THE RESILIENCE OF CORAL REEF COMMUNITIES TO CLIMATE-DRIVEN DISTURBANCES

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ABSTRACT

Laura Mudge: The resilience of coral reef communities to climate-driven disturbances
(Under the direction of John F. Bruno)

Climate change is expected to increase the intensity and frequency of natural disturbances which are important drivers of coral reef community structure and functioning. Past work has often quantified the effect of singular, isolated events on living coral cover (mainly on pristine, high cover reefs), yet we know little about how disturbances affect coral community structure on contemporary, degraded reefs. Additionally, we know that disturbances, including hurricanes, coral bleaching, and coral disease, have the potential to interact, but we do not have a general understanding of the outcomes of these interactions on coral communities. Disturbances interact by altering the likelihood, extent, or severity of a subsequent event, or by altering the recovery time after the next event. These interactions have the potential to create novel or compound effects, which could affect coral community resilience.

My dissertation quantifies how disturbances drive changes in scleractinian coral communities through a framework that evaluates the impacts of disturbances as multiple, interacting events. First, I investigated the ecological conditions related to recent recovery of elkhorn coral (*Acropora palmata)* and found that regrowth correlated strongly with abundant herbivore populations, particularly *Diadema antillarum*. Second, I quantified the resilience of contemporary Caribbean coral reefs to hurricane impacts by compiling a regional database of coral surveys from ~2000 unique reef locations between 1970-2017. I found that coral reef communities are becoming more resistant to storm damage (i.e. less immediate coral loss), but are not recovering to pre-disturbance states. The number of historical storms a particular reef experienced is a significant predictor of decreased recovery and increased resistance, suggesting that multiple disturbance events can influence resilience capacity. Additionally, if recovery time becomes limited with more frequent disturbances, understanding reef resistance may give us greater insight into which reefs can persist under predicted changes to disturbance regimes. Third, I tested hypotheses of disturbance interactions between hurricanes, coral bleaching, and coral disease events and found mixed evidence of these interactions across broader temporal and spatial scales. Lastly, I consider the context in which we communicate and quantify changes to coral condition by developing site-appropriate baselines to use in coral reef reporting indices.

To Keith and Wilder

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Introduction

Coral decline over the last few decades has greatly changed the structure and functioning of coral reef ecosystems. In the Caribbean, an important component of this decline was the loss of habitat-forming acroporid corals, particularly elkhorn coral (*Acropora palmata*). Elkhorn coral dominated shallow reef habitats until the 1980s when an outbreak of white-band disease decimated populations region-wide (Aronson and Precht, 2001b). The recovery of elkhorn coral is a conservation priority because its unique branching structure provides habitat for countless other reef organisms, its critical role in reef accretion due to fast growth, and its role in buffering coastlines from wave action (Aronson and Precht, 2001b; Bellwood et al., 2004; National Marine Fisheries Service, 2015). A second critical component of reef change in the Caribbean has been the decline of herbivore populations. Regionally, parrotfishes have been removed from reefs via overfishing (Hughes, 1994) and the long-spined sea urchin, *Diadema antillarum*, was nearly extirpated regionally by a pathogen outbreak in the 1980s (Lessios et al., 1984). The reduction of herbivory has led to an increased cover and biomass of macroalgae (Hughes, 1994; Aronson and Precht, 2000). This in turn, when extreme, can reduce coral settlement and recruitment and slow population recovery (Knowlton, 1992; Hughes, 1994; Edmunds and Carpenter, 2001; Mumby, 2009).

Despite the region-wide declines in major reef-building corals, there are some instances of patchy and isolated coral recovery documented in the Caribbean (Macintyre and Toscano, 2007; Zubillaga et al., 2008; Larson et al., 2014; Muller et al., 2014). Recently, a “re-sheeting” phenomenon, in which elkhorn tissue grows over relict coral skeletons (Bonito and Grober-Dunsmore, 2006), was observed along the reefs in the Mexican Yucatán peninsula (Bruno, 2014; Rodríguez-Martínez et al., 2014). Re-sheeting can be identified in the field (Figure 1.1) whereby thin, healthy tissue takes the shape of the substrate beneath it (in this case, usually the smoothed or flattened edges of relict skeletons) and the edge is not overgrown by another spatial competitor. Little is known about the ecological factors contributing to this re-sheeting phenomenon, and more generally, to the establishment of individual colonies and the regrowth of new populations (Graham et al., 2011). Coral recovery, in general, is complex and any number of ecological or environmental mechanisms can contribute to the recovery of coral species, including recruitment and post-settlement survival (Ritson-Williams et al., 2009), capacity to cope with additional stressors (Mora et al., 2016), interactions with predators and competitors (Grober-Dunsmore et al., 2006), or variation in geographic area and management status (Graham et al., 2011). However, we do know that grazing of benthic algae by herbivorous fishes and urchins is one mechanism of coral recovery which generally facilitates the survival and growth of juvenile or remnant corals (Edmunds and Carpenter, 2001; Hughes et al., 2007). This top-down control by herbivores suppresses the growth of macroalgae, enabling corals to settle and grow by reducing competition for space (Knowlton, 1992; Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006; Kuempel and Altieri, 2017). Increasing herbivore populations (Kramer et al., 2015; McField et al., 2018), and thus increased grazing activity, may be contributing significantly to the regrowth of elkhorn coral observed in Mexico, where it appears recovery is restricted to locations with numerous herbivores and little seaweed.

Scientists have been calling for management initiatives that will aid in the recovery of herbivore populations as one way to boost coral recovery. In the Caribbean, much of this focus is placed on increasing the populations of herbivorous parrotfish species (Jackson et al., 2014; Adam et al., 2015; Cramer et al., 2017). Understanding the impacts of multiple grazer populations is important for management, and an ongoing debate of the relative importance of parrotfish and urchin populations in controlling macroalgal growth, specifically, has not been resolved (Adam et al., 2015; Russ et al., 2015; Bruno et al., 2019). *Diadema* populations remain low throughout the Caribbean, but locally high populations may contribute more grazing pressure to the top-down control of macroalgae. However, we may not have an accurate understanding of the contribution of *Diadema* to coral recovery on contemporary coral reefs. *Diadema* can be hard to detect on structurally complex reefs due to their nocturnal feeding behavior, as they are known to seek refuge from predators during the day (Ogden, 1976; Levitan and Genovese, 1989). If urchins are left out of management interventions, we may miss out on a critical component for coral reef recovery.

Akumal, Mexico, is a small coastal Caribbean town, located approximately 105 km south of Cancún, along the Riviera Maya in Quintana Roo. Patterns of coral ecosystem degradation in Akumal mirror past Caribbean region-wide decline of herbivores and corals from overfishing, hurricanes, and disease (Roy, 2004). Additionally, heavy coastal development and remarkable increases in tourism-based activities over the past decade are associated with deteriorating reef conditions in Akumal Bay, particularly in the backreef lagoon that is frequently visited by tourists (Gil et al., 2015; Figueroa-Zavala and Munoz Arroyo, 2018). Conservation efforts resulted in a fish sanctuary being announced in 2015 (Yucatan Times, 2019) and a larger (1,653 hectare) Marine Refuge for Protected Species in 2016 (Official Gazette of the Federation, 2016), yet formal protection and management measures are still being developed. Despite deteriorating conditions from coastal development, ecological monitoring along the Mesoamerican Barrier Reef indicated recent increases to elkhorn coral (Rodríguez-Martínez et al., 2014; McField et al., 2018) and herbivore populations (Kramer et al., 2015; McField et al., 2018). Yet, little is known about the abundance of elkhorn populations in Akumal and what factors may be contributing to the re-sheeting phenomenon observed on these spur-and-groove reefs.

The purpose of this study was to evaluate the status of elkhorn populations in forereef habitats of Akumal, Mexico and determine if historically important herbivore groups, namely *Diadema* urchins or parrotfishes, are associated with higher elkhorn abundance and less macroalgae. Specifically, we tested hypotheses that higher local density or biomass of herbivores corresponds to increased elkhorn presence, higher elkhorn live area index (LAI), and lower macroalgal percent cover. Additionally, we investigated the sampling bias of *Diadema* density by conducting paired day/night transects.

Methods

Research Site

We conducted this study on the coral reefs of Akumal, Mexico (Figure 1.2), where elkhorn re-sheeting was observed in recent years. There are three distinct sets of spur-and-groove reefs in Akumal, moving perpendicular from the shoreline. The shallowest spur and groove set has a depth range generally ≤11m, the middle set is approximately 12-16m deep, and the deepest set is > 16m deep. We sampled in the first two spur and groove sets (referred to as “shallow” and “deep” throughout), as the third deepest set is beyond the expected depth range of elkhorn coral. Survey locations were chosen based on published locations of previous elkhorn coral assessments (Rodríguez-Martínez et al., 2014) and monitoring sites used by a local non-governmental organization, Centro Ecológico Akumal (CEA). Due to rarity of elkhorn coral presence across Akumal, we surveyed some locations known to have elkhorn coral to ensure that we would find spurs with elkhorn colonies, but there was no pre-determined surveying gradient of low-to-high abundance. Table 1.1 documents the total number of transects and which transects contained elkhorn colonies. We conducted 55 transect surveys from May to August 2016 at 12 reef sites, covering approximately 2,200m^2 of benthic habitat over a 10 km stretch of coastline. Transects were 20m long, with all benthic information recorded within 1m on each side and parrotfish observed within 2m on either side.

Live Area Index of elkhorn coral

For each elkhorn colony or patch observed, we measured the colony size (length, width, and height in cm); estimated percent mortality; and documented observations of lesions from disease or predation, bleaching, fish bites, worms, and overgrowth. Colonies and patches were measured if the center or base of a colony was inside the 2m belt. The calculation used for live area index (LAI) is: (W * L * % Live tissue) / 100 in units cm^2 (Larson et al., 2014). Elkhorn colonies and patches were grouped into three size classes (<60cm^2, 60-1,600cm^2, and >1600cm^2) based on reproductive potential (Larson et al., 2014). For patches or thickets of elkhorn coral in which it was not possible to delineate individual colonies, the total width and length of the thicket was measured, and estimated percent coverage of live tissue documented (similar to the estimation of percent mortality).

Herbivore abundance, biomass, density

We recorded parrotfish species and phase (initial or terminal, which is related to the hermaphroditic lifecycle of most species), number of individuals of each species and estimated size (cm). Parrotfish biomass was calculated from published length-weight ratios found on www.fishbase.org (see Table 1.2 for coefficient values used), using the equation: $W = a \times L^b$ (Froese and Pauly, 2018). In the equation, W represents weight (grams), L represents length (cm) and the letters a and b represent standard coefficients based on the species. Parrotfish biomass for all species was pooled together for a biomass value for each transect (g/m^2). Parrotfish species were assigned functional groups based on feeding strategy and the proportion of biomass and total individuals observed was calculated for each group (browser, scraper, and excavator). Browsers typically feed on fleshy macroalgae, grazers on turf algae, and excavators on endolithic algae but take large bites that usually excavate the reef framework (Adam et al., 2015b, 2018). The biomass (g/m^2) and density (individuals per m^2) of browser species was also calculated for each transect.

We counted all *Diadema antillarum* urchins observed within the 2m belt, and density of *Diadema* was calculated for each transect (individuals/m^2). We searched for urchins under crevices and included them in a count even if only the spines were visible. Transects were geolocated using surface GPS waypoints and starting points marked with flagging tape so we could return to the exact same spurs at night to recount *Diadema* urchins, for a total of 16 paired day-night *Diadema* surveys. On the paired transects only, reef topography was visually assessed by divers, whereas “complex” spurs had relatively higher reef relief and more available crevices or overhangs for organisms to seek refuge (Wilson et al., 2007).

Benthic Cover

Go-Pro cameras (Hero 4) in underwater housings were used to record benthic images along each transect, remaining approximately 25 cm above the benthos. A total of 30-35 images were collected per transect and uploaded to CoralNet for analysis (Beijbom et al., 2015). Ten points were randomly assigned to each image and we manually identified the benthic component for each tag. Identification was made to species level when possible and all ID tags were pooled into relevant functional groups (hard coral, soft coral, gorgonian, macroalgae, turf algae, crustose coralline algae (CCA), coralline-turf-bare (CTB), etc.). CTB refers to a combined category of coralline algae, turf algae, and bare substrate, and is used when the identification at the specific point cannot be resolved in the images.

Statistical Analyses

A two-step hurdle modeling approach was used to evaluate the relationship between elkhorn coral and six predictor variables: total parrotfish biomass, biomass of parrotfish browser species, density of parrotfish browser species, *Diadema* density, maximum depth, and site. Due to low sample size (n=16), we could not include night time urchin density as a predictor in the models. This approach was used over other strategies to 1) aid in determining if either herbivore is associated with the presence/absence of elkhorn coral in addition to the amount of live tissue measured; 2) account for the existence of zeros in the response variable, as elkhorn coral is considered a rare species and was not observed on every transect. This is a well-accepted approach in ecological statistics for measuring the abundance of rare species (Welsh et al., 2002; Fletcher et al., 2005; Zuur et al., 2009). Prior to analysis, raw data were analyzed for normality, heteroscedasticity, outliers, and collinearity. Two outlier observations were removed prior to analysis. Total parrotfish density was not used as a predictor variable due to high collinearity with biomass and fish biomass is the more ecologically relevant variable for this study. Only *Diadema* density from day-time surveys was included in the models. Maximum depth, measured in meters, was used as the fixed effect because depth category of the spurs (deep or shallow) is confounding with site: meaning that sites were either deep or shallow, but not both. In all models, total parrotfish biomass, biomass of parrotfish browser species, density of parrotfish browser species, *Diadema* density, and depth were treated as fixed effects and site used as a random effect.

The first step tested the effect of these predictor variables on the presence of elkhorn colonies, using glmer generalized linear mixed-effects models from the lme4 package in R (Bates et al., 2015), with presence/absence of elkhorn colonies as a binomial response. In step two, for transects in which elkhorn colonies were present, we used mixed-effect lmer models from the lme4 package to test for the effect of these predictor variables on elkhorn LAI (a continuous response variable). Macroalgae was observed on every transect, so the step two mixed-effects structure was used to estimate the effect of the predictor variables on percent cover of macroalgae. All predictor variables were centered and scaled prior to modeling. Values are centered by subtracting variable means and scaled by standard deviations, using the center and scale functions, respectively, from base R. This results in standardized coefficients that can be compared directly. Chi-squared tests were used to evaluate if predictors could be dropped from the full model. Akaike information criterion (AIC) values were used to evaluate competing models. We used paired t-tests to evaluate the difference in *Diadema* density between day and night surveys. All statistical analyses were completed using R version 3.5.0.

Results

Description of elkhorn and herbivore populations in Akumal

The heterogeneity of the spur and groove reef ecosystem in Akumal, Mexico, was indicated by the high variability in the presence and abundance of elkhorn coral and herbivores across sampling sites (Figure 1.3). Elkhorn coral was most common and had the highest live area index in shallow areas and was not found on the deepest transects (~15m) at sites LR, YP, and

HMBP (Figure 1.3, Table 1.1). We measured 85 elkhorn colonies or patches and found that a majority (n=60) had a LAI greater than 1,600cm^2 (Figure 1.4). Of those in the larger size class, we documented 15 colonies of a typical branching form, 25 observations of continuous re-sheeting over relict elkhorn skeleton, 12 observations of patchy re-sheeting colonies, and 8 thickets which contained a series of branching colonies (see Figure 1.1 for examples of form classification). Average percent cover of elkhorn coral was determined from the point-count image analysis and ranged from 0- 6.5% (Table 1.1). At two sites, ESC and YS, elkhorn coral did not appear under the transect tape where images were taken for point-count analysis, but colonies did originate within the 2m belt, which explains why there is a 0% cover but positive LAI value for these sites. The average percent cover of major benthic categories are: 32.56% for macroalgae, 23.5% for turf algae, 13.02% for CTB, and 11.65% for scleractinian corals (including elkhorn coral).

The abundance and density of herbivores also varies by site and depth (Figure 1.3). *Diadema* density recorded in the day-time ranged from 0-1.2 individuals per m^2, with an average of 0.18 individuals/m^2 across all sites. *Diadema* urchins were more common in shallow sites (max density: 1.2/m^2, mean density: 0.35/m^2) and present but rare at sites deeper than 12m (mean density: 0.017/m^2). *Diadema* were not observed in belt transects in 3 out of our 12 sites (BPS, LR, HMBP).

We observed 7 different species of parrotfishes, with species, average length (cm) and average weight (grams) reported in Table 2. Parrotfish biomass ranged from approximately 2-43 g/m^2. with an average of 12 g/m^2. Parrotfish were observed in all transects but had higher average biomass in deeper sites (15 g/m^2) compared to shallower sites (9 g/m^2) (Figure 1.3). Browser species, which typically feed on fleshy macroalgae, comprised the largest proportion of biomass and individuals observed (42% and 51% respectively), although excavator species made up a comparable 39% of the total biomass (Figure 1.5).

Herbivore populations and the presence of elkhorn coral

Herbivore population metrics of total parrotfish biomass and *Diadema* density have a positive statistical effect on the presence of elkhorn coral and accounted for 73.7% of variance explained in the model (Figure 1.6A-B and Table 3, marginal R^2= 0.737, conditional R^2=0.929). The significance of *Diadema* density (*estimate= 5.7, p= 0.023)* was slightly higher, yet comparable to parrotfish biomass (*estimate= 2.33, p= 0.046*). Model selection revealed that browser density, browser biomass, and maximum depth were not significant predictors and were not included in the final model (Table 1.4).

Herbivore populations and the amount of elkhorn coral tissue (LAI)

Linear mixed-effects models revealed that *Diadema* urchins have a statistically significant positive correlation on the amount of live elkhorn tissue (*estimate=1.66, p= 0.032*) and total parrotfish biomass has a small, nearly statistically significant correlation (*estimate=0.04, p= 0.094*) (Table 1.3, Figure 1.6 C-D). Browser density, browser biomass, and maximum depth were not significant terms and dropped from the final model. However, model comparison indicated that the final model had a lower AIC but was only marginally different from the null model (*p=0.06*, Table 1.4), which only had site as a random effect. Even though *Diadema* density was a significant predictor of elkhorn LAI, fixed effects in the final model did not account for a substantial amount of the variance (Table 1.3, marginal R^2= 0.158).

Herbivore populations and macroalgal cover

Diadema density (*estimate= -5.84; p= 0.001*) and browser species biomass (*estimate= -3.95, p=0.032)* had statistically significant negative correlations with macroalgal cover. Browser species density had a significant positive correlation to macroalgal cover (*estimate= 4.0, p= 0.007)* (Figure 1.7, Table 1.3). These predictors (fixed effects) accounted for 27.9% of the variance explained in the model. Total parrotfish biomass and maximum depth were not significant terms and were dropped from the final model (Table 1.4).

Significant temporal variance in Diadema urchin counts

Analysis of paired day and night transect surveys revealed there is a significantly higher number of *Diadema* urchins observed at night (Figure 5, *df=15, t=-3.36, p=0.004*). This difference is more pronounced in the shallower, higher relief reefs (*df=9, t=-4.6, p=0.001*). *Diadema* were present on deeper, lower relief sites, yet there was no difference between *Diadema* counts during day and night surveys (Figure 1.8). Because of the mixture of variables (depth, complexity) we cannot statistically attribute the differences in *Diadema* count due to any covariates other than time of day.

Discussion

The goal of this study was to evaluate the status of elkhorn populations in Akumal, Mexico and determine if *Diadema* urchin or parrotfish populations are associated with higher elkhorn abundance and lower algal cover. The majority of elkhorn colonies observed were large in size (>1600cm^2) and exhibited the re-sheeting growth form. We found that, overall, the presence of elkhorn coral and amount of live tissue increased with increasing herbivore density or biomass. Most strikingly, we found that both herbivore populations contributed significantly to the presence of elkhorn coral. Complementary linear mixed-effects models indicate that *Diadema* density was a better predictor than parrotfish biomass of total elkhorn tissue live area index, although the fixed effects only contributed to a small portion of the variance. We also found that higher *Diadema* density and parrotfish browser species biomass was correlated with lower macroalgal cover, even at low abundances. We observed higher *Diadema* density during our night surveys especially at shallower, high relief reef sites. While this result is not surprising because it corresponds to the expected nocturnal behavior of urchins (Carpenter 1984), it suggests we may be underestimating population densities, and therefore grazing activity, of *Diadema* urchins when only considering day-time measurements. Our findings support the argument that recovering herbivore populations may be contributing significantly to controlling algal growth and facilitating high elkhorn abundance or re-sheeting on contemporary Caribbean shallow water forereef habitats (Morrison, 1988; Edmunds and Carpenter, 2001; Precht et al., 2015).

Top-down control of macroalgal growth is one ecological factor imperative for coral recovery, as this process provides physical space on the benthos for corals to settle or grow (Knowlton, 1992; Edmunds and Carpenter, 2001). We hypothesized that the "re-sheeting" phenomenon of elkhorn coral observed in Mexico was related to this top-down control of algal growth, since coral tissue is growing over bare surfaces of relic corals, not up into newly formed 3D structures. Of the 85 colonies surveyed, 43 were classified as re-sheeting and 37 of those colonies were in the largest size class (Figure 1.4); indicating that re-sheeting is contributing to a large portion of the total LAI and elkhorn cover on Akumal reefs.

Our study revealed that even at low biomass, parrotfish browser species, which feed specifically on macroalgae, have a significant negative correlation with macroalgal cover. Parrotfish biomass in the Mesoamerican Barrier Reef has been increasing slightly in the past few years, and the populations observed here in Akumal are comparable to country and region-wide parrotfish population sizes (Jackson et al., 2014; McField et al., 2018), indicating that recovering populations may be reaching a threshold in which they can exert effective top down control of algal growth (Williams et al., 2016). Even though total parrotfish biomass was not correlated to lower macroalgal cover, fish grazing activity from non-browser species may have other positive benefits such as contributing to increased coral calcification (Suchley and Alvarez-Filip, 2017) or overall reef accretion (Cramer et al., 2017). Conversely, we found increasing macroalgal cover with increasing browser species density. The high number of small bodied Redtail parrotfish species may be contributing to this trend (Table 1.2).

Our results also revealed increased coral presence and cover with increasing urchin populations and confirmed previous studies demonstrating that higher *Diadema* densities are associated with coral recovery (Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007) and lower macroalgal cover (Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007; Williams et al., 2016; Rodríguez-Barreras et al., 2018) in the Caribbean. This correlation may also be due to positive feedbacks associated with structural complexity and *Diadema* populations (Lee, 2006). The physical structure of the reef, and elkhorn skeletons in particular, may provide enough refuge to support larger *Diadema* populations, which results in increased grazing pressure. A 2013 study in Akumal Bay also demonstrated a positive relationship between habitat structural complexity and *Diadema* density (Lacey et al., 2013).

The spatial extent of grazing pressure can also influence effectiveness of top-down control of macroalgal growth. Previous evidence suggests that herbivory from urchins is more effective for promoting coral growth due to the high grazing intensity and spatially constrained grazing behavior of *Diadema* urchins (Carpenter, 1986; Sandin and McNamara, 2012), particularly in shallow-water reef zones (Morrison, 1988). Additionally, herbivorous fishes have larger foraging ranges (up to 0.5 hectares) so the grazing pressure from fish is more diffuse due to their roaming behavior (Carpenter 1986; Adam et al. 2015; Sandin and McNamara 2012). This is one potential explanation for higher *Diadema* estimates in our models.

Implications for local management

Our results support recommendations to enhance herbivore populations as one mechanism to promote coral recovery and control macroalgal growth on degraded coral reefs (Adam et al., 2015a; Williams et al., 2016). Efforts to protect and potentially enhance fish populations are already underway through designation of a fish sanctuary and marine reserve in Akumal (Official Gazette of the Federation, 2016; Yucatan Times, 2019). Consideration of the full life-history of parrotfish species is also critical to ensure that ecological functions from all parrotfish groups (browsers, scrapers, and excavators) are maintained (Adam et al 2015). A robust parrotfish guild can provide complementary functions to promote reef recovery, including removal of different species of algae (macro vs. turf) and removal of dead coral which can provide space for new coral settlement or growth (Cardoso et al., 2009). We demonstrated that browser species specifically contribute to reduced macroalgae cover, and other studies have found that browser foraging behavior may result in higher rugosity reefs, as bites from browser species typically do not erode reef substrate. Population metrics and behaviors of excavator species, however, should be monitored to prevent excessive substrate erosion or corallivory, which could lead to coral mortality of other reef-building corals (Rotjan and Lewis, 2006; Cardoso et al., 2009; Burkepile, 2012; Bruno et al., 2019).

Strong associations between elkhorn abundance and *Diadema* populations in Akumal suggest that *Diadema* reintroduction may be an appropriate tool for local managers when developing holistic coral recovery or restoration plans (Adam et al., 2015a; Precht and Precht, 2015). Managers and researchers could work together towards finding and cultivating ideal site-specific *Diadema* population sizes: large enough to exhibit top-down control of macroalgal growth and promote coral recovery, but not so dense that urchin grazing harming coral recruitment by consuming coral spat or further eroding the reef substrate (Sammarco, 1980; Korzen et al., 2011; Sandin and McNamara, 2012). *Diadema* urchins are known bioeroders, meaning they can remove the hard carbonate substrate of the reef; therefore, benthic habitats with poor or no coral recruitment can also be flattened by grazing of extremely high-density urchin populations (Bak, 1994). The role of grazing by smaller urchins, namely *Echinometra spp.*, has been noted in other Caribbean locations (Sangil and Guzman, 2016; Kuempel and Altieri, 2017); however, *Echinometra* spp. are not common on the exposed spur-and-groove forereef habitats in Akumal. These urchins are typically found in shallow, intertidal zones or protected leeward reefs (Brown-Saracino et al., 2007; McClanahan and Muthiga, 2007) and a 2013 study in Akumal documented variable populations densities of *E.lucunter* (0-12 individuals per m^2) in a shallow, lagoon portion of Akumal Bay. However, the bay area in Akumal is a distinctly different reef structure than the spur-and-groove forereef. The habitat and spatial heterogeneity of both coral and *Diadema* populations demonstrates the need for location-specific information for evaluating associations between herbivory and coral recovery. To address the issue of inaccurate population estimates of *Diadema* urchins, day-time survey protocols should be supplemented with evening or night surveying, especially on high relief reefs where more urchins may be completely hidden during daylight hours. More robust information on herbivore population dynamics may also benefit in-water conservation projects, such as coral nurseries, as knowledge of local herbivore densities can provide guidance on geographic areas where outplanted coral fragments might have a higher competitive advantage due to grazing of macroalgae (Sandin and McNamara, 2012; Adam et al., 2015; Precht et al., 2015). This study demonstrates the importance for considering *Diadema* population metrics in coral recovery efforts.

Local management interventions may be limited in the scope of problems that can be addressed; however, without mitigation of underlying causes of coral mortality such as ocean warming and coastal development, we should not expect herbivore protection or enhancement alone to increase coral resilience (Edmunds and Elahi 2007; Adam, Burkepile, et al. 2015; Cox et al. 2017; Arias-González et al. 2017; Bruno, Cote, and Toth 2019).

Limitations and other considerations

Bottom-up forces, such as eutrophication from terrestrial runoff, which counter grazing pressure may also contribute to a shift toward algal dominance (Arias-González et al., 2017). This study did not test for bottom-up forcing from nutrients; although previous studies demonstrated a correlation between tourism, a proxy for nutrient influx, and declining reef condition in Akumal Bay (Gil et al., 2015; Renfro and Chadwick, 2017) and documented sources of anthropogenic nutrient input to Akumal waters (Hernández-Terrones et al., 2015).

While this study finds statistical correlations between *Diadema* density and parrotfish biomass with elkhorn live tissue cover, experimental manipulations of herbivore abundance and coral growth are needed to establish a causative effect. Herbivore exclusion studies have been conducted before (Lirman, 2001; Hughes et al., 2007; Sotka and Hay, 2009); however, in the Caribbean these particular studies involve “weedy” coral species that have different growth forms and rates and thus different ecological roles from “competitive” coral species, such as elkhorn coral (Bellwood et al., 2004; Darling et al., 2012). Additionally, we used a visual estimate for reef relief; however, studies quantifying rugosity and *Diadema* abundances would be more informative in quantifying the relationship not only between *Diadema* and reef complexity but also in developing predictions of accurate *Diadema* densities based on reef rugosity.

Lastly, even when elkhorn recovery is documented, tissue damage from predatory snails (e.g. C*oralliophila abbreviata*) and damselfish grazing (from the cultivation of turf algal “gardens”) may stifle the full potential for regrowth (Grober-Dunsmore et al., 2006). In Akumal, high damselfish density and turf algae cover has been observed the past few years (Figueroa-Zavala and Munoz Arroyo, 2018). These sources of tissue damage should be closely monitored.

Conclusion

In summary, our results suggest that *Diadema* urchins and parrotfishes are associated with the presence and higher abundance of elkhorn coral in Akumal, Mexico, likely through the top-down control of macroalgae growth. We found that even at low abundances, these herbivore groups are associated with less macroalgal cover, although experimental grazing studies are needed to quantify the magnitude of this effect. While gaps in our knowledge persist regarding the ecological factors contributing to coral recovery, results here suggest that both herbivore groups contribute to elkhorn abundance. Additionally, we highlight the importance of estimating accurate urchin counts using night-time surveys in order to fully understand the influence of Diadema grazing on macroalgal growth and coral recovery on contemporary Caribbean reefs.

Table 1.1 Elkhorn coral survey and demographic information

Reported for each site is: latitude, longitude, maximum depth in meters, depth category of the site, number of transects completed, number of transects in which elkhorn coral was observed at that site, average live area index (LAI) of elkhorn colonies or patches that were measured, and average percent cover of elkhorn coral calculated from the benthic photo analysis.

Site	Latitude	Longitude	Max depth (m)	Site depth category	# transects completed	# transects with elkhorn	Elkhorn LAI (cm^2): Mean (SD)	Percent Elkhorn Cover: Mean (SD)
161ACROP	20.40559	-87.30202	9.14	shallow	6	6	105,809.45 (160867.48)	5.96 (10.91)
161DEEP	20.40478	-87.30074	12.19	deep	5	5	66,576.97 (74302.57)	4.33 (5.61)
BAK5	20.38302	-87.31755	7.31	shallow	4	3	28,700.06 (42725.79)	6.57 (7.54)
BPS	20.37073	-87.322	10.67	shallow	4	4	11,706.43 (10205.53)	3.57 (4.12)
ESC	20.38927	-87.3102	13.72	deep	4	1	1,766.33 (3532.65)	0
HMBP	20.4012	-87.30149	16.15	deep	3	0	0	0
HMBS	20.40339	-87.30288	9.75	shallow	4	3	15,368.76 (15814.95)	4 (4.69)
LR	20.38829	-87.30881	15.24	deep	4	0	0	0
MX4	20.40732	-87.29943	13.41	deep	6	4	39,895.78 (60556.80)	2.12 (5.2)
MX6	20.38264	-87.31803	8.23	shallow	4	2	38,736.63 (76344.12)	0.75 (1.5)
YP	20.41203	-87.29575	15.54	deep	5	0	0	0
YS	20.41321	-87.29728	10.67	shallow	4	4	64,076.05 (69338.72)	0

Table 1.2 Parrotfish species observed and coefficient values used in biomass calculations

Summary of parrotfish species observed across all transects, species functional group assignment, the values of coefficient a and b used to calculate biomass, and the average length of an individual fish for each species. Functional groups assigned based on analysis from Adam et al. 2018.

Common name	**Scientific name**	**Functional group**	**Value of coefficient a**	**Value of coefficient b**	**Total number fish observed**	**Average length of individual (cm)**	**Average mass of individual (grams)**
Redband	*Sparisoma aurofrenatum*	Browser	0.00468	3.4291	174	14.89	83.42
Stoplight	*Sparisoma viride*	Excavator	0.025	2.921	93	21.16	259.39
Striped	*Scarus iserti*	Scraper	0.0166	3.02	74	15.79	76.73
Princess	*Scarus taeniopterus*	Scraper	0.0135	3	9	17.54	81.42
Redtail	*Sparisoma chrysopterum*	Browser	0.0099	3.1708	2	24	236.92
Yellowtail	*Sparisoma rubripinne*	Browser	0.0156	3.0641	16	21.56	198.22
Queen	*Scarus vetula*	Scraper	0.0138	3.03	3	32.67	565.06

Table 1.3 Results of mixed effects models

Estimated regression parameters, standard error, z-value or t-value, and p-values from the final linear mixed-effects models. All predictor variables were centered and scaled prior to modeling. Terms were dropped from models using chi-square test. Z-values are reported for the binomial presence/absence of elkhorn coral model, while all other models report t-values.

Approach & Fixed effects	**Estimate**	**Standard error**	**z or t value**	**p value**
Presence/Absence of elkhorn coral				
(Intercept)	2.135	1.3	1.63	**0.103**
Diadema density	5.7	2.51	2.27	**0.023 ***
Parrotfish biomass	2.33	1.12	1.99	**0.046 ***
Marginal R^2= 0.737; Conditional R^2 = 0.929				
Amount of elkhorn tissue (LAI)				
(Intercept)	9.90	0.24	41.61	**<0.001 *****
Diadema density	0.44	0.20	2.15	**0.032 ***
Parrotfish biomass	0.37	0.22	1.68	0.094
Marginal R^2= 0.158; Conditional R^2 = 0.158				
Percent cover of macroalgae				
(Intercept)	32.77	2.49	13.14	**<0.001 *****
Diadema density	-5.84	1.70	-3.43	**0.001 ****
Browser biomass	-3.05	1.42	-2.15	**0.032 ***
Browser density	4.00	1.49	2.69	**0.007 ****
Marginal R^2 = 0.279; Conditional R^2= 0.676				

Signif. codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1**

Table 1.4 Summary of model comparisons.

For each linear mixed-effect model, the model terms, degrees of freedom, Akaike information criterion (AIC), Bayesian information criterion (BIC), log likelihood (LogLik), deviance, chi-square, and p-value are reported.

