FEATURE ARTICLE

Cryptic regime shift in benthic community structure on shallow reefs in St. John, US Virgin Islands

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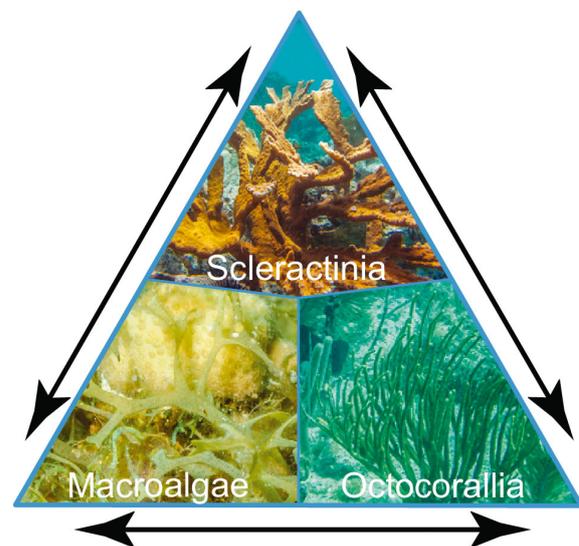[1]Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303, USA
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ABSTRACT: We evaluated whether long-term changes on fringing reefs (7–9 m depth) around St. John, US Virgin Islands, conformed to the 'coral reef crisis' involving ongoing collapse of community structure. Annual photoquadrats at 6 sites were used to measure octocoral abundance (by genus) and the cover of scleractinians (by species), macroalgae, crustose coralline algae, algal turf, and bare space. Community structure changed between 1992 and 2014, but did not correspond to large changes in response to pulse disturbances; octocoral abundance declined from 1992 to 2002, but increased to 2014, scleractinians remained uncommon (~4.5% cover), and macroalgae became more abundant. Richness and diversity of octocorals and scleractinians increased following 2000, and together defined 2 communities characterized by distinct taxonomic assemblages and temporally segregated to 1992–2001 versus 2002–2014. Smoothed temporal variation in community structure assessed at generic (Octocorallia) and species (Scleractinia) level was associated most strongly with rainfall, and to a lesser extent with hurricane intensity, thereby underscoring the roles of chronic disturbances in driving gradual changes in community structure. Together, these changes did not conform to the typical coral reef crisis construct, and instead summed to cryptic regime change that has escaped attention by researchers focused on scleractinians and macroalgae.

KEY WORDS: Scleractinia · Octocorallia · Ecology · Caribbean · Coral

Shallow reefs (7–9 m) in St. John, US Virgin Islands, have shown a cryptic regime change over the last 23 yr involving subtle covariation of abundance of scleractinians, macroalgae, and octocorals.

Photos: P. J. Edmunds

INTRODUCTION

The impacts of anthropogenic disturbances on ecosystems define a new epoch (Lewis & Maslin 2015), in which human 'fingerprints' are evident in virtually every biome (Walther et al. 2002). Some of the strongest effects are caused by climate change (Walther et al. 2002), but a wide variety of natural and local-scale human disturbances are acting in concert to drive changes in ecosystem structure and function (Mouillot et al. 2013). Dramatic changes attract the greatest attention, and large and rapid changes in community structure often are described as regime shifts (Walther et al. 2002). One of the best examples of dramatic change is provided by coral reefs, where decades of declining cover of scleractinian corals have fueled the notion of a coral reef crisis (Hoegh-Guldberg et al. 2007). For scleractinians, declining cover often has been associated with increasing abundances of macroalgae (Bruno et al.

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2009), especially in the Caribbean (Roff & Mumby 2012). However, changes in abundance of scleractinians and macroalgae alone do not fully capture the range of community dynamics occurring on coral reefs (Norström et al. 2009).

Although most studies of community change on coral reefs have focused on scleractinians and macroalgae (Mumby et al. 2013 and references therein), other transitions in community structure have occurred (Norström et al. 2009), and they have received little attention. These alternative transitions include changeovers from scleractinians to corallimorpharians or soft corals in the Indo-Pacific (Work et al. 2008), and to sponges (Loh & Pawlik 2014) or gorgonian soft corals (Ruzicka et al. 2013, Lenz et al. 2015) in the Caribbean. Transitions in community structure favoring octocorals are particularly interesting, because octocorals have long been recognized as important constituents of coral reef faunas (Kinzie 1973), even though ecological studies of this ecosystem rarely give them much attention. In the Caribbean, octocoral populations historically have been recorded over large areas of reef with their colonies interspersed at low densities among scleractinians (Kinzie 1973). Recent analyses indicate that octocorals may be becoming more common throughout the region (Ruzicka et al. 2013, Lenz et al. 2015), including in habitats formerly dominated by scleractinians (Ruzicka et al. 2013). These changes may reflect a widespread and gradual transition in benthic community structure to favor octocorals, which has important implications for the structure and function of coral reefs.

Scleractinian-to-macroalgal transitions have been described as a phase change or alternate stable state. This distinction has been debated for over a decade (Fung et al. 2011), and both concepts remain in use. The phrase 'regime shifts' provides an alternative terminology to describe large changes in community structure independent of the causes and the ecological stability of the phases (Conversi et al. 2015). In contrast to the rapid scleractinian-to-macroalgal transitions (Done 1992), it has also been recognized that in some cases the rate of change in community structure will occur over decades to centuries, which reflect time spans that are commensurate with the generation times of long-lived scleractinians. These more gradual changes have been referred to as 'cryptic regime shifts' (Hughes et al. 2013). Recognizing cryptic regime change is important, as the slow speed of the process creates the capacity to detect changes before a stable endpoint is reached, and therefore the possibility of preventative resource management (Hughes et al. 2013).

We quantified the community structure of fringing reefs (7–9 m depth) in St. John, US Virgin Islands, using annual records extending from 1992 to 2014. The record describes the abundance of octocoral genera, and the cover of scleractinians at mostly species resolution, macroalgae, and CTB (crustose coralline algae, algal turf, and bare space combined; Aronson & Precht 2000). Changes in cover of scleractinians, macroalgae, and CTB are described elsewhere (Edmunds 2013), and a subset of these data has been used to show that octocorals increased in abundance between 1992 and 2013 (Lenz et al. 2015). Using all the data from 1992 to 2014, and quantifying octocoral and scleractinian communities, we evaluate whether this record conforms to the commonly referenced 'coral reef crisis' (Hughes et al. 2010, Bellwood et al. 2004) that refers to sites facing imminent collapse of the coral reef community. We address 2 questions: (1) is there evidence of a regime change affecting multiple aspects of community structure, and (2) to what extent have changes in community structure been associated with both episodic and chronic changes in physical environmental conditions?

