Received: 30 November 2023 | Revised: 12 February 2024 | Accepted: 9 April 2024

DOI: 10.1002/ecy.4360

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Decadal-scale time series highlight the role of chronic disturbances in driving ecosystem collapse in the Anthropocene

Peter J. Edmunds

Department of Biology, California State University, Northridge, California, USA

Correspondence
Peter J. Edmunds
Email: peter.edmunds@csun.edu

Funding information
Biological Oceanography, Grant/Award Number: OCE 20-19992

Handling Editor: Richard B. Aronson

Abstract

Biome degradation characterizes the Anthropocene Epoch, and modern ecology is deeply involved with describing the changes underway. Most research has focused on the role of acute disturbances in causing conspicuous changes in ecosystem structure, which leads to an underappreciation of the chronic effects causing large changes through the cumulative effects of small perturbations over decades. Coral reefs epitomize this trend, because the changes in community structure are profound, yet the data to quantify these effects are usually insufficient to evaluate the relative roles of different disturbance types. Here, four decades of surveys from two coral reefs (9 and 14 m depth) off St. John, US Virgin Islands, are used to quantify the associations of acute and chronic events with the changes in benthic community structure. These reefs profoundly changed over 36 years, with coral death altering species assemblages to depress abundances of the ecologically important coral *Orbicella* spp. and elevating the coverage of macroalgae and crustose coralline algae/turf/bare space (CTB). Linear mixed models revealed the prominent role of chronic variation in temperature in accounting for changes in coverage of corals, macroalgae, and CTB, with rising temperature associated with increases in coral cover on the deep reef, and declines on the shallow reef. Hurricanes were also associated with declines in coral cover on the shallow reef, and increases on the deep reef. Multivariate analyses revealed strong associations between community structure and temperature, but weaker associations with hurricanes, bleaching, and diseases. These results highlight the overwhelming importance of chronically increasing temperature in altering the benthic community structure of Caribbean reefs.

KEYWORDS
Caribbean, climate change, coral reef, ecology, Scleractinia

INTRODUCTION

The Anthropocene Epoch marks an era in the global history of biota in which humans have become the dominant drivers of change (Kidwell, 2015). Through the engineering of planetary features, consumption of resources, and increases in atmospheric CO_2 in the pursuit of energy assets (Syvitski et al., 2020), humans have altered the ecology of every biome (Parmesan & Yohe, 2003). Ecologists are focusing on documenting these effects (Poloczanska et al., 2013), with efforts often dominated by acute events, such as forest fires, floods, diseases, and storms (Lafferty, 2009; Turner, 2010; Ummenhofer & Meehl, 2017). Acute events usually appear to have substantial ecological significance when they are captured in studies spanning only a few years, but as studies extend to multiple decades, it is more likely that they will reveal the ecological significance of chronic events (Luo et al., 2011). Underappreciation of chronic events causing communities to change can lead to inaccurate projections of a future state, and a mismatch of conservation efforts intended to alleviate the effects of the putative drivers of change.

Coral reefs provide an interesting case in which to consider these issues, because they have been studied for centuries, with the last few decades underscoring the large changes that have occurred relative to the 1960s (and earlier) (Cramer et al., 2021). Acute events have prominently featured in these studies, including storms (Woodley et al., 1981), outbreaks of corallivores (Chesher, 1969), diseases (Aronson & Precht, 2001), and more recently, bleaching (Hughes, Kerry, et al., 2017), new coral diseases (Brandt et al., 2021), and ocean acidification (Doney et al., 2009). The capacity of acute disturbances to cause profound changes in coral communities supported the emergence of the alternative stable state theory positing that large disturbances can transition a community into an alternative stable state under identical background conditions (Dudgeon et al., 2010). Together, the aforementioned effects have promoted a narrative emphasizing that coral reef degradation (Hughes, Kerry, et al., 2017), particularly in the Caribbean (Roff & Mumby, 2012), is strongly associated with acute disturbances (e.g., Hughes et al., 2010).

With ecological analyses of coral reefs extending decades (e.g., Jackson et al., 2014), the roles of chronic versus acute events in changing these communities can objectively be evaluated. Because chronic effects require decades to detect, it is reasonable to expect that they will only be identified in the longest studies. The reefs of St. John, US Virgin Islands, provide a record of suitable length for this purpose, because they have been studied since the 1980s, thereby capturing replicated acute events acting against a backdrop of chronically changing environmental conditions. Because this project began in 1987, the study reefs have been dominated by the corals *Orbicella annularis*, *Orbicella faveolata*, and *Orbicella franksi*, and while most colonies of these species were alive in 1987, by 2022 many had died leaving their skeletons dead in place. Prior to this project, thickets of *Acropora cervicornis* were common at ~16 m depth adjacent to the Tektite reef (Lee et al., 1975), and stands of *Acropora palmata* were growing ~3 km away at John's Folly Bay. *A. cervicornis* probably was killed by disease in the 1980s (Aronson & Precht, 2001) and was not seen when this study began, but the *A. palmata* at John's Folly Bay persisted until 1989, when it was destroyed by Hurricane Hugo. It is reasonable to infer, therefore, that the history of the present reefs is similar to that of other Caribbean reefs in comparable habitats where *Acropora* spp. have been absent for decades and the reef is dominated by a framework of *Orbicella* spp.

Here a 36-year record is used to compare the roles of different environmental conditions in statistically explaining changes in coverage of corals and other benthic space holders on the reefs of St. John. The study tests the hypothesis that chronically changing conditions are strongly associated with community degradation. I follow previous literature in considering hurricanes, bleaching, and disease outbreaks as acute events, and seawater temperature and rainfall regimes as chronic events (Ceccarelli et al., 2020; Hughes & Connell, 1999), but recognize that the distinction between the two types of conditions is qualitative.

METHODS

The study began in December 1987 to evaluate the effects of coral bleaching. Three, 10-m long, permanently marked transects were established at 14-m depth at the Tektite reef, and at 9-m depth at Yawzi Point. These reefs were selected because of their high percentage cover of *Orbicella* spp. and ease of access from a field station with small boats.

Each transect was sampled using 10 contiguous photoquadrats (1 × 1 m), recorded annually between May and December beginning in December 1987 and ending in July 2022 (Appendix S1: Table S1). The reefs were sampled twice each year in 1988, 1989, and 2017 to evaluate the effects of hurricanes, and initially were recorded using color slide film, and from 2001, digitally (Appendix S1: Table S1). A strobe was used with all cameras, each image contained a scale bar, and slides were digitized (4000 dpi) for analysis. Images were analyzed using CPCe (Kohler & Gill, 2006) or CoralNET (Beijbom et al., 2015) software, with 200 randomly located points image $^{-1}$ that were manually annotated to resolve coral (scleractinians and *Millepora*), macroalgae, and crustose coralline algae + algal turf + bare space (CTB). Objects to ~5 mm diameter were identified, although the taxonomic resolution was occasionally restricted by shadows, leading to a consensus list of 23 space holders that were quantified (Appendix S1: Table S2) for percentage cover (mean ± SE).

Environmental conditions were quantified through continuous measures of seawater temperature and rainfall, and nominal measures of hurricanes, bleaching, and diseases. From 1989, temperature was measured at 9-m depth at Yawzi Point using mostly Hobo temperature loggers (±0.2°C), with occasional gaps in the record filled with measurements from the same model of logger at 14-m depth at Tektite (9% of 11,995 daily records). Loggers were recorded at 0.001 Hz, and values were averaged by day. Temperatures for 1987 and 1988 were obtained from remote sensing of monthly SST in the NOAA global coral bleaching monitoring database with a 5-km resolution (version 3.1, accessed through ERDAPP, 2 January 2023, for an ~11 km grid centered at 18.2537° N, 295.2265° E). The comparison of in situ (9-m depth at Yawzi Point) and SST temperatures for 1989 revealed a strong correlation between the two (Appendix S1: Figure S1). Because discrepancies between the two were trivial, SST for 1987 and 1988 were combined with in situ temperature for 1989–2022 without adjustment. Daily records were summarized as annual means (±SE), the means (±SE) of the 12 monthly values between August and July, and the mean (±SE) of the hottest 3 months of each year. Rainfall (in centimeters) was obtained from the southeastern regional climate center (SERCC) using rain gauges on St. John for 1987–2011, and from 2012, using a rain gauge on the north shore (station VI-SJ-3, https://wys.cocorahs.org). Daily rainfall was summarized by month and expressed as the mean (±SE) by year, as well as for the 12 months between August and July of each year.