Approach & model terms	df	AIC	BIC	LogLik	Deviance	Chisq	p-value
Presence/Absence of elkhorn coral							
Null model: (1|site)	2	60.1	64.0	-28.0	56.1	-	-
Full model: *Diadema* density + Parrotfish biomass + browser biomass + browser density + depth + (1|site)	7	47.2	60.9	-16.6	33.2	4.58	0.205
Final model: *Diadema* density + Parrotfish biomass + (1|site)	4	45.8	53.7	-18.9	37.8	18.3	**0.0001*****
Amount of elkhorn tissue (LAI)							
Null model: (1 | site)	3	116.4	120.8	-55.2	110.4	-	-
Full model: *Diadema* density + Parrotfish biomass + browser biomass + browser density + depth + (1|site)	8	120.1	131.9	-52.1	104.1	0.98	0.80645
Final model: *Diadema* density + Parrotfish biomass + (1|site)	5	115.1	120.4	-52.6	105.11	5.3	**0.06972 .**
Percent cover of macroalgae							
Null model: (1 | site)	3	402.1	408.0	-198.1	396.1	-	-
Full: *Diadema* density + Parrotfish biomass + browser biomass + browser density + depth + (1 | site)	8	396.3	412.1	-190.2	380.3	0.82	0.663973
Final: *Diadema* density + browser biomass + browser density + (1 | site)	6	393.1	404.2	-190.6	381.1	14.99	**0.001825 ****

Signif. codes: 0 ‘*’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1**

Figure 1.1 Examples of elkhorn coral (*Acropora palmata*) growth forms.

A) on the top-left is a typical branching colony growth form. B) on the right is an example of re-sheeting growth over a relict elkhorn colony. C) on the bottom left is an elkhorn thicket, and in this case contains both growth forms, with re-sheeting regrowth on the left side of the thicket and more typical branching colonies on the right and upper side of the thicket.

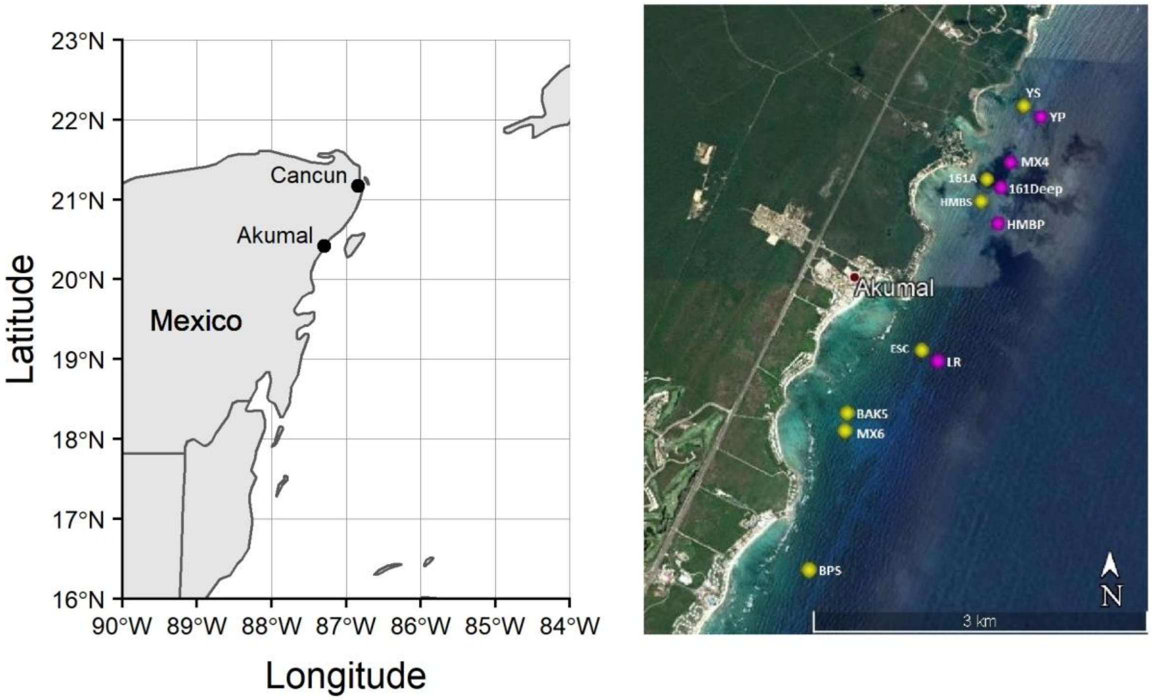

Figure 1.2 Map of the study region

(A) Location of Akumal, Mexico on the Yucatán Peninsula; (B) Survey site locations on Akumal coral reefs, made with Google Earth. Yellow dots indicate sites on the shallower spur-and-groove set (≤11m), and pink dots indicate sites on the deeper set of spur-and-grooves (12-17m).

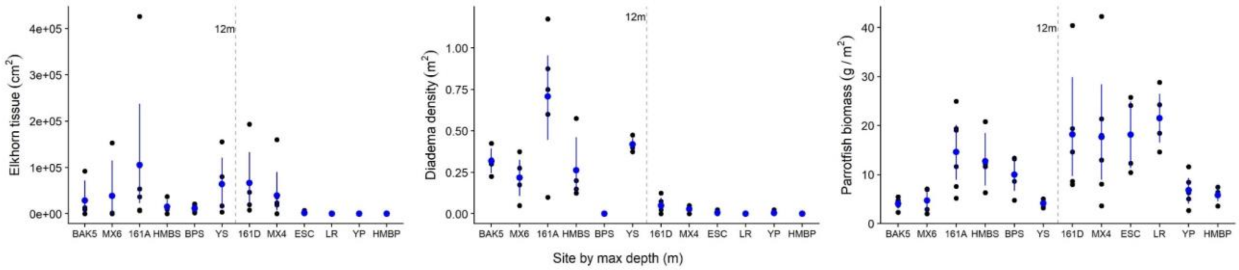

Figure 1.3 Variation in elkhorn and herbivore populations across survey sites in Akumal, Mexico.

Each black dot represents one transect survey (or spur). Blue dots indicate average values at each site with bootstrapped standard errors. On the x-axis, sites are in order of increasing recorded maximum depth (m). The 12m line indicates the separation between the “shallow” and “deep” sets of spur and groove reef areas. (A) Elkhorn tissue LAI (cm^2); (B) *Diadema* urchin density (individuals/m^2); (C) Parrotfish biomass (g/m^2).

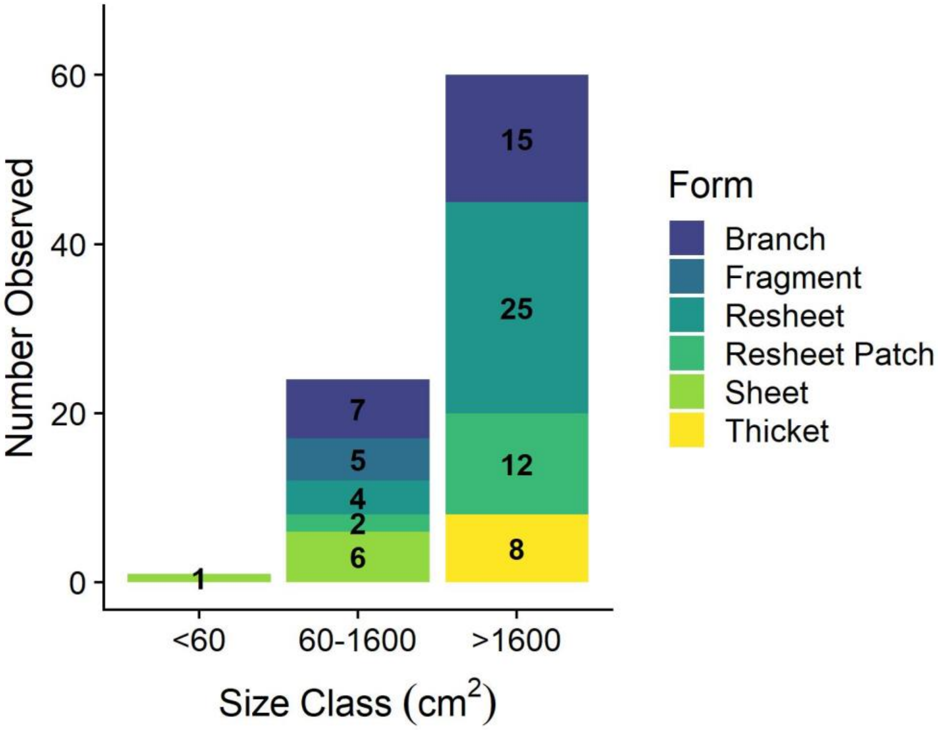

Figure 1.4 Elkhorn colony size class distribution.

Definition of size classes from Larson et al. (2014) and classification of a colony or patch determined from LAI measurement (cm^2).

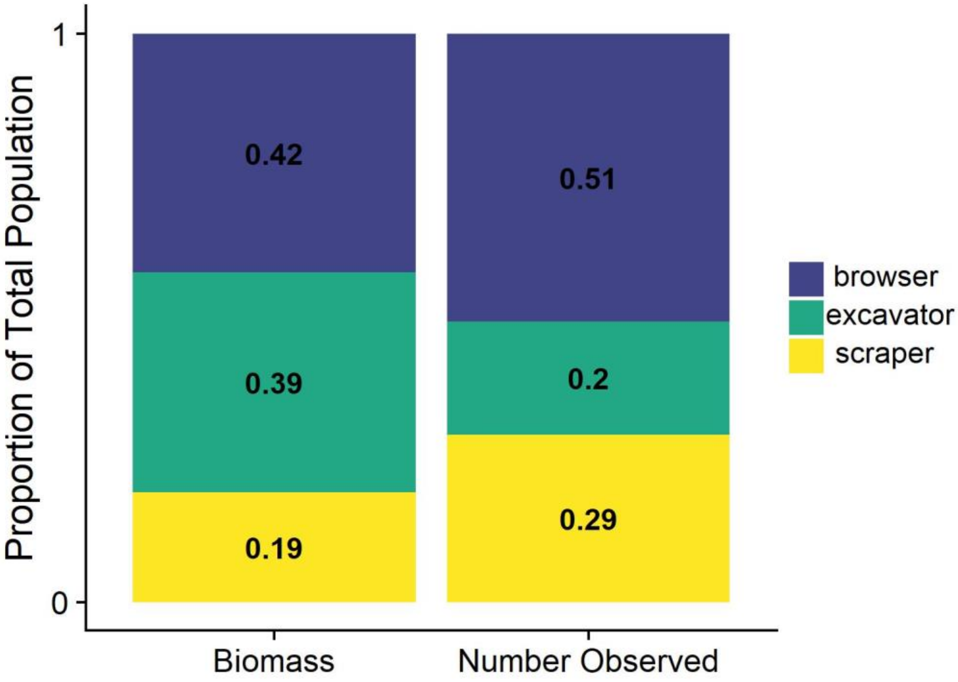

Figure 1.5 Proportional biomass and count of parrotfish functional groups.

Species were classified as browser, scraper, or excavator based on previous analysis from Adam et al 2018.

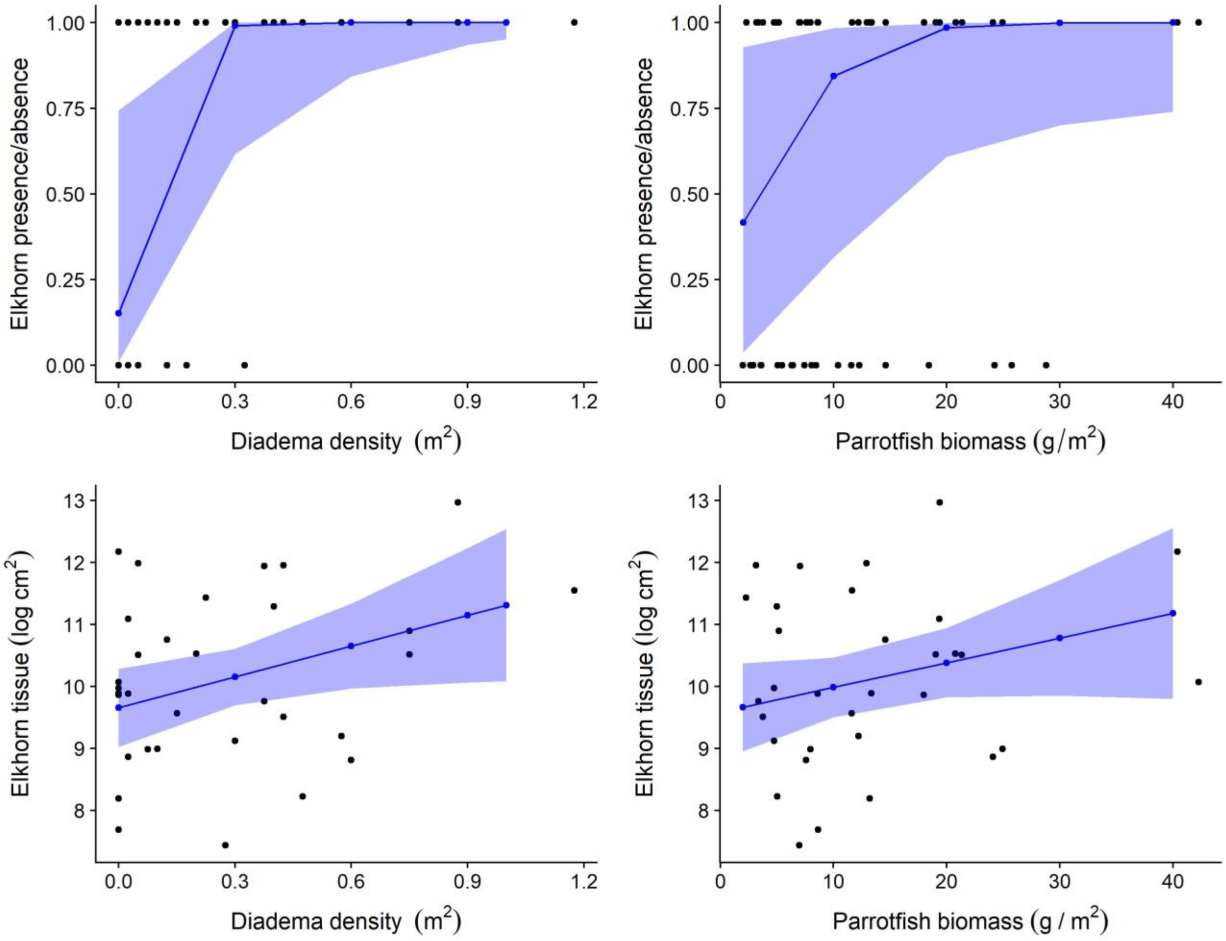

Figure 1.6 Relationship between herbivore groups and elkhorn coral.

For all plots, black dots represent raw data points, blue dots and lines represent unscaled model estimates and 95% confidence intervals from the final model. Top panel A-B) Relationship between elkhorn coral presence and *Diadema* density and parrotfish biomass; Lower panel C-D) Relationship between elkhorn LAI and *Diadema* density and parrotfish biomass.

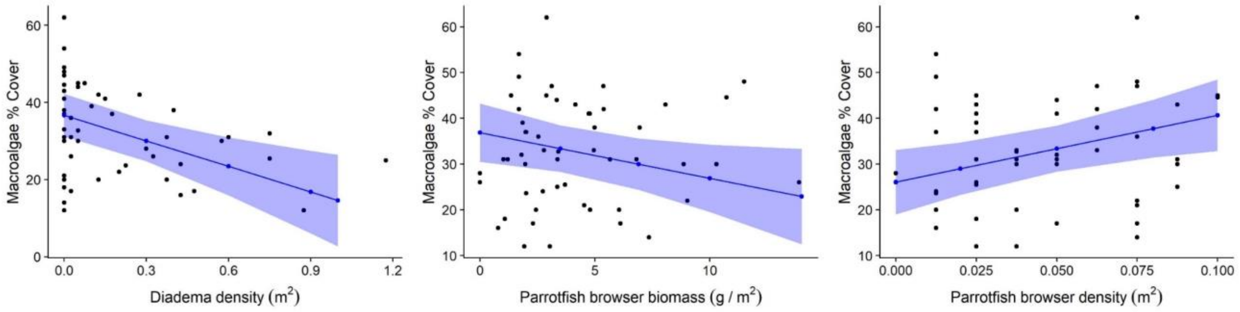

Figure 1.7 Relationship between herbivores and macroalgae cover.

For all plots, black dots represent raw data points, blue dots and lines represent unscaled model estimates and 95% confidence intervals from the final model. A) Negative association between *Diadema* density and macroalgae; B) Negative association between parrotfish browser species biomass and macroalgae; C) Positive association between parrotfish browser density and macroalgae.

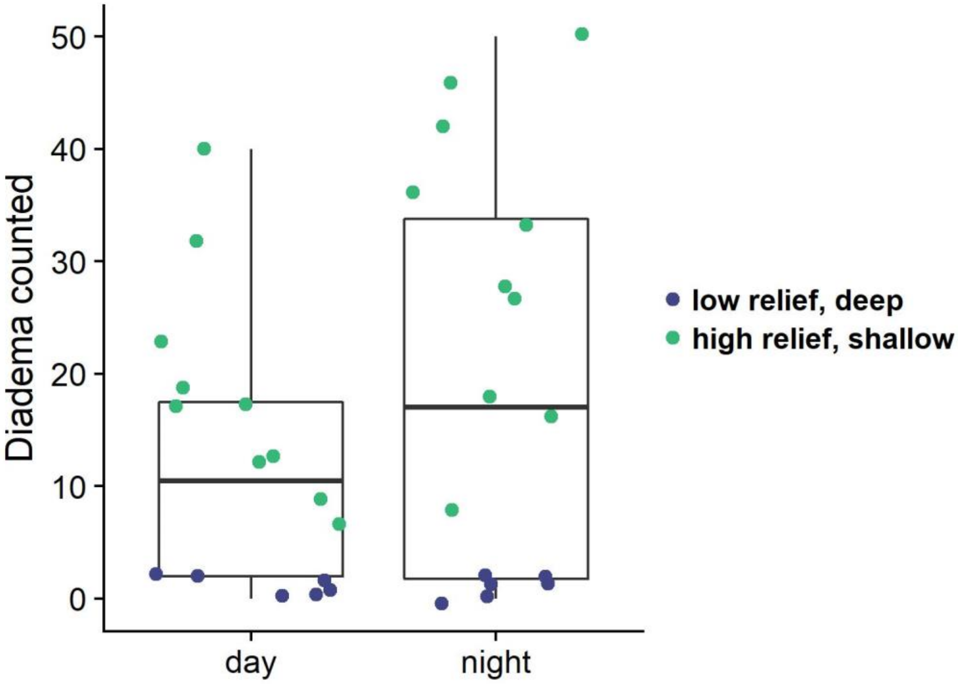

Figure 1.8 *Diadema* counts from paired day/night transects.

Colored dots indicate the depth zone of the survey (shallow: ≤ 11m, deep: 12-17m), which also correspond to structural complexity in this case (shallow= high relief; deep= low relief).

CHAPTER 2 : LONG TERM TRENDS OF TROPICAL STORM IMPACTS ON CARIBBEAN CORAL REEFS

Introduction

Disturbances are ubiquitous in all ecosystems and are important drivers of community structure and function (White and Pickett, 1985; Connell, 1997; Hughes et al., 2003). Individual disturbance events result in wide-ranging impacts from large-scale physical damage caused by natural disasters to localized mortality events. Variations in disturbance intensity, frequency, and scale of impact contribute to habitat heterogeneity and maintenance of diversity in a community (Sousa, 1985; White and Pickett, 1985; Connell, 1997; White and Jentsch, 2001), and at any given time, community composition will be a function of the disturbance history and the subsequent recovery and successional processes.

In coral reef ecosystems, hurricanes are an important disturbance driving ecological community structure and functioning across biological and spatial scales (Harmelin-Vivien, 1994; Blanchon, 1997; Connell, 1997; Aronson and Precht, 2001a; Gardner et al., 2003). Immediate impacts from storms include fragmentation or uprooting of benthic organisms (Edmunds and Witman, 1991), "sand-blasted" reefs (i.e. the removal of coral tissue from sand abrasion or smothering of tissue from suspended sediments that have settled on reefs), or physiological stress to organisms due to decreased salinity and increased turbidity from heavy rainfall (Harmelin-Vivien, 1994; Heron et al., 2008). Longer term consequences of these impacts include replacement of uprooted species by algae and other benthic species, selective removal of branching coral species that are susceptible to strong wave action (Harmelin-Vivien, 1994), and shifts in coral species composition after strong storms (Álvarez-Filip et al., 2009). However, it is important to note that not all hurricane impacts are destructive. Passing storms can alleviate stress from high seasonal sea surface temperatures via evaporative cooling, upwelling, or shading from storm clouds (Heron et al., 2008), which has the potential to mitigate coral bleaching (Manzello et al., 2007).

Most work quantifying changes to coral communities from hurricane impacts evaluates the changes to percent coral cover, a quantitative measurement that provides a crude yet robust estimate for coral reef condition. The seminal meta-analysis conducted by Gardner et al. on Caribbean coral reefs found that on average, a coral reef site that experiences a hurricane will lose ~17% relative coral cover, which is significantly higher than "background decline" at non-impacted sites (2005). The authors did not find evidence of recovery to a pre-disturbed state by 8 years after impact (Gardner et al., 2005), although other estimates suggest it can take decades for a reef to recover to a pre-impact state (Dollar and Tribble, 1993; Harmelin-Vivien, 1994; Graham et al., 2011).

Spatial variability in coral community response to hurricanes exists both between and within storm events. Hurricanes can result in substantial coral mortality, including complete decimation of coral populations in some cases, and changes to the physical reef structure (Dollar and Tribble, 1993; Harmelin-Vivien, 1994; Hughes, 1994; Connell, 1997; Anticamara and Go, 2017). However, there are also documented instances of minimal structural damage or reduction in coral cover from hurricanes (Coles and Brown, 2007; Edmunds, 2019). Even within a single storm event at a single location the coral community response may vary across a reef landscape. For example, a study from the U.S. Virgin Islands found significant differences in hurricane-induced coral mortality and subsequent changes to coral diversity at sites that were only a few hundred meters apart (Bythell et al., 2000). Other studies also demonstrate a wide range of differential impacts (e.g difference in coral cover loss 30-70%) between nearby sites hit by the same storm (Woodley et al., 1981; Rogers et al., 1982; Precht and Aronson, 2005; Coles and Brown, 2007; Anticamara and Go, 2017). This spatial variability in coral response can be a result of the individual storm characteristics (intensity, frequency, duration), site-specific disturbance history, habitat heterogeneity (reef depth, profile/slope, exposure), environmental gradients along reef sites, or differences in the initial conditions (coral cover, species abundance and diversity) at a reef site (Harmelin-Vivien, 1994; Jordán-Dahlgren and Rodríguez-Martínez, 1998; Bythell et al., 2000; Gardner et al., 2005; Coles and Brown, 2007; Anticamara and Go, 2017).

Recent observations of hurricane impacts reveal temporal variation in coral response to storms. A decadal comparison of hurricane impacts in the Caribbean showed that storms in the 1990s contributed less to overall coral decline compared to storms that occurred in the 1980s (Gardner et al., 2005). Additionally, a 30-year time-series study of multiple hurricane impacts demonstrated a stronger response (more coral mortality) to severe storms in the 1980s and 90s compared to severe storms during the 2017 hurricane year (Edmunds, 2019). Changing reef conditions, including the marked loss of branching *Acropora* species in the Caribbean, and changing disturbance dynamics (such as increased storm frequency or increased relative importance of other stressors) may be contributing to these patterns of temporal variation (Gardner et al., 2005; Edmunds, 2019). Factors contributing to spatial and temporal variation in coral response to hurricanes also influence the overall resilience of coral reefs.

Resilience, the capacity for a community to persist after disturbance, is an important component in maintaining community structure and function over large spatial and temporal scales (Holling, 1973; Hodgson et al., 2015). This capacity is based on both community resistance to and recovery from disturbance. Resistance refers to the capacity of a system to absorb impacts caused by disturbance. Recovery refers to the capacity of a system to return to its original, pre-disturbed state (Holling, 1973). Gardner et al. posit four potential post-storm trajectories in coral cover: 1) recovery, in which coral cover initially increases before continuing background decline; 2) stasis, in which coral cover remains stable post-storm before declining again; 3) resumption, in which coral cover immediately resumes its pre-storm decline; and 4) synergy, in which post-storm coral decline continues at a rate greater than pre-storm decline, likely due to a synergistic interaction between the hurricane and another stressor (2005). All of these trajectories assume that coral cover is declining before a storm event occurs.

Coral community resilience is influenced by a variety of endogenous and exogenous variables, including the ecology of individual reef sites, and characteristics of distinct storm episodes and historical disturbance regimes. Initial coral cover and species composition can directly influence the magnitude of resistance (Zhang et al., 2014). Reefs with overall high initial cover or relative abundance of competitive, branching species may experience more substantial initial loss, as these communities are more susceptible to wave action from storms, compared to reefs with low cover or communities dominated by boulder or encrusting species that can better withstand wave action (Steneck et al., 2019). Because coral species have different growth rates and reproduction modes, the composition and abundance of species remaining post-disturbance can influence recovery rates. Post-storm recovery is also strongly influenced by coral recruitment (Harmelin-Vivien, 1994; Coles and Brown, 2007), so close proximity to other reef locations can increase community resilience if larval recruitment can occur. Lastly, the unique physical structure of the reef, such as depth, slope, exposure, etc. can influence the magnitude of impact from wave action, and therefore coral community response to storms (Rogers, 1992; Harmelin-

Vivien, 1994). Generally, more intense storms result in more substantial coral loss and longer recovery times (Gardner et al., 2005). Storms of similar intensity may have varying effects on coral resistance or recovery depending on the time elapsed since a previous storm, as storms occurring back to back likely will not elicit the same response as two storms occurring years apart (Mumby et al., 2011). Additionally, the proximity of a hurricane can result in varying levels of coral loss, depending on the distance and "direction of approach" to a reef (Bythell et al., 2000). Long-term spatial and temporal patterns of hurricane events can also contribute substantially to coral resilience. Average historical return time (measured as years between events) is negatively correlated to coral resistance, meaning that coral sites with more time between events had greater immediate coral loss compared to coral reef sites that did not (Gardner et al., 2005). Temporal clustering of hurricanes, the repeated pattern in which storms occur (regular, random, or clustered intervals), can have an impact on the ecological response of coral reefs to storms. Coral recovery models in the Caribbean and Great Barrier Reef, Australia suggest that reefs remain healthier (higher coral cover, delayed onset of degradation) for longer under a clustered storm regime, likely due to less compounded coral decline, more time for recovery, and therefore more time in which we observe late-successional conditions on the reef (Mumby et al., 2011; Wolff et al., 2016).

The resilience capacity of Caribbean coral reefs is precarious because natural and anthropogenic disturbances have resulted in vast changes to coral communities in the past few decades (Hughes, 1994; Gardner et al., 2003; Bruno et al., 2009; Schutte et al., 2010). High coral mortality with little to no recovery is commonly documented throughout the Caribbean (Connell, 1997; Aronson and Precht, 2001b; Graham et al., 2011). Additionally, shifts between previously dominant and less dominant species, whether due to competitive exclusion during recovery or changing environmental conditions and disturbance regimes, can have consequences for reef functioning (Connell, 1997; White and Jentsch, 2001; Alvarez-Filip et al., 2013). Recent observed changes in Caribbean reef communities are mostly attributed to disturbances influenced by climate change, including hurricanes, bleaching, and disease outbreaks (Aronson and Precht, 2001a; Hughes et al., 2003) and the frequency and intensity of such disturbances are projected to increase with increasing ocean temperatures (Christensen et al., 2013; Heron et al., 2016). In fact, direct observations and modeling studies already show that storm frequency and intensity is increasing in the Atlantic Ocean basin as a result of climate change (Elsner et al., 2008; Emanuel, 2013).

While coral species have evolved under the selective pressures of hurricanes, the changing disturbance dynamics, paired with simultaneous decline in coral condition and the environmental context, has the potential to alter contemporary coral reefs in very unexpected ways (Heron et al., 2008; Hughes et al., 2017). As a result, we do not have broad generalization of how coral communities respond to present-day hurricane regimes, particularly those in a degraded state with low coral cover. The effect of multiple or sequential tropical storms on coral community structure and how these patterns are changing is documented to a lesser degree. Greater emphasis is also being placed on evaluating changes to reef communities in terms of the relative abundances of coral species and life history groups, as these parameters can be more informative regarding ecological structure and function than coral cover alone (Darling et al., 2012; Alvarez-Filip et al., 2013). Shifts in the coral assemblages after hurricanes has been documented in site-specific studies (Woodley et al., 1981; Aronson and Precht, 2001a; Álvarez-Filip et al., 2009; Edmunds, 2019); however, we do not know if these patterns hold across coral reef communities throughout the Caribbean.

The purpose of this study was to assess Caribbean coral resilience to tropical storm disturbances on contemporary, degraded reefs. Specifically, I: 1) quantified coral resistance and recovery to hurricanes over a broad spatial and temporal scale; and 2) quantified how the relative abundances of coral life history groups are affected by hurricanes. In this paper, I define resistance as the immediate change (within 1 year) to percent coral cover after a storm event, and recovery as the post-storm temporal trend in coral cover, accounting for initial pre-storm conditions and "background decline". This study fills specific gaps in our knowledge regarding coral resilience through a region-wide assessment of hurricane impacts by providing a generality of disturbance response while accounting for expected local level variability.

Methods

Coral Survey Data Acquisition

Coral reef benthic survey data was obtained from primary source databases, peer-reviewed literature, and grey literature. Databases included widely-used and publicly available coral reef monitoring programs, such as Reef Check, Reef Life Survey, and the Atlantic and Gulf Rapid Reef Assessment (AGRRA). Primary databases with download date are listed in Table 2.1. This study combined a previous version of a Caribbean coral cover database used for analysis in Selig and Bruno 2010 and Schutte et al. 2010, with more recent coral survey data from longitudinal studies and monitoring datasets. I relied heavily on data from monitoring programs because they provide large amounts of repeated measurements over long time frames and cover broad spatial scales, both of which are essential for making conclusions regarding regional trends and possibly help mitigate the effects of publication bias (Gardner et al., 2005;

Coles and Brown, 2007). Most surveys were not conducted on permanent transects, and GPS coordinates were used to verify the location on the reef for resurveying over time. All monitoring programs collect data on characteristics of the habitat surveyed (e.g. reef zone, such as bank reef or patch reef), which aids in verifying that the same reef area is resurveyed.

Absolute living scleractinian coral cover was measured using quantitative techniques including line transect intercept (in-situ counts along a transect line) and point count (randomized points taken from video transects or photo quadrats). Despite differences in survey methodology and possibly precision and accuracy, the metric of percent cover of the benthos is recognized as a fairly coarse measurement, resulting in negligible differences that are not statistically affected by the method of collection (Carleton and Done, 1995; Rogers and Miller, 2001; Leujak and Ormond, 2007; Wilson et al., 2007; Graham et al., 2011). The data collection methods for obtaining coral species data were similar (AGRRA or modified-AGRRA protocols) and conducted by trained scientists.

Studies were included if they reported a reef site location, survey date (or year), and a measure of absolute percent cover for scleractinian corals. When latitude and longitude coordinates of survey locations were not provided in the reference, I used site location descriptions and maps from the text to identify approximate coordinates using Google Earth, when possible. In addition to manual data entry from primary literature, three tools were used to extract data from pdf resources: the tabulizer package in R (Leeper, 2018) was used to extract raw percent cover data from tables, and ImageJ (from previous Bruno lab database only, see Schutte et al., 2010) and/or Web Digitizer (Rohatgi, 2018) was used to extract raw percent cover data from figures. If more than one survey was conducted at the same reef site on any given day, percent coral cover was averaged to produce one value per day/location combination. Coral reef survey locations were considered unique based on the latitude and longitude coordinates provided from the dataset or study. The resulting database includes survey data from 3,144 unique reef locations throughout the Caribbean with 11,490 measurements of coral cover between 1971 and 2017 (Figure 2.1, Supplement Figure 1). Approximately 23% of the data came from peer-reviewed literature sources and 77% from coral reef monitoring programs.

Coral Cover by Life History Group

Absolute percent cover of distinct coral species was obtained from three sources, mostly focused in Florida and the US Virgin Islands (Table 2.1 Data sources for coral cover Table 2.1 sources with **). Coral species were assigned a life history group (LHG) of either competitive, stress tolerant, or weedy based on classifications made in Darling et al. Figure S3 (2012). These assignments are based on qualities related to species specific growth and reproduction (Supplement Table 2). Coral species not yet assigned to a LHG were labeled as "unclassified". The relative cover for each life history group was calculated by site and year using the calculation:

$$Relative\ \%\ Cover\ of\ LHG = \frac{Absolute\ \%\ Cover\ of\ LHG}{Total\ Coral\ \%\ Cover}\ x\ 100$$

Building a hurricane and coral reef intersection database

Historical storm track data was downloaded directly from the National Oceanic and Atmospheric Administration (NOAA) Atlantic Hurricane Database (HURDAT) using the HURDAT package in R (Trice and Landsea, 2020). These historical records contain storm track location (latitudinal and longitudinal coordinates), wind speed (knots), low pressure (millibar), status (landfall, hurricane classification), date and time, with variables recorded every 6-hours. Historical track information from the earliest year (1851) to present was used to analyze overall storm patterns in the Atlantic basin. Linear models were used to investigate changing trends in the frequency and intensity of tropical storms over time in the Atlantic.

Functional programming in R was used to catalog which hurricanes cross which reef sites in the coral reef survey dataset. Code for these procedures was adapted from Elsner and Jagger (2013). For each reef, I searched for all historical storms occurring within a 100km radius of the reef site coordinates. Storms of any strength were retained within a 35km radius of the reef coordinates, storms of category 3-5 on the Saffir-Simpson scale were further retained between 35-60km, and only category 4 and 5 storms retained between 65-100km. These buffers are based on previously published hurricane path impacts to coral reefs (Done, 1992; Treml et al., 1997; Gardner et al., 2005). Each observation in the database is a unique reef-storm intersection. Therefore, reef locations appear multiple times in the database, if more than one storm has hit the reef since 1851, and individual storms appear multiple times if they struck multiple coral reef locations along their path.

