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SPECIAL ISSUE: IMPACT OF 2017 HURRICANES

Impacts of Hurricanes Irma and Maria on Coral Reef Sponge Communities in St. Thomas, U.S. Virgin Islands

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Abstract

Many studies have evaluated the impacts of hurricanes on coral communities, but far less is known about impacts, recovery, and resilience of sponge communities to these extreme events. In September 2017, St. Thomas, U.S. Virgin Islands, was impacted by two Category 5 hurricanes within 2 weeks: Hurricanes Irma and Maria. Such extreme events occurring in such rapid succession are virtually unprecedented. Pre-hurricane (2015, 2016) surveys of permanent transects at six sites around St. Thomas were compared with those at 10 weeks post-hurricanes (December 2017) to evaluate storm impacts on sponges and on benthic coral reef constituents. These surveys also established a baseline for evaluating future recovery. Percent cover of sponges declined by 24.9% post-hurricanes. In contrast, sponge density increased by 43.9% from 2015 to 2016 and declined slightly after the hurricanes. Overall sponge volume did not vary over time, and whereas sponge diversity was similar in 2015 and 2016, it increased post-hurricanes. Sponge morphologies were differentially affected by the hurricanes; the proportion of upright sponges declined by 36.9%, while there was a 24.4% increase in encrusting sponges. Coral and macroalgal cover did not change significantly over the sampling period, while percent cover of epilithic algae increased and non-living substrata decreased from 2015 to 2016 but did not change further post-hurricanes. At all sites, recruitment and/or regrowth of sponges was observed within 10 weeks post-hurricanes, indicating potential resilience in Caribbean sponge communities. Whether these sponge communities return to pre-hurricane conditions and how long that will take remains to be seen.

Keywords Hurricane impacts · Sponge community · Coral reef community · Sponge morphology · U.S. Virgin Islands

Introduction

Natural and anthropogenic disturbances can have profound consequences for marine ecosystems, particularly coral reefs (Hughes and Connell 1999; Gardner et al. 2005; Wilkinson and Souter 2008). Coral reef ecosystems demonstrate a gradient of resilience to disturbance, which can range from resistance to damage, recovery after damage, and irreversible damage. However, the frequency and intensity of disturbance also influences how reefs recover. Many anthropogenic disturbances, such as runoff of pollutants or sediment due to poor land use practices (Nemeth and Nowlis 2001; Smith et al. 2008; Ennis et al. 2016), are chronic and, therefore, do not provide opportunities for ecosystem recovery. Conversely, extreme but intermittent disturbances, such as hurricanes, can alter the structure and function of the benthic community over very short time scales, with long potential recovery times. However, severe hurricanes have become increasingly common due to climate change (Emanuel 2005; Hosseini et al.

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2018), which has reduced the time available for reef recovery between these events. The interplay between extreme events and chronic stressors may impair the ability of coral reefs to recover (Hughes and Connell 1999; Gardner et al. 2005; Jackson et al. 2014), and dramatic changes in community structure can result in phase shifts and/or alternative stable states (Dudgeon et al. 2010).

As coral community resilience declines in the face of multiple stressors (Hoegh-Guldberg et al. 2007; Anthony et al. 2011), phase shifts are increasingly likely (Nyström et al. 2000; Dudgeon et al. 2010; Roff and Mumby 2012). Particularly on Caribbean reefs, shifts from coral-dominated to macroalgal-dominated communities have been widely described (e.g., Hughes 1994; Rogers and Miller 2006; Norström et al. 2009; Dudgeon et al. 2010; Arias-Gonzalez et al. 2017). However, such changes are not restricted to macroalgae, and shifts to sponge-dominated systems have also been reported (Aronson et al. 2002; Ward-Paige et al. 2005; McMurray et al. 2010; Bell et al. 2013, 2018; Chaves-Fonnegra et al. 2018).

