Frequent disturbances and chronic pressures constrain stony coral recovery on Florida's Coral Reef

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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 populations on reefs with lower exposure to chronic pressures are often presumed to have increased resilience, enabling them to recover quickly following disturbance, but decades of anthropogenic stress and degradation may undermine the systematic recovery and reassembly of benthic communities. This study explored spatiotemporal changes in benthic community structure over a 15 yr 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). We 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 due to increased recovery following disturbance and generally had higher cover than stony corals on Florida's Coral Reef, while sponge cover was very stable over the study period. Acute disturbances, which affected sites on average once every 3 yr, negatively impacted stony coral and/or octocoral cover in every region and habitat, contributing to the region-wide 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 in Florida, even in locations with lower chronic pressure, recovery is severely limited.

Keywords Florida reef tract · Long-term monitoring · Octocoral · Sponges · Macroalgae · Benthic community

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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 absorb a disturbance and recover (i.e., resilience) fundamentally influences the contemporary

state and trends in the composition of benthic communities. Under moderate disturbance regimes, stony coral cover on reefs exposed to limited chronic pressures is expected to recover (Wilkinson 1999; Graham et al. 2015; Pratchett et al. 2020), however, on 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 cover and community composition 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). 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 the resilience of coral communities, 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 & Meier 1992; Precht & 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). In contrast, stony coral abundance following the 1997/98 bleaching event 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 (2004–2018), explicitly testing variability in the resilience of benthic communities at a range of spatial scales. To do this, we 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 (SEC-REMP) 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 cover 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. We hypothesize these regional

differences predispose them to variations in resilience, 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 with stony coral cover increasing toward pre-disturbance levels 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 toward 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
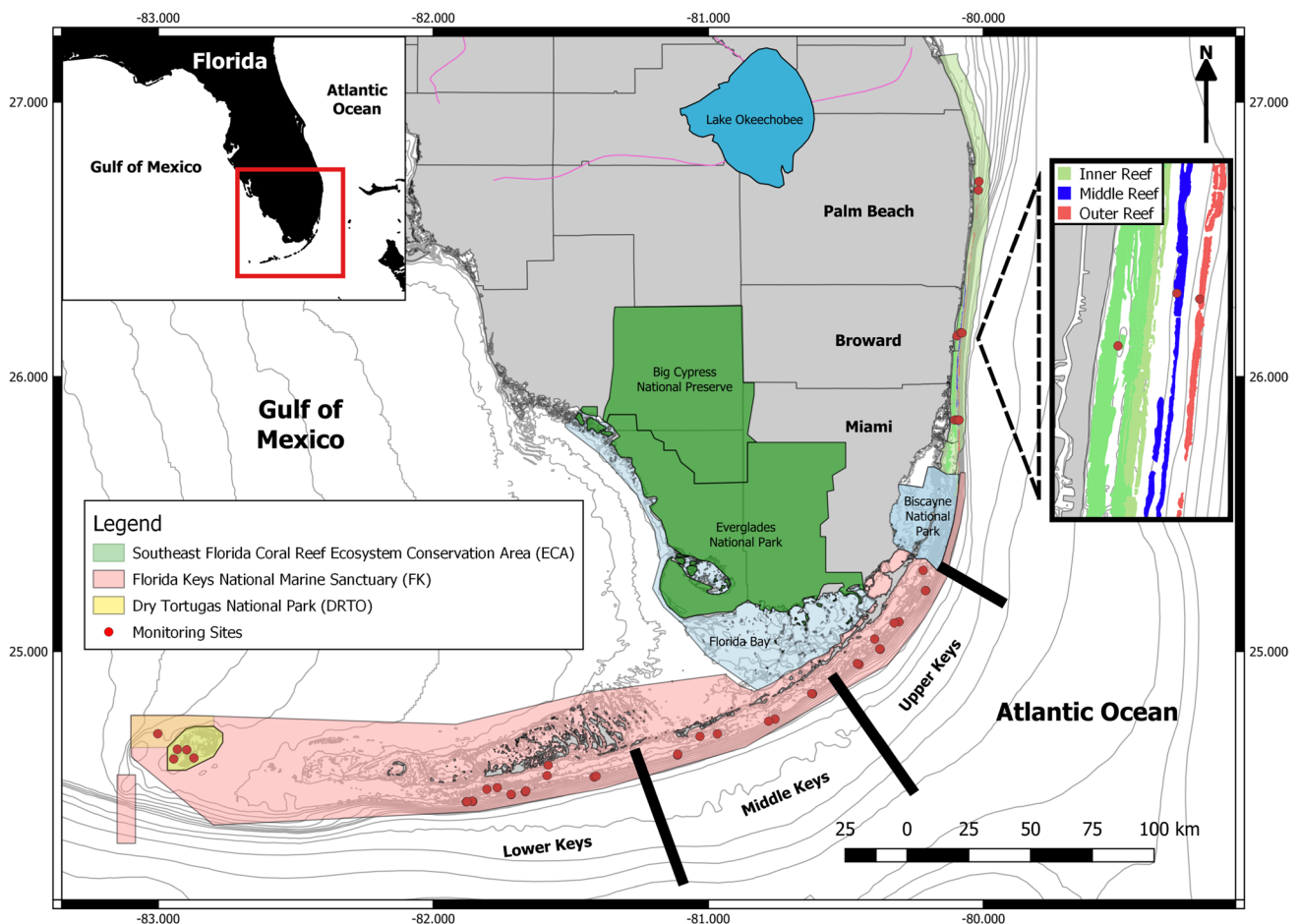