MATERIALS AND METHODS

Data collection

Benthic coral reef communities were monitored on the south shore of St. John. In 1992, 6 sites were selected using random coordinates constrained to hard bottom on fringing reefs (<9-m depth) between Cabritte Horn and White Point (Fig. S1 in the Supplement at www-int-res.com/articles/suppl/m559p001_supp.pdf), and were permanently marked. Three sites (RS5, RS11 and RS15; Fig. S1) resemble gorgonian plains (sensu Williams et al. 2015a), but the remainder have greater topographic complexity than gorgonian plains due to the presence of igneous boulders and cliffs.

The 6 study sites were censused annually using photoquadrats randomly positioned along a marked transect parallel to the depth contour. From 1992 to 1999, each site was sampled with approximately 18 photoquadrats along a 20 m transect, with images recorded using a Nikonos V camera fitted with a 28 mm lens, strobes, and Kodachrome 64 film. Color slides were scanned at 4000 dpi for analysis. In 2000, each transect was extended to 40 m in length, and the sampling was increased to 40 photoquadrats distributed randomly along each transect. Increased

sampling was made possible with the advent of digital cameras (3.3 to 16.2 megapixels). All cameras were mounted on a framer and recorded a 0.5 × 0.5 m quadrat that resolved objects ≥1 cm.

Photoquadrats were analyzed for the percentage cover of scleractinians, macroalgae, and CTB by identifying the benthic substratum beneath 200 randomly placed points on each image using CPCe software (Kohler & Gill 2006). Scleractinians were resolved to 26 taxa (see Table S1 in the Supplement, and macroalgae were defined as ≥1 cm thalli of mostly *Lobophora*, *Halimeda*, *Padina*, and *Dictyota*. Using the same photoquadrats, octocorals were resolved to 11 genera (Table S1), and colonies that could not be identified were categorized as 'unknown'. Octocorals were counted in each photoquadrat, with arborescent taxa scored by the presence of holdfasts, and encrusting *Erythropodium caribaeorum* (henceforth *Erythropodium*) scored based on the number of discrete patches (i.e. colonies). As colonies of *Erythropodium* undergo fission and fusion, colony abundance could provide a misleading indication of ecological trends affecting this species. To explore this possibility, the percentage cover of *Erythropodium* was also calculated using the same methods as described above for scleractinians, macroalgae, and CTB.

Local- and regional-scale measurements of the physical environment were tested in a multivariate framework for their ability to account for temporal variance in the biotic data. Seawater temperature was measured at 9–11 m depth in Great Lameshur Bay using loggers (Edmunds 2013) and was averaged by day to calculate the mean, minimum, and maximum temperature, as well as the number of hot days (mean >29.3°C) and cold days (mean ≤26.0°C) (Edmunds 2004). The 29.3°C cut-off for defining hot days was based on the local coral bleaching threshold, as determined by the United States National Oceanic and Atmosphereic Administration, National Environmental Satellite Data and Information Service (http://coralreefwatch.noaa.gov/vs/index.php). The 26.0°C cut-off for defining cold days is an arbitrary value defined as the 15th percentile of daily temperatures (Edmunds 2004). Winters with cooler than average temperatures will have greater numbers of 'cold days', and the index was employed to evaluate the potentially valuable effects of cold winters in promoting elevated coral biomass (Fitt et al. 2000). Rainfall (cm yr^{-1}) was compiled for St. John (Edmunds & Gray 2014), and hurricanes were evaluated on a categorical scale (H_{index}) (Gross & Edmunds 2015). Hurricanes impacted the study areas after the annual monitoring, and their effects appear in coral community data from the year following each event. Temporal variation in the regional-scale physical environment was evaluated through a detrended index reflecting the effect of the Atlantic Multidecadal Oscillation (AMO) as reported in Steinman et al. (2015) and provided courtesy of the first author.

Statistical analysis

Sites were treated as statistical replicates, and abundance and cover data from photoquadrats were averaged by site to describe community structure with 6 replicates per year. To evaluate the implications of increasing the sample size (no. of quadrats) from ~18 to ~40 in 2000, analysis of multivariate community structure in 2000 (scleractinians by species, octocorals by genus, CTB, and macroalgae) based on the initial 18 quadrats was compared with the analysis based on the additional quadrats using PERMANOVA (Anderson 2001). Data were standardized (z-scores) to address their measurement on different scales, and fourth-root transformed prior to calculating resemblance matrices using Bray–Curtis similarities. Univariate contrasts were also conducted between the initial 18 quadrats and the additional quadrats using t-tests with Bonferroni-adjusted alpha values to reduce the risks of Type I errors. Changes over time in the abundance of octocorals and scleractinians are displayed using line graphs showing means ± SE for untransformed values. Based on the taxonomic resolution described above, community structure was characterized by site using Shannon–Wiener diversity (H'), Pielou's evenness (J'), and richness (number of taxa); in this application, these metrics refer to alpha diversity (Whittaker 1960). For scleractinians, H' and J' were calculated using percentage cover as a measure of abundance, and for octocorals, abundance was evaluated by density (colonies 0.25 m^{-2}).

PERMANOVA (Anderson 2001) was used to test for changes in community structure among years (repeated measures) and sites (random effect) based on 4 assemblages: (1) the whole community (scleractinians, octocorals, macroalgae, and CTB), (2) octocorals by genus, (3) scleractinians by species, and (4) octocorals and scleractinians combined, to genus or species, respectively. The same design was used in a univariate mode to test for time and site effects using H', J', and richness as dependent variables. Comparisons of scleractinian and octocoral community structure over time were conducted using PERMANOVAs of resemblance matrices composed of Bray–Curtis

similarities. Analyses were repeated for scleractinians and octocorals combined, and then for each separately. In the combined scleractinian and octocoral analysis, data were normalized and square-root transformed. Analyses of scleractinians alone or octocorals alone used square-root or fourth-root transformed data, respectively. Significance was tested in a permutational framework (999 permutations) and evaluated through Pseudo-F and the probability of obtaining the statistic values by chance alone (p_{perm}).

To detect years between which significant changes in community structure occurred, planned contrasts were used between sequential years, and unplanned contrasts were used to compare sites. The same techniques were used for H', J', and richness, except values were square-root transformed, and similarities were determined using Euclidian distance. To evaluate rates of change in dependent variables over time, data were tested for temporal autocorrelation using the Durbin–Watson statistic (Durbin & Watson 1951). Model I regressions were used where there was no autocorrelation, and where autocorrelation was detected, Model I linear regressions were adjusted using the Cochrane–Orcutt model (Cochrane & Orcutt 1949).

Multivariate variation in community structure was described using multidimensional scaling (MDS) applied to the community structure averaged across sites within years, and described at 2 resolutions: (1) by functional group consisting of scleractinians (summed among taxa), octocorals (summed among genera), macroalgae, and CTB, and (2) scleractinians by species, octocorals by genus, macroalgae, and CTB. Data were standardized (z-scores) to address their measurement on different scales, and fourth-root transformed prior to calculating resemblance matrices using Bray–Curtis similarities. MDS ordinations were prepared using 100 restarts until stress stabilized, and similarity contours were applied where they enhanced the interpretation of groupings. Principle coordinate analyses (PCoA) were prepared using the same resemblance matrices, and were overlaid with vectors displaying Spearman correlations between dependent variables and PCO1 and PCO2. The length (scaled to ≤1) of the vectors shows the influence of dependent variables in causing separation along each axis.