Historically (1851-2017), approximately 32% of named storms in the Atlantic basin have hit a coral reef location (1,604 named storms, 521 hit a reef) (Figure 2.2). Between 1970-2017, the time period of coral survey sampling, there were 547 storms total, 28% of which crossed over at least one coral reef site, for a total of 10,058 unique site-storm intersections. Out of 3,144 unique coral reef survey sites, 2,754 sites experienced at least one tropical storm since the beginning of storm records in 1851 (87.6% of reefs impacted, 12.4% of reefs unimpacted). Sites that were not impacted were located in the SW Caribbean, along the coast of Panama, Colombia, and Costa Rica.

For each unique reef site, I calculated several measurements pertaining to the disturbance regime of tropical storms, including the total number of storms to ever hit that reef, historical return time (average number of years between storm events), storm dispersion patterns, and the average historical maximum intensity of all storms, weighted by their distance to the reef. All of these variables were calculated from coral-storm intersections that occurred between 1851-2017. The dispersion statistic is used to assess the temporal clustering of hurricanes and has demonstrated ecological impacts on coral reef ecosystems (Mumby et al., 2011; Wolff et al., 2016) (Mumby et al 2011, Wolff et al 2016). Using previously described methods, we tabulated a count vector (Y) of storm events per reef for each year between 1851-2017. The dispersion statistics (ψ) is calculated as:

$$\psi(Y) = \frac{variance\ (Y)}{mean\ (Y)} - 1$$

Storm dispersion patterns were characterized as follows (Mumby et al 2011, Wolff et al 2016):

- Stochastic (random): Ψ (Y) = 0 ; (variance = mean)
- Clustered (over-dispersed): Ψ (Y) > 0; (variance > mean)
- Regular (under-dispersed): Ψ (Y) < 0; (variance < mean)

Control Reefs

A subset of the larger coral cover database was identified to serve as a "control" dataset. This included coral cover data from sites that were either 1) never hit by a storm; 2) had a substantial amount of time (>10 years) between storm events. For sites that had been hit by a storm, coral cover data was only retained for a period of 10 years after a previous storm until the next storm hit. This is to ensure that we were not including potential storm recovery trajectories as part of a control condition. For each reef site, we calculated the annual rate of change in coral cover (CR) to use as a comparison against the rate of change in coral cover at storm-impacted sites (Gardner et al., 2005). The CR value was also calculated for each Caribbean subregion in order to account for anticipated spatial variation in coral cover and potential local conditions contributing to coral decline.

Quantifying Resilience

Resistance

Coral resistance to tropical storm damage was measured as the absolute change in coral cover from initial conditions (one year prior to a storm) and one-year post-storm. Paired Wilcoxon tests were used to quantify differences in cover before and after each individual storm event at each reef (i.e. each site-storm combination is one observation for this test). A Kruskal-Wallis test was used to test the hypothesis that coral resistance is greater (meaning less coral loss from storms) in more recent decades.

Recovery

Temporal patterns in coral recovery were quantified in two ways: as (1) the relative change in coral cover at any year pre- or post-storm, relative to coral cover in the year preceding a storm, here referred to as the initial conditions; and (2) as the annual rate of change in absolute coral cover (CR), post-storm (Cote et al., 2005; Gardner et al., 2005; Graham et al., 2011).

(1) Relative recovery = % cover at year relative to storm - % cover before impact

(2) Annual rate of change in coral cover (CR) = $\frac{pca - pcb}{d}$

Quantifying the relative change in coral cover for years both before and after a storm event allows us to compare the impact of storms on pre-disturbance trends. First, I used regression models to evaluate the trend in relative recovery for the time periods pre- and post-storm. Upon visual review of linear regression (using ordinary least squares models), it became apparent that that one linear relationship did not persist throughout the time period of recovery, but rather multiple piecewise relationships might exist. I used the segmented package in R to estimate the appropriate breakpoints for the regressions (Muggeo, 2008). I then compared the slopes in the piecewise regressions for several time periods pre- and post- storm to describe patterns of recovery. Next, I quantified the annual rate of change in coral cover (CR) after a storm event. CR is measured over each individual storm event time series, in which pca is the percent cover at the end of the time series, pcb is the coral cover immediately after a storm (post one-year), and d is the duration of the time series, calculated as the number of years between pcb and pca. If two or more storms occurred in the same year/site, the CR time series was kept for the stronger storm and/or later storm. Resistance and recovery were quantified for both absolute coral percent cover (all species) and the relative abundances of coral life history groups.

Linear mixed models were used to quantify the effects of a variety of disturbance characteristics on coral resistance and recovery. Predictors included a mix of event specific characteristics and disturbance regime characteristics (Table 2.2). All predictors were treated as fixed effects, except for reef location, which was treated as a random effect to account for variation amongst individual reef sites. Prior to modeling, raw data were analyzed for normality, heteroscedasticity, outliers, and collinearity via pairs plots and variance inflation factors (VIF). Predictors with a VIF > 2 were removed from the model. Historical return time and the historical number of storms were collinear and had high VIF and for each model, whichever variable had the higher VIF was removed. In the resistance models for coral life history groups, storm distance was also removed due to high collinearity with wind speed and high VIF. Response variables had a non-normal distribution and included both zeros and negative values, so a cube-root transformed was performed prior to modeling. All continuous fixed effects were scaled prior to modeling. Model residuals were also evaluated to meet assumptions of normality and homoscedasticity. All models were run using the lme4 package (Bates et al., 2015) in R version 3.6.1.

Results

Evidence for increasing storm frequency and intensity in the Atlantic

Between 1851 and 2017, the maximum recorded wind speed for any storm to form in the Atlantic increased (Figure 2.3) along with overall storm frequency (Figure 2.4). Maximum intensity increased by approximately 50 knots (max wind speed in 1851=100knots, maximum wind speed in 2017= 150 knots), although there is a lot of year-to-year variation in wind speeds. The frequency of storms per year in the Atlantic has a significant positive trend, likely driven by the increase in tropical storms and category 4 and 5 hurricanes (Figure 2.4).

Trends in Caribbean coral cover over time

Coral cover has declined throughout the Atlantic and Caribbean since the 1970s (Figure 2.5), and these patterns confirm previous regional reports of coral degradation (Hughes, 1994; Gardner et al., 2003). The uptick in coral cover in the 1990s (Figure 2.5, panel A) is a result of increased sampling at the Flower Garden Banks in the Gulf of Mexico, a slightly deeper (60ft) coral reef site with historically high coral cover.

When all data are pooled, the rate of change in coral cover (CR) was not significantly different at control vs. storm-impacted sites (Table 2.3, Wilcoxon test, W = 50397, p-value = 0.4693). However, there were significant temporal and spatial differences in CR rates between control and impacted sites (Figure 2.6). Each time series CR value was assigned a decade based on the end year of the study. CR is significantly different between control and impacted sites in the 2010s (Wilcoxon test, W = 12712, p-value = 0.002748), with control sites having a positive rate of change (0.53 ± 0.25(se)%) , while impacted sites continue to have a negative rate of change (-0.46 ± 0.19(se)%). CR of impacted vs. unimpacted sites differs significantly in two subregions (Figure 2.6). In Florida, the CR at control sites was slightly positive at 0.09 ± 0.23% (mean ± se), while impacted sites were slightly negative at -0.13 ± 0.16 (mean ± se) (Wilcoxon test, W = 4092, p= 0.01119). In the Western Caribbean, control sites had a significantly greater rate of negative change (-4.60 ± 1.48%) compared to impacted sites (-1.52 ± 0.54%) (Wilcoxon test, W = 750.5, p= 0.025).

The relative abundance of coral life history groups varied between 1992-2017, with a significant decrease in unclassified coral groups (Paired wilcoxon, p= 5.5×10^{-7}) and significant increase in the weedy coral group (Paired wilcoxon, p=1.9×10^{-6}) when comparing the relative cover between the beginning and end points of each time series (Figure 2.7). Stress tolerant corals remained in high abundance since the early 1990s (p=0.88), while competitive corals have maintained low abundance (p=0.5). It should be noted that this dataset does not precede the white-band disease outbreak in the 1980s and 1990s, which decimated populations of competitive coral species in the genus Acropora, and therefore did not capture the resulting stark decline in competitive species during the late 80s and early 90s.

Coral resilience to hurricanes: by coral cover

Resistance

Coral resistance is measured as the immediate change in coral cover from a storm disturbance. We were able to compare coral resistance for 210 reef-storm intersections. There was variation in response to storms: coral cover increased, decreased, or stayed relatively the same depending on the storm episode. There was an overall small but significant decrease in coral cover after a storm, with a loss of -1.32 ± 0.37 % (mean ± sd) between the year prior and year post-storm (Figure 2.8, Wilcoxon paired test, p= 0.00015). Coral resistance has also increased significantly over time, from a median loss of from -5.78% in the 1980s to -0.57% in the 2010s (Figure 2.8-B, Kruskal-Wallis chi-squared= 36.526, df=3, p= 5.8x10-8).

Recovery

We evaluated change in coral cover, relative to percent cover at the time of impact, for up to 10 years prior and 10 years post-storm (Figure 2.9). These trends in pre- and post- storm coral cover are based on 569 unique reef/storm intersections from 55 storms. In the years leading up to a storm event, coral cover is generally declining (slope = -0.3% per year), but declines at a greater rate due to the impact of the storm (comparing one year prior to one-year post, slope = -0.7% per year). After a storm event, we see patterns of both stasis and potential synergy. For approximately 5 years post-storm, on average coral cover does not appear to change significantly (stasis, slope = -0.04% per year). However, after 5 years, coral cover decline resumes, but at a steeper rate than the pre-storm ("background") decline (synergy, slope = -0.75% per year). However, if we "reset" coral cover trajectories between events, the post-storm recovery pattern changes slightly (see Figure 2.9 B-C). Panel B appears to show some evidence for coral recovery; however, that trend is being driven by the positive changes in relative coral cover at 9 years post-storm. Upon further investigation, the values at year 9 are driven by one set of reefs in Jamaica, and therefore should not be considered a regional pattern. In panel C, I only consider the patterns for up to 8 years post-storm (thus removing the bias from Jamaican reefs); and the pattern of stasis followed by resumption is observed.

The annual rate of change (CR) in coral cover post-storm was -0.23 ± 0.13% (mean ± se) (n= 282, min= -10.25%, max= 13.76%). CR rates varied between Caribbean subregions (Figure 2.10), with a general pattern of lower (more negative) CR rates in the Gulf of Mexico and

Western Caribbean, compared to the eastern subregions, including Florida, the Lesser Antilles, and Northern Caribbean.

Predictors of Coral Cover Resilience

Significant predictors of resistance

We found that initial coral cover, storm year, storm distance, maximum wind speed, and historical storm intensity are significant predictors of coral resistance to hurricane impacts (Figure 2.11, Table 2.4, marginal r^2= 0.244, conditional r^2= 0.279). Storm year and distance have a positive relationship with resistance, meaning that storms occurring more recently or further away from a reef site are correlated with increased resistance. Resistance is negatively correlated with higher initial cover and more intense storms (both max wind speed of individual events and historical storm intensity). Storm dispersion patterns (stochastic, regular, clustered), historical return time, and days since the last storm were not significant predictors of resistance.

Significant predictors of recovery

The relative year to year change in coral cover for up to 8 years post-storm was positively correlated to the storm year, maximum wind speed, time passed since a previous storm (days), and initial change (Figure 2.11, Table 2.4). These fixed effects accounted for almost 50% of model variance (marginal r^2 = 0.48, conditional r^2= 0.651).

The annual rate of change (CR) was negatively correlated to initial post-storm cover and clustered dispersion patterns, but positively correlated to historical return time and stochastic dispersion patterns (Figure 2.11, Table 2.4). Fixed effects accounted for 16.4% of the variance, with random effects (site) contributing to an additional 58.7% of the variance (marginal r^2= 0.164, conditional r^2= 0.751). It is not surprising that reef location (random effects) accounted for a large portion of model variance, given the significant differences in CR rates based on subregion (Figure 2.10). Stochastic storm patterns have a positive effect on the annual rate of change (CR), compared to reef sites under a clustered storm pattern (Supplement Figure 3, CR clustered: median = -0.21, IQR = 0.73; stochastic: median = -0.04, IQR = 0.71, Wilcox p = 0.012).

Coral resilience to hurricanes: relative abundance of coral life history groups

Resistance

We compared coral resistance by life history group for 142 reef-storm intersections, from 15 distinct storms that occurred between 1998-2011. The relative abundance of competitive species decreased significantly by -3.12 ± 0.81% (mean ± se) after a storm (Figure 2.12, p = 0.0045). There was no statistically significant change in the relative abundance of weedy, stress tolerant, or unclassified species from one year prior to one-year post storm.

Relative recovery (year to year change)

We were able to evaluate recovery trajectories for 215 reef-storm intersections, representing 19 distinct storms that occurred between 1998-2017. The patterns in year-to-year changes in the relative abundance of life history groups varies both among groups and differs from the pattern seen with overall percent coral cover. Competitive species are declining pre-storm; however, even with a negative impact at the time of the storm, we see evidence for potential recovery (positive slope) between 1-5 years post-impact. After 5 years, the relative abundance of competitive species begins to decline again, at a rate almost 10x higher than its pre-storm decline (Figure 2.13A). Stress tolerant species appear to follow a cyclic pattern of change pre- and post- impact. Relative abundance declines between 3-10 years before a storm, but is generally already increasing at the time of impact. After a storm impact, relative abundance declines at a rate steeper than pre-storm decline, before eventually increasing again at

5 years post-storm (Figure 2.13B). The trends in relative abundance of weedy and unclassified species are not negatively affected by storm impacts (Figure 2.13C-D). The slope of decline in unclassified species remains the same pre- and post- storm. However, it appears that weedy species may benefit from storm impacts in the years following a storm, as the post-storm yearly trend (slope =0.95) has a steeper, more positive slope compared to the pre-storm increasing trend (0.63).

Rate of Change in Cover (CR) Post-Storm

The annual rate of change in coral cover after storm events differs significantly between life history groups (Figure 2.14, n=176, Wilcoxon p = 4.8x10-10). Competitive group CR was -0.4 ± 0.34% (mean ± se) and unclassified group CR was -0.02 ± 0.08% (mean ± se), although both groups had a median rate of 0. The annual rate of change in the stress group was -0.7 ± 0.32% (mean ± se), with a median value of -0.26%. The annual rate of change in the weedy group was 1.12 ± 0.38%, with a median value of 0.41%.

Significant predictors of LHG resilience

Regression analysis revealed that storm and disturbance-regime characteristics were not significant predictors of coral LHG resistance to storms (Figure 2.15). Initial relative cover was the only variable correlated to resistance accounting for ~27% of model variance (estimate = -1.12, $p < 0.001$, $\sigma2$ =2.35, n= 568, marginal r^2= 0.268, conditional r^2= 0.506).

The post-storm annual rate of change (CR) was also negatively correlated to initial cover (post-disturbance) for all life history groups. The average historical return time had significant, but opposite relationships for stress tolerant and competitive species (Figure 2.15). Historical return time was negatively correlated to the post-disturbance rate of change in stress tolerant species (estimate= -0.29, p=0.04), but positively correlated to recovery of competitive species (estimate= 0.23, p= 0.005).

Discussion

Hurricanes can have a significant impact on coral reef cover and composition, although the magnitude of this impact has declined in recent years. Previous work demonstrated significant reductions in coral cover due to tropical storms; however, reef degradation since the 1970s, marked by declining or low initial coral cover, is contributing to increased resistance of reefs to storm impacts. My analysis also revealed a continuation of previously described recovery patterns, in which there appears to be a period of stasis in coral cover post-storm, followed by a continuation of pre-storm decline. However, this recovery pattern varies greatly between coral life history groups, with evidence that weedy coral species may be benefitting from storm impacts.

Increased resistance yet lack of recovery to hurricane impacts

Temporal trends in resistance suggest that hurricanes are not having the same magnitude of impact as they did in earlier decades. Change in response to storm events has been decreasing in each decade and is currently not significantly different from zero, indicating that storms may no longer be having an immediate measurable effect on some reefs in terms of living coral cover. The significant negative correlation between initial coral cover and resistance suggests that coral reefs with a higher initial cover are less resistant, while degraded reefs are more resistant due to their low initial cover (Gardner et al., 2005; Graham et al., 2011; Zhang et al., 2014). Our finding supports recent reports of storm impacts in the US Virgin Islands, where degraded reefs were more resistant to storm damage in 2017, compared to storms occurring in the 1980s and 90s (Edmunds, 2019). Increased resistance to storm impacts is likely due to these patterns in reef degradation (i.e. low coral cover) or shifts in community assemblages dominated by stress-tolerant or weedy species.

Coral resistance to storm impacts is also correlated to storm-specific factors including storm year, maximum wind speed, and minimum distance. These results align with previous findings that more intense storms result in more coral loss, while more recent storms and storms that pass further from a reef result in less immediate coral loss (Gardner et al., 2005). The negative correlation between historical average storm intensity and resistance suggests that sites which previously experienced intense storms had less immediate coral loss, i.e., their resistance has increased due to the loss of storm-sensitive taxa. Strong, compound disturbances are selective and are known to remove or damage coral groups susceptible to high wave action, namely the branching, competitive species in the Caribbean (Harmelin-Vivien, 1994; Jordán-Dahlgren and Rodríguez-Martínez, 1998). As a result, it is possible that previous storms left behind a landscape of individual coral colonies that could withstand physical damage to subsequent storms.

Overall, I did not find evidence for coral recovery in terms of coral cover returning to a pre-storm state (Figure 2.9). When considering either compounded impacts or a period up to 8 years post-storm, these are similar to those reported by Gardner et al 2005, in which there is a short (<5 year) period of stasis before coral cover continues to decline again. The annual rate of change (CR) post-storm was less than overall CR rates for both impacted and unimpacted sites (Figure 2.6, average CR at control sites was -1.08, impacted sites -1.18, post-storm -0.23). The lower CR rate following a tropical storm may be due to the ~5 year period of stasis before decline continues again. However, CR rates post-storm varied significantly between Caribbean subregions, with sites on the western half of the basin (including the Gulf of Mexico and

Western Caribbean) having higher rates of post-storm decline compared to the eastern side of the basin (Florida, Northern Caribbean, Lesser Antilles).

Storm return time is a significant predictor of recovery. Both measures of recovery were positively correlated to at least one return time metric (time elapsed since previous event or average historical return time). This result is unsurprising as more time elapsed between events allows more opportunity for regrowth (from fragmentation) or recruitment of new colonies. Temporal dispersion patterns of storms also correlated significantly with coral recovery. Annual rate of change (CR) was positively correlated to stochastic storm regimes, meaning that sites that are hit by storms at a random interval had a more positive annual rate of change, whereas reef sites hit by storms in a clustered pattern had an overall negative rate of change (Supplement Figure 3). This contrasts with previous findings suggesting that reefs experiencing a clustered storm regime generally had less coral loss (Mumby et al., 2011; Wolff et al., 2016). However, these studies reported modeled predictions of functionally different reef ecosystems dominated by competitive *Acropora* species or model assumptions including high herbivory, no sedimentation, no acidification, and no coral bleaching, which is not the current environmental context for most Caribbean reefs in this study.

My results may also signal a potential synergy between storms and additional stressors or disturbances on reefs, although this is not explicitly tested in this study. First, the slope of decline in the year to year changes in coral cover after the stasis period is higher (more negative) than the pre-storm decline when considering compounding storm events, a pattern similar to expected synergy. Additionally, when comparing the CR between storm impacted and unimpacted sites, we found that storm impacted sites still have a negative recovery rate in the 2010s while unimpacted sites have a slightly positive CR rate (Figure 2.6A). We know that coral reefs experience a simultaneous myriad of disturbances and stressors, including storms, thermal stress (leading to coral bleaching), disease, and localized impacts from pollution, overfishing, and development. Therefore, there is a substantial probability that concurrent or subsequent disturbances or stressors interact with storm impacts to further exacerbate coral cover decline. For example, synergistic interactions between hurricanes and coral disease, in which storm damaged sites have a higher prevalence of coral disease compared to unimpacted sites, has been documented in the Caribbean (Brandt and Mcmanus, 2009; Miller et al., 2009; Brandt et al., 2013).

Storms may facilitate shifts in coral community composition

In general, Caribbean reefs are experiencing a shift in the relative abundances of coral life history groups, with a decline in competitive species and increase in weedy species (Green et al., 2008; Alvarez-Filip et al., 2013; Toth et al., 2014; McWilliam et al., 2020). However, the contribution of hurricanes to this shift is not substantial for all groups. Each life history group has a unique pattern in the year to year changes both pre- and post- storm. Competitive and unclassified species follow a similar pre-storm decline; however, competitive species appear to have a short (<5 year) period of recovery post-storm before declining again, while unclassified appear unaffected by storm events.

The short-term recovery of competitive species may be due to survivorship and reattachment of coral fragments post-storm. Fragmentation is a part of the life history of the competitive *Acropora* species as a form of asexual reproduction and fragments are known to fuse to substrate (or rubble) and regenerate (Harmelin-Vivien, 1994; Williams et al., 2008). Some studies have documented high survivorship and tissue regrowth of *A. palmata* fragments within a few months to a year after hurricane damage (Highsmith et al., 1980; Rogers et al., 1982).

Therefore, successful survival and regrowth of coral fragments could contribute to an increase in measured percent cover in the years following a storm. However, while coral fragmentation might initially increase the relative abundance, there are potential negative consequences. Fragment lesions and increased sedimentation from storm damage can lead to increased contact between pathogens and coral tissue, resulting in delayed, disease-related mortality of surviving fragments or colonies (Williams et al., 2008; Brandt et al., 2013). Additionally, decreased colony size, either of remnant colonies or new fragments, leads to a decrease in fecundity and viability and contributes to the already low sexual recruitment rates of Atlantic *Acropora* species (Williams et al., 2008). While competitive species are typically fast growing (mean growth rate of 71.09 ± 50.13 mm/year), a substantial lack of recruitment can hinder the long term recovery processes (Coles and Brown, 2007; Williams et al., 2008; Darling et al., 2012). In this study, recovery of competitive species was positively associated with return time, fitting assumptions that more time between storm events allows for more opportunity for coral recruitment and regrowth. However, estimates of coral recovery times (10-20 years) are generally greater than storm return time (mean return time this study = 11.4 years, Florida mean return time = 8.69 years, SW Caribbean 20 years) (Coles and Brown, 2007; Williams and Miller, 2012). Therefore, the precipitous decline in competitive species abundance after 5 years may be due to a synergistic effect of frequent, compound disturbances, which inhibit competitive species recovery and allows for colonization and subsequent dominance of more opportunistic species (Adjeroud et al., 2018).

Stress tolerant species have high resistance to storm impacts and appear to follow a cyclic pattern of increase and decline surrounding storm events, which is similar to the overall temporal pattern observed in the Caribbean. Our results are concordant with previous studies documenting high resistance of stress tolerant species to storm impacts in Jamaica and Mexico (Aronson and Precht, 2006; Álvarez-Filip et al., 2009). The cyclical pattern could also be due to differential species response within the stress tolerant group. For example, after a hurricane and subsequent bleaching event in Bonaire, some stress tolerant species declined in abundance, each to a different degree, (*O. annularis, O. faveolata, C. natans*), while other species increased (*M. cavernosa*) (Steneck et al., 2019). Based on our results, it does not appear that hurricanes have substantial influence on the relative abundance of stress tolerant corals as a group.

Weedy species, on the other hand, are clearly increasing in relative abundance both pre- and post-storm. While the storm event itself doesn't lead to a significant increase in cover from year prior to year post, the post-storm increase in abundance is higher/steeper than the pre-storm increase, suggesting that overall weedy species may benefit from storm impacts. Our results align with previous studies demonstrating an increase in weedy coral species after storm disturbances (Álvarez-Filip et al., 2009; Steneck et al., 2019). Wave action from hurricanes displaces benthic organisms including coral and algae, and the increase in relative abundance of weedy species after a disturbance can occur due to their ability to quickly colonize space left behind by competitors (Grime 1977). Weedy coral species are mostly brooders, meaning they do not spawn but rather release larvae that are generally able to settle on benthic substrate once released. This represents a potential reproductive advantage post-disturbance because weedy species generally are able to colonize benthic substrate first and adults generally have longer reproductive seasons compared to spawning species (Aronson and Precht, 2001b; Álvarez-Filip et al., 2009; Darling et al., 2012). Conversely, the increase in relative abundance could just be due to the fact that overall coral cover is declining, but weedy species are making up a larger portion of the coral cover that remains due to their high survivorship. Our results support the hypothesis that weedy species are predicted to become the dominant coral group as disturbances increase in intensity and frequency due to their high resistance to storms and increased abundance post-storm (Aronson and Precht, 2001b; de Bakker et al., 2016).

Event-specific variables (such as storm wind speed, distance, etc.) do not appear to be significant predictors of resistance or recovery of life history groups. Initial cover (relative abundance) was negatively correlated to both resistance and recovery of all life history groups, again reinforcing previous findings that substantial impact from a storm might only be observed if the initial cover is higher to begin with (Graham et al., 2011; Zhang et al., 2014). Average historical return time of storms was the only disturbance regime characteristic correlated to LHG recovery. The negative trend between historical return time and stress tolerant species recovery could be a result of their slow growth rates, which is on average 5.33 mm/year, slowest of all groups or reproductive modes (Darling et al., 2012). So, while individual colonies may persist through storm damage, there can be a lack of expansion of leftover colonies or recruitment of new colonies to the space opened by storms, paired with colonization of opportunistic, weedy species.

Implications for coral reef resilience, in light of reef degradation and changing disturbance regimes

In this study and others in the Caribbean, it is clear that disturbances have been contributing to a shift in coral assemblages, from historically high coral cover reefs dominated by competitive species to contemporary reefs now marked by low coral cover and dominated by weedy and stress tolerant species (Green et al., 2008; Toth et al., 2014; Precht et al., 2019). While contemporary reefs may be more resistant to hurricane impacts, contemporary coral assemblages will likely not provide the same reef functionality compared to historical assemblages. Previous studies quantifying changes to reef assemblages based on functional traits conclude that a shift in dominance from competitive to weedy or stress tolerant species results in the loss of various reef functions such as structural complexity, calcification, and facilitation of invertebrate and fish diversity (Idjadi and Edmunds, 2006; Alvarez-Filip et al., 2011b, 2013). In the Caribbean, competitive coral species, and some stress tolerant species in the *Orbicella* genera, disproportionately contribute to increased structural complexity and calcification, whereas many weedy species do not because of their smaller colony sizes and rounder morphologies. The loss of structural complexity is of unique importance due to the established links between complexity and multiple ecosystem services and because changes to complexity are highly influenced by hurricane impacts, compared to other disturbances (Alvarez-Filip et al., 2011b, 2011c). More complex reef habitats can dissipate wave energy during storms and provide predator refuge space for both invertebrates and fish. Declines in herbivore populations after disturbances can further inhibit coral recovery as a decrease in grazing activity can lead to an increase in macroalgae cover (Aronson and Precht, 2001b). Additionally, weedy species have lower calcification and extension rates, leading to concerns that rates of erosion will eventually outpace rates of reef accretion (Alvarez-Filip et al., 2013).

Another important consideration is whether contemporary Caribbean coral assemblages are resilient to multiple types of disturbances or stressors. Reef degradation may actually contribute to increased resistance to future climate disturbances as coral communities become dominated by disturbance-tolerant species (Côté and Darling, 2010; Darling et al., 2012). There is some evidence of trade-offs in reef traits exhibited by weedy species, that may contribute to increased resilience to other types of disturbances. A study in the Great Barrier Reef showed that assemblages remaining after initial storm disturbances had compact, less complex corals, similar to weedy species morphologies of the Caribbean, which were not affected by a subsequent mass bleaching event (Zawada et al., 2019). A case study in Moorea, French Polynesia also documented a shift towards domination of opportunistic weedy species after multiple, severe disturbances, including storms, COT outbreaks, and bleaching. These new coral assemblages were able to recover, and avoid collapse, after subsequent disturbances (Adjeroud et al., 2018). Additionally, thermally tolerant corals, usually classified as stress tolerant or weedy but defined by the type of symbiotic algae they host, may ensure persistence of coral colonies through times of high thermal stress caused by climate change (Edmunds et al., 2014). Therefore, the survivability and colonization success of weedy and stress tolerant species in disturbed environments may be crucial for persistence of coral communities as the intensity and frequency of hurricanes and other disturbances increases.

Quantifying coral identity in contemporary assemblages will be crucial for understanding how coral communities respond to future disturbances. Some evidence suggests that higher species richness does not necessarily lead to increased resilience to disturbance (Zhang et al., 2014); but rather some combination of resistant and resilient (quick recovery) coral species will be needed to ensure ecological resilience (Baskett et al., 2014). Homogenized reefs post a threat to coral persistence by the potential loss of trait and response diversity, therefore, measuring coral traits of remaining species may be more informational than species richness or coral cover alone. Quantifying changes in coral percent cover is important for an overall view of coral health, but changes to percent cover can mask underlying functional changes to reefs, such as structural complexity, calcification, and thermal tolerance, as mentioned above (McWilliam et al., 2020). For example, a high coral cover reef is generally considered healthy, but if it were composed only of small size, weedy species the community might not maintain appropriate levels of accretion or have substantial structural complexity to support fish and invertebrate populations (Alvarez-Filip et al., 2011b, 2013). If loss of function occurs, management and conservation actions could then focus on restoration of species to enhance complexity or calcification, such as those in the *Acropora* or *Orbicella* genera.

Managing for ecological resilience in coral ecosystems has thus far placed greater emphasis on habitat protection (via marine protected areas) and enhancing coral recovery (via small scale restoration) (Bruno et al., 2019; Steneck et al., 2019; Boström-Einarsson et al., 2020; Hein et al., 2020). However, our results suggest that a greater emphasis on managing coral resistance to disturbance could be more effective. Managing for greater resistance will be imperative due to decreased opportunity for coral recovery as acute disturbance frequency increases and/or the role of chronic stressors (such as thermal stress and ocean acidification), which inherently might not have a recovery window, becomes more prevalent (Côté and Darling, 2010). Our results support this argument, as we found an increasing frequency and return time of hurricanes on Caribbean reefs and an overall lack of post-storm recovery both in percent cover and community reassembly. Regional causes of coral mortality from acute disturbances have been more influential in reshaping coral communities compared to local causes of coral decline (Precht et al., 2019). This suggests climate-induced changes to disturbance regimes, in the form of increased frequency and intensity of disturbances, may preclude opportunity for coral recovery. Therefore, the ubiquity of resistant coral communities may be the best hope in ensuring Caribbean coral reef persistence in the context of climate change.

Conclusion

The contribution of hurricane impacts to coral decline in the Caribbean has decreased over the past few decades; however, localized immediate impacts from storms can still be substantial on reefs with high coral cover or longer time between storm events. We found no evidence of coral recovery post-storm and a possible synergistic decline in coral cover occurring 5 years after a storm event. Additionally, storms appear to be facilitating a shift towards coral assemblages dominated by weedy species. This shift has negative implications in terms of reef functionality, but may also provide increased resistance for other types of stressors or disturbances. This study provides a comprehensive, up to date analysis of Caribbean coral resilience to hurricanes, including a novel, region-wide analysis in the trends of coral life history groups as related to storm events.

Table 2.1 Data sources for coral cover

Includes primary databases and monitoring programs. (**) indicates sources that also had coral percent cover for individual species.

Database or monitoring program	**Date of data access or download**	**Reef locations surveyed**	**Years of data coverage**
Bruno Lab database (Schutte et al., 2010): includes earlier reef check, AGRRA, and literature sources	March 2017	Region wide	1971-2006
Atlantic and Gulf Rapid Reef Assessment **	March 2018	Region wide	1998-2016
Florida Fish and Wildlife Conservation Commission: Coral Reef Evaluation and Monitoring Project (CREMP) **	January 2019	Florida	1996-2017 (coral cover) 1992-2015 (species cover)
Reef Check	March 2018	Region wide	1997-2017
Reef Life Survey	August 2018	Region wide	2010-2012
NSF Coral Time Series, Virgin Islands (Edmunds 2019)	June 2019	USVI	1987-2015
CSUN and NPS USVI time series **	August 2018	Guest et al 2018	2003-2015
US Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP) **	June 2019	USVI	2001-2010 (coral cover) 2001-2016 (species cover)
CARICOMP (Linton and Fisher, 2004)	July 2019	Region wide	1993-2003
Stokes et al., 2010	July 2019	Bonaire	1982-2008
Steneck et al., 2019	July 2019	Bonaire	2004-2017
Toth et al., 2014	July 2019	Florida	1998-2011

Table 2.2 Potential predictors of resistance or recovery

Site-specific characteristics
Coral reef location
Initial percent coral cover
Initial absolute change in coral cover (for recovery models only)
Storm-specific characteristics (per event)
Maximum sustained wind speed (knots)
Minimum distance between storm track and reef site (nautical miles)
Year of the storm
Time passed since last storm (days)
Disturbance regime characteristics (per site)
Total number of storms experienced since 1851
Average historical return time between storms (years)
Average historical intensity of storms (knots, weighted by storm distance)
Dispersion pattern of storm events (regular, stochastic, or clustered)

Table 2.3 Annual rate of change in coral cover at control vs. impacted sites

Data is pooled for all years and subregions. (n) is the number of sites in the dataset

Category	n	Mean	Standard deviation	Standard error	Median	Min	Max	IQR
Control sites	193	-1.08	4.41	0.32	-0.15	-25.52	9.53	2.27
Impacted reefs	508	-1.18	5.13	0.23	-0.27	-39.38	16.25	2.09

Table 2.4 Linear mixed model results

Estimated regression parameters, standard errors, confidence intervals, t-values, and p-values from linear mixed effects models on percent coral cover.