Fig. 1 Florida's Coral Reef with the three regions (Southeast Florida Coral Reef Ecosystem Conservation Area, Florida Keys and Dry Tortugas), sub-regions (Palm Beach, Broward, Miami, Upper Keys, Middle Keys, Lower Keys, Dry Tortugas) and monitoring sites. Note: DRTO sites are within the Dry Tortugas National Park and North

Tortugas Ecological Reserve. Site depths ranged from 2 to 22 m. 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

the three regions. In each region, there are multiple reef habitats found on an inshore to offshore gradient.

Spatial designations

Changes in benthic 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 with 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 were 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, 2018; Lirman et al. 2011). 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 to 2017, Upper Keys from 2016 to 2018 and Middle Keys from 2017 to 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 were compiled from annually repeated surveys conducted during summer months (May–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 was 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 backward 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., Eq. 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.

$$\text{Logit (Stony coral cover)} = \text{Year x Region} \\ + \text{Depth} + (1|\text{Habitat/Site})$$
(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 2004–2018 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

We 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 nonparametric analysis of variance. We 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 was 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

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)	46,915.0		
	Year × Region + (1|Habitat/Site)	46,469.6		
	Year × Habitat + (1|Habitat/Site)	45,789.8		
	Year × Regional Habitat + (1|Habitat/Site)	44,849.8		
	Year × Sub-Region + (1|Habitat/Site)	45,125.7		
	Year × Regional Habitat + Depth + (1|Habitat/Site)	**44,847.2**	**0.317**	**0.244**
Macroalgae	Year + (1|Habitat/Site)	174,437.9		
	Year × Region + (1|Habitat/Site)	146,063.3		
	Year × Habitat + (1|Habitat/Site)	141,892.2		
	Year × Regional Habitat + (1|Habitat/Site)	134,350.8		
	Year × Sub-Region + (1|Habitat/Site)	**131,462.6**	**0.241**	**0.133**
	Year × Sub-Region + Depth + (1|Habitat/Site)	131,464.5		
Octocoral	Year + (1|/Site)	71,834.1		
	Year × Region + (1|/Site)	69,130.2		
	Year × Habitat + (1|/Site)	66,844.8		
	Year × Regional Habitat + (1|/Site)	**64,156.8**	**0.156**	**0.02**
	Year × Sub-Region + (1|/Site)	64,412.0		
	Year × Regional Habitat + Depth + (1|/Site)	64,158.6		
Sponge	Year + (1|/Site)	25,879.0		
	Year × Region + (1| /Site)	25,024.1		
	Year × Habitat + (1|/Site)	24,230.5		
	Year × Regional Habitat + (1|/Site)	24,153.0		
	Year × Sub-Region + (1|/Site)	24,576.1		
	Year × Regional Habitat + Depth + (1|/Site)	**24,136.4**	**0.284**	**0.212**

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

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.