The BEST procedure in PRIMER (Clarke & Gorley 2006) and DISTLM in PERMANOVA+ (Anderson et al. 2008) were used evaluate the extent to which community structure was associated with physical conditions. The BEST procedure is based on rank correlations (ρ) between the resemblance matrix defining the community structure and a suite of resemblance matrices defining physical conditions. Where community structure included variables measured on multiple scales, values were standardized and square-root transformed. Collinear variables were excluded, and variables were standardized and square-root transformed. Resemblance matrices were prepared for both data types using Bray–Curtis similarities (biotic data) or Euclidean distances (physical conditions). To evaluate associations between biotic and physical data, analyses were conducted first, with data obtained in the year of measurement. To test for delayed responses in community structure, the biotic data for each year were also compared with the physical conditions 1 yr earlier, 2 yr earlier, and averaged over the 3 yr starting with the measurement year and extending back 2 yr. Testing for delayed responses was motivated by the possibility that physical conditions in any one year initiated biological responses that were not evident until one or more years had passed. Finally, biotic and environment conditions were compared using 3 yr moving averages to smooth stochastic variation from year to year. Significance of ρ was determined within a permutational framework (999 permutations) as the probability of occurrence by chance alone (p_{perm}).

The BEST procedure does not model the multivariate data, rather, it detects the best rank order match between dissimilarities in 2 data sets; often it identifies multiple associations including those with differing numbers of variables. To determine the best linear model between physical conditions and biological data, we used the DISTLM procedure, which distinguished among the multiple associations identified in the BEST procedure. Where BEST identified significant associations, DISTLM was used to identify the most effective combination of variables explaining the biological data in a linear model, with the best fit identified by the corrected Akaike's information criterion (AIC_c) (Anderson et al. 2008). All possible combinations of predictor variables were considered. Values reported are combinations of physical conditions that are significantly associated with the biological data (i.e. as detected with the BEST procedure), and have the greatest explanatory capacity.

The BEST procedure was used for the regional-scale physical data (i.e. the AMO index), in which one environmental dependent variable was tested, and this was not smoothed further than in the primary analysis in which the AMO was reported (Steinman et al. 2015).

Multivariate statistics based on resemblance matrices were conducted using PRIMER version 6 (Clarke & Gorley 2006) and PERMANOVA+ for PRIMER

(Anderson et al. 2008). Statistics related to autocorrelation and the correction of Model I regressions against time were conducted using XLStat 2015 (Addinsoft SARL).

RESULTS

Community structure

Fig. 1 shows the changes in abundance of the major groups over 23 yr. In 1992, communities consisted of 35.2 ± 6.2% cover of CTB, 14.4 ± 6.5% cover of macroalgae, 3.8 ± 1.0% cover of scleractinians, and 3.1 ± 1.6 colonies m^{-2} of octocorals (mean ± SE, n = 6 sites). In 2000, the sample size (no. of quadrats at each site) was increased from ~18 to ~40 by sampling along a 40 m transect rather than a 20 m transect. The longer transects sometimes sampled more heterogeneous areas of reef, and in 2000, multivariate community structure (31 benthic groups) differed between the initial and augmented portions of the transects, in patterns that differed among sites (i.e. there was an interaction between site and transect portion; Pseudo-F = 1.678, df = 5, 202, p_{perm} = 0.004). Univariate analyses (α = 0.002) revealed that CTB was more abundant in the augmented (76%) versus the initial (44%) portion of the transect at Cabritte Horn (p < 0.001), and in the augmented (51%) versus the initial (29%) portion of the transect at Europa Bay

(RS11, Fig. S1); no other contrasts were significant. The increased sample size did not affect the patterns of change in community structure that were detected (described below). By 2014, CTB cover had increased to 51.4 ± 3.5%, the cover of macroalgae had increased to 24.6 ± 3.7%, but there were virtually no changes in the cover of scleractinians (3.5 ± 0.9%) or octocoral abundance (2.5 ± 0.7 colonies 0.25 m^{-2}). However, the abundances of all taxa were more dynamic over time than the endpoints of the time series suggest. Between 1992 and 2014, there were significant year-to-year changes in benthic community structure among sites and times, some, but not all, of which were associated with the 2 yr of bleaching and 3 hurricanes that occurred over the study period (Fig. 1, Table S2 in the Supplement).

Bleaching and hurricanes sometimes were followed by declines in cover of scleractinians and reduced abundance of octocorals. For example, the abundance of octocorals declined following Hurricanes Marilyn and Luis in 1995, the cover of scleractinians declined the year following Hurricanes Jose and Lenny in 1999, and both were negatively affected for 1–2 yr by bleaching in 1998 (Fig. 1A). However, the cover of scleractinians did not change following Hurricanes Marilyn and Luis in 1995, and the abundance of octocorals was unaffected in the year following Hurricanes Jose and Lenny in 1999 (Fig. 1A). Cover of CTB increased following each of the 3 years with hurricanes, but exhibited no consistent response to
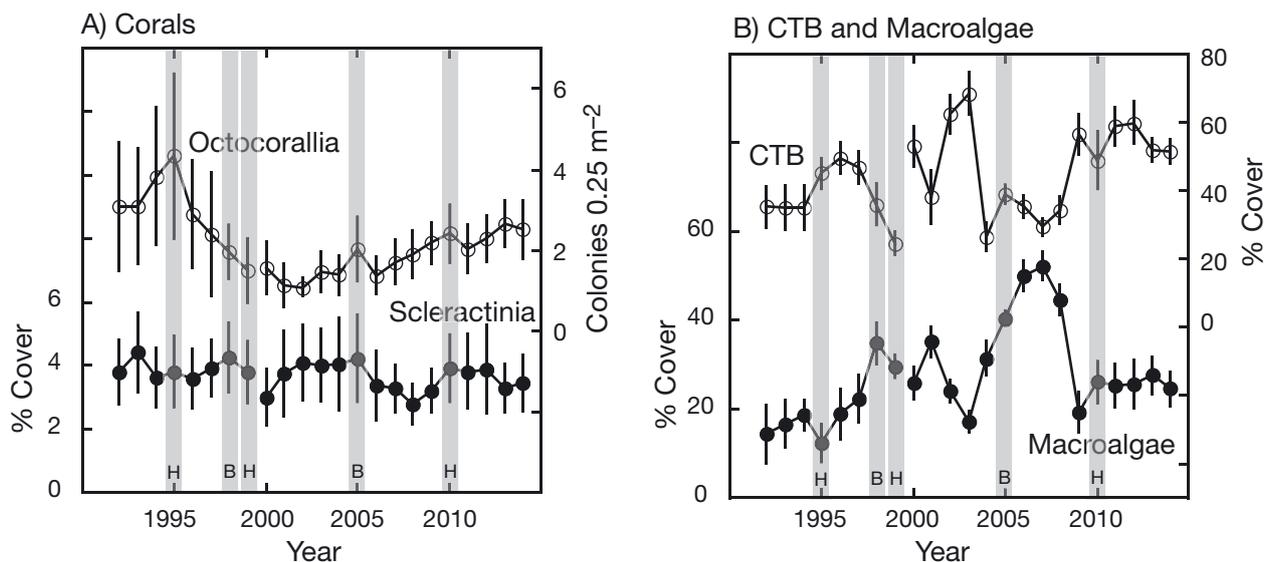