Response Variable & Fixed effects	Estimate	Standard Error	Confidence Intervals	t-value	p value	Direction of slope
Resistance						
(Intercept)	-0.404	0.216	-0.82 – 0.03	-1.832	0.067	
Initial Cover	-0.219	0.097	-0.39- -0.01	-2.056	**0.040 ***	neg
Storm Year	0.397	0.124	0.16- 0.64	3.206	**0.001 ****	pos
Distance	0.489	0.164	0.15- 0.79	2.869	**0.004 ****	pos
Max Wind Speed	-0.412	0.163	-0.73- -0.09	-2.483	**0.013 ***	neg
Historical Return Time	0.025	0.104	-0.18- 0.23	0.207	0.836	
Dispersion (regular)	-0.312	0.350	-0.98- 0.39	-0.853	0.394	
Dispersion (stochastic)	0.134	0.247	-0.33- 0.64	0.635	0.526	
Days Since Previous Storm	0.128	0.100	-0.07- 0.32	1.258	0.208	
Historical Storm Intensity	-0.276	0.100	-0.47- -0.07	-2.661	**0.008 ****	neg
Marginal R^2 *= 0.244; Conditional* R^2 *= 0.279; Random effects variance:* $\sigma^2 = 1.36$; *n= 209*						
Relative recovery (up to 8 years post-storm)						
(Intercept)	-0.23	0.15	-0.52 - 0.06	-1.56	0.12	
Storm Year	0.64	0.06	0.52 - 0.76	10.28	< **0.001 *****	pos
Distance	-0.17	0.10	-0.36 - 0.02	-1.77	0.08	
Max Wind Speed	0.24	0.10	0.05 – 0.43	2.44	**0.015 ***	pos

Days Since Previous Storm	0.33	0.05	0.23 - 0.42	6.53	< **0.001** ***	pos
Historical Return Time	0.05	0.07	-0.08 - 0.18	0.70	0.49	
Historical Storm Intensity	0.04	0.06	-0.08 - 0.17	0.69	0.49	
Initial Change (resistance)	0.67	0.05	0.58 - 0.77	13.69	< **0.001** ***	pos
Dispersion (regular)	-0.32	0.25	-0.81 - 0.18	-1.26	0.21	
Dispersion (stochastic)	0.04	0.17	-0.30 – 0.38	0.23	0.82	
Marginal R^2*= 0.482; Conditional* R^2 *= 0.651; Random effects variance:* $\sigma^2 = 0.73$; *n= 866*						
Annual rate of change (CR)						
(Intercept)	-0.483	0.166	-0.81 – -0.16	-2.908	**0.004** **	neg
Storm Year	0.088	0.052	-0.014 - 0.189	1.698	0.089	
Max Wind Speed	-0.024	0.044	-0.111 - 0.062	-0.552	0.581	
Days Since Previous Storm	0.026	0.049	-0.070 - 0.122	0.522	0.602	
Historical Return Time	0.193	0.069	0.058 - 0.328	2.810	**0.005** **	pos
Historical Storm Intensity	0.059	0.066	-0.071 - 0.189	0.889	0.374	
Initial Cover	-0.303	0.067	-0.434 - -0.172	-4.526	< **0.001** ***	neg
Dispersion (regular)	0.221	0.232	-0.234 - 0.676	0.951	0.341	
Dispersion(stochastic)	0.405	0.188	0.037 - 0.774	2.154	**0.031***	pos
Marginal R^2 *= 0.164 ; Conditional* R^2*= 0.751; Random effects variance:* $\sigma^2 = 0.25$; *n= 282*						

Signif. codes: 0 ‘*’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1**

Table 2.5 Linear mixed model results for relative abundances of coral life history groups

Estimated regression parameters, standard errors, confidence intervals, t-values, and p-values from the linear mixed-effects models on resistance and recovery of coral life history groups.

Response Variable & Fixed effects	Estimate	Standard Error	Confidence Intervals	t-value	p value	Direction of slope
Resistance						
(Intercept)	0.252	0.565	-0.86-1.36	0.445	0.656	
Initial Cover	-1.123	0.101	-1.321- -0.925	-11.118	**< 0.001 *****	negative
Storm Year	0.023	0.077	-0.128 - 0.174	0.300	0.764	
Max Wind Speed	-0.072	0.080	-0.229 - 0.084	-0.904	0.366	
Days Since Previous Storm	-0.053	0.082	-0.213 - 0.107	-0.644	0.520	
Historical Return Time	-0.020	0.080	-0.177 - 0.137	-0.249	0.804	
Historical Storm Intensity	-0.002	0.078	-0.155 - 0.151	-0.024	0.981	
Dispersion (regular)	-0.353	0.291	-0.923 - 0.218	-1.212	0.225	
Dispersion (stochastic)	-0.269	0.215	-0.690 - 0.153	-1.250	0.211	
Marginal R^2 = 0.268, Conditional R^2 = 0.506, Random effects variance: σ^2 = 2.35, n =568						
CR: Stress						
(Intercept)	-0.194	0.329	-0.84-0.45	-0.590	0.555	
Storm Year	6.89E-04	0.085	-0.166 - 0.167	0.008	0.994	
Max Wind Speed	0.0014	0.089	-0.173 - 0.176	0.016	0.988	
Days Since Previous Storm	0.0524	0.092	-0.127 - 0.232	0.571	0.568	

Historical Return Time	-0.2906	0.144	-0.572 - -0.009	-2.024	**0.043 ***	negative
Historical Storm Intensity	0.0326	0.116	-0.196 - 0.261	0.280	0.779	
Initial post-disturbance cover	-0.7054	0.107	-0.915 - -0.496	-6.596	**< 0.001 *****	negative
Dispersion (regular)	-0.2412	0.418	-1.060 - 0.578	-0.577	0.564	
Dispersion (stochastic)	-0.1028	0.381	-0.850 - 0.644	-0.270	0.787	
Marginal R^2 = 0.237, Conditional R^2 = 0.660, Random effects variance: σ^2 = 0.71, n =176						
CR: Competitive						
(Intercept)	-0.238	0.190	-0.61-0.13	-1.251	0.211	
Storm Year	0.064	0.048	-0.030 - 0.158	1.328	0.184	
Max Wind Speed	0.016	0.050	-0.082 - 0.114	0.321	0.748	
Days Since Previous Storm	0.033	0.052	-0.069 - 0.134	0.634	0.526	
Historical Return Time	0.233	0.084	0.068 - 0.399	2.766	**0.006 ****	positive
Historical Storm Intensity	0.014	0.067	-0.117 - 0.146	0.215	0.830	
Initial post-disturbance cover	-0.428	0.062	-0.550 - -0.306	-6.878	**< 0.001 *****	negative
Dispersion (regular)	-0.040	0.241	-0.512 - 0.432	-0.165	0.869	
Dispersion (stochastic)	0.274	0.221	-0.160 - 0.707	1.238	0.216	
Marginal R^2 = 0.260, Conditional R^2 = 0.689, Random effects variance: σ^2 = 0.22, n =175						
CR: Weedy						
(Intercept)	0.533	0.299	-0.05-1.12	1.780	0.075	
Storm Year	-0.143	0.079	-0.298 - 0.011	-1.821	0.069	

Max Wind Speed	0.006	0.078	-0.146 - 0.158	0.074	0.941	
Days Since Previous Storm	-0.104	0.080	-0.260 - 0.052	-1.304	0.192	
Historical Return Time	0.066	0.129	-0.187 - 0.319	0.509	0.611	
Historical Storm Intensity	0.010	0.105	-0.195 - 0.215	0.097	0.922	
Initial post-disturbance cover	-0.528	0.097	-0.718 - -0.339	-5.461	**< 0.001 *****	negative
Dispersion (regular)	0.290	0.378	-0.451 - 1.030	0.766	0.444	
Dispersion (stochastic)	-0.179	0.349	-0.863 - 0.505	-0.513	0.608	
Marginal R^2 = 0.230, Conditional R^2 = 0.679, Random effects variance: σ^2 = 0.53, n =175						
CR: Unclassified						
(Intercept)	-0.249	0.129	-0.5-0.0	-1.925	0.054	
Storm Year	-0.031	0.036	-0.101 - 0.040	-0.849	0.396	
Max Wind Speed	0.001	0.038	-0.073 - 0.075	0.020	0.984	
Days Since Previous Storm	0.020	0.039	-0.057 - 0.097	0.515	0.606	
Historical Return Time	-0.047	0.057	-0.158 - 0.064	-0.823	0.410	
Historical Storm Intensity	0.018	0.047	-0.073 - 0.110	0.392	0.695	
Initial post-disturbance cover	-0.323	0.037	-0.396 - -0.251	-8.741	**< 0.001 *****	negative
Dispersion (regular)	0.153	0.166	-0.173 - 0.479	0.922	0.357	
Dispersion (stochastic)	0.127	0.149	-0.166 - 0.420	0.851	0.395	
Marginal R^2 = 0.313, Conditional R^2 = 0.643, Random effects variance: σ^2 = 0.13, n =175						

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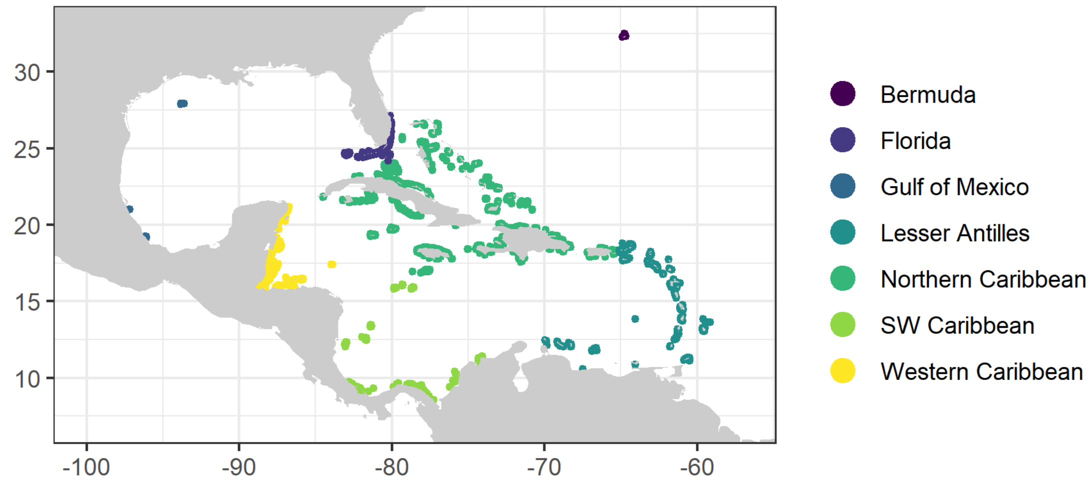


Figure 2.1 Coral reef survey locations

Each dot represents a unique coral reef site, based on latitude and longitude coordinates.

Colors represent ecoregions within the Caribbean.

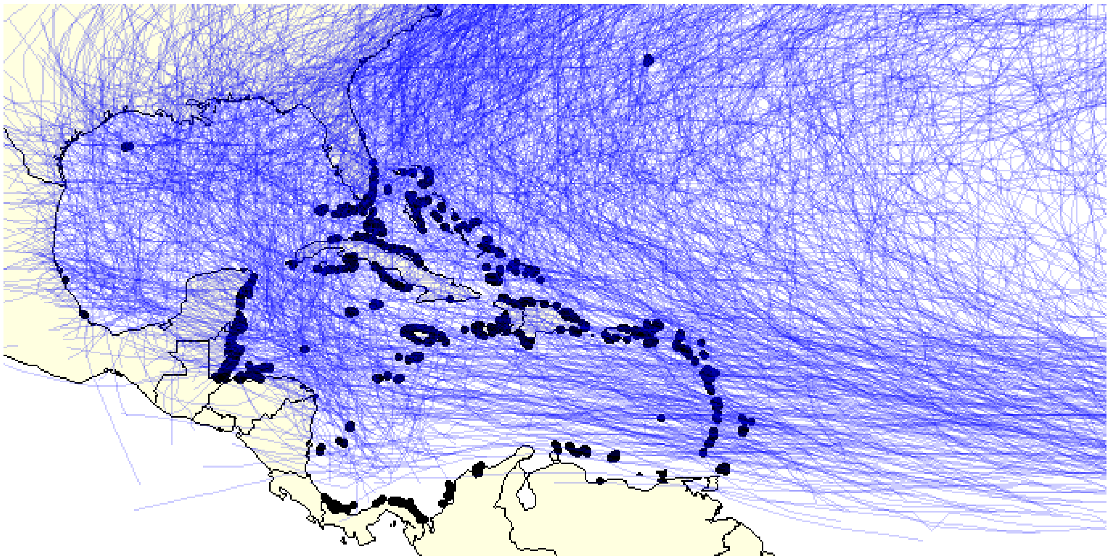


Figure 2.2 Atlantic storm tracks from 1851-2017

Blue lines represent individual tracks for all hurricanes and tropical storms originating in the Atlantic Ocean basin. Black dots are coral reef survey locations.

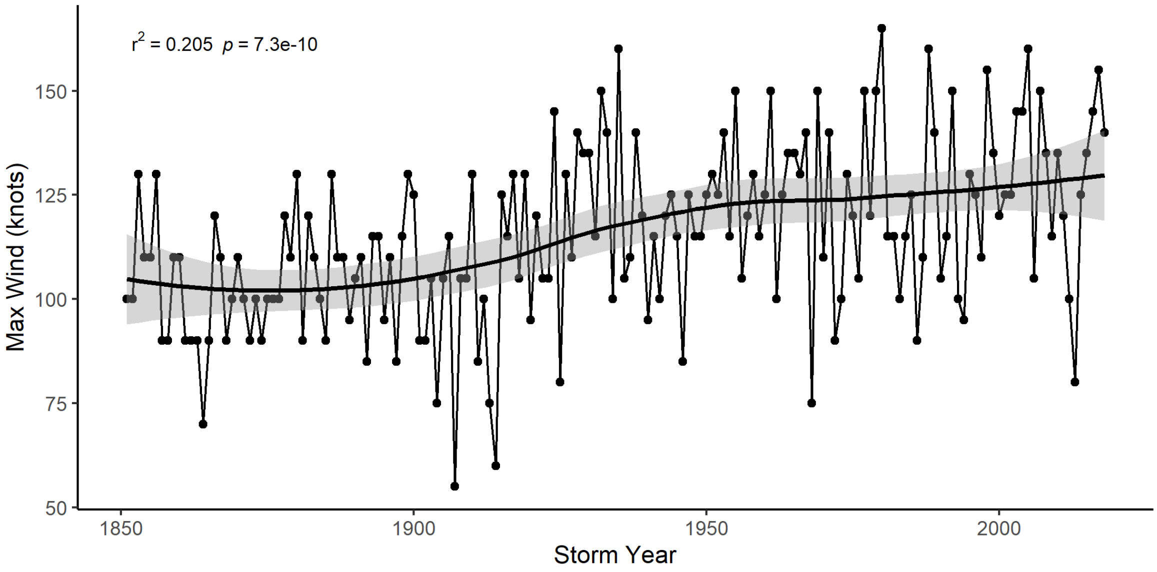


Figure 2.3 Increasing maximum winds

Data points represent the maximum wind speed (knots) of any storm occurring in the Atlantic Ocean Basin, per year. Trend line is a linear regression (loess smoother) +/- standard error.

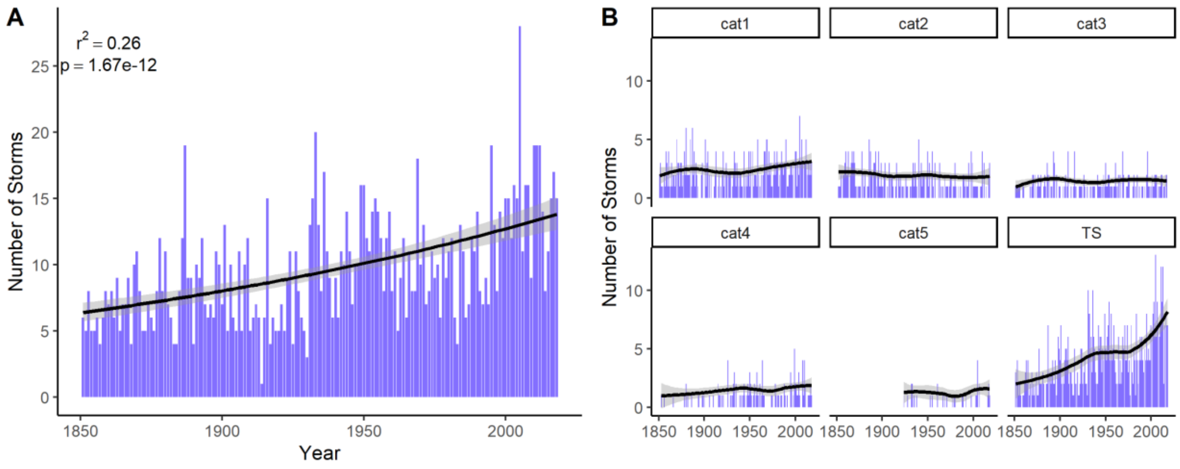


Figure 2.4 Increasing storm frequency

A) Frequency of storms in the Atlantic Ocean basin per year since 1851. B) Frequency of Atlantic storms by category, per year since 1851.

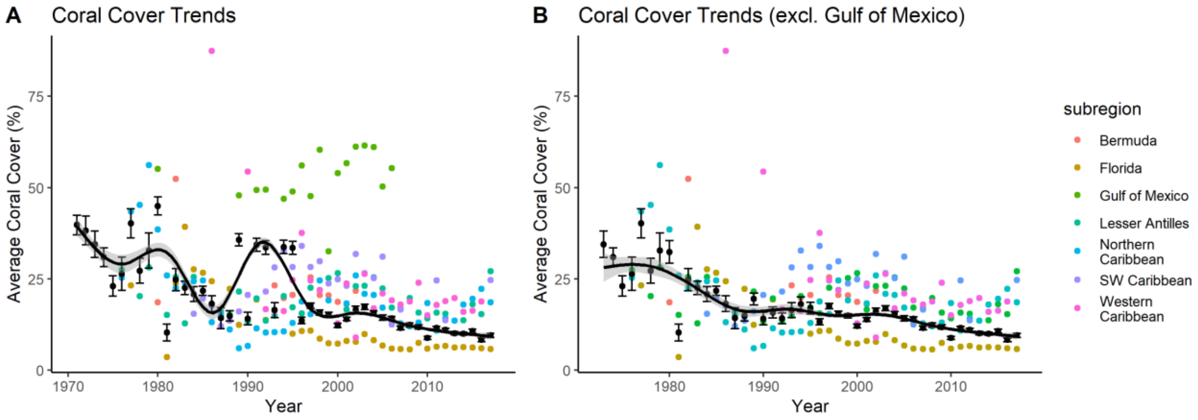


Figure 2.5 Caribbean coral cover decline since 1970

Colored data points represent subregional annual averages in coral percent cover. Black data points represent basin wide annual averages in percent cover (+/- standard error). A) Coral cover decline including all Caribbean subregions. B) Caribbean coral cover decline, excluding the Gulf of Mexico.

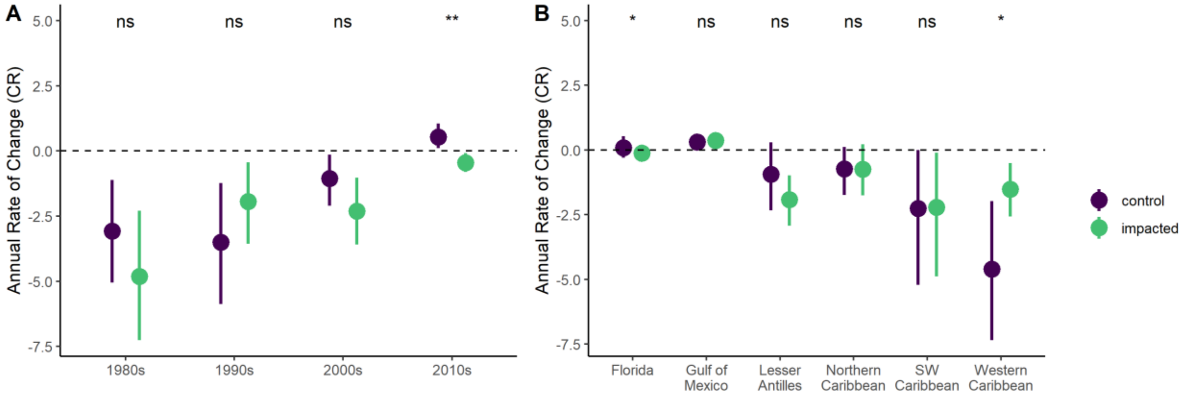


Figure 2.6 Annual rate of change in coral cover between control and storm-impacted sites

A) by decade; B) by subregion. Bermuda is not included in the subregional comparison due to low sample size (1 site per condition).

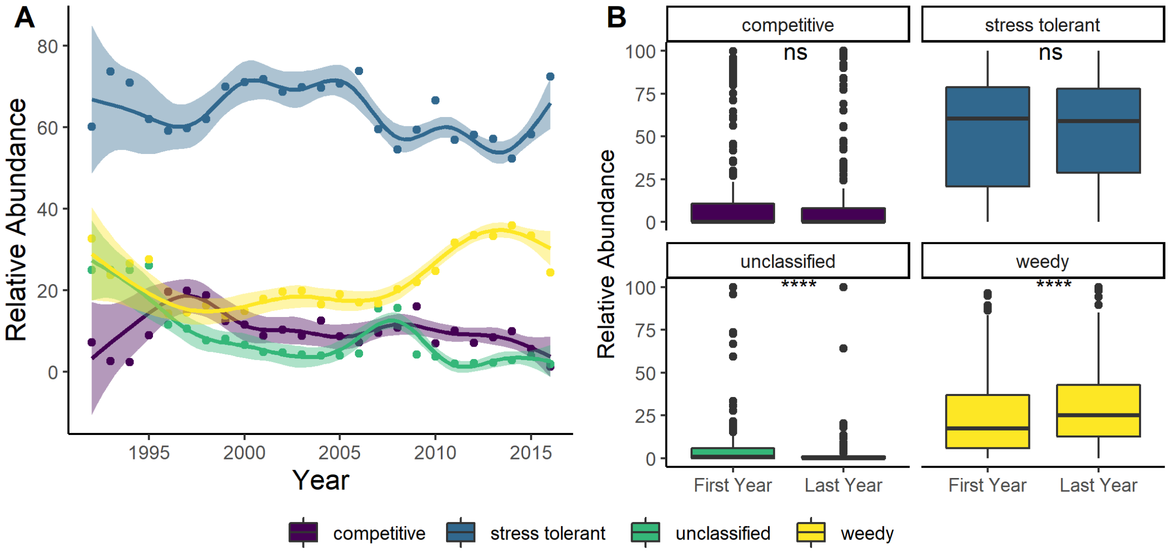


Figure 2.7 Temporal trends in the relative abundances of coral life history groups

A) Trend in each life history group between 1992-2017; B) Difference in relative abundance of life history groups between the beginning and end of the time series per site.

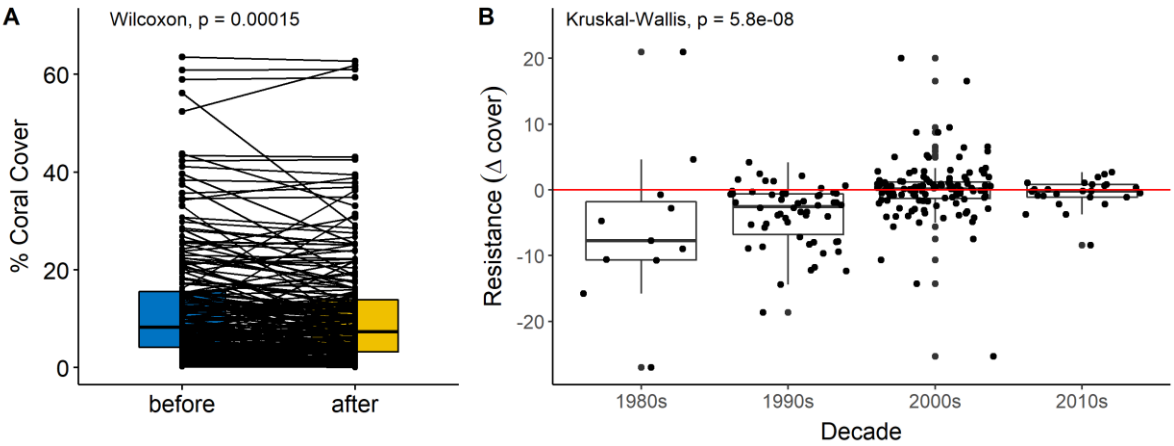


Figure 2.8 Coral resistance to storm impacts

A) Paired differences in coral cover immediately before and after (<1 year) a storm event; B) Temporal trends in absolute resistance for individual storm events.

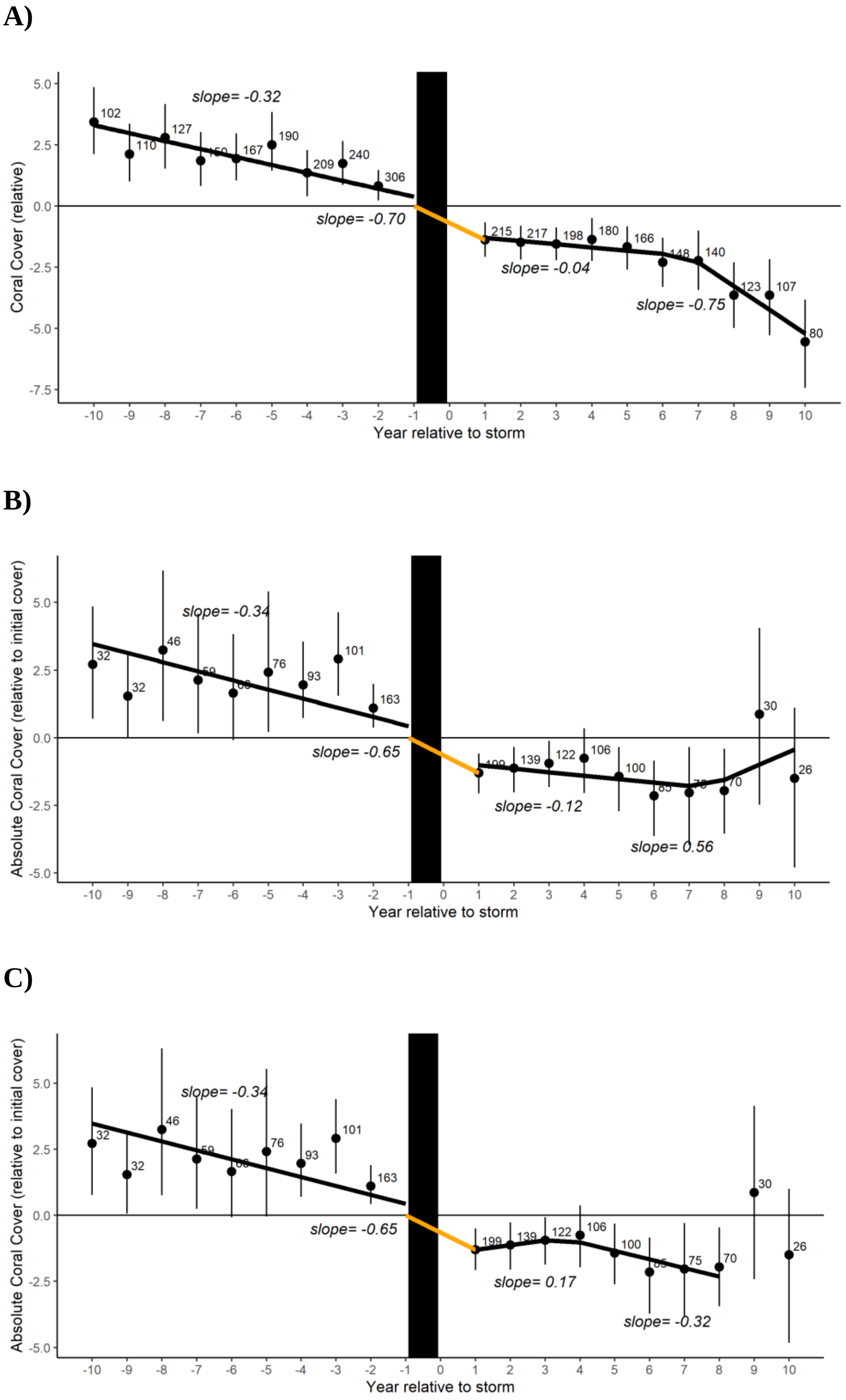


Figure 2.9 Year-to-year change in coral cover, post-storm

The vertical black bar represents a storm event on a reef. Black dots are the Caribbean-wide average change in coral cover for any year pre/post storm (+/- bootstrapped confidence intervals), relative to initial cover (percent cover at one year prior to storm). Numbers represent n values for averages. Lines represent the slope of change in coral cover pre- and post- storm, with the orange line representing resistance (change from initial cover to one-year post-storm). A) Year to year change with compounding storm events; B) Year to year change with trajectories reset at each event; C) Post-storm trends up to 8 years after storm.

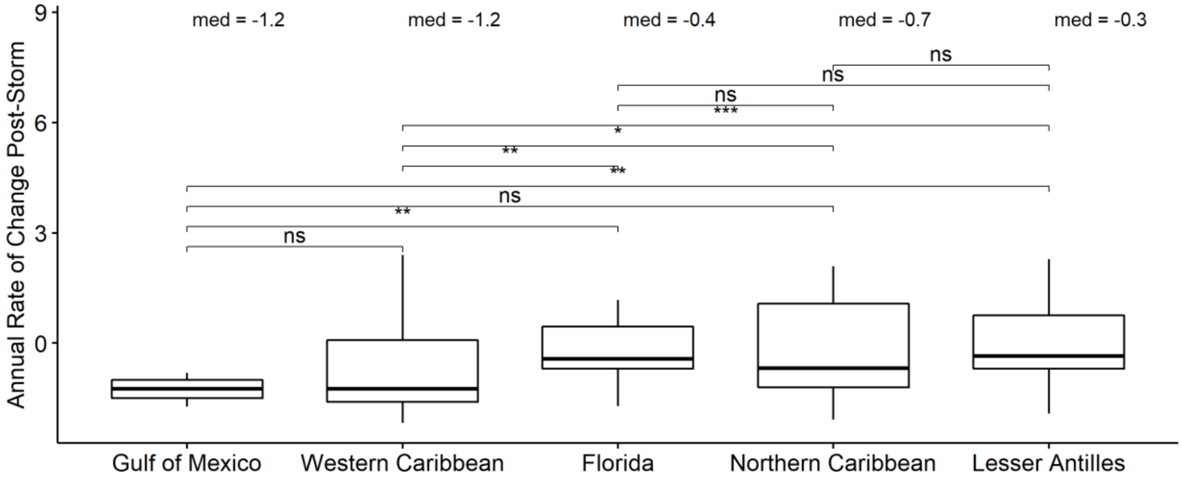


Figure 2.10 Annual rate of change in coral cover post-storm, by subregion

Median annual rate of change (CR) compared between subregions using a Wilcoxon test. Asterisks denote level of significance (ns: p > 0.05, * p <= 0.05, ** p <= 0.01, *** p <= 0.001).

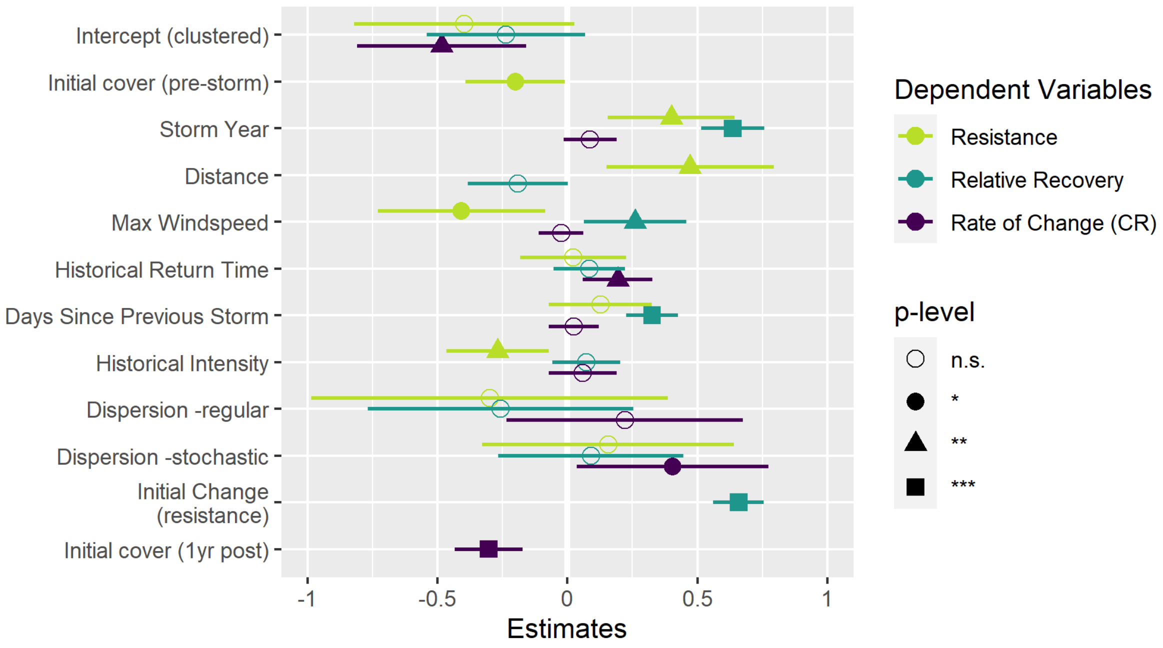


Figure 2.11 Effect of storm parameters of coral resistance and recovery

Model estimates are from linear mixed effects models in which all predictors were treated as fixed effects and site as a random effect. Dependent variables were cube root transformed and all fixed effects scaled prior to modeling. Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

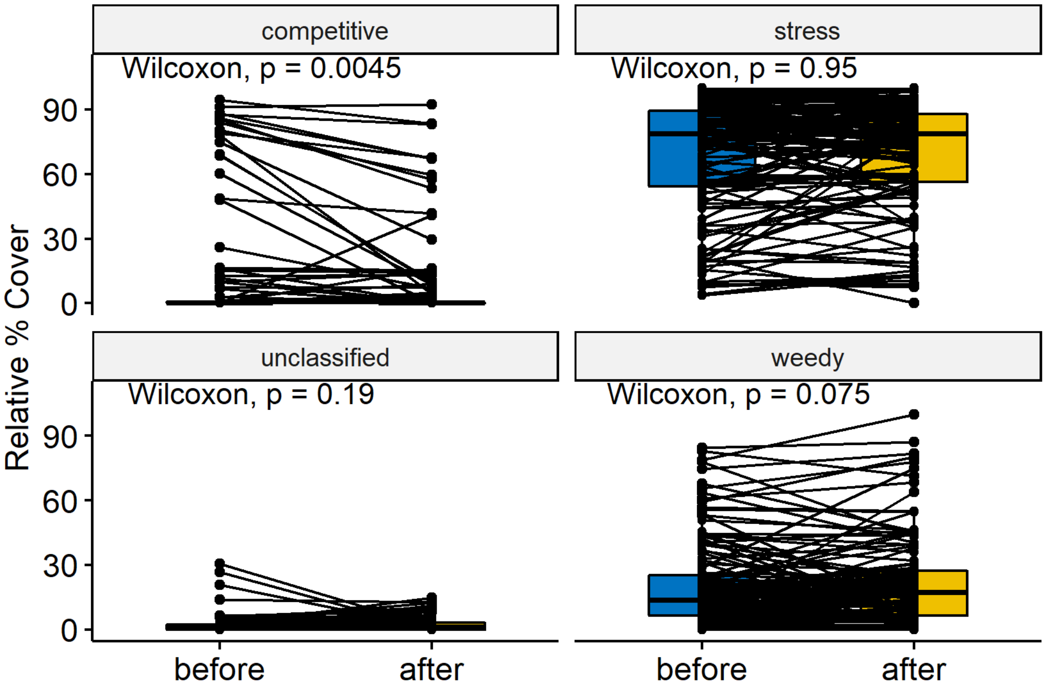


Figure 2.12 Coral resistance to storms, by life history group

Differences in the relative abundance of each life history group before and after a storm even were evaluated using paired Wilcoxon tests.

