	1	=
ECA	**Inner**	**2004-2018**	**-0.95691**	**0.2796**	**2316**	**-3.422**	**0.0459**	**+**
ECA	Middle	2004-2005	-0.08609	0.2007	2316	-0.429	1	=
ECA	Middle	2005-2006	-0.09686	0.1982	2316	-0.489	1	=
ECA	Middle	2006-2007	-0.08483	0.1935	2316	-0.439	1	=
ECA	Middle	2007-2008	-0.0958	0.1876	2316	-0.511	1	=
ECA	Middle	2008-2009	0.098518	0.1868	2316	0.527	1	=
ECA	Middle	2009-2010	-0.13511	0.1867	2316	-0.724	1	=
ECA	Middle	2010-2011	-0.27628	0.1846	2316	-1.496	0.9769	=
ECA	Middle	2011-2012	0.174894	0.1835	2316	0.953	0.9998	=
ECA	Middle	2012-2013	0.125614	0.1852	2316	0.678	1	=
ECA	Middle	2013-2014	-0.04234	0.1862	2316	-0.227	1	=
ECA	Middle	2014-2015	-0.14734	0.185	2316	-0.797	1	=
ECA	Middle	2015-2016	0.168714	0.1845	2316	0.914	0.9999	=
ECA	Middle	2016-2017	-0.24885	0.185	2316	-1.345	0.9914	=
ECA	Middle	2017-2018	0.278774	0.1856	2316	1.502	0.976	=
ECA	**Middle**	**2004-2018**	**-0.367**	**0.2594**	**2316**	**-1.415**	**0.9861**	**=**
ECA	Outer	2004-2005	-0.00416	0.1389	2316	-0.03	1	=
ECA	Outer	2005-2006	-0.11041	0.1385	2316	-0.797	1	=
ECA	Outer	2006-2007	-0.24044	0.1341	2316	-1.793	0.9014	=
ECA	Outer	2007-2008	0.140043	0.1314	2316	1.066	0.9993	=
ECA	Outer	2008-2009	-0.1829	0.1308	2316	-1.398	0.9876	=
ECA	Outer	2009-2010	-0.15095	0.1292	2316	-1.168	0.998	=
ECA	Outer	2010-2011	0.013287	0.1289	2316	0.103	1	=
ECA	Outer	2011-2012	-0.1056	0.1284	2316	-0.822	1	=
ECA	Outer	2012-2013	0.167997	0.1286	2316	1.307	0.9935	=
ECA	Outer	2013-2014	0.08744	0.1298	2316	0.674	1	=
ECA	Outer	2014-2015	0.014789	0.1303	2316	0.114	1	=
ECA	Outer	2015-2016	0.001642	0.1303	2316	0.013	1	=

ECA	Outer	2016-2017	-0.16237	0.1301	2316	-1.248	0.9959	=
ECA	Outer	2017-2018	0.160265	0.1307	2316	1.226	0.9966	=
ECA	**Outer**	**2004-2018**	**-0.37136**	**0.1813**	**2316**	**-2.048**	**0.7689**	**=**

Table S6. Results from Permanova for benthic community cover composition, using Type III sum of squares based on 9999 permutations of residuals under a reduced model: Model structure = Region (fixed), Year (fixed), Sub-region (Fixed, nested in Region), Regional Habitat (Fixed, nested in Region), Site (Random, nested with Regional Habitat, Sub-region, Region).

Source	Df	SS	Pseudo-F	P(perm)	Unique Permutations	Square root - Estimates of components of variation
Region	2	49958	4.9803	0.0002	9939	6.3233
Year	14	55179	40.011	0.0001	9877	6.6573
Sub-region	4	31376	1.6568	0.0779	9917	3.0892
Regional Habitat	5	167490	6.988	0.0001	9909	10.017
Region x Year	28	21074	7.6343	0.0001	9837	4.4255
Sub-region x Year	56	18444	3.3101	0.0001	9788	3.2099
Regional Habitat x Year	70	7589.9	1.0991	0.1883	9752	0.7061
Site	27	122960	46.3	0.0001	9829	9.1652

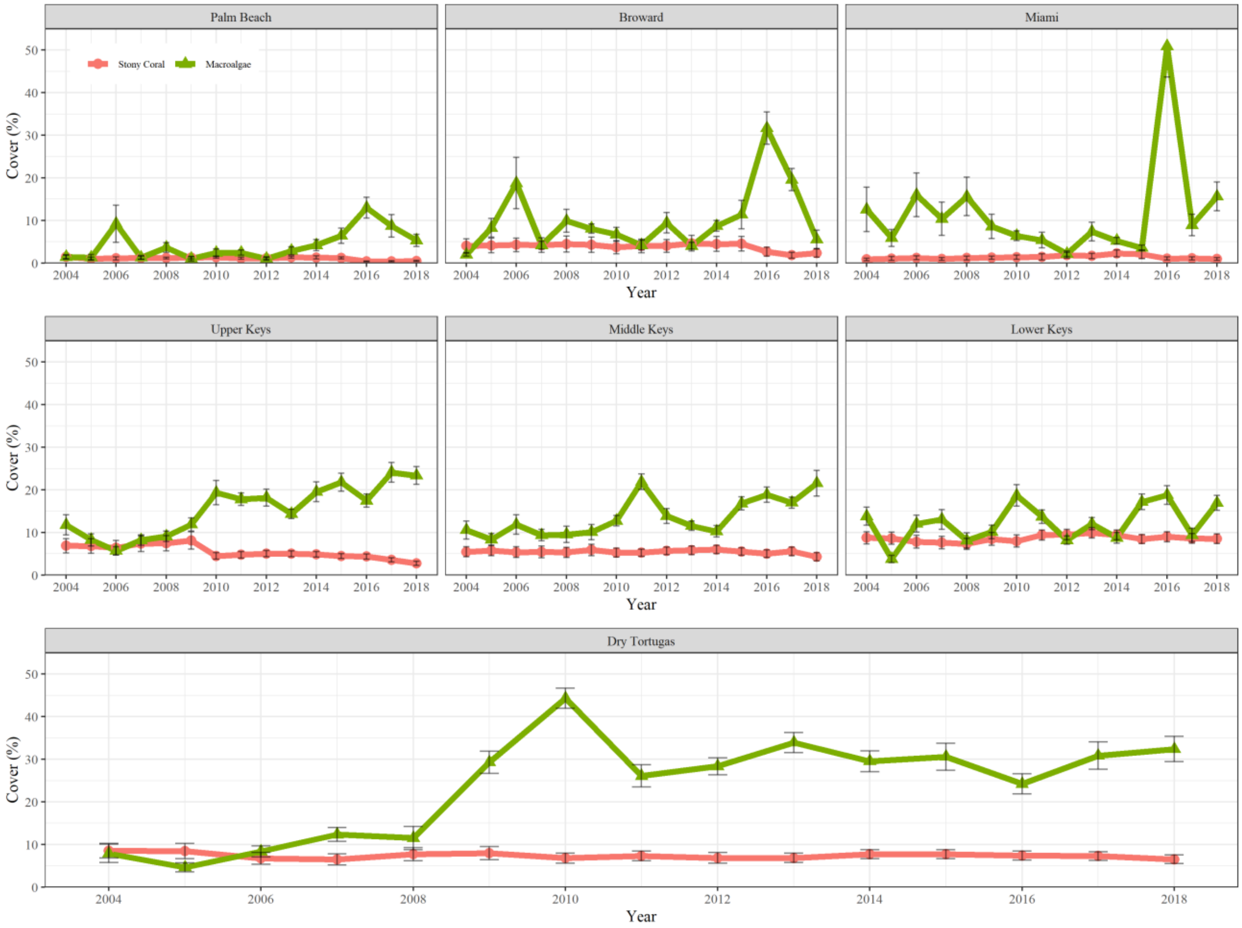

Figure S1. Mean percent cover (±SE) of stony coral and macroalgae on the FCR. Top panel = ECA sub-regions, Middle Panel = FK sub-regions, Bottom Panel = Dry Tortugas sub-region. Sub-regions ordered from North East to South West L – R.

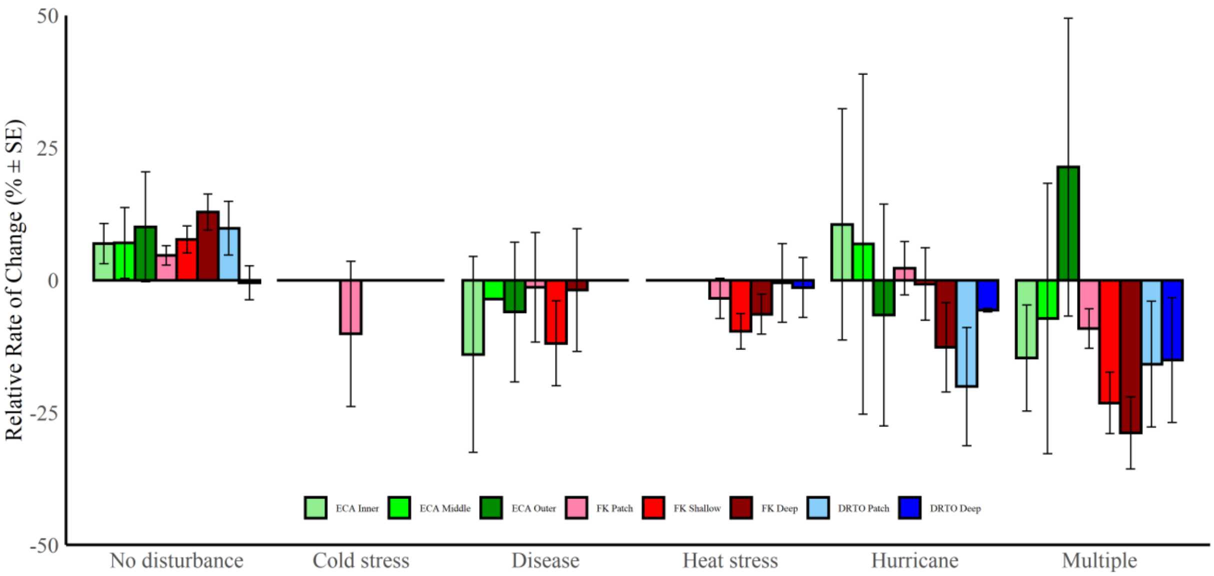

Figure S2. Stony coral cover relative rate of change in each regional habitat following periods of no disturbance and major disturbances. The absence of bars indicate disturbance did not occur in the regional habitat over the course of the study. Note, the ECA did not experience heat stress alone, but heat stress in conjunction with hurricanes in 2005 and disease in 2014 and 2015.

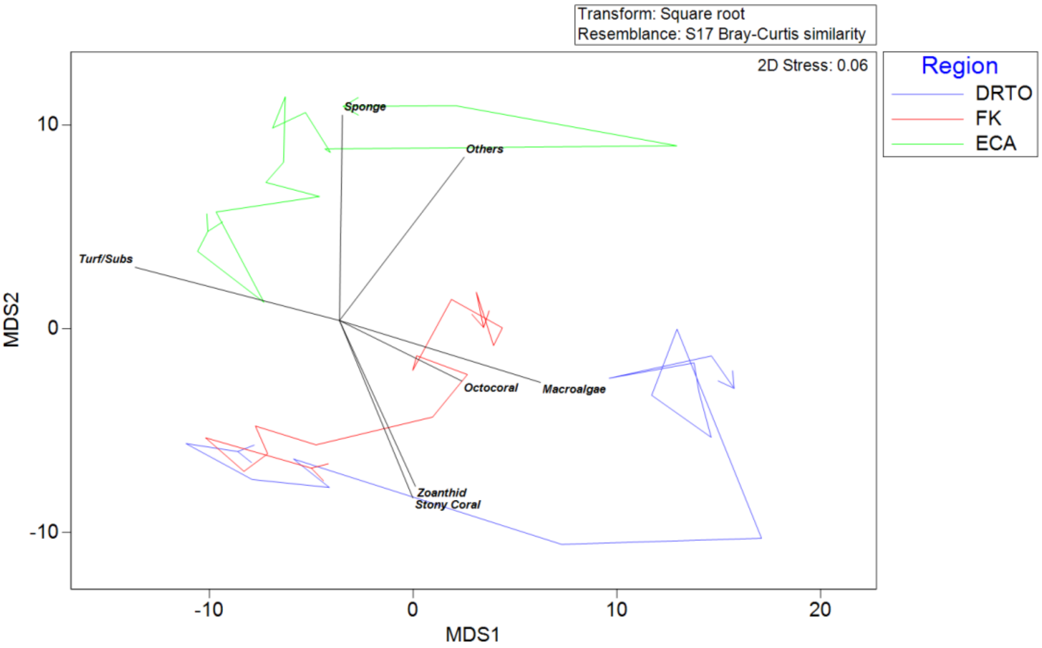

Figure S3. Threshold metric MDS plot showing benthic community trajectories from 2004 to 2018. Each line represents temporal trajectory in each region, based upon the distance among centroids calculation. Arrows represent direction of community change. Vectors represent relative importance of taxa in dissimilarity.

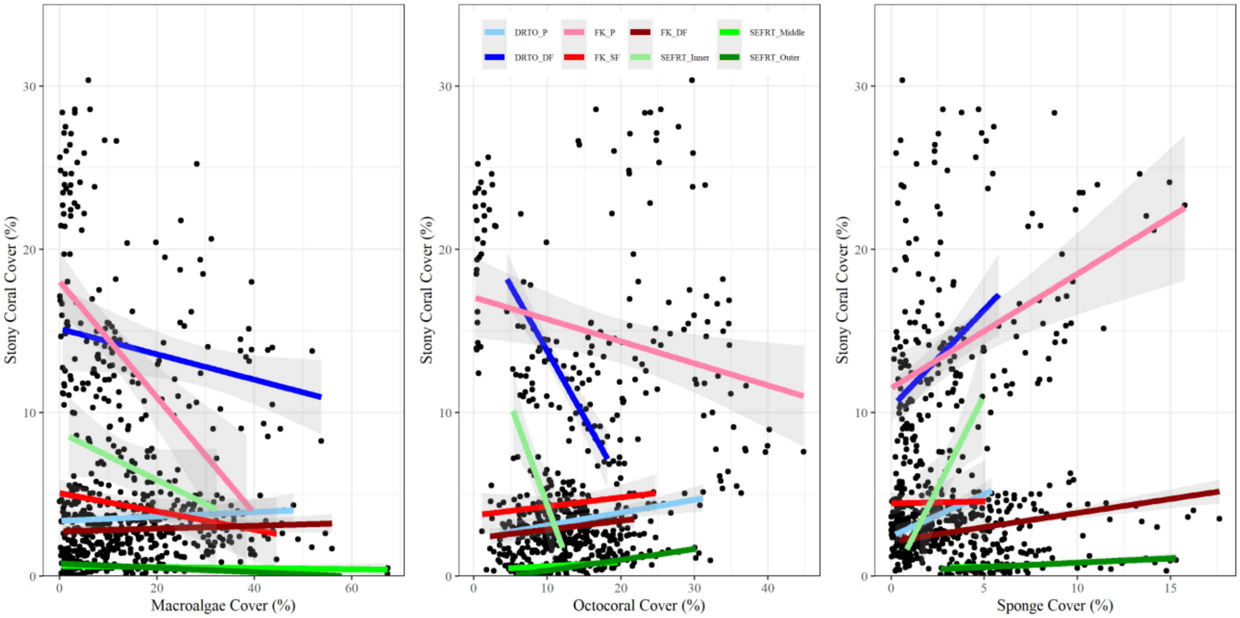

Figure S4. Regression plots of potential phase shifts. Points represent mean cover per site per year, lines represent line of best fit (± SE). Left: Stony Coral vs Macroalgae; Middle: Stony Coral vs Octocoral; Right: Stony Coral vs Sponge.

Chapter 2. High incidence of partial colony mortality constrains realized growth for three coral species (*Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea*) in southeast Florida

Abstract

Growth rates of individual coral colonies are a key demographic trait which can reveal fundamental changes in population health and resilience. With changing environmental conditions on coral reefs, assessing spatial, temporal and taxonomic variation in net coral growth (accounting for growth and partial mortality) is fundamental to understanding the changing structure and dynamics of coral populations and communities. In recent years, the high-latitude Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) has experienced mass coral mortality from heat stress and disease, thus increased focus has been placed on restoration. Yet it is unclear how growth rates vary within and between species spatially and whether there is growth suppression which reduces recovery potential. To assess this, interannual changes in growth rate and linear extension of the three most abundant species, *Montastraea cavernosa*, *Porites astreoides*, and *Siderastrea siderea*, were quantified between 2000 and 2020 to specifically test for spatiotemporal variations in net growth rate and partial mortality prevalence in Broward County, Florida. Of 136 tracked colonies, 33% died and 89% had partial mortality. Small *M. cavernosa* and *P. astreoides* colonies generally grew faster than large colonies and had less partial mortality, but *S. siderea* consistently had high partial mortality. *M. cavernosa* and *S. siderea* net growth rates primarily declined following excess heat stress or disease outbreaks, which caused partial and whole colony mortality, but growth rates in all species were often negligible during inter-disturbance periods. Maximum annual growth rates of each species align with those found elsewhere in the Caribbean, but partial mortality prevalence and extent was exceptionally high, particularly in large colonies, resulting in allometric net growth. As a result, colonies of each species reached just a third of their theoretical maximum size after 20 years which hampers recovery capacity.

Keywords: Long-term monitoring, net growth, linear extension, disturbance, inter-disturbance

Introduction

Much of the recent research on coral reefs has been focused on measuring the effects of acute disturbances, such as severe tropical storms or marine heatwaves, on coral communities (Hughes et al. 2018, Ortiz et al. 2018, Mellin et al. 2019). Moreover, the effects of acute disturbances on coral communities are mostly assessed based on changes in cover or abundance of major taxa (e.g., De'ath et al. 2012, Hughes et al. 2018, Chapter 1). Such studies fail to consider the demographic mechanisms or chronic pressures which often determine recovery and underpin resilience (Hughes and Jackson 1980, Edmunds and Riegl 2020). Growth rates of individual coral colonies are a key demographic trait which can reveal fundamental changes in population health and resilience, the ability to absorb a disturbance and recover (Pratchett et al. 2015), and will affect the future abundance, size structure, and viability of coral populations.

For colonial coral species, growth mostly occurs by addition of coral polyps (Madin et al. 2020), though it is also possible that some polyps die or are lost, effectively reducing colony size. When the incidence or extent of this partial mortality exceeds the rate of coral growth then colonies will get smaller over time. Net growth of coral colonies (accounting for both growth and partial mortality) may vary spatially, temporally and taxonomically (Kuffner et al. 2013, Manzello et al. 2015, Madin et al. 2020), depending on environmental conditions and disturbance regimes. Importantly, acute disturbances and chronic anthropogenic pressures, such as poor water quality, not only increase rates of partial mortality, but may also constrain rates of coral growth. For some coral species, growth can be suppressed immediately after acute heat stress (Cantin and Lough 2014, Gold and Palumbi 2018, but see Crabbe 2009), irrespective of whether corals bleach (Carilli et al. 2010, Neal et al. 2017). Elevated turbidity and nutrients can also suppress growth (Dodge et al. 1974, Dodge and Vaisnys 1977, Crabbe and Carlin 2007) and increase the prevalence or extent of partial mortality (Vega Thurber et al. 2014). Elevated turbidity may conflate (Anthony and Connolly 2004) or mediate (Cacciapaglia and van Woesik 2016, Rippe et al. 2018) the effects of heat stress, thereby differentially affecting net growth rate (Helmle et al. 2011, Cooper et al. 2012). With changing environmental conditions and disturbance regimes on coral reefs (Nyström et al. 2000, Mellin et al. 2019, Pratchett et al. 2020), understanding spatial, temporal and taxonomic variation in net coral growth is fundamental in understanding the changing structure and dynamics of coral populations and communities.

The predominant method used in long-term studies to account for both growth and partial mortality is to measure changes in the horizontal planar area of individual coral colonies (e.g., Crabbe 2009, Pratchett et al. 2015; Gold and Palumbi 2018, Madin et al. 2020). Proportional changes in planar area generally decline with increasing colony size, partly due to increasing prevalence and extent of partial mortality in larger colonies (Tanner 1995, Dornelas et al. 2017, Madin et al. 2020, Fong and Todd 2021). While long-term studies using this method find most colonies have net growth, particularly in small size classes (Dornelas et al. 2017, Brito-Millan et al. 2019), high rates of colony fission or shrinkage may occur under environmental stress (Riegl and Purkis 2015, Riegl et al. 2017). Hughes and Tanner (2000) found two-thirds of surviving *Orbicella annularis* shrank in a six-year period (1987-1993) in Jamaica and Edmunds et al. (2004) found 25% of juvenile corals shrank or did not grow over one year in the Florida Keys. These suggest that even while population density or cover may be stable or increase, underlying barriers to increasing colony size may represent chronic pressures which suggest low resilience. Measuring planar growth may therefore capture intrinsic differences and the impact of extrinsic factors which cause partial mortality, such as acute disturbances or chronic pressures (Neal et al. 2017, Gold and Palumbi 2018, Rippe et al. 2018, Madin et al. 2020).

This study examined spatiotemporal variation in net colony growth, partial mortality prevalence and whole colony mortality prevalence of the three most abundant coral species (*Montastraea cavernosa*, *Porites astreoides*, and *Siderastrea siderea*) in the high-latitude Southeast Florida Coral Reef Ecosystem Conservation Area (ECA). Heat stress and SCTLD caused mass coral mortality from 2014 to 2017 (Walton et al. 2018), which has increased focus on restoration of massive, reef-building species. Yet it is unclear whether small increases in coral cover from 2004 to 2014 (see Chapter 1), mask chronic growth suppression which reduces recovery potential and whether net growth rates vary within and between species spatially. I tracked 136 coral colonies from the three species for 5 to 21 years between 2000 and 2020, a period that spanned multiple acute disturbances: heat stress related bleaching in 2005, 2014 and 2015, major hurricanes in 2005 and 2017 and a severe disease outbreak, stony coral tissue loss disease (SCTLD), which peaked in 2016 (Chapter 1). Proportional interannual changes in horizontal planar live tissue area (i.e., relative colony growth rate) and the annual change in the arithmetic mean radius (i.e., linear extension) were quantified to specifically test for spatiotemporal variations in growth rate and partial mortality prevalence to assess a demographic mechanism that influences the potential resilience to acute disturbances and chronic pressure of these species in southeast Florida.

Methods

Spatiotemporal variation in net coral growth, partial mortality prevalence and whole colony mortality prevalence were examined from 2000 to 2020 by tracking 136 coral colonies from three species at 19 sites in three reef habitats in southeast Florida (26.3114 N to 26.0042 N; Table S1). Each individual colony was tracked annually for 5 to 21 years, depending on time of recruitment into the study area or whole colony mortality, between 2000 and 2020, whereby the horizontal 2D area was recorded photographically every year, except in 2009 when no surveys were conducted. A five-year minimum time period was selected to avoid assessing colonies that appeared visibly healthy but had underlying conditions leading to immediate mortality and restricting growth, and as this timespan was hypothesized to sufficiently capture interannual variation and trend in growth of each colony. Surveys were typically conducted from October to December in each sample year. Habitats varied with depth and distance offshore. The inner reef habitat, 275-780 m offshore at a depth range of 4-10 m, comprises the nearshore ridge complex and linear inner reef. The middle reef habitat is 770-2000 m offshore at 11-16 m depth. The outer reef habitat is 1500-3000m offshore at 16-18 m depth. Sites were also divided into three sub-regions, by latitude/by ports and inlets as per Jones et al. (2020). The Deerfield sub-region, furthest north, is between Boca and Hillsboro inlets (~9 km). The Broward/Fort Lauderdale sub-region is between Hillsboro Inlet and Port Everglades (~18 km). The Hollywood/Miami sub-region is furthest south, between Port Everglades and the Broward/Miami-Dade County line (~13 km).

Study Species

The three study coral species are expected to have different stress tolerances (Darling et al. 2012, Jones et al. 2020). *Montastraea cavernosa* is a massive, gonochoric broadcast spawning coral, which dominates in the study area. Despite being considered relatively stress tolerant (Darling et al. 2012), recent bleaching and disease events have resulted in significant declines in *M. cavernosa* density and cover (Walton et al. 2018, Jones et al. 2020). *Porites astreoides* is a brooding, encrusting species, which has increased in cover and density on the ECA in recent years (Jones et al. 2020) and has previously been classified as resilient/weedy (Darling et al. 2012). *Siderastrea siderea* is a massive, gonochoric broadcast spawning species, is considered stress tolerant (Darling et al. 2012), and was not heavily impacted by recent disease and has a high recruitment rate in Florida (Walton et al. 2018). Each species grows primarily in the horizontal plane in southeast Florida (Goldberg 1973, Lirman 2000).

Coral Health and Growth Rate

Replicate colonies of *Montastraea cavernosa* (n=53), *Porites astreoides* (n=46) and *Siderastrea siderea* (n=37) were surveyed over successive years in the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA). Change in horizontal planar colony area was chosen as the most suitable metric to assess net growth as it captures increases and decreases in colony size, the area of occupancy and allows conversion to arithmetic mean radius (AMR; Pratchett et al. 2015). Photographic images of each colony were taken annually using an Olympus c5060 camera and Ikelite housing mounted at a fixed distance onto a $0.75m^2$ quadrat parallel to the colony surface. A 2-dimensional scale bar of known width was attached to the quadrat, parallel to the coral colony. Incidences of partial or whole colony mortality were recorded on every colony and verified by in situ diver assessment. Images were qualitatively inspected for skew, distortion or obstruction of the colony boundary and images with inferred high parallax error or that did not capture the colony boundary were removed. Fifteen colonies were omitted from quantitative growth analysis due to high parallax error. To calculate coral growth rate, the living tissue planar area of the remaining 121 colonies was measured annually from photographic images (n = 42 *M. cavernosa*, n = 42 *P. astreoides*, n = 37 *S. siderea*). Planar live tissue area was measured using Image J software (Schneider et al. 2012). Images were calibrated using the scale bar of known width and the outline of the colony carefully traced to calculate the total area of living tissue at each timepoint (cm^2). From this, the growth rate of each colony was calculated as the relative change in live tissue area (% yr^{-1}; Equation 1). The AMR was calculated as the square root of the live tissue area divided by pi (cm), the annual change in AMR (cm yr^{-1}) and the colony diameter (cm).

$$\text{Growth Rate}\left(\%\ \text{yr}^{-1}\right)=\frac{((\text{Area in Year X+t})\text{-Area in Year X})/\text{t}}{\text{Area in Year X}}\ \text{x}\ 100$$

Equation 1. Relative growth rate in percent per year, where X is the live tissue area in year X, X + t is the live tissue area in the next timepoint and t is the time between monitoring periods.

Potential vs realized growth of juvenile colonies (< 5 cm diameter) was assessed by comparing the potential increase in AMR with the actual realized increase in AMR. Where the potential increase in AMR is calculated as the mean of the maximum interannual change in AMR per colony and assumes isometric growth over time. The actual realized increase in AMR is the measured increase in AMR over time of juvenile colonies.

Statistical Analysis

Statistical analysis of intraspecific, interspecific and spatiotemporal variation in annual relative growth rate (% yr^{-1}) was conducted in R (R Core Team 2020). A Linear Mixed Effects Model (LMM) was used to assess variation in growth rate in relation to Species, Minimum Colony Age, Colony Diameter, Survey Year, Depth, Habitat and Sub-region using the “lme” function from the “nlme” package (Pinheiro et al. 2017). LMMs using the lme function were used as growth rate was normally distributed, and it allowed us to incorporate both random effects and variance structure into the model. Species (3 levels), Survey Year (19 levels), Habitat (3 levels) and Sub-region (3 levels) were considered as categorical factors. Minimum Colony Age (i.e., recorded as the number of years the coral was surveyed, not the exact age of the colony), Colony Diameter (calculated from projected area and considered at each timepoint as the live tissue diameter the previous year) and Depth were considered as continuous factors. A single model approach was used, starting with the modified full model, consisting of all factors and the interaction between Species and each factor (Equation 2) and the fitted minimum adequate model selected by the Akaike Information Criterion (AIC) from multiple candidate models. More complex models assessing interactions between all factors were not assessed as many model combinations could not be fitted due to lack of convergence and my interest was primarily between the factors and how each species related to them. In the event of equivalent models (i.e., within an AIC score of 2; Burnham and Anderson 2004), the simplest model was selected. Repeat measurements of the same colony were accounted for by incorporating Colony ID as a random intercept in all models after assessment of candidate random effects, including random intercept Colony ID, random intercept Colony ID nested within Site and random slope Colony ID. Model validation was conducted by plotting residuals vs fitted values and residuals versus each factor. Heteroscedasticity was found in the residuals and a variance structure was added using the weights argument in “lme” to account for heterogeneity in variance by Species and increased variance with Colony Diameter. Multiple possible variance structures were fitted as per Zuur et al. (2009), re-performed model selection and selected a Constant Plus Power Variance Structure, using the “varConstPower” function (Pinheiro and Bates 2000) which incorporated heterogeneity in the variance of both Colony Diameter and Species (Equation 2). Model validation of the fitted model containing variance structure indicated no problems. Post-hoc, pairwise assessment of retained variables in the minimum adequate model was conducted using the package “emmeans” and Tukey method, where differences in the response variable were analyzed between levels of a factor (e.g., Species) or interaction (e.g., Species x Minimum Colony Age) based on model predictions (Lenth 2019). Emmeans contrasts was used to assess significant variation in levels of a factor against the mean value. For interactions between categorical and continuous factors (covariates), the “emtrends” function was used to assess covariate trends between levels of the categorical factor.

Growth Rate = Species ij + Sub-region ij + Habitat ij + Survey Year ij + Minimum Colony Age ij + Colony Diameter ij + Depth ij + Species ij x Sub-region ij + Species ij x Habitat ij + Species ij x Survey Year ij + Species ij x Minimum Colony Age ij + Species ij x Colony Diameter ij + Species ij x Depth ij + Colony ID i + ε ij

Growth Rate ij ~ Gaussian(μ ij)

Colony ID ~ N(0, σ^2)

Var(ε ij) = σ^2 x (δ1 + |Species ij |Diameter ij|δ2$)^2$

Equation 2. LMM examining variation in growth rate, where growth rate ij refers to the jth observation at Colony ID i. Random intercept Colony ID is assumed to be normally distributed with mean 0 and variance σ^2. Residual variance (ε) is proportional to the constant δ1 plus the power of the variance covariates Species and Colony Diameter.

Temporal variation in the change in AMR was assessed for each species using Kruskal-Wallis non-parametric analysis of variance due to violation of assumptions of normality and homogeneity of variance despite transformation or centering of data. For the same reason, the relationship between the change in AMR and colony size was assessed for each species independently with Theil-Sen non-parametric linear regression.

Results

Colony Health

Of the 136 coral colonies monitored, 33% of the colonies died and 89% of colonies experienced partial colony mortality between 2000 and 2020 (n=45 and n=121 respectively; Figure 1). Only five *M. cavernosa* and three *S. siderea* colonies had no partial or whole colony mortality. All *P. astreoides* had whole and/or partial colony mortality. Of the 45 colonies that died, 37 died between fall 2013 and 2016 when multiple acute disturbances occurred; 17 *M. cavernosa* colonies died from 2014 to 2015 and seven from 2015 to 2016, seven *P. astreoides* colonies died from 2015 to 2016 and four *S. siderea* colonies died between 2013 and 2015. Ninety-one colonies were still alive in 2020; 12% had shrunk, two *M. cavernosa* on the inner reef, two *P. astreoides* on the inner reef, one *P. astreoides* on the middle reef and three *S. siderea* on each of the middle and outer reefs. Only 58% of the 45 colonies surveyed in 2000 survived until 2020: 50% of *M. cavernosa* colonies (12 of 24), 45% of *P. astreoides* colonies (5 of 11) and 90% of *S. siderea* colonies (9 of 10).

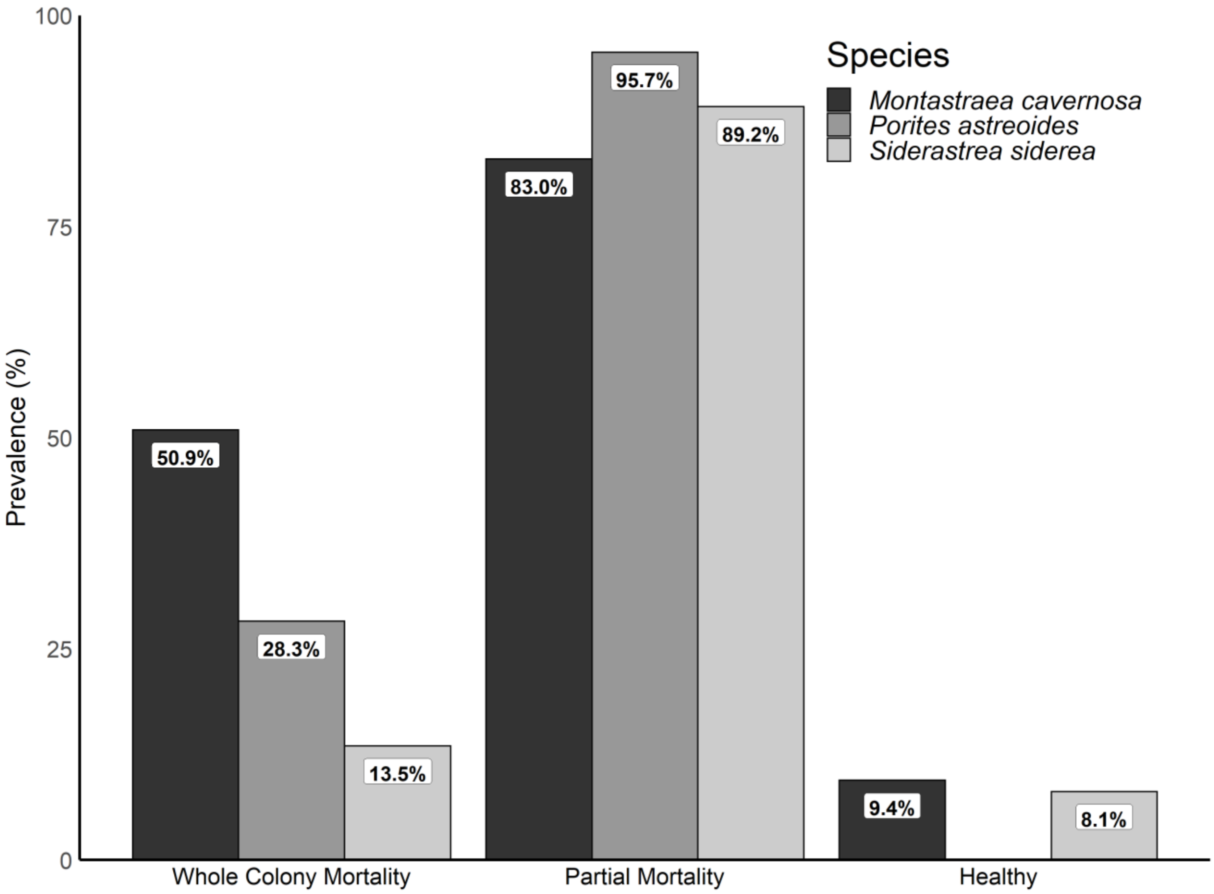

Figure 1. Coral colony health (recorded as partial or whole colony mortality) from 2000 to 2020. Healthy colonies recorded as those with no partial or whole colony mortality.