Hurricane impacts were evaluated on a nominal scale through storm intensities and tracks (https://www.nhc.noaa.gov), and anecdotal descriptions of local impacts. Evaluations of their underwater effects from wind speed, proximity, and diameter proved unreliable. Storms were assigned a value of 1 when they impacted St. John, with other years assigned a zero (Appendix S1: Table S3). Because hurricanes occurred after annual samplings, their effects were registered in the year following their occurrence. The effects of bleaching were assigned a value of 1 (bleaching) or 0 (no bleaching) based on published and anecdotal records (Appendix S1: Table S3), as well as records of high temperature. Bleaching occurred after annual sampling (except 1987 when the photoquadrats were recorded in December), and its impacts were registered in the year following occurrence. Coral diseases were chronic (Edmunds, 1991), but three acute disease events were evaluated on a nominal scale (1 = disease, 0 = no disease): the effect of white pox and other diseases in late 2005 (Miller et al., 2009) were registered in the following year; stony coral tissue loss disease (SCTLD) appeared around St. Thomas in early 2019 (Brandt et al., 2021), and its effects were registered in 2019 and 2020; and in 2022, the sea urchin *Diadema antillarum* declined 98% in population size through disease (Levitan et al., 2023), and the effects were registered in that year.

Statistical analyses

Differences over time in the cover of each benthic group were evaluated from contrasts of means and nonoverlapping SEs. Linear mixed models (LMM) were used to test for the effects of time, average annual temperature (in degrees Celsius), rainfall (in millimeters), hurricanes (0 or 1), disease (0 or 1), and bleaching (0 or 1) (fixed effect) on the percentage cover of corals, macroalgae, and CTB. Quadrats were averaged by transect within each site ($n = 3$) because transects were haphazardly selected and repeatedly surveyed; transects were introduced as a random factor. Models were fitted using restriction maximum likelihood methods (REML), and were also run in simplified forms with nonsignificant fixed effects excluded. Models were evaluated using the corrected Akaike information criterion for small sample sizes ($\mathrm{AIC_c}$) (Burnham & Anderson, 2004). Interaction terms were not included because of the potential for multicollinearity among predictors. The influence of the fixed effects was evaluated through the model estimates and 95% CI about these values.

Multivariate changes were displayed with 2-dimensional ordinations using nonmetric multidimensional scaling (MDS) with Bray–Curtis dissimilarities based on square-root transformed data and 999 permutations until stress stabilized. MDS plots were prepared for community structure (coral, macroalgae, and CTB), and coral taxa (Appendix S1: Table S2), with significance tested using SIMPROF.

To test for associations between the environment and multivariate benthic community (by both functional groups and coral genera) environmental conditions were screened for collinearity using Pearson correlations, and where a significant association was detected (at $p \leq 0.05$ with $r > 0.341$ and 35 years of data), one member of each pair was excluded based on weak clarity of interpretation of the environmental condition. The association of biological and environmental ordinations was tested using the BEST routine in Primer 7.0 software (Clarke & Gorley, 2015), in which Spearman rank correlation (ρ) identified the best match within a permutational framework. One analysis was completed with the biological and environmental data calculated by year, and one using a centered 3-year running mean to smooth variation. Environmental data were square-root transformed and converted to a resemblance matrix using Gower distances (Gower, 1971). BIO-ENV detects multiple associations, sometimes with different combinations of variables, among which the relative role of each variable in causing changes in community structure was evaluated using distance-based linear modeling (DISTLM). This procedure distinguishes among associations identified through the BEST routine using AIC, and it attributes variance to components in the model (Burnham & Anderson, 2004).

Descriptive statistics and LMMs were completed using Systat 13 (Inpixon, San Jose, CA), and multivariate tests were completed using Primer 7.0 and PERMANOVA+ (Clarke & Gorley, 2015). Statistical assumptions of LMM were evaluated through graphical analyses of residuals. Although MDS, SIMPROF, and DISTLM make no explicit assumptions about the distribution of the data, attention was paid to stress and avoidance of collinearity in the DISTLM (Clarke & Gorley, 2015). Data are available in Dryad (Edmunds, 2024 at https://doi.org/10.5061/dryad.x0k6djht1) and Appendix S1: Table S3.

RESULTS

Community structure at Yawzi Point

In 1987, mean (±SE) coral cover was 44.6 ± 3.4% ($n = 29$), macroalgae cover was 2.2 ± 0.4%, and CTB cover was 35.4 ± 3.7%. Coral cover declined by 39% from April to October 1989, and a protracted decline began after 1994. From 1994 to 1999, mean coral cover declined by 67%, and then to 3.8 ± 1.2% ($n = 30$) in 2022 (a 92% loss cf. 1987). Concurrently, macroalgal cover rose to 40.0 ± 2.8%, and CTB to 43.0 ± 2.6% in 2022 (Figure 1A), and there was a weak trend for reciprocal variation in cover between these space holders, with dissimilar effects between ~1987–1999 and ~2000–2022 (Appendix S2: Figure S1). From 1987 to 2022, the reef was affected by 11 hurricanes (Hugo in 1989, Marilyn and Luis in 1995, Bertha and Hortense in 1996, Georges in 1998, Lenny in 1999, Debbie in 2000, Earl in 2010, and Irma and Maria in 2017), three bleachings, and three disease outbreaks, with the largest declines in coral cover occurring 1–5 years after hurricanes in 1989 and in the late 1990s. LMM showed that the coverage of each of the space holders changed (Table 1), but their responses to the other fixed effects varied. Coral changed in association with hurricanes and temperature; macroalgae changed in association with hurricanes; and CTB marginally changed in association with bleaching (Table 1; Appendix S2: Table S1). The plots of effects estimates (Figure 2) showed that coral cover declined with rising temperature and hurricanes, and that hurricanes were followed by an increase in macroalgal cover (Appendix S2: Table S1). The random effect of the transect was not significant, and models excluding nonsignificant fixed effects were less good fits (Appendix S2: Table S1). Most of these results did not change when the LMM was repeated with hurricanes scored as absent (0) present (1) and severe (2 = Hugo in 1989 and Irma/Maria in 2017), and the effects of SCTLD were extended through 2021; in this model, there was no association between CTB and bleaching (Appendix S2: Table S2).

Multivariate analysis created a robust ordination (stress = 0.06), revealing the transition from coral

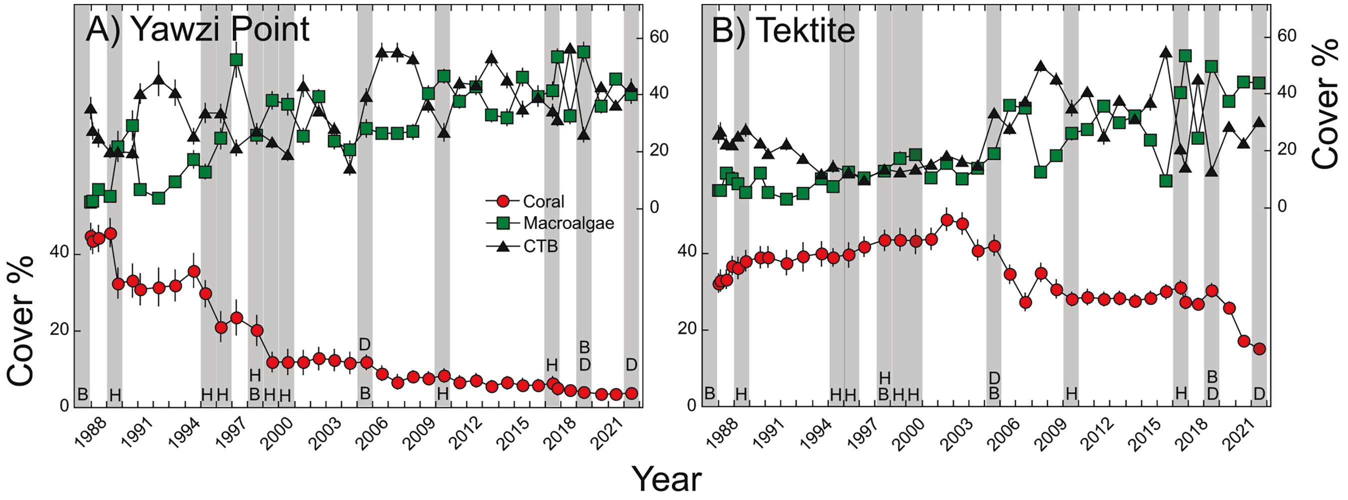

FIGURE 1 Coral reef community structure at Yawzi Point (A) and Tektite (B) from 1987 to 2022. Mean (±SE, $n = 18–30$ photoquadrats year ^{1}) with percentage cover of coral, macroalgae, and crustose coralline algae/turf/bare space (CTB) shown, and environmental events indicated as gray bars (B, bleaching, D, disease; H, hurricanes).