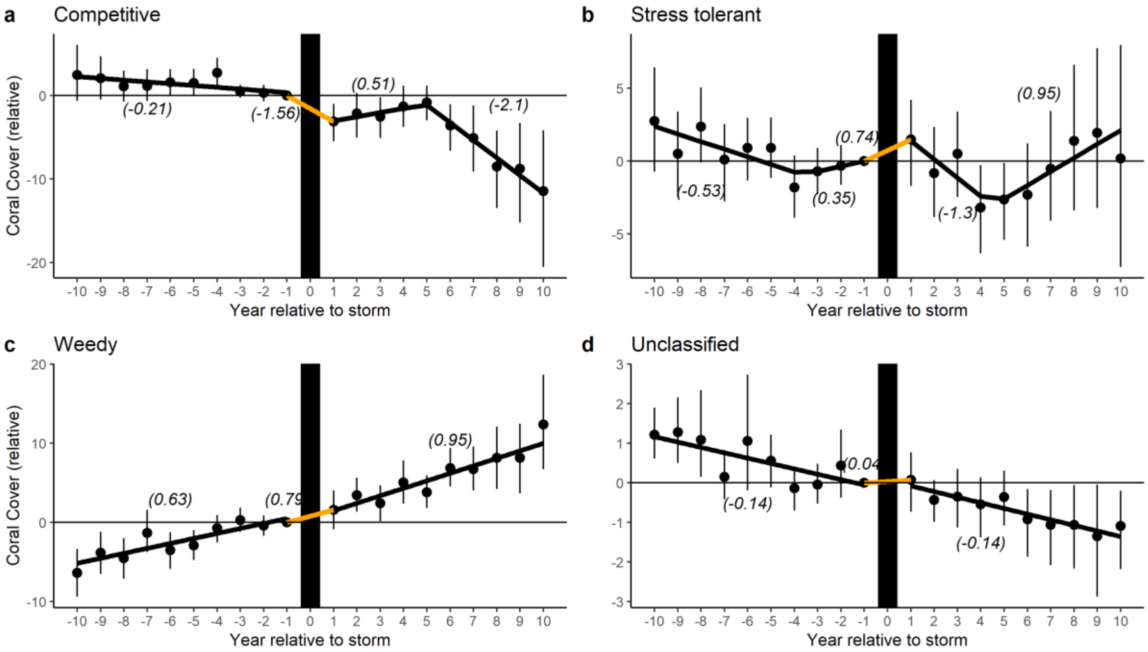


Figure 2.13 Year to year change in cover, by life history group

Year to year changes in relative abundance of coral life history groups before and after storms. Black dots represent Caribbean-wide averages in relative percent cover +/- bootstrapped confidence intervals. Trends fitted using breakpoint regressions.

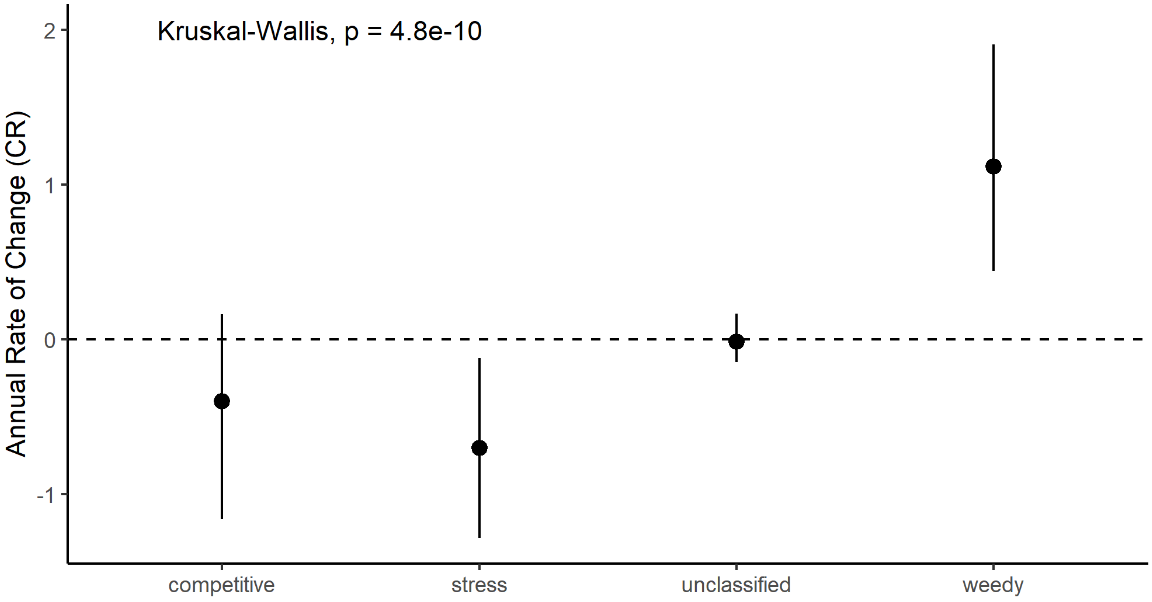


Figure 2.14 Annual rate of change post-storm, by life history group

Comparison of CR rates between coral life history groups, from all sites in the Caribbean (n=176). Black dots represent regional average in CR rate +/- bootstrapped confidence intervals.

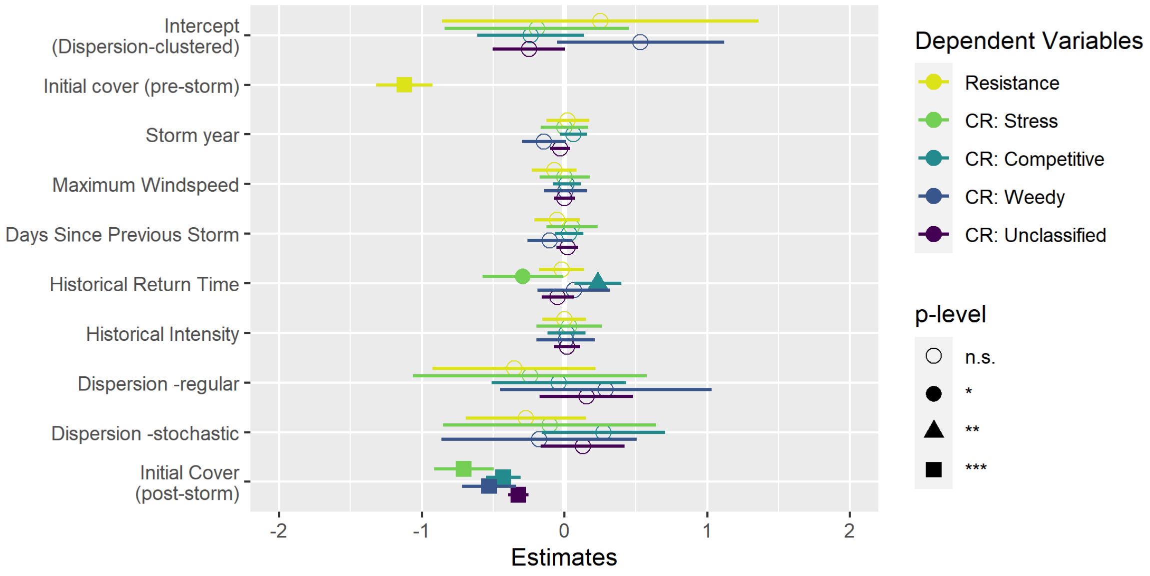


Figure 2.15 Effect of storm parameters on relative abundance of life history groups

Model estimates for life history group resistance and recovery. Dependent variables were cube root transformed and all fixed effects scaled prior to modeling. In the resistance model, life history group was treated as a random effect. In the recovery models, coral reef site was treated as a random effect.

CHAPTER 3 : HOW DO MULTIPLE, INTERACTING DISTURBANCES DRIVE CHANGES TO CORAL COMMUNITIES?

Introduction

The importance of evaluating interactions between different types of natural disturbances across broad spatial and temporal scales is recognized in ecology as critical for understanding processes that drive community structure and function (Paine et al., 1998; Wilson et al., 2006; Darling and Côté, 2008; Graham et al., 2011; De'ath et al., 2012; Ban et al., 2014; Buma, 2015). Ecological communities experience multiple disturbance events and types and the impact of any one disturbance may influence the impact of a subsequent disturbance. This occurs because each individual disturbance event leaves behind a unique legacy, which is a physical and biological template for the next disturbances to interact with (Pickett and White, 1985; Paine et al., 1998; Wilson et al., 2006; Buma, 2015). There are two ways in which disturbances interact: 1) the first disturbance will alter the likelihood, extent, or severity of the subsequent disturbance event; or 2) by altering recovery mechanisms between events (Buma and Wessman, 2011; Buma, 2015). Most often, disturbance interactions are assumed to be synergistic; however, this is rarely tested and there is substantial evidence for antagonistic and additive disturbance interactions (Darling and Côté, 2008; Ban et al., 2014).

Interactions have the potential to create novel disturbance effects that result in unexpected or non-linear changes to communities and ecosystems. These novel or compounded disturbance outcomes can have substantial consequences for community and ecosystem resilience (Paine et al., 1998; Darling and Côté, 2008; Buma and Wessman, 2011; Buma, 2015). It is possible for disturbances to have a large enough magnitude to overcome the resilience mechanisms of a system and change the community structure or lead to a complete regime shift recognized as an alternate stable state (Holling, 1973; Graham et al., 2011). While this phenomenon is not necessarily common in nature (Bruno et al., 2009), disturbance interactions can potentially push communities beyond resilience thresholds more often than what is currently anticipated, especially if the effect is amplified by climate change.

Elevated Sea Surface Temperatures as a driver of disturbances on coral reefs

Disturbance interactions can be quantified if we understand the underlying drivers of the disturbances and their individual legacies (Buma, 2015). In coral reef ecosystems, anomalously warm sea surface temperatures (SST) are a driver for several types of disturbances, including hurricanes, coral bleaching, and disease outbreaks, which are substantial causes of change to Caribbean coral reefs (Precht and Aronson, 2005). In 2005, the Northern Hemisphere experienced an excessively hot year, which translated to anomalously warm SST in the Atlantic and Caribbean region. The first warm hotspots, visible by satellites, were observed as early as May, extended throughout the region by mid-August, and persisted until the end of the year (Wilkinson and Souter, 2008). Warming was not uniform throughout the region, but at a maximum SST increased to 1.2°C above normal conditions (Eakin et al., 2010). Intense hurricane activity, massive coral bleaching, and disease outbreaks were observed across the Caribbean region in 2005 as a direct result of these anomalously warm SST.

Hurricanes are fueled by warm water and there is substantial evidence of correlations between warming oceans and increased hurricane intensity (Elsner et al., 2008; Knutson et al., 2010; Emanuel, 2013). Hurricanes physically damage coral reefs by fragmenting or uprooting living coral colonies and other benthic organisms. Rainfall and wave action from storms can cause decreased water salinity and increased water turbidity, which can result in physiological stress to reef organisms (Harmelin-Vivien, 1994). The legacy of any storm will vary based on storm metrics, such as strength, duration, or distance to the reef, but extreme, although patchy, losses to coral cover and shifts in benthic community structure or species composition have been widely documented after intense storms (Woodley et al., 1981; Harmelin-Vivien, 1994; Gardner et al., 2005; Álvarez-Filip et al., 2009; Edmunds, 2019). The anomalously warm SST event in 2005 resulted in a destructive Atlantic hurricane season, with 27 total storms (14 hurricanes), including three category 5 hurricanes on the Saffir-Simpson scale. These storms resulted in substantial physical damage to coral reefs, particularly on the Mesoamerican Barrier Reef in Mexico where up to 56% decline in coral cover was documented after being hit by two Category 5 storms (Álvarez-Filip et al., 2009).

There is also a direct link between warm SST and coral bleaching. Warm ocean temperatures are a stressful condition for coral colonies and lead to the expulsion of their symbiotic algae, resulting in the pale or white color that is associated with bleached corals. Direct observations of increased or anomalously warm SST followed by coral bleaching events are well documented (Glynn, 1990; Williams and Bunkley-Williams, 1990; Winter et al., 1998; McWilliams et al., 2005; van Oppen and Lough, 2009; Eakin et al., 2010). During the Caribbean warm event in 2005, the first signs of coral bleaching were reported in June, with region-wide bleaching reports by July and August. Coral bleaching was severe in 2005; however, there was a lot of variation in bleaching severity and prevalence between sites, likely attributed to other risk factors of bleaching, including local nutrient conditions and coral species composition (Wilkinson and Souter, 2008; Eakin et al., 2010). Severe or prolonged coral bleaching can result in substantial coral mortality. With bleaching induced mortality, the bare coral skeleton remains and other benthic organisms, particularly bacterial mats and algae, can colonize, resulting in changes to overall benthic composition of reefs.

Coral diseases are also known to be more prevalent during periods of elevated SST (Precht and Aronson, 2005; Bruno et al., 2007; Randall and Woesik, 2015). Two hypothesized mechanisms linking SST and coral disease include (1) pathogen abundance or virulence increases with high temperatures (Miller et al., 2009, Toren et al 1998, Rosenberg and Ben-Haim 2002) or conversely, (2) high SST results in an increased susceptibility of coral hosts to disease pathogens (Harvell et al 2002, Lesser et al 2007). The 2005 warm SST anomalies in the Caribbean were followed by an increase in disease outbreaks across several locations and in multiple coral species (Muller et al., 2008; Miller et al., 2009). In severe cases like that in Trinidad and Tobago, up to 73% disease-related mortality was observed in *Colpophyllia sp.* and *Diploria sp.* (Wilkinson and Souter, 2008). This phenomenon is not unique to the Caribbean, as a six-year region-wide study of the Great Barrier Reef in Australia revealed significant positive correlations between warm SST anomalies and white syndrome disease (Bruno et al., 2007). Similar to coral bleaching, coral diseases, especially outbreaks that affect large portions of a coral population, can result in substantial coral mortality, as live tissue dies with disease progression across a colony (Precht and Aronson, 2005). The physical substrate remains and dead corals are then typically colonized by other benthic organisms, such as algae, sponges, and bacterial mats.

Evidence for interactive effects between storms, bleaching and disease

The individual impacts of hurricanes, bleaching, and disease are well known and there is emerging evidence of their potential interactive effects. An antagonistic interaction by which hurricanes cool SST and decrease the severity of coral bleaching on reefs has been observed on several occasions (Manzello et al., 2007; Brandt et al., 2013). Hurricanes can cool water temperatures by three different mechanisms: evaporative cooling, local upwelling of cooler, deeper waters, and by providing shading from storm clouds (Heron et al 2008). Passing storms can cool water temperatures by 5°C over a much wider spatial area than the path of physical damage and a study of hurricanes in Florida revealed that SST were cooled by up to 3.2°C for 1-40 days after a storm (Manzello et al., 2007). During the 2005 warm SST event, Florida reefs were affected by four separate storms and experienced a decrease in bleaching prevalence and quicker recovery from bleaching, compared to reefs in the US Virgin Islands (USVI), which had similar levels of coral bleaching but no storm impacts (Manzello et al., 2007; Wilkinson and Souter, 2008) (Manzello et al 2007, Wilkinson and Souter 2008). Bleaching mortality along the Mesoamerican Barrier Reef in the Western Caribbean during 2005 was also lower compared to other Caribbean regions due cooling SST after storms, although intense storms such as Hurricane Wilma (Category 5) resulted in substantial storm-induced mortality (Wilkinson and Souter, 2008). The antagonistic interaction between hurricanes and coral bleaching was also documented in 2010 when Hurricane Earl (Category 2) passed by the USVI during a time of high coral bleaching and resulted in decreased SST and mitigation of bleaching (Brandt et al., 2013).

Conversely, coral reefs impacted by tropical storms and/or coral bleaching can have increased prevalence of coral disease (Brandt and Mcmanus, 2009; Miller et al., 2009; Brandt et al., 2013). Physical damage from tropical storms, such as coral fragmentation and increased sedimentation, may provide more opportunity for contact between pathogens and live coral tissue (Harmelin-Vivien, 1994; Miller and Williams, 2007). The interaction between coral disease and hurricanes has largely been observational as well. For example, in La Parguera, Puerto Rico outbreaks of multiple coral diseases (white plague, blank band, and patchy necrosis) were observed within a few weeks after the passing of Hurricane Hortense in 1996. Up to 47% of the coral population was affected on some reefs, even though water temperatures remained at normal or below normal levels (Bruckner and Bruckner, 1997). Similarly, a “white-disease” outbreak was documented in Navassa Island in 2004 after the passing of two hurricanes (Miller and Williams, 2007). Neither study provides a causal effect of hurricanes on disease outbreaks and in both cases other anthropogenic and environmental factors, such as localized damage from boating activities, variation in hydrodynamics, or chronic water turbidity may also have contributed to increased disease prevalence. However, a 2010 study of the impacts of Hurricane Earl in the USVI provided experimental evidence of storm-induced colony fragmentation as a mechanism for the interaction between coral disease and hurricanes. After the passing of Hurricane Earl, SST decreased and bleaching was mitigated, but an outbreak of ‘rapid tissue loss disease’ was observed almost immediately afterwards, with significantly higher prevalence on coral fragments (compared to intact colonies) and on fragments in contact with sediments (Brandt et al., 2013).

While both coral bleaching and coral disease are associated with warm SST, a pattern exists in which coral disease typically follows a severe bleaching event (Selig et al., 2006; Bruno et al., 2007; Muller et al., 2008; Wilkinson and Souter, 2008). Physiological stress from coral bleaching may increase the susceptibility of a colony to coral disease, known as the “compromised-host” hypothesis (Muller et al., 2008; Miller et al., 2009). A test of this hypothesis on elkhorn coral (*Acropora palmata*) found that tissue loss from disease was substantially greater on bleached vs. unbleached corals during the 2005 Caribbean warm event (Muller et al., 2008). The authors concluded that host susceptibility was the more important factor driving disease severity. During the same 2005 Caribbean high SST event, the highest levels of coral mortality were observed in areas in which coral disease followed bleaching, also suggesting a synergistic interaction (Wilkinson and Souter, 2008; Miller et al., 2009; Rogers et al., 2009). In most cases, increased coral disease prevalence is observed during or after a bleaching event; however, this may depend on the coral species affected and the disease type (Muller et al., 2008; Bruckner and Hill, 2009; Rogers et al., 2009; Rogers and Muller, 2012). The opposite relationship, in which coral disease occurs before bleaching, was observed on *Siderastrea siderea* corals in the Florida Keys during the 2005 event: colonies infected with Dark Spot disease appeared to bleach more severely than non-diseased corals (Brandt and Mcmanus, 2009).

Patterns of disturbance interactions on coral reefs

Direct observations of interactions between hurricanes, coral bleaching, and coral disease support the theoretical underpinnings of disturbance interactions: that each disturbance event leaves a legacy for which another event can act upon, changing the trajectory of community or ecosystem state. However, we have minimal knowledge regarding the generality of these interactions on coral reefs and community-level responses to multiple, interacting disturbance events (Ban et al., 2014). Much of what we know about these specific disturbance interactions come from observations during the anomalously warm 2005 year in the Caribbean, which represents an extreme case of thermal stress and consequently one of the most active hurricane years on record. There is no test of coral reef disturbance interactions between storms, bleaching, and disease on a region-wide scale and in less-extreme conditions. Thus, the question remains, are the outcomes of these disturbance interactions detectable on an annual/regular basis, or should we only expect to see them during times of extreme events?

The purpose of this study is to characterize the generality of potential interactions between three SST-driven disturbances on coral reef ecosystems (hurricanes, bleaching, and disease) on a decadal scale across the Caribbean region. Specifically, I tested three disturbance interaction hypotheses: 1) Tropical storms decrease the severity of coral bleaching; 2) Tropical storms increase the prevalence of coral disease; 3) Coral disease correlates with bleaching extent. My aim is to describe the regularity of these disturbance interactions, quantify their effect on coral cover, and determine the direction and magnitude of their cumulative effects. This investigation will provide critical understanding of how disturbance interactions are changing coral reef communities and influencing reef resilience, particularly at a time when disturbance dynamics are being modified due to anthropogenic climate change.

Methods

Data Aggregation

Coral Health Data: Percent cover, bleaching, and disease

Coral monitoring data was aggregated from the Atlantic and Gulf Rapid Reef Assessment (AGRRA) and Reef Check Caribbean monitoring databases. Surveys covered 1,081 unique reef locations between 2006-2017 and included metrics such as percent live coral cover, percent bleaching of population, and percent of coral population exhibiting disease. Both programs employ in-situ, point count transect protocols to monitor coral reef health. These are not permanent transects; however, both monitoring programs record GPS coordinates and information about the habitat (e.g. reef zone) to ensure that the same reef area is resurveyed over time. Percent bleaching and disease in corals is recorded as the percent of total corals observed that exhibit any type of disease or bleaching (pale, partially bleached, fully bleached).

In the AGRRA protocol, each transect is 20 meters long and benthic organisms recorded every 10cm. On average, for each sampling date, 2.5 surveys were conducted at a site to get values for percent bleaching and disease and an average of 6 surveys were conducted to get percent live coral cover. AGRRA data was downloaded directly from the site level coral disease and benthic point cover summary products (Marks and Lang 2018). In the Reef Check protocol, each transect is 100m long, split into four 20m segments, with a 5-meter un-surveyed gap between each section. The total segments completed per transect were counted as one survey, with an average of 1.2 surveys were conducted at each site per sampling date. Raw data from the Reef Check database was obtained directly from Reef Check headquarters in March 2018, but is also publicly available online (Reef Check Foundation, data.reefcheck.org).

Locations of each unique coral reef site were assigned a Caribbean ecoregion based on the World Wildlife Fund (WWF) marine ecoregions classification (Spalding et al 2007). Ecoregions included in this dataset are: Florida, Bahamas, Western Caribbean, Southwestern Caribbean, Eastern Caribbean, Southern Caribbean, and the Greater Antilles (Figure 3.1).

Historical Storm Impacts

Tropical storm tracks from 1851-2017 were downloaded directly from the National Ocean and Atmospheric Administration (NOAA) Atlantic Hurricane Database (HURDAT), using the Hurdat package in R (Trice and Landsea 2019). These historical records contain storm track location (latitudinal and longitudinal coordinates), wind speed (knots), low pressure (millibar), status (landfall, hurricane classification), date and time of track record, with variables recorded every 6-hours. We only included historical storm tracks from 2006-2017, which overlaps with the years in which coral reef survey data were available. Functional programming in R was used to catalog which hurricanes cross which reef sites in the coral reef survey dataset. Code for these procedures was adapted from Elsner and Jagger (2013). A search radius of 100 km (~54 nautical miles) was used to capture all tropical storm and hurricane strength storms that may have physically damaged a coral reef (Gardner et al., 2005; Manzello et al., 2007). To test for the effects of tropical storms on coral bleaching, a search radius of 400 km (~216 nautical miles) was used to select storms within a distance wide enough to offer potential cooling (Manzello et al., 2007).

Disturbance Interactions

For each unique reef, we created an annual time series from 2006-2017 that documents reef coordinates, reef name, country, ecoregion, number of coral monitoring surveys conducted, date of coral surveying, average percent coral cover, average percent bleaching of population, average disease of population, the total number of storms a reef experienced, the average return time (number of days since a previous storm), the average max windspeed (knots) of all storms to hit that reef in that year, the average distance between the reef site and center of storm track (units), and the date of the earliest storm to hit that reef that year. If more than one storm hit a site in any given year, the average maximum wind speed of all storms was weighted by the distance of each storm.

For each hypothesis, I evaluated the interactions on a year to year basis. This was to account for potential variation in annual temperatures, bleaching severity, storm activity, or disease prevalence.

H1: Tropical storms decrease the severity of coral bleaching.

To test this hypothesis, I quantified the differences in the proportion of coral colonies bleached (measured as a percent of population bleached) amongst sites that were unaffected by tropical storms and those that were impacted by at least one storm. If coral reef monitoring surveys were conducted at a site before the first storm of the season occurred, that data point was considered “unaffected”. Coral bleaching in the Caribbean typically peaks in the late summer, but can be observed for several months after it begins. This time frame for peak bleaching overlaps with the Atlantic hurricane season, which runs June 1-November 30th. Therefore, to account for seasonality in these disturbance impacts, we limited the comparison to surveys conducted between July and December of any given year. Results supporting this hypothesis would reveal a lower proportion of bleached corals at sites with a storm compared to storm unaffected sites. A Wilcoxon test was used to quantify differences in bleaching at storm impact vs. storm unimpacted sites, as data are not normally distributed.

H2: Tropical storms increase the prevalence of coral disease.

To test this hypothesis, I quantified differences in the proportion of diseased corals at sites affected and unaffected by tropical storms. Sites were considered unaffected by a storm if either no storm occurred in that year or the coral health surveys were conducted before the first storm of the season. Results supporting this hypothesis would reveal a higher proportion of diseased colonies at storm-impacted reefs, compared to sites unaffected by storms. A Wilcoxon test was used to quantify differences in disease at storm impact vs. storm unimpacted sites, as data are not normally distributed.

H3: Coral disease correlates with bleaching extent.

From the literature, the true hypothesis is that coral bleaching increases the prevalence of coral disease. However, in the monitoring surveys, disease and bleaching are recorded simultaneously; therefore, it was not possible to test for sequential events. Based on previous observations, we would still expect that reefs experiencing higher bleaching prevalence also have higher disease prevalence and would see a co-occurrence of these two events.

To test this hypothesis, I quantified differences in the proportion of diseased corals at sites affected and unaffected by bleaching. Results supporting this hypothesis would indicate a higher proportion of diseased colonies on bleached reefs compared to sites unaffected by bleaching. A Wilcoxon test was used to quantify these differences as data are not normally distributed. Ordinary least squares regression was used to evaluate the correlation between bleaching severity (% of population coral bleached) and disease prevalence (% population of corals diseased).

Effect of disturbance interactions on coral cover:

To quantify the cumulative effects of disturbances and their interactions, I tested how coral bleaching, coral disease, and tropical storms affect absolute percent coral cover and annual rate of change in coral cover (CR). The annual rate of change in cover was calculated using equations from Gardner et al 2005 and Cote et al 2003; in which pca is the percent of coral cover at the end of the time series, pcb is the coral cover at the beginning of the time series, and d is the duration of the time series.

$$Rate\ of\ Change\ (CR) = \frac{pca - pcb}{d}$$

For predictors, I calculated the total number of storms that hit each reef, the average bleaching extent and average disease extent over each reef timeseries. Only reefs that were surveyed more than two times during the sampling period of 2006-2017 were retained for this analysis (n=112). CR values were square root transformed and all predictors were scaled before modeling. I used linear mixed effects models to quantify the effect of disturbance predictors on coral response (CR or absolute difference), with ecoregion as a random effect to account for potential spatial variation. All models were run using the lme4 package in R (Bates et al 2015).

Results

H1: Tropical storms decrease the severity of coral bleaching

Between 2006-2017 there were five years with a significant difference in bleaching at storm unaffected vs. storm impacted sites (Figure 3.2). In three of those years storm-impacted reefs had lower median percent bleaching compared to sites unimpacted by a storm, supporting this hypothesis. In 2007 and 2008 there was a median difference in -5.2% bleaching at storm impacted sites (p= 0.0078, p= 0.0012, respectively) and in 2013 there was a median difference in -2.1% bleaching at storm-impacted sites (p=0.029). However, in 2011 and 2017 the opposite pattern was observed, in which storm impacted sites had higher median percent compared to non-impacted sites (2011: +7.4%, p= $6.4\text{x}10^{-7}$; 2017: + 4.5%, p= $3\text{x}10^{-7}$). In 2011, the increase in post-storm bleaching appears to be driven by patterns observed in the Bahamas and Western Caribbean specifically, while the 2017 increase in post-storm bleaching appears to be limited to the Greater Antilles (Supplement Figure 5). In 2009 and 2016 there was a low sample size (n<5) for surveys in either the storm impacted or unaffected category. In the remaining five years of the dataset (2006, 2010, 2012, 2014, 2015), there was no detectable difference in coral bleaching at unaffected vs. impacted sites.

H2: Tropical storms increase the extent of coral disease

Overall, I did not find strong support for this hypothesis. There were only six years in which coral disease data existed for both storm-impacted and unimpacted reefs (Figure 3.3), and only one year in which disease was higher at storm impacted sites (2007: +6.6%, p =0.028). In 2011, there was a statistically significant, yet small difference in coral disease between impacted and unimpacted sites (-0.4%, p =0.0011). This small difference in median recorded disease is likely not ecologically significant, and I would expect it to fall within a margin of error for detecting disease during in-situ surveys. For both 2007 and 2011 comparisons, the sample size between impacted and unimpacted reefs is skewed. For all other years, there was no significant difference in coral disease at storm impacted vs. unaffected sites.

I also assessed the effects of other potential covariates in the hypothesized relationship between coral disease and storms. There was no significant relationship between the amount of disease and storm intensity (windspeed) ($p=0.89$, $r^2=0$) or the amount of disease and the number of tropical storms (Kruskal-Wallis =0.059 when all data pooled; by year all $p > 0.05$ with low R^2).

To account for a potential time lag between a storm occurring and the observable onset of coral disease, I also evaluated coral disease for up to one-year post storm when data was available. There was no significant difference in disease at storm impacted vs. unaffected sites at one-year post storm (Supplement Figure 7). A paired t-test for impacted sites that were surveyed in consecutive years did not reveal a significant difference in disease levels between the year of impact and one-year post-impact ($t = -0.166$, $df = 91$, p-value = 0.8).

H3: Coral disease correlates with bleaching extent

On average in any given year, a coral reef that experienced bleaching had a higher disease extent (+1.5%, $p < 2.2e^{-16}$, Figure 3.4), supporting hypothesis 3. Additionally, there is a weak but statistically significant increase in disease extent with higher bleaching severity (Figure 3.5, $r^2 = 0.04$, $p= 1.16^{-16}$). However, because the measurements for coral bleaching and disease were taken simultaneously, these results only demonstrate co-occurrence of the disturbances, not a sequential pattern of bleaching to disease.

Disturbance interactions on coral cover:

Storms and disease have a negative synergistic effect on both the absolute difference in coral cover over time (p=0.017) and the rate of change in coral cover (CR) over the time series (p=0.011). No other disturbance or interaction had a significant effect on the difference in cover or CR. However, these disturbance events accounted for very little model variance, with a larger amount of model variance being explained by spatial differences (ecoregion) (Table 3.2, Figure 3.6).

Discussion

We know that extreme temperature related events, such as the anomalously warm year in 2005, can result in localized disturbance interactions and potentially negative impacts to coral reef communities (Manzello et al., 2007; Muller et al., 2008; Wilkinson and Souter, 2008; Brandt and Mcmanus, 2009; Miller et al., 2009). The purpose of this study was to test hypotheses of how storms, bleaching, and disease interact and quantify their cumulative effects on coral cover over broad temporal and spatial scales. I leveraged long-term coral reef monitoring data in the Caribbean to characterize the generality in which these disturbances occur. I found support for an antagonistic interaction between storms and bleaching, a positive correlation between coral bleaching and disease extent, and a synergistic interaction between storms and disease that results in greater loss in absolute coral cover and a more negative rate of change in coral cover over time. These patterns were inconsistent year to year, in both the direction of interaction (positive or negative) and magnitude of change. It is surprising that we didn’t detect a stronger signal of disturbance interactions, seeing as that during the timeframe of the study (2006-2017), there was a 3 year global bleaching event (2014-2017), several active hurricane seasons, (see Table 3.1) and outbreak of a novel disease on the Florida reef tract that spread to other localities in the Caribbean (Alvarez-Filip et al., 2019; Eakin et al., 2019; Muller et al., 2020). Inconsistencies in the disturbance interaction patterns found in this study could be due to both methodological limitations and ecological responses specific to contemporary Caribbean reefs.