Coral growth was quantitively assessed on 121 colonies, 86 of which were still alive in 2020. Of these, 76 had a net increase in size (AMR) from their first to last survey point: 21 of 23 *M. cavernosa*, 29 of 31 *P. astreoides* and 26 of 32 *S. siderea*. Mean increase in AMR (i.e., linear extension) in the 76 colonies with net growth was 0.13 cm yr^{-1} (±0.02 SE) for *M. cavernosa*, 0.2 cm yr^{-1} (±0.02 SE) for *P. astreoides* and 0.12 cm yr^{-1} (±0.01 SE) for *S. siderea*.

Coral Growth Rate

Net growth of larger colonies was negligible for all species (Figure 2) and all large colonies tracked (> 20cm diameter) shrank during at least one interannual period (Year X to Year X+1; Table 1). Juvenile *M. cavernosa* and *P. astreoides* colonies (< 5cm diameter) generally had less partial mortality than larger colonies and smaller colonies had positive net growth, but partial mortality in *S. siderea* was more consistent with colony size (Table 1 and 2).

Table 1. Percentage of colonies which declined in AMR during at least one interannual period by size class (Colony Diameter in cm). Note: While some colonies declined in size multiple times, each unique colony is only counted once per size class. No *S. siderea* colonies larger than 20 cm diameter were surveyed.

Species	Colony Size Class			
	Juvenile: < 5 cm	Small: 5-10cm	Medium: 10-20cm	Large: > 20cm
Montastraea cavernosa	61%	73%	79%	100%
Porites astreoides	25%	51%	75%	100%
Siderastrea siderea	71%	65%	67%	NA

Table 2. Mean colony diameter during every interannual growth rate record, mean number of years each was colony tracked (all species had colonies tracked for 5 years and colonies tracked for 20 years), colony diameter (calculated from projected colony area) and minimum colony age during each increase or decrease in net AMR per time period.

Species	All colonies (±SE)		Diameter (cm ±SE)		Minimum Colony Age (yrs. ±SE)	
	Diameter (cm)	Years Tracked	Increase AMR	Decrease AMR	Increase AMR	Decrease AMR
Montastraea cavernosa	11.3 ±0.4	8.8 ±0.2	10.2 ±0.5	13.8 ±0.9	8.6 ±0.3	9.3 ±0.4
Porites astreoides	8.3 ±0.2	7.8 ±0.2	7.9 ±0.2	9.5 ±0.4	7.1 ±0.2	10.4 ±0.5
Siderastrea siderea	4.9 ±0.1	7.7 ±0.3	4.8 ±0.2	5.2 ±0.3	7.4 ±0.3	8.7 ±0.5

Interspecific differences in coral growth rate (assessed as proportional change in planar live tissue area (% yr^{-1})) by Survey Year, Minimum Colony Age and Colony Diameter were found (Table S2; Linear Mixed Effects Model (LMM)). The relationship between growth rate and colony diameter varied significantly between *M. cavernosa* and both *P. astreoides* and *S. siderea* (emmeans pairwise comparison with Tukey test (Tukey pairwise), $p < 0.001$). *Montastraea cavernosa* had relatively consistent growth rate with increasing colony diameter, after a sharp decline for small colonies (LMM, $p = 0.1$), while *S. siderea* and *P. astreoides* growth rate declined with colony diameter (LMM, $p < 0.0001$; Figure 2). Change in AMR declined with colony diameter in all three species (non-parametric regression, $p < 0.001$; Figure S1). The relationship between growth rate and minimum colony age varied between *M. cavernosa* and *S. siderea* (Figure S2, Tukey pairwise, $p = 0.03$), but not between *M. cavernosa* and *P. astreoides* or *P. astreoides* and *S. siderea* (Tukey pairwise, $p > 0.05$). *S. siderea* had relatively consistent growth rate with minimum colony age. *M. cavernosa* and *P. astreoides* growth rate declined with minimum colony age (LMM, $p = 0.0004$ and $p = 0.02$ respectively). Spatial variations in growth rate were less pronounced and the fitted model suggested only moderate interactions between Species and

Habitat (p = 0.07), Species and Sub-region (p = 0.2) and Species and Depth (p = 0.3). *S. siderea* had a slightly, but not significantly higher growth rate inshore, while *M. cavernosa* and *P. astreoides* had marginally higher growth rates offshore, largely due to increased partial mortality on larger colonies on the inner reef. *M. cavernosa* and *P. astreoides* had marginally higher growth rates in the southern sub-region. Growth rate fluctuated widely for each species (Table 3), but model estimates suggest *P. astreoides* growth rates were 11.7 % (± 3.8 SE) faster than *S. siderea* (Tukey pairwise, p = 0.007).

Table 3. Annual growth rates for the three coral species (mean ± SD). Relative growth rate = mean percentage change in planar area per year; AMR = mean arithmetic radius of colonies at their initial survey timepoint; Max change in AMR = species mean of the maximum change in AMR per colony.

Species	Relative growth rate (% yr^{-1})	Planar change in area (cm^2 yr^{-1})	AMR (cm)	Change in AMR (cm yr^{-1})	Max change in AMR (cm yr^{-1})
Montastraea cavernosa	8.42 ± 28.8	-1.11 ± 43.2	5.1 ± 5.1	0.03 ± 0.6	0.48 ± 0.26
Porites astreoides	18.6 ± 39.1	4.18 ± 17.5	2.2 ± 1.3	0.17 ± 0.6	0.75 ± 0.36
Siderastrea siderea	20.1 ± 42.3	2.04 ± 7.3	1.6 ± 1.2	0.12 ± 0.3	0.51 ± 0.18

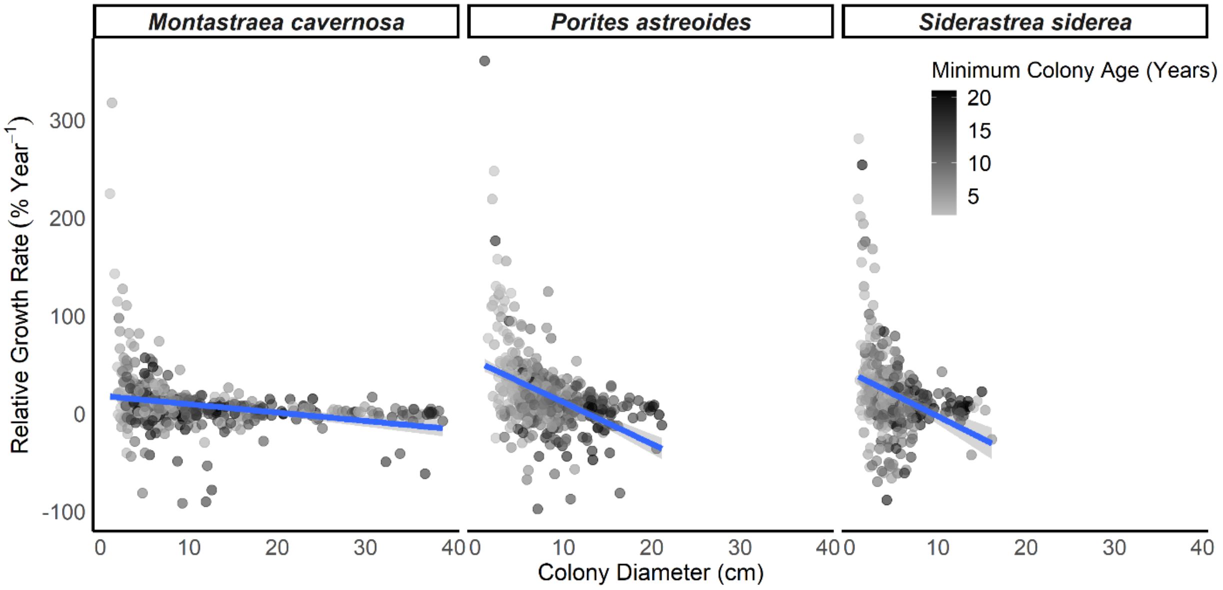

Figure 2. Relative growth rate (proportional change in colony area) vs colony size (colony live tissue diameter). Blue regression line represents trend in mean relative growth rate. Points represent the relative growth rate of each coral colony during each timepoint.

Interannual Growth Pattern

Growth rate fluctuated widely by survey year (Figure 3). Averaged across all colonies surveyed in that year, *M. cavernosa* growth rate ranged from 0.42% yr^{-1} (± 3.5) from 2017 to 2018 to 16.6% yr^{-1} (± 32.5 SE) from 2018 to 2019. *P. astreoides* growth rate ranged from -1.05 % yr^{-1} (± 5.0) from 2019 to 2020 to 53% yr^{-1} (± 13.1) from 2006 to 2007. *S. siderea* growth rate ranged from -8.4% yr^{-1} (± 7.7) from 2005 to 2006 to 45.8% yr^{-1} (± 12.8) from 2010 to 2011. The only significant interannual difference in growth rate occurred in *M. cavernosa*, where the growth rate from 2019 to 2020 exceeded that from 2015 to 2016 (Tukey pairwise, $p = 0.009$). Growth rates were particularly low for *M. cavernosa* from 2004 to 2005 and from 2015 to 2016 (emmeans contrasts, $p < 0.05$) and for *S. siderea* from 2005 to 2006 and 2006 to 2007 (emmeans contrasts, $p < 0.05$).

Regionwide, *M. cavernosa* linear extension (measured as change in AMR) ranged from -0.73 cm yr^{-1} (± 0.36) from 2015 to 2016 to 0.20 cm yr^{-1} (± 0.08 SE) from 2019 to 2020. *P. astreoides* linear extension ranged from -0.14 cm yr^{-1} (± 0.15) from 2019 to 2020 to 0.54 cm yr^{-1} (± 0.12) from 2006 to 2007. *S. siderea* linear extension ranged from -0.22 cm yr^{-1} (± 0.16) from 2005 to 2006 to 0.25 cm yr^{-1} (± 0.06) from 2001 to 2002. No significant interannual variation in linear extension was found for *M. cavernosa* (Kruskal-Wallis, $H = 20.28$, $p = 0.3$). Significant interannual variation in linear extension was found for *P. astreoides* Kruskal-Wallis, $H = 46.29$, $p = 0.0003$) and *S. siderea* (Kruskal-Wallis, $H = 31.98$, $p = 0.02$). *Porites astreoides* linear extension from 2006 to 2007 and from 2010 to 2011 was significantly greater than from 2019 to 2020 ($p < 0.05$). No significant differences were found in year-to-year comparisons of *S. siderea* linear extension.

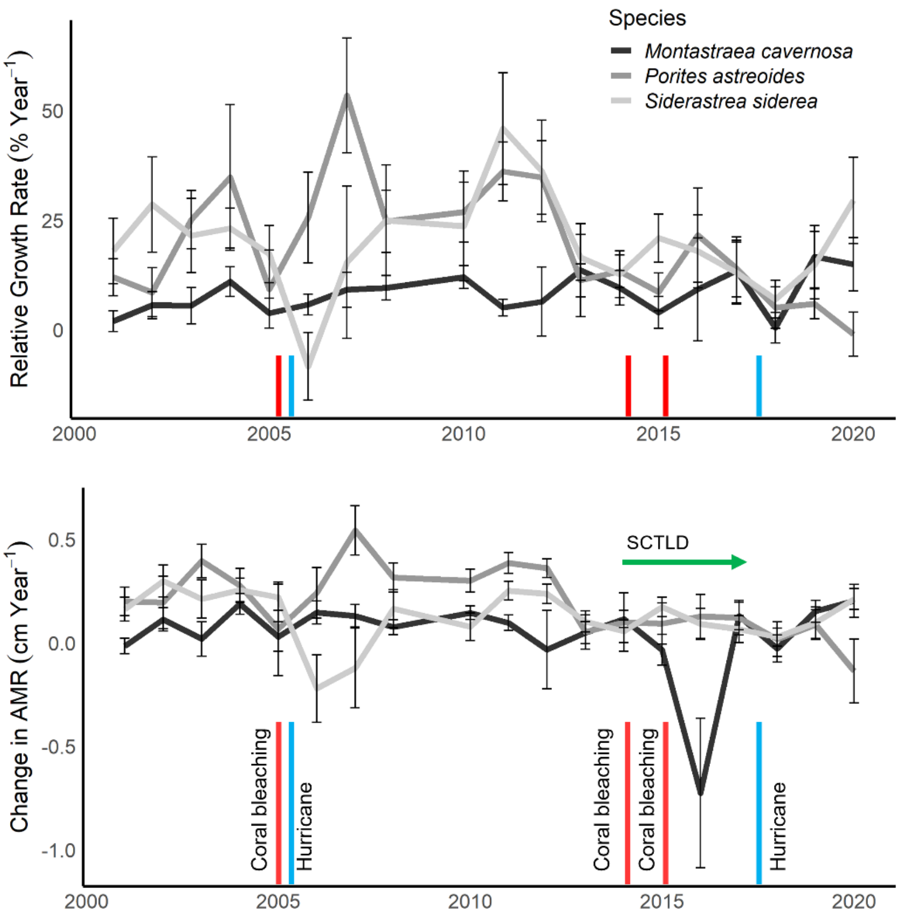

Figure 3. Interannual growth pattern of the three coral species. Top) Mean relative growth rate ±SE, based on proportional change in planar area (% change yr^{-1}); bottom) Mean change in AMR ±SE (cm yr^{-1}). Major acute disturbances during study period noted. Stony coral tissue loss disease was prevalent in the ECA from 2014 to 2017.

Realized vs Potential Growth

Linear extension of 81 colonies tracked as juveniles (< 5cm diameter) declined with minimum colony age for all three species, most noticeably in *P. astreoides* (Figure 4). Mean maximum annual linear extension of juveniles was 0.46 cm yr^{-1} (± 0.01 SE), 0.72 cm yr^{-1} (± 0.1) and 0.52 cm yr^{-1} (± 0.01) for *M. cavernosa*, *P. astreoides* and *S. siderea* respectively, but mean annual linear extension was substantially lower (0.13 cm yr^{-1} (± 0.02), 0.23 cm yr^{-1} (± 0.03) and 0.12 cm yr^{-1} (± 0.02) respectively). After 20 years, realized increases in colony size were three times lower than potential growth (assuming isometric growth), such that after 20 years the mean AMR of juveniles was only 3.27 cm (± 0.6) for *M. cavernosa*, 5.0 cm (± 0.0) for *P. astreoides* and 3.7 cm (± 0.8) for *S. siderea*.

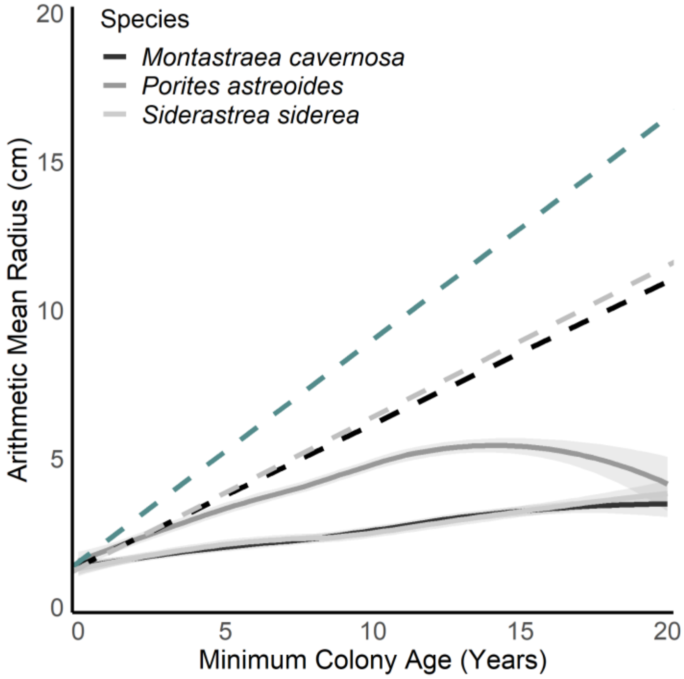

Figure 4. Potential vs realized size progression with minimum colony age of juveniles (colonies < 2.5 cm AMR at first measurement). Dashed line (Potential AMR) represents mean maximum potential increase in AMR (mean of maximum change in AMR per colony; Table 1) with time. Solid line represents mean measured AMR over time of juveniles (shading = SE).

Discussion

Coral growth in the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) was limited in the most abundant species, *Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea* from 2000 to 2020. Maximum observed growth rates of all three species align with those found elsewhere in the Caribbean (Hughes and Jackson 1985, Huston 1985, Elahi and Edmunds 2007, Crabbe 2009), but partial mortality prevalence and extent was very high, particularly in large colonies, which limited realized growth. In addition to 33% of the tracked colonies dying, 89% of colonies had partial mortality and 85% of measured colonies shrank during at least one interannual period, frequently in the two years following a known acute disturbance, but also during supposed inter-disturbance periods. Partial mortality can cause allometric growth in modular organisms constraining growth and resulting in populations with small colony size (Hughes and Jackson 1980, Dornelas et al. 2017, Riegl et al. 2017, Madin et al. 2020, Pisapia et al. 2020). Every large colony (>20 cm diameter) shrank during at least one interannual period and 12% of the colonies still alive in 2020 had shrunk compared to their initial size. Of these, 19% of *S. siderea* had shrunk and no colonies observed here grew into the largest size class. In recent years, a growing focus in the ECA has been placed on the restoration of massive reef-building colonies like *M. cavernosa*. My findings suggest that under current conditions long-term recovery from restoration alone is unlikely.

Linear extension (measured as change in AMR) declined with size in all three species, growth rate declined with size in *P. astreoides* and *S. siderea* and growth rate declined with minimum colony age in *M. cavernosa* and *P. astreoides*. Small, relatively young *M. cavernosa* and *P. astreoides* colonies generally had less partial mortality than older, large colonies giving them significantly increased growth capacity. This may lead to short-term increases in coral cover, but consistent colony growth currently appears to be prevented by cumulative stress and acute disturbances (Hughes and Jackson 1985, Pisapia and Pratchett 2014). *S. siderea* growth rate declined with colony size, but not minimum colony age, thus low whole colony mortality likely favors old, small colonies (Elahi and Edmunds 2007). This may explain the high abundance of small, fecund colonies found in southeast Florida (Moyer et al. 2003, St Gelais et al. 2016) but may prevent this species from contributing greatly to reef growth.

Interspecific differences in growth rate and mortality suggest variable resilience to acute disturbances resulting in different population trajectories. As predicted, *P. astreoides* growth rate was highest which may allow them to recover quickly following partial colony mortality. *P. astreoides* growth rate was significantly greater than *S. siderea*. Growth rate and linear extension increased in many colonies following disturbance, with growth rate and linear extension highest from 2006 to 2007, but *P. astreoides* growth rate was consistently low from 2016 onwards and linear extension declined overall from 2019 to 2020. Low recent growth rates and high partial mortality suggest the population may not be as healthy as suspected. *Montastraea cavernosa* colonies suffered extensive partial and whole colony mortality from 2014 to 2017 from heat stress and disease (Walton et al. 2018), with the largest decline in live tissue planar area in colonies surveyed from the first few years of the study (i.e., the oldest colonies). Since 2016, *M. cavernosa* linear extension has been comparatively high, with the growth rate highest from 2018 to 2019, linear extension highest from 2019 to 2020 and the growth rate from 2019 to 2020 significantly higher than 2015 to 2016. Potential explanations include colonies resistant to heat stress and disease or recruited during the thermal stress event have intrinsic resilience (Darling and Cote

2018, Madin et al 2020), or that environmental conditions are facilitating increased growth rate (Cooper et al. 2012). Mean and minimum sea surface temperature have risen in the ECA since 2007 (Jones et al. 2020) and with no extreme thermal stress events experienced since 2015, higher mean annual temperature may be facilitating increased growth (Lough and Barnes 2000, Cooper et al. 2012, Manzello et al. 2015). Whether this increase in growth and linear extension is resulting in increased calcification requires further investigation (Helmle et al. 2011), but this does suggest that *M. cavernosa* may have increased capacity to recover during inter-disturbance periods.

There was no clear evidence of any location where growth was not limited in any of the species. In the Florida Keys, the local climate has been suggested to buffer *S. siderea* and *Pseudodiploria strigosa* from growth decline in nearshore areas (Rippe et al. 2018). This study suggested *S. siderea* also grew marginally faster at inshore sites in the adjoining high-latitude ECA, but 60% of the colonies alive in 2020 had still shrunk in at least one interannual period. *M. cavernosa* and *P. astreoides* growth rates were slightly lower on the inner reef and higher on the outer reef, but this is likely largely a function of colony size (Pratchett et al. 2015, Dornelas et al. 2017). Despite some account of colony size in the model, most large *M. cavernosa* and *P. astreoides*, which experienced the greatest decline in live tissue planar area from partial mortality, are found on the inner reef. Huston (1985) also found *M. cavernosa* growth rates were highest at intermediate depths, and in this study twice as many *M. cavernosa* and *P. astreoides* colonies died on the inner reef than outer reef suggesting there may be some depth related stress resistance (Bongaerts and Smith 2019). No clear pattern in growth rate variation by sub-region was seen for any species, reflective of minimal difference in latitude which may influence changes in growth rate (Cooper et al. 2012). However, model predictions suggest growth rate of *P. astreoides* decreased slightly moving northwards and 80% of *P. astreoides* that died were in the northernmost sub-region.

Whole and partial colony mortality were most prevalent following years with known acute disturbances or disease outbreaks, which effectively slowed the growth rate of the reef-building species *M. cavernosa* and *S. siderea*. This study spanned multiple acute disturbances that impacted the ECA: El Niño related bleaching in 2005, 2014 and 2015, major hurricanes in 2005 and 2017 and a severe disease outbreak, stony coral tissue loss disease (SCTLD), which peaked in 2016 (Wilkinson and Souter 2008, Eakin et al. 2010, Walton et al. 2018, Chapter 1). Whole colony mortality was primarily observed rapidly after acute disturbance (i.e., the year of or after acute disturbance). Of the 45 colonies that died, 82% died from late 2013 to 2016 and *M. cavernosa* and *S. siderea* growth rates were lowest following acute disturbances. *M. cavernosa* linear extension was lowest from 2015 to 2016 and growth rate lowest from 2017 to 2018. Heat stress in combination with local environmental stress has previously been suggested to limit *M. cavernosa* growth rate in the Florida Keys (Manzello et al. 2015) and coupled with disease has limited growth in the ECA (Walton et al. 2018). *S. siderea* growth rate and linear extension were lowest from 2005 to 2006 and both remained low from 2006 to 2007. *S. siderea* is generally considered to be resistant to acute disturbance, often maintaining growth rates despite thermal stress (Darling et al. 2012, Kuffner et al. 2013, Rippe et al. 2018). The evidence suggests that in the ECA intense thermal stress may reduce *S. siderea* growth rate and kill whole colonies, as it likely did to the four colonies which died from late 2013 to 2015, but that growth rate generally recovers within a couple of years. No clear effect of acute disturbance on *P. astreoides* growth rate was detected here, but 16% of colonies surveyed between 2015 to 2016 died suggesting even species with increased thermal tolerance are not immune to extreme marine heatwaves (Manzello et al. 2015, Jones et al. 2020).

Acute disturbances correlated with some interannual declines in *M. cavernosa* and *S. siderea* growth rate and most instances of whole colony mortality, but low growth rates and high rates of partial mortality were frequently observed on colonies during supposed inter-disturbance periods suggesting local pressures are contributing significantly to limited net growth (Hughes and Jackson 1980, Elahi and Edmunds 2007, Crabbe 2009, Ortiz et al. 2018). For instance, *P. astreoides* growth rate and linear extension were lowest during the inter-disturbance period from 2019 to 2020, when *M. cavernosa* and *S. siderea* growth rates were high. Two probable causes seem most likely: *P. astreoides* has an encrusting growth form, which increases their susceptibility to overgrowth interactions with macroalgae that increases in cover during periods devoid of major hydrodynamic action (Lirman 2000, Mumby et al. 2005). Additionally, the cumulative effect of local stress, such as nutrient pollution or sedimentation, or repeat bleaching has increased partial mortality and limited net growth (Cantin and Lough 2014, Grottoli et al. 2014, Pisapia and Pratchett 2014, Manzello et al. 2015, Kim et al. 2019).

After 20 years, *M. cavernosa*, *P. astreoides* and *S. siderea* colonies reached just a third of their potential size if they had maintained mean maximum annual growth rates, contributing to low resilience which hampers recovery capacity (Chapter 1). Coral growth rates at high latitude are generally found to be lower than in the tropics (Grigg 1981, Anderson et al. 2015). I found that *M. cavernosa*, *P. astreoides* and *S. siderea* can attain similar growth rates to the tropical western Atlantic (e.g., Hughes and Jackson 1985, Huston 1985, Elahi and Edmunds 2007, Crabbe 2009), but they rarely sustain them in southeast Florida. This may suggest that acute disturbances and chronic pressures constrain coral growth, particularly of large colonies, reducing recovery capacity in reef-building and weedy species and leading to a community dominated by small colonies (Riegl et al. 2017, Pisapia et al. 2020). This has important restoration implications in Florida, where the fragmentation of large colonies and subsequent reattachment to maximize growth has become commonplace (Page et al. 2018). My findings suggest the initial growth rate may be high, but these will not be sustained without minimizing acute disturbances and chronic pressures. I found differences in stress tolerance and resilience between *M. cavernosa*, *P. astreoides* and *S. siderea* which align with their predicted life-history strategy (Darling et al. 2012) and their susceptibility to temperature stress in the ECA (Jones et al. 2020), but high partial colony mortality prevalence was found in all species. Previously, we found sub-regional increasing trends in stony coral cover from 2007 to 2014 in the ECA, before acute heat stress and disease caused a 43% regionwide decline in cover from 2015 to 2016 (Jones et al. 2020). Here, there was no clear evidence of any reef locations in the ECA where growth rate and linear extension were not significantly constrained among larger coral colonies, but *M. cavernosa* colonies that survived acute heat stress and disease from 2014 to 2017 were growing faster at the end of the study period than at any point in the previous 20 years. Here, I also captured the impact of acute disturbance on coral growth and mortality, but growth measurements also suggest the increasing trend in coral cover seen previously (Chapter 1, Jones et al. 2020), masked underlying demographic changes which limited net growth and recovery capacity.

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Supplementary Materials

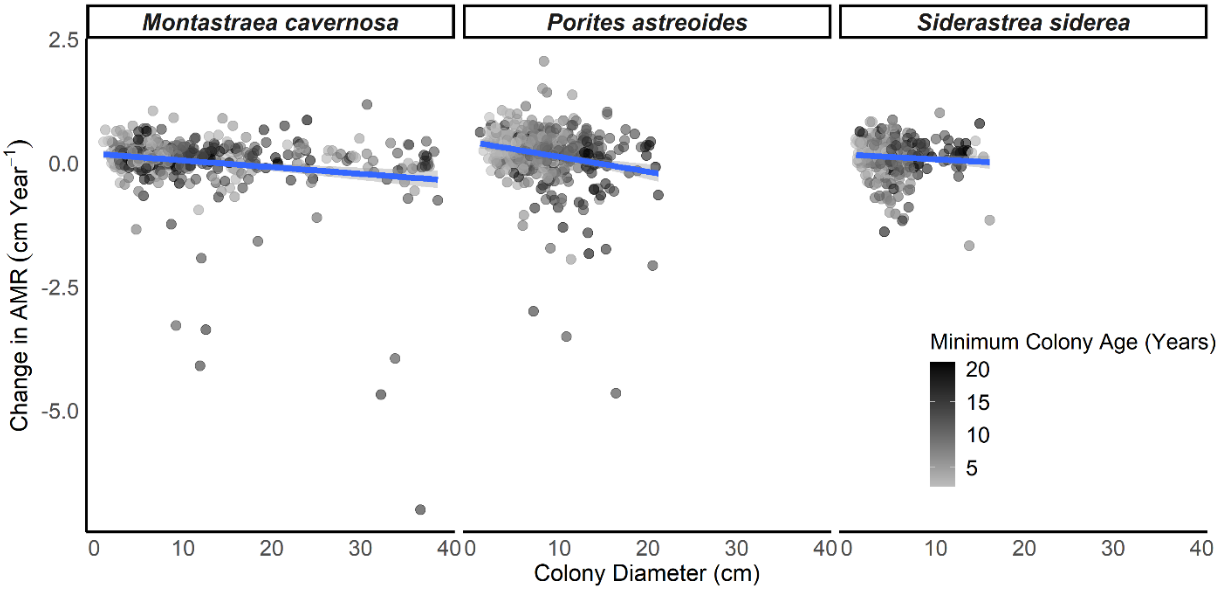

Figure S1. Change in AMR with size. Points represent changes in AMR of each individual colony between timepoints. Blue line represents linear regression of change in AMR vs Colony Diameter.

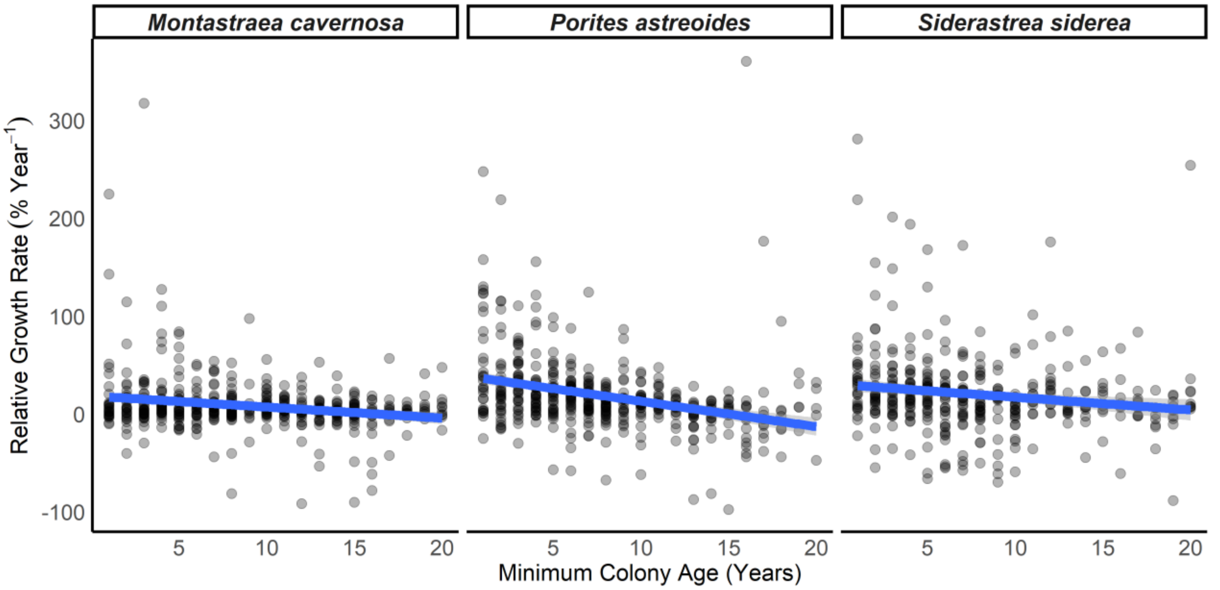

Figure S2. Relative growth rate (proportional change in colony area) vs Minimum Colony Age (i.e., years surveyed). Blue regression line represents the trend in relative growth rate. Points represent the relative growth rate of each coral colony during each timepoint.

Table S1. Monitored coral colonies. Location, duration of monitoring and size changes. All colonies not surveyed until 2020 died. Most colonies with start year after 2000 were monitored from recruits. Images at site DB2 were unusable in 2000. Site FTL5 was first monitored in 2003. Whether colony was measured or used solely for mortality prevalence noted (Y or N).