TABLE 1 Results of linear mixed models analysis of percentage cover of coral, macroalgae, and crustose coralline algae/turf/bare space (CTB) in which year, rainfall, temperature, hurricanes, bleaching, and diseases were fixed effects, and transect was a random effect.

		Type III test of fixed effects				
Site and DV	**Fixed effect**	***F***	**df**	***p***	**(1) AIC$_c$**	**(2) AIC$_c$**
Yawzi Point						
Coral	Time	122.628	1, 104	<0.001	752 [0]	758 [6]
	Hurricanes	14.848	1, 104	<0.001		
	Temperature	5.950	1, 104	0.016		
Macroalgae	Time	32.495	1, 103	<0.001	865 [0]	880 [16]
	Hurricanes	13.728	1, 103	<0.001		
CTB	Time	10.999	1, 103	0.001	862 [0]	876 [15]
	Bleaching	3.938	1, 103	0.050		
Tektite						
Coral	Time	48.402	1, 104	<0.001	724 [0]	724 [0]
	Hurricanes	8.770	1, 104	0.004		
	Bleaching	4.473	1, 104	0.037		
	Temperature	10.770	1, 104	0.001		
Macroalgae	Time	78.974	1, 104	<0.001	791 [0]	803 [12]
	Disease	7.277	1, 104	0.008		
CTB	Time	19.938	1, 104	<0.001	854 [0]	858 [4]
	Temperature	4.706	1, 104	0.032		
	Disease	3.962	1, 104	0.049		

Note: Significant effects shown with full results in Appendix S2: Table S1. Refer to Figure 2 for effects estimates for the best model.
Abbreviations: AIC$_c$, corrected Akaike information criterion for the full (1) [ΔAIC$_c$] and simplified (2) model; DV, dependent variable.

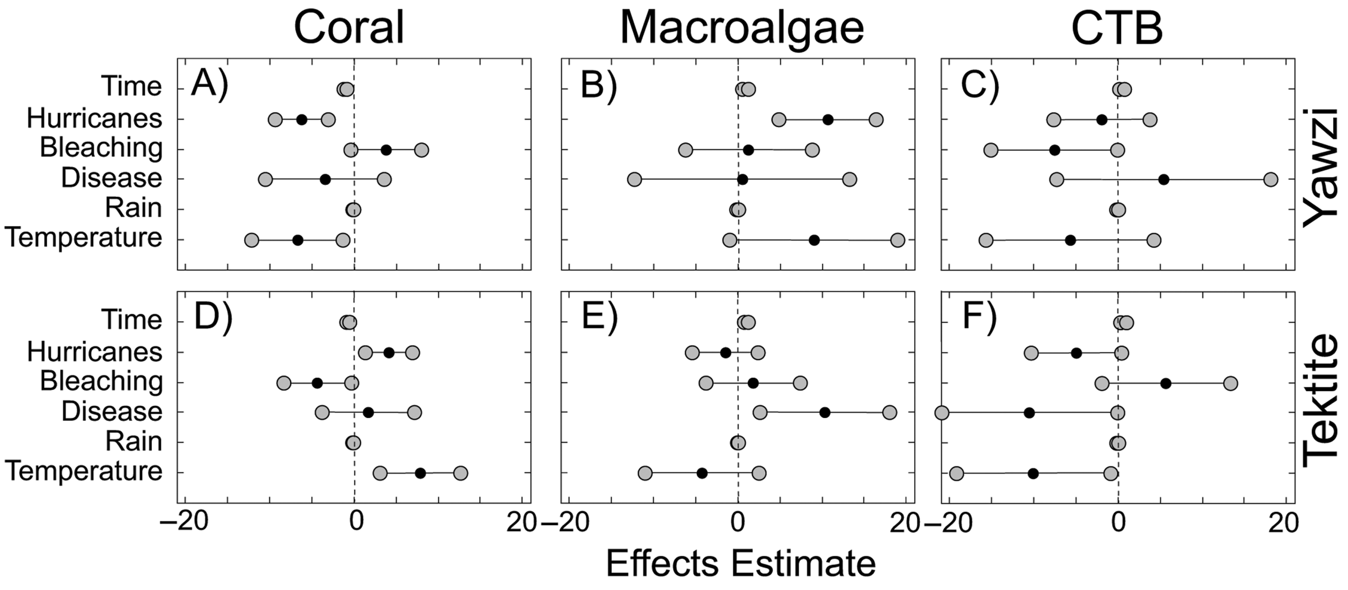

FIGURE 2 Fixed effects estimate from linear mixed models for the percentage coverage of coral (A, D), macroalgae (B, E), and crustose coralline algae/turf/bare space (CTB) (C, F) at Yawzi Point and Tektite from 1987 to 2021 (Figure 1). Values shown for time, hurricanes, bleaching, rain, and temperature (small central symbol) with 95% CI (flanking and joined larger symbols).

(Figure 3A) in the first decade, to macroalgal and CTB co-dominance in the final decade. The largest differences occurred from 4/1989 to 10/1989, 1990 to 1991, 2004 to 2005, and 2018 to 2019 (Figure 3A), and were associated with Hurricane Hugo (1989), and macroalgae and their encroachment on/off of CTB. The ordination revealed a change from the 1980s and 1990s to the 2010s and 2020s, with SIMPROF identifying five clusters of years ($\rho \geq 0.44$, $n = 999$, $p \leq 0.015$) that highlight differences in community structure around 2000, and over the following 20 years. 2022 clustered with nine other years, revealing decadal-scale homogeneity of community structure (Figure 3A). Multivariate analysis by coral genera (Appendix S2: Figure S2) revealed a stringent ordination (stress = 0.09) with the largest differences from 1998 to 1999, 2005 to 2006 and 2011 to 2012, which corresponded to bleaching, disease, and hurricanes, respectively (Appendix S1: Table S3). The ordination revealed a separation of years associated with the transition between 1998 and 1999, with SIMPROF identifying four clusters ($\rho \geq 1.13$, $n = 999$, $p \leq 0.003$), three prior to 1999, and one from 1999 to 2022 (Figure 3).

Community structure at Tektite

In 1987, mean (±SE) coral cover was 32.2 ± 2.5% ($n = 30$), macroalgae cover was 5.9 ± 0.7%, and CTB cover was 25.8 ± 3.0%. Over 15 years, mean coral cover increased by 52% to 48.8 ± 2.9% ($n = 30$) in 2002, mean macroalgal cover tripled to 15.5 ± 2.0%, and the mean cover of CTB declined by 30% to 18.2 ± 1.9%, all while these reefs were affected by six hurricanes and bleaching in 1998 (Figure 1B). There was reciprocal variation in abundance between CTB and macroalgae, with the effect intensifying between 1987–2004 and 2005–2022 (Appendix S2: Figure S1). By 2022, mean coral cover had declined by 69% to 15.3 ± 1.0% ($n = 30$), macroalgal cover increased