Fig. 1. Community structure at sites between Cabritte Horn and White Point from 1992 to 2014. (A) Cover of scleractinians (left abscissa) and abundance of octocorals (right abscissa), and (B) cover of macroalgae (left abscissa) and CTB (crustose coralline algae, algal turf, and bare space combined; right abscissa). Means ± SE displayed with n = 6 sites. Grey blocks show years in which disturbances occurred (H: hurricane; B: bleaching); break in line plots between 1999 and 2000 reflects the change from 35 mm slide film (1992–1999, n ≈ 18 photoquadrats site^{-1} yr^{-1}) to digital images (2000–present, n ≈ 40 photoquadrats site^{-1} yr^{-1})

bleaching events (Fig. 1B). The cover of CTB and macroalgae were inversely associated (r = −0.503, df = 21, p = 0.009). Macroalgae did not exhibit a consistent response to either bleaching events or hurricanes. When CTB and macroalgae were included in multivariate comparisons of community structure over time, there were significant changes following hurricanes in 1999 and 2005 (Table S2), following bleaching in 1998, and in the years immediately following 2001 and 2004 when neither hurricanes nor bleaching occurred (Table S2).

The 6 most common scleractinians were *Siderastrea siderea* (1.0% cover averaged among years), *Orbicella annularis* (0.6%), *Porites astreoides* (0.6%), *Montastraea cavernosa* (0.3%), *Agaricia* spp. (0.3%), and branching *Porites* (0.2%). These taxa and the other scleractinians changed asynchronously in abundance (Fig. 2). *Porites astreoides* and branching *Porites* were in decline early in the study, and increased in abundance during the last third of the study, whereas the other 4 taxa showed the reverse trend (Fig. 2). The 5 most common octocorals were
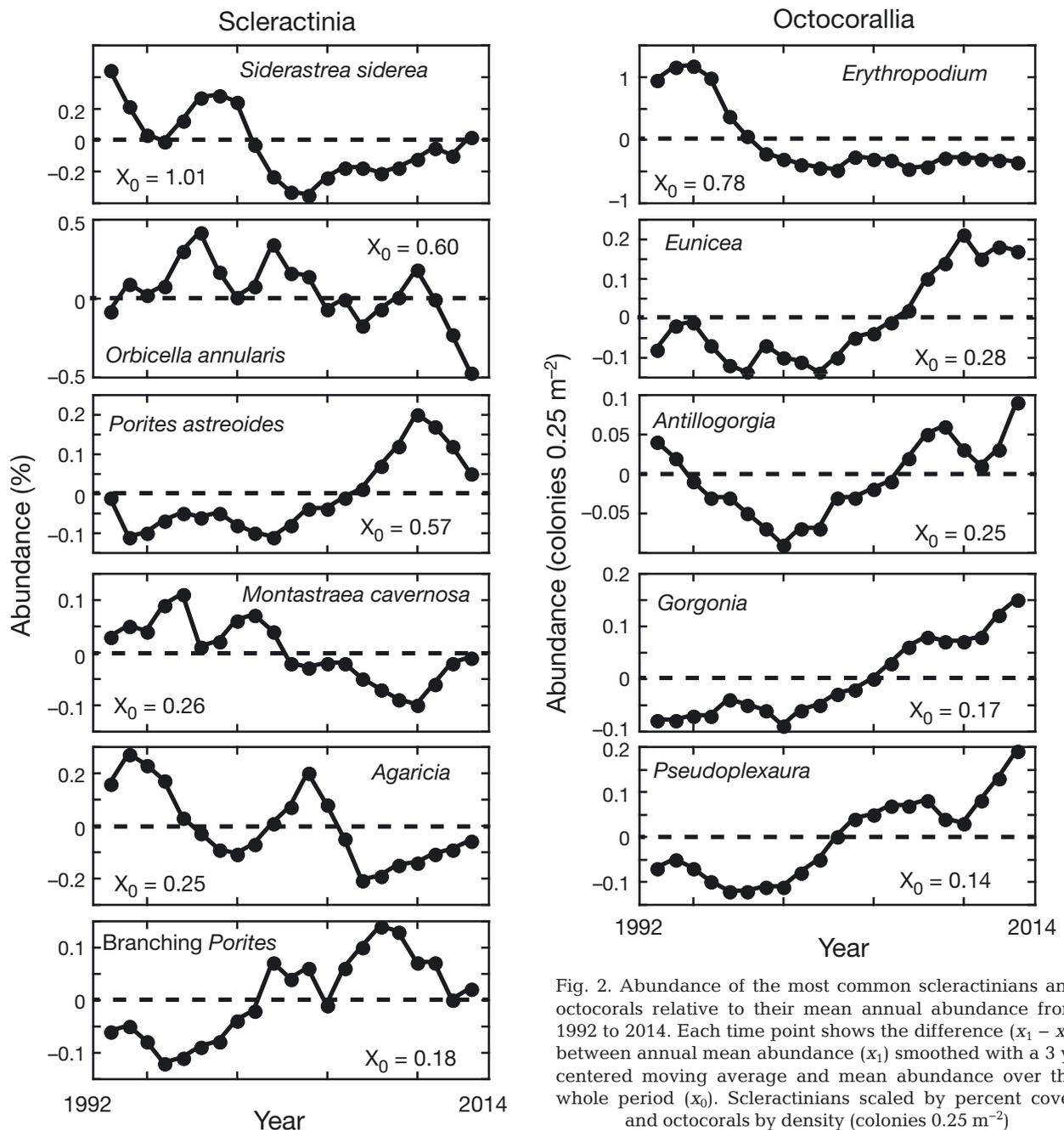

Fig. 2. Abundance of the most common scleractinians and octocorals relative to their mean annual abundance from 1992 to 2014. Each time point shows the difference $(x_1 - x_0)$ between annual mean abundance (x_1) smoothed with a 3 yr centered moving average and mean abundance over the whole period (x_0). Scleractinians scaled by percent cover and octocorals by density (colonies 0.25 m^{-2})

Erythropodium (0.8 colonies m^{-2} averaged among years), unidentified octocorals (0.4 colonies m^{-2}), *Eunicea* (0.3 colonies m^{-2}), *Antillogorgia* (0.3 colonies m^{-2}), *Gorgonia* (0.2 colonies m^{-2}), and *Pseudoplexaura* (0.1 colonies m^{-2}). Relative to the long-term average, abundance (colonies m^{-2}) of *Erythropodium* declined in all but a single year after 1997. The abundance of *Erythropodium* was strongly and positively correlated with the percentage cover of this taxon (r = 0.801, df = 21, p < 0.001), and decreases over time were observed on both scales (Fig. S2 in the Supplement). Together with the low mean percent cover of this taxon (≤1.1% in 1992), these results demonstrate that abundances of *Erythropodium* based on colony count data did not hide large changes in colony size or cover. The abundance of the other octocorals followed patterns of decreasing abundance early in the study, and then increasing abundance towards the end of the study, although the timing of the transition from decline to increase was spread across 4 successive years (Fig. 2).