Species	Site	Habitat	Sub-region	Depth (m)	Start Year	End Year	Years Surveyed	Initial Diameter (cm)	End Diameter (cm)	Measured
MCAV	DB2	Middle	Deerfield	11	2001	2015	15	2	7.3	Y
MCAV	DB2	Middle	Deerfield	11	2001	2016	17	8.1	3.7	Y
MCAV	DB2	Middle	Deerfield	11	2000	2015	16	7	9.1	Y
MCAV	DB2	Middle	Deerfield	11	2000	2015	16	3.1	5.7	Y
MCAV	DB2	Middle	Deerfield	11	2000	2020	21	14.8	25.7	Y
MCAV	DB2	Middle	Deerfield	11	2004	2019	16	1.9	5.7	Y
MCAV	DB2	Middle	Deerfield	11	2000	2020	21	5.4	14.3	Y
MCAV	FTL2	Middle	FTL	15	2010	2020	11	2.9	4.9	Y
MCAV	FTL2	Middle	FTL	15	2015	2020	6	2.8	5.9	Y
MCAV	FTL2	Middle	FTL	15	2015	2020	6	1.1	5.8	Y
MCAV	FTL3	Outer	FTL	18	2007	2016	10	2	3.5	Y
MCAV	FTL3	Outer	FTL	18	2007	2016	10	3.5	2.9	Y
MCAV	FTL3	Outer	FTL	18	2000	2020	21	10	11.2	Y
MCAV	FTL3	Outer	FTL	18	2002	2020	19	2.4	8.5	Y
MCAV	FTL4	Inner	FTL	6	2000	2015	16	16.3	12.7	Y
MCAV	FTL4	Inner	FTL	6	2000	2015	16	26.5	28.9	Y
MCAV	FTL4	Inner	FTL	6	2000	2016	17	36.3	22.9	Y
MCAV	FTL4	Inner	FTL	6	2000	2020	21	21.8	24.4	Y
MCAV	FTL4	Inner	FTL	6	2000	2015	16	5.9	9.9	Y
MCAV	FTL4	Inner	FTL	6	2000	2015	16	11.6	10.7	Y
MCAV	FTL5	Inner	FTL	8	2003	2016	14	35.4	26	Y
MCAV	FTL5	Inner	FTL	8	2003	2020	18	37.7	37.7	Y
MCAV	FTL5	Inner	FTL	8	2003	2015	13	17.7	18.1	Y
MCAV	FTL5	Inner	FTL	8	2003	2020	18	23.1	4.2	Y
MCAV	HB2	Middle	Deerfield	11	2000	2020	21	6.2	13.7	Y
MCAV	HB2	Middle	Deerfield	11	2000	2016	17	29.2	22.7	Y
MCAV	HB2	Middle	Deerfield	11	2015	2020	6	1.6	4.9	Y
MCAV	HB3	Outer	Deerfield	15	2007	2015	9	6.1	7.5	Y
MCAV	HB3	Outer	Deerfield	15	2008	2020	13	2.9	5.9	Y
MCAV	HB3	Outer	Deerfield	15	2010	2020	11	2.3	6.4	Y
MCAV	HB3	Outer	Deerfield	15	2001	2016	16	7.7	11.8	Y
MCAV	JUL2	Outer	Hollywood	16	2000	2020	21	15.4	20.6	Y
MCAV	JUL8	Outer	Hollywood	18	2000	2020	21	6.9	8.9	Y
MCAV	JUL8	Outer	Hollywood	18	2008	2020	13	2.5	4.4	Y
MCAV	JUL8	Outer	Hollywood	18	2000	2020	21	2.7	6.6	Y
MCAV	POMP3	Outer	FTL	16	2000	2020	21	3.1	4.3	Y
MCAV	POMP3	Outer	FTL	16	2000	2015	16	4.3	7.1	Y
MCAV	POMP3	Outer	FTL	16	2000	2020	21	5	8.7	Y
MCAV	POMP3	Outer	FTL	16	2000	2020	21	6.2	16.5	Y
MCAV	POMP3	Outer	FTL	16	2000	2012	13	7.7	2.6	Y
MCAV	POMP5	Inner	FTL	9	2000	2020	21	13.6	7.2	Y
MCAV	POMP6	Middle	FTL	16	2012	2020	9	6.1	6.8	Y
PAST	DB2	Middle	Deerfield	11	2000	2018	19	7.6	10.6	Y
PAST	DB2	Middle	Deerfield	11	2000	2016	17	9.9	8.1	Y
PAST	FTL1	Inner	FTL	6	2000	2011	12	9.8	16.1	Y
PAST	FTL1	Inner	FTL	6	2006	2020	15	2.5	8.2	Y
PAST	FTL1	Inner	FTL	6	2005	2020	16	2.5	13.7	Y
PAST	FTL1	Inner	FTL	6	2008	2017	10	3.3	10.2	Y
PAST	FTL1	Inner	FTL	6	2010	2020	11	3.6	10.1	Y
PAST	FTL1	Inner	FTL	6	2000	2015	16	5.4	10	Y
PAST	FTL2	Middle	FTL	15	2010	2020	11	2.3	7.6	Y

PAST	FTL2	Middle	FTL	15	2000	2020	21	4.4	10	Y
PAST	FTL4	Inner	FTL	6	2004	2020	17	2.6	11.9	Y
PAST	FTL4	Inner	FTL	6	2000	2016	17	8.9	11.8	Y
PAST	FTL5	Inner	FTL	8	2003	2020	18	5.4	6.8	Y
PAST	FTL5	Inner	FTL	8	2003	2020	18	1.5	6.9	Y
PAST	HB2	Middle	Deerfield	11	2006	2020	15	3.2	17.5	Y
PAST	HB2	Middle	Deerfield	11	2010	2020	11	3.8	2.9	Y
PAST	HB3	Outer	Deerfield	15	2008	2016	9	2.6	5.4	Y
PAST	HB3	Outer	Deerfield	15	2010	2020	11	3.5	5.9	Y
PAST	HB3	Outer	Deerfield	15	2010	2020	11	2.4	11.5	Y
PAST	HB3	Outer	Deerfield	15	2010	2020	11	4.3	11.1	Y
PAST	HB3	Outer	Deerfield	15	2007	2020	14	4.1	7.8	Y
PAST	HB3	Outer	Deerfield	15	2006	2020	15	6.8	9.5	Y
PAST	HB3	Outer	Deerfield	15	2008	2016	9	4.2	3.3	Y
PAST	JUL2	Outer	Hollywood	16	2004	2020	17	3.6	10.1	Y
PAST	JUL2	Outer	Hollywood	16	2008	2020	13	2.1	9.4	Y
PAST	JUL6	Inner	Hollywood	4	2000	2020	21	9.2	7.3	Y
PAST	JUL6	Inner	Hollywood	4	2002	2020	19	2.8	12.9	Y
PAST	JUL6	Inner	Hollywood	4	2000	2020	21	9.4	9.7	Y
PAST	JUL7	Inner	Hollywood	10	2008	2016	9	3.4	7.2	Y
PAST	JUL7	Inner	Hollywood	10	2002	2020	19	2	4.5	Y
PAST	JUL8	Outer	Hollywood	18	2000	2020	21	8.6	20.7	Y
PAST	JUL8	Outer	Hollywood	18	2007	2020	14	2.7	3.8	Y
PAST	JUL8	Outer	Hollywood	18	2000	2020	21	8.2	13.6	Y
PAST	POMP1	Inner	FTL	6	2011	2020	10	2.1	10.9	Y
PAST	POMP1	Inner	FTL	6	2010	2016	7	2.7	3.9	Y
PAST	POMP1	Inner	FTL	6	2005	2016	12	3	11	Y
PAST	POMP1	Inner	FTL	6	2011	2020	10	1.9	5.7	Y
PAST	POMP1	Inner	FTL	6	2011	2020	10	2.8	9.5	Y
PAST	POMP2	Middle	FTL	15	2013	2020	8	3.7	9.6	Y
PAST	POMP2	Middle	FTL	15	2010	2020	11	4.3	9.2	Y
PAST	POMP3	Outer	FTL	16	2010	2020	11	2.8	7	Y
PAST	POMP3	Outer	FTL	16	2010	2020	11	5.2	5.6	Y
SSID	DB2	Middle	Deerfield	11	2004	2014	11	2.8	6.3	Y
SSID	DB2	Middle	Deerfield	11	2015	2020	6	2.4	5.1	Y
SSID	DB2	Middle	Deerfield	11	2000	2020	21	4.3	3.9	Y
SSID	DB3	Outer	Deerfield	17	2011	2020	10	2.1	5.3	Y
SSID	DB3	Outer	Deerfield	17	2006	2020	15	1.9	4.9	Y
SSID	DB3	Outer	Deerfield	17	2013	2020	8	2.7	3.5	Y
SSID	FTL2	Middle	FTL	15	2000	2020	21	4.1	9.2	Y
SSID	FTL2	Middle	FTL	15	2013	2020	8	2.3	5.2	Y
SSID	FTL2	Middle	FTL	15	2014	2020	7	1.8	3.1	Y
SSID	FTL3	Outer	FTL	18	2010	2020	9	3.4	4.2	Y
SSID	FTL3	Outer	FTL	18	2010	2020	11	2.3	6.2	Y
SSID	FTL3	Outer	FTL	18	2008	2020	13	1.2	5.4	Y
SSID	FTL5	Inner	FTL	8	2003	2007	5	5.9	8.3	Y
SSID	HB2	Middle	Deerfield	11	2010	2020	11	2.5	5	Y
SSID	HB2	Middle	Deerfield	11	2011	2020	10	1	4.5	Y
SSID	HB2	Middle	Deerfield	11	2010	2020	11	4.3	3.6	Y
SSID	HB2	Middle	Deerfield	11	2010	2020	11	1.8	5.2	Y
SSID	HB2	Middle	Deerfield	11	2010	2020	11	1.5	3.4	Y
SSID	HB2	Middle	Deerfield	11	2013	2020	8	1.7	3.2	Y
SSID	HB3	Outer	Deerfield	15	2008	2020	13	3.6	3	Y
SSID	HB3	Outer	Deerfield	15	2010	2020	11	3.6	2.2	Y
SSID	JUL1	Middle	Hollywood	12	2010	2020	11	1	5.2	Y
SSID	JUL2	Outer	Hollywood	16	2000	2020	21	1.3	4.9	Y
SSID	JUL2	Outer	Hollywood	16	2005	2014	10	3.4	4	Y

SSID	JUL2	Outer	Hollywood	16	2007	2020	14	1.5	4.2	Y
SSID	JUL7	Inner	Hollywood	10	2014	2020	7	1.3	4.2	Y
SSID	JUL7	Inner	Hollywood	10	2000	2020	21	8.1	13.8	Y
SSID	JUL7	Inner	Hollywood	10	2008	2020	13	3.1	6.5	Y
SSID	POMP1	Inner	FTL	6	2000	2020	21	4.1	9.8	Y
SSID	POMP1	Inner	FTL	6	2000	2020	21	3	14.1	Y
SSID	POMP2	Middle	FTL	15	2000	2020	21	2.3	8.2	Y
SSID	POMP2	Middle	FTL	15	2000	2020	21	14.1	16.6	Y
SSID	POMP2	Middle	FTL	15	2008	2020	13	3.5	8.6	Y
SSID	POMP2	Middle	FTL	15	2010	2020	11	3.6	2.4	Y
SSID	POMP2	Middle	FTL	15	2000	2015	16	4.4	9.1	Y
SSID	POMP3	Outer	FTL	16	2000	2020	21	3.7	2.7	Y
SSID	POMP3	Outer	FTL	16	2006	2015	10	1.2	5.5	Y
MCAV	DB2	Middle	Deerfield	11	2010	2015	6	21.2	25	N
MCAV	DB2	Middle	Deerfield	11	2001	2015	15	5.5	1.5	N
MCAV	DB2	Middle	Deerfield	11	2006	2015	10	10.1	11.5	N
MCAV	FTL3	Outer	FTL	18	2015	2020	6	8.8	11.3	N
MCAV	FTL4	Inner	FTL	6	2000	2015	16	18.8	24.6	N
MCAV	FTL4	Inner	FTL	6	2000	2018	19	22.7	6.9	N
MCAV	FTL5	Inner	FTL	8	2003	2015	13	14	3.5	N
MCAV	FTL5	Inner	FTL	8	2010	2020	11	24.9	31.4	N
MCAV	FTL5	Inner	FTL	8	2003	2015	13	27.6	30.3	N
MCAV	FTL5	Inner	FTL	8	2003	2020	18	34.1	40.1	N
MCAV	FTL5	Inner	FTL	8	2003	2015	13	27.6	29.7	N
PAST	DB2	Middle	Deerfield	11	2010	2020	11	7.3	8.8	N
PAST	FTL1	Inner	FTL	6	2000	2017	18	14.8	7.7	N
PAST	FTL1	Inner	FTL	6	2002	2014	13	10.7	11.7	N
PAST	JUL6	Inner	Hollywood	4	2010	2020	11	23.8	18.4	N

Table S2. Summary table of the fitted linear mixed effects model of coral growth rate.

	Value	Std.Error	DF	t-value	p-value
(Intercept)	10.937	9.94213	1136	1.100066	0.2715
SpeciesPAST	16.59035	14.14634	103	1.172766	0.2436
SpeciesSSID	21.25169	15.88305	103	1.33801	0.1838
SpeciesMCAV:Survey.Year	-1.6468	0.466653	1136	-3.52897	0.0004
SpeciesPAST:Survey.Year	-1.26361	0.557866	1136	-2.26507	0.0237
SpeciesSSID:Survey.Year	0.14687	0.525403	1136	0.279546	0.7799
SpeciesMCAV:Last.Diameter	-0.23376	0.153964	1136	-1.51831	0.1292
SpeciesPAST:Last.Diameter	-1.97822	0.45057	1136	-4.39047	0.000
SpeciesSSID:Last.Diameter	-3.33264	0.689124	1136	-4.83605	0.000
SpeciesMCAV:fYear2002	7.73056	5.3626	1136	1.44157	0.1497
SpeciesPAST:fYear2002	1.5902	10.29123	1136	0.15452	0.8772
SpeciesSSID:fYear2002	11.3283	10.95569	1136	1.03401	0.3014
SpeciesMCAV:fYear2003	5.46623	5.434303	1136	1.005875	0.3147
SpeciesPAST:fYear2003	13.66311	9.730756	1136	1.404116	0.1606
SpeciesSSID:fYear2003	3.6544	12.56234	1136	0.290901	0.7712
SpeciesMCAV:fYear2004	14.97622	5.339074	1136	2.805022	0.0051
SpeciesPAST:fYear2004	9.13247	9.556798	1136	0.955599	0.3395
SpeciesSSID:fYear2004	5.36373	11.36756	1136	0.471845	0.6371
SpeciesMCAV:fYear2005	8.32054	5.555553	1136	1.497697	0.1345
SpeciesPAST:fYear2005	2.42155	9.7064	1136	0.249479	0.8030
SpeciesSSID:fYear2005	7.28376	10.08042	1136	0.722565	0.4701
SpeciesMCAV:fYear2006	16.23967	5.542949	1136	2.929789	0.0035
SpeciesPAST:fYear2006	12.15347	9.432927	1136	1.288409	0.1979
SpeciesSSID:fYear2006	-19.7196	9.80334	1136	-2.01152	0.0445
SpeciesMCAV:fYear2007	16.87731	5.74355	1136	2.938481	0.0034
SpeciesPAST:fYear2007	30.55403	9.437023	1136	3.237677	0.0012
SpeciesSSID:fYear2007	-22.9309	10.22675	1136	-2.24225	0.0251
SpeciesMCAV:fYear2008	16.71665	5.76847	1136	2.897935	0.0038
SpeciesPAST:fYear2008	15.51145	9.271367	1136	1.673049	0.0946
SpeciesSSID:fYear2008	-1.13232	10.34587	1136	-0.10945	0.9129
SpeciesMCAV:fYear2010	23.08141	6.385157	1136	3.614854	0.0003
SpeciesPAST:fYear2010	19.46847	9.327471	1136	2.087218	0.0371
SpeciesSSID:fYear2010	-11.5945	11.27267	1136	-1.02855	0.3039
SpeciesMCAV:fYear2011	20.89347	6.742151	1136	3.098932	0.0020
SpeciesPAST:fYear2011	24.25852	9.321864	1136	2.602326	0.0094
SpeciesSSID:fYear2011	7.17153	10.47005	1136	0.684956	0.4935
SpeciesMCAV:fYear2012	17.39185	7.348004	1136	2.36688	0.0181
SpeciesPAST:fYear2012	21.74427	9.36384	1136	2.322153	0.0204
SpeciesSSID:fYear2012	6.77368	10.39621	1136	0.651553	0.5148

SpeciesMCAV:fYear2013	21.58544	7.387406	1136	2.921924	0.0035
SpeciesPAST:fYear2013	9.25109	9.415079	1136	0.982582	0.3260
SpeciesSSID:fYear2013	-4.35493	10.43095	1136	-0.4175	0.6764
SpeciesMCAV:fYear2014	25.24579	7.586345	1136	3.327794	0.0009
SpeciesPAST:fYear2014	12.10745	9.62013	1136	1.258554	0.2085
SpeciesSSID:fYear2014	-7.929	10.39782	1136	-0.76256	0.4459
SpeciesMCAV:fYear2015	23.63998	7.94293	1136	2.976229	0.0030
SpeciesPAST:fYear2015	12.47543	9.852505	1136	1.266219	0.2057
SpeciesSSID:fYear2015	4.39316	10.7183	1136	0.409875	0.6820
SpeciesMCAV:fYear2016	9.25084	8.362212	1136	1.106267	0.2688
SpeciesPAST:fYear2016	14.85071	10.02906	1136	1.480767	0.1389
SpeciesSSID:fYear2016	-2.7072	10.8431	1136	-0.24967	0.8029
SpeciesMCAV:fYear2017	27.19263	8.953692	1136	3.03703	0.0024
SpeciesPAST:fYear2017	13.67494	10.31015	1136	1.326357	0.1850
SpeciesSSID:fYear2017	-4.87111	10.99133	1136	-0.44318	0.6577
SpeciesMCAV:fYear2018	21.58038	9.137773	1136	2.361668	0.0184
SpeciesPAST:fYear2018	10.02577	10.68457	1136	0.938341	0.3483
SpeciesSSID:fYear2018	-10.0909	11.30525	1136	-0.89258	0.3723
SpeciesMCAV:fYear2019	31.24789	9.575969	1136	3.263157	0.0011
SpeciesPAST:fYear2019	14.38056	11.04266	1136	1.302273	0.1931
SpeciesSSID:fYear2019	-1.16761	11.61395	1136	-0.10054	0.9199
SpeciesMCAV:fYear2020	34.74087	9.846926	1136	3.528092	0.0004
SpeciesPAST:fYear2020	8.18631	11.31367	1136	0.723576	0.4695
SpeciesSSID:fYear2020	4.91589	11.70982	1136	0.419809	0.6747
SpeciesMCAV:Sub.regionFTL	4.37928	5.822813	103	0.75209	0.4537
SpeciesPAST:Sub.regionFTL	8.42646	5.999934	103	1.404426	0.1632
SpeciesSSID:Sub.regionFTL	5.9582	6.18091	103	0.963968	0.3373
SpeciesMCAV:Sub.regionHollywood	8.02606	7.451667	103	1.077083	0.2840
SpeciesPAST:Sub.regionHollywood	9.99441	5.820187	103	1.717198	0.0889
SpeciesSSID:Sub.regionHollywood	2.41043	8.055446	103	0.29923	0.7654
SpeciesMCAV:HabitatMiddle	21.59898	11.80877	103	1.829063	0.0703
SpeciesPAST:HabitatMiddle	15.70365	11.41509	103	1.375692	0.1719
SpeciesSSID:HabitatMiddle	-13.6338	11.25939	103	-1.21089	0.2287
SpeciesMCAV:HabitatOuter	24.91228	16.28243	103	1.53001	0.1291
SpeciesPAST:HabitatOuter	16.5811	15.07187	103	1.100136	0.2738
SpeciesSSID:HabitatOuter	-25.3482	15.51335	103	-1.63396	0.1053
SpeciesMCAV:Depth	-2.21515	1.6068	103	-1.37861	0.1710
SpeciesPAST:Depth	-1.49216	1.256421	103	-1.18763	0.2377
SpeciesSSID:Depth	0.77824	1.463658	103	0.531707	0.5961

Chapter 3. Temperature and local anthropogenic pressures limit stony coral assemblage viability in southeast Florida

Abstract

Global climate change is viewed as the primary threat to coral reefs worldwide, where acute thermal stress events have contributed to extensive bleaching, disease and mortality in recent years. Concurrently, chronic local pressures have exacerbated stony coral cover decline and community change. The consensus is that improving water quality may increase the resilience of stony coral communities to acute disturbances, but it is unclear whether this extends to marginal habitats already subject to environmental pressure. The Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) is a high-latitude reef system offshore of a highly urbanized coastline. Extensive stony coral mortality from 2014 to 2018, following heat stress, disease and Hurricane Irma has established focus on assessing recovery potential. Here, the influence of temperature and water quality on benthic community structure and spatiotemporal changes in the benthic community were assessed from 2018 to 2021. Photographic and stony coral demographic data were collected on 72 fixed transects to quantify benthic community structure, stony coral recruit and adult community structure and interannual changes in the benthic community. Daily temperature data was collected at these fixed sites and water quality data was collected monthly at adjacent reef sites. I used Distance-based Linear Models and Random Forests to analyze the relationship between the benthic community and specific in situ temperature and water quality parameters. Temperature accounted for most of the observed variation, recruitment doubled and interannual increases in stony coral abundance tripled when mean annual temperature reached 27 °C, until threshold temperatures were exceeded (>31 °C) at which point coral abundance and recruitment did not increase as much. Benefits associated with warmer temperatures were negated by poor water quality, as nutrient enrichment was related to increased macroalgae cover, reduced coral recruitment and higher partial mortality. Increased total suspended solids was associated with reduced partial mortality in the dominant reef-building coral, *Montastraea cavernosa*, but was also related to reduced coral species richness and increased macroalgae cover. I suggest reducing local chronic pressures may reduce macroalgae cover and enhance stony coral recovery potential, but that temperature is the predominant influence on stony coral assemblages in southeast Florida.

Key words: Water quality, chronic pressure, recovery, recruitment, nutrients, turbidity

Introduction

The persistence of coral reef communities is threatened by a suite of anthropogenic stressors (Hughes et al. 2017; Hoegh-Guldberg et al. 2019). On a global scale, acute disturbances (short term stochastic events such as marine heatwaves or hurricanes) and chronic pressures (such as ocean warming or acidification) have caused the most significant changes to stony coral assemblages (order Scleractinia) and continue to impair recovery potential (Hughes et al. 2018; Hughes et al. 2019). Additionally, many coral reefs are subject to local pressures such as poor water quality or sedimentation which further impact stony corals and shape benthic community structure, particularly near urbanized coastlines (Jackson et al. 2001; Ortiz et al. 2018; Lapointe et al. 2019; Otaño-Cruz et al. 2019). The combined effect of such stressors has raised the likelihood of coral reef ecosystem collapse (Pratchett et al. 2021).

Recent studies have begun to quantify the cumulative effects of local chronic pressures and acute disturbances (MacNeil et al. 2019; Mellin et al. 2019; Donovan et al. 2021). However, the influence of global chronic pressures (e.g., ocean warming) and local chronic pressures (e.g., water quality) in shaping community structure and the viability of stony coral populations are understudied. The conventional view is that local action to improve water quality will decrease the vulnerability of corals to climate change (Knowlton and Jackson 2008), allowing recovery to occur during inter-disturbance periods. This assumes that local water quality exacerbates acute and chronic global stressors to negatively influence stony coral health (Ortiz et al. 2018; Ellis et al. 2019; Mellin et al. 2019; Donovan et al. 2021). However, in some locations chronic local pressures are predicted to reduce the impact of thermal stress on coral communities by reducing irradiance (Cacciapaglia and Woesik 2016; Morgan et al. 2017; Koester et al. 2020), while in others the impact of ocean warming overwhelms any impact of water quality (Côté and Darling 2010; Bruno et al. 2019; MacNeil et al. 2019).

Marginal stony coral communities are already living towards their physiological limits, but under ocean warming, these range edges may become tropicalized (Beger et al. 2014; Verges et al. 2014). A major constraint to this potential is that many high-latitude reefs are close to urbanized coastlines, placing stony coral assemblages under the combined stress of temperature (heat and cold stress) and water quality (Fabricius and McCorry 2006; Muir et al. 2015; Toth et al. 2021). Excess nutrients and sedimentation, either through prolonged exposure or by exceeding thresholds, can have profound effects on stony coral health and benthic community composition. Imbalanced nitrogen to phosphorous ratios can reduce stony coral bleaching resistance (Wiedenmann et al. 2013; Wang et al. 2018), nitrogen and phosphorous enrichment and excess suspended sediment can induce disease (Pollock et al. 2014; Vega-Thurber et al. 2014; Zaneveld et al. 2016; Lapointe et al 2019), sedimentation and eutrophication can reduce coral recruitment (Fabricius 2005), turbidity and total suspended solids strongly influence community composition (Fabricius 2005; Thompson et al. 2014; Weijerman et al. 2018) and eutrophication increases macroalgal density which hinders coral recovery potential (De'ath and Fabricius 2010; Graham et al. 2018). Assessing the influence of temperature, nutrients, and sedimentation on benthic community structure, stony coral community structure and key demographic features, such as recruitment and mortality, may help identify the key drivers of change in the stony coral community and determine how to maximize the viability of stony corals.

The Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) is a high-latitude reef system offshore of a heavily urbanized coastline, with multiple international ports, sewage outfalls and widespread coastal construction. Acute disturbances, primarily heat stress in 2014 and 2015 and stony coral tissue loss disease (SCTLD; prevalent from 2014 to 2017), reduced stony coral cover and density over the past decade (Walton et al. 2018; Jones et al. 2020; Chapter 1). Minimal recovery in stony coral cover has been seen during inter-disturbance periods (Chapter 1), possibly due to high partial mortality limiting net growth of the three most abundant species, *Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea* (Chapter 2). Jones et al. (2020) found temperature and thermal stress explained some of the variability in benthic community structure and trends in stony coral cover, but multiple anthropogenic sources of nutrient pollution and sedimentation are suspected to also influence interannual changes in the benthic community and stony coral populations.

In this study, I investigate how water quality and temperature influence benthic community structure and drive interannual changes in the benthic community in the ECA. This was assessed by analyzing interannual changes in the benthic community, stony coral colony health and stony coral diversity from 2018 to 2021, a period without any known acute disturbances, in order to determine the underlying influence that water quality and temperature have on the benthic community. My primary interest was to assess which environmental predictors were most strongly related to the spatiotemporal variation in each benthic metric. Within this I was specifically interested in whether water quality may be impacting stony coral recovery capacity in the ECA, or whether temperature variability was the dominant factor. I hypothesize that local water quality presents a barrier to stony coral recovery and will prevent tropicalization in the high-latitude coral communities of southeast Florida (Verges et al. 2014; Toth et al. 2021).

Methods

Study area

The Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) is a high-latitude reef system (~27.1 N to 25.6 N) offshore of a highly urbanized coastline which includes the major cities West Palm Beach, Fort Lauderdale and Miami, where coastal construction and beach nourishment are prevalent. Nine inlets and ports connect the ECA with inland waterways and rivers, bringing elevated nutrients and freshwater influx. Six ocean outfalls discharge partially treated wastewater at depth one to five kilometers offshore (Figure 1). The ECA is divided north to south into multiple sub-regions by major port channels and biogeographic boundaries (Walker 2012; Jones et al. 2020). Previous studies have shown substantial variation between environmental conditions and benthic community structure in the northernmost sub-region of the ECA, Martin County, with those further south (Jones et al. 2020), therefore I only assessed the five southern sub-regions here.

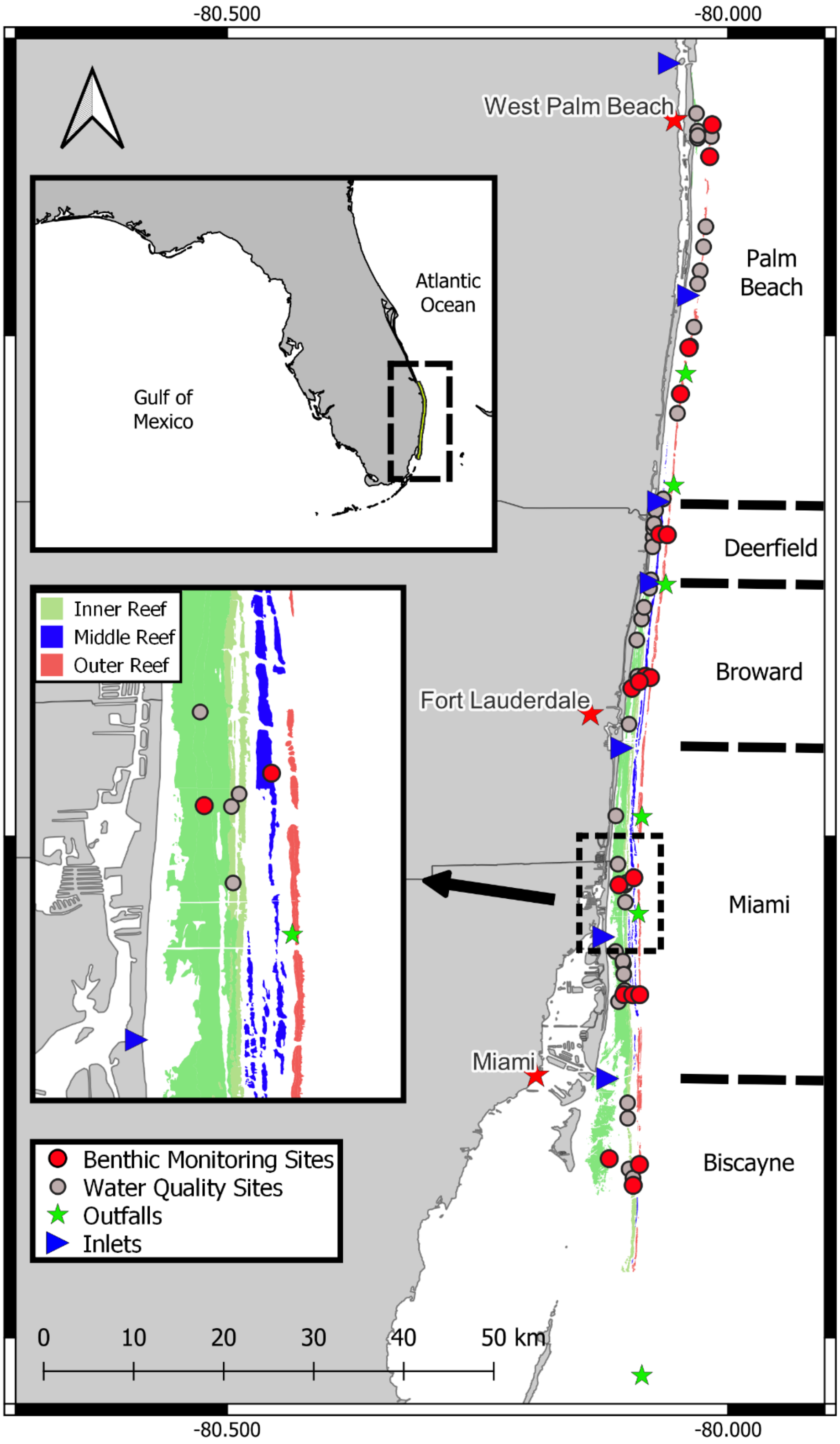

Figure 1. Study area, monitoring sites, sub-regions and key features. Inset top: Florida, USA with Southeast Florida Coral Reef Ecosystem Conservation Area highlighted. Inset middle: Reef habitats and monitoring sites.

Benthic data collection

Benthic community data were collected annually from 2013 to 2021 at 18 sites permanently monitored as part of the Southeast Florida Coral Reef Evaluation and Monitoring Program (SECREMP). At each site, four permanent belt transects were monitored. Benthic data were collected in two forms: along the full 22 x 1 m long belt transect, every stony coral (Scleractinian) colony greater than or equal to 2 cm diameter was identified to species, measured and percent partial colony mortality estimated (from 2013 to 2017 only colonies ≥ 4cm were measured). Along the same belt transect from 2018 to 2021, every visible stony coral colony smaller than 2 cm (i.e., Scleractinian recruit) was identified to the lowest taxonomic level and the abundance tallied. Secondly, ~ 60 abutting photographic images, each 40 cm wide, were taken linearly along the same transect at a fixed distance from the substrate covering ~ 8.8 m^2. Images were analyzed using PointCount '99 to determine percent substrate coverage (Dustan et al. 1999); for each image, the benthic taxa were identified at 15 randomly placed points, for a total of 900-1000 points per transect. Benthic taxa were categorized as stony corals (Scleractinians and Milleporids), octocorals, sponges, macroalgae (grouped with cyanobacteria), zoanthids, turf algae/substrate, and other taxa (e.g., hydroids, anemones etc.).

Benthic community change metrics

Stony coral cover and stony coral abundance were assessed in relation to known acute disturbances (Chapter 1). Benthic community cover structure, stony coral recruit community structure (colonies < 2cm) and stony coral adult community structure (colonies ≥ 2 cm) were assessed and multiple univariate response variables were calculated to assess specific interannual changes in composition, stony coral colony health, or stony coral diversity. For each transect (n = 72), the interannual change in the abundance of stony coral adult colonies (≥ 2 cm diameter), the interannual change in the abundance of the three most abundant coral species in the ECA, *Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea* and the interannual change in the cover of each benthic taxa were calculated (e.g., the absolute change in stony coral cover from 2018 to 2019). Stony coral recruit (< 2 cm diameter) abundance, average percent partial colony mortality of all stony coral species (mean partial mortality was estimated per colony during in situ survey), percent partial colony mortality of *M. cavernosa*, *P. astreoides* and *S. siderea* were calculated annually. Adult stony coral species richness, Shannon-Weaver diversity index (H', Shannon 1948) and Pielou's evenness index (J, Pielou 1966) at each transect each year was also calculated (Equations 1 and 2).

$$H' = -\sum_{i=1}^{s} pi \ln pi$$

Equation 1. Shannon-Weaver diversity index, where pi is the relative abundance of species i, and s is the total number of species.

$$J' = H'/H'max = H'/\ln S$$

Equation 2. Pielou's J for evenness where H'max is the maximum possible diversity and S is the total number of species.

Each of these response variables was specifically chosen to represent stony coral colony health, stony coral diversity or a change within the community which likely influences the recovery potential of stony coral assemblages in the ECA. Annual recruit abundance and interannual change in stony coral adult abundance reflect recruitment, retention and mortality in the system and determine population viability. Interannual change in benthic taxa cover relate either directly to stony coral health (i.e., stony coral cover), to competing benthic taxa which influence stony coral recovery potential (i.e., macroalgae cover) or to the future trajectory of the benthic community (i.e., octocoral cover). Partial colony mortality represents a measure of individual colony and population fitness and influences population viability.