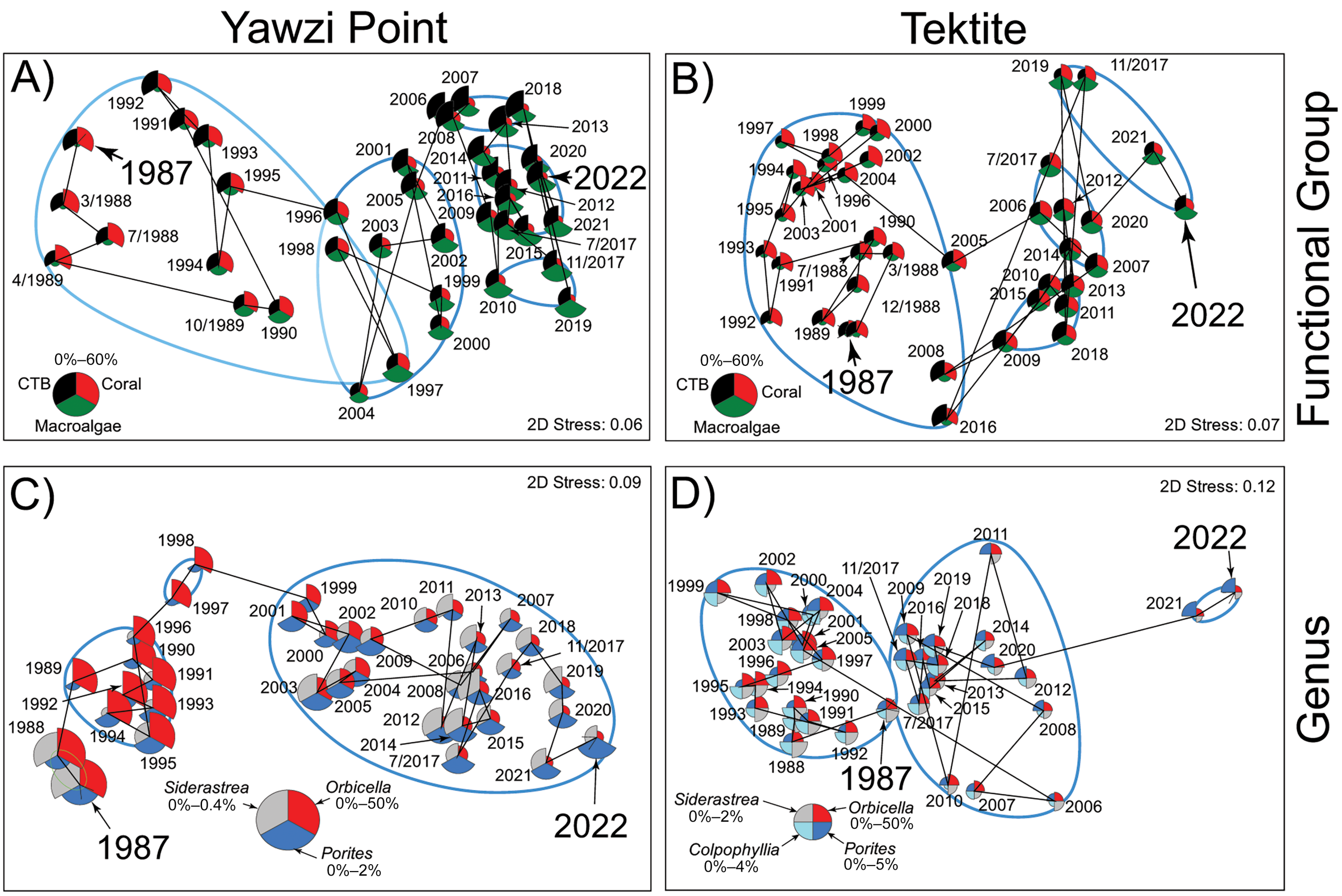

FIGURE 3 Multidimensional scaling displaying changes in community structure at Yawzi Point (A, C) and Tektite (B, D). Functional groups (A, B) based on coral, macroalgae, and crustose coralline algae/turf/bare space (CTB); (C, D) based on analysis by coral genera. Vectors link sequential samplings, which are labeled where feasible for clarity. Sectors of symbols scaled (differentially by taxon) and colored to show the percentage cover of the dominant space holders ([A, B] = coral, macroalgae, and CTB, [C, D] = *Orbicella*, *Siderastrea*, and *Porites* at Yawzi Point, and *Orbicella*, *Siderastrea*, *Colpophyllia*, and *Porites* at Tektite). Blue contours show significant clusters.

2.8-fold to 43.9 ± 1.9%, and CTB increased 1.7-fold to 30.2 ± 1.4%. From 2002 to 2022, the reef was affected by three hurricanes (with two in 2017), two bleachings, and three disease events. Coral diseases in 2005 and 2019 were followed by the largest 3-year declines in coral cover recorded at this site: 35% from 2005 to 2007, and 43% from 2019 to 2022. LMM showed that the coverage of each of the space holders changed (Table 1), but their responses to the other fixed effects varied. Coral cover changed in association with hurricanes, bleaching, and temperature; macroalgae changed in association with diseases; and CTB changed in association with temperature and diseases (Table 1; Appendix S2: Table S1). The plots of effects estimates (Figure 2) showed that coral cover was elevated in association with hurricanes and rising temperature, with a stronger effect for temperature, but declined in association with bleaching. Diseases were associated with increased cover of macroalgae and depressed coverage of CTB, and elevated temperature was associated with reduced cover of CTB (Figure 2). The random effect of transect was not significant, and models excluding nonsignificant fixed effects were less good fits (Appendix S2: Table S1). Some results changed when the LMM was repeated with hurricanes scored as absent (0) present (1) and severe (2, as described above), and the effects of SCTLD were extended through 2021. In these models, coral cover was no longer associated with bleaching, macroalgal cover was additionally associated with rainfall, and CTB was additionally associated with hurricanes (Appendix S2: Table S2, cf. Table 1).

Multivariate analysis of coral, macroalgae, and CTB created a robust 2-D ordination (stress $= 0.07$), revealing a transition from coral dominance (Figure 3B) in the first decade, to co-dominance by macroalgae and CTB ~2005, to macroalgal dominance in the final four samplings. The largest differences occurred from 2004 to 2005, 2015 to 2016, and 2016 to July 2017 (Figure 3B), and were associated with macroalgae and their spread onto/off CTB. The ordination revealed a transition from the 1980s and 1990s to the 2010s and 2020s, with SIMPROF identifying four clusters of years ($\rho \geq 0.49$, $p \leq 0.025$) that highlighted differences associated with the new millennium and the following 20 years (Figure 3B). Multivariate analysis by coral genus (Appendix S2: Figure S1) created a less stringent ordination (stress $= 0.12$), in which the largest differences occurred from 2005 to 2006, 2010 to 2011, and 2020 to 2021 (Figure 3D). These were associated with bleaching and diseases (2005–2006), Hurricane Earl and heavy rain (2010–2011), and SCTLD (2020–2021) (Appendix S1: Table S3). SIMPROF revealed transitions in coral community structure (Figure 3D), first around 2000 ($\rho = 0.96$, $n = 999$ permutations, $p = 0.001$), and second, between 2020 and 2021 ($\rho = 1.68$, $n = 999$ permutations, $p = 0.001$). These trends were associated with a reduction in cover of *Orbicella* spp. and *Colpophyllia* spp., and an increased cover of *Porites* spp.

Association between biological and environmental variation

Records of some environmental conditions extended from 1987 to 2022, but not rainfall, and tests for association with biological data excluded 2022 (Appendix S1: Table S1). Tests for collinearity reduced environmental data to mean temperature by calendar year, mean rainfall by calendar year, hurricanes, bleaching, and diseases. Mean temperature increased over time ($F = 29.415$, df $= 1$, 33, $p < 0.001$) at 0.2 ± 0.1°C decade ^{1}, but rainfall did not linearly vary ($F = 4.424$, df $= 1$, 33, $p = 0.129$).

For all data by year at Yawzi Point, variation in the multivariate coral community defined by functional group was best explained by temperature, and both temperature and bleaching (Table 2). DISTLM outputs for both relationships were indistinguishable (difference in AIC between models $[\Delta\text{AIC}] < 2.0$), but other associations were supported by models that fit less well ($\Delta\text{AIC} > 2$). The linear model with temperature explained 40.0% of the variation, and the model with temperature and bleaching explained 43.0% (temperature $= 40.0\%$, bleaching $= 3.0\%$). In the multivariate community defined by coral genera, variation was best explained by temperature, which accounted for 43.3% of the variation (Table 2). Smoothed biological and environmental data were more strongly associated (Table 2), and the best associations explained 67.3%–73.7% of the variation in community structure. Temperature accounted for most (68.3%) variation in functional groups, and for coral genera, temperature, and rainfall accounted for most for the variation (52.9% and 8.3%, respectively).

For all data by year at Tektite, variation in the multivariate coral community defined by functional group was best explained by temperature, rainfall, and disease, although several combinations of variables were also effective at explaining variation (Table 2). DISTLM provided a best-fit solution using two predictors, of which temperature explained 21.2% and rainfall 2.2% of the variation (Table 2). In the multivariate community defined by coral genera, variation was not associated with any combination of environmental conditions (Table 2). Smoothed biological and environmental data again were more strongly associated (Table 2), and the best associations explained 55.0%–65.3% of the variation in community structure. Temperature accounted for most (34.8%) variation in functional groups, and for coral genera, temperature,

TABLE 2 Multivariate tests of association between community structure and environmental conditions (Appendix S1: Table S3).