Limitations of monitoring data in detecting disturbance interactions

It is important to acknowledge some of the limitations of monitoring data in testing these hypotheses. First, monitoring data is not paired at the site level for this analysis. Ideally, for each coral reef site we would have survey data from immediately before and after any disturbance event, yet this data doesn't exist on a broad temporal and spatial scale. Monitoring programs are subject to several budgetary and time constraints and the survey program itself may be impacted by disturbances. Sampling can get delayed by storms, both by direct disruption to sampling plans but also post-storm water turbidity can make it difficult to conduct in-situ scuba surveys. Additionally, some monitoring data has an issue of scale because it doesn't capture changes to individual coral colonies over time. Studies that tag and track individual coral colonies over time repeatedly demonstrate interactions of bleaching, disease, and hurricanes on colony level mortality (Brandt and Mcmanus, 2009; Bruckner and Hill, 2009; Rogers and Muller, 2012; Brandt et al., 2013; Brodnicke et al., 2019). Additionally, monitoring programs used in this study counted fragments, but did not report on the status (such as living, bleached, diseased), which may influence how disease prevalence is documented post-storm (AGRRA coral protocol). Coral colonies can survive fragmentation and reattach to substrate (Highsmith et al., 1980; Fong and Lirman, 1995; Smith and Hughes, 1999), so more studies that also quantify disease on coral fragments may provide greater insight into the storm-disease disturbance interaction.

Not unique to monitoring data, but to study sampling in general, is the fact that the timing and robustness of surveying can impact results and their interpretation. For example, due to species specific responses to thermal stress and the onset of bleaching symptoms, survey timing may impact interpretations about which species are most sensitive and what proportion of corals experienced bleaching, especially if some colonies have either recovered or died (Claar and Baum, 2019). Additionally, it can be difficult to make temporal comparisons of disturbance impacts to coral communities when some years are sampled less than others. In the Caribbean, 2010 was another thermal “extreme” year with high SST, bleaching, and a busy hurricane season, but less records of these events and their impacts exist compared to the 2005 events. Some speculate this is due to the fact that several assessment programs documenting disturbance impacts no longer existed (Eakin et al., 2019). This was evident in our dataset as well, evidenced the low sample sizes for surveys conducted in 2010 (Supplement Table 4).

Lastly, this study likely did not capture the impact of Stony Coral Tissue Loss Disease (SCTLD), a novel disease that spread throughout the Florida Reef Tract beginning in 2014. As information about this disease was just emerging, it was not immediately recorded separately in the monitoring databases and did not appear in other regions of the Caribbean until a few years later (Alvarez-Filip et al., 2019). This outbreak was emerging during the time frame of this study, so is not surprising we did not capture a region-wide effect from disease due to this because many Caribbean regions were not affected until 2017 or later.

Disturbance interactions are hard to detect on degraded reefs

Between 2014-2017, warm sea surface temperatures resulted in a global, multi-year coral reef bleaching event (Eakin et al., 2019). This bleaching caused devastation in terms of coral mortality on many of the world’s reefs, most notably the Great Barrier Reef in Australia. However, it is important to note that impacts were not uniform across all locations, either globally or within the Caribbean basin (Muñiz-Castillo et al., 2019). In the Caribbean, it appears that bleaching onset and severity varied across subregions, but reports on bleaching and mortality during this event are still being compiled (NOAA, 2018). Hurricanes were also a major impact during this time, with “active” seasons in several years (Table 3.1); therefore, it is surprising that a stronger signal of the mitigative effects of hurricanes on bleaching was not detected.

Once we consider the state of contemporary Caribbean reefs, it may not be so surprising that we did not see strong evidence for disturbance interactions as expected. In recent decades, Caribbean coral reefs have been degraded to low coral cover reefs, many of which are dominated by weedy and stress tolerant species (Green et al., 2008; Alvarez-Filip et al., 2013; Toth et al., 2014; McWilliam et al., 2020). And in fact, I previously demonstrated the reduced effect of tropical storms on coral cover, due to the already degraded state (Mudge and Bruno, in prep, chapter 2).There is also evidence that in recent years, the onset of bleaching is occurring at higher temperature thresholds, suggesting that coral communities may either have acclimatized to thermal stress or that a higher proportion of thermally tolerant species remain (Sully et al., 2019). Therefore, it’s possible that contemporary coral reefs are becoming more resistant to thermally induced disturbances such as bleaching. If this is the case, it might be more difficult to detect a strong interaction or cumulative effect of bleaching and tropical storms on coral cover specifically because reefs are more resistant to these disturbances in the first place.

There are still many unknowns regarding the future of coral reefs and how disturbance interactions will drive changes to coral communities. While it appears there is a reduced effect of hurricanes on coral cover, we should still be concerned about them, and other disturbances, because disturbance regimes are changing. An increase in the intensity and frequency of thermal stress events is already well documented (Lough et al., 2018; Muñiz-Castillo et al., 2019; Skirving et al., 2019), and subsequently so is an increase in the frequency and intensity of thermally-induced disturbances (Webster et al., 2005; Bruno et al., 2007; Elsner et al., 2008; Cheal et al., 2017; Eakin et al., 2019; Sully et al., 2019). Altered disturbance regimes are frequently quantified by changes to disturbance frequency and intensity, yet other metrics are also changing. For example, Atlantic hurricane seasons may be getting longer. A record was set in 2019 in which the previous five consecutive years (2014-2019) had a named storm form in the Atlantic before the official start of the season. Lengthening hurricane seasons decreases the time for recovery between hurricane events. There is also evidence of increasing/broader temporal and spatial extents to which heat stress has been documented on coral reefs in the past decade. An increase in bleaching observations could be due to more areas being affected or more days SST are elevated during peak events (Skirving et al., 2019).

Cascading effects

To fully understand consequences of disturbance interactions, it is important to consider indirect or cascading effects on other aspects of coral biology and the broader reef community. The primary effect on coral outlined in this study is the change in coral cover, presumably due to coral mortality. However, we know that combinations of bleaching, disease, and storms have negative impacts on the reproduction, recruitment, and growth of coral reef organisms - all of which are crucial for the survivorship of coral reef communities. Decreased coral recruitment (Fabricius et al., 2008; Mallela and Crabbe, 2009), reduced fecundity (Williams et al., 2008; Weil et al., 2009; Fisch et al., 2019), and reduced growth rates (Goreau and Macfarlane, 1990; Carilli et al., 2009) are some well documented responses to disturbances. Most of what we know about disturbance impacts on coral biology and physiology comes from individual events; more research is needed to quantify the effects of interactions on these processes.

Corals are foundational species of coral reef ecosystems, therefore we would expect disturbance-induced changes to coral assemblages to also affect populations of other reef organisms. Corals are facilitators for the larger reef community because they provide habitat and predator refuges for fishes and benthic invertebrates and reef structural complexity is well documented as a predictor of fish assemblage characteristics (Idjadi and Edmunds, 2006; Darling et al., 2017; Richardson et al., 2017). A decline in structural complexity of reefs post-disturbance, particularly after strong storms, reduces habitat availability for these organisms (Alvarez-Filip et al., 2011a). Concomitant declines in coral feeding fishes is also well documented (Adjeroud et al., 2002; Wilson et al., 2006; Stuart-Smith et al., 2018); however, fish communities can be differentially impacted depending on how much of the physical reef structure remains intact. Additionally, SST are also impacting populations of fishes, algae, and benthic invertebrates (Maharaj et al., 2018; Robinson et al., 2018; Stuart-Smith et al., 2018), but more research is needed to understand interactions between SST and changes to coral assemblages on the broader reef community structure.

Conclusion

This is a novel investigation of the generality of disturbance interactions between storms, bleaching, and disease on Caribbean coral reefs across a wide spatial and temporal scale. I found some support for these hypotheses and their cumulative effects on reefs; but overall, patterns were inconsistent on a year to year basis. However, some of the inconsistencies in these patterns could arguably be due to limitations in monitoring data for this type of study or due to the already degraded condition of contemporary Caribbean reefs. Increasing sea surface temperatures are still the greatest threat to coral reef ecosystems and understanding how SST will drive changes to reefs- both directly and indirectly through cascading effects of disturbances and their interactions- is critical for predicting future reef condition.

Table 3.1 Summary of Atlantic storms between 2006-2017

Data summarized from NOAA's HURDAT dataset for the Atlantic Ocean Basin. Storms were filtered to include both tropical storms and hurricanes, but not tropical depressions.

Year	# Total Storms	# Hurricanes	# Cat 4-5 Hurricanes
2006	11	5	0
2007	16	7	2
2008	16	9	4
2009	9	3	1
2010	19	12	4
2011	19	7	2
2012	19	10	0
2013	14	2	0
2014	8	6	1
2015	11	4	1
2016	15	7	2
2017	17	10	4

Table 3.2 Disturbance interaction model results

Cumulative impacts of disturbances on the annual rate of change in coral cover (CR) and absolute difference in coral cover (from beginning to end of time series).

Response Variable & Fixed effects	**Estimate**	**Standard Error**	**Confidence Intervals**	**t-value**	**p value**	**Direction of slope**
Dependent variable = Annual rate of change in coral cover (CR)						
Intercept	-.11	0.39	-0.87-0.66	-0.27	0.786	
Total # Storms	0.4	0.34	-.028-1.07	1.15	0.250	

Bleaching	0.08	0.23	-0.38 – 0.54	0.33	0.738	
Disease	0.04	0.23	-0.41 – 0.48	0.16	0.873	
Total Storms x Bleaching	0.63	0.44	-0.24 – 1.50	1.41	0.159	
Total Storms x Disease	-0.53	0.22	-0.97 – -0.09	-2.38	**0.017**	negative
Bleaching x Disease	-0.18	0.20	-0.58 – 0.23	-0.86	0.393	
Total Storms x Bleaching x Disease	-0.05	0.15	-0.35 – 0.26	-0.30	0.763	
Random effects variance: σ^2*= 2.77 n= 112, in 6 ecoregions* *Marginal* R^2 = 0.053; *Conditional* R^2 *= 0.225*						
Dependent variable = Absolute difference in % cover over the time series						
Intercept	-0.28	2.3	-4.79 – 4.23	-0.12	0.9	
Total # Storms	0.76	1.67	-2.50 – 4.02	0.46	0.65	
Bleaching	0.21	1.1	-1.95 – 2.37	0.19	0.85	
Disease	-.016	1.04	-2.19 – 1.88	-0.15	0.88	
Total Storms x Bleaching	3.35	2.03	-0.63 – 7.34	1.65	0.1	
Total Storms x Disease	-2.59	1.02	-4.60 – -0.59	-2.53	**0.011**	neg
Bleaching x Disease	-0.78	0.94	-2.63 – 1.06	-0.83	0.406	
Total Storms x Bleaching x Disease	-0.25	0.71	-1.64 – 1.13	-0.36	0.716	
Random effects variance: σ^2*= 57.95 n= 112, in 6 ecoregions* *Marginal* R^2 = 0.057; *Conditional* R^2 *= 0.34*						

Signif. codes: 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1**

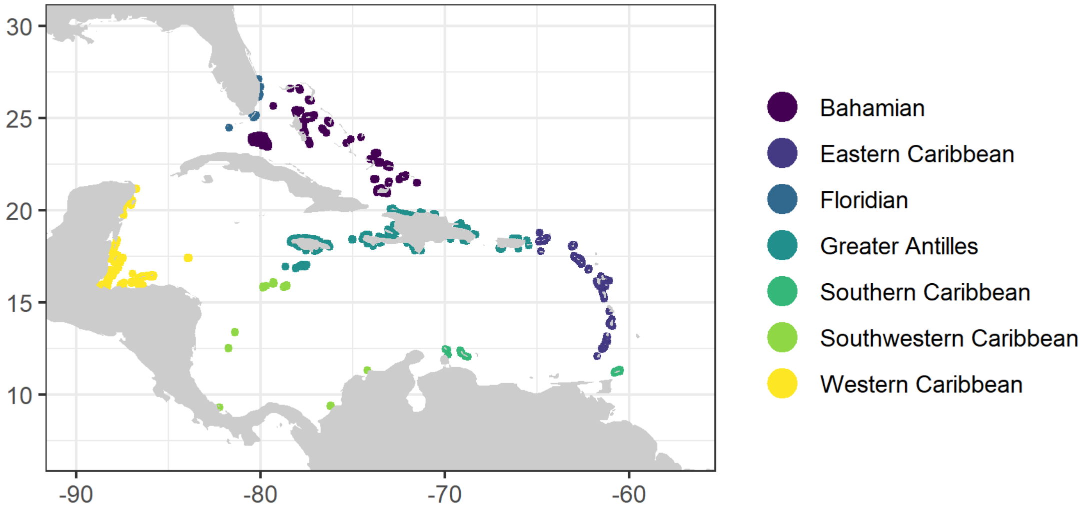


Figure 3.1 Map of study locations

Coral reef survey sites aggregated from the AGRRA and ReefCheck databases. There is a total of 1,081 unique sites surveyed between 2006-2017.

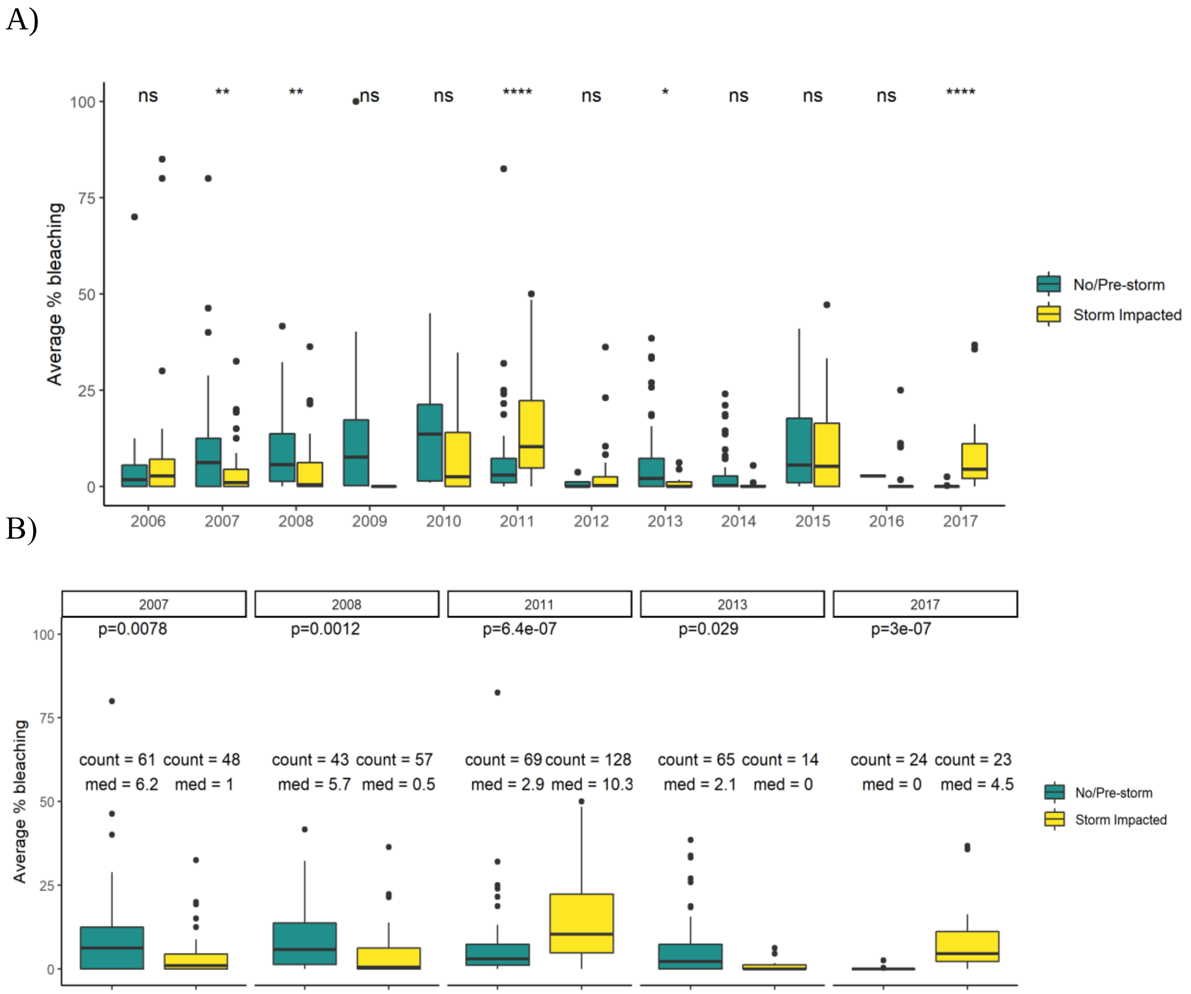


Figure 3.2 Bleaching at storm impacted vs. unimpacted sites

Annual coral bleaching between impacted and unimpacted sites in the Caribbean. Differences were evaluated using non-paired Wilcox tests. A) All years. Asterisks denote level of significance (ns: $p > 0.05$, * $p <= 0.05$, ** $p <= 0.01$, *** $p <= 0.001$).; B) Only years that had a significant difference ($p < 0.05$).

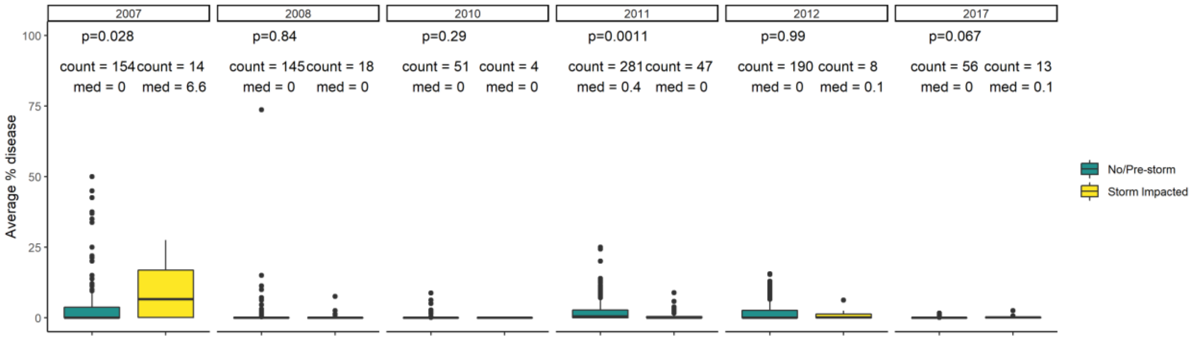


Figure 3.3 Coral disease at storm impacted vs. unimpacted sites

Only years with both no/pre-storm and post-storm data were retained. Differences at impacted vs. unimpacted sites were evaluated using non-paired Wilcoxon tests.

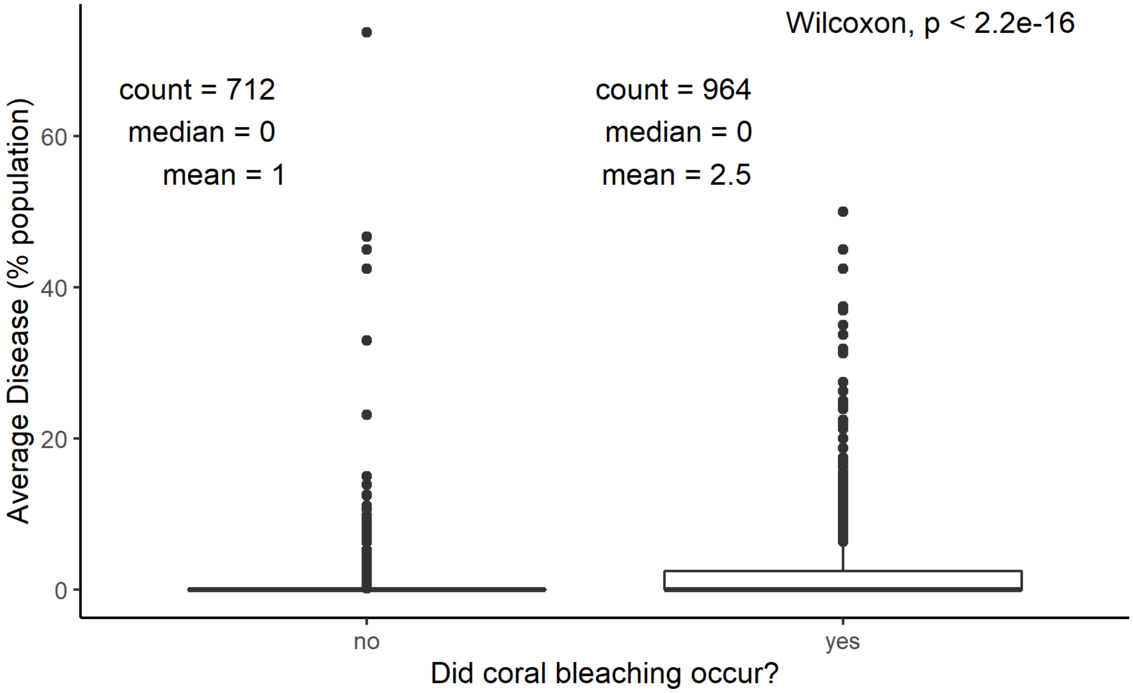


Figure 3.4 Disease at bleached vs. unbleached sites

Differences in disease prevalence when bleaching was observed vs. not observed at a site.

Data is pooled for all years and locations in the Caribbean.

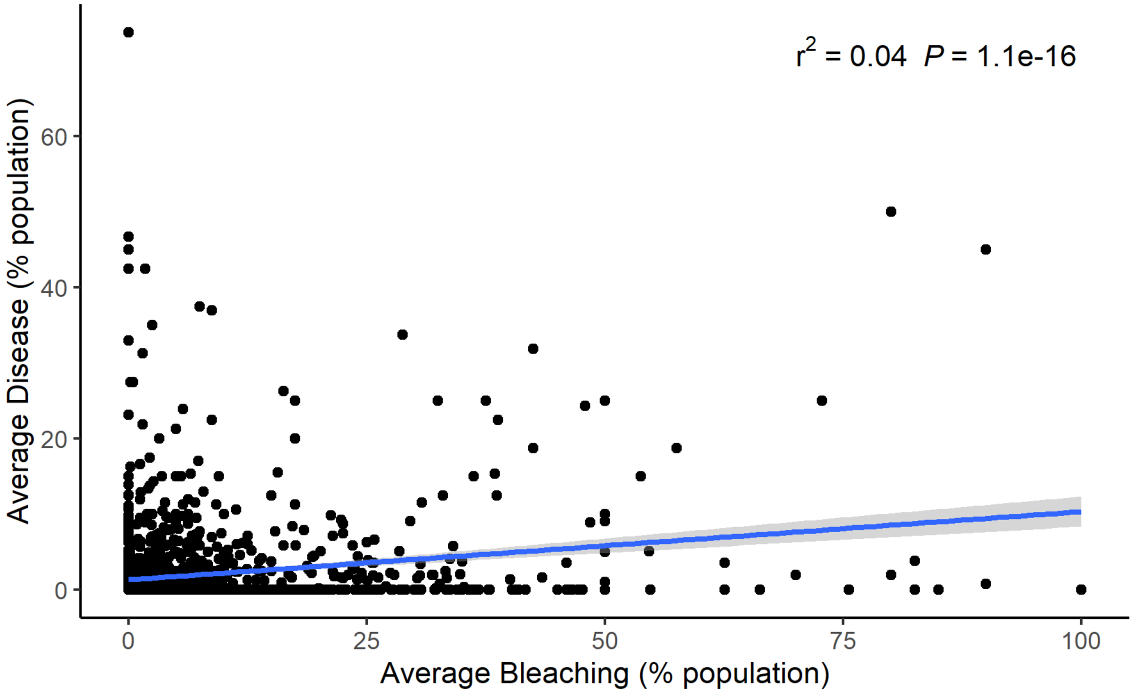


Figure 3.5 Effect of bleaching extent on disease prevalence

Results of ordinary least squares regression of bleaching extent (over the entire surveyed population) on the disease prevalence (% of population).

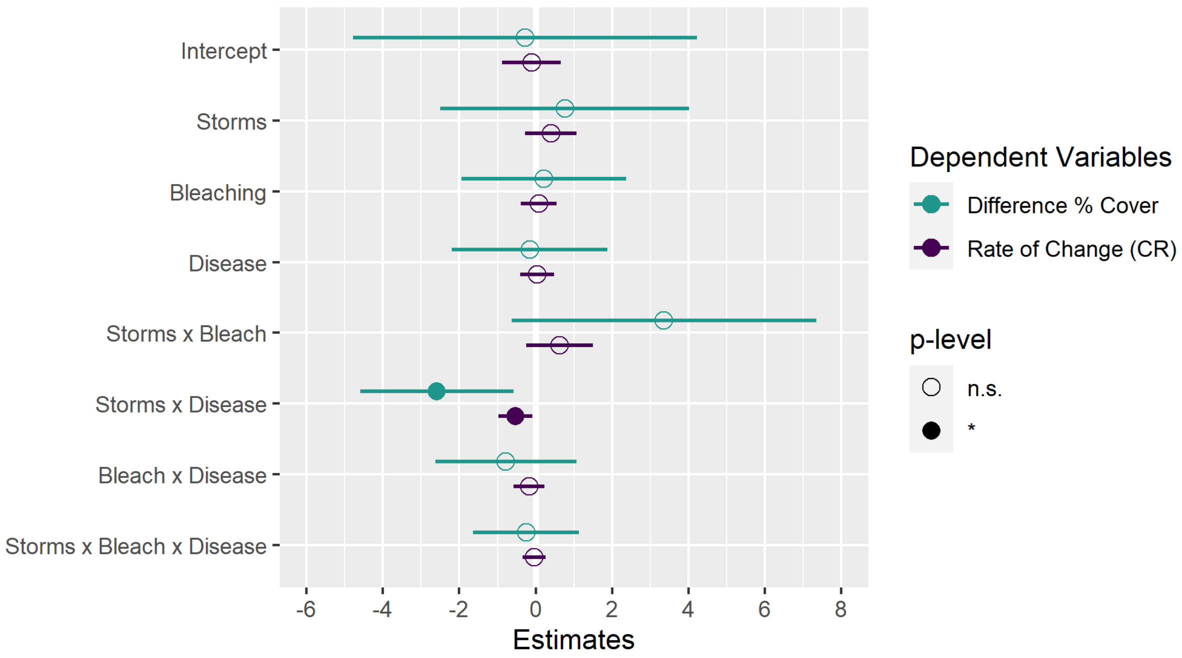


Figure 3.6 Interactive effects of disturbances on coral cover

Effect of individual disturbances and their hypothesized interactions were evaluated using a linear mixed effects model. All predictors (disturbances) treated as fixed effects and site as a random effect. Asterisks represent significance (ns = $p > 0.05$, * $p < 0.05$).

CHAPTER 4 : USING BASELINE DATA TO COMMUNICATE CHANGES TO CORAL REEF COMMUNITIES

Introduction

One critical aspect of effective resource management is understanding current ecosystem condition and how it has changed over time or in response to disturbance (Stoddard et al., 2006; Tulloch et al., 2018). Ecosystem condition is often evaluated through a selected set of indicator variables relevant to the ecological function of that specific system (Harwell et al., 1999; Mcfield and Kramer, 2007). Some types of ecological indicators, such as physio-chemical variables like water pH, dissolved oxygen, and nutrient levels, have scientifically derived, clearly defined thresholds for what is considered healthy (Hallock, 2002; Ecocheck, 2011; U.S. Environmental Protection Agency, 2020). Indicators may also be evaluated by assessing trends or comparing a recent measurement to a reference or baseline value (Kramer, 2003; Díaz-Pérez et al., 2016; Eddy et al., 2018; Hansen and Phillips, 2018).

Baselines are used to evaluate changes in ecosystem or community condition over time and can serve as reference points or benchmarks for management and restoration (Campbell et al., 2009; Bruno et al., 2014; Gatti et al., 2015). Ecological baselines are usually considered to be the initial, pre-impact state of an ecosystem or community before disturbances or degradation, commonly described as a "pristine" state (Stoddard et al., 2006; Bruno et al., 2014). The scientific consensus is that no single baseline value exists for most ecosystem or community level metrics, but rather a range of potential values, dependent upon disturbance history, timing of succession, and natural variation along environmental gradients (Morgan et al., 1994;

Stoddard et al., 2006; Bruno et al., 2014; Tulloch et al., 2018) The concept of “historical range of variability” uses historical data to define the boundaries for ecosystem variables as they vary over contemporary temporal and spatial scales (Morgan et al., 1994). Understanding this historical variation in ecosystem dynamics can be useful for communicating changes to ecosystem status and effects of management interventions.

Obtaining historical quantitative data, when possible, can be paramount to determining what represents an accurate baseline condition and can provide a contrast against “shifting baselines”. By definition, “shifting baselines” means that with each generation, the idea of what represents a baseline condition for an ecosystem is changing due to large fluctuations in ecosystem condition over a short period of time, and users are more apt to accept the condition of their first observation as the baseline (Pauly, 1995). The “shifting baselines” phenomenon is widely documented, particularly in fisheries (Knowlton and Jackson, 2008; Pinnegar and Engelhard, 2008; Gatti et al., 2015). A recent survey of coral reef experts and recreational SCUBA divers did not find evidence of the shifting baseline phenomenon on estimates of baseline coral cover on tropical reefs, perhaps a result of information sharing among generations (Eddy et al., 2018). Therefore, it may be possible to combat the shifting baseline syndrome if we properly utilize and convey historical information when evaluating contemporary coral reef condition.

In many cases, quantitative historical data is lacking or it is difficult to integrate historical information due to different methodologies or types of observations documented. For coral reef ecosystems, we gain an understanding of the persistence (or lack thereof) of reefs species from past specimen collections (Hoeksema et al., 2011) and coral cores (Johnson et al., 2017) and the decline in extent of reef habitat from old shipping logs and maps (McClenachan et al., 2017) on the scale of centuries. These types of documentation provide invaluable information regarding past reef condition, but are hard to reconcile with data from underwater in-situ surveying, which began in the 1960s, and has become the standard currency for obtaining quantitative reef data.

Determining a "pristine" baseline is particularly difficult because quantitative survey data was collected post-human impact (i.e. post-industrial revolution) when ecosystems were already experiencing anthropogenic disturbances (Knowlton and Jackson, 2008; McLean et al., 2016; Eddy et al., 2018). When quantitative historical (pre-1950s) survey data is available, bias may exist from limitations in habitat accessibility or study design. The selection of survey location, "snapshot studies" that survey at only one time point, and disturbance context of a site (e.g. if there was a recent physical disturbance such as a hurricane or ship grounding) can influence whether a study truly represents the average reef condition at that time. However, imperfect historical data should not discount its use in developing baseline or reference values (Alagona et al., 2012). Understanding past conditions, or changes between past and present conditions, is invaluable for understanding the magnitude and composition of changes to ecological communities. Quantitative historical data can be used to develop baseline conditions if potential biases and limitations are acknowledged and accounted for when communicating comparisons between present day and baseline ecosystem conditions.

Communicating the status of ecosystem health is imperative to advise on policy and management decisions, and inform the broader public about the status of ecosystems important to them. "Report Cards" are one example of a commonly used tool to communicate the state of an ecosystem to the broader public. Most types of ecosystem report cards use a familiar system of grading which reports on individual scores for indicator variables as well as summary score when all indicators are considered together (Harwell et al., 1999; Fennessy et al., 2007;

Ecocheck, 2011; McField et al., 2018). For coral reef ecosystems, there are at least two widely used indices to “score” coral reef condition for use in report cards of Caribbean coral reefs. The Reef Health Index (RHI) developed by the Healthy Reef Initiative (Mcfield and Kramer, 2007) and the Coral Health Index (CHI) developed by the Nature Conservancy (Kaufman et al., 2011) are both used to report on overall coral reef condition from a scale of “critical/poor” condition to “good” or “very good” condition . Each index is a summation of slightly different indicators but both contain measures to evaluate benthic condition using percent coral cover, which is the percentage of a benthic space that is comprised of living scleractinian coral species. Percent cover is a quantitative measurement calculated as the proportion of points from a transect line or quadrat grid. High percent coral cover on a reef is considered healthy because it signals potentially high abundance of reef-building species, which provide habitat for many other reef dwelling organisms and contributes to habitat growth and ecosystem functionality (Risk, 1972; Carpenter et al., 1981; Gratwicke and Speight, 2005; Wilson et al., 2007; Dustan et al., 2013).

There is a lot of value in using report cards as a communication tool to managers and the public: it’s a familiar, succinct format to convey the complexities of changing coral reef dynamics. However, when it comes to the coral cover indicator specifically, current reporting methods lack a nuanced, quantitative way to assign a “grade” that takes into account the natural or historical variability of coral cover at a particular location. For example, both the HRI and CHI indices use standard threshold values for all reef localities and environments (e.g. backreef and forereef), without consideration for expected variation in coral cover over time or across natural environmental or bathymetric gradients. This may result in undue pressure or target values being placed on a coral reef where a “very good” coral cover percentage was not historically observed or even possible to obtain in certain marginal habitats. Additionally, there is a lack of transparency in how the cutoff values for each health category was assigned. The Healthy Reefs Initiative report cards provide descriptions for the index development; but no specific guidance on how the grading categories were assigned numerically (Mcfield and Kramer, 2007; Healthy Reefs Initiative, 2008), while the CHI methods created five equal bins from a scale of 0-1 (Kaufman et al., 2011) . To address these issues, the use of quantitative, historical data, when available, can be used to determine habitat or site-specific threshold values on which grades are based.

The purpose of this study is to use historical, quantitative baseline data to develop a standardized approach for communicating changes in coral reef condition. I demonstrate the utility of these methods by applying them to the National Coral Reef Monitoring Program (NCRMP) benthic data from Florida, an area which has high habitat heterogeneity and availability of historical quantitative surveys. Where possible, I used historical data to create baseline distributions based on location and reef attributes, which are then divided by quantiles to create bins for related report card “grades”, ranging from critical to excellent (similar to Figure 1 in Stoddard et al., 2006). This study addresses the limitations of current reporting metrics by providing mathematically defensible baseline indicator values for Florida reefs that can be easily understood by managers and science practitioners.