Environmental data collection

A suite of environmental predictors was assessed from water quality and temperature data collected in situ from 2018 to 2021. Water temperature data were collected bi-hourly at each SECREMP site using HOBO Pro v2 loggers (5-18 m depth). The maximum, mean, minimum and standard deviation in water temperature between annual benthic monitoring events were calculated for each site. Additionally, the heat stress duration and cold stress duration, reflective of temperatures above the bleaching threshold and below the equivalent cold stress threshold, were calculated between monitoring events as per Jones et al. (2020). Heat stress duration was defined as the number of days in situ water temperature was 1 °C above the maximum of the mean summertime (July-September) sea surface temperature (SST). Cold stress duration was defined as the number of days in situ water temperature was 1 °C below the minimum of the mean wintertime

(January-March) SST. Thermal stress thresholds were calculated independently for each sub-region during the study period using modelled SST data from the Hybrid Coordinate Ocean Model (HYCOM) and the thermal stress duration calculated for each site (Jones et al. 2020).

Water quality data, pertaining to a suite of environmental analytes, were obtained from the Southeast Florida Reef Tract Water Quality Assessment Project, part of the Florida Department of Environmental Protection’s Watershed Information Network (https://floridadep.gov/dear/watershed-services-program/content/winstoret). Water samples were collected on a monthly basis at 115 sites within the ECA by a team from Nova Southeastern University (NSU). A detailed description of the sampling design can be found in Whitall et al. (2019). Briefly, each site is associated with one of nine major inlets, St Lucie, Jupiter, Lake Worth, Boynton, Boca Raton, Hillsboro, Port Everglades, Baker’s Haulover or Government Cut, and is positioned to capture water quality data associated with an inlet, a sewage outfall or a reef. At Inlet sampling sites surface (collected approximately 0.5 m below the surface) and bottom (collected near the seafloor using niskin bottles, 3-18 m depth) water samples were collected around each inlet. At Outfall sampling sites surface samples were collected around each sewage outfall. At Reef sampling sites surface and bottom samples were collected from randomly selected reef sites throughout the ECA. Water samples were analyzed for a suite of analytes, including Ammonium, Nitrate/Nitrite, Total Nitrogen, Orthophosphate, Total Phosphorous, Silicate, Total Suspended Solids (TSS) and Turbidity, using methods described in detail in Whitall et al. (2019). I extracted specific analytes from the dataset and additionally calculated the monthly Nitrate and Dissolved Inorganic Nitrogen concentration (product of ammonium, nitrate and nitrite) at each site (Table 1). For this study, only bottom samples were used as these were considered to most closely influence the benthic community. Due to the point source nature of water quality sampling, but fluidity of water movement which I wanted to account for, a spatial join was used to link the closest three water quality monitoring sites with each benthic monitoring site to represent the potential environmental conditions experienced by the benthic community. As my interest was in the relationship between environmental conditions and benthic community dynamics and because water quality, temperature and benthic data were collected on different temporal scales, annual environmental metrics that were predicted to influence interannual changes in benthic community structure were calculated between each annual benthic monitoring event. For each water quality analyte, the annual maximum, mean and standard deviation was calculated for each benthic monitoring site. I also calculated the mean annual total nitrogen: total phosphorous ratio (TN: TP) at each benthic monitoring site to give 37 environmental predictors (Table 1).

Table 3. Environmental predictors calculated from bottom samples collected at reef sites in the ECA from July 2018 to July 2021, where each predictor = the metric of an analyte. Retained predictors are those used in statistical analysis after the removal of covariates. Yes = Predictor present in full model. Blank = predictor covaried and not used in full models. At least one predictor for each analyte was retained after the removal of covariates. Value = mean value of environmental predictor across all time points and sites (±SE). Heat stress and cold stress duration = mean thermal stress duration per site, per year during study period.

Analyte	**Metric**	**Unit**	**Retained**	**Value (±SE)**
Temperature	Maximum	°C	Yes	30.5 ±0.06
	Mean	°C	Yes	26.9 ±0.04
	Minimum	°C	Yes	22.4 ±0.1
	Standard Deviation (SD)	°C	Yes	2.1 ±0.04
	Heat Stress Duration	Days yr^{-1}	Yes	0.72 ±0.4
	Cold Stress Duration	Days yr^{-1}	Yes	2.37 ±0.6
Ammonium (NH_4^+)	Maximum	mg/l		0.05 ±0.008
	Mean	mg/l		0.009 ±0.001
	SD	mg/l	Yes	0.01 ±0.002
Nitrate (NO_3^-)	Maximum	mg/l	Yes	0.01 ±0.001
	Mean	mg/l	Yes	0.003 ±2e^{-04}
	SD	mg/l		0.003 ±3e^{-04}
Nitrite (NO_2^-)	Maximum	mg/l	Yes	0.003 ±3e^{-04}
	Mean	mg/l	Yes	0.0004 ±5e^{-05}
	SD	mg/l		0.0007 ±6e^{-05}
Dissolved Inorganic Nitrogen (DIN)	Maximum	mg/l	Yes	0.05 ±0.008
	Mean	mg/l	Yes	0.01 ±0.001
	SD	mg/l		0.01 ±0.002
Total Nitrogen (TN)	Maximum	mg/l		0.2 ±0.02
	Mean	mg/l		0.04 ±0.006
	SD	mg/l	Yes	0.04 ±0.006
Total Phosphorous (TP)	Maximum	mg/l	Yes	0.03 ±0.003
	Mean	mg/l	Yes	0.005 ±5e^{-04}
	SD	mg/l		0.007 ±7e^{-04}
Orthophosphate (HPO_4^{2-})	Maximum	mg/l	Yes	0.006 ±0.001
	Mean	mg/l	Yes	0.0009 ±2e^{-04}
	SD	mg/l		0.002 ±3e^{-04}
TN: TP	Mean	mg/l	Yes	8: 1 ±0.7
Silicate (SiO_4^{4-})	Maximum	mg/l		0.06 ±0.009
	Mean	mg/l	Yes	0.02 ±0.003
	SD	mg/l		0.003 ±0.02
Total Suspended Solids (TSS)	Maximum	mg/l	Yes	9.6 ±1.1
	Mean	mg/l	Yes	2.2 ±0.09
	SD	mg/l		2.3 ±0.2
Turbidity	Maximum	NTU	Yes	1.6 ±0.3
	Mean	NTU	Yes	0.36 ±0.03
	SD	NTU	Yes	0.32 ±0.05

Data analysis

Two approaches were taken to assess the impact of environmental variation on the benthic community. Multivariate Distance-based Linear Models (DISTLM) and Distance-based Redundancy Analysis (dbRDA) were used to assess the relationship between benthic community structure and environmental predictors (Primer v7; Legendre and Anderson 1999). Random forest regression was conducted to identify which environmental predictors correlated most strongly with interannual changes in the benthic community composition, stony coral colony health (quantified as coral recruitment, change in colony abundance or partial colony mortality) or stony coral diversity (Species richness, H' or J'). Prior to statistical analysis, environmental predictors were tested for collinearity by calculating the Pearson's correlation coefficient. One of the predictors with a PCC > 0.95 were removed from statistical analysis (predictors which correlated with two or more predictors were removed first), leaving 25 potential environmental predictors (Table 1). In the event that a predictor correlated with a predictor from another analyte (e.g., NH4 max with DIN max), the removal of covariates was conducted such that at least one predictor remained from each analyte.

Benthic community structure

Multivariate analyses were conducted in Primer 7 (Clarke and Gorley 2006). Three Distance-based Linear Models (DISTLM) were used to assess the relationship between benthic community structure and environmental predictors. The first model assessed benthic community cover composition, the second assessed stony coral recruit community structure (colonies < 2 cm diameter) and the third assessed stony coral adult community structure (colonies ≥ 2 cm diameter). Benthic community cover composition was averaged by site to provide an average of the benthic community structure within a site and stony coral community structure summed by site to capture total colony abundance within a site, then each were square root transformed prior to the generation of Bray-Curtis similarity coefficients. Spatiotemporal variation in benthic community cover composition, recruit stony coral community structure and adult stony coral community structure were statistically analyzed using Permutation Analysis of Variance (PERMANOVA; Anderson 2001; McArdle and Anderson 2001). Type 3 PERMANOVA was performed with 9999 permutations of residuals under a reduced model with sites in each survey year as samples (n = 54). Community composition was assessed by the factors: Year, Habitat and Sub-region. Multivariate results were considered significant at $p < 0.05$. The three-way interaction, Year x Habitat x Sub-region, was pooled when analyzing recruit and adult community structure after results suggested it accounted for minimal variation. Pooling removes a factor which accounts for minimal variation from the model and combines the factors sum of squares and degrees of freedom to another term with equivalent estimated mean squares (Anderson et al. 2008). The interactions Year x Habitat and Year x Sub-region were also pooled for adult community structure. DISTLM analysis was performed under the BEST selection procedure with 9999 permutations and the best model determined using the corrected Akaike Information Criterion (AICc) from all possible combinations of environmental predictors. In the event that multiple models had equivalent AICc's (i.e., < 2 difference between models; Burnham and Anderson 2004), the simplest model with the fewest predictor variables was selected as the model which explained the most variation in the response matrix. The most parsimonious model was ordinated using Distance-based Redundancy Analysis (dbRDA; Legendre and Anderson 1999), where each point represented the mean benthic community structure or stony coral community structure at each site in each year and vectors represent either the origin of differences in the community or the environmental predictors which explain the variation. Environmental predictors were normalized prior to analysis.

Identifying drivers of benthic community change

Univariate analyses were conducted in R studio (R Core Team 2020). The relationship between interannual changes in the benthic community, stony coral colony health and stony coral diversity with environmental predictors was analyzed using random forest models. A random forest model is a decision tree ensemble method of machine learning which creates multiple uncorrelated decision trees and combines their results to model the relationship between the response variable and multiple predictors (Breiman 2001). Random forests have the advantage of being insensitive to overfitting by using multiple decision trees, can handle non-linear relationships and are a reliable way to assess variable importance using the out of bag samples (Breiman 2001; Strobl et al. 2007). Random forest regression models were created for 17 response variables with transects as samples to account for variability within sites (n = 216): the interannual change in stony coral, *M. cavernosa*, *S. siderea* or *P. astreoides* colony abundance, the interannual change in stony coral, octocoral, sponge, macroalgae or zoanthid cover, recruit abundance (number of colonies < 2 cm diameter), stony coral species richness (N), Shannon diversity (H') or evenness (Pielou's J), and mean percent partial mortality of stony coral colonies, *M. cavernosa* colonies, *S. siderea* colonies or *P. astreoides* colonies. The 'randomForest' function from the randomForest package (Liaw and

Wiener 2002) was used to create random forest regression models which assessed each response variable against all 25 environmental predictors. The default number of variables randomly sampled as candidates at each split (i.e., 1/3 the number of predictors sampled to split each node) was used as statistical comparisons have shown these to be suitable for random forest regression analysis (Liaw and Wiener 2002; Prasad et al. 2006). Variable importance is relatively insensitive to the number of trees (Liaw and Wiener 2002), but to increase confidence in identifying the most important drivers of change the number of trees was set as the number of trees per model which achieved over 95% correlation in variable importance between two equivalent random forest models (Brieuc et al. 2018). From each model I assessed how much variation in each response variable was explained by all 25 potential environmental predictors. My primary interest was to assess which environmental predictors were most strongly related to the spatiotemporal variation in each benthic metric. Within this I was interested in whether water quality was constraining stony coral recovery capacity in the ECA, or whether temperature variability was the dominant factor. As such, variable importance of each environmental predictor was assessed to identify the main drivers of change using the increase in mean sum of squares, which measures the mean decrease in model accuracy when each predictor is removed. Cross-validation is generally not required for random forest regression as feature selection is randomized and the out of bag samples are used to calculate the error rate and variable importance (Prasad et al. 2006; Oliveira et al. 2012). However, to further ensure model reliability and goodness of fit, the cross-validation error rate was plotted against the number of trees and the correlation between fitted model predictions with the out of bag samples and the correlation between fitted model predictions and the observed data was visually assessed. Models assessing the interannual change in *M. cavernosa* and *P. astreoides* abundance, interannual change in stony coral and zoanthid cover, Shannon diversity, evenness and *S. siderea* and *P. astreoides* partial colony mortality were omitted as they had negative variance estimates and/or very low error rates suggesting overfitting. In the nine remaining models (Table 1), a heat map of variable importance was created by extracting the mean squared error (MSE) for each environmental predictor (i.e., how much worse model fit was by removing the variable) and dividing that by the total MSE to give relative variable importance. The relationship between each response variable and the environmental predictors with the highest variable importance were then assessed, using partial regression plots.

Results

Recent disturbance history

From 2013 to 2018, the ECA experienced multiple acute disturbances and a severe disease outbreak, stony coral tissue loss disease (SCTLD), which caused extensive mortality. During this period 17 of the 18 sites lost 34% to 85% relative stony coral cover (cover remained stable at one site). The greatest declines followed acute disturbances, with stony coral cover declining 40% on average (± 7% SE) from 2015 to 2016 and a further 21% (± 6% SE) from 2017 to 2018 (Figure 2). From 2015 to 2016 stony coral abundance also declined 23% (± 4% SE), before increasing again at some sites such that the change in stony coral abundance ranged from -42% to +51% from 2013 to 2018 (Figure S1). During the subsequent inter-disturbance period from 2018 to 2021, stony coral cover increased negligibly, but abundance increased 17% (± 5% SE).

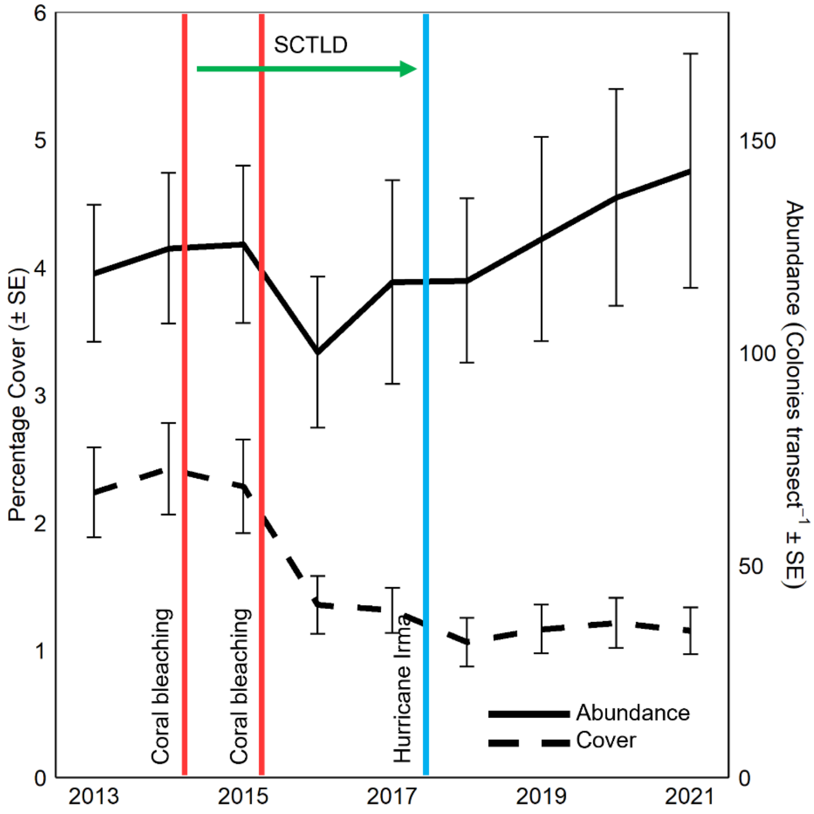

Figure 2. Temporal change in stony coral cover (left y-axis) and abundance (colonies ≥ 4cm diameter; right y-axis) during the multi-disturbance period from 2013 to 2017 and the inter-disturbance period from 2018 to 2021. Vertical lines = Major acute disturbances. Stony coral tissue loss disease (SCTLD) was prevalent from 2014 to 2017.

Benthic community structure

During the inter-disturbance period from 2018 to 2021 benthic community structure significantly varied spatially, by habitat and sub-region, but not temporally (PERMANOVA, $p = 0.0001$). A gradient of community structure change was evident with depth with stony coral and macroalgae cover higher on the shallower inner reef and octocoral and sponge cover higher on the deeper outer reef ($p < 0.01$; Figure 3a). Palm beach had higher octocoral and sponge cover and had significantly different community structure than all sub-regions to the south ($p < 0.05$). Miami generally had higher macroalgae and stony coral cover than Deerfield or Broward ($p < 0.05$). While overall benthic community structure did not vary significantly over time, changes in community structure, particularly macroalgae were evident at the site level (Figure 3A). Benthic community structure was most strongly influenced by temperature and turbidity (DISTLM, $R^2 = 0.45$; Figure 3B). Sites with relatively high stony coral and zoanthid cover were associated with high maximum annual temperature, but with relatively low heat or cold stress duration, while sites with high macroalgae/cyanobacteria cover had high maximum annual temperature, high heat and cold stress duration and high mean turbidity. Sites with high turf algae/substrate, sponge or other fauna cover were associated with high variability in turbidity and lower maximum annual temperature. High octocoral cover sites occurred within a smaller temperature range, with high minimum annual temperatures, but low maximum annual temperatures and low mean turbidity.

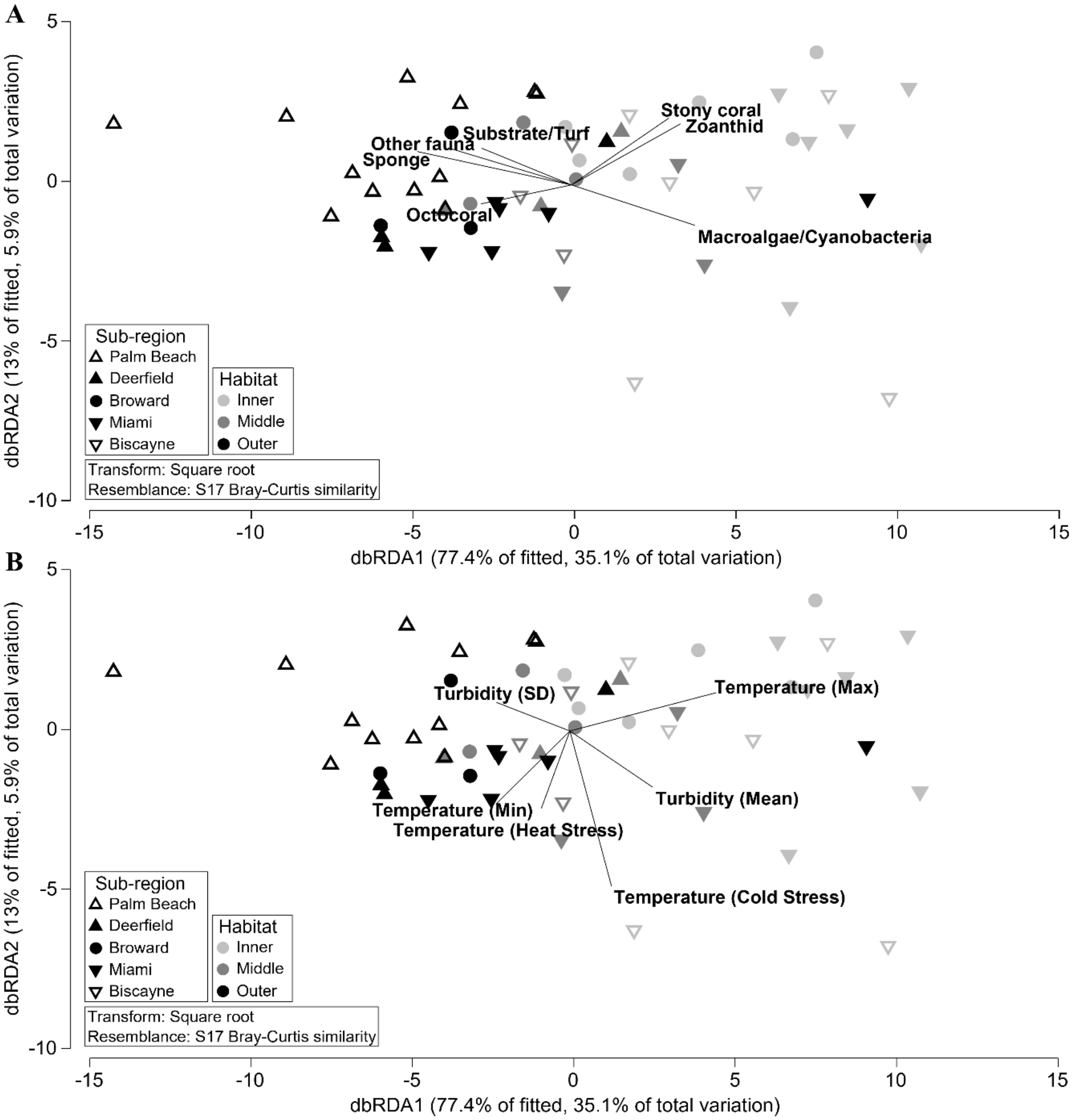

Figure 3. dbRDA ordination of the relationship between A) benthic community structure and B) key environmental predictors identified in DISTLM. Vectors explain 41.0 % variation in benthic community structure.

Stony coral recruit community structure (colonies < 2 cm diameter) varied significantly by habitat and sub-region (PERMANOVA, $p < 0.01$). Stony coral recruit community structure varied marginally, but not significantly by year ($p = 0.07$). Recruit abundance was lower and less diverse in Palm Beach, than in Broward or Miami ($p < 0.05$), and on the middle and outer reefs than on the inner reef ($p = 0.0001$; Figure 4A). *Montastraea cavernosa* and *P. astreoides* recruitment was particularly high in 2021 and *S. siderea* recruitment twice as high in 2020 and 2021 as it was in 2019. Stony coral recruit community structure was most strongly influenced by minimum temperature and temperature standard deviation (DISTLM, $R^2 = 0.20$; Figure 4B). The most abundant recruits were *P. astreoides* and *S. siderea* (Figure 4A). Sites with high minimum temperatures generally had higher abundance of *Stephanocoenia intersepta*, *Dichocoenia stokesii* and *M. cavernosa* recruits. Sites with high temperature standard deviation, predominantly southern shallow sites, generally had higher Shannon diversity, including higher abundance of *P. astreoides* recruits and higher abundance of *S. siderea* recruits.

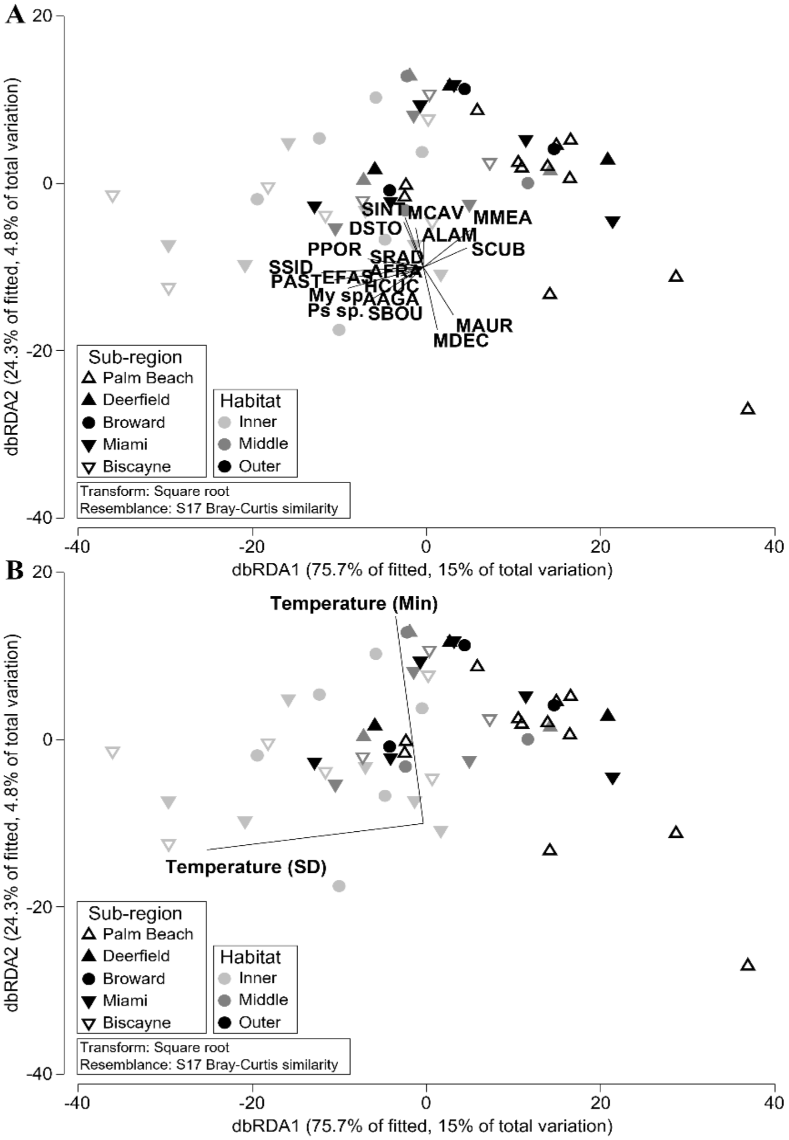

Figure 4. dbRDA ordination of the relationship between A) stony coral recruit community structure and B) key environmental predictors identified in DISTLM. Vectors explain 19.8% variation in stony coral recruit community structure. Species names correspond to four letter code (First letter of Specie and first three letters of genus) for brevity if colony only identified to genus, first two letters of genus listed. Full list of species names in Table S1.

Stony coral adult community structure (colonies ≥ 2cm diameter) significantly varied by habitat and sub-region, with a significant interaction between the two (PERMANOVA, $p < 0.001$). Shannon diversity and species richness were generally higher inshore and in the southern sub-regions, but varied widely spatially (Figure 5A). Similarly, to benthic community structure, stony coral community structure did not significantly change temporally overall, but fluctuations in community structure, particularly in *M. cavernosa*, *P. astreoides*, *P. porites* and *S. siderea* abundance, were seen at certain sites. Stony coral adult community structure was most strongly influenced by total suspended solid concentration (TSS), total nitrogen to total phosphorous ratio (TN: TP) and total nitrogen (TN) concentration (DISTLM, $R^2 = 0.26$; Figure 5B). Sites dominated by *M. cavernosa* and with higher relative abundance of *Meandrina meandrites* had higher mean annual TSS concentration relative to sites with higher Shannon diversity, but low maximum annual TSS concentration (Figure 5B). Sites with higher stony coral Shannon diversity had low mean TSS, high TN variability and low TN: TP ratio. Water quality metrics influenced adult stony coral community structure more strongly than temperature.

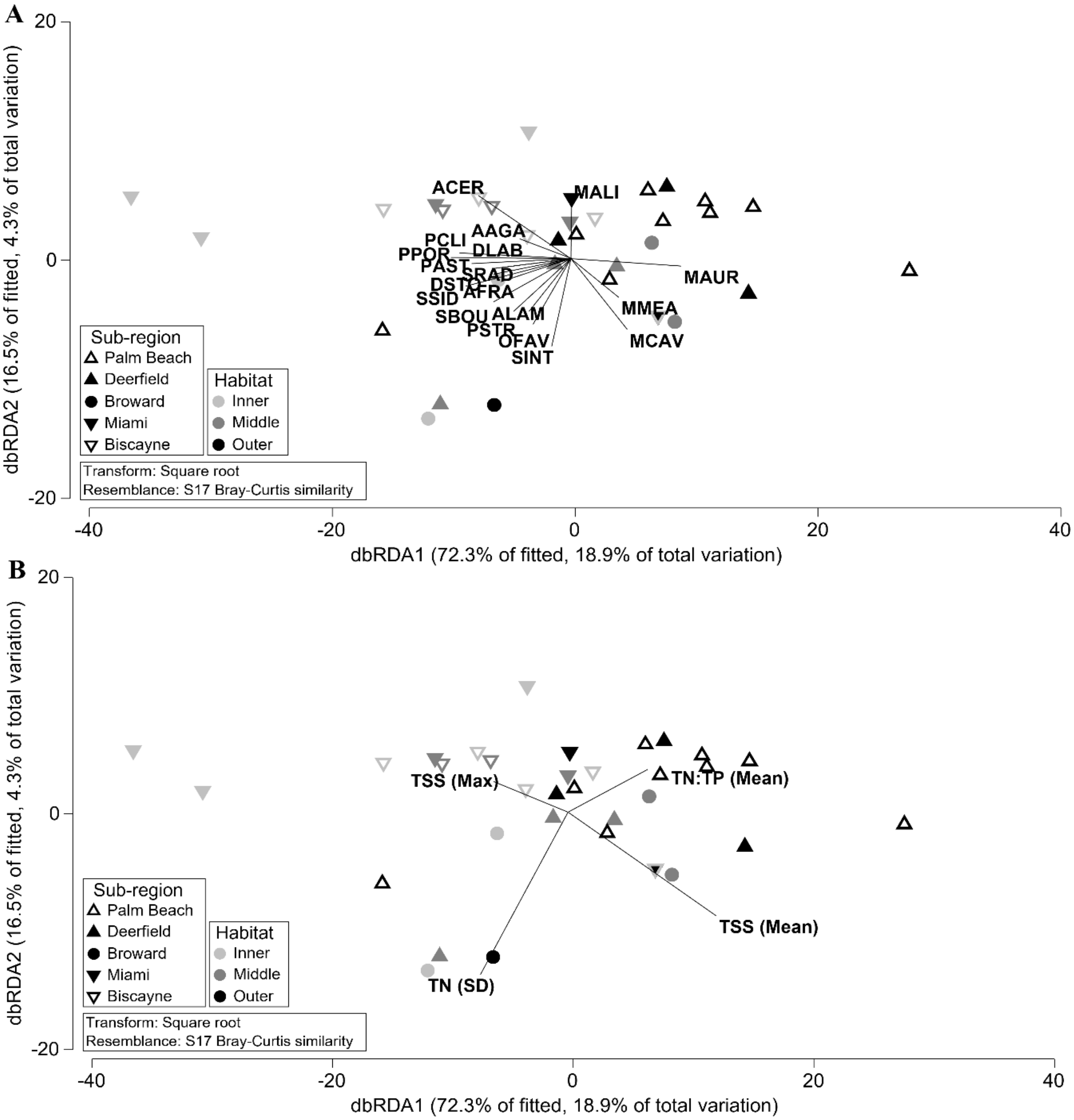

Figure 5. dbRDA ordination of the relationship between A) stony coral adult community structure (colonies ≥ 2cm diameter) and B) key environmental predictors identified in DISTLM. Vectors explain 23.2% variation in adult stony coral community structure. Species names correspond to four letter code (First letter of Species and first three letters of genus) for brevity, full list of species names in Table S1.

Drivers of benthic community change

Temperature generally had the greatest effect on interannual changes in the benthic community, stony coral colony health and stony coral species richness (Figure 6), while increased nutrients, turbidity and TSS had a negative relationship with stony coral abundance, colony health and species richness (Table 2; Figure 7). Random forest regression models were successfully developed for nine metrics and the environmental predictors explained 9 to 79% of variation within them (Figures S2-S10). Increasing annual mean temperature, particularly above 27 °C, had a strong positive relationship with increases in stony coral abundance, *S. siderea* abundance and stony coral recruitment (Figure 7A-C), as well as with interannual increases in octocoral (Figure 7G) and sponge cover (Figure S16B). Macroalgae cover had a strong negative relationship with mean annual temperature (Figure S14A). Locations which had higher, but not too high (~30.5 to 31° C), maximum temperature had a greater interannual increase in stony coral abundance (Figure S11), higher recruitment (Figure S12A) and increased sponge cover (Figure S16A), while octocoral and macroalgae cover declined when maximum temperatures were high (Figure S15 and Figure S14B). Low minimum temperature (< 22° C) was associated with sites which had lower stony coral species richness (Figure S13) and had higher partial colony mortality, particularly in *M. cavernosa* when cold stress duration was also high. Interannual increases in stony coral and *S. siderea* abundance were particularly high at intermediate temperature standard deviation (SD). Recruitment and *M. cavernosa* partial mortality increased with temperature SD, stony coral species richness declined slightly with temperature SD and the greatest interannual increases in macroalgae cover were when temperature SD was below 2° C (Figure 7I).

Nutrients, turbidity and TSS were important predictors of variation in all response metrics and were strongly related to partial colony mortality, stony coral species richness and interannual changes in sponge cover. Where maximum nitrate concentrations were high, partial colony mortality increased and recruitment declined (Figure 7C-E). Where total phosphate or mean nitrate concentrations were higher interannual increases in coral abundance were low and where total nitrogen concentrations were most variable (i.e., TN SD > 0.05 mg/l) *S. siderea* density changes were negligible (Figure 7B). Stony coral species richness was higher where mean nitrite was higher but declined with maximum and mean TSS concentration and with mean turbidity and turbidity SD. *Montastraea cavernosa* partial mortality declined with mean TSS concentration and where mean TSS concentration was either particularly high or low, recruitment was higher. Recruitment also had a parabolic relationship with mean TN: TP (Figure S12B). Mean TSS also had strong importance in interannual changes in sponge and macroalgae cover. Mean TSS above 2.5 mg/l was associated with declining sponge cover (Figure 7H), but interannual increases in macroalgae cover (Figure S14D). Areas with excess nutrients, particularly those with high maximum TP, high mean silicate (SiO4) and high TN SD concentrations (Figure 7I, Figures S14C and S14E), but with low TN: TP ratio (i.e., phosphate overload) were related to the largest increases in macroalgae cover (Figure S14F). Mean DIN concentrations over 0.04 mg/l were associated with declining octocoral cover (Figure 7G).