	BIO_ENV			DISTLM		Contribution to R^2 (%)				
Data, site, and assemblage type	**DV**	**ρ**	**p_{perm}**	**ΔAIC**	**R^2 (%)**	**DV1**	**DV2**	**DV3**	**DV4**	**DV5**
Annual										
Yawzi Point										
(A) Functional group	1	0.333	0.006	0	40.0	40.0				
	1, 5	0.248	0.040	0.1	43.0	40.0				3.0
(B) Coral genus	1	0.321	0.011	0	43.3	43.3				
Tektite										
(A) Functional group	1, 2, 4	0.217	0.008	0.1	23.5	15.1	3.0		9.0	
	1, 2	0.197	0.018	0	23.5	21.2	2.2			
	2, 4	0.193	0.021	3.0	17.3		6.8		10.5	
(B) Coral genus	n/a	0.220	0.053							
3 years smoothed										
Yawzi Point										
(A) Functional group	1	0.691	<0.001	2.7	68.3	68.3				
	1, 2	0.587	<0.001	3.0	69.7	69.7	1.5			
	1, 2, 5	0.482	<0.001	0	73.7	68.3	1.5			3.9
(B) Coral genus	1, 2	0.645	<0.001	3.8	61.1	53.0	8.1			
	1	0.618	<0.001	7.4	52.9	52.9				
	1, 2, 3	0.534	<0.001	0	67.3	52.9	8.3	6.1		
Tektite										
(A) Functional group	1, 2	0.431	<0.001	8.4	51.5	34.8	16.7			
	1, 2, 4	0.395	<0.001	2.6	60.6	34.8	16.7		9.2	
	1, 2, 3, 4	0.382	<0.001	0	65.3	34.8	16.7	4.7	9.2	
(B) Coral genus	1, 2	0.420	<0.001	6.5	38.1	27.8	10.3			
	1, 2, 4	0.392	<0.001	2.7	48.1	27.8	10.3		10.0	
	1, 2, 3, 4	0.377	<0.001	0	55.0	27.8	10.3	6.9	10.0	

Note: Analyses tested for associations between community structure and environmental conditions in the preceding year (Annual), and over a running, centered average of 3 years (3 years smoothed). The strongest associations were revealed by BIO_ENV, with the best-fit and up to the next two best-fits reported. Analyses were completed with five environmental conditions (dependent variable [DV], 1 = temperature [in degrees Celsius], 2 = rainfall [in centimeters], 3 = hurricane, 4 = disease, and 5 = bleaching [Appendix S1: Table S3]) and associations between resemblance matrices are reported with the rank correlations (ρ) and its probability ($n = 999$ permutations, p_{perm}). For significant associations, DISTLM was used to fit linear models of environmental conditions, with the best model identified by ΔAIC and reported with the proportion of the variance explained (R^2), and the contribution of each DV to this variance. Analyses for: (A) community structure by functional group (coral, macroalgae, and crustose coralline algae/turf/bare space), and (B) coral community by genus (Appendix S1: Table S2).

Abbreviations: ΔAIC; difference in Akaike information criterion between models; DISTLM, distance-based linear modeling; n/a, not applicable.

and rainfall accounted for most for the variation (27.8% and 10.3%, respectively).

DISCUSSION

Rapid changes in ecosystems are defining features of the Anthropocene Epoch, and while many of these effects originated with the Industrial Revolution (Kidwell, 2015), they have only been featured in ecological science for ~20 years (Walther et al., 2002). Causation for these effects often can be attributed to climate change (Poloczanska et al., 2013), with the effects of acute disturbances garnering strong attention (Hughes, Kerry, et al., 2017; Turner, 2010). Quantifying the relative importance of multiple disturbances in causing ecosystems to change is important for accurate assessment of risks, and to advance solution-oriented science (Miller et al., 2014), yet the data required for these purposes can be sparse. Coral reefs have become the poster child for ecosystem degradation and solution-oriented science (Hughes et al., 2010, 2023), but changes in this ecosystem are often explained through an incomplete set of causes, for example, through bleaching (Hughes, Kerry, et al., 2017), storms (Woodley et al., 1981), and diseases (Brandt et al., 2021). Chronic coral mortality and depressed coral population growth are less commonly associated with declining coral abundance (cf. Ceccarelli et al., 2020; Connell et al., 1997).

Here, two reefs were used to quantify the effects of chronic and acute events in changing benthic communities. Although many corals have been killed on these reefs by acute events (e.g., hurricanes; Edmunds & Witman, 1991 and white pox disease; Miller et al., 2009), thus creating distinctive signatures in coral reef community structure (Figure 1), the chronic effects of varying temperature had particularly strong associations with the ecological trends over 36 years. These effects were expressed in univariate models through the association of rising temperature with reduced coral cover at Yawzi Point, and with increased coral cover and lower cover of CTB at Tektite. In multivariate models, temperature explained the greatest proportion of the variance in dissimilarities of benthic community structure among samplings, with this effect rising to 68% for functional groups at Yawzi Point when a 3-year running mean was implemented. Rainfall had little explanatory capacity in the LMMs, but it accounted for 1.5%–16.7% of the variance in the multivariate analyses (Table 2), suggesting chronic variation in rainfall might indirectly affect holistic community structure (Edmunds & Lasker, 2016). In some years, acute disturbances caused large and rapid changes in community structure (Figure 1), and while these effects were revealed in the statistical analysis through significant effects of hurricanes, bleaching, and disease (Table 1), they differed between sites, and were inconsistent among dependent variables (Figure 2).

The types and magnitudes of the changes affecting the reefs at Yawzi Point and Tektite since 1987 are well known in the Caribbean (Jackson et al., 2014; Roff & Mumby, 2012; Steneck et al., 2019), and as is common for the region, signs of coral community recovery have not emerged for St. John (cf. Connell, 1997; Steneck et al., 2019). Yawzi Point and Tektite were dominated by *O. annularis* in 1987, like many forereef communities throughout the Caribbean (Hughes & Tanner, 2000), but they transitioned from 32% to 45% coral cover in 1987, to 4%–15% by 2022, with increased coverage of macroalgae and CTB (Edmunds, 2013, 2019). Additionally, the coral assemblages changed (Figure 3C,D), driven in large part by the replacement of long-lived, mass spawning, and framework-building *Orbicella* spp. by weedy corals with brooding life history strategies (e.g., *Porites* spp.), and stress tolerant (including to elevated temperature) corals like *Siderastrea siderea* (Castillo et al., 2012; Darling et al., 2012). Caribbean-wide, these trends began with *Acropora* spp. mortality in the 1980s (Aronson & Precht, 2001), which probably affected *Acropora* spp. thickets that were growing near the present study sites in the 1970s (Lee et al., 1975), and continued with declining abundances of *Orbicella* spp. (Edmunds & Elahi, 2007; Toth et al., 2019), biotic homogenization (Burman et al., 2012), and a protracted recruitment failure of mass spawning corals (Hughes & Tanner, 2000; Williams et al., 2008). Together with changes in other biotic and abiotic factors, including a region-wide depression of reef fish abundances (Paddack et al., 2009), these events have advanced community transitions to favor weedy corals (Toth et al., 2019).

As coral cover changed at Yawzi Point and Tektite, the cover of macroalgae and CTB increased, with their cover strongly and inversely related at Tektite, and weakly inversely related Yawzi Point; in both cases, this relationship differed in intensity between groups of years separating around the early 2000s (Appendix S2: Figure S2). At Yawzi Point, the separation corresponded to the start of a period of low coral cover, and at Tektite, to the start of declining coral cover. A reciprocal relationship between macroalgae and CTB is well known in the Caribbean (Aronson et al., 2005; Aronson & Precht, 2000) where it is mediated by the intensity of herbivory (Aronson & Precht, 2000). In the present case, the relationship between the coverage of macroalgae and CTB, and its intensification over time at Tektite, highlights the potential for interactions between the availability of space on dead corals, herbivory, and reef flattening (Alvarez-Filip et al., 2009) to mediate covariance of abundance of these benthic space holders.

Unlike ecological studies of many Caribbean reefs, the length and temporal resolution of the present analysis demonstrate a gradual transition in the community phase (Figures 1 and 2). Although this transition has been punctuated by multiple examples of the same acute events (e.g., hurricanes), statistical analyses highlight the association of the ecological events with both chronic and acute events. A 36-year study provides an ecologically meaningful context within which acute events like Hurricane Hugo in 1989 (Edmunds & Witman, 1991), bleaching in 1998 (Rogers et al., 2008), bleaching and disease in 2005 (Miller et al., 2009), Hurricanes Irma and Marie in 2017 (Edmunds, 2019), and SCTLD in 2019 (Brandt et al., 2021), can objectively be evaluated. SCTLD is an interesting example of an acute event, because its effects extended over at least 2 years in St. John, and its lethality differed among coral species (e.g., leaving *Siderasterea* spp. relatively unaffected), with effects tempered by historical contingencies. For example, earlier disturbances spared some corals (e.g., *Dendrogyra cylindrus* and *Colpophyllia natans*) only to leave them vulnerable to SCTLD. It was the death by SCTLD around 2019/2020 of these corals at Tektite that caused the differences in coral community structure distinguishing 2021 and 2022 from other years in this millennium (Figure 3D). Without decadal-scale insights, it would be tempting to conclude that the changes in community structure caused by acute events at Yawzi Point and Tektite were the primary drivers of the multidecadal community dynamics at these sites.