Diversity (*H'*), evenness (*J'*), and richness averaged among sites changed over time for both taxa, with all 3 metrics increasing linearly (1992–2014) (Fig. S3, Table S3 in the Supplement). The distribution of taxa among the 6 study sites over time (Fig. S4 in the Supplement) indicates that the increases in diversity were driven largely by taxa becoming more equitably distributed among sites over time, rather than through the appearance of new taxa within the study area. Among the octocorals, almost all of the genera were present throughout the study, *Pterogorgia* being the one exception to that pattern (Fig. S4). When considered site by site, 7 of the 11 genera were found at more sites in 2014 than in 1992.

Clear temporal patterns emerged when community structure was analyzed at the level of species and genera for octocorals and scleractinians (and including macroalgae and CTB). MDS of community structure defined 2 groups, one including 1992 to 2001, and the other 2002 to 2014 (Fig. 3A). These 2 groups separated at the 96% similarity level (SIMPROF, π = 0.30, p_{perm} = 0.001). PCoA revealed that separation by time along PCO1 was driven by increased abundance of *Erythropodium* and unknown octocorals to the right, and increased abundance of *Gorgonia*, *Pseudoplexaura*, *P. astreoides*, and *Eunicea* to the left (Fig. 3B). Having fewer images from transects during
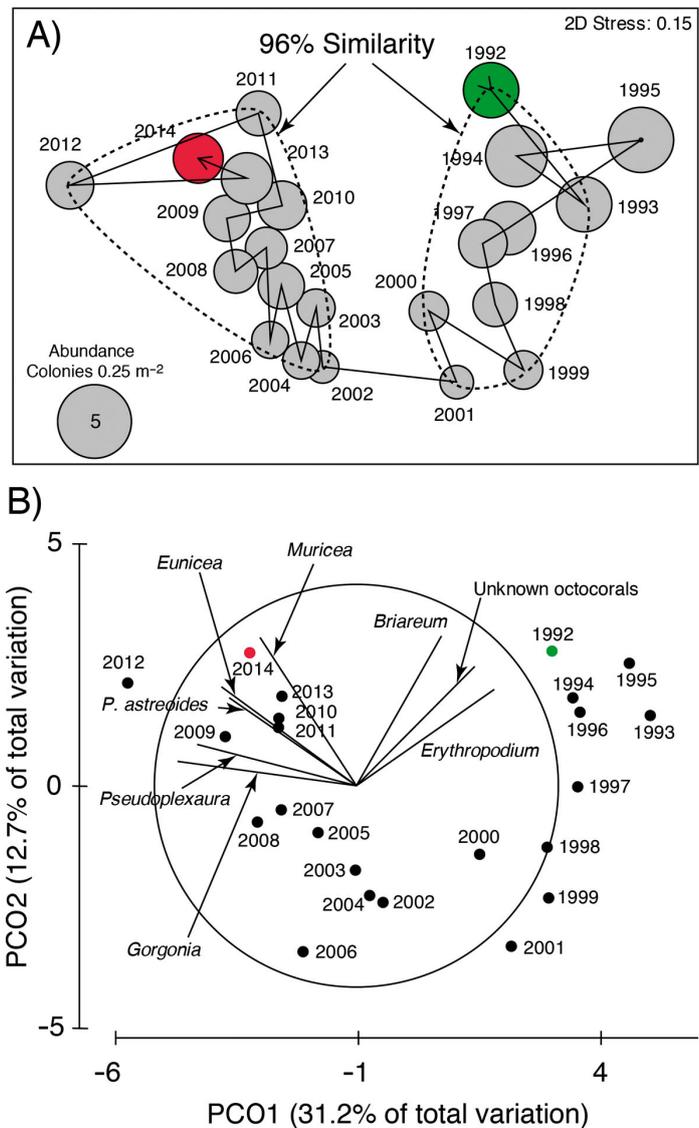

Fig. 3. Multivariate community structure from 1992 (green) to 2014 (red) for Octocorallia, Scleractinia (both by lowest taxon), macroalgae, and CTB (crustose coralline algae, algal turf, and bare space combined), averaged among sites. (A) Multidimensional scaling plot with bubbles scaled to the abundance of octocorals, and dashed line showing a significant (p = 0.001) 96% similarity contour. (B) Principal coordinate analysis (PCoA) of resemblance matrix showing years arrayed along PCO1 and PCO2; vectors display Spearman correlations between dependent variables and PCO1 and PCO2, screened to values >0.6. Separation along PCO1 is associated mostly with increasing abundance of *Erythropodium*, and unknown octocorals (to the right) and increased abundance of *Gorgonia*, *Pseudoplexaura*, *Porites astreoides*, and *Eunicea* (to the left); separation along PCO2 is associated mostly with increased abundance of *Briareum* and *Muricea* (up)

the first 8 yr of the study did not introduce systematic bias (Fig. S5 in the Supplement), and the trends for variation in multivariate community structure broadly were the same when *Erythropodium* was measured

on a percentage cover scale (Fig. S6 in the Supplement). Analyses of similarities among years based only on scleractinians or octocorals (i.e. excluding macroalgae and CTB) suggested that much of the distinction between these periods (Figs. 3 & S5) was a result of octocorals, for which assemblages from 2002 through 2014 formed a distinct cluster in the MDS (Fig. S7B,D in the Supplement).

Analysis of community structure by functional group (all scleractinians, all octocorals, macroalgae, and CTB) also revealed separation among years (Fig. S8A in the Supplement), but the trends were less clear than those obtained with lower taxonomic resolution (Fig. 3), and there was no consistent temporal trend across the study. The 1992–1996 assemblages were somewhat distinct from other years, which reflected lower macroalgal cover (Fig. S8B). The community structure at the turn of the century was similar among some years (1998–2005), but not all years in this range clustered together (e.g. 2000, 2002 and 2003). PCoA revealed that separation among years (along PCO1) was driven by macroalgae, with weaker separation (along PCO2) driven by scleractinians, CTB, and octocorals (Fig. S8B).