Methods

Project development and site selection

This study was developed in partnership with the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Conservation Program (CRCP), which runs the National Coral Reef Monitoring Program (NCRMP). An emerging project of the CRCP and NCRMP is to create coral reef report cards that will communicate the status of coral reef ecosystems within

U.S. jurisdictions. Florida was chosen for this particular case study due to the timing of report card development within U.S. Atlantic coral reefs and the known availability of historical data for the Florida Reef Tract. Florida is also the only location with extensive shallow-water reef habitats in the continental United States and contains several protected zones including the Florida Keys National Marine Sanctuary, the Dry Tortugas National Park, Biscayne National Park, several state parks and coastal National Wildlife Refuges.

The Florida Reef Tract is a barrier reef system that stretches approximately 300 miles from Martin County in Southeast Florida to the Dry Tortugas, situated beyond the Florida Keys (Figure 4.1). The NCRMP, which conducts biannual ecological and socioeconomic surveys of U.S. jurisdictional reef systems, designates Florida reefs into three distinct sampling regions: Southeast Florida (SEFL), stretching from Martin County southward to Miami; the Florida Keys (FLK) stretching from Miami southward to Key West, and the Dry Tortugas (DT) which are found west of the keys (Figure 4.1). Each subregion contains a different part of the Florida Reef Tract system and can vary in habitat type, depth, and vertical relief. Reef habitats in SEFL are mostly marginal, relict reef habitats with an abundance of hard bottom habitat and historically low coral cover. The FLK reefs consist of both shallow (<6m) and deep (>6m) patch reefs and spur and groove systems. The Dry Tortugas are mostly patch reefs, with some spur and groove formations.

Historical Data Acquisition

I conducted a literature review for historical references and reports of coral cover on Florida reefs targeting the earliest data available through the end of the 1990s. Searches were conducted in the NOAA Institutional Repository and Web of Science and included terms such as “florida reefs”, “historical florida reefs”, “florida coral”, as well as search terms for individual locations such as “Looe Key”, “Florida Keys”, “Dry Tortugas”, “Broward County”, etc., although this list is non-exhaustive. Long-term monitoring data from the Florida Coral Reef Evaluation and Monitoring Project (CREMP) from 1996 to 1999 was also included. A reference was included in this study if it provided a specific reef location (providing GPS coordinates or a reef name and location description or map), year of survey, and percentage of hard coral cover. Experts from NOAA’s CRCP and benthic monitoring team reviewed locational information provided from historical resources to verify study location and attributes from historical surveys. If historical data was only provided in figures (not tables), data points were extracted using Web Plot Digitizer (Rohatgi, 2018).

A total 18 references (Table 4.1) were retained which included 982 data points (either one survey or a study with averages of multiple surveys), each representing a percent coral cover value for a particular time and location. The earliest data comes from surveys conducted in 1974 and we used the end of the CREMP monitoring program (year 2000) as a cutoff point for what constitutes “historical” data for this particular study. These references provide quantitative data across a range of natural gradients and disturbance states. Historical disturbances to Florida reefs include hurricanes, the white-band disease outbreak which dramatically reduced populations of *Acroporid* corals, and physical damage from boat anchors or ship groundings.

Creating baseline distributions

Historical coral cover data were divided by NCRMP sampling regions: Southeast Florida (SEFL), the Florida Keys (FLK) and the Dry Tortugas (DT). The distribution of coral cover and summary statistics were calculated for each region. The current NCRMP benthic sampling protocol also considers a complex combination of “strata” within each subregion. These sampling strata are defined by local reef attributes such as habitat type or substrate characteristics, depth, vertical relief, and location relative to shore. To provide meaningful targets for specific regions or habitats within each region, I evaluated coral cover distributions based on reef attributes, when possible, such as habitat type, reef relief, and depth of reef site. Information on these specific attributes were generally available in the historical literature and are used as distinguishing reef attributes for the various NCRMP sampling strata. The purpose of this exercise was to examine natural breaks in the data as a means of determining subcategories within each region which could be scored in order to avoid assigning meaningless target values to specific regions or habitats within a region. Additionally, the aim was to create baseline distributions which provide an adequate comparison against current-day NCRMP monitoring data. Wilcoxon tests were used to validate decisions for either pooling or separating reef attributes into distinct baseline distributions. Significant breaks between reef attribute categories were used only if enough baseline data existed to make a baseline distribution and it was a relevant category for scoring current NCRMP data. Figure 4.2 demonstrates the decision-making process in both a general application (A) and how we applied this process to the Florida Reef Tract (B).

Determining report card scoring metrics

Similar to other ecological scoring indices, I developed a five-bin scoring index ranging from “critical” to “excellent” condition. Distribution quantiles were used as cut off points for establishing thresholds between each scoring level (

Table 4.2). The median historical coral cover value was used as cutoff between an overall positive score and neutral (fair) or negative (poor, critical) scores (i.e. if present day coral cover is above the historical median value, the reef is considered to be in good or excellent condition). Some historical distributions are left-skewed (e.g. Figure 4.3), therefore the median was a more appropriate descriptor than historical average coral cover for determining this break. This method is advantageous in that a standardized methodology can be applied for determining scoring threshold cutoffs, but when applied to each distinct baseline distribution, the specific coral cover values to create these scores are unique and relevant to each region and, when applicable, reef attributes.

Results

Baseline distributions by region and reef attribute

Data Summary

The number of observations, mean, standard deviation, median, minimum, maximum, and range of percent hard coral values are reported for each distinct Florida region or reef attribute combination in Table 4.3. The percent cover values for each scoring threshold are reported in

Table 4.4.

Florida Keys (FLK)

The Florida Keys region is well sampled in the historical literature. I aggregated 817 data points from 13 references with sampling occurring between 1974-2000 (Table 4.1). Historical survey data exists for reefs described as bank (forereef or spur and groove), patch, hardbottom, and reef flat. Current NCRMP sampling classifies FLK reefs into 7 strata: 3 of which are of patch reef habitats (inshore, mid-channel, and offshore) and 4 of which are bank reefs (shallow linear, mid-channel linear, deep low relief, high relief). Enough historical data existed to create separate baseline distributions for patch reefs (n=202) and bank reefs (n=484). This decision was verified by the significant difference in historical coral cover documented in bank and patch reefs (Supplement Figure 8, Wilcox $p=9.9\times10^{-10}$).

Next, I evaluated within habitat differences in historical coral cover reef relief and depth. Descriptions of reef relief were unknown (n=799) for most of the data, so relief could not be used as a distinguishing feature. However, all sources indicated a depth of the historical surveys. There is a significant difference between historical coral cover at shallow (<6m depth) and deep (>6m) patch reefs (Supplement Figure 9, Wilcoxon, p=.0004); however, current NCRMP sampling strata for patch reefs evaluates location (inshore, mid channel, offshore), not depth specifically. Therefore, all historical patch reef data was pooled together for one distribution. There is also a significant difference in historical coral cover between shallow and deep bank reefs (Supplement Figure 10, Wilcoxon p= 0.00041). Based on this current classification and the natural breaks in the historical data, I created baseline distributions for patch reefs, shallow bank reefs (<6m depth) and deep bank reefs (>6m depth) (Figure 4.3). The historical data for hardbottom and reef flat areas were not used for these baseline distributions.

Dry Tortugas (DT)

Historical data for the DT region consists of 91 data points from 5 sources spanning 1975-1977 and 1999 (Table 4.1). Current NCRMP sampling classifies DT reefs into 4 strata, based on substrate characteristics (contiguous, spur and groove, isolated, rubble) and vertical reef relief (low <0.3m; mid= 0.3-0.7m; high > 0.7m). However, there is a mismatch in the NCRMP substrate classifications and historical reference descriptions of habitat type, making this reef attribute difficult to score. However, historical descriptions of reefs in the DT area provided both qualitative and quantitative information on reef relief, described as low, mid, mixed, or high relief. There are significant differences in historical coral cover between reefs of low, mid, and high relief (Supplement Figure 11). However, reefs described as having "mixed" relief were not significantly different from the "mid" relief category (Wilcoxon $p = 0.31$), and were pooled together into one mid-relief category. Therefore, based on the NCRMP classification and historical data available, I created distributions for low, mid, and high relief reefs (Figure 4.4) in the Dry Tortugas. Historical surveys that did not provide information on reef relief (n=18) were excluded from these baseline distributions.

Southeast Florida (SEFL)

The SEFL region is the least sampled region historically. I gathered 74 data points from two baseline resources, spanning 4 years of sampling (1979, 1985, 1989, 1992) (Table 4.1). Current NCRMP sampling classifies SEFL reefs into 8 strata, using a complex combination of descriptors, including location (nearshore, midshore, and offshore), and substrate quality or rugosity (homogenous habitat or edge/transition reef). However, not enough detail exists in the historical data to further segregate baseline distributions according to the specific NCRMP sampling strata definitions. The reef descriptions from historical resources indicate that reef habitat would be classified as “hardbottom”, with no other marked or distinguishing reef attributes. Therefore, we pooled all historic SEFL survey data into one baseline distribution for the subregion (Figure 4.5).

Scoring thresholds and comparison to other indices:

Using distribution quantiles, the percent coral cover thresholds for each scoring metric (critical to excellent) are reported in Table 4. Thresholds for the RHI index and CHI index are also reported for comparison. The RHI index thresholds are for percentage of hard coral cover, which is the same as this study; however, the thresholds for the CHI contain a combined percent cover of hard corals and crustose coralline algae (CCA), a type of calcified red algae that contributes to reef calcification and also provide a hard substrate for larval settlement. Therefore, the thresholds for the CHI index are not directly comparable to this study or the RHI index.

Comparison between scoring thresholds in this study and those defined by RHI are markedly different for some Florida reefs. The range for what constitutes a “good” reef in SEFL and on low/mid relief reefs in DT would likely be categorized as poor or fair condition using the RHI index (Figure 4.6). This suggests that the RHI index is likely not appropriate for scoring lower relief and hardbottom habitats. The baseline scoring thresholds for FLK patch and FLK shallow bank reefs are most similar to the RHI index; although reefs categorized as “poor” by RHI standards would be classified as “fair” using the baseline standards from this study. Only the DT high relief reefs have thresholds higher than those presented by the RHI index. Note that for all scores in Figure 4.6, any coral cover above the “good” threshold would be considered “excellent”

Discussion

The goal of this study was to demonstrate the utility of using historical baseline data to establish metrics for how changes in coral cover are communicated. Using the Florida Reef Tract as an example system, I obtained historical percent coral cover data for all three subregions of Florida reefs (Southeast Florida, Florida Keys, Dry Tortugas) spanning 1974-2000. I found that baseline distributions of coral cover varied significantly between subregion and reef attributes such as habitat type, vertical relief and depth. These results suggest that standardized thresholds for scoring coral condition may not be appropriate for all coral reef locations or zones, as there is no accounting for variation across natural environmental or bathymetric gradients, nor consideration of site-specific historical condition. However, a standardized method for defining such thresholds, as outlined in this study, maintains a standard score ranking system (i.e. "critical" to "excellent" condition), but accounts for variation across reef locations and habitats, thus providing a more individualized approach for scoring unique reefs.

Low relief reefs and marginal habitats such as those found in DT and SEFL had a narrow distribution of historical values for coral cover (Table 4.3, range= 10.6% (DT), 27.34% (SEFL) cover) and high relief, shallow reef habitats had a much wider distribution of historical cover values (Table 4.3, range= 47%, 58% cover). As a result, the threshold values for scoring bins (critical to excellent) varied between reefs, with "excellent" status varying from as low as ~7% coral cover (Dry Tortugas low relief reefs) to as high as ~57% coral cover (Dry Tortugas high relief reefs). Out of the 7 baseline distributions made for Florida reefs in this study, only 1 reef system (DT high relief reefs) resulted in scoring thresholds that were higher than the RHI index; all other Florida reefs had lower percent cover thresholds between score categories. Scoring thresholds of reefs in marginal habitats or with low vertical relief (e.g. SEFL, DT low relief, DT mid relief reefs) were markedly different from the RHI index, with the exception that thresholds for "critical" reef status remained less than 5% cover. This demonstrates that standardized thresholds from indices like RHI may not be appropriate for all reef locations and habitats, and may result in more negative scoring results (i.e. poor and critical condition reefs), even if present-day reefs have a similar coral cover to what was historically observed. It was not possible to make a direct comparison between the methods in this study and the CHI index, as the CHI index includes percent cover of both hard corals and crustose coralline algae (CCA). There was not enough information in the historical literature to include CCA in this study.

Limitations to interpreting historical ecological data

The amount of historical coral cover data from Florida reefs is comparatively robust; however, like most coral reef studies, data are recent on an ecological timeframe (post 1950s) and recorded after human influence (Dustan and Halas, 1987; Glynn et al., 1989; Toth et al., 2014). Therefore, our baseline coral cover data is not a measure of "pre-human impact" conditions and should not be considered a reconstruction of pristine reef conditions. However, the thresholds we present here may be a more attainable benchmark for restoration and management, even though they are predicated on anthropogenic influences. Societies are reckoning with the fact that no ecosystem, even remote coral reefs are untouched by human activity, so returning to a true pre-human impact state may be an unrealistic expectation placed on resource managers. One alternative is to set ecologically relevant, yet attainable, benchmarks for restoration and management that consider anthropogenic impacts, using historical information as a guide.

Certain biases may exist in the historical ecological survey data aggregated in this study. First, site selection bias can result in a disproportionately higher amount of coral cover documented. For example, if researchers chose to survey the "best" reefs (i.e. ones known to have high cover) without any stratified sampling methodology, we are left with data that reflect only those best reefs and not a general understanding of historical reef condition (Eddy et al., 2018). Second, disturbance ecology was a trending topic in the 1970s with many disturbance studies undertaken on reef habitats, particularly in Florida (Porter et al., 1982; Voss, 1983; Connell and Keough, 1985; Dustan and Halas, 1987). Conversely to the site selection bias, studies evaluating post-disturbance impacts to coral reefs may contribute to lower than expected values of percent coral cover. However, we know that disturbances, particularly tropical storms, are ubiquitous on reefs, so post-disturbance states are representative of reefs along a natural successional trajectory. Lastly, we recognize that historical survey data is limited and not every reef location will have the abundance of historical survey data that exist for heavily researched areas like Florida. Therefore, the insights we can make about past reef condition rely on the type and amount of historical information available.

Aside from historical in-situ ecological surveys, other types of data exist which can provide insight on historical reef condition, and although challenging, should be incorporated into our contextual understanding of reef condition over time (Alagona et al., 2012). For example, coral core samples have demonstrated the persistence of coral reef communities in the Great Barrier Reef through geological time, and researchers have pinpointed specific drivers of change (water depth) to coral composition (Roche et al., 2011; Johnson et al., 2017). Nautical charts from the 18th century revealed an overall loss of 52% in coral extent in the Florida Keys, most notably from inshore areas, which are now dominated by seagrasses or bare substrate (McClenachan et al., 2017). Documenting changes to the spatial extent of reef habitat suggests that even coral cover data from the 1960s will inherently underestimate coral cover due to the fact that the amount of extant coral habitat has declined.

When historical survey data is not available, space-for-time comparisons are often implemented to evaluate current reef condition compared to a different, relatively undisturbed or "archetypal" reef (Knowlton and Jackson, 2008; Sandin et al., 2008; Coté et al., 2013; Bruno et al., 2014). In the absence of time-series data, researchers compared reef condition between inhabited and uninhabited reefs in the Northern Line Islands and showed that reefs were in better condition when further away from human communities and intact food webs, which were associated with higher coral cover and lower coral disease, on isolated reefs became the "baseline" condition (Sandin et al., 2008). However, the negative relationship between human population density and coral degradation does not appear to be a global phenomenon (Bruno and Valdivia, 2016), so we should exercise caution when extrapolating baseline conditions from one location and applying them to a broad geographical scale. Similarly, reefs along the island of Jamaica had been viewed as an "archetypal" reef for changing ecological dynamics in the Caribbean (Woodley, 1992). However, researchers showed that the decline of coral reef condition in Jamaica was worse, not typical, when compared to reef degradation in other parts of the Caribbean (Woodley, 1992; Coté et al., 2013). Space-for-time comparisons can be an appropriate substitute when historical quantitative data is lacking; however, care should be taken to ensure that comparisons are made between sites that have similar ecological histories.

Is a high score meaningful?

How we define indicator thresholds has significant impact on the conclusions we draw regarding ecosystem condition (Stoddard et al., 2006). Therefore, any assumptions, value judgements, and biases in historical data must be explicitly stated in order to assess if a high score is meaningful (Campbell et al., 2009). The first assumption is that we equate high coral cover with a healthy reef. We make this assumption knowing that much research indicates this pattern is mostly true, as high coral cover reefs provide more habitat for other reef organisms and support higher species diversity (e.g. Risk, 1972; Gratwicke and Speight, 2005). However, this assumption can be misleading in cases when a degraded reef maintains high coral cover. For example, high coral cover reefs composed of weedy species or a single-species community likely doesn't provide the same habitat or ecosystem services to other reef organisms (Alvarez-Filip et al., 2011a; Tulloch et al., 2018).

On the reverse end, a low coral cover reef is not always synonymous with "unhealthy" reef condition. Marginal reefs with low coral cover are often limited by natural conditions (ocean conditions, substrate, etc.), so while coral cover is comparatively low, it may be at an appropriate or maximal level for that particular habitat. The CHI index report acknowledges this limitation when reporting on reefs scored as "poor" (Kaufman et al., 2011); however, the distinction between a poor reef due to degradation and a poor reef due to biotic or abiotic limiting factors is not evident in their scoring methods. Our methods of scoring reefs based on reef attributes, such as habitat type and location, can provide some distinction. In our scoring of SEFL and Dry Tortugas reefs, we were able to create scoring distributions based on attributes associated with limiting factors. By scoring reef habitats known to have limited coral cover (hardbottom, low relief) separately from reef habitats known to have abundant cover (high relief spur and groove reefs), comparative changes in those habitats over the years may be more insightful regarding reef degradation.

The second assumption we make is that historical reef condition is healthier than today's coral reefs. Studies confirm that this is generally the case, with widespread documentation of recent reef degradation in the Caribbean and knowledge that contemporary reefs face more anthropogenic impacts from climate change (Gardner et al., 2003; Jackson et al., 2014; Bruno et al., 2019). Both historical data and expert opinion indicate this is true for Florida reefs. Coral cover and condition varied through time based on disturbance history and recovery trajectory, so it is important to discuss the disturbance history when drawing conclusions between studies at different time points. Not every historical study will yield a higher coral cover or more “pristine” reef condition if data were collected after disturbance impact or at a time of stressor overload for that particular system.

Lastly, in this study we make a value judgement that historical coral cover is an appropriate target for management and conservation of Florida reefs. Pristine reef conditions may be unrealistic management goals in an era of accelerated ocean warming and anthropogenic impacts. In the case of most Florida reefs, achieving historical, not necessarily pristine, coral cover would be an improvement to reef condition and provides a tangible, data supported restoration goal to convey to the broader public. Additionally, historical distributions of coral cover represent the range of possible conditions a reef can be in and may be important for assessing post-disturbance reef condition. For example, coral loss is common after a hurricane (Gardner et al., 2005), but managers could assess if the change in coral percent cover post-disturbance is still within a natural range of variability for that particular location or reef habitat.

Conclusion

Baseline distributions of ecological indicators demonstrate the range of conditions an ecosystem can maintain and provide reasonable reference conditions or conservation targets, assuming current ecosystem condition has degraded. This is not a novel concept and ecologists have discussed several ways in which historical data can be used to define reference conditions of ecosystems (Stoddard et al., 2006; Alagona et al., 2012). Although challenging, identifying what constitutes an ecological baseline and incorporating historical data or knowledge into our evaluation of ecosystem condition can increase our understanding of how ecosystems change over time and provide deeper insight into the magnitude of ecological variation. This study demonstrated the utility of using baseline distributions of a coral reef benthic indicator, percent coral cover, to develop metrics for measuring ecological change across a variety of reef locations, habitats, and attributes. These methods provide a clear, transparent way to rank coral cover for ecosystem report cards, based on comparison to site or attribute-specific historical condition.

Table 4.1 Historical references

Reference	Survey location(s)	Years surveyed
(Alevizon and Porter, 2015)	KEYS	1974, 2000
(Antonius et al., 1978)	KEYS	1977
(Aronson et al., 1994)	KEYS	1992
(Blair and Flynn, 1984)	SEFL	1979, 1985, 1989
(Burns, 1985)	KEYS	1981
Coral Reef Evaluation and Monitoring Program (CREMP) of the Florida Fish and Wildlife Conservation Commission	KEYS, DT	1996-1999 (KEYS); 1999 (DT)
(Dustan, 1985)	DT	1975
(Dustan and Halas, 1987)	KEYS	1975,1982, 1983
(Glynn et al., 1989)	Keys	1985
(Hocevar, 1993)	SEFL	1992
(Jaap, 1978)	Keys	1977-1978
(Jaap et al., 1989)	DT	1975-1976
(Murdoch and Aronson, 1999)	DT, Keys	1995
(Bohnsack, 1983)	Keys	1983
(Porter et al., 1982)	DT	1976-1977
(Porter and Meier, 1992)	Keys	1984-1986, 1988-1991
(Voss, 1983)	Keys	1980, 1981, 1983
(White and Porter, 1985)	Keys	1984

Table 4.2 Scoring thresholds

The threshold for each category was determined using quantiles of a distribution.

Score	Quantile	Percentage of data points
Excellent	90%	10%
Good	median-90%	40%
Fair	Q1-median	25%
Poor	10%-Q1	15%
Critical	10%	10%

Table 4.3 Historical coral cover by region and attribute

Summary statistics from the historical references. “n” represents the number of data points used to create the baseline distribution.

Region	Attribute	n	mean	sd	median	min	max	range
FLK	Patch	202	16.28	11.58	16.21	0	48.61	48.61
FLK	Bank; shallow	184	13.79	13.25	10.34	0.37	58	57.63
FLK	Bank; deep	300	9.09	10.00	6.1	0	63	63
SEFL	All	74	5.26	4.9	3.89	0.2	27.34	27.14
DT	Low relief	30	3.45	2.7	2.65	0	10.6	10.6
DT	Mid relief	17	8.4	5.16	6.32	1.58	17.9	16.32
DT	High relief	26	41.85	12.08	43.05	16.84	63.9	47.06

Table 4.4 Comparison of scoring categories

Scoring threshold breakdowns for baseline distributions created here, and previously created coral reef scoring metrics, RHI and CHI.

Index	**Scored Attribute**	**Critical**	**Poor**	**Fair**	**Good**	**Excellent**
This study	FLK: patch reefs	< 1.3%	1.3-6%	6-16.2%	16.2-32.3%	> 32.3%
	FLK: Shallow bank reefs	< 1.5	1.5-3.4%	3.4-10.3%	10.3-30.8%	>30.8%
	FLK: Deep bank reefs	< 2%	2-3.5 %	3.5-6 %	6-21.2%	> 21.2%
	SEFL	< 0.8%	0.84-1.7%	1.7-3.9%	3.9-11.6%	>11.6%
	DT: Low relief	< 0.7%	0.7-1.5%	1.5-2.7%	2.65-6.8%	>6.8%
	DT: Mid Relief	< 3.3%	3.3-4.6%	4.6-6.3%	6.3-16.3%	>16.3%
	DT: High relief	< 25%	25-36.4%	36.4-43%	43-56.6%	>56.6%
Reef Health Index (RHI)	All reefs	< 5%	5-10%	10-20%	20-40%	> 40%
CHI	All reefs, includes % coral + CCA	≤ 0.20	0.21-4	0.41-6	0.61-8	0.81-1

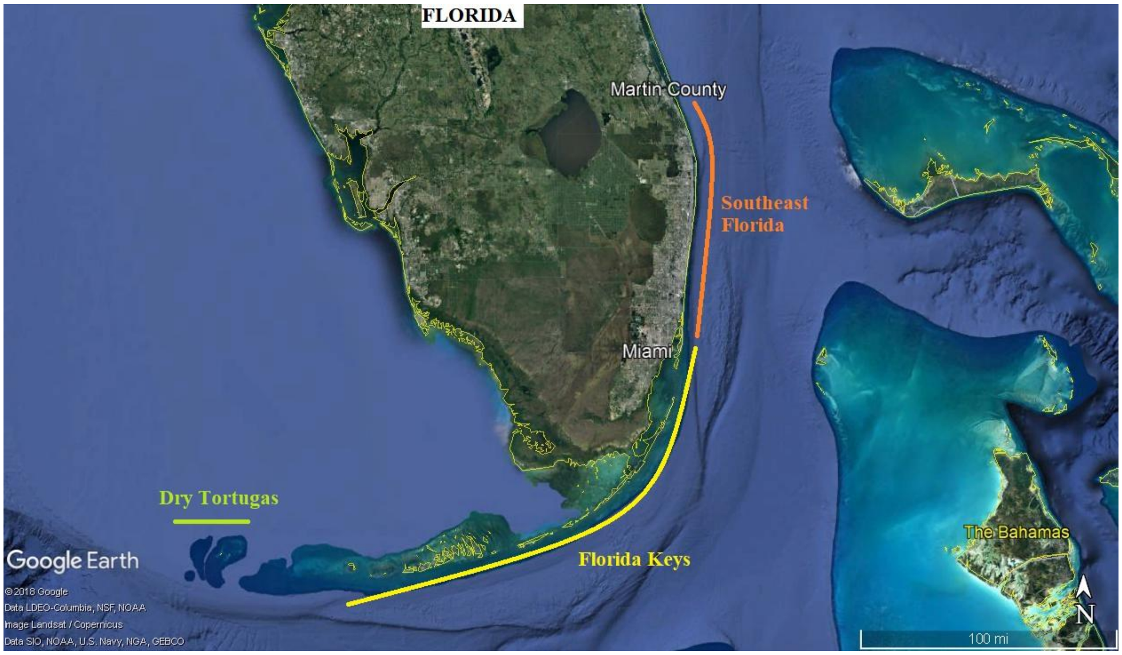


Figure 4.1 Study location

Geographical extent of the Florida Reef Tract (FRT). Lines represent the three subregions within the FRT: Southeast Florida, Florida Keys, and Dry Tortugas.

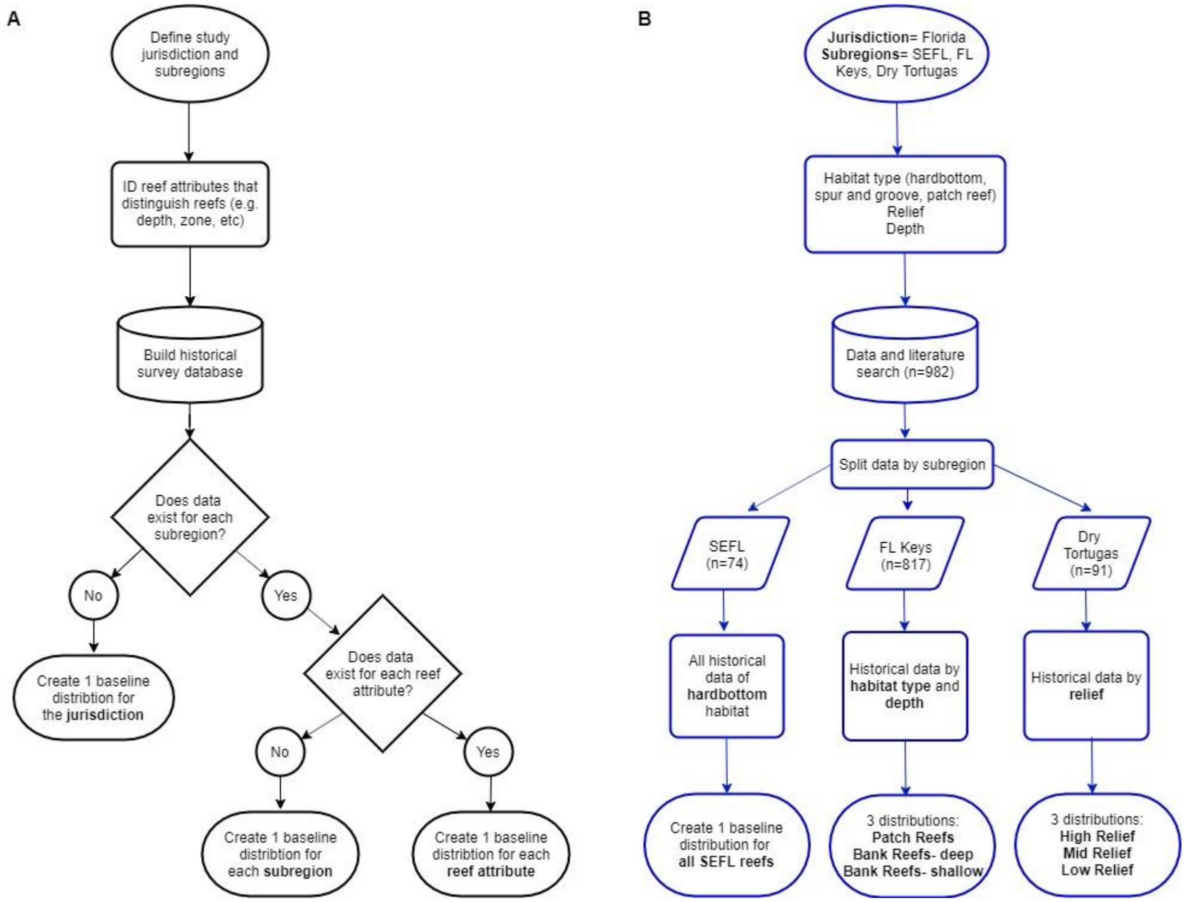


Figure 4.2 Decision making flowchart

A) General guiding principles on how to delineate baseline data; B) Flow of decisions and data splits for this case study.

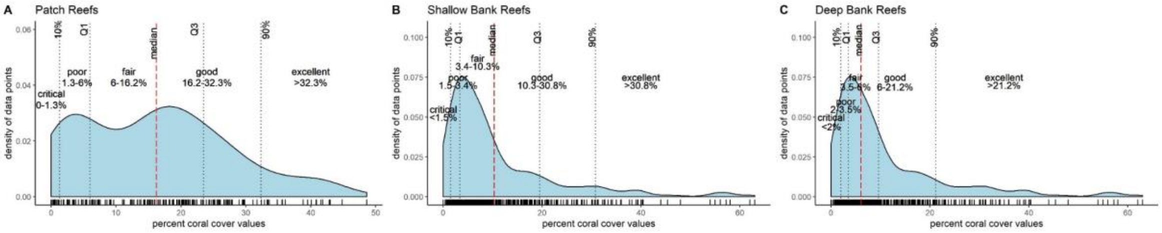


Figure 4.3 Baseline distribution for FLK reefs

Baseline data comes from the historical references and is broken down by habitat type and depth. A) Patch reefs; B) Shallow (<6m) bank reefs; C) Deep (≥6m) bank reefs. Vertical lines represent quantile marks (10%, 25%, median, 75%, 90%).

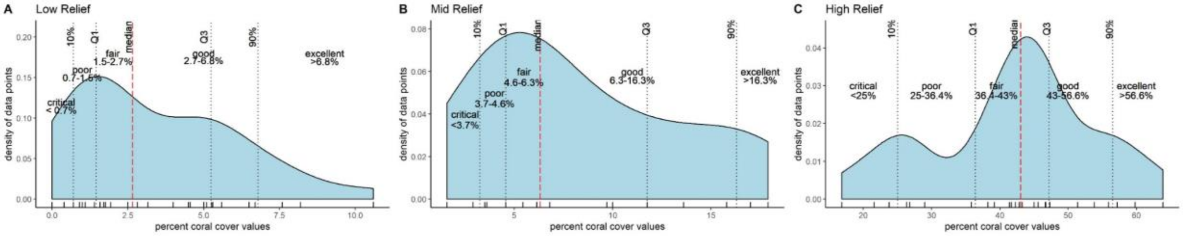


Figure 4.4 Baseline distribution for the Dry Tortugas

Baseline data comes from historical references and is broken down by reef relief. A) Low relief reefs; B) Mid relief reefs; C) High relief reefs. Vertical lines represent quantile thresholds (10%, Q1= 25%, median= 50%, Q3= 75%, and 90%).

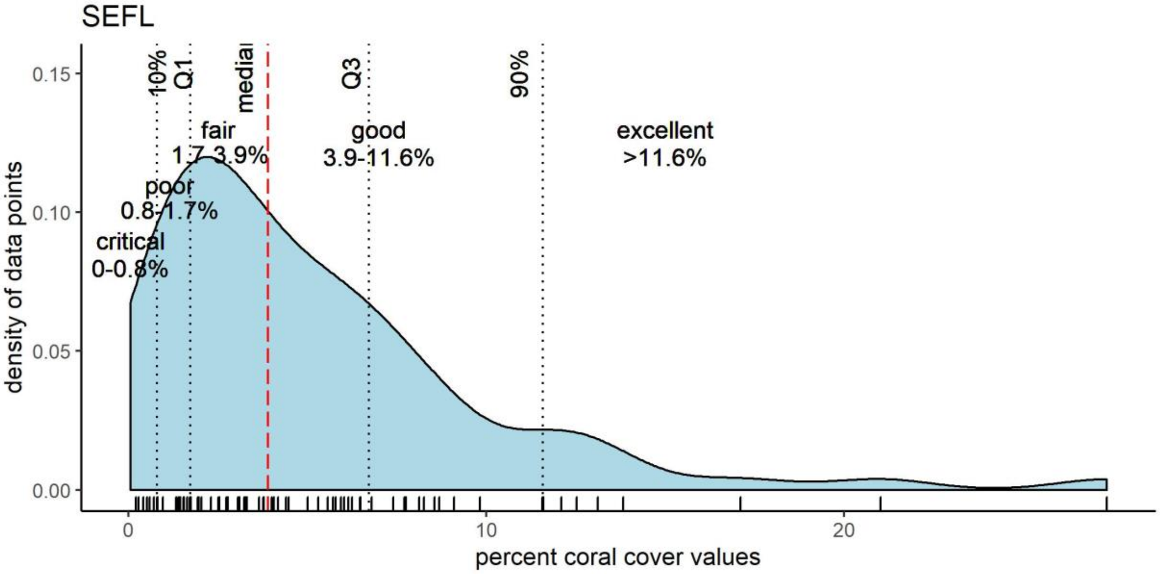


Figure 4.5 Baseline distribution of SEFL reefs

All historical data was pooled together and represents a hardbottom reef habitat. Vertical lines represent quantile thresholds (10%, Q1= 25%, median= 50%, Q3= 75%, and 90%).