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
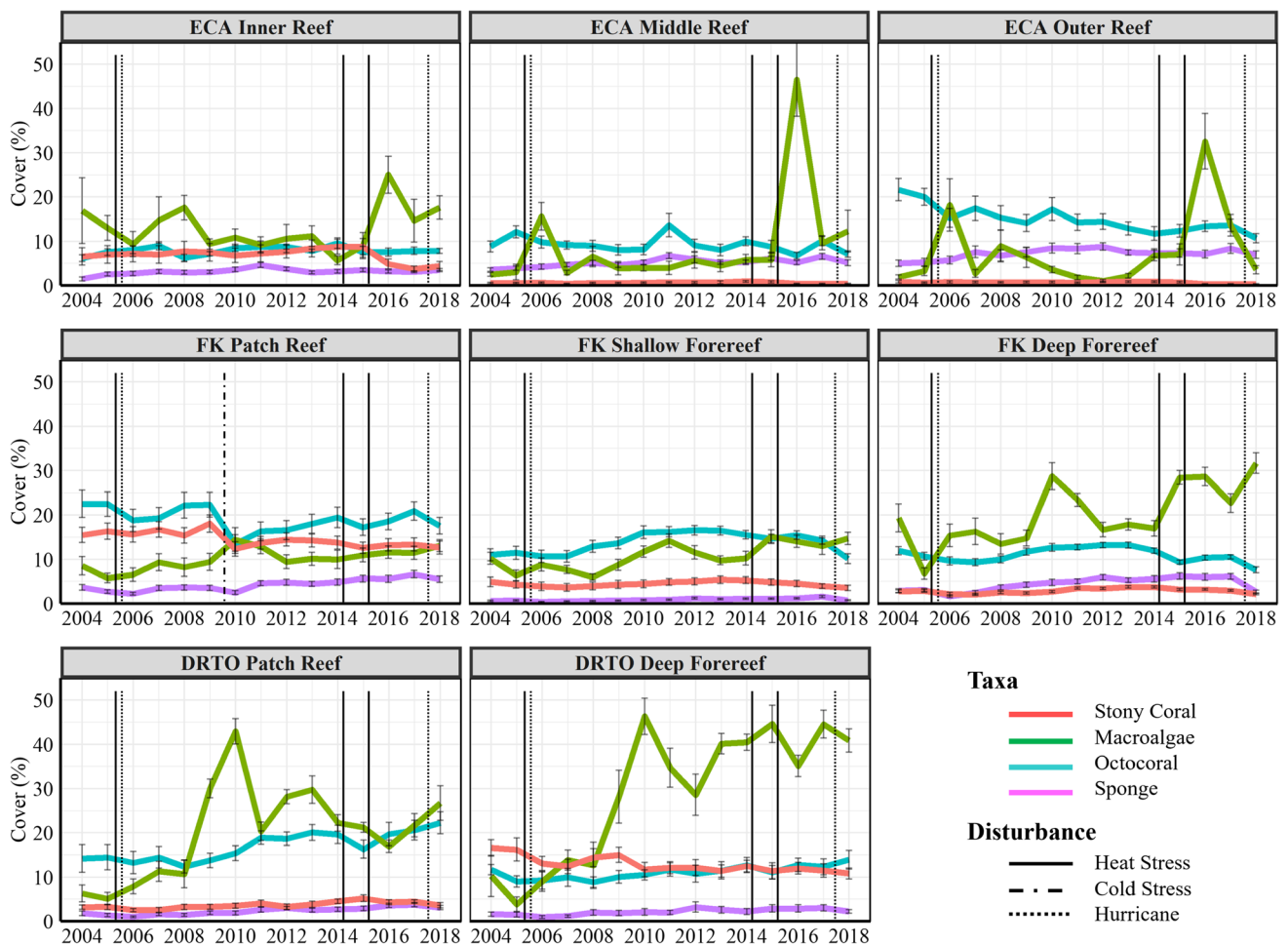
Fig. 2 Mean percent cover (± SE) of stony coral, macroalgae, octocoral and sponge on Florida's Coral Reef. Top panel = ECA habitats, Middle Panel = FK habitats, Bottom Panel = DRTO habitats. Depth increases L – R. FK patch and shallow forereefs are at comparable depths. Interannual significant differences in cover of each taxon can be found in Tables S2-S5. Disturbance event indicated by verti- cal 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 onward, is not noted on the figure to avoid misinterpretation, as it was recorded on a site-by-site basis annually

($p < 0.001$). 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 ($11.8 \pm 2.3\%$ to $23.4 \pm 2.1\%$), Middle Keys ($10.6 \pm 2.2\%$ to $21.6 \pm 3.0\%$) and the DRTO ($7.9 \pm 2.2\%$ to $32.4 \pm 3.0\%$).