Sponges have long been recognized as important structural and functional components of coral reefs, contributing to primary production, nutrient cycling and bentho-pelagic coupling, consolidation and bioerosion of reef substrata, and habitat and food for other reef taxa (Diaz and Rützler 2001; Bell 2008; Wulff 2012; de Goeij et al. 2013). Thus, increases in sponges have significant implications for coral reef biodiversity and overall ecosystem functioning. In spite of their unequivocal contributions to coral reef ecology, sponge responses to stressors are not well understood. Sponge assemblages are known to vary with exposure to sedimentation and land-based sources of pollution (e.g., Rose and Risk 1985; Ward-Paige et al. 2005; Gochfeld et al. 2007; Biggerstaff et al. 2017). To date, relatively few studies have described effects of hurricanes on sponge assemblages (reviewed in Bell et al. 2017a, 2018), and whereas some studies have reported dramatic storm-induced declines in sponge numbers and/or biomass (e.g., Stoddart 1969; Woodley et al. 1981; Alvarez-Filip and Gil 2006; Wulff 1995, 2006; Stevely et al. 2011), at least one study reported only minor changes in the sponge community (e.g., Fenner 1991).

The rate of recovery or establishment of sponges following disturbances will vary, depending on the severity and type of disturbance, exposure to other stressors, and species-specific characteristics related to type or degree of damage, and reproductive and growth strategies (Zea 1993; Maldonado and Riesgo 2008; Wulff 2013; Chaves-Fonnegra et al. 2016, 2018). Stevely et al. (2011) reported different patterns of sponge mortality from exposure to algal blooms and Hurricane Wilma, with recovery also occurring over different time scales (10–15 years for blooms and 2 years for hurricane impacts; see also Fenner 1991; Wulff 1995; Cropper and DiResta 1999). On shallow Caribbean reefs, sponges represent the highest animal biodiversity (Miloslavich et al. 2010; Diaz and Rützler 2011), resulting in a tremendous diversity of reproductive strategies (both asexual and sexual), dispersal capabilities, recruitment and post-settlement survival rates, and subsequent growth rates (Zea 1993; Maldonado and Young 1996; Maldonado and Riesgo 2008; DeBiasse et al. 2010; Chaves-Fonnegra et al. 2015; Richards et al. 2016). On newly established substratum, such as a shipwreck, sponge occupation may be relatively slow initially, but it is most likely the result of larval recruitment, given the absence of a pre-established sponge community, and may favor rapidly growing species (Pawlik et al. 2008). In contrast, physical disturbances to extant coral reef communities may leave behind living remnants of damaged sponges or physically detached fragments of sponges that may survive, reattach, and continue to grow (Wulff 1991, 2006; Stevely et al. 2011; Easson et al. 2013). Surviving sponges may also produce larvae that can recruit to exposed substrata (Wulff 1995; Stevely et al. 2011).

The 2017 Atlantic hurricane season was the most active in decades (e.g., Camp et al. 2018), and St. Thomas, U.S. Virgin Islands (USVI), was directly impacted by the passage of two Category 5 hurricanes (wind speed ≥ 252 km h^{-1}) in September 2017. Hurricane Irma was the strongest Atlantic hurricane since Wilma in 2005 and had the second highest accumulated cyclone energy index for an Atlantic hurricane since 1970 (Camp et al. 2018). Hurricane Irma reached a peak wind speed of 155 kt (287 km h^{-1}) and 915 mb of pressure when it made landfall at 1600 UTC on 6 September 2017 in Virgin Gorda, British Virgin Islands, about 55 km northeast of St. Thomas (Cangialosi et al. 2018). Two hours later, the center of Irma passed within 32 km to the north of St. Thomas (Fig. 1a), with a peak wind speed of 150 kt (278 km h^{-1}) and 914 mb of pressure (NOAA Office for Coastal Management, 2018). The Caribbean Integrated Coastal Ocean Observing System (CarICOOS) station 41058, located north of St. Thomas, recorded a maximum wave height of 6.9 m at 1800 UTC and 11.85 m at 1900 UTC, although waves breaking over the buoy at that time make the data less reliable; buoy power failure occurred at 1930 UTC (D. Wilson, personal communication). Widespread, catastrophic damage occurred throughout the USVI, particularly on St. Thomas and St. John, which received significant rainfall, causing extensive flooding and compounding wind-generated damage to buildings and vegetation. Hurricane Maria passed about 20 km southeast of St. Croix (80 km from St. Thomas; Fig. 1a) at 0600 UTC on 20 September 2017, with a peak intensity of 140 kt (259 km h^{-1}) and 913 mb of pressure (NOAA Office for Coastal Management, 2018). CarICOOS station 41052, located south of St. John, recorded a maximum wave height of 7.9 m during Hurricane Maria (NOAA National Buoy