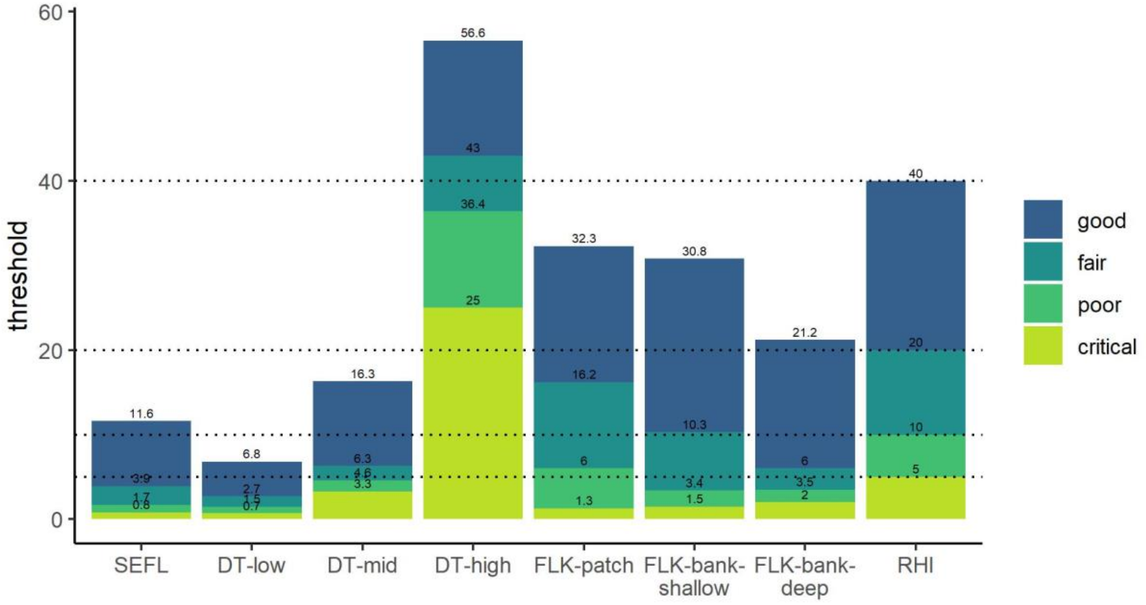
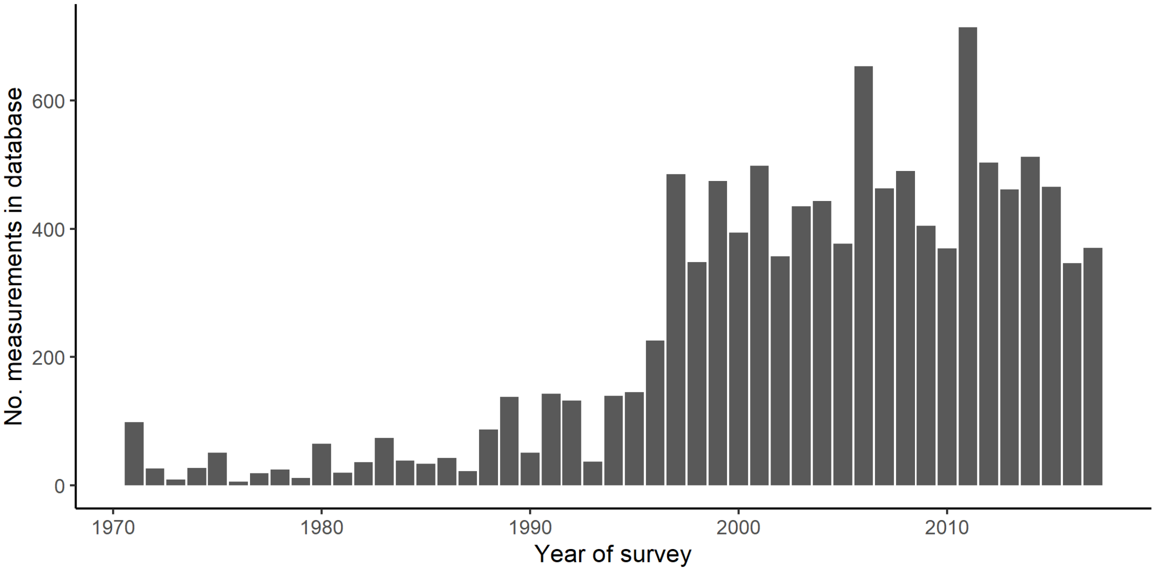


Figure 4.6 Comparison of scoring thresholds

Threshold values are the cutoff points between the different score categories. Any hard coral cover value above the "good" threshold is considered excellent. Horizontal dotted lines indicate the threshold cutoffs for the RHI index.

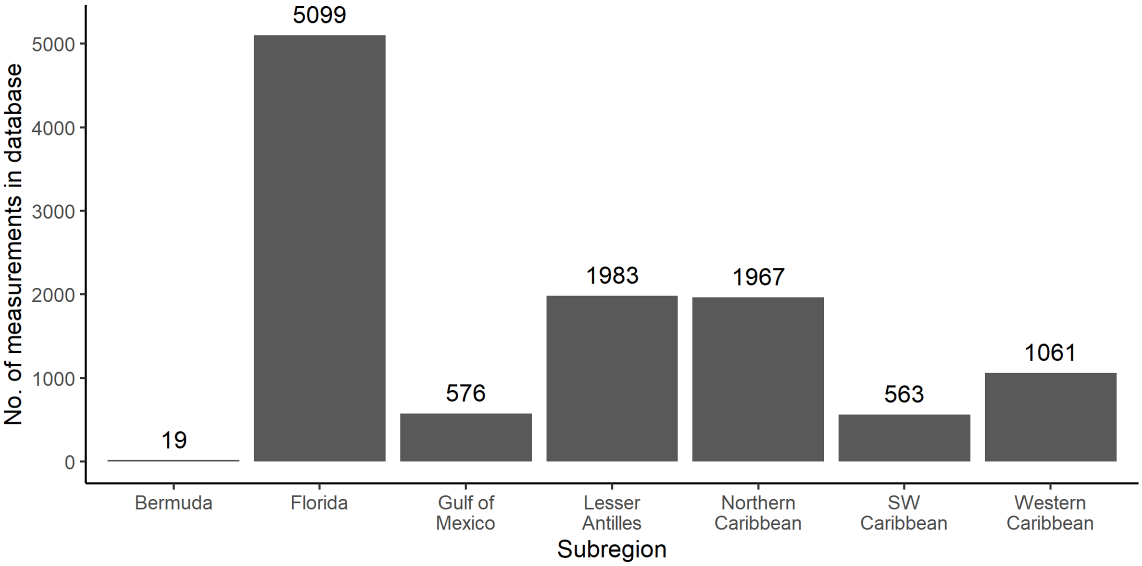
APPENDIX A: SUPPLEMENTARY MATERIAL FOR CHAPTER 2

A1. Supplemental Figures

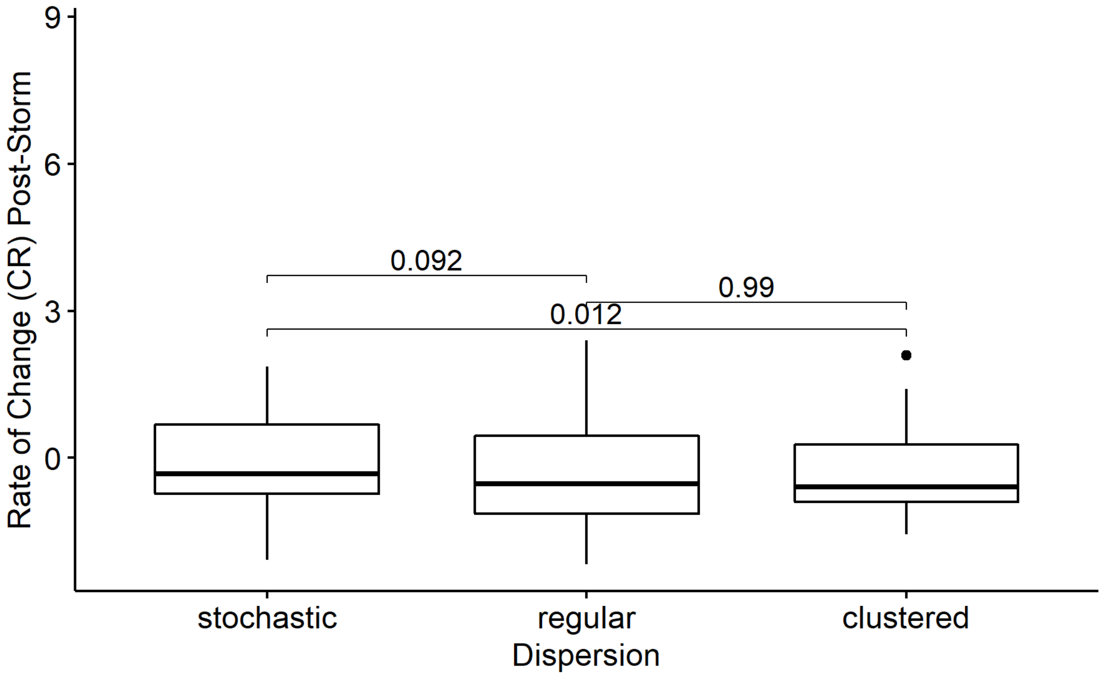


Supplement Figure 1: Coral data sampling by year

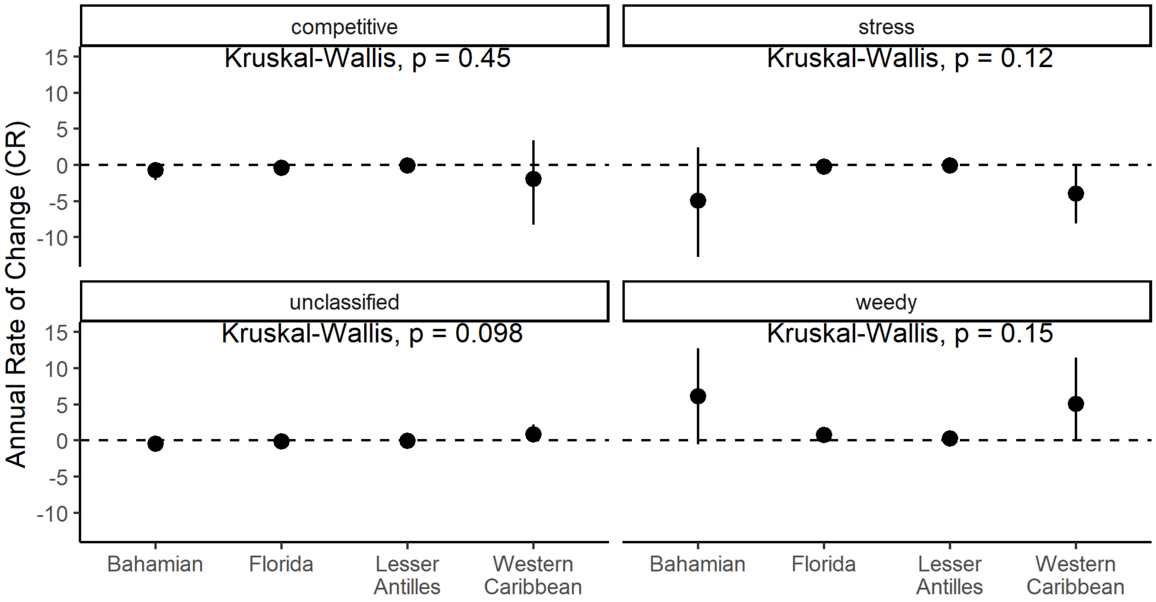
The temporally skewed distribution of datasets is due to the emergence of monitoring programs in the 1990s, citizen science programs, and massive efforts in recent years to compile and make coral data accessible to the public (Reef Check, Graham et al 2011, Guest et al 2018).



Supplement Figure 2: Coral cover sampling by subregion



Supplement Figure 3: Differences in annual rate of change (CR) post-storm, by dispersion



Supplement Figure 4: Annual rate of change in coral LHG, by subregion

A2. Supplemental Tables

Supplement Table 1: Coral cover summary statistics, by subregion

For each subregion, the number of observations along with summary statistics are reported for scleractinian percent coral cover.

subregion	n	mean	sd	std.error	median	min	max	range	IQR
Bermuda	19	21.50	8.72	2.00	20.55	8	52.40	44.40	4.23
Florida	5094	7.46	8.98	0.13	3.86	0	63.00	63.00	8.59
Gulf of Mexico	576	47.02	18.32	0.76	49.00	0	100.00	100.00	24.00
Lesser Antilles	1982	19.50	14.47	0.32	15.80	0	81.25	81.25	21.13
Northern Caribbean	1967	16.34	11.05	0.25	14.30	0	84.38	84.38	13.17
SW Caribbean	563	24.39	16.00	0.67	21.94	0	93.95	93.95	20.07
Western Caribbean	1061	18.70	11.90	0.37	16.88	0	87.41	87.41	12.50

Supplement Table 2: Classification of coral species by life history group

Life History Group	Coral Species
Competitive	*Acropora cervicornis*
	Acropora palmata
	Acropora prolifera

	Acropora sp.
Stress Tolerant	*Colpophyllia natans*
	Dichocoenia stellaris
	Dichocoenia stokesii
	Diploria labyrinthiformis
	Diploria sp.
	Eusmilia fastigiata
	Favia fragum
	Favia sp.
	Meandrina meandrites
	Montastraea cavernosa
	Montastraea sp.
	Orbicella annularis
	Orbicella faveolata
	Orbicella franksi
	Orbicella sp.
	Pseudodiploria clivosa
	Pseudodiploria sp.
	Pseudodiploria strigosa
	Siderastrea siderea

	Stephanocoenia intersepta
Weedy	*Agaricia sp.*
	Agaricia agaricites
	Agaricia fragilis
	Agaricia grahamae
	Agaricia humilis
	Agaricia lamarcki
	Agaricia tenuifolia
	Agaricia undata
	Isophyllia sinuosa
	Madracis auretenra (mirabilis)
	Madracis decactis
	Madracis formosa
	Madracis pharensis
	Madracis sp.
	Manicina areolata
	Mycetophyllia ferox
	Porites astreoides
	Porites cf. branneri
	Porites divaricata

	Porites furcata
	Porites porites
	Porites sp.
	Siderastrea radians
Unclassified	*Cladocora arbuscula*
	Leptoseris (Helioseris) cucullata
	Isophyllia rigida
	Isophyllia sp.
	Isopyhyllastrea rigida
	Meandrina jacksoni
	Meandrina sp.
	Mussa angulosa
	Mycetophyllia sp.
	Mycetophyllia aliciae
	Mycetophyllia danaana
	Mycetophyllia lamarckiana
	Oculina diffusa
	Oculina robusta
	Oculina sp.
	Oculina varicosa

	Scolymia
	Scolymia cubensis
	Scolymia lacera
	Scolymia sp.
	Scolymia wellsi
	Siderastrea sp.
	Siderastrea stellata
	Solenastrea bournoni
	Solenastrea hyades
	Solenastrea sp.
	Tubastraea coccinea
	Unknown Scleractinia species

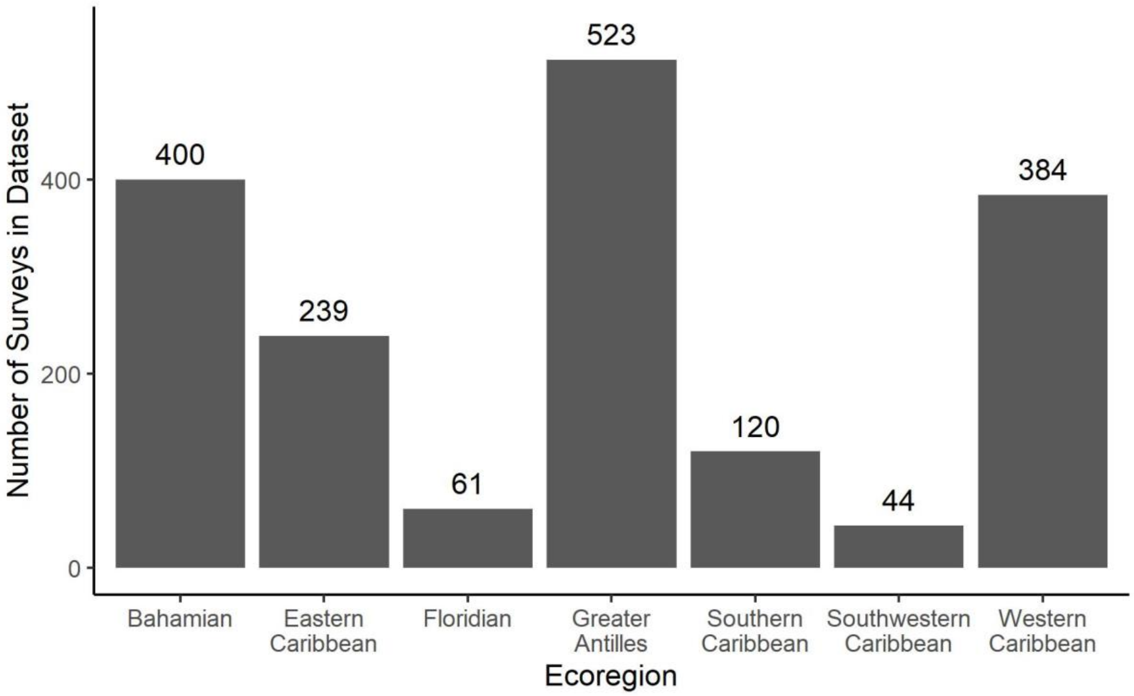
Supplement Table 3: Coral resistance to storms, by decade

Reported for each decade are: the number of reef-storm interactions, mean loss of coral cover +/- standard deviation and standard error, median loss of coral cover, highest about of coral loss (minimum), largest positive amount of change post-storm (maximum), total range of coral change values, and interquartile range.

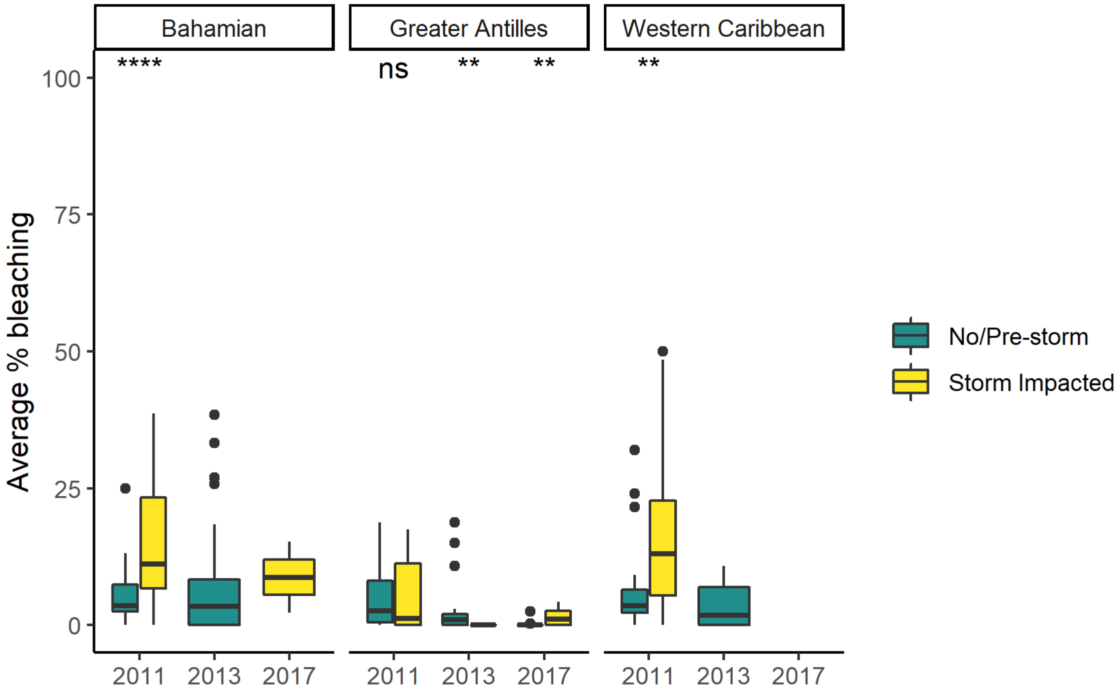
decade	n	mean	sd	std.error	median	min	max	range	IQR
1980s	11	-5.78	12.13	3.66	-7.75	-27.02	20.97	47.99	8.86
1990s	58	-3.88	4.59	0.60	-2.54	-18.64	4.18	22.82	7.07
2000s	121	0.03	4.64	0.42	0.13	-25.31	20.00	45.31	2.64
2010s	25	-0.57	2.29	0.46	-0.18	-8.43	2.70	11.13	1.94

APPENDIX B: SUPPLEMENTARY MATERIAL FOR CHAPTER 3

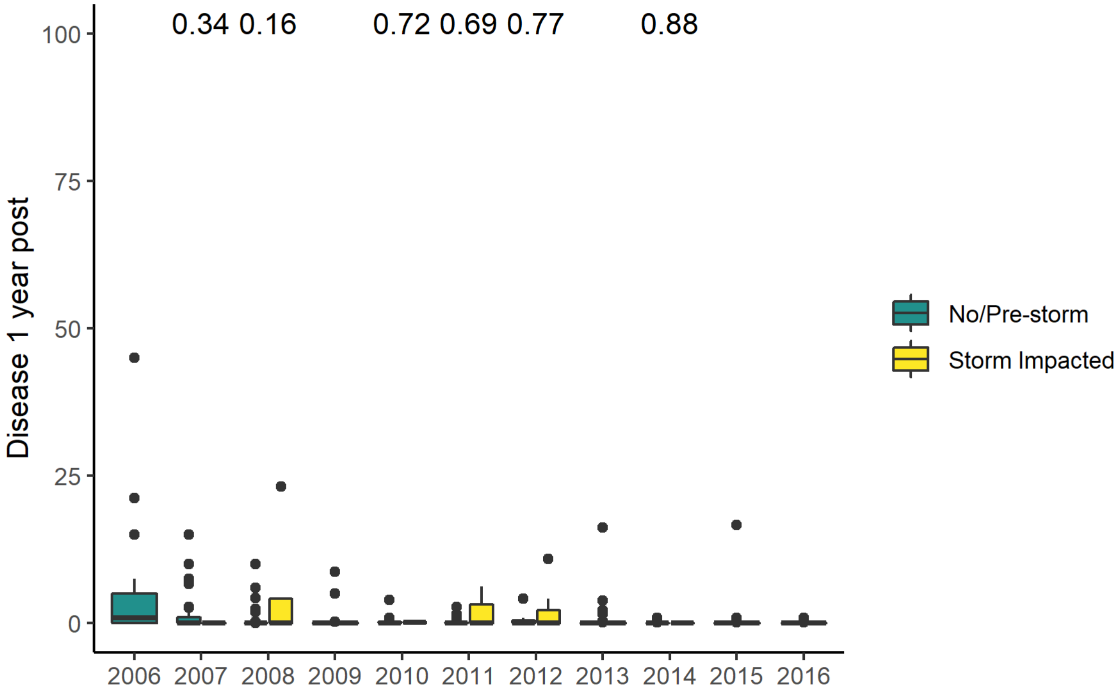
A1. Supplemental Figures



Supplement Figure 5: Coral health surveys by ecoregion



Supplement Figure 6: Coral bleaching by ecoregion



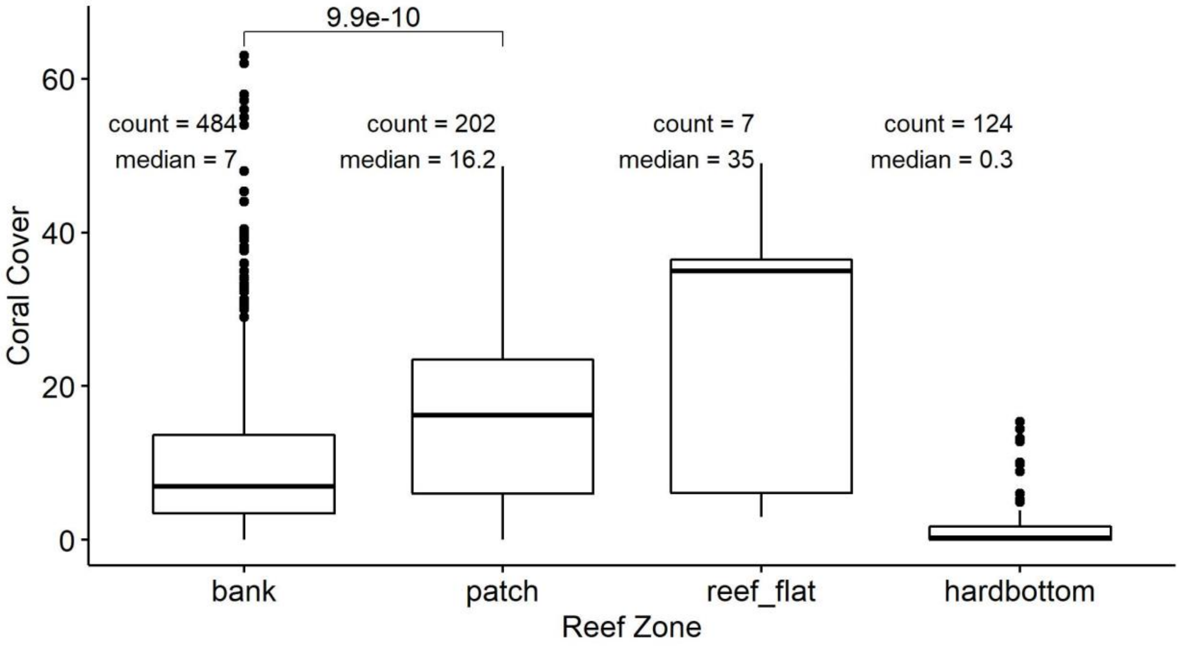
Supplement Figure 7: Coral disease one year post-storm

A2. Supplemental Tables

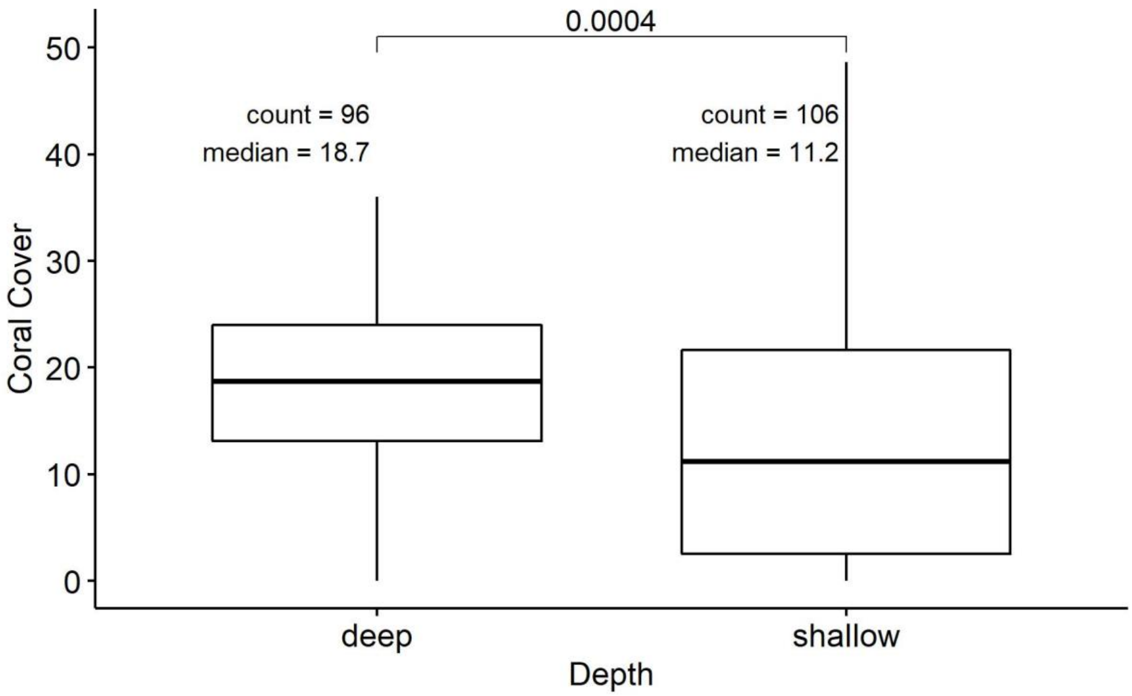
Supplement Table 4: Number of coral health surveys per year

Year	Number of surveys in the dataset
2006	171
2007	181
2008	173
2009	123
2010	58
2011	329
2012	201
2013	150
2014	125
2015	131
2016	60
2017	69

APPENDIX C: SUPPLEMENTARY MATERIAL FOR CHAPTER 4

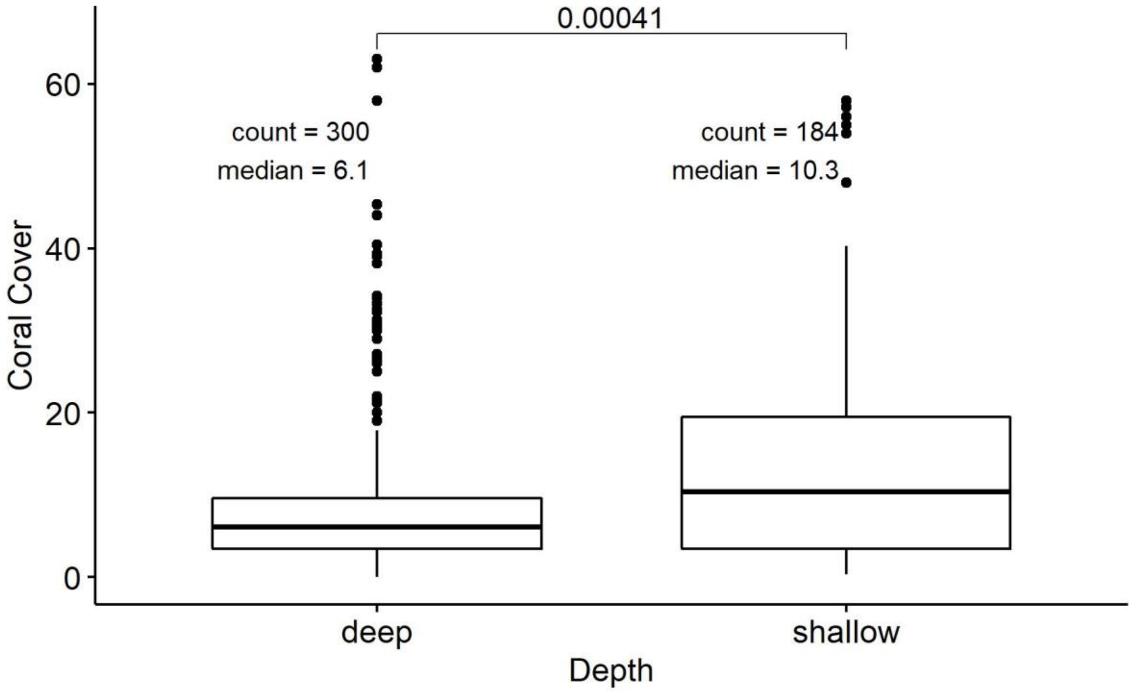


Supplement Figure 8: Coral cover by reef zone in the Florida Keys



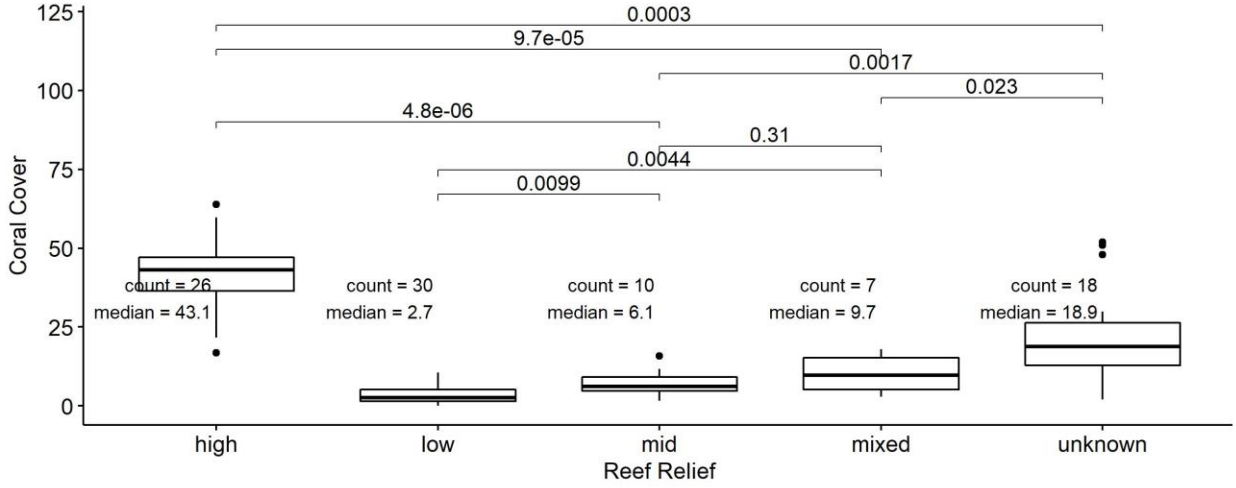
Supplement Figure 9: Coral cover by depth in Florida Keys patch reefs

Significant difference in historical coral cover between shallow (<6m) and deep (>6m) patch reefs in the Florida Keys.



Supplement Figure 10: Coral cover by depth in Florida Keys bank reefs

Significant difference in historical coral cover between shallow (<6m) and deep (>6m) bank reefs in the Florida Keys.



Supplement Figure 11: Coral cover by relief in Dry Tortugas

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