Spatiotemporal changes in benthic cover

Interannual variation in cover of stony corals, octocorals, sponges and macroalgae was found throughout the study, especially between periods with acute disturbance: 2005–2006, 2009–2010, 2014–2015, 2015–2016, and 2017–2018 (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

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

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*

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 that, although macroalgae cover varied most strongly by sub-region (Table 1 & Fig S2), cover change by regional habitat is included here for comparison

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 (2006–2007, 2007–2008; p < 0.05) and only declining twice after hurricanes on both shallow and deep forereefs (2005–2006, 2017–2018; 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).

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; chi-squared = 58.274, df = 5, p < 0.0001; chi-squared = 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 (2006–2009; GLMM, p < 0.0001), on FK shallow and deep forereefs (2006–2013; GLMM, p < 0.0001) and on DRTO patch reefs (2006–2013; 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).
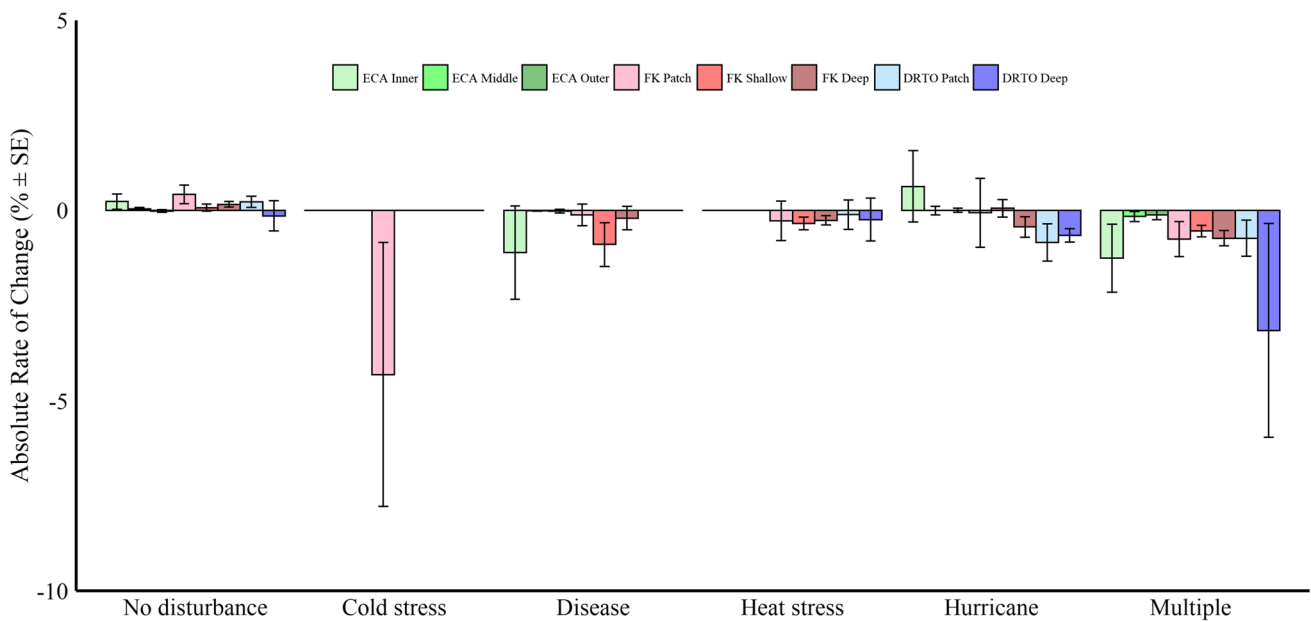
Fig. 3 Stony coral cover absolute rate of change in each regional habitat following periods of no disturbance and major disturbances. The absence of bars indicate disturbance did not occur in the regional habitat over the course of the study. Note that, the ECA did not experience heat stress alone, but 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).