Physical variation

Local-scale physical conditions describe hurricane intensity, seawater temperature, and rainfall between 1989 and 2013. Local-scale physical conditions varied among years (see Table S4 in the Supplement) and displayed several linear trends over time (Table S5 in the Supplement). Rainfall increased at a rate of 1.6 cm yr^{-1}, mean temperature increased at a rate of 0.02°C yr^{-1}, maximum daily temperature increased at a rate of 0.03°C yr^{-1}, and the number of hot days increased at a rate of 2 d yr^{-1}; no other physical conditions changed linearly over time. Multivariate local-scale physical conditions were represented by 2 separate, but overlapping clusters in MDS ordination (Fig. S7A) that differed (SIMPROF, $\pi = 0.1$, $p_{perm} = 0.001$). One cluster included mostly years from 1989 to 2002, and the other included mostly years from 2003 to 2014. PCoA (Fig. S9B in the Supplement) revealed that the separation of the clusters along PCO1 was associated with seawater temperature. Early years in the study were characterized by large numbers of cold days, few hot days, low mean temperature, low minimum, and low maximum temperatures, with later years characterized by the reverse. An exception to that pattern was 1998, a particularly warm year, which clustered with the post-2002 years.

Association between biological and physical data

Of the 7 variables describing variation in the local-scale physical environment (Table S4 in the Supplement), 3 were collinear with temperature (minimum, maximum, and number of hot days), and were excluded from tests of association with the biological data. When the biological and physical data were compared by year in which measurements were made, none of the associations were significant for any combinations of dependent variables ($p \geq 0.601$; Table S6 in the Supplement). Likewise, there were no associations between biological data in the year of measurement and the physical conditions lagged 2 yr (Table S7 in the Supplement). When physical conditions were lagged 1 yr, there were significant associations in 2 cases: overall community structure with genus resolution for octocorals and species resolution for scleractinians, and for the octocorals (by genus) and scleractinians (by species) ($p_{perm} \leq 0.050$; Table S7).

When biological and physical data were smoothed, there were significant associations between the two (Tables S6 & S7, Fig. S10 in the Supplement). All analyses in BEST identified rainfall and mean seawater temperature as key variables driving associations between biological and physical data (Tables S6 & S7). As all analyses using smoothing produced similar results, subsequent analyses with DISTLM focused on associations based on 3 yr centered-moving averages, which smooths stochastic variation without implying mechanisms of temporal integration. Based on AIC_c values in DISTLM, rainfall explained variation in all assemblage types, and accounted for the largest proportion of this variation (Table S6). Unexplained variation was large (80%) for the overall community structure with functional group resolution, but smaller for the 4 other assemblages (39–54%). For these assemblages, hurricane intensity explained the next largest portion of the variation in community structure (12–15%). Although seawater temperature was associated with community structure (Table S6), it did not play a strong role in the best linear models explaining variation in community structure (i.e. $R^2 = 8–9\%$). Together, covariation in biological and physical data is captured by the ordination prepared by PCoA that included octocorals (by genus), scleractinians (by species), macroalgae, and CTB (Fig. S10 in the Supplement). The vectors reveal the roles of mostly octocorals (*Plexaura*, *Pseudoplexaura*, *Gorgonia*, and *Pterogorgia*), as well as the scleractinians *Favia fragum* and *Madracis decactis*, in characterizing a cryptic regime shift in association with rainfall, hurricanes, and

seawater temperature (Fig. S10). Smoothed variation (3 yr centered) in overall community structure (genus and species resolution) between 1992 and 2012 was associated with the AMO for the internal component of North Atlantic sea surface temperature ($\rho = 0.279$, $p_{perm} = 0.003$).

DISCUSSION

Overview

The long-term dynamics of benthic communities are well described for many reefs in the Caribbean (Jackson et al. 2014) and Indo-Pacific (Bruno & Selig 2007). However, the taxonomic scope of these studies typically is narrow, with most focusing on 'coral cover' (i.e. scleractinians) and macroalgae, and they report changes that differ from those reported here. Unlike many Caribbean reefs over the last few decades, the present reefs in St. John did not undergo rapid transitions in community structure (sensu Done 1992), and their dynamics do not conform to changes expected within the 'coral reef crisis' construct (Bellwood et al. 2004, Hughes et al. 2010).

The study sites on St. John had only 3.8% cover of scleractinians in 1992, and therefore large absolute declines in coral cover, like those recorded in Jamaica (Hughes 1994) and elsewhere, were not possible (although relative declines in scleractinian cover reached 34% between 2005 and 2008). Benthic community structure in St. John did change over the 23 yr study, but exhibited trajectories that were more complex and slower in developing than is characterized by the scleractinian–macroalgae dichotomy that is prevalent throughout the region (Roff & Mumby 2012). Understanding these disparate trajectories of change in benthic community structure is important, and they should not be left as unexplained variance components in meta-analyses focused on elucidating region-wide trends in coral reef community dynamics.

Overall, the benthic community trajectories for the near-shore fringing reefs in St. John suggest that: (1) these reefs have undergone a cryptic regime change (sensu Hughes et al. 2013) defining 2 domains of community structure separating around 2001 and characterized by gradual changes in species abundances of scleractinians and genus-level abundances of octocorals, and (2) the changes were associated with local-scale physical conditions as well as the regional weather and climate as captured in the AMO.

Cryptic regime change in St. John

The changing community structure at our study sites represents a cryptic regime change (sensu Hughes et al. 2013). The scleractinians found at these sites are representative of present-day Caribbean reefs in shallow water (Williams et al. 2015b), and scleractinian cover neither followed a consistent trajectory nor displayed a large absolute decline (Edmunds 2013). Scleractinian cover was depressed after disturbances in 1998/1999 (when bleaching and a hurricane occurred) and 2005 (another year affected by bleaching), but these declines were reversed within 3 yr. Although there was little scleractinian cover to lose, cover was relatively stable, and quickly recovered from small perturbations, suggesting ecological stability (Gross & Edmunds 2015). However, order-level stability obscured more complex patterns of change in abundance of individual taxa. When scleractinian cover was analyzed at this finer taxonomic level, changes in cover were clear, but different among taxa.

Overall, *Orbicella annularus* covered only 0.6% of the benthos (averaged over sites and year), and therefore mortality of this species (e.g. Hughes & Tanner 2000) is unlikely to have played a strong role in the changes affecting this scleractinian community. Instead, the changes in scleractinian cover reflect the summed outcomes of smaller changes affecting multiple species. *Agaricia* spp. for instance, underwent large relative changes in cover, with declines following high temperature in 1998 and 2005, and recovery thereafter; *Porites astreoides* increased in cover from 2002 to 2010, before declining after 2010; and branching *Porites* generally increased in cover throughout the study. Changing abundances of juvenile scleractinians (<40 mm diameter) that differ among genera have been found in adjacent shallow water (~5 m) (Edmunds 2013), and more broadly, similar effects involving taxonomic variation in the response of scleractinians to environmental conditions are widespread (Darling et al. 2012). Three of the 6 common scleractinians in St. John brood their larvae and have traits generally characterized as a weedy life history strategy (e.g. branching *Porites*, *P. astreoides*, and *Agaricia*; Fadlallah 1983). The traits associated with this strategy (Darling et al. 2012) may have been important factors contributing to the high relative ecological stability of this community (Gross & Edmunds 2015). The results indicate that not all scleractinians are ecological losers (or winners) under present-day conditions (Loya et al. 2001), and it is possible that this scleractinian community in St. John is an example of regional-scale biotic homogenization favor-

ing eurytopic species and ecological stability (Burman et al. 2012).