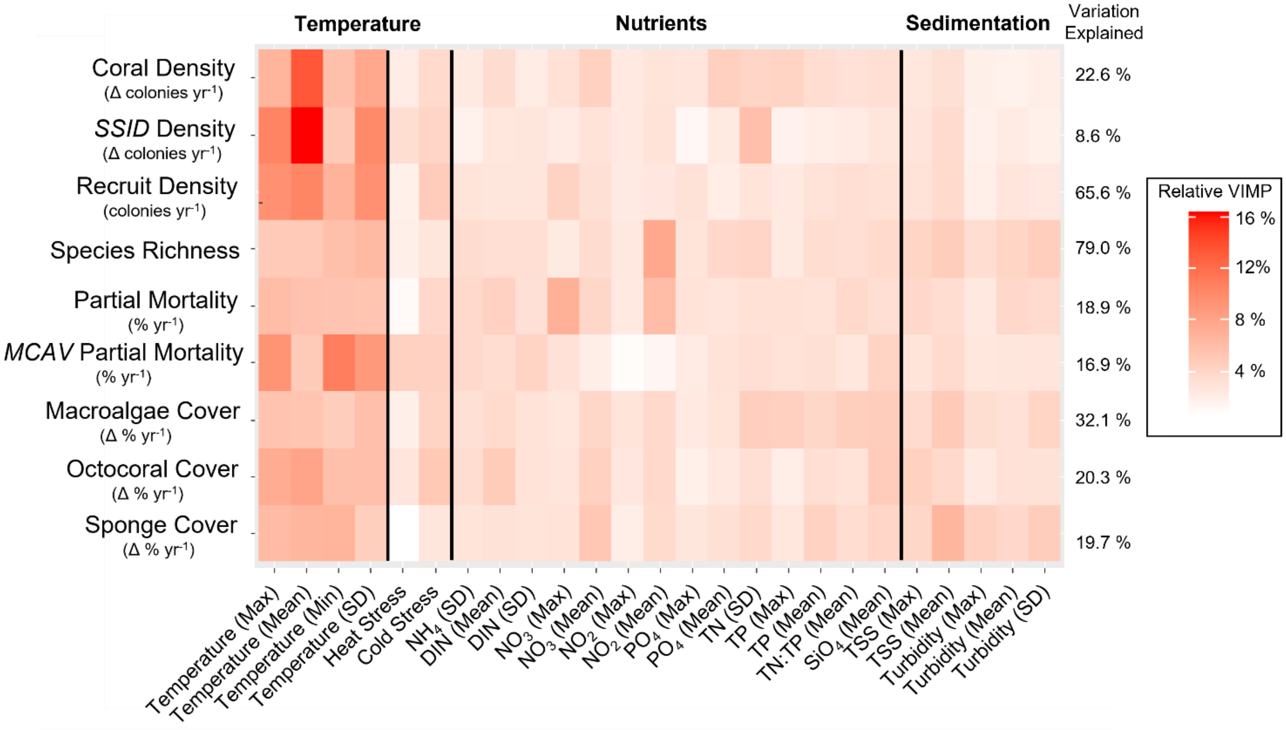

Figure 6. Heat map of relative variable importance (VIMP) based on mean squared error (MSE) of each predictor. Figure is subdivided by environmental predictor (temperature, thermal stress, nutrients, sedimentation). The darker the red the greater the importance of that predictor in explaining variation in the response metric. % Variation explained by model noted

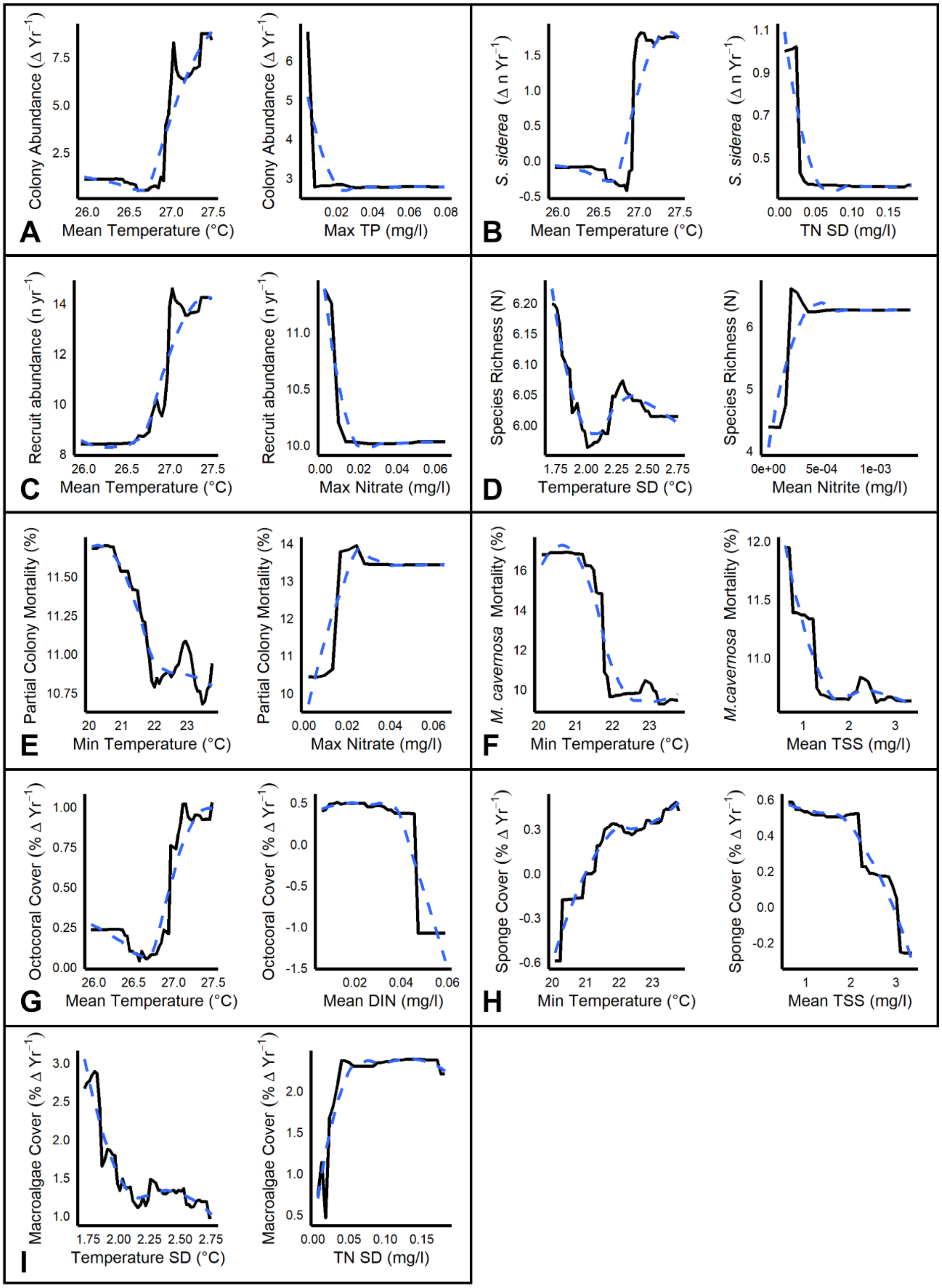

Figure 7. Partial regression plots from random forest regression models of the most important temperature (left) and water quality (right) predictor of A) Change in colony abundance, B) Change in *Siderastrea siderea* colony abundance, C) Stony coral recruit abundance, D) Stony coral species richness, E) Partial Colony Mortality, F) *Montastraea cavernosa* partial colony mortality, G) Change in octocoral cover, H) Change in sponge cover and I) Change in macroalgae cover. Black line = random forest prediction, Blue dashed line = loess smoothed regression.

Table 4. Modeled responses of benthic metrics and environmental predictors which accounted for > 50% of mean squared error (MSE) in random forest models. Variables are listed in order of importance with percent increase in mean square error when they were removed noted in brackets. Δ = interannual change in metric. All other metrics are annual values.

Metric	Variation Explained	Variables that positively affected metric	Variables that negatively affected metric	Variables that had non-linear relationships with metric
Stony coral abundance (Δ)	22.6%	Mean temperature (34.5), max temperature (18.9), min temperature (15.3), TN SD (11.1)	Max TP (11.9), mean NO_3^- (11.9)	Temperature SD (21.5), mean HPO_4^{2-} (12.4)
Siderastrea siderea abundance (Δ)	8.6%	Mean temperature (32.1), max temperature (21.1), min temperature (10.3)	TN SD (12.4), cold stress (7.9)	Temperature SD (20.7)
Recruit abundance	65.6%	Mean temperature (26.1), temperature SD (24.1), max temperature (24.1)	Cold stress (12.2), max NO_3^- (10.9)	Min temperature (16.4), mean TSS (10.0), mean TN:TP (9.1)
Stony coral species richness	79.0%	Mean NO_2^- (22.5), min temperature (17.4), mean temperature (17.3)	Temperature SD (19.1), mean TSS (15.5), turbidity SD (15.4), max TSS (13.4), mean turbidity (13.1)	TN SD (12.7), max temperature (16.3)
Partial colony mortality	18.9%	Max NO_3^- (20.0), cold stress (12.3), NH_4^+ SD (12.3)	Mean NO_2^- (17.1), min temperature (16.9), mean temperature (16.0), mean DIN (12.5), max TSS (11.8)	Max temperature (16.0), SD temperature (15.8)
Partial *Montastraea cavernosa* mortality	16.9%	Max temperature (25.3), temperature SD (24.0), heat stress (11.6), cold stress (11.6)	Min temperature (29.4), mean temperature (11.6), mean TSS (11.4), mean SiO_4^{4-} (11.1)	
Macroalgae cover (Δ)	32.1%	TN SD (18.0), mean TSS (17.7), mean SiO_4^{4-} (16.7), max TP (16.0)	Temperature SD (22.3), max temperature (20.6), mean temperature (18.9), mean TN:TP (17.5)	Min temperature (17.5), mean NO_3^- (15.1)
Octocoral cover (Δ)	20.3%	Mean temperature (21.4), min temperature (16.1), cold stress (13.5), mean SiO_4^{4-} (13.0)	Max temperature (20.3), temperature SD (16.1), max TSS (12.2), mean DIN (12.8), mean NO_3^- (12.5)	
Sponge cover (Δ)	19.7%	Min temperature (15.3), mean temperature (14.1), max temperature (13.7), mean NO_3^- (11.4), turbidity SD (11.1), max turbidity (10.1), max TSS (9.8)	Mean TSS (16.1), temperature SD (10.2),	

Discussion

Temperature was the primary correlate of spatiotemporal differences in benthic community structure, stony coral recruitment and interannual changes in the stony coral community in the ECA from 2018 to 2021. Consecutive heat stress events, Hurricane Irma and a severe disease outbreak caused mass stony coral mortality in the ECA from 2014 to 2018, reducing cover by up to 85% and abundance by up 40% (Walton et al. 2018; Jones et al. 2020; Chapter 1). In the subsequent inter-disturbance period stony coral colony density recovered above pre-disturbance levels, but cover did not. I found that increasing temperature enhanced recovery potential, with elevated recruitment and interannual increases in coral abundance when mean annual in situ water temperature exceeded ~27 °C. However, the benefit of increasing temperature, particularly reduced cold stress and higher minimum temperature (Toth et al. 2021), were reduced when maximum water temperature exceeded 31 °C or when water quality was poor.

Multiple acute disturbances from 2014 to 2017 significantly changed the benthic community in the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA; Chapter 1). Spatiotemporal variation in benthic community structure in the subsequent few years was most strongly influenced by temperature and turbidity, which combined limit coral recovery in many locations in the ECA (Howells et al. 2016; Sommer et al. 2018; Evans et al. 2020). Stony coral cover was higher in areas with higher maximum annual temperature, but with low heat stress, as was found in the pre-disturbance community (Jones et al. 2020). Historically, reduced reef development in the high-latitude ECA has been attributed to cooler water temperature, particularly from winter cold fronts (Toth et al. 2021), with acute heat stress causing contemporary declines in coral cover (Jones et al. 2020). When cold (< ~22 °C) or heat stress (> ~31°C) thresholds were exceeded, conditions favored increased macroalgae cover over stony coral cover and reduced recruitment and adult coral colony survival. Further, low minimum annual water temperature was related to increased partial colony mortality which constrains colony growth in the ECA (Chapter 2), emphasizing that coral communities in the ECA may exist close to the lower limits of their thermal maximum (Kleypas et al. 1999; Toth et al. 2021).

Increased mean turbidity was associated with higher macroalgae and stony coral cover, while sites where turbidity was highly variable had higher turf algae and sponge cover. Turbid conditions are often associated with reducing the impact of thermal stress on corals by limiting irradiance (e.g., Cacciapaglia and van Woesik 2016; Koester et al. 2020). Partial colony mortality of the predominant reef-building stony coral in the ECA, *M. cavernosa*, was lower when turbidity and total suspended solids were elevated suggesting it may mitigate environmental stress in some species, but stony coral species richness declined with turbidity, as has been seen on reefs in the Pacific Ocean (De'ath and Fabricius 2010). Overall turbid conditions, particularly when seasonal fluctuations were substantial supported macroalgae and sponges. Some sponge species can photoacclimate to extreme fluctuations (Marlow et al. 2018) and the increase in suspended food may benefit filter feeding sponges (Fabricius et al. 2012).

Recruitment and subsequent survival, indicated here by change in colony abundance are fundamental to population viability and recovery (McClanahan et al. 2012; Riegl et al. 2018; Edmunds et al. 2018; Pisapia et al. 2020). Stony coral recruitment and colony survival increased most strongly with increasing annual water temperature, until maximum temperature thresholds were exceeded. Recruitment nearly doubled and change in colony abundance tripled when mean annual temperature was above 27 °C, as it was on inshore reefs, in Biscayne and throughout the ECA between the 2019 and 2020 monitoring periods. However, while recruitment and colony survival increased with mean and maximum annual temperature, when temperature exceeded 31 °C these positive relationships began to decline. Previous estimates suggest prolonged temperature above 30.5 °C to induce coral bleaching in Florida (Manzello et al. 2007), but the models here suggest coral abundance and recruitment still increase above this threshold, at least if it is exceeded temporarily.

Stony coral recruit diversity was generally low, with the community dominated by *P. astreoides* and *S. siderea*. Water quality had limited influence on recruit community structure, with temperature variability, which ranged from 1.72 °C to 2.75 °C (SD), and minimum temperature, 20.08 °C to 23.77 °C, explaining most of the variation in recruit community structure. This largely related to very low recruitment in the northernmost sub-region, Palm Beach, which had cooler and less variable temperatures, and high *S. siderea* recruitment at inshore sites (2.2 ±0.3 SE recruits m^{-2}) where temperatures fluctuate more widely. Stony coral recruit abundance and diversity is frequently lower on high-latitude reefs than in the tropics but the thermally tolerant *S. siderea* has relatively high recruitment success and dominates the recruit community in the ECA (Darling et al. 2012; Vega-Rodriguez et al. 2015; St. Gelais et al. 2016). There was evidence of temporal variability in recruit community structure and abundance, with recruit species richness nearly 50% higher and density nearly 70% higher in 2021 than in 2019, when annual mean and minimum temperatures were lower, but recruit density was still low, averaging only 0.57 ±0.09 recruits m^{-2} (±SE).

Temperature was the dominant environmental factor influencing recruitment and survival, but excess nutrients also negatively affected both and water quality had a large impact on colony health and stony coral community structure. Partial colony mortality was 40% higher and recruit abundance declined when maximum nitrate concentration approached 0.02 mg/l. This concentration is lower than thresholds proposed around coral reefs in American Samoa, but within the range of those proposed near Hawaiian coral reefs (Houk et al. 2020). Excess nitrogen can induce oxidative stress in corals, impairing symbiosis with zooxanthellae, leading to reduced coral colony fitness, including constrained growth rates and enhanced bleaching and disease susceptibility (Renegar and Riegl, 2005; D'Angelo and Wiedenmann 2014; Zaneveld et al. 2016; Wang et al. 2018; Lapointe et al. 2019; Zhao et al. 2021). I also found the interannual change in coral colony and *S. siderea* colony abundance halved when maximum total phosphorous concentration (which covaried with TP SD) reached nearly 0.01 mg/l or total nitrogen concentration SD (which covaried with TN max and TN mean) exceeded 0.03 mg/l respectively.

Water quality had the strongest influence on stony coral adult community structure, with reduced diversity where total suspended solids (TSS) concentration and total nitrogen: phosphorous ratio (TN: TP) were higher throughout the year. Suspended solids may increase light attention and sedimentation, limiting growth and recruitment (Carilli et al. 2009; Mellin et al. 2019; Otaño-Cruz et al. 2019), but can be a dominant food source for some coral species (Anthony and Fabricius 2000). TSS was higher in Deerfield (mean = 2.4 ±0.3 mg/l, max = 20.1 mg/l), which is situated between two inlets and two sewage outfalls and had the lowest number of species. In contrast, the more developed coral communities in Broward and Miami, with Broward in particular supporting extensive *Acropora cervicornis* thickets (Goergen et al. 2020), had slightly lower annual mean TSS and substantially lower maximum TSS (5.3 and 7.0 mg/l respectively). *Montastraea cavernosa* and *M. meandrites*, which was abundant in the pre-disturbance community, were both positively related to high mean annual TSS. *Montastraea cavernosa* have high rates of heterotrophy in low light conditions (Lesser et al. 2010) and have large polyps which can effectively remove sediment (Loya 1976; Lasker 1980), while *M. meandrites* have a high rate of mucus excretion which is suspected to aid sediment removal (Loya 1976). Increased TN: TP ratio, which was also generally higher in Deerfield, can lower coral resistance to temperature and light by phosphate starving symbionts and increasing bleaching susceptibility (Wiedenmann et al. 2013). Variability in total nitrogen concentrations (TN), which covaried with maximum and mean TN, also strongly influenced stony coral community structure, including increased relative abundance of the massive corals *Orbicella* spp. and *Pseudodiploria strigosa*. Further, stony coral species richness was most strongly influenced by mean nitrite concentration. This may be related to nitrogen limitation in some species, as has been suggested in some parts of the Red Sea (Ellis et al. 2019) which may also explain the negative relationship between coral colony abundance and total phosphorous, but it may be purely circumstantial. For instance, TN variability and mean nitrite concentrations were both highest in the two southern sub-regions, Miami and Biscayne, which had the highest species richness.

Nutrient enrichment, particularly high total nitrogen or total phosphorous concentrations, was correlated with increased macroalgae cover, reinforcing conditions detrimental to coral recruitment and survival (Box and Mumby 2007; Doropoulos et al. 2016; Ellis et al. 2019; Donovan et al. 2021). Macroalgae cover also increased when annual temperature was cooler and more stable. Previous studies have predicted macroalgae cover would increase in the ECA with rising temperature (Jones et al. 2020). While macroalgae cover was higher at sites with higher maximum temperature, interannual increases in cover were greatest under eutrophic conditions when temperature was stable (Ellis et al. 2019). Reducing anthropogenic nutrient input could be an immediate action which limits macroalgae growth and enhances the potential of stony corals to recruit and survive (Lapointe 1997; Zaneveld et al. 2016; Donovan et al. 2021).

Temperature had a similar effect on octocoral and sponge cover as on stony corals. Octocoral cover also increased when mean temperature exceeded 27 °C and sponge cover declined if minimum temperatures dropped below 22 °C. However, while octocoral cover declined when nutrients were elevated (Fabricius and McCorry 2006), sponge cover increased with mean nitrate concentration (Graham et al. 2018). Both octocoral and sponge cover declined with mean total suspended solid concentration. Despite the suspected increase in available particulate food, zooxanthellate octocorals can still have a negative energy budget in low light conditions (Anthony and Fabricius 2000) and while high turbidity can increase food availability for sponges (Fabricius et al 2012), extended periods of high suspended solids can compromise sponge feeding ability and increase tissue necrosis (Pineda et al. 2017).

Our central question was motivated by understanding whether reducing local chronic pressures, such as sedimentation and nutrient enrichment would enhance stony coral recovery capacity (e.g., Mellin et al. 2019), or whether temperature variability, influenced primarily by global climate change, was the dominant factor. Water temperature has been increasing in the ECA (Jones et al. 2020) and I found a positive relationship between higher water temperature stony coral recruitment, abundance and health, particularly when annual mean temperature surpassed 27 °C, until threshold maximum temperatures were exceeded. However, I also found evidence that excess nutrients and sedimentation reduced stony coral recruitment, diversity and health, favoring increased sponge or macroalgae cover. Under current conditions any potential for tropicalization of these high-latitude urbanised coastlines, which is already hindered by temperature (Jones et al. 2020; Toth et al. 2021), is further reduced by local chronic pressures from anthropogenic sources of pollution.

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Supplementary Materials

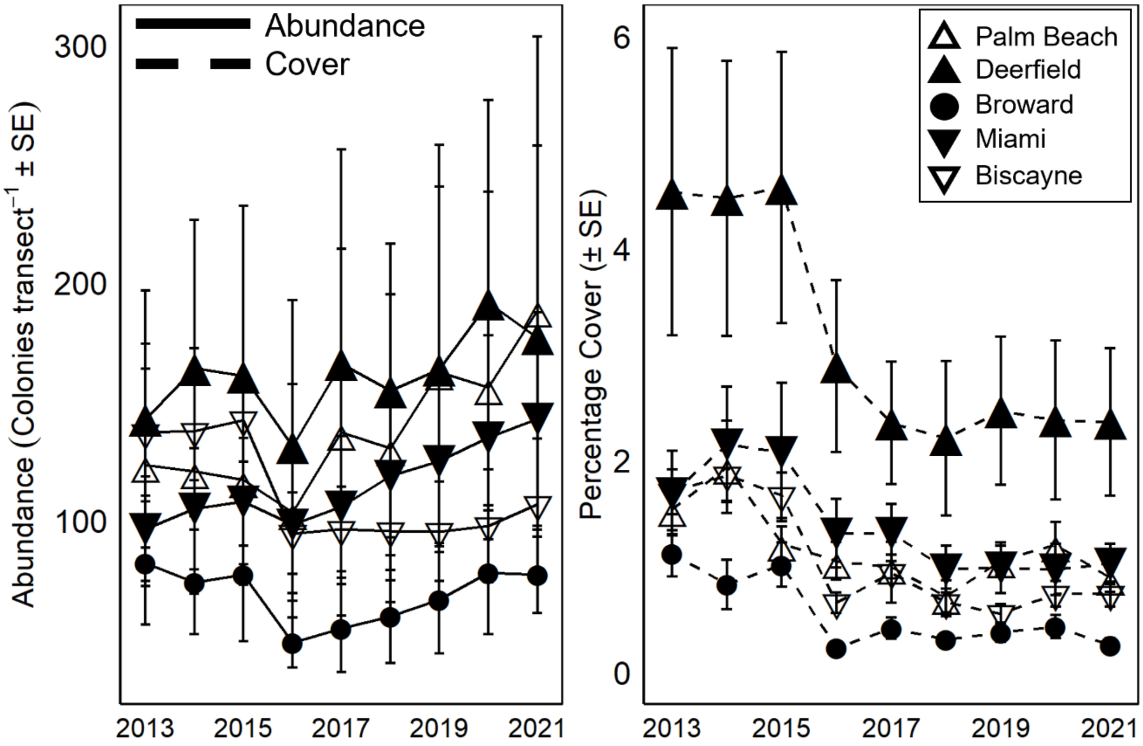

Figure S1. Temporal change in stony coral cover and abundance in each sub-region during the multi-disturbance period from 2013 to 2018 and inter-disturbance period from 2018 to 2021.

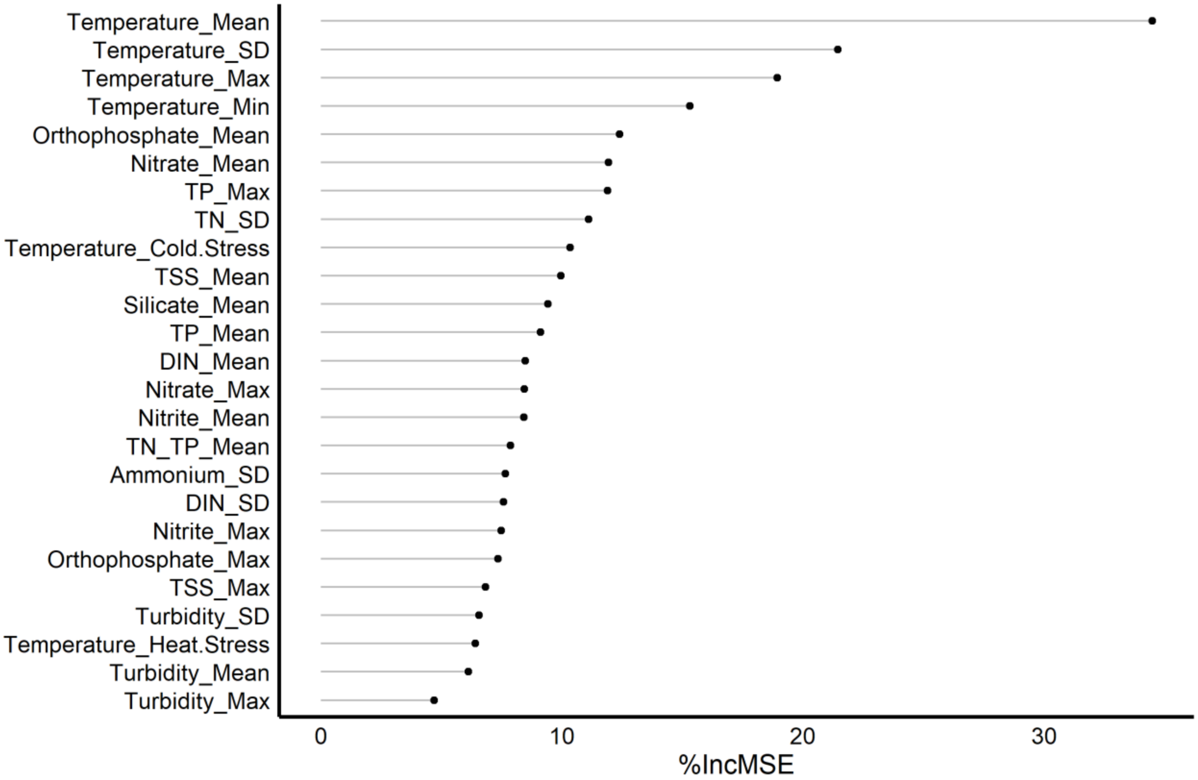

Figure S2. Importance of environmental predictors to interannual change in stony coral abundance calculated by random forest regression model. %IncMSE = increase in mean sum of squares if variable is permuted i.e., the mean decrease in random forest model accuracy if the variable is removed. Variables are ordered by importance.

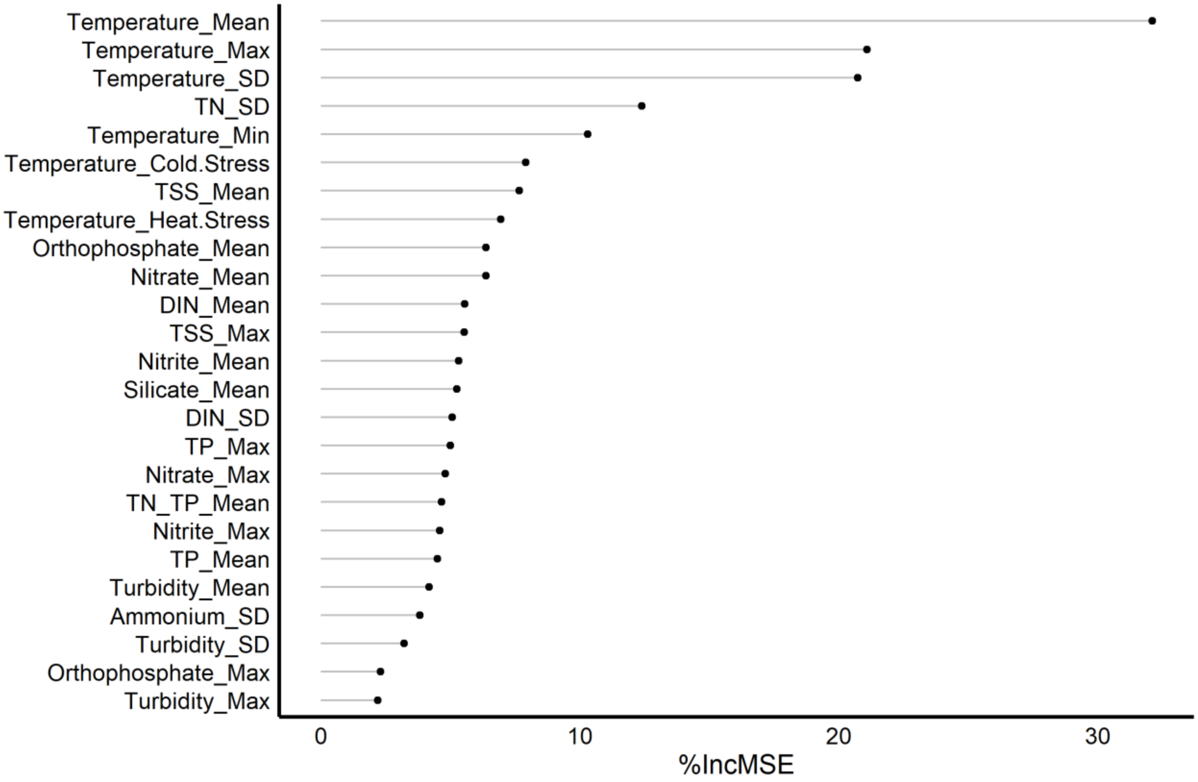

Figure S3. Importance of environmental predictors to interannual change in *Siderastrea siderea* abundance calculated by random forest regression model.

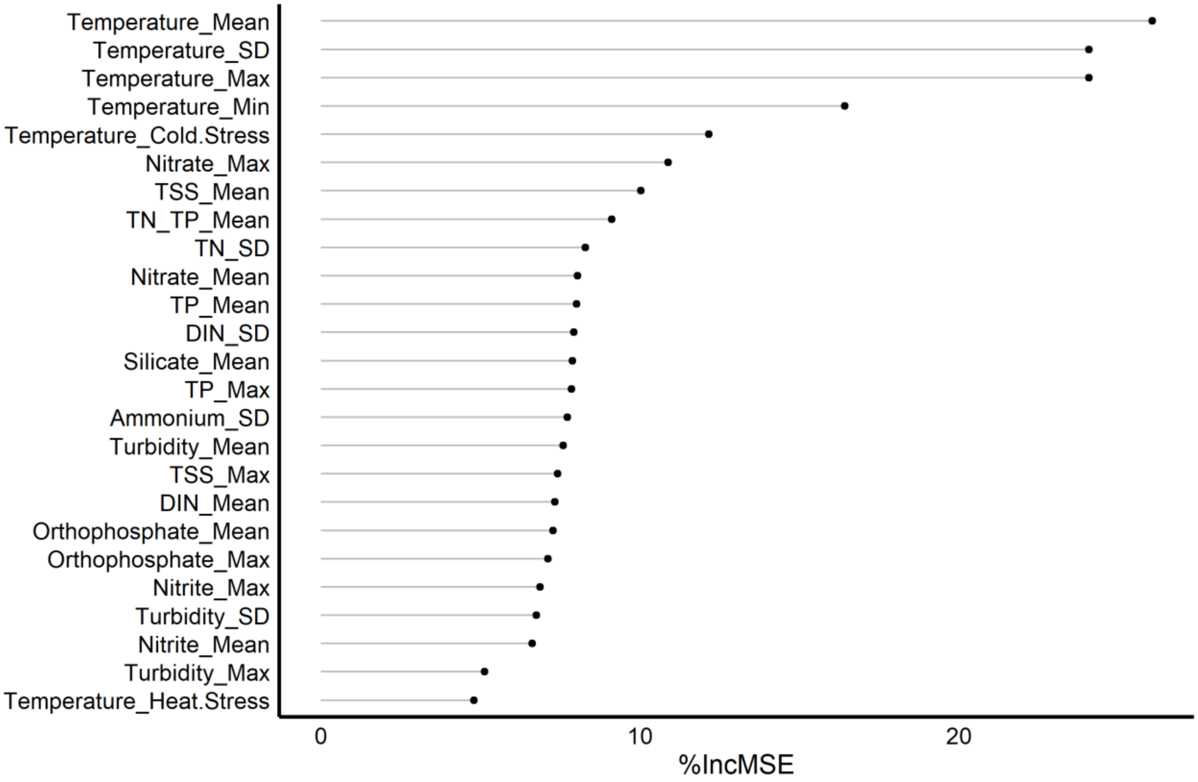

Figure S4. Importance of environmental predictors to realized stony coral recruitment calculated by random forest regression model.

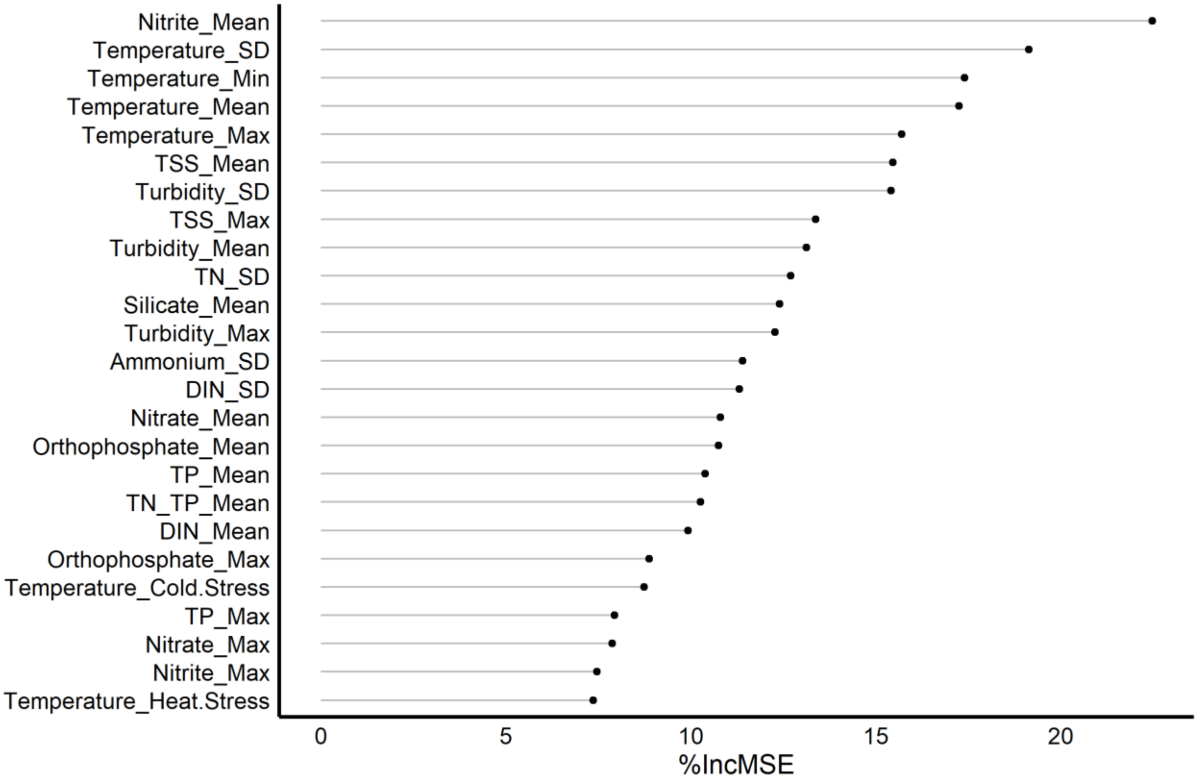

Figure S5. Importance of environmental predictors to species richness calculated by random forest regression model.