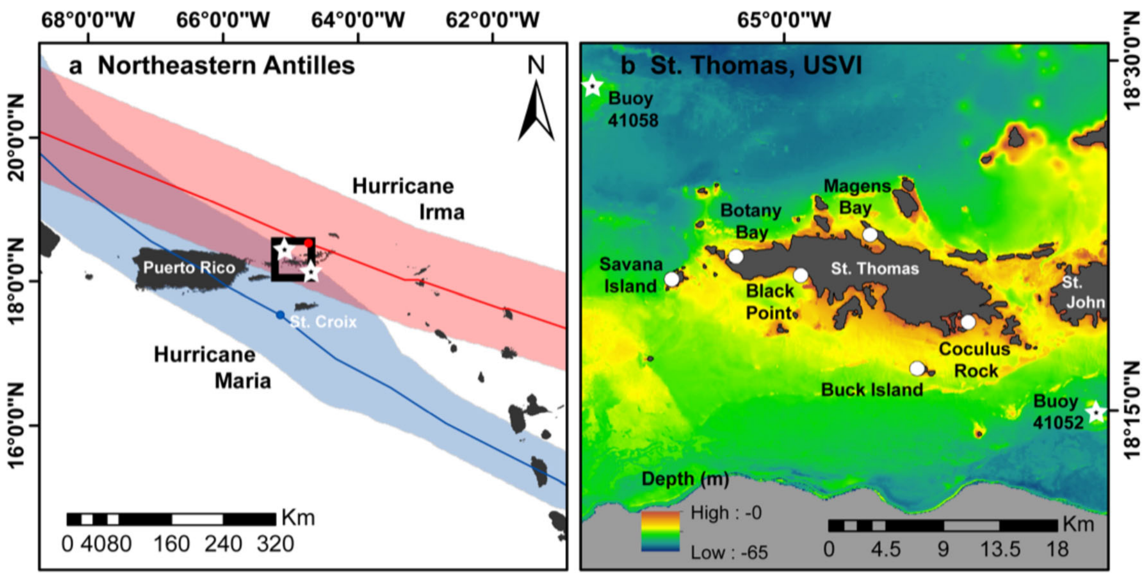

Fig. 1 Study area affected by Hurricanes Irma and Maria in the USVI. **a** The Northeastern Antilles islands in the Western Atlantic Ocean, with hurricane tracks (lines) and hurricane force wind swaths (> 64 kt (120 km h^{-1})) indicated for Hurricanes Irma (pink) and Maria (blue). Bold box outlines St. Thomas, USVI. Dots on track lines represent points of closest passage to St. Thomas. White stars show the location of CarICOOS buoys 41058 (upper left star, north of St. Thomas) and 41052 (lower right star, south of St. John). St. Thomas was subjected to hurricane force winds during both storms. Hurricane spatial data from the National Hurricane Center (2018). **b** Study sites around St. Thomas (white dots) and location of CarICOOS buoys 41058 and 41052 (white stars)

Data Center, 2018). Hurricane Maria caused further wind damage and produced torrential rains, resulting in massive flooding and landslides on an already damaged landscape (Pasch et al. 2018). As meaningful recovery was unlikely to have occurred in the brief interval between the storms, they presumably represent a single event of unprecedented scope and intensity that affected marine ecosystems throughout the USVI and the entire region.

While the 2017 Atlantic hurricane season was unusually destructive, predictions of more frequent intense storms in the future (Knutson et al. 2010; Emanuel 2013; Sobel et al. 2016) reinforce the importance of understanding impacts of these storms on coral reef communities as a whole. Given the amount of terrestrial destruction and historical effects of severe hurricanes on Caribbean coral reef ecosystems, we expected to see dramatic impacts on coral reef communities. We predicted that sponges, which are generally soft bodied and susceptible to breakage or abrasion, yet represented high density, biomass, and biodiversity on St. Thomas' reefs prior to these storms, would suffer significant damage, ranging from abrasion to fragmentation to mortality. We tested the hypotheses that (1) there would be significant detrimental effects of the hurricanes on sponge cover, density, volume, and diversity; (2) different sponge morphologies would be differentially affected by the hurricanes, with upright sponges most likely to be damaged; and (3) there would be significant declines in coral cover concomitant with increases in percent cover of macroalgae, epilithic algae, and non-living substrata following the hurricanes.