Interpretation of temporal trends in the benthic communities of the shallow reefs of St. John changed when octocorals were included in the analyses. For instance, when the analysis was based on abundances of the 4 functional groups, community structure differed strongly among years, with high cover of macroalgae in most years from 1998 to 2008, and a biphasic transition in octocoral abundance, with a decline from 1995 to 2002, and an increase thereafter. Changes in cover of 'coral' (i.e. scleractinians) and macroalgae alone (Edmunds 2013) were not sufficient to capture the complexity of events affecting these reefs, and arguably the same will likely be true for other tropical reefs.

Overall, 11 octocoral genera were found in the photoquadrats, which is similar to the octocoral fauna at ≤20 m depth throughout the Caribbean (Williams et al. 2015b). Generic resolution, however, includes a richness of 51 species region-wide (Bayer 1961, Williams et al. 2015b) and 39 in St. John (H. R. Lasker unpubl. data). Most octocorals in the photoquadrats could not be identified to species, and therefore evaluating the role of individual species in driving changes in the octocoral community largely was not possible. However, *Erythropodium* is exclusively represented by *E. caribaeorum*, and *Gorgonia* almost exclusively by *G. ventalina* on the shallow reefs included in the present analysis. In both cases, population trends over time were clear and contrasting. Over 23 yr, *E. caribaeorum* declined 84% in abundance (colonies 0.25 m^{-2}), which accounted for 36% of the decline in octocoral abundance between 1995 and 2001; the trend was similar when *E. caribaeorum* was measured on a percentage cover scale. In contrast, *G. ventalina* was 4.8-fold more abundant in 2014 than in 1992. *Eunicea*, the most speciose of the Caribbean octocoral genera, exhibited more complex changes in abundance, which may be a result of the summed effects of dissimilar species-specific patterns of changing abundance. This raises the possibility that the biphasic change in octocoral abundance (Fig. 1) reflects dissimilar responses of 2 species assemblages to the environmental conditions, with one assemblage declining in abundance, and the other becoming more abundant. Finally, while our data suggest a subtle, but clearly discerned, change in the octocoral community around the start of the 21st century, we cannot assume that the 1990s provide a baseline representative of even earlier times. In 1970, for example, Birkeland & Gregory (1975) surveyed the octocoral community close to the Tektite underwater habitat at 9–17 m depth, which is close to 2 of the transects censused repeatedly in the present study (Fig. S1). They reported octocoral densities (6.4 colonies m^{-2}) that are 37% of the highest mean reported here for 1995, 148% of the lowest density recorded in 2002, and 63% of the density in 2014. The results of Birkeland & Gregory (1975) suggest that regime change in the benthic community structure of the coral reefs of St. John, at least at one site, has been ongoing for over 45 yr and perhaps displays repeatable trends.

Have changes in community structure been associated with physical environmental conditions?

The history of Caribbean reefs over the last 50 yr has been characterized by a series of major disturbances including hurricanes, the die-off of the sea urchin *Diadema antillarum*, and bleaching events. These disturbances have caused rapid and large reductions in scleractinian cover, and usually have been followed by further gradual declines in cover, and increased abundances of macroalgae (Hughes 1994, Edmunds 2013). While the same disturbances affected St. John, the responses in the reef community were not uniform across events, and did not involve changes in community structure that were particularly striking. Had our surveys begun in the 1980s, we probably would have observed higher scleractinian cover at the start of our study, because St. John was severely damaged by Hurricane Hugo in 1989 (Rogers 1993). Thus, our results do not challenge the notion that Caribbean reefs have changed substantially since at least the 1960s (Jackson et al. 2014). Between 1992 and 2014, St. John was affected by 4 hurricanes and 2 bleaching events, all of which created ecological signatures of modest scope in our study sites (Fig. 1). Most strikingly, the 1998 El Niño, which caused extensive bleaching and coral mortality throughout the region (Bruno et al. 2015), was associated with relatively small effects on our study reefs. Mean scleractinian cover, for example, changed from 3.9% in 1997 to 4.3% in 1998 and 3.6% in 1999. Octocorals also declined after the summer of 1998, but the decline started after Hurricanes Luis and Marilyn in 1995 and then continued throughout 1998, with no apparent effect from Hurricanes Jose and Lenny in 1999 (Fig. 1).

Overall changes in community structure (see Fig. 3) were not associated with the changes during these episodic events, but rather changes that occurred as the abundances of octocorals recovered following 1999. This implies that the causal agents of these

changes were physical and biotic factors acting over time scales longer than those characterized by the perturbed conditions of El Niño. The environmental factors having the greatest effects on community structure, rainfall and hurricanes, have strong effects on scleractinians and coral reefs. Rainfall modulates terrestrial runoff, salinity, sedimentation, and nutrient concentrations, all of which can negatively affect scleractinians (Rogers 1990, Fabricius 2005). The association between multivariate community structure and rainfall is likely to reflect the role of this variable in integrating the effects of other factors including seawater temperature, storms, underwater light intensity, and the AMO. For instance, cloud cover (associated with rain) reduced light intensities and ameliorated bleaching in French Polynesia in 1998 (Mumby et al. 2001), and hurricanes (also usually associated with heavy rainfall) in the Caribbean during 2005 reduced thermal bleaching in the Virgin Islands through vertical mixing of seawater (Manzello et al. 2007). In the present study, smoothed rainfall was correlated with smoothed mean temperature (with a 3 yr centered average 1992–2013, r = 0.566, df = 20, p = 0.006), and there is a well-established framework describing the pervasive effects of temperature on ectothermic reef organisms (Bruno et al. 2015).

Smoothed rainfall was also correlated with the AMO index (1992–2012, r = 0.733, df = 19, p < 0.001). The AMO is a broad measure of North Atlantic sea surface temperature and multiple aspects of hemispherical weather and climate, and has a periodicity of ~70 yr (Steinman et al. 2015). There are associations between the AMO and rainfall in a number of Caribbean locations (Stephenson et al. 2014), and the AMO is associated with the density of scleractinian skeletons in the Florida Keys (Helmle et al. 2011), as well as the oxygen isotope composition of at least one coral in Venezuela (Hetzinger et al. 2008). The current phase of the AMO appears to be reaching the apogee of its cycle, and therefore is likely to decline in coming decades (Steinman et al. 2015). Although it will require a decade or more to accrue the necessary data, a declining intensity of the AMO will provide opportunities to evaluate its role in causing future changes in coral reef community structure. Potentially, it will create the opportunity to deconvolve the effects of natural drivers of coral reef community dynamics (i.e. the AMO) from those attributed to anthropogenic climate change, thereby sharpening the focus of research on changes that are cyclic versus novel.