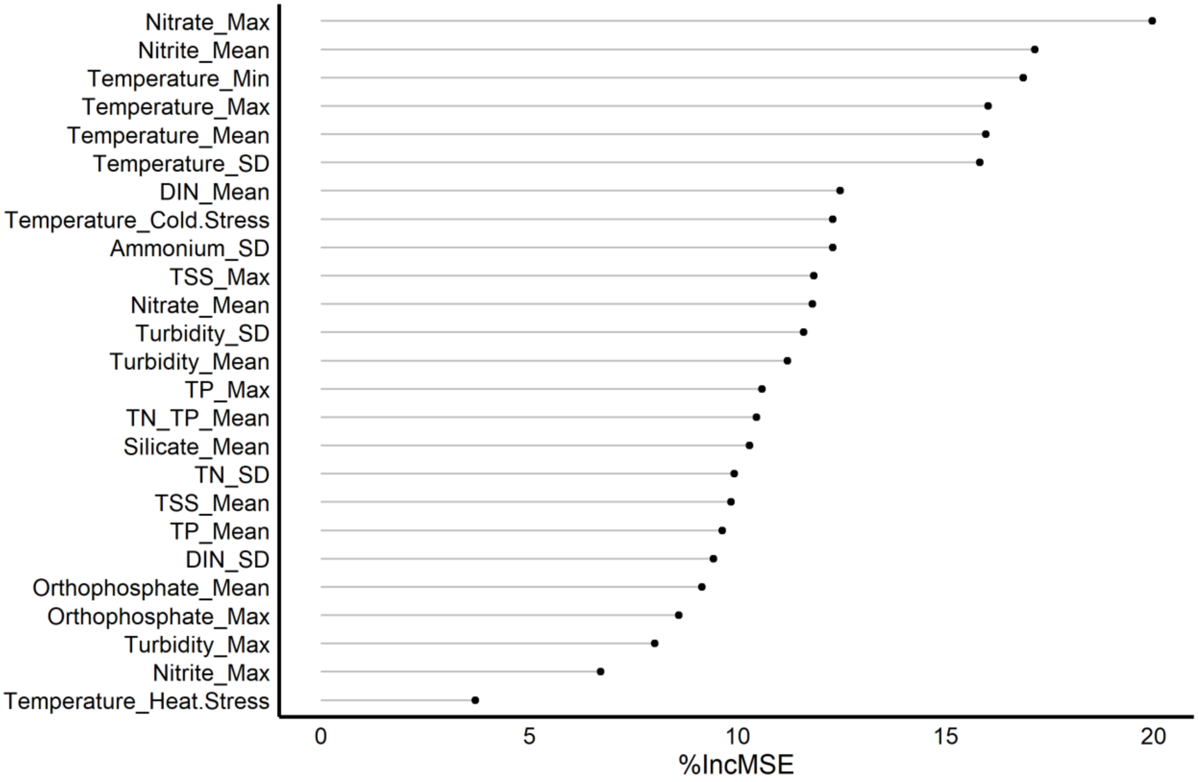

Figure S6. Importance of environmental predictors to partial colony mortality calculated by random forest regression model.

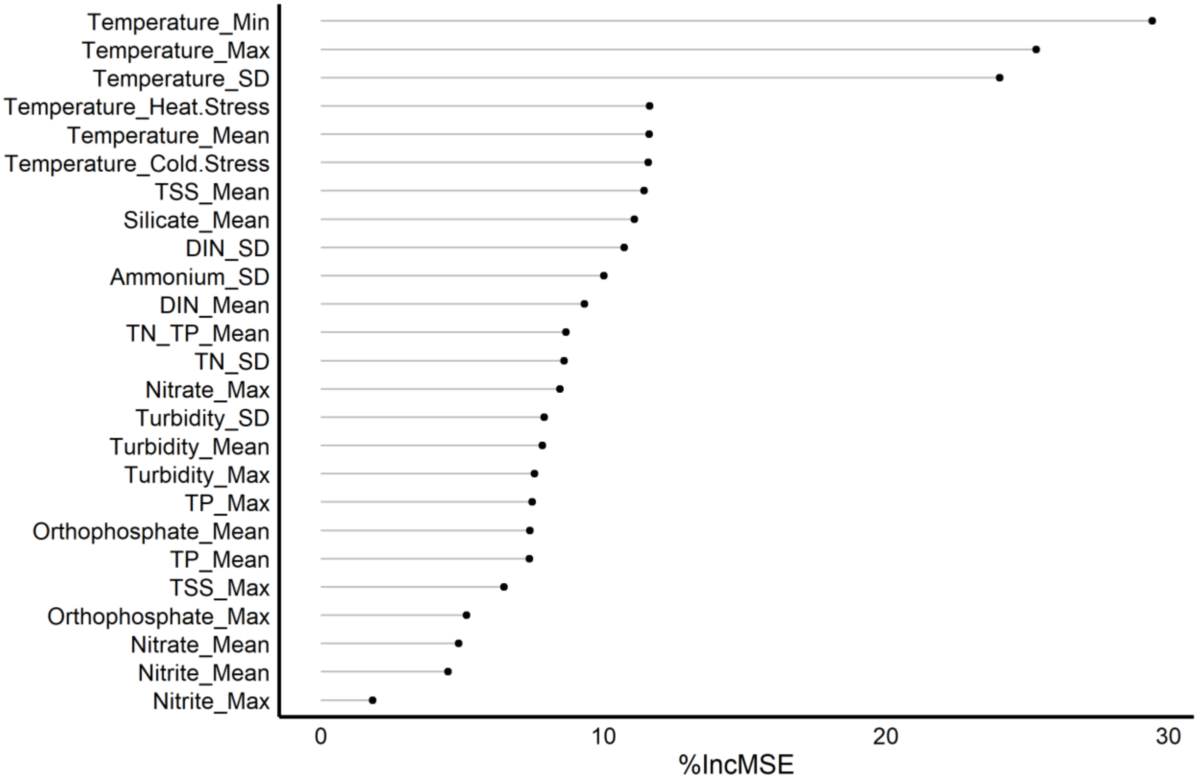

Figure S7. Importance of environmental predictors to partial *Montastraea cavernosa* mortality calculated by random forest regression model.

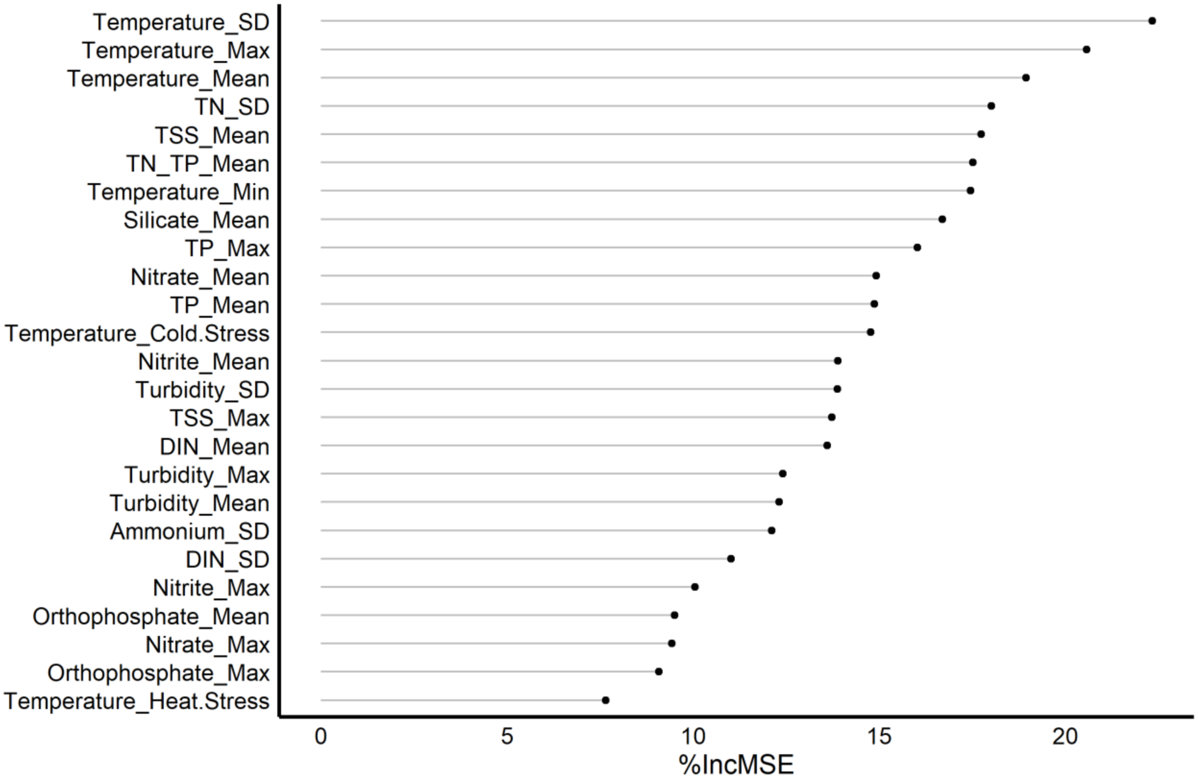

Figure S8. Importance of environmental predictors to interannual change in macroalgae cover calculated by random forest regression model.

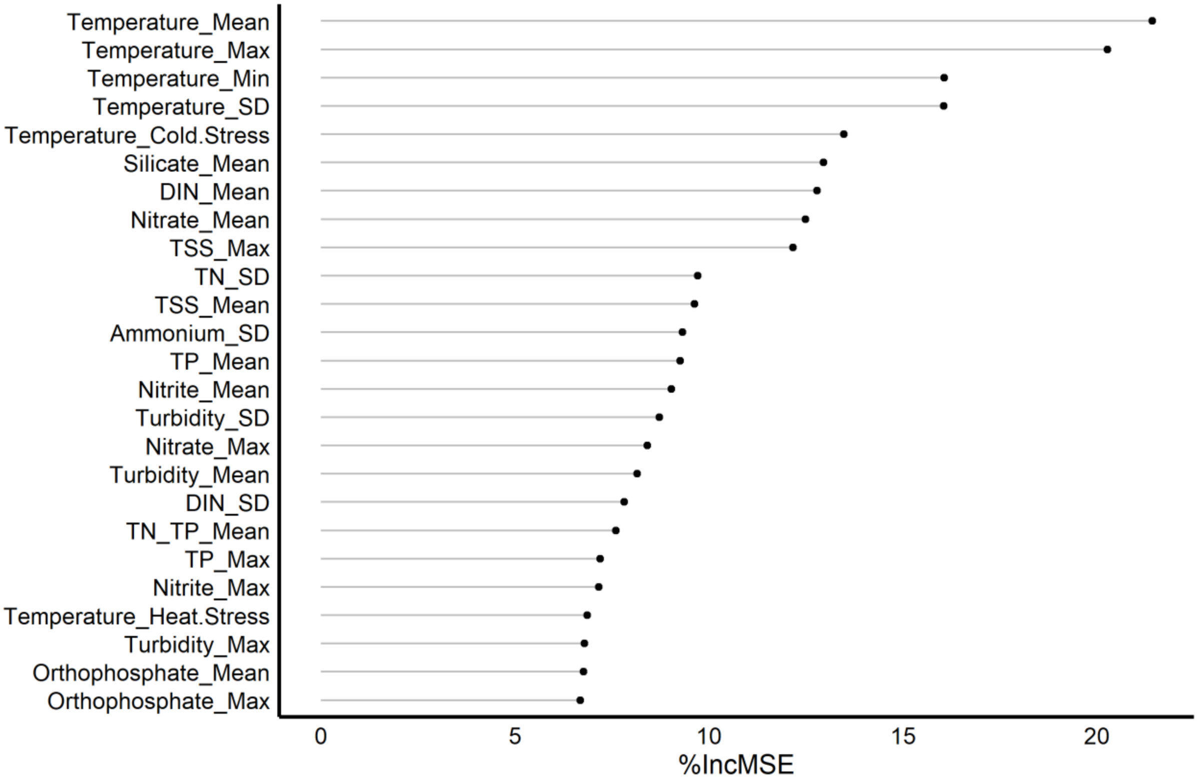

Figure S9. Importance of environmental predictors to interannual change in octocoral cover calculated by random forest regression model.

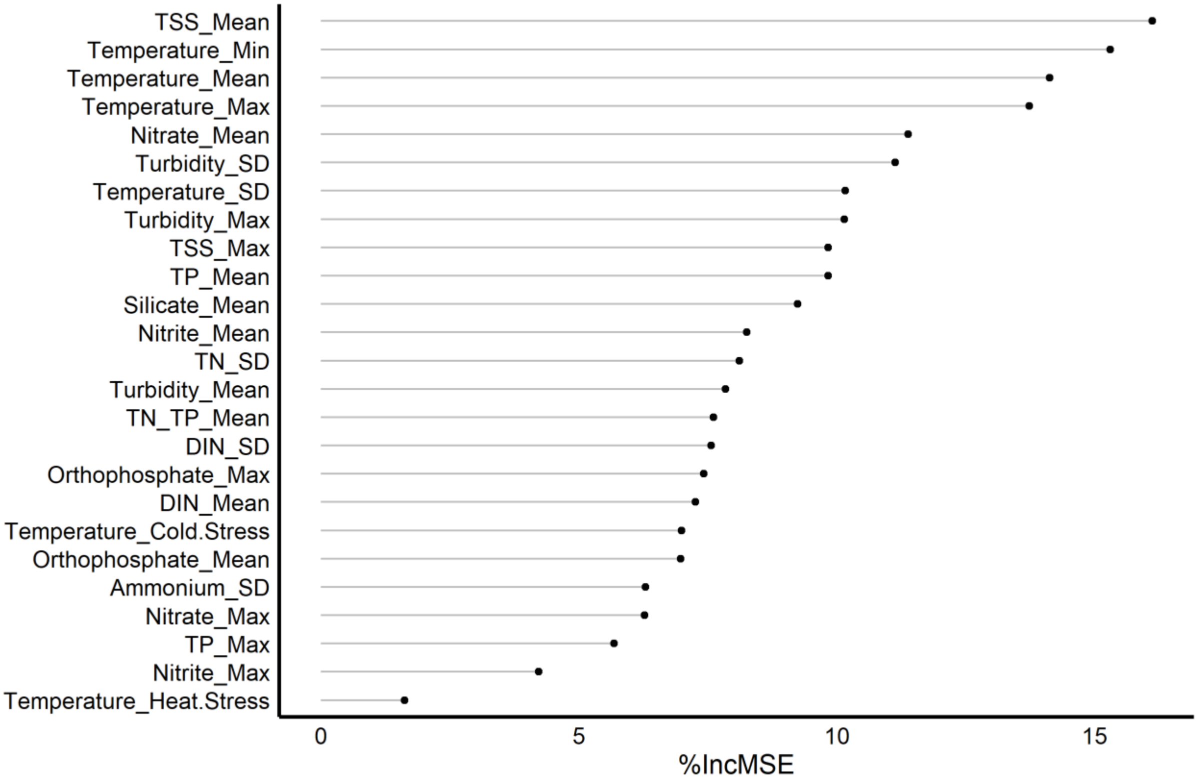

Figure S10. Importance of environmental predictors to interannual change in sponge cover calculated by random forest regression model.

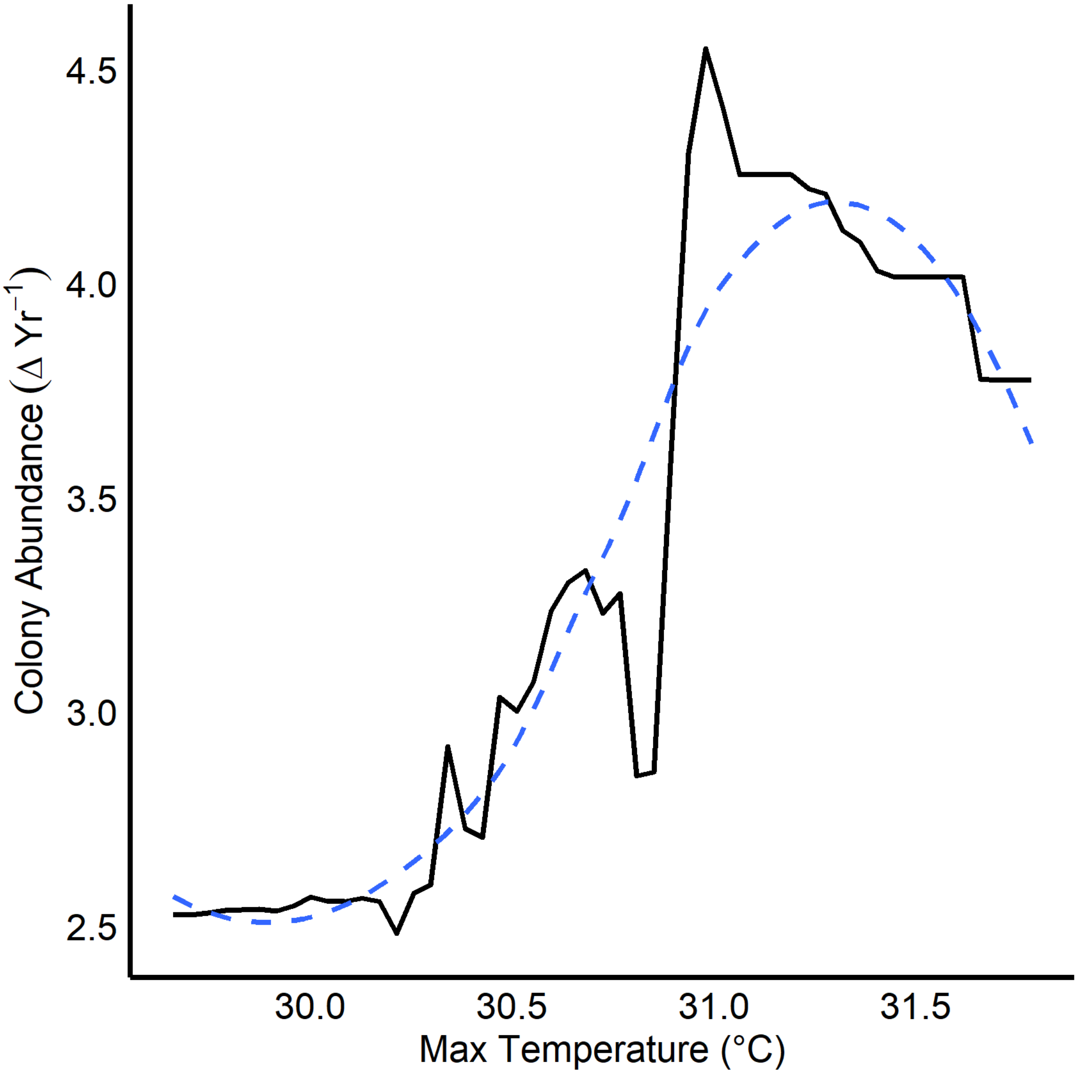

Figure S11. Partial regression plots from random forest regression models of change in colony abundance with maximum temperature. Black line = random forest prediction, Blue dashed line = loess smoothed regression.

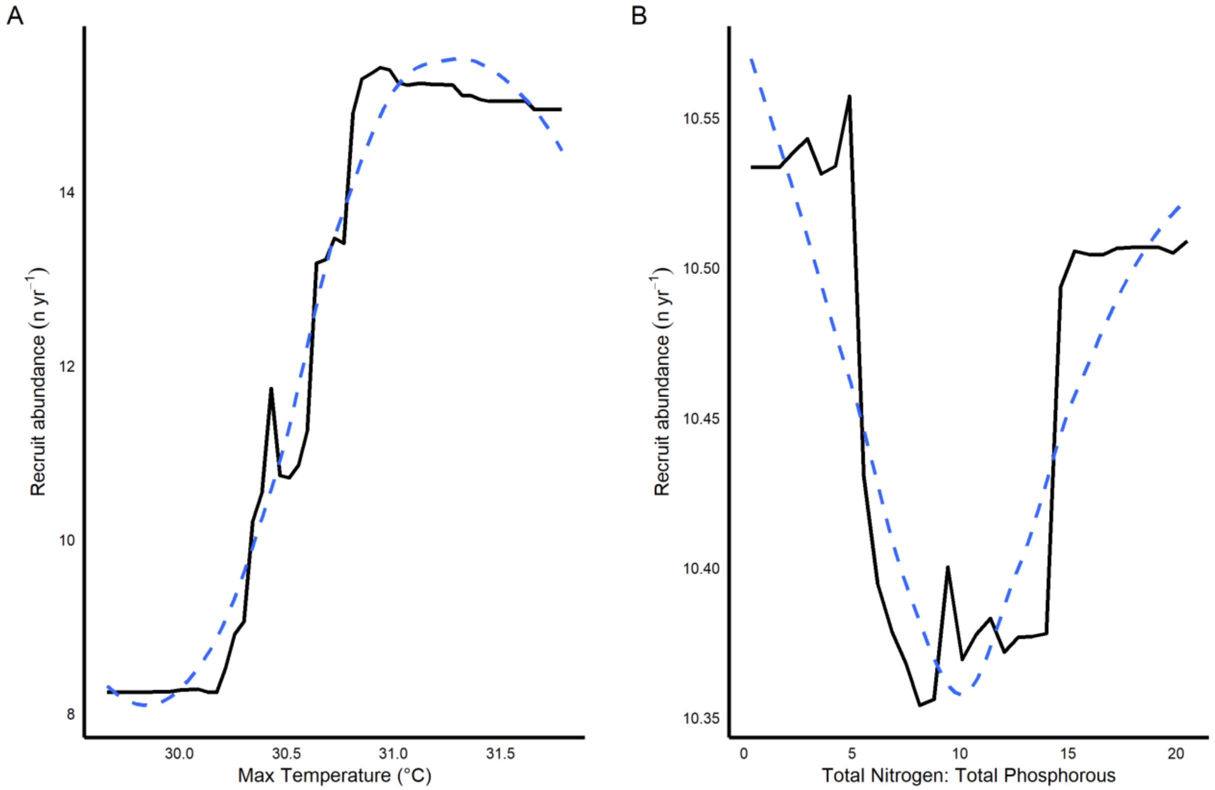

Figure S12. Partial regression plots from random forest regression models of recruit abundance with A) Maximum temperature; B) mean TN:TP ratio. Black line = random forest prediction, Blue dashed line = loess smoothed regression.

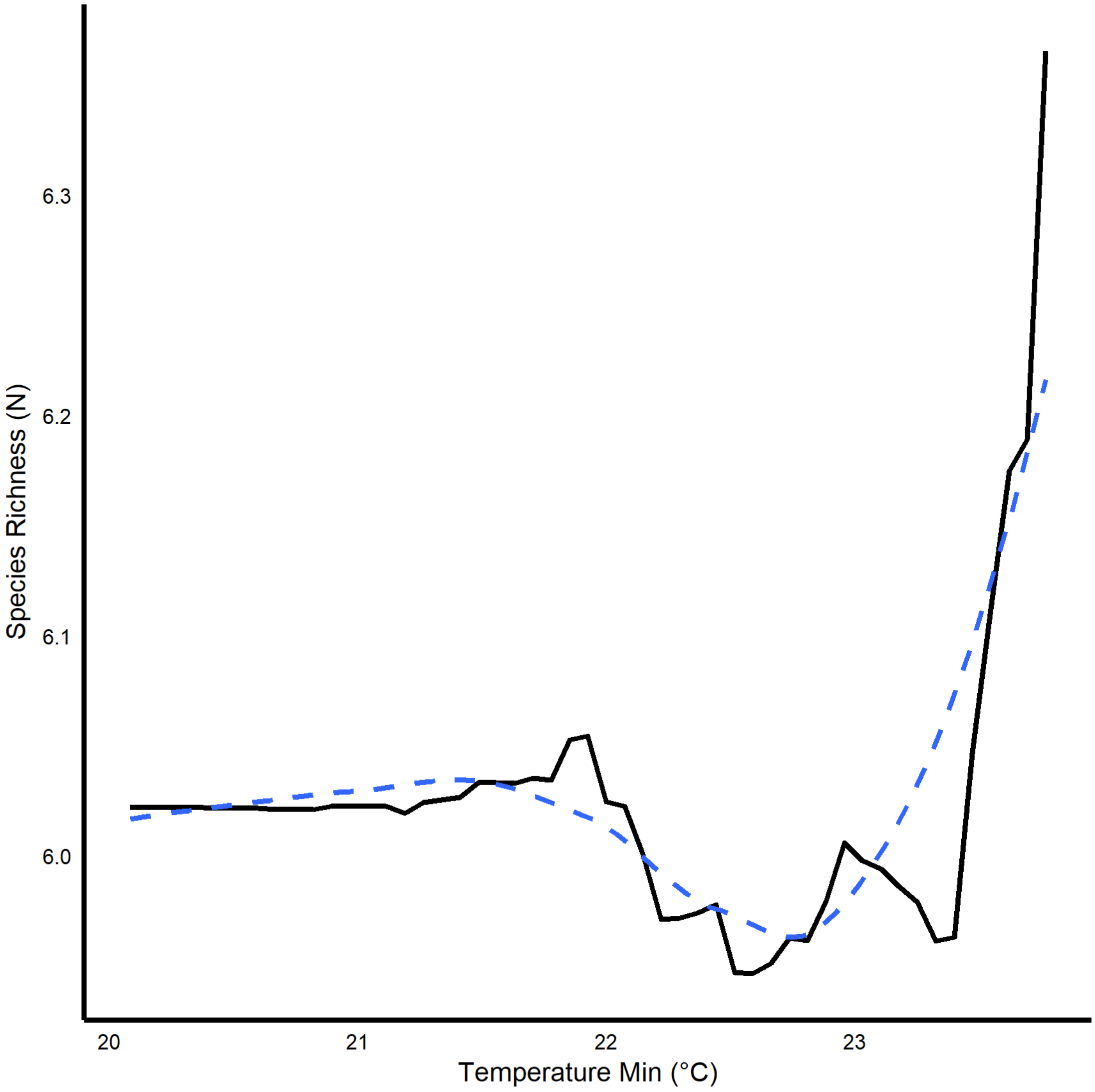

Figure S13. Partial regression plots from random forest regression models of species richness with minimum temperature. Black line = random forest prediction, Blue dashed line = loess smoothed regression.

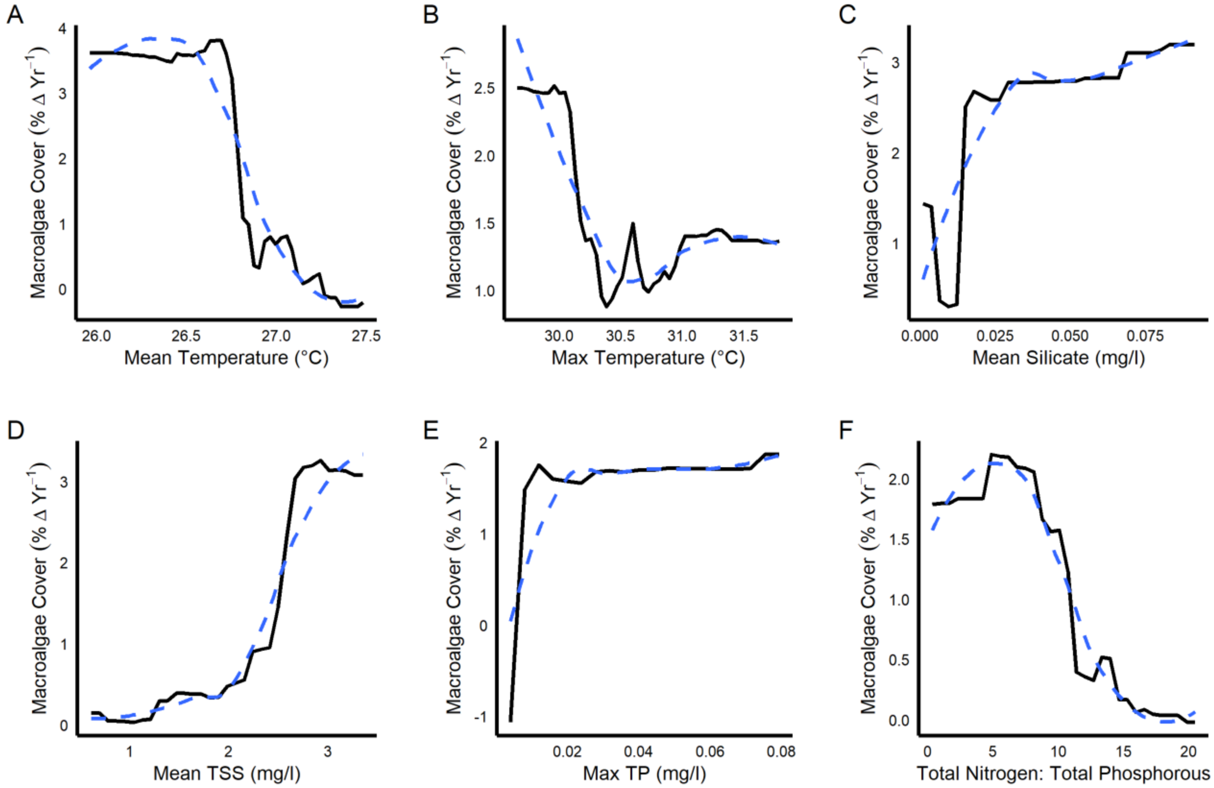

Figure S14. Partial regression plots from random forest regression models of change in macroalgae cover with A) Mean temperature; B) Maximum temperature; C) Mean silicate; D) Mean TSS; E) Maximum TP concentration; F) mean TN:TP ratio. Black line = random forest prediction, Blue dashed line = loess smoothed regression.

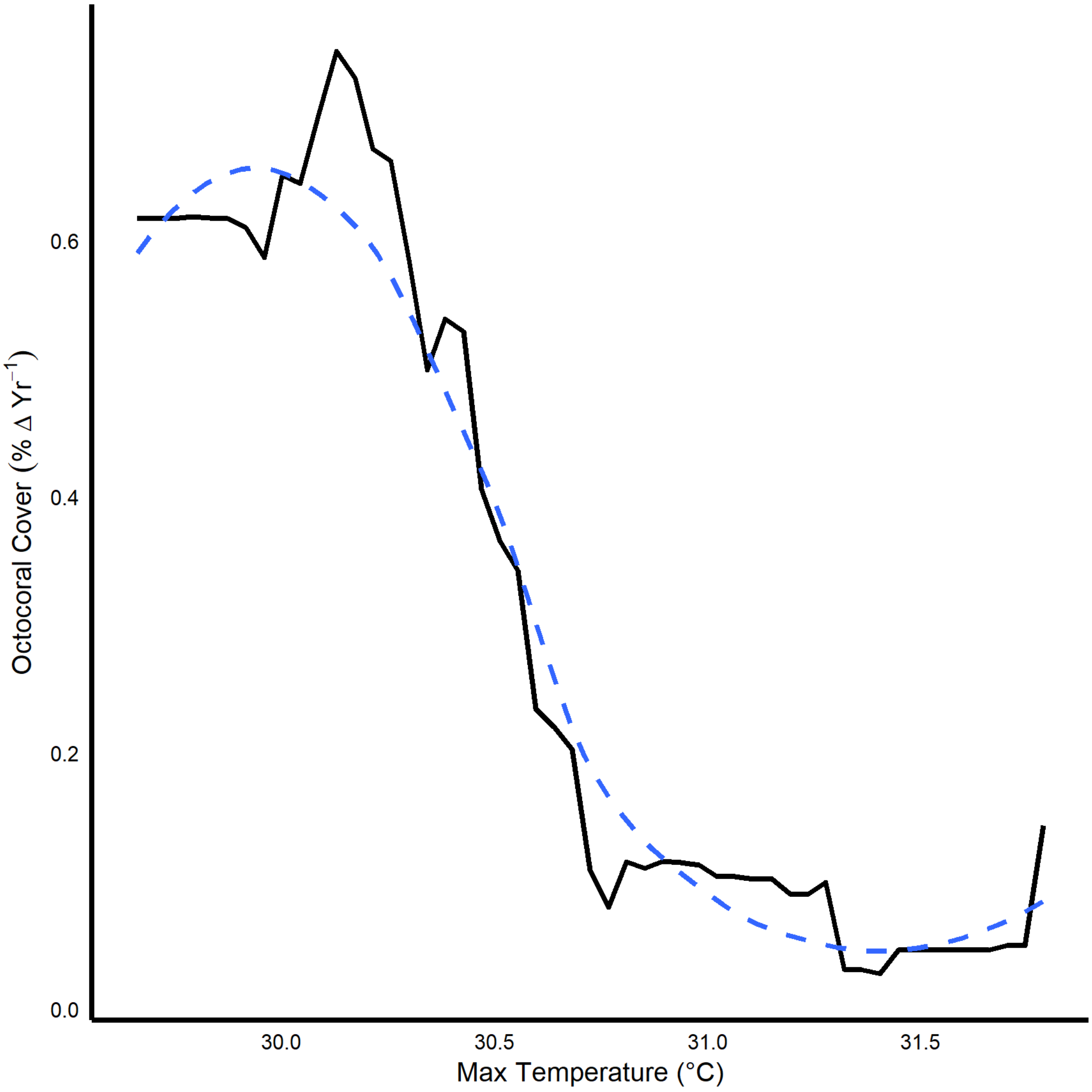

Figure S15. Partial regression plots from random forest regression models of change in octocoral cover with maximum temperature. Black line = random forest prediction, Blue dashed line = loess smoothed regression.