Methods

Study Sites

Prior to the 2017 hurricanes, six shallow (8–15-m depth) reef sites had been selected from the 33 Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP)'s permanent monitoring sites to study variation in sponge communities in St. Thomas (Fig. 1b). These sites included Black Point (N 18° 20.665′, W 64° 59.107′), Coculus Rock (N 18° 18.734′, W 64° 51.613′), and Magens Bay (N 18° 22.459′, W 64° 56.077′), which are in embayments with heavily developed watersheds. Buck Island (N 18° 16.717′, W 64° 53.925′) and Savana Island (N 18° 20.437′, W 65° 04.939′) are located near undeveloped offshore cays. Botany Bay (N 18° 21.433′, W 65° 02.071′) is a nearshore site in a bay with a low level of watershed development. For this study, we used three randomly selected transects out of the six permanently established 10-m TCRMP transects at each site. The same three transects at each site were resurveyed repeatedly over time.

Effect of Hurricanes on Sponges

At each site, the benthic communities were repeatedly surveyed in August 2015, August 2016, and early December 2017 (10 weeks after Hurricane Maria). The abundance of sponges on reefs is often assessed as percent cover, which may be ecologically relevant for encrusting species that occur on open substrata, but given their tremendous morphological variation and the large number of species that grow in crevices, the number of individuals (i.e., density), volume, or biomass are additional ecologically relevant metrics by which to measure sponge contributions to the benthic community (Wulff 2012). Additionally, for spatial and temporal comparisons, the use of more than one metric is preferable (discussed in Wulff 2012; Bell et al. 2017b). Therefore, this study used multiple metrics to assess sponge abundance on these reefs to obtain the broadest perspective of hurricane impacts on sponge communities.

Percent cover of sponges was determined from videos of the three transects at each site following established TCRMP methods (Smith et al. 2016a). Briefly, a diver on SCUBA swam at a uniform speed while videoing the substrata from a height of approximately 0.4 m (the height of a guide wand). Consecutive, non-overlapping images, each approximately 0.64 × 0.48 m in planar area, were captured for each transect, for an average of 21 images per transect. Twenty random points were superimposed on each image (average of 1282 points per site, per sampling period), and the benthic cover underneath each point was identified to the lowest identifiable taxonomic level and used in the calculation of percent cover by transect. Specific sponges were not identified in the benthic cover analysis and were instead grouped into the overarching category of "Sponge." The number of points per image required to adequately characterize the percent cover of sponges, and each of the other benthic categories detailed below, was determined by visual inspection of the running means. For all categories, the mean value stabilized at no more than 17 points per image per transect, indicating that the 20 points analyzed per image were sufficient to accurately reflect the percent cover at these sites (Online Resource 1).

Sponge density was quantified by counting every sponge individual (i.e., ramet) within 0.5 m on one side of each transect (resulting in 0.5 × 10 m belt transects) for all sites except Black Point, where 0.5 m on both sides of the transects (resulting in 1 × 10 m belt transects) were surveyed. Density was calculated as the total number of individual sponges per transect, divided by the transect area, to yield the number of sponges per m^2. Because many sponges are cryptic and cannot be quantified in photos or videos, surveys of sponge density were performed in situ by a diver, who also identified them to the lowest possible taxonomic level. For sponges that could not be identified in situ, voucher specimens were collected for subsequent identification in the laboratory.

Sponge volume was calculated within permanent 1-m^2 quadrats centered on the transect line within the initial and/or final meter of each transect. Sponge volume was calculated for 3–5 quadrats per site. As there were over 100 sponge species within our survey areas, representing a diversity of morphologies, we chose to use a standardized approach to measure all sponges, rather than calculating the true volumetric measurement for each sponge based on its actual morphology. Thus, sponges were essentially treated as cuboids. We used a flexible sewing tape to measure the longest dimension of the sponge, then one to several width measurements perpendicular to the initial length measurement, and finally, one to several height measurements, as needed to represent the shape and dimensions of each sponge. Multiple measurements for each dimension were averaged, and length × width × height was calculated. For large tubes, of which there were relatively few, we subtracted the dimensions of the interior cavity from the exterior dimensions of the sponge.

Whereas other researchers have characterized sponge volume by calculating the actual volumetric dimensions of each sponge based on its morphology (e.g., cylinder, tube, fulcrum of a cone), most of those studies focused on a single or small number of sponge species (e.g., Wulff 1991; McMurray et al. 2010). Here, we chose to use a single approach for calculating the sponge volume of all species due to the large number of species and morphologies represented in this community, as it would not be practical to do otherwise, given our time constraints in the field. However, to estimate the difference between these approaches, in 2015, we calculated the dimensions of all of the sponges in all quadrats in both manners and found that our approach overestimated actual sponge volume by 10.53 ± 3.34% (across 23 quadrats consisting of 768 sponges from 55 species). Thus, while this approach is somewhat less conservative than calculating volumes based on actual shapes of each sponge, the mean difference in outcomes is low and consistent.