This conclusion does not capture the complexities of the statistical analyses of 36 years of associations between community structure and environmental conditions. The contrasting trajectories of changing community structure between sites (Figure 1), as well as the ways in which the changes are differentially associated with environmental conditions, highlight the limitations of "single causation" constructs to explain the state of Caribbean reefs. Hurricanes significantly affected coral cover at Yawzi Point and Tektite (Table 1), but their effects were only strongly negative at Yawzi Point (Figure 1). Shortly after Hurricane Hugo in 1989, the storm was described as "severely damaging" to the *O. annularis* community at Yawzi Point (causing a 34% decline in cover, Edmunds & Witman, 1991), yet the ecological importance of this loss was blunted by the subsequent 23 years of cumulative damage. Hurricanes in 1995 and 1998, bleaching in 1998, and decades of small annual reductions in coral cover culminated in 3.8% coral cover by 2022. Multiple disease and bleaching events killed corals at Yawzi Point and Tektite between 1987 and 2022 (P. J. Edmunds, personal observation; Rogers et al., 2008), but the statistical analyses showed that declines in coral cover were only associated with bleaching at Tektite. The effects of diseases were not statistically discernible on coral cover at either site (Table 1), even when the effects of SCTLD were extended to a third year in the LMM (Appendix S2: Table S2). In the LMMs using coral cover as the dependent variable, the changes emerged as negative effect estimates at Yawzi Point, largely through the death of corals during hurricanes, following by macroalgal blooms (Edmunds & Witman, 1991), which caused positive effect estimates (Figure 2A,B). Hurricanes appeared to have positive effects for coral cover at Tektite, indicating that damage was attenuated in seawater 5 m deeper than at Yawzi Point. The greater depth reduces the impacts of storm waves (Davis et al., 2021), and the positive effect on coral cover probably resulted from the removal of macroalgae (to expose coral tissue) that emerged as nonsignificant negative effect estimates at this site (Figure 2E,F).

The association of temperature with coral cover was stronger than for hurricanes (Figure 2A,D), with coral cover declining with rising temperature at Yawzi Point, but increasing at Tektite. Multiple mechanisms could generate these outcomes, but because in situ temperatures typically differ ≤0.04°C between these sites (Edmunds, 2020), it is parsimonious to suggest they reflect the effect of deeper water at Tektite in attenuating light. At Yawzi Point, periods of elevated temperature had a greater probability of interacting with light to cause bleaching (Gonzalez-Espinosa & Donner, 2021) and led to reduced coral cover. In contrast, at Tektite where downwelling irradiance is reduced by 40% relative to Yawzi Point (calculated from the diffuse attenuation coefficient; Edmunds et al., 2018), the effects of temperature on coral growth might remain stimulatory (Pratchett et al., 2015). In the case of CTB at Tektite, the negative effects estimate for temperature is a plausible outcome of the inhibitory effects of high temperature on calcification of the crustose coralline algae (Comeau et al., 2016), and the reduction in algal growth that might be expected under reduced irradiances in deeper water (Tebbett & Bellwood, 2021). Because diseases were associated with enhanced coverage of macroalgae at Tektite, probably because they preempted space created by the death of corals, CTB also declined in abundance in association with diseases.

Coral reefs in the 21st century are different from those of 50 years ago (Jackson et al., 2014). Despite recognition of the large extent to which coral reefs have changed, the strong role of anthropogenic factors in driving these changes (Hughes, Barnes, et al., 2017), and the high probability of coral extirpations (Jones et al., 2021) and extinctions (Carpenter et al., 2008), elucidating the importance of different disturbance events in contributing to the state of coral reefs remains a research priority (Castro-Sanguino et al., 2021; Ceccarelli et al., 2020). In part, this is because disturbances like storms and bleaching are easy to document because of their conspicuous effects, whereas the consequences of subtle events can take decades to emerge (Hughes & Connell, 1999).

Major disturbances cause large changes in coral reef communities (Hughes, Barnes, et al., 2017; Hughes, Kerry, et al., 2017; Woodley et al., 1981) and can transition reefs from one benthic phase (e.g., coral) to another (e.g., algae) (Dudgeon et al., 2010). However, there are many chronic factors that can also mediate large changes in coral reefs that can play dominant roles in driving ecological states (Ceccarelli et al., 2020). Untangling the roles of the complex suite of disturbances affecting coral reefs is challenging, but progress in this task has benefited from categorizing disturbances as contrasts of abiotic versus biotic events (Huston, 1985), anthropogenic versus natural phenomena (Pearson, 1981), or chronic versus acute effects (Connell, 1997). Although disturbances in the natural world do not correspond well to binary constructs, the chronic-acute framework has been particularly useful in advancing the understanding of coral reefs (Connell et al., 1997; Hughes & Connell, 1999).

For several decades, studies of the response of coral reefs to temperature have been dominated by bleaching (Hughes, Kerry, et al., 2017). While bleaching can have profound ecological importance, the focus on this stressor has led to the other implications of rising temperature for coral reefs being overlooked. For reef corals, these implications include effects on metabolism (Jurriaans & Hoogenboom, 2019), reproductive phenology (Shlesinger & Loya, 2019), pelagic larval dispersal (O'Connor et al., 2007), and microbial diseases (Miller & Richardson, 2015). As described here, and elsewhere (González-Barrios et al., 2023), the chronic effects of variation in temperature can be important long-term drivers of change in coral reef communities.

Although working with shorter temporal records than employed herein, several studies have sought to explain changes in the coral reefs at Yawzi Point and Tektite through environmental conditions. Gross and Edmunds (2015) used multivariate autoregression (MAR) models with 20 years of data to explore community stability with respect to temperature and hurricanes. They showed these reefs had responded in a directional manner to sustained changes in environmental conditions. Both were sensitive to rising temperature, Yawzi Point (but not Tektite) was sensitive to hurricanes, and both displayed chronic losses that could not be attributed to hurricanes or temperature. Working with results from six nearby sites at 7–9 m depth, Edmunds and Lasker (2016) evaluated the roles of temperature, rainfall, and hurricanes in mediating changes from 1992 to 2014. They found that changes in the community structure of scleractinians and octocorals were best explained by rainfall and, to a lesser extent, hurricanes, although 39%–80% of the variation remained unexplained. In Gross and Edmunds (2015) and Edmunds and Lasker (2016), long-term variation in community structure was best explained by chronically changing environmental conditions.

The present study extends these analyses to four decades over which the reefs were impacted by multiple acute events. Acute disturbances were associated with reductions in coral cover, supporting the common narrative that the degradation of many reefs (Roff & Mumby, 2012), has been "driven" by acute events (e.g., Hughes et al., 2010). Acute events have conspicuously killed corals in St. John and throughout the Caribbean (Jackson et al., 2014), but here I reveal the extent to which long-term changes in community composition have been associated with both acute and chronic disturbances. Instead of accounting for the demise of coral reefs solely by acute events, causation is complex (Hughes & Connell, 1999) and akin to a "death by a thousand cuts" (Hughes, Barnes, et al., 2017) as described for insects (Wagner et al., 2021).

In the 1990s, the concept of self-organized criticality (SOC) posited that the accumulation of numerous small events could drive an ecological system to stochastic instability (Solé et al., 1999), which suggests that a coral reef dying from a thousand cuts faces impending but unpredictable collapse (Hughes et al., 2013). While it is beyond the scope of the present study to test this possibility for the reefs of St. John, it is interesting to note the lengthy period over which low cover has stabilized at Yawzi Point (Figure 1), and on nearby sites (Edmunds, 2018). The long-term stability of a low coral cover state might indicate that the ultimate collapse of these coral reefs (i.e., local extirpation of coral) hypothesized through SOC, has been avoided. Alternatively, it is possible that full "collapse" already has occurred, and the current low coral cover state is the new persistent state for these reefs.

Of the environmental factors tested for associations with changes in community structure, hurricanes and chronic changes in temperature were effective in explaining variation, which cautions against overlooking the chronic effects of temperature on reef corals (González-Barrios et al., 2023). While a more informed interpretation of the likely causes of reef degradation is provided by 36 years of data, the high portion of the variance in community structure that remains unexplained highlights the ongoing need for multidecadal, holistic time series from coral reefs (Hughes & Connell, 1999). These needs include extending time series, broadening consideration of drivers of ecological change, and increasing replication to enhance the statistical power in tests for the effects of drivers of ecological change.

AUTHOR CONTRIBUTIONS

Peter J. Edmunds designed and implemented the study, and sampled these reefs from 1987 to present. He is responsible for analysis and writing of this paper.

ACKNOWLEDGMENTS

This research has been funded from multiple sources, most recently through Biological Oceanography (OCE 20-19992), and has been permitted through the National Park Service (most recently VIIS-2022-SCI-0010). I thank S. Burgess for statistical advice and comments that improved earlier drafts of this paper. This is contribution number 384 of the CSUN marine biology program.

CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Edmunds, 2024) are available in Dryad at https://doi.org/10.5061/dryad.x0k6djht1.

ORCID

Peter J. Edmunds https://orcid.org/0000-0002-9039-9347

REFERENCES

Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. "Flattening of Caribbean Coral Reefs: Region-Wide Declines in Architectural Complexity." *Proceeedings of the Royal Society B: Biological Sciences* 276: 3019–25.

Aronson, R. B., I. G. Macintyre, S. A. Lewis, and N. L. Hilbun. 2005. "Emergent Zonation and Geographic Convergence of Coral Reefs." *Ecology* 86: 2586–2600.

Aronson, R. B., and W. F. Precht. 2000. "Herbivory and Algal Dynamics on the Coral Reefs at Discovery Bay, Jamaica." *Limnology and Oceanography* 45: 251–55.

Aronson, R. B., and W. F. Precht. 2001. "White-Band Disease and the Changing Face of Caribbean Coral Reefs." *Hydrobiologia* 460: 25–38.

Beijbom, O., P. J. Edmunds, C. Roelfsema, J. Smith, D. I. Kline, B. P. Neal, M. J. Dunlap, et al. 2015. "Towards Automated Annotation of Benthic Survey Images: Variability of Human Experts and Operational Modes of Automation." *PLoS One* 10: e0130312.

Brandt, M. E., R. S. Ennis, S. S. Meiling, J. Townsend, K. Cobleigh, A. Glahn, J. Quetel, V. Brandtneris, L. M. Henderson, and T. B. Smith. 2021. "The Emergence and Initial Impact of Stony Coral Tissue Loss Disease (SCTLD) in the United States Virgin Islands." *Frontiers in Marine Science* 8: 715329.

Burman, S. G., R. B. Aronson, and R. van Woesik. 2012. "Biotic Homogenization of Coral Assemblages along the Florida Reef Tract." *Marine Ecology Progress Series* 467: 89–96.

Burnham, K. P., and D. R. Anderson. 2004. "Multimodel Inference: Understanding AIC and BIC in Model Selection." *Sociological Methods and Research* 33: 261–304.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, et al. 2008. "One-Third of Reef-Building Corals Face Elevated Extinction Risk from Climate Change and Local Impacts." *Science* 321: 560–63.

Castillo, K. D., J. B. Ries, J. M. Weiss, and F. P. Lima. 2012. "Decline of Forereef Corals in Response to Recent Warming Linked to History of Thermal Exposure." *Nature Climate Change* 2: 756–760.

Castro-Sanguino, C., J. C. Ortiz, A. Thompson, N. H. Wolff, R. Ferrari, B. Robson, M. M. Magno-Canto, M. Puotinen, K. E. Fabricius, and S. Uthicke. 2021. "Reef State and Performance as Indicators of Cumulative Impacts on Coral Reefs." *Ecological Indicators* 123: 107335.

Ceccarelli, D. M., R. D. Evans, M. Logan, P. Mantel, M. Puotinen, C. Petus, G. R. Russ, and D. H. Williamson. 2020. "Long-Term Dynamics and Drivers of Coral and Macroalgal Cover on Inshore Reefs of the Great Barrier Reef Marine Park." *Ecological Applications* 30: e02008.

Chesher, R. H. 1969. "Destruction of Pacific Corals by the Sea Star *Acanthaster planci*." *Science* 165: 280–83.

Clarke, K. R., and R. N. Gorley. 2015. *PRIMER v7: User Manual*. Plymouth: PRIMER-E.

Comeau, S., R. C. Carpenter, C. A. Lantz, and P. J. Edmunds. 2016. "Parameterization of the Response of Calcification to Temperature and pCO_2 in the Coral *Acropora pulchra* and the Alga *Lithophyllum kotschyanum*." *Coral Reefs* 35: 929–939.

Connell, J. H. 1997. "Disturbance and Recovery of Coral Assemblages." *Coral Reefs* 16: S101–S113.

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. "A 30-Year Study of Coral Abundance, Recruitment, and Disturbance at Several Scales in Space and Time." *Ecological Monographs* 67: 461–488.

Cramer, K. L., M. K. Donovan, J. B. Jackson, B. J. Greenstein, C. A. Korpanty, G. M. Cook, and J. M. Pandolfi. 2021. "The Transformation of Caribbean Coral Communities since Humans." *Ecology and Evolution* 11: 10098–118.

Darling, E. S., L. Alvarez-Filip, T. O. Oliver, T. R. McClanahan, and I. M. Côté. 2012. "Evaluating Life-History Strategies of Reef Corals from Species Traits." *Ecology Letters* 15: 1378–86.

Davis, K. A., G. Pawlak, and S. G. Monismith. 2021. "Turbulence and Coral Reefs." *Annual Review of Marine Science* 13: 343–373.

Doney, S. C., V. J. Fabry, R. A. Feely, and J. A. Kleypas. 2009. "Ocean Acidification: The Other CO_2 Problem." *Annual Review of Marine Science* 1: 169–192.

Dudgeon, S. R., R. B. Aronson, J. F. Bruno, and W. F. Precht. 2010. "Phase Shifts and Stable States on Coral Reefs." *Marine Ecology Progress Series* 413: 201–216.

Edmunds, P. J. 1991. "Extent and Effect of Black Band Disease on a Caribbean Reef." *Coral Reefs* 10: 161–65.

Edmunds, P. J. 2013. "Decadal-Scale Changes in the Community Structure of Coral Reefs of St. John, US Virgin Islands." *Marine Ecology Progress Series* 489: 107–123.

Edmunds, P. J. 2018. "The Hidden Dynamics of Low Coral Cover Communities." *Hydrobiologia* 818: 193–209.

Edmunds, P. J. 2019. "Three Decades of Degradation Lead to Diminished Impacts of Severe Hurricanes on Caribbean Reefs." *Ecology* 100: e02587.

Edmunds, P. J. 2020. "Vital Rates of Small Reef Corals Are Associated with Variation in Climate." *Limnology and Oceanography* 66: 901–913.

Edmunds, P. J. 2024. "Data from: Decadal-Scale Time Series Highlight the Role of Chronic Disturbances in Driving Ecosystem Collapse in the Anthropocene." Dryad, Dataset. https://doi.org/10.5061/dryad.x0k6djht1.

Edmunds, P. J., and R. Elahi. 2007. "The Demographics of a 15-Year Decline in Cover of the Caribbean Reef Coral *Montastraea annularis*." *Ecological Monographs* 77: 3–18.

Edmunds, P. J., and H. R. Lasker. 2016. "Cryptic Regime Shift in Benthic Community Structure on Shallow Reefs in St. John, US Virgin Islands." *Marine Ecology Progress Series* 559: 1–12.

Edmunds, P. J., G. Tsounis, R. Boulon, and L. Bramanti. 2018. "Long-Term Variation in Light Intensity on a Coral Reef." *Coral Reefs* 37: 955–965.

Edmunds, P. J., and J. D. Witman. 1991. "Effect of Hurricane Hugo on the Primary Framework of a Reef along the South Shore of St. John, US Virgin Islands." *Marine Ecology Progress Series* 78: 201–4.

González-Barrios, F. J., N. Estrada-Saldívar, E. Pérez-Cervantes, F. Secaira-Fajardo, and L. Álvarez-Filip. 2023. "Legacy Effects of Anthropogenic Disturbances Modulate Dynamics in the world's Coral Reefs." *Global Change Biology* 29: 3285–3303.

Gonzalez-Espinosa, P. C., and S. D. Donner. 2021. "Cloudiness Reduces the Bleaching Response of Coral Reefs Exposed to Heat Stress." *Global Change Biology* 27: 3474–86.

Gower, J. C. 1971. "A General Coefficient of Similarity and Some of Its Properties." *Biometrics* 27: 857–871.

Gross, K., and P. J. Edmunds. 2015. "Stability of Caribbean Coral Communities Quantified by Long-Term Monitoring and Autoregression Models." *Ecology* 96: 1812–22.

Hughes, T. P., A. H. Baird, T. H. Morrison, and G. Torda. 2023. "Principles for Coral Reef Restoration in the Anthropocene." *One Earth* 6: 656–665.

Hughes, T. P., M. L. Barnes, D. R. Bellwood, J. E. Cinner, G. S. Cumming, J. B. C. Jackson, J. Kleypas, et al. 2017. "Coral Reefs in the Anthropocene." *Nature* 546: 82–90.