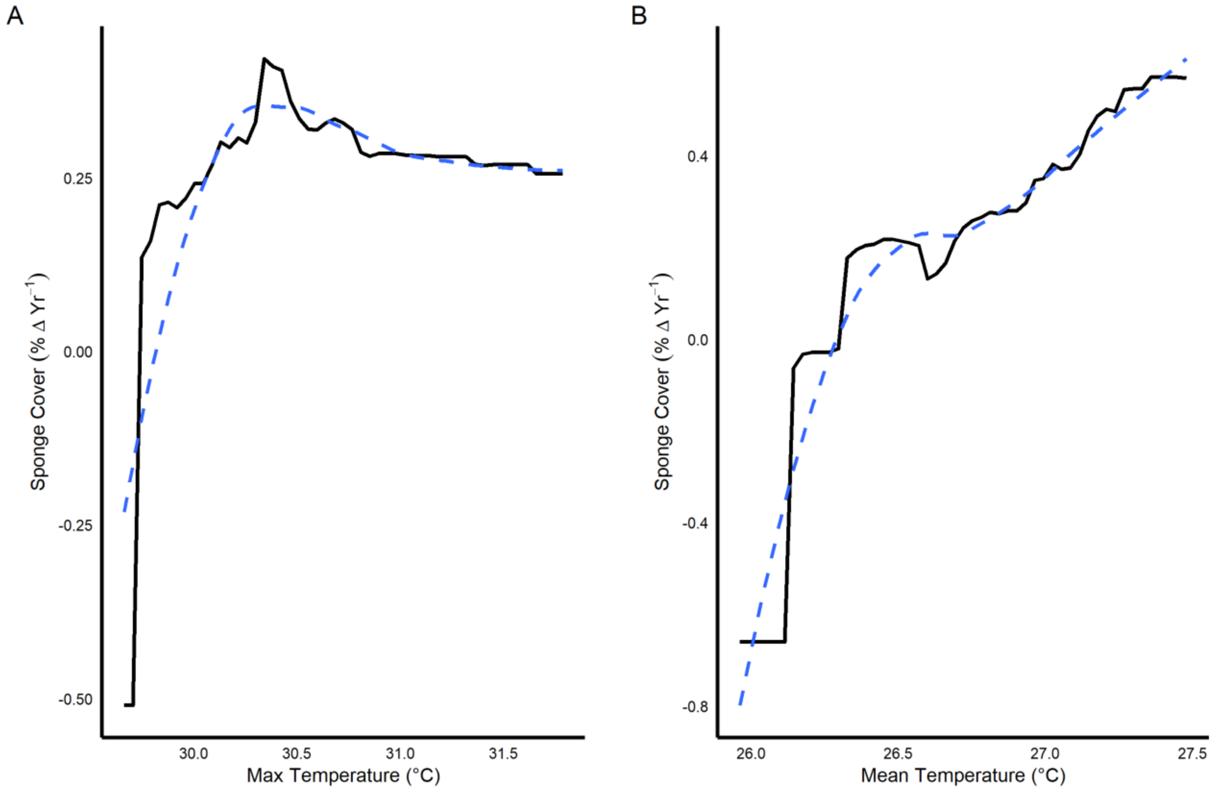

Figure S16. Partial regression plots from random forest regression models of change in sponge cover with A) Maximum temperature; B) Mean temperature. Black line = random forest prediction, Blue dashed line = loess smoothed regression.

Table S5. Stony coral species recorded during study period, four letter code and predominant growth form.

Four letter code	Species	Growth form
AAGA	*Agaricia agaricites*	Encrusting
ACER	*Acropora cervicornis*	Arborescent
AFRA	*Agaricia fragilis*	Laminar
ALAM	*Agaricia lamarcki*	Laminar
CNAT	*Colpophyllia natans*	Massive
DLAB	*Diploria labyrinthiformis*	Massive
DSTO	*Dichocoenia stokesii*	Submassive
EFAS	*Eusmilia fastigiata*	Corymbose
HCUC	*Helioseris cucculata*	Laminar
MALI	*Mycetophyllia aliciae*	Laminar
MAUR	*Madracis auretenra*	Caespitose
MCAV	*Montastraea cavernosa*	Massive
MDEC	*Madracis decactis*	Digitate
MMEA	*Meandrina meandrites*	Submassive
MSEN	*Madracis senaria*	Encrusting
My sp.	*Mycetophyllia sp.*	
OFAV	*Orbicella faveolata*	Massive
OFRA	*Orbicella franksi*	Massive
PAST	*Porites astreoides*	Encrusting
PCLI	*Pseudodiploria clivosa*	Massive
PDIV	*Porites divaricata*	Digitate
PPOR	*Porites porites*	Digitate
PSTR	*Pseudodiploria strigosa*	Massive
Ps sp.	*Pseudodiploria sp.*	Massive
SBOU	*Solenastrea bournoni*	Massive
SCUB	*Scolymia spp.*	Solitary
SINT	*Stephanocoenia intersepta*	Submassive
SSID	*Siderastrea siderea*	Massive
SRAD	*Siderastrea radians*	Encrusting

Chapter 4. Spatial disconnect between recruitment, growth and survival prevents population growth of stony coral assemblages in southeast Florida

Abstract

The size structure of stony coral populations can reveal underlying demographic barriers to population growth or recovery. Recent declines in coral cover from acute disturbances are well documented, but few studies assess size structure and the demographic processes which determine population growth. Vital rates, such as recruitment and survival vary spatially and temporally in response to environmental conditions, in turn influencing community composition. The Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) is a high-latitude reef system offshore of a heavily urbanized coastline. Stony coral cover and density have significantly declined on the ECA in recent years, primarily from heat stress and disease, with limited recovery of stony coral cover during inter-disturbance periods. I quantified variation in stony coral recruitment, size structure and community composition across depth and latitude at permanent sites over three years (2019-2022) to assess the viability of stony coral assemblages. I found spatial decoupling in recruitment, adult colony density and cover that maintains a preponderance of small colonies and skewed size structure in the ECA. At sites close to shore where recruitment was high, there was limited evidence of survival and growth of recruits, while at sites where large colonies were sampled or cover was relatively high, there was limited recruitment. The majority (>75%) of recruits sampled were *Siderastrea siderea*, but there was little evidence these grew into larger size classes. Diversity increased moving offshore, but recruits of most species were uncommon throughout the study area. I suggest low recruitment and high mortality, particularly in small colonies, even during inter-disturbance periods, limits population growth of stony coral assemblages in southeast Florida.

Keywords: Demographics, community, *Montastraea cavernosa, Porites astreoides*, *Siderastrea siderea*, size structure

Introduction

As coral reef communities continue to undergo declines in coral cover (Gardner et al. 2003; De'ath et al. 2012; Hughes et al. 2018; Chapter 1), understanding demographic barriers to the recovery and expansion of stony coral (order Scleractinian) assemblages is key to assessing their viability (Dietzel et al. 2020; Edmunds and Riegl 2020). Vital rates, such as recruitment and survival, drive changes in population growth and size structure (Holbrook et al. 2018; Pisapia et al., 2020). These are influenced by acute disturbances and chronic pressures which can reduce fecundity, impair growth and drive mortality (Bellwood et al. 2004; Baker et al. 2008; Carilli et al. 2009; De'ath et al. 2009; Bauman et al. 2013). The size structure of populations can therefore be used to infer the underlying impact of environmental pressures on stony corals and their potential to persist (Pisapia et al. 2020). Populations dominated by small colonies suggests high disturbance frequency or chronic pressures constrain growth and survival despite consistent recruitment (Bak and Meesters 1998; Bauman et al. 2013; Riegl et al. 2017). A preponderance of intermediate sized colonies may reflect pulses of recruitment (Riegl et al. 2018), and a high ratio of large to small colonies may indicate an aging population with limited recruitment (Bak and Meesters 1999; Miller et al. 2016; Riegl et al. 2018).

Spatial and taxonomic variations in stony coral demographics may reflect differential resilience and influence community composition (Bak and Meesters 1999; Bauman et al. 2013; Holbrook et al. 2018; Edmunds and Riegl 2020; Kramer et al. 2020). In many regions, recent changes to community composition following disturbance have been exemplified by the loss of reef-building species and relative increases in stress tolerant species (Bellwood et al. 2004; de Bakker et al. 2016; Hughes et al. 2019; Jones et al. 2020). In the Pacific, high recruitment of fast-growing species has driven recovery (Edmunds 2018; Holbrook et al., 2018), but recovery has been limited in the Caribbean (Gardner et al. 2005; Hughes et al. 2017; Roff 2020). This is often presumed to relate to chronic anthropogenic pressures (Connell 1997; Gardner et al. 2005; Mumby 2009), but there is growing recognition that spatial disconnects between recruit sinks and locations where stony corals survive and grow can also impair population growth and influence community composition (Miller et al. 2000; van Woesik et al. 2014; Edmunds 2021). As such, it is necessary to assess spatial variation in recruitment, size structure and community composition to determine the impact of environmental conditions and potential demographic bottlenecks which may limit stony coral persistence.

The Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) is a high-latitude reef system offshore of a heavily urbanized coastline. The ECA is located towards the northern limit of stony coral distribution in the western Atlantic. Historically, temperature has limited stony coral population growth and diversity (Toth et al. 2021), but increasing temperature under climate change may precipitate more suitable conditions (Vergés et al. 2019). However, with a human population of ~7 million and widespread coastal construction, stony corals in the ECA are also subject to chronic anthropogenic pressures which may limit this potential (Chapter 3). Over recent years, stony corals in the ECA experienced significant declines in cover and density from thermal stress and stony coral tissue loss disease (SCTLD; Walton et al. 2018; Jones et al. 2020). Although there is evidence of recovery in density during the recent inter-disturbance period (Chapter 3), increases in coral cover have generally been very limited in the ECA (Chapter 1) suggesting underlying barriers to population growth (Bellwood et al. 2004; Edmunds and Elahi 2007; Hughes et al. 2011).

To assess the contemporary condition of stony coral assemblages in southeast Florida, I quantified variation in stony coral recruitment, size structure and community composition across depth and latitude over three years. Limited monitoring of the deep outer reef habitat in the ECA (~20-30 m depth) has been conducted, with focus placed on the shallower inner (4-10 m), middle (11-16 m) and outer (16-18 m) reef habitats. All four habitats, and three sub-regions divided by latitude, were monitored in Broward County, Florida between 2019 and 2022. I tested for spatial, temporal and taxonomic differences in recruitment and size structure to understand the viability of stony coral populations, focusing predominately on the three most abundant stony coral species, *Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea*. Further, spatial differences in stony coral recruit and adult community composition were analyzed. I predict recruitment, size structure and community composition to vary spatially in relation to anthropogenic pressures, with stony coral health and diversity suspected to improve with depth and distance offshore, as has been seen in other anthropogenically impacted areas (Mellin et al. 2019; Otaño-Cruz et al. 2019).

Methods

Study Sites

Scleractinian (stony coral) assemblages were monitored annually for three years between 2019 to 2022 at 27 permanently defined sites offshore Broward County, Florida (Figure 1). Sites were spatially distributed between reef habitats and sub-regions. Habitats varied with depth and distance offshore. The inner reef habitat, 275-780 m offshore at a depth range of 4-10 m, comprises the nearshore ridge complex and linear inner reef. The middle reef habitat is 770-2000 m offshore at 11-16 m depth. The outer reef habitat is 1500-3000m offshore at 16-18 m depth. The deep outer reef habitat was furthest offshore at the eastern edge of the outer reef at 23-26 m depth. Sites were also divided into three sub-regions, by latitude and by ports and inlets as per Jones et al. (2020). The Deerfield sub-region, furthest north, is between Boca and Hillsboro inlets. The Broward/Fort Lauderdale sub-region is between Hillsboro Inlet and Port Everglades. The Hollywood/Miami sub-region is furthest south, between Port Everglades and the Broward/Miami-Dade County line. Surveys on the inner, middle and outer reef habitats were conducted from late September to December in each sample year. Surveys on the deep outer reef habitat were conducted in March and April every year.

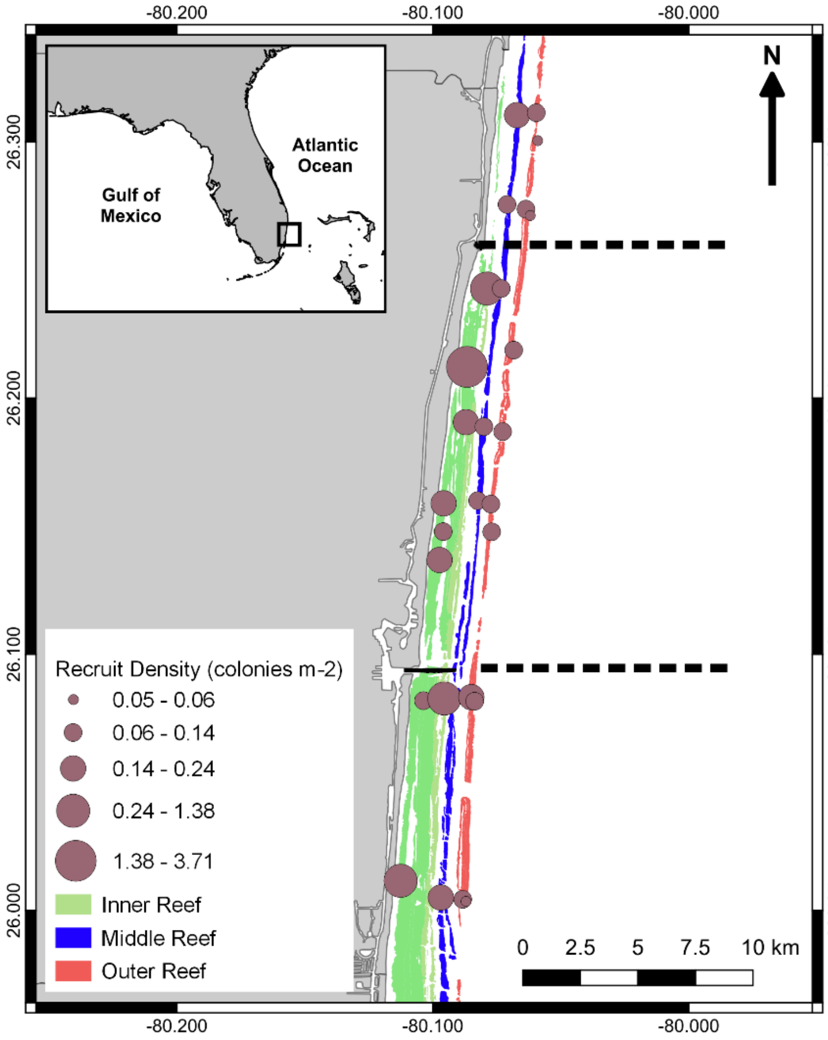

Figure 1. Map of study area and monitoring sites. Reef habitats run parallel from shore, inshore to offshore: Inner reef (comprised of a nearshore ridge complex and linear inner reef), middle reef and outer reef (deep outer reef sites on the eastern edge of the outer reef). Divisions of northern, central and southern sub-regions identified by dashed lines perpendicular to shoreline. Size of the site points corresponds to recruit density (colonies/m^2). Inset map: Study location marked with black box.

Data Collection

Each site consisted of a single 20 m by 1.5 m belt transect, defined by 40, 0.75 m^2 quadrats. Stony coral colonies were identified to species in each quadrat. The maximum diameter, perpendicular width and height of every colony at least 2 cm in diameter were measured to the closest centimeter and percent colony mortality estimated. Live tissue length and width within the quadrat was also measured on every colony in order to calculate percent cover on each transect. Recruits (defined here as colonies under 2 cm diameter) were identified to species and tallied. Recruit and adult colony density was calculated for each 30 m^2 site. Each coral species was assigned to one of eight coral growth forms (arborescent, corymbose, digitate, encrusting, laminar, massive, solitary or submassive) based on the Coral Trait Database (Madin et al. 2016).

Data analysis

Spatial and temporal variation in recruitment, stony coral colony density, live tissue cover and mean colony diameter was statistically assessed in R studio (R Core Team 2020). Generalized linear models (GLM) were used to analyze each metric in relation to the Habitat (Inner, Middle, Outer or Deep outer reef), Sub-region (from north to south Deerfield, Broward, Miami) and Survey year (Year 1, Year 2, Year 3). Five different recruitment response variables were assessed: total recruit abundance, the abundance of the three most abundant species (*Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea*) and the abundance of all other species. Poisson GLMs were used for each recruit response variable with an offset, survey area, to account for differences in survey area and hence represent recruit density. Overdispersion was detected in the model containing all species and *S. siderea* and a negative binomial GLM was fitted. A single model was used for each of adult stony coral density (negative binomial GLM with survey area offset), live tissue cover (gamma distribution and log link) and mean colony length (gamma distribution and log link). Evidence of spatial structure was detected in the residuals of the live tissue cover and mean colony length models. A generalized linear mixed model (GLMM) from the package glmmTMB (Brooks et al. 2017), with random effect site was therefore used for these two metrics to account for the spatial dependency. Full model selection was performed from all potential candidate models and the fitted minimum adequate model selected by the Akaike Information Criterion (AIC). In the event of equivalent models (i.e., within an AIC score of 2; Burnham and Anderson 2004), the simplest model was selected. Model validation was conducted by plotting residuals vs fitted values and residuals versus each factor. Spatial and temporal autocorrelation were tested using the package “DHARMa”. Post-hoc, pairwise assessment of retained factors in the fitted model was conducted using the package “emmeans” and Tukey method, where differences in the response variable are analyzed between levels of a factor (e.g., Habitat) or interaction (e.g., Survey Year x Habitat) based on model predictions (Lenth, 2019).

Size frequency distributions of the maximum colony diameter were constructed for *M. cavernosa*, *P. astreoides*, *S. siderea* and all other species combined. Size class distributions were compared between species and within species by habitat and survey year using Kolmogorov-Smirnov (KS) two sample tests. Size data were then pooled into size classes (<2 cm, 2-4 cm, 5-10 cm, 11-20 cm, 21-30 cm, 31-40 cm, 41-50 cm and > 51 cm) for visual assessment and to allow comparison with other benthic monitoring projects.

Multivariate analyses of spatial and temporal variation in recruit and adult stony coral community composition were conducted in Primer 7 (Clarke and Gorley 2006). Prior to generation of Bray-Curtis similarity coefficients, data were square root transformed. Spatiotemporal variation in recruit stony coral community composition and adult stony coral community composition were statistically analyzed using Permutation Analysis of Variance (PERMANOVA, Anderson 2001; McArdle and Anderson 2001). Type 3 PERMANOVA based on 9999 permutations of residuals under a reduced model was used with sites in each survey year as samples. Similarity matrices were assessed by the fixed factors: Survey year, Habitat and Sub-region. Multivariate results were considered significant at $p < 0.05$. The three-way interaction, Survey year x Habitat x Sub-region, was pooled when analyzing recruit and adult community composition after results suggested it accounted for minimal variation. The interactions Survey Year x Habitat and Survey year x Sub-region were also pooled for adult community composition. Similarity profile routine (SIMPROF) was used to identify significant groups of samples (Clarke et al. 2008). For visual assessment of similarity between habitats, sub-regions or survey years threshold metric multidimensional scaling (tmMDS) plots were created. Each sample in the tmMDS represents each site at each time point and the distance between samples depicts the similarity in community composition (i.e., the closer a sample, the more similar the community composition). SIMPROF groups were overlayed and the spatiotemporal differences visually assessed by plotting species vectors onto the tmMDS.

Species richness, Shannon-Weaver diversity index (H') and Pielou's evenness index (J') were calculated for each site, habitat, sub-region and survey year (Equations 1 and 2).

$$H' = -\sum_{i=1}^{s} pi \ln pi$$

Equation 1. Shannon-Weaver diversity index, where pi is the relative abundance of species i, and s is the total number of species.

$$J' = H'/H'max = H'/lnS$$

Equation 2. Pielou's J for evenness where H'max is the maximum possible diversity and S is the total number of species.

Results

Density and Cover

Recruit density was low at most sites (Figure 1), averaging 0.95 ±0.2 recruits m^{-2} (± SE). Recruit density varied most strongly by habitat (Table 1; negative binomial GLM, $R^2 = 0.43$) and was significantly higher on the inner reef than all other habitats (Figure 2a; emmeans pairwise comparison with Tukey test (Tukey pairwise), $p < 0.0001$). Adult colony density (negative binomial GLM; $R^2 = 0.15$) and live tissue cover (gamma GLMM; conditional $R^2 = 0.96$, marginal $R^2 = 0.27$) also varied most strongly by habitat (Figure 2b and 2c). In comparison to recruitment, adult colony density was significantly higher on the outer reef than on the inner reef (Tukey pairwise, $p = 0.01$) or middle reef (Tukey pairwise, $p < 0.01$; Table 1) and cover was significantly higher on the deep outer reef than the middle reef (Tukey pairwise, $p = 0.01$) and marginally higher on the deep outer reef than the inner reef (Tukey pairwise, $p = 0.08$). Recruitment, adult density and cover did not vary significantly by sub-region or by survey year, but mean recruit density was twice as high overall in year 2 than year 3 (Figure S1). Mean colony length varied by survey year and habitat (gamma GLMM, conditional $R^2 = 0.96$, marginal $R^2 = 0.18$). Mean colony length increased over time and was significantly higher in survey year 3 than it was in years 1 and 2 (Tukey pairwise, $p < 0.05$). Mean colony length was highest on the deep outer reef (10.8 ±0.3 cm), but not significantly (Tukey pairwise, $p > 0.05$). Model validation of the final fitted models (GLM or GLMM) indicated no problems.

Table 6. Spatial and temporal variation in stony coral demographics and diversity. Habitats listed from inshore to offshore. Sub-regions listed North to South. Year of survey listed with survey year.

Metric	**Habitat**				**Sub-region**			**Survey Year**		
	Inner	**Middle**	**Outer**	**Deep**	**Deerfield**	**Broward**	**Miami**	**1**	**2**	**3**
								2019/20	**2020/21**	**2021/22**
Recruit Density (colonies m^{-2} ±SE)	1.9 ±0.5	0.5 ±0.1	0.5 ±0.1	0.3 ±0.1	0.4 ±0.1	1.1 ±0.3	1.1 ±0.2	1.0 ±0.3	1.2 ±0.4	0.6 ±0.1
Density (colonies m^{-2} ±SE)	2.0 ±0.2	1.9 ±0.1	2.8 ±0.3	2.4 ±0.7	2.3 ±0.2	2.2 ±0.1	2.2 ±0.2	2.3 ±0.2	2.2 ±0.2	2.2 ±0.2
Cover (% ±SE)	1.9 ±0.4	0.8 ±0.1	1.3 ±0.2	3.1 ±0.4	1.4 ±0.1	2.2 ±0.3	1.4 ±0.3	1.8 ±0.3	1.8 ±0.3	1.8 ±0.3
Species Richness	14	16	19	16	19	23	21	23	22	23
H'	1.74	1.72	1.74	2.01	1.96	2.08	2	2.07	2.05	2.08
J'	0.66	0.62	0.73	0.66	0.67	0.66	0.66	0.66	0.66	0.66
Mean Length (cm ±SE)	8.6 ±0.4	6.6 ±0.2	7.1 ±0.1	10.8 ±0.3	7.4 ±0.2	9.3 ±0.3	7.4 ±0.2	8.3 ±0.3	8.1 ±0.2	8.6 ±0.2
Max Length (cm)	170	90	50	97	65	170	50	170	170	130
Max Height (cm)	80	40	24	48	30	80	32	80	80	45

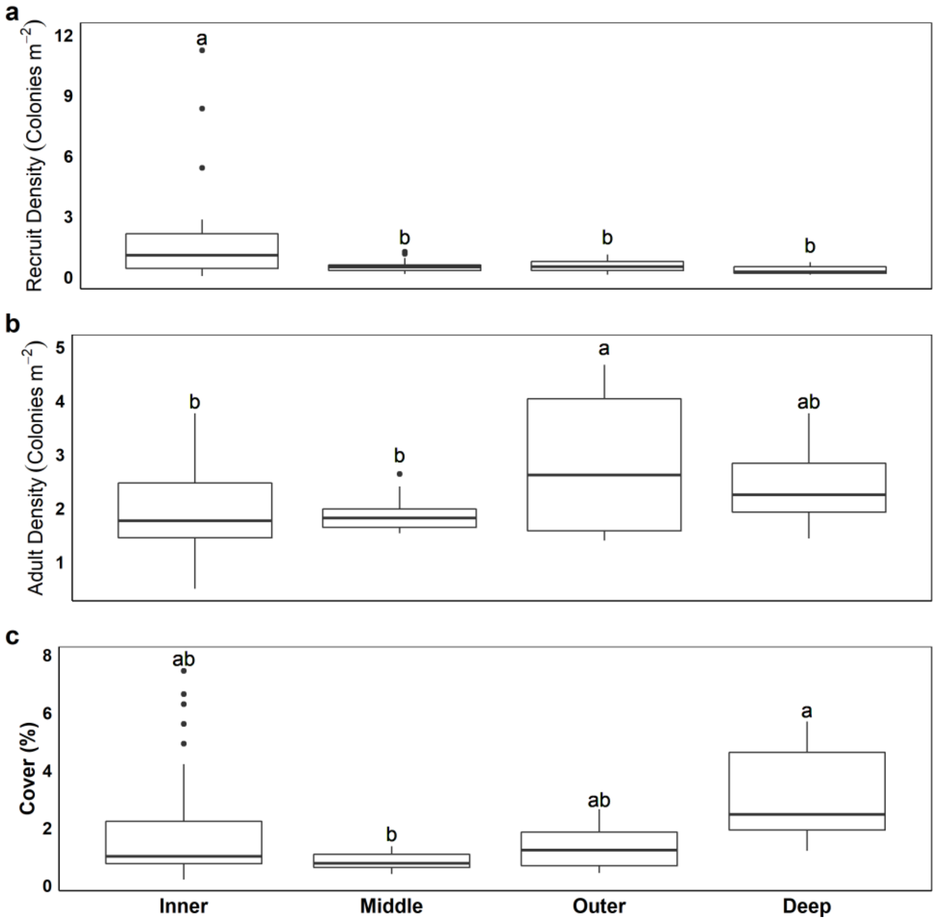

Figure 2. Spatial variation in a) Recruit density; b) Adult colony density; and c) Live tissue cover, based on reef habitat.

Recruitment and Size Structure

I sampled 2177 stony coral recruits from 18 species (< 2 cm diameter) and 5408 adult colonies from 24 species (≥ 2 cm diameter). Three quarters of recruits were *S. siderea*, with density varying by habitat (negative binomial GLM, $R^2 = 52.8\%$) and being nearly 10 times higher on the inner reef than elsewhere (Tukey pairwise, $p < 0.01$; Figure 3c). *Montastraea cavernosa* recruit density varied by habitat, sub-region and year, with a significant interaction between habitat and sub-region (Poisson GLM, $R^2 = 68.1\%$). *Montastraea cavernosa* recruit density was highest on the middle and outer reefs, significantly so on the middle reef than on the deep outer reef (Tukey pairwise, $p < 0.01$) and was higher in the Miami sub-region than Broward (Tukey pairwise, $p = 0.001$; Figure 3a). Further, *M. cavernosa* recruit density on the inner, middle and outer reefs in Miami were higher than on those habitats in Broward (Tukey pairwise, $p < 0.05$). *Montastraea cavernosa* recruit density on the deep outer reef in Broward was significantly higher than the same habitat in Deerfield or Miami (Tukey pairwise, $p < 0.05$) and was marginally higher than on the inner reef in Broward (Tukey pairwise, $p = 0.1$) where the largest *M. cavernosa* colonies were found and where cover is traditionally highest. *Montastraea cavernosa* recruitment was marginally higher in year 1 (2019/20) than in year 3 (2021/22; Tukey pairwise, $p = 0.05$). *Porites astreoides* recruit density was fairly consistent over time and space and did not vary significantly by any spatial or temporal factor (Poisson GLM; $R^2 = 2.6\%$; Figure 3b). All other recruit species, except for *P. porites* on the inner reef, were generally rare and were grouped together for analysis. Recruitment of these species varied by habitat and sub-region (Poisson GLM, $R^2 = 24.4\%$), with marginally higher recruitment on the inner than middle reef (Tukey pairwise, $p = 0.1$) and significantly higher recruitment in Miami than Broward (Tukey pairwise, $p = 0.02$; Figure 3d).

Size frequency distribution was skewed for all species and most colonies were smaller than 10 cm diameter (Figure 3). *Montastraea cavernosa* size frequency distribution was significantly different to the non-target species and to *S. siderea*, but not to *P. astreoides* (KS, $p < 0.0001$). The largest colonies surveyed were *M. cavernosa*, with the largest colony measuring 170 cm on the inner reef in Broward (Table 1). *Montastraea cavernosa* size frequency distribution varied significantly by habitat (KS, $p < 0.0001$), with a dearth of intermediate sized colonies on the inner reef and a more normal distribution on the deep outer reef (Figure 3a). *Porites astreoides* size frequency distribution was relatively similar on the inner, middle and outer reefs, with most colonies measuring 5-10 cm diameter and few to none being larger than 30 cm diameter. It was significantly different on the deep outer reef (KS, $p < 0.001$) where the spread of colonies from under 2 cm to 31-40 cm diameter was relatively even (Figure 3b). *Siderastrea siderea* size frequency distribution was heavily positively skewed and significantly different to all other species (KS, $p < 0.0001$; Figure 3c). It also varied significantly by habitat (KS, $p < 0.0001$) with the bulk of recruits and small adult colonies on the inner reef and less skewness moving offshore. *Siderastrea siderea* size frequency distribution was significantly different in years 1 (2019/20) and 2 (2020/21) than in year 3 (2021/22) when recruit density was low and the size frequency distribution less positively skewed (Figure S2). Non-target size frequency distribution significantly varied to all others, with density comparatively consistent with size (Figure 3d). Size frequency distribution was significantly different on the deep outer reef than all other habitats (KS, $p < 0.001$), with more 5-10 cm diameter colonies. Non-target size frequency distribution was also significantly different between year 1 (2019/20) and year 3 (2021/22; $p < 0.05$), with evidence that recruits and small colonies in year 1 were growing into larger size classes by year 3, particularly on the inner reef (Figure S2).

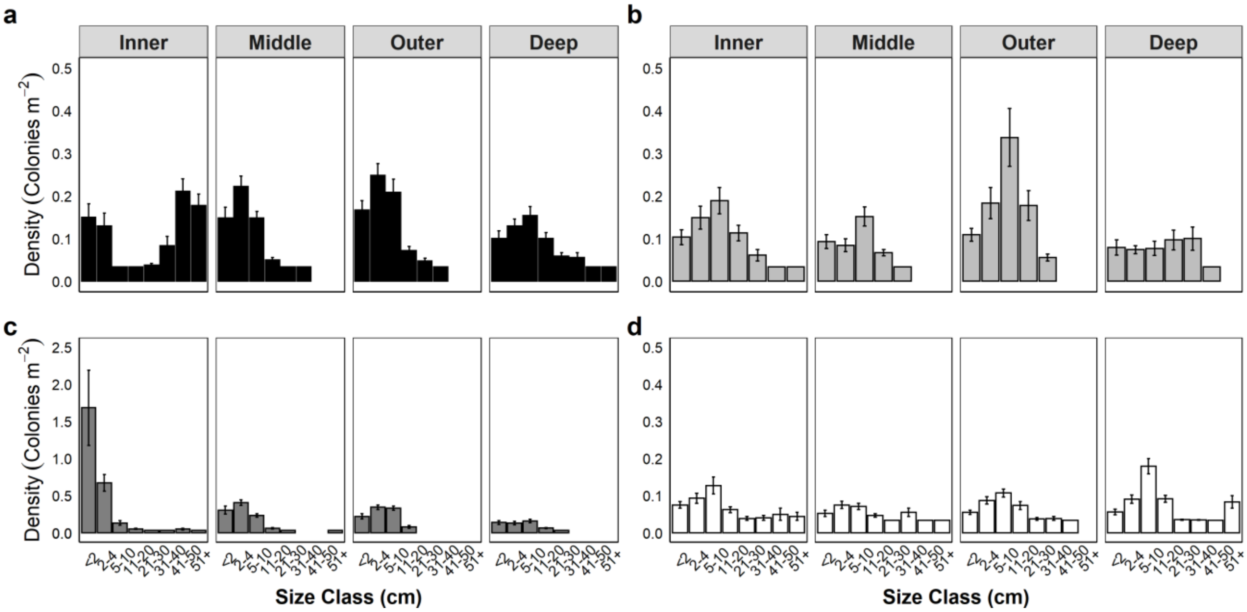

Figure 3. Spatial variation in size frequency distributions of a) *Montastraea cavernosa*; b) *Porites astreoides*; c) *Siderastrea siderea*; d) All other species. Size class is based upon maximum diameter of each colony and the y axis is the density of the species in each size class (<2 cm, 2-4 cm, 5-10 cm, 11-20 cm, 21-30 cm, 31-40 cm, 41-50 cm, 51+ cm). Note: y-axis on different scale in plot c to a, b, and d.