Associations between community structure and the physical environment were only evident when the physical data were smoothed over 3 yr. Apparently, the linkage between changes in environmental conditions and population size took multiple years to develop, suggesting that chronic effects were mediating changes in recruitment and post-settlement success, which are difficult to measure, especially using photoquadrats. It is also noteworthy that the change in community structure and its association with environmental conditions were most striking when octocorals and scleractinians were resolved to genera and species (respectively), and were weak for the community structure resolved to functional groups. This again suggests that the processes effecting community structure were more complex, and more taxon-specific than those attributed to acute disturbances that tend to have taxonomically broad effects (Glynn 1993, Rogers 1993).

LITERATURE CITED

Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. Can J Fish Aquat Sci 58:626–639

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Aronson RB, Precht WF (2000) Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. Limnol Oceanogr 45:251–255

Bayer FM (1961) The shallow-water Octocorallia of the West Indian region. Martinus Nijihoff, The Hague

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

Birkeland C, Gregory B (1975) Foraging behavior and rates of feeding of the gastropod *Cyphoma gibbosum* (Linnaeus). Los Angeles Co Nat Hist Mus Sci Bull 20:57–67

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLOS ONE 2:e711

Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90:1478–1484

Bruno JF, Carr LA, O'Connor MI (2015) Exploring the role of temperature in the ocean through metabolic scaling. Ecology 96:3126–3140

Burman SG, Aronson RB, van Woesik R (2012) Biotic homo-

genization of coral assemblages along the Florida reef tract. Mar Ecol Prog Ser 467:89–96

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/ Tutorial. PRIMER-E, Plymouth

Cochrane D, Orcutt GH (1949) Application of least squares regression to relationships containing auto-correlated error terms. J Am Stat Assoc 44:32–61

Conversi A, Möllmann C, Folke C, Edwards M (2015) Marine regime shifts around the globe: theory, drivers and impacts. Philos Trans R Soc B 370:20130260

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM, Bellwood D (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Done TJ (1992) Phase shifts in coral reef communities their ecological significance. Hydrobiologia 247:121–132

Durbin J, Watson GS (1951) Testing for serial correlation in least squares regression II. Biometrika 38:159–178

Edmunds PJ (2004) Juvenile coral population dynamics track rising seawater temperature on a Caribbean reef. Mar Ecol Prog Ser 269:111–119

Edmunds PJ (2013) Decadal-scale changes in the community structure of coral reefs of St. John, US Virgin Islands. Mar Ecol Prog Ser 489:107–123

Edmunds PJ, Gray SC (2014) The effects of storms, heavy rain, and sedimentation on the shallow coral reefs of St. John, US Virgin Islands. Hydrobiologia 734:143–158

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs review and synthesis. Mar Pollut Bull 50:125–146

Fadlallah YH (1983) Sexual reproduction, development and larval biology in scleractinian corals. Coral Reefs 2:129–150

Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnol Oceanogr 45:677–685

Fung T, Seymour RM, Johnson CR (2011) Alternative stable states and phase shifts in coral reefs under anthropogenic stress. Ecology 92:967–982

Glynn PW (1993) Coral bleaching: ecological perspectives. Coral Reefs 12:1–17

Gross K, Edmunds PJ (2015) Stability of Caribbean coral communities quantified by long-term monitoring and autoregression models. Ecology 96:1812–1822

Helmle KP, Dodge RE, Swart PK, Gledhill DK, Eakin CM (2011) Growth rates of Florida corals from 1937 to 1996 and their response to climate change. Nat Commun 2:215

Hetzinger S, Pfeiffer M, Dullo WC, Keenlyside N, Latif M, Zinke J (2008) Caribbean coral tracks Atlantic Multidecadal Oscillation and past hurricane activity. Geology 36:11–14

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, and others (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265: 1547–1551

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience. Trends Ecol Evol 25:633–642

Hughes TP, Linares C, Dakos V, van de Leemput IA, van Nes EH (2013) Living dangerously on borrowed time during slow, unrecognized regime shifts. Trends Ecol Evol 28:149–155

Jackson JBC, Donovan M, Cramer K, Lam V (2014) Status and trends of Caribbean coral reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland

Kinzie RA (1973) The zonation of West Indian gorgonians. Bull Mar Sci 23:93–155

Kohler KE, Gill SM (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. Comput Geosci 32:1259–1269

Lenz EA, Bramanti L, Lasker HR, Edmunds PJ (2015) Long-term variation of octocoral populations in St. John, US Virgin Islands. Coral Reefs 34:1099–1109

Lewis SL, Maslin MA (2015) Defining the Anthropocene. Nature 519:171–180

Loh TL, Pawlik JR (2014) Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. Proc Natl Acad Sci USA 111:4151–4156

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122–131

Manzello DP, Brandy M, Smith TB, Lirman D, Hendee JC, Nemeth RS (2007) Hurricanes benefit bleached corals. Proc Natl Acad Sci USA 104:12035–2039

Mouillot D, Grahamn NAJ, Villeger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177

Mumby PJ, Chisholm JRM, Edwards AJ, Andrefouet S, Jaubert J (2001) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. Mar Ecol Prog Ser 222:209–216

Mumby PJ, Steneck RS, Hastings A (2013) Evidence for and against the existence of alternate attractors on coral reefs. Oikos 122:481–491

Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Mar Ecol Prog Ser 376:295–306

Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. Trends Ecol Evol 27:404–413

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202

Rogers CS (1993) Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. Coral Reefs 12:127–137

Ruzicka RR, Colella MA, Porter JW, Morrison JM and others (2013) Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. Mar Ecol Prog Ser 489:125–141

Steinman BA, Mann ME, Miller SK (2015) Atlantic and Pacific multidecadal oscillations and Northern Hemisphere temperatures. Science 347:988–991

Stephenson TS, Vincent LA, Allen T, Van Meerbeeck CJ and others (2014) Changes in extreme temperature and precipitation in the Caribbean region 1961–2010. Int J Climatol 34:2957–2971

Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. Nature 416:389–395

Whittaker RH (1960) Vegetation of the Siskiyou mountains, Oregon and California. Ecol Monogr 30:279–338

Williams SM, Chollett I, Roff G, Cortés J, Dryden CS, Mumby PJ (2015a) Hierarchical spatial patterns in Caribbean reef benthic assemblages. J Biogeogr 42:1327–1335

Williams SM, Mumby PJ, Chollette I, Cortés J (2015b) Importance of differentiating *Orbicella* reefs from gorgonian plains for ecological assessments of Caribbean reefs. Mar Ecol Prog Ser 530:93–101

Work TM, Aeby GS, Maragos JE (2008) Phase shift from a coral to a corallimorph-dominated reef associated with a shipwreck on Palmyra Atoll. PLOS ONE 3:e2989