Hughes, T. P., and J. H. Connell. 1999. "Multiple Stressors on Coral Reefs: A Long-Term Perspective." *Limnology and Oceanography* 44: 932–940.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. "Rising to the Challenge of Sustaining Coral Reef Resilience." *Trends in Ecology and Evolution* 25: 63–3642.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, et al. 2017. "Global Warming and Recurrent Mass Bleaching of Corals." *Nature* 543: 373–77.

Hughes, T. P., C. Linares, V. Dakos, I. A. van de Leemput, and E. H. van Nes. 2013. "Living Dangerously on Borrowed Time during Slow, Unrecognized Regime Shifts." *Trends in Ecology and Evolution* 28: 149–155.

Hughes, T. P., and J. E. Tanner. 2000. "Recruitment Failure, Life Histories, and Long-Term Decline of Caribbean Corals." *Ecology* 81: 2250–63.

Huston, M. A. 1985. "Patterns of Species Diversity on Coral Reefs." *Annual Review of Ecology and Systematics* 16: 149–177.

Jackson, J. B. C., M. Donovan, K. Cramer, and V. Lam. 2014. *Status and Trends of Caribbean Coral Reefs: 1970–2012*. Gland: Global Coral Reef Monitoring Network, IUCN.

Jones, N. P., L. Kabay, K. Semon Lunz, and D. S. Gilliam. 2021. "Temperature Stress and Disease Drives the Extirpation of the Threatened Pillar Coral, *Dendrogyra Cylindrus*, in Southeast Florida." *Scientific Reports* 11: 14113.

Jurriaans, S., and M. O. Hoogenboom. 2019. "Thermal Performance of Scleractinian Corals along a Latitudinal Gradient on the Great Barrier Reef." *Philosophical Transactions of the Royal Society B* 374: 20180546.

Kidwell, S. M. 2015. "Biology in the Anthropocene: Challenges and Insights from Young Fossil Records." *Proceedings of the National Academy of Sciences of the United States of America* 112: 4922–29.

Kohler, K. E., and S. M. Gill. 2006. "Coral Point Count with Excel Extensions (CPCe): A Visual Basic Program for the Determination of Coral and Substrate Coverage Using Random Point Count Methodology." *Computers and Geosciences* 32: 1259–69.

Lafferty, K. D. 2009. "The Ecology of Climate Change and Infectious Diseases." *Ecology* 90: 888–900.

Lee, C. C., E. L. Lee, and J. S. Bunt. 1975. "Distribution of Biomass in a Coral Reef Transect." *Bulletin of the Natural History Museum of Los Angeles County* 30: 69–75.

Levitan, D. R., R. M. Best, and P. J. Edmunds. 2023. "Sea Urchin Mass Mortalities 40 y Apart Further Threaten Caribbean Coral Reefs." *Proceedings of the National Academy of Sciences of the United States of America* 120: e2218901120.

Luo, Y., J. Melillo, S. Niu, C. Beier, J. Clark, A. T. Classen, E. Davidson, et al. 2011. "Coordinated Approaches to Quantify Long-Term Ecosystem Dynamics in Response to Global Change." *Global Change Biology* 17: 843–854.

Miller, A. W., and L. L. Richardson. 2015. "Emerging Coral Diseases: A Temperature-Driven Process?" *Marine Ecology* 36: 278–291.

Miller, J., E. Muller, C. Rogers, R. Waara, A. Atkinson, K. R. T. Whelan, M. Patterson, and B. Witcher. 2009. "Coral Disease Following Massive Bleaching in 2005 Causes 60% Decline in Coral Cover on Reefs in the US Virgin Islands." *Coral Reefs* 28: 925–937.

Miller, T. R., A. Wiek, D. Sarewitz, J. Robinson, L. Olsson, D. Kriebel, and D. Loorbach. 2014. "The Future of Sustainability Science: A Solutions-Oriented Research Agenda." *Sustainability Science* 9: 239–246.

O'Connor, M. I., J. F. Bruno, S. D. Gaines, B. S. Halpern, S. E. Lester, B. P. Kinlan, and J. M. Weiss. 2007. "Temperature Control of Larval Dispersal and the Implications for Marine Ecology, Evolution, and Conservation." *Proceedings of the National Academy of Sciences of the United States of America* 104: 1266–71.

Paddack, M. J., J. D. Reynolds, C. Aguilar, R. S. Appeldoorn, J. Beets, E. W. Burkett, P. M. Chittaro, et al. 2009. "Recent Region-Wide Declines in Caribbean Reef Fish Abundance." *Current Biology* 19: 590–95.

Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems." *Nature* 421: 37–42.

Pearson, R. G. 1981. "Recovery and Recolonization of Coral Reefs." *Marine Ecology Progress Series* 4: 105–122.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, et al. 2013. "Global Imprint of Climate Change on Marine Life." *Nature Climate Change* 3: 919–925.

Pratchett, M. S., K. D. Anderson, M. O. Hoogenboom, E. Widman, A. H. Baird, J. M. Pandolfi, P. J. Edmunds, and J. M. Lough. 2015. "Spatial, Temporal and Taxonomic Variation in Coral Growth—Implications for the Structure and Function of Coral Reef Ecosystems." *Oceanography and Marine Biology: An Annual Review* 53: 215–295.

Roff, G., and P. J. Mumby. 2012. "Global Disparity in the Resilience of Coral Reefs." *Trends in Ecology and Evolution* 27: 404–413.

Rogers, C. S., J. Miller, E. M. Muller, P. Edmunds, R. S. Nemeth, J. P. Beets, A. M. Friedlander, et al. 2008. "Ecology of Coral Reefs in the US Virgin Islands." In *Coral Reefs of the USA*, edited by B. M. Riegl and R. E. Dodge, 303–373. Berlin: Springer.

Shlesinger, T., and Y. Loya. 2019. "Breakdown in Spawning Synchrony: A Silent Threat to Coral Persistence." *Science* 365: 1002–7.

Solé, R. V., S. C. Manrubia, M. Benton, S. Kauffman, and P. Bak. 1999. "Criticality and Scaling in Evolutionary Ecology." *Trends in Ecology and Evolution* 14: 156–160.

Steneck, R. S., S. N. Arnold, R. Boenish, R. de León, P. J. Mumby, D. B. Rasher, and M. W. Wilson. 2019. “Managing Recovery Resilience in Coral Reefs against Climate-Induced Bleaching and Hurricanes: A 15 Year Case Study from Bonaire, Dutch Caribbean.” *Frontiers in Marine Science* 6: 265.

Syvitski, J., C. N. Waters, J. Day, J. D. Milliman, C. Summerhayes, W. Steffen, J. Zalasiewicz, et al. 2020. “Extraordinary Human Energy Consumption and Resultant Geological Impacts Beginning around 1950 CE Initiated the Proposed Anthropocene Epoch.” *Communications Earth & Environment* 1: 32.

Tebbett, A. B., and D. R. Bellwood. 2021. “Agal Turf Productivity on Coral Reefs: A Meta Analysis.” *Marine Environmental Research* 168: 105311.

Toth, L. T., A. Stathakopoulos, I. B. Kuffner, R. R. Ruzicka, M. A. Colella, and E. A. Shinn. 2019. “The Unprecedented Loss of Florida’s Reef-Building Corals and the Emergence of a Novel Coral-Reef Assemblage.” *Ecology* 100: e02781.

Turner, M. G. 2010. “Disturbance and Landscape Dynamics in a Changing World.” *Ecology* 91: 2833–49.

Ummenhofer, C. C., and G. A. Meehl. 2017. “Extreme Weather and Climate Events with Ecological Relevance: A Review.” *Philosophical Transactions of the Royal Society, B: Biological Sciences* 372: 20160135.

Wagner, D. L., E. M. Grames, M. L. Forister, M. R. Berenbaum, and D. Stopak. 2021. “Insect Decline in the Anthropocene: Death by a Thousand Cuts.” *Proceedings of the National Academy of Sciences of the United States of America* 118: e2023989118.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. “Ecological Responses to Recent Climate Change.” *Nature* 416: 389–395.

Williams, D. E., M. W. Miller, and K. L. Kramer. 2008. “Recruitment Failure in Florida Keys *Acropora palmata*, a Threatened Caribbean Coral.” *Coral Reefs* 27: 697–705.

Woodley, J. D., E. A. Chornesky, P. A. Clifford, J. B. C. Jackson, L. S. Kaufman, N. Knowlton, J. C. Lang, et al. 1981. “Hurricane Allen’s Impact on Jamaican Coral Reefs.” *Science* 214: 749–755.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Edmunds, Peter J. 2024. “Decadal-Scale Time Series Highlight the Role of Chronic Disturbances in Driving Ecosystem Collapse in the Anthropocene.” *Ecology* e4360. https://doi.org/10.1002/ecy.4360