Community Composition

Recruit community composition significantly varied by habitat (PERMANOVA, $p = 0.0001$) with a significant interaction between habitat and sub-region ($p = 0.02$), but did not vary temporally. Recruit community composition varied significantly between all habitats except the middle and outer reefs ($p < 0.01$). Inner reef sites had higher relative *S. siderea* and *P. porites* recruit density and low diversity and evenness (H’ = 0.6; J’ = 0.2; Figure 4). Recruit diversity and evenness increased moving offshore and was highest on the deep outer reef (H’ = 1.5; J’ = 0.7). Recruit community composition did not significantly vary between sub-regions on inner or deep outer reefs, but recruitment in the northernmost sub-region (Deerfield) was significantly different to the central sub-region (Broward) on the middle reef ($p = 0.008$), and the recruit community in Broward and the southernmost sub-region (Miami) varied on the outer reef ($p = 0.02$). The middle reef in Deerfield had twice as many recruits (primarily *S. siderea* and *Stephanocoenia intersepta*) as the middle reef in Broward. The outer reef in Miami had three times as many *M. cavernosa* recruits as the outer reef in Broward. SIMPROF analysis found recruit community composition split into two groups ($p = 0.02$; Figure 4). One group was made up of two low cover sites within 500 m of the shoreline, HH2 and Pomp4, which had twice as many *S. siderea* recruits than at any other site. The other group contained all other samples and was comparatively diverse. No recruits with arborescent or corymbose morphologies were found. Two sites had recruits with laminar morphologies and only one *Orbicella* sp. recruit was found (Figure S3).

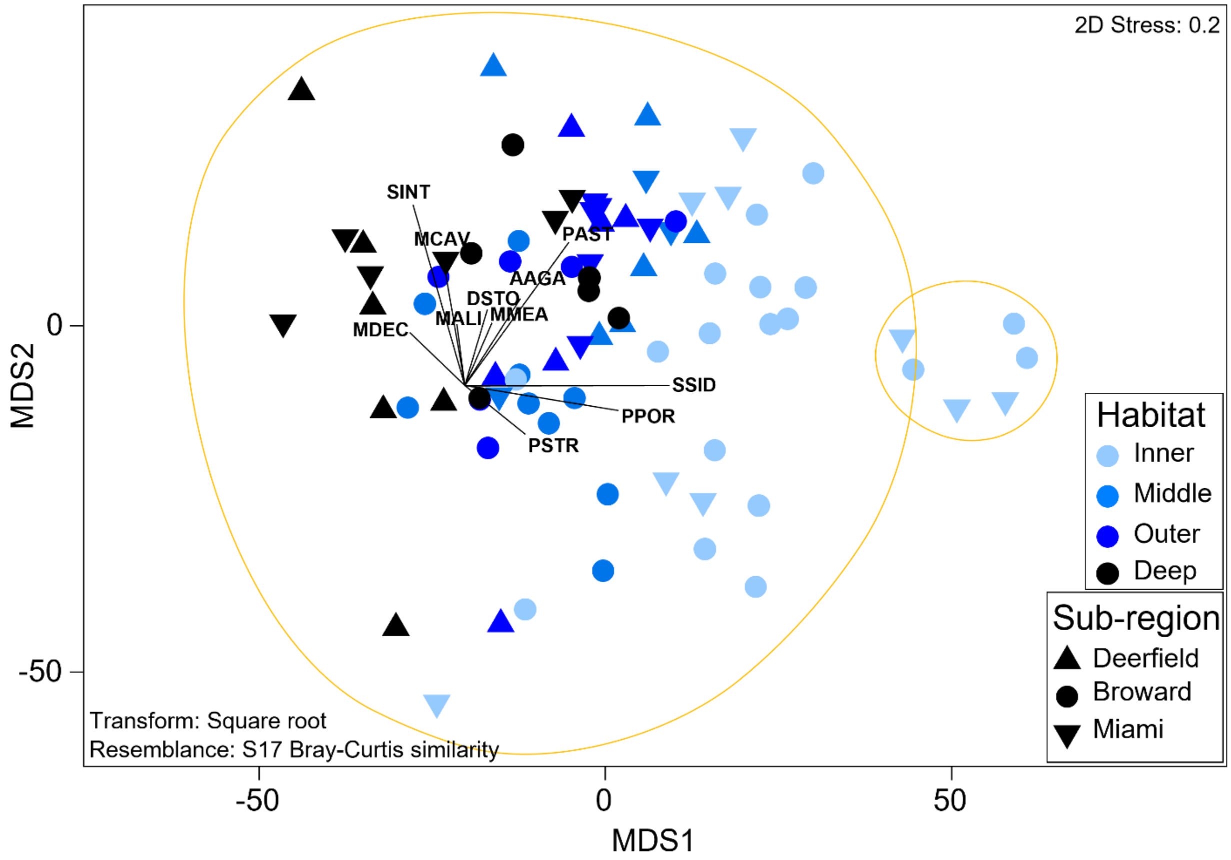

Figure 4. Threshold metric multidimensional scaling plot of recruit community composition. Each sample represents the community composition at one site during one survey year. Orange circles symbolize significant groups identified by SIMPROF. Vectors represent coral species. Labels comprise the first letter of the species and the first three letters of the genus (Table S1).

Adult stony coral community composition also significantly varied most strongly by habitat (PERMANOVA, p = 0.0001), with a significant interaction between habitat and sub-region (p = 0.02). Community composition significantly varied between every habitat, with a depth-based gradient of species distribution and relative abundance (Figure 5). Inner reef sites were dominated by *S. siderea* and *P. porites*, with higher relative *Solenastrea bournoni* density. A clear depth-based split between shallow and deeper sites from *P. porites* to *Madracis decactis* as the only digitate coral was seen (Figure S4). Diversity (H') and evenness (J') was highest on the deep outer reef and lowest on the middle reef. No species representing corymbose, laminar or solitary morphologies were found at inner reef sites. The single arborescent species, *Acropora cervicornis*, was only found on the inner reef at two of nine sites. Community composition on the inner or outer reefs did not vary significantly by sub-region (p > 0.05). Community composition in the northernmost sub-region (Deerfield), was significantly different to both sub-regions to the south on the middle reef ($p < 0.05$) with lower species richness, evenness and diversity. Community composition in Deerfield was also significantly different to Broward on the deep outer reef ($p < 0.05$), with lower species richness and density, but higher evenness. Sites generally clustered together or clustered with the closest site in the same habitat into significant SIMPROF groups ($p = 0.001$).

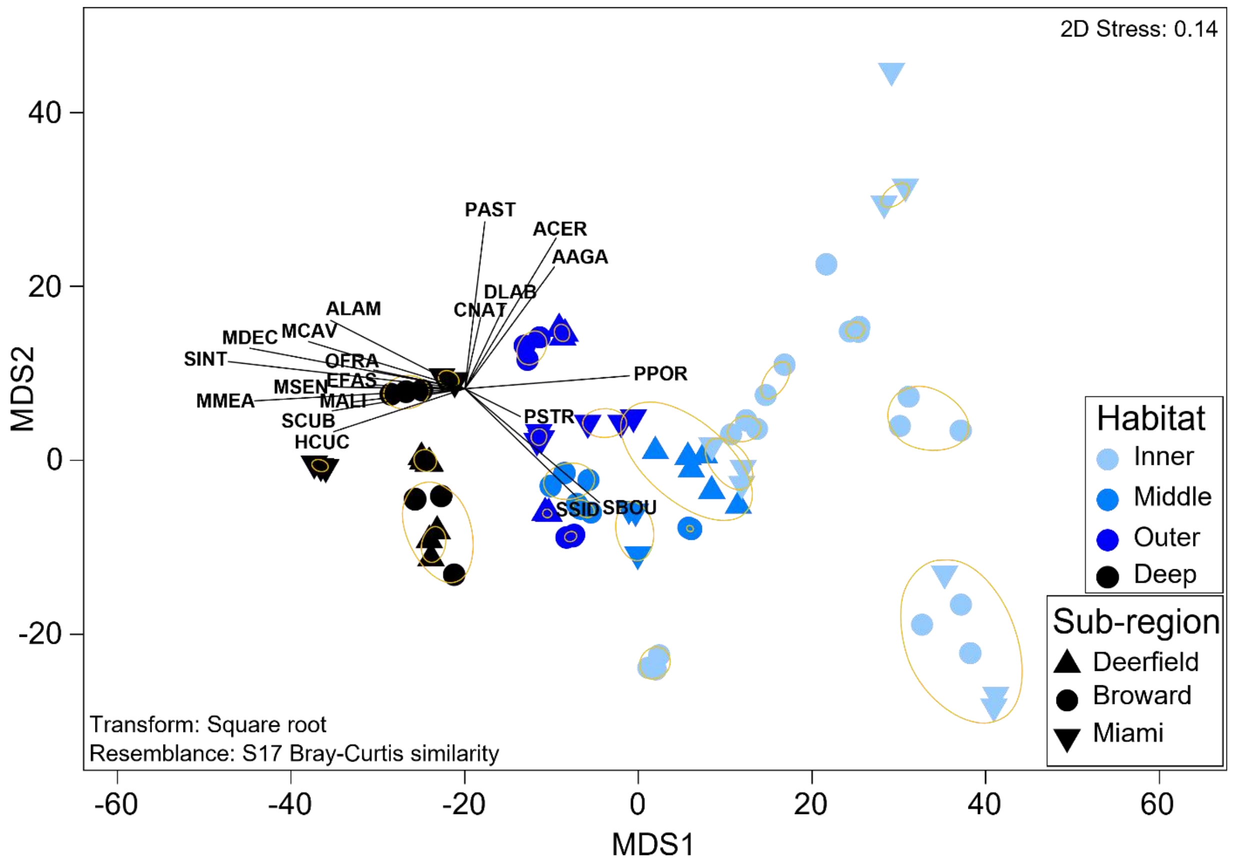

Figure 5. Threshold metric multidimensional scaling plot of adult coral community composition. Each sample represents the community composition at one site during one survey year. Orange circles symbolize significant groups identified by SIMPROF. Vectors represent coral species. Labels comprise the first letter of the species and the first three letters of the genus (Table S1).

Discussion

In this study, I identified a spatial disconnect between stony coral recruitment, adult colony density, size structure and cover that suggests a bottleneck to population growth in southeast Florida (Miller et al. 2000; Edmunds 2021). Recruitment was four times higher inshore, while adult colony density, diversity, mean colony size and cover were all higher offshore. At sites with higher recruitment there was limited evidence of recruit survival or growth into larger size classes.

Conversely, where larger colonies were more common, there was limited recruitment, particularly in species which contributed most strongly to cover. As a result, there is a preponderance of small colonies in the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) that suggests high colony mortality, potentially from environmental pressure (Bauman et al. 2013; Riegl et al. 2017).

Historically, *Montastraea cavernosa* is the dominant hermatypic species in the ECA, with a high density of larger colonies (51+ cm) just north of Port Everglades on the inner reef in the Broward sub-region (Moyer et al. 2003). Despite being heavily impacted by stony coral tissue loss disease (SCTLD) from 2014 to 2017 (Walton et al. 2018), there was still a relatively high abundance of large *M. cavernosa* colonies here, but very few recruits. Subsequently, *M. cavernosa* had a bimodal size structure on the inner reef, with a latitudinal divide between recruitment and adult colonies. *Montastraea cavernosa* recruitment was comparatively high at southern sites and those offshore, where large adults were sporadic. The enhanced ability of *M. cavernosa* to effectively removing sediment (Loya 1976), which may reduce partial mortality (Chapter 3), has often been assumed to enable them to survive and grow faster in inshore conditions (Goodbody-Gringley et al. 2015). While the presence of large colonies inshore corroborates this, a dearth of intermediate size classes suggests they were most heavily impacted by SCTLD (Walton et al. 2018). Further, the lack of recruits suggests larvae are not settling, post settlement mortality is particularly high (Doropoulos et al. 2016; Price et al. 2019; Edmunds 2021) or that thermal stress and disease caused fecundity and recruitment to decline (Hughes et al. 2019). Regardless of the demographic mechanism, recovery of the inner reef population will be limited without sufficient recruitment (Holbrook et al. 2018; Pisapia et al. 2020).

Recruit density was 500% higher on the inner reef than on the deep outer reef. This was predominately due to *S. siderea*, which represented three quarters of the 2177 recruits sampled. Despite higher recruitment in years 1 and 2 (1.8 ±0.9 recruits m^{-2} and 2.3 ±1.2 recruits m^{-2}; ±SE), there was little survival or growth into larger size classes and cover did not change over the study as seen in the Florida Keys (van Woesik et al. 2014). *Siderastrea siderea* is considered resistant to most stressors (Darling et al. 2012) and regularly forms large colonies on inshore reefs in the Florida Keys (Lirman and Fong 2007). However, on the ECA inner reef, size structure was heavily skewed, indicative of a highly disturbed habitat with high mortality and slow growth rate (Miller et al. 2000; Bauman et al. 2013; Kramer et al. 2020; Pisapia et al. 2020; Chapter 2). Nowhere was this more evident that at the two sites with the highest recruit density, HH2 and Pomp4, where *S. siderea* accounted for 99% of recruits. Recruit density was 3.6 ± 0.9 colonies m^{-2} (±SE) and 7.4 ±2.5 colonies m^{-2} respectively, but adult colony density was 1.4 ±0.3 colonies m^{-2} and 2.2 ±0.3 colonies m^{-2} and the largest *S. siderea* colony was just 6 cm diameter. Further, at one site (Pomp4) adult colony abundance declined by 33 colonies from 2020 to 2021 despite 337 recruits in 2020 (only 81 recruits were recorded in 2021). *Siderastrea siderea* size structure was more normally distributed at middle, outer and deep outer reef sites where temperatures tend to be more stable and turbidity is lower (Chapter 3).

Porites astreoides had a comparatively normal size structure and recruit density was ubiquitous over time and space. An encrusting, generalist, brooding species, *P. astreoides* is thermally tolerant and has been increasing in cover in the ECA over the last 15 years (Jones et al. 2020). In Chapter 2, I found high partial mortality in *P. astreoides*, which may prevent growth into larger size classes and explain the high frequency of 5-10 cm colonies. Despite this, *P. astreoides* was the only species where no spatial decoupling between recruitment and adult density was evident suggesting the population is comparatively healthy. As frequently suggested (Toth et al. 2019; Jones et al. 2020), this provides further evidence that *P. astreoides* will continue to be a dominant part of the stony coral community.

Recruit density was generally low, averaging 0.95 ±0.2 recruits m^{-2} (± SE). Similar recruit densities have been recorded using similar survey methods in Biscayne Bay (Miller et al. 2000) and the Florida Keys (Chiappone and Sullivan 1996), but recruit density at most sites in the ECA was substantially lower than recorded elsewhere in the Caribbean. Edmunds et al. (2004) recorded ~8 recruits m^{-2} in the Florida Keys, while Williams et al. (2017) recorded ~8 recruits m^{-2} in Antigua and ~18 recruits m^{-2} in Barbados, although these surveys counted all colonies below 4 cm in diameter. Only *S. siderea* recruit density at one inner reef site (Pomp4) was comparable (7.4 ±2.5 recruits m^{-2}), with most other sites having an order of magnitude less. The measure of recruitment used in this study, identifying colonies under 2 cm diameter using 0.75 m^{2} quadrats, was designed to quantify settlement success, to only capture recruits that were below reproductive size once during the study period (St. Gelais et al. 2016) and provides an ecologically relevant way to assess recruitment success (Miller et al. 2000; Price et al. 2019). This is particularly pertinent on reefs with high macroalgae cover, like the ECA (Jones et al. 2020), where as few as 1% of newly settled corals survive (Doropoulos et al. 2016). My findings provide indication of high mortality in recruits that do survive settlement which presents a substantial barrier to population growth.

Diversity was low at most sites, particularly in recruits, with multiple growth forms absent in each habitat. Eighteen species, representing six growth forms were sampled as recruits, however only *M. cavernosa*, *P. astreoides*, *S. siderea* and *S. intersepta* were found at over 50% of sites, with most other species rare. Many species heavily impacted by SCTLD were sampled as recruits (Figure S2), but low recruit diversity at many sites is still likely largely a result of an Allee effect for most species, particularly following the loss of many colonies of reproductive size from disease (Walton et al. 2018). Twenty-four species were sampled as adults, representing eight growth forms, with *M. cavernosa*, *P. astreoides*, *S. siderea* and *S. intersepta* again most abundant. A slight latitudinal and inshore to offshore gradient in stony coral diversity was found. Shannon diversity and species richness were lower in the northernmost sub-region, Deerfield, which lacked the only arborescent species, *Acropora cervicornis*. Diversity was highest on the outer and deep outer reef habitats and lowest on the inner reef, as seen in other locations with inshore sediment stress (Otaño-Cruz et al. 2019).

I hypothesized depth and distance from shore may have provided some refugia to stony corals on the deep outer reef during thermal stress, disease and Hurricane Irma from 2014 to 2018 (e.g., Sturm et al. 2022). On the deep outer reef, farthest from anthropogenic stress, stony coral cover was highest and adult density and diversity were relatively high, but recruit density was low. There was higher relative abundance of species with massive and laminar morphologies, as is frequent at depth (Kramer et al. 2020), but encrusting, digitate and submassive species, which did not substantially contribute to cover, were more common as recruits. Despite this, size structure was more evenly spread in each species on the deep outer reef, suggesting the habitat is less disturbed and recruits do grow into larger size classes (Kramer et al. 2020).

Following significant declines in cover and density from thermal stress, disease and Hurricane Irma from 2014 to 2018 (Walton et al. 2018; Jones et al. 2020), there was evidence of stony coral recovery during the 2018 to 2021 inter-disturbance period (Chapter 3). Here, there was little evidence that recruits consistently grow into larger size classes, with over 75% of adult colonies sampled under 10 cm diameter. Further, despite an increase in mean colony size, stony coral cover did not change during the study. Instead, my findings suggest the loss of smaller colonies even during the inter-disturbance period when temperature has been relatively stable and no major acute disturbances have been recorded. Temperature is frequently suggested to restrict reef accretion in the ECA (Toth et al. 2021), with local chronic pressures limiting recovery potential (Chapter 3). Here, I suggest that spatial decoupling in recruitment, size structure and survival also presents a substantial barrier to population growth.

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Supplementary Materials

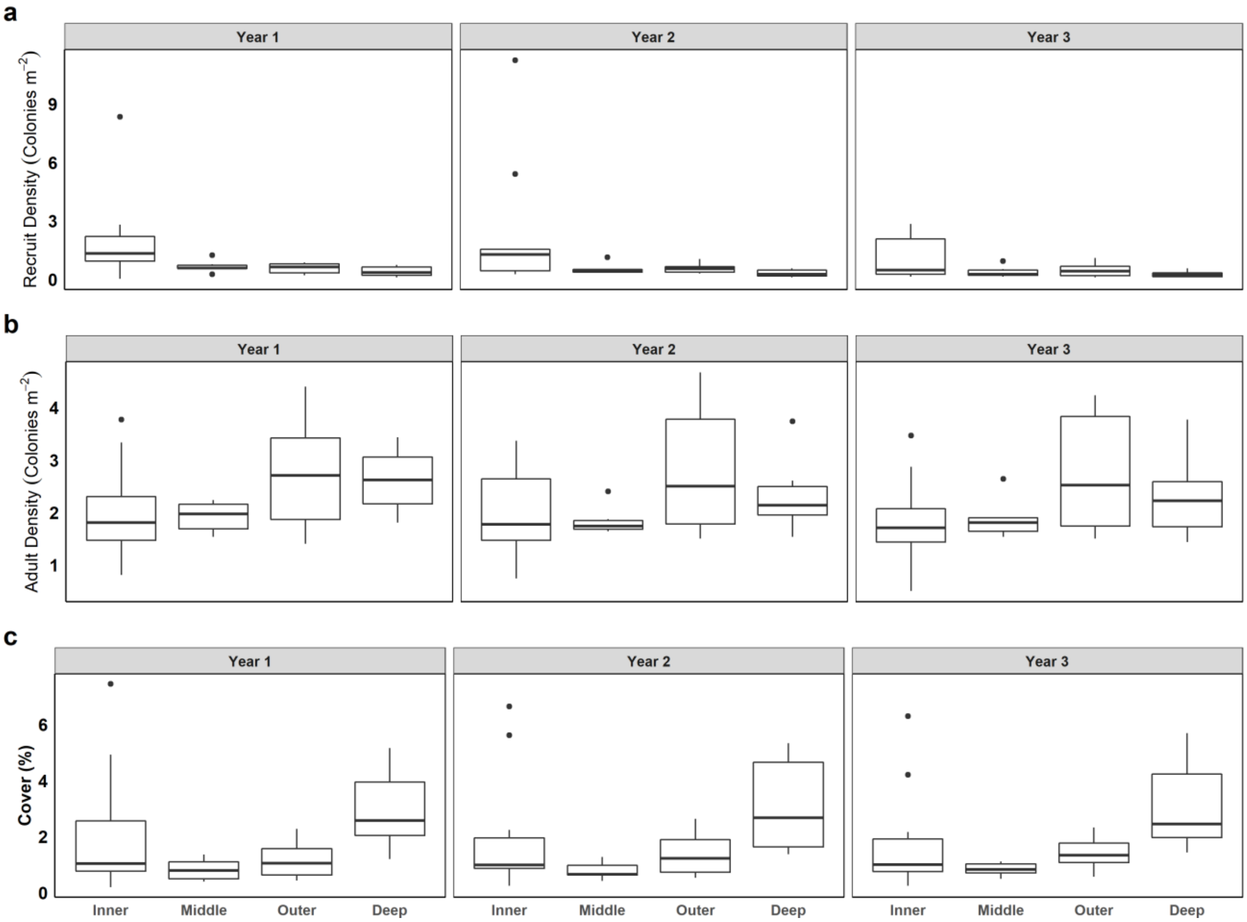

Figure S1. Spatial and temporal variation in a) Recruit density; b) Adult colony density; c) Live tissue cover based on survey year and reef habitat.

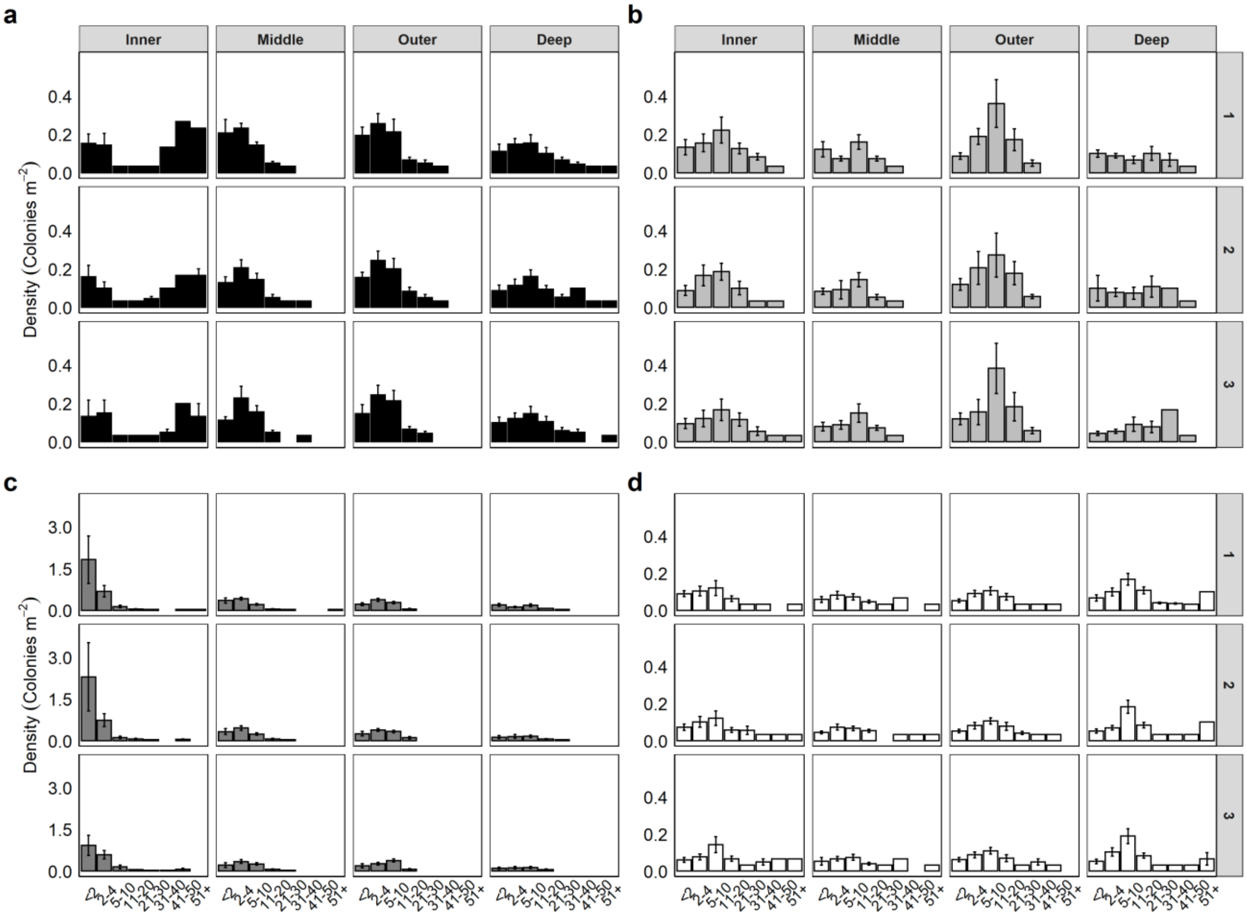

Figure S2. Spatial and temporal variation in size frequency distributions of a) *Montastraea cavernosa*; b) *Porites astreoides*; c) *Siderastrea siderea*; d) All other species. Size class is based upon maximum diameter of each colony and the y axis is the density of each size class.

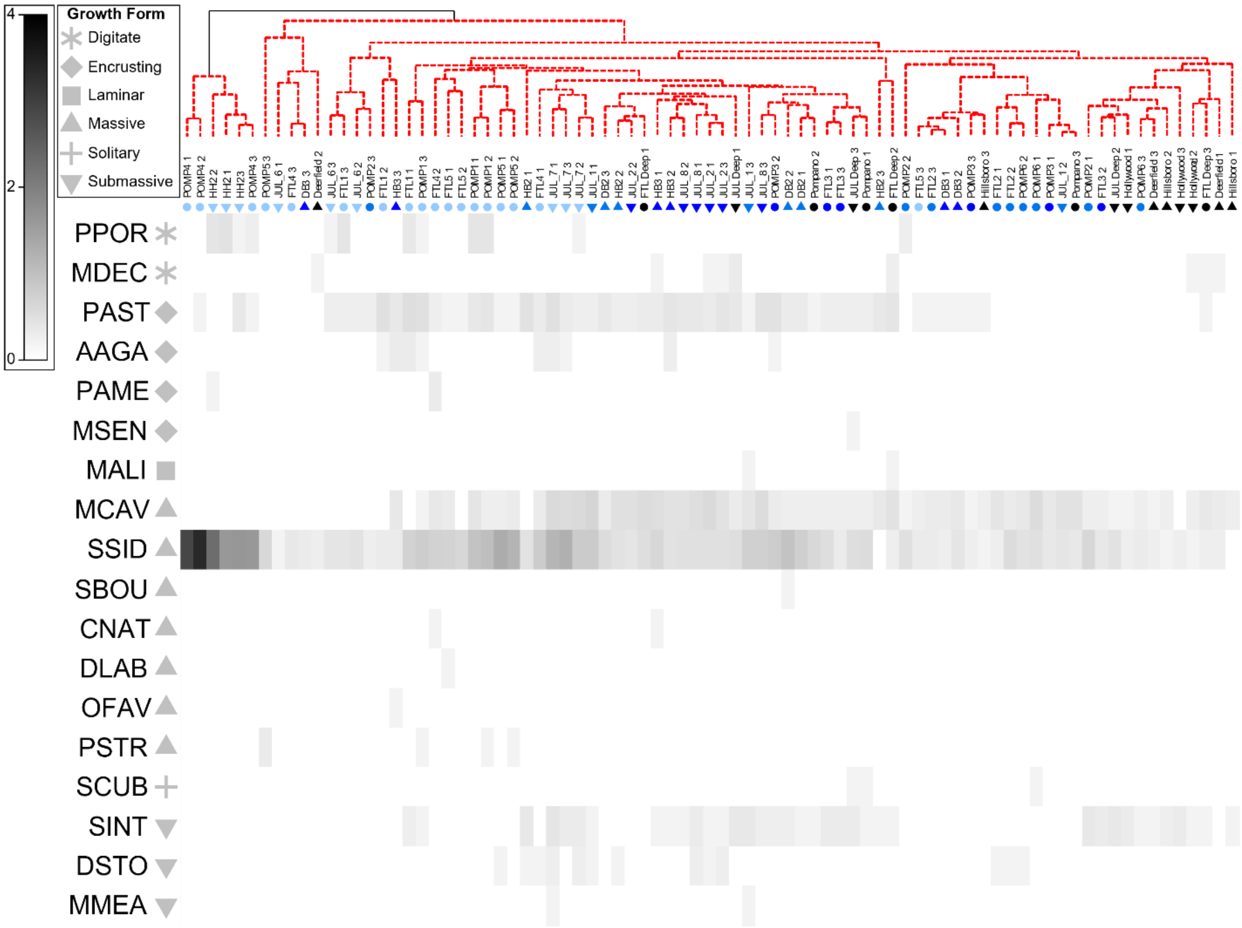

Figure S3. Recruit community composition shade plot. X axis shows results of cluster analysis and significant groups identified by SIMPROF. Y axis shows each species and the predominant growth form.

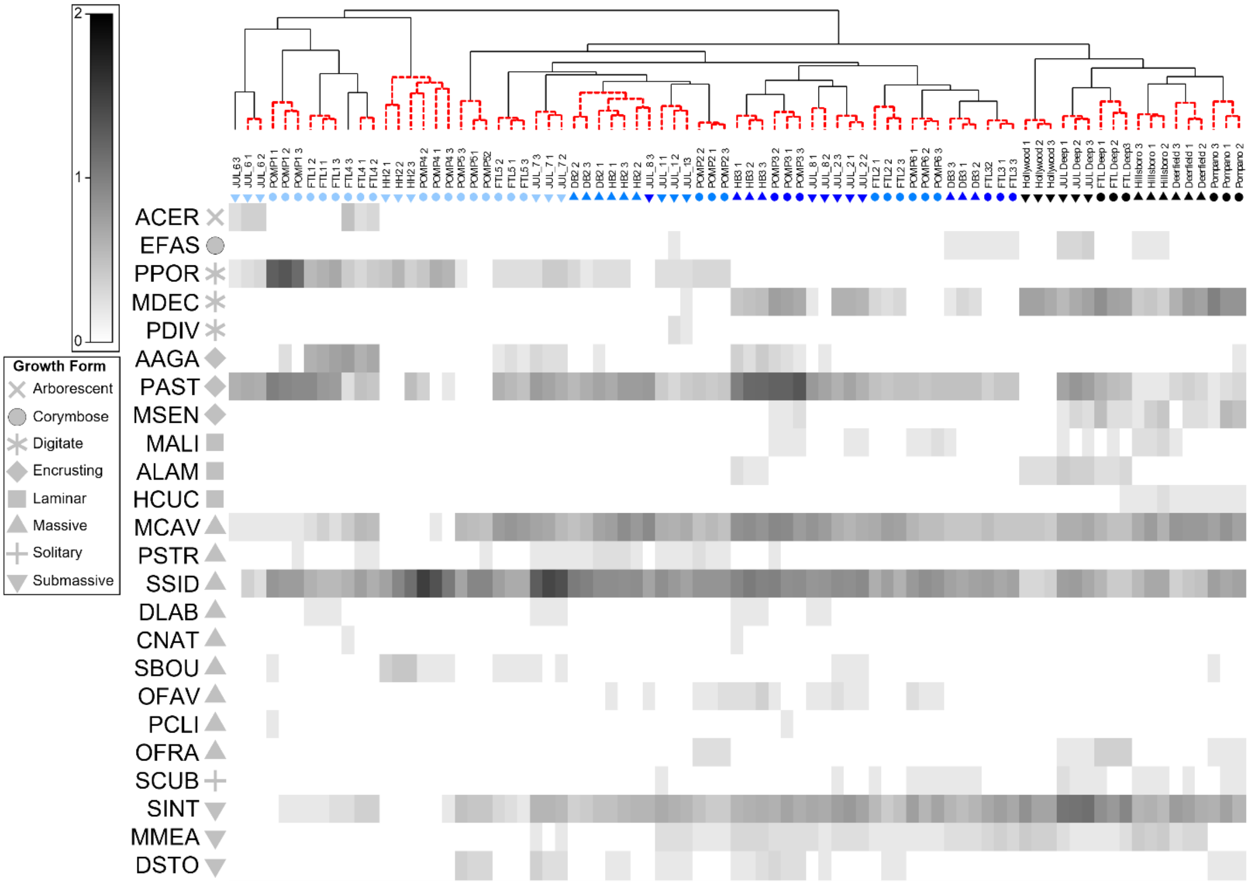

Figure S4. Adult coral community composition shade plot. X axis shows results of cluster analysis and significant groups identified by SIMPROF. Y axis shows each species and the predominant growth form.

Table 7. Stony coral species with four letter code and predominant growth form.

Four letter code	Species	Growth form
AAGA	*Agaricia agaricites*	Encrusting
ACER	*Acropora cervicornis*	Arborescent
ALAM	*Agaricia lamarcki*	Laminar
CNAT	*Colpophyllia natans*	Massive
DLAB	*Diploria labyrinthiformis*	Massive
DSTO	*Dichocoenia stokesii*	Submassive
EFAS	*Eusmilia fastigiata*	Corymbose
HCUC	*Helioseris cucculata*	Laminar
MALI	*Mycetophyllia aliciae*	Laminar
MCAV	*Montastraea cavernosa*	Massive
MDEC	*Madracis decactis*	Digitate
MMEA	*Meandrina meandrites*	Submassive
MSEN	*Madracis senaria*	Encrusting
OFAV	*Orbicella faveolata*	Massive
OFRA	*Orbicella franksi*	Massive
PAME	*Phyllangia americana*	Encrusting
PAST	*Porites astreoides*	Encrusting
PCLI	*Pseudodiploria clivosa*	Massive
PDIV	*Porites divaricata*	Digitate
PPOR	*Porites porites*	Digitate
PSTR	*Pseudodiploria strigosa*	Massive
SBOU	*Solenastrea bournoni*	Massive
SCUB	*Scolymia spp.*	Solitary
SINT	*Stephanocoenia intersepta*	Submassive
SSID	*Siderastrea siderea*	Massive