Fig. 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
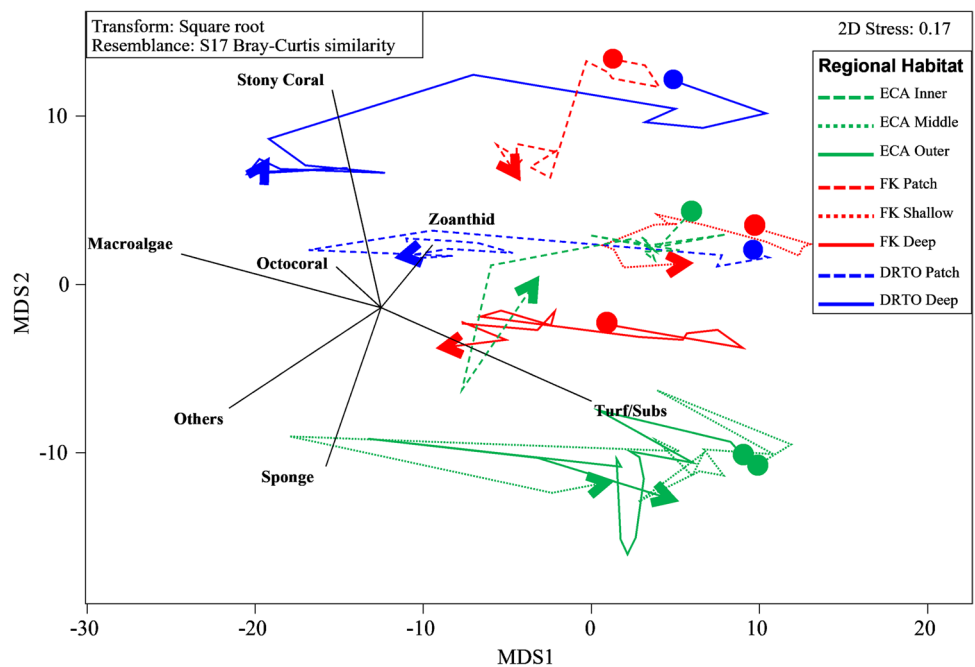
Stony coral cover was higher on FK patch reefs and DRTO deep forereefs relative to all other regional habitats. ECA middle and outer reefs had relatively higher turf algae/substrate and sponge cover. Benthic community structure trends followed similar patterns in many regional habitats despite 2004 baseline 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.

Discussion

From 2004 to 2018, stony corals failed 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 of this and greater octocoral resilience, 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. We determined that high acute disturbance frequency coupled with limited stony coral recovery during inter-disturbance periods continues to reshape the benthic community of FCR and was largely irrespective of regional differences in chronic pressures.

We hypothesized that benthic community dynamics on the FCR would vary regionally, with increased stony coral cover 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 cover 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, 2018; Lirman et al. 2011; 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 coral and octocoral colonies (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 were 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 our study. Instead, we suspect disturbance frequency is too high across the FCR and coupled with local chronic pressures, suppresses recovery rate (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). We found that octocoral cover was frequently declined following disturbance, but demonstrated resilience and generally increased faster than stony coral cover during inter-disturbance periods. 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 suggest 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 that 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 onward. We expected 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, to be most resilient but macroalgae cover is now four times higher than stony coral cover. Our data suggest that increasing macroalgae cover, which averaged $13.3 \pm 0.2\%$ ($\pm$ SE) across FCR, combined with high disturbance frequency, contributes to the continued degradation of the FCR under current conditions.

We found low stony coral resilience 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. We suggest that 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 our evidence suggests that FK patch reefs are still comparatively resilient. Our model suggested stony coral cover increased slightly with depth, but the deepest reefs surveyed, DRTO deep forereefs, which we expected would 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 with 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, and so they are not assessed here (Walker et al. 2012). Our 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 1000 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 contrains recovery potential of stony corals on Florida's coral reefs. Under global climate change, the frequency and intensity of acute disturbances are predicted to increase further (Pachauri et al. 2014; Hughes et al. 2017, 2018b; Lough et al. 2018). Our results suggest that 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 that 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.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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