Sponge diversity was calculated using the sponge density data from the in situ transects. Over 100 distinct sponge taxa were used to calculate the diversity metrics. Those that could not be identified to the species level in situ were still differentiated as distinct taxa (species A, B, etc.) pending future taxonomic characterization. Species richness (S), the Shannon index (H'), and the inverse Simpson index (D) were calculated in the Primer v6 software package (Clarke and Warwick 2001). Transect area was twice as large at Black Point than at the other five sites, which could affect measures of sponge diversity; therefore, we omitted Black Point from these analyses. However, a comparison of the analyses with and without Black Point yielded the same overall patterns as those reported in the results.

To determine whether different sponge morphologies were differentially affected by hurricanes, each sponge from each transect was assigned to a broad morphological category (*sensu* Wulff 2006). These categories included excavating sponges ("excavating"); low-relief (≤ 1–2 cm in depth) encrusting sponges ("encrusting"); thicker cushions, massive, tube, vase, or other amorphous shapes of medium relief ("massive"); and upright, branching, and rope sponges of high relief ("upright"). These groupings differ slightly from those used by Wulff (2006) but are representative of the sponge morphologies found within the transects in St. Thomas.

Representative taxa included within each category are listed in Online Resource 2. The proportion of the entire sponge community represented by each morphological category was calculated as the number of individuals in each category divided by the total number of individuals for each transect.

Effect of Hurricanes on the Overall Benthic Community

Percent cover of other benthic constituents of the reef community was determined from video transects, as described above, and following Smith et al. (2016a). In addition to sponges, percent cover of hard corals, macroalgae, the epilithic algal community (EAC) (i.e., diminutive turf algae and other low complexity filamentous algal communities), non-living substrata, calcareous algae, cyanobacterial mats, gorgonians, zoanthids, and other/unknown living substrata were determined.

Data Analysis

Effect of Hurricanes on Sponges

To test for hurricane effects on various metrics of the sponge community, repeated-measures analyses of variance (RM-ANOVAs) were performed on sponge percent cover, density, and volume, as well as species richness, Shannon index, and inverse Simpson index, with site as a random factor. These analyses were performed in R using the lmer function in the lme4 (linear mixed effects using ‘Eigen’ and S4) package (Bates et al. 2015), and p values were determined using the Satterthwaite approximation. Prior to analyses, all data were tested for normality using Shapiro-Wilk tests and for homogeneity of variance using Bartlett’s tests. To meet assumptions, square root transformations were performed on sponge density and volume and species richness was log transformed; no transformations were necessary for the other metrics. For significant effects, post hoc comparisons among years were performed using the lsmeans function with the Tukey correction specified in R. Results of the post hoc comparisons are presented in Online Resource 3. To characterize hurricane effects on sponges with differing morphologies, a RM-ANOVA was also performed on arcsine-transformed proportions to test for the main effect of year, using site as a random factor, followed by least square means post hoc tests where warranted.

Effect of Hurricanes on the Overall Benthic Community

Sponges, hard corals, macroalgae, EAC, and non-living substrata represented over 90% of the overall benthic substrata. Percent cover of these major benthic community constituents was compared individually among years using RM-ANOVAs as described above, following logarithmic or square root transformation if necessary. Post hoc comparisons among years were performed using least square means as described above. Other benthic constituents either were of such low representation or did not meet the assumptions of parametric analysis even after transformation, and they were not analyzed independently.

Results

Effect of Hurricanes on Sponges

Following the hurricanes, many dislodged massive and upright sponges were observed at the six sites, some of which still had areas of live tissue 10 weeks post storms. Large clusters of dislodged sponges were observed rolling around in sandy areas at the base of some reefs. Unless the dislodged sponge fragments became trapped in the reef structure where they could reattach to hard substrate, the sponge gradually disintegrated. There was also evidence of sponge remnants, with remaining live tissue from which portions of the sponge had obviously been broken off. These attached sponges often displayed lesions that had already healed and appeared able to recover and grow, at least over the short term.

There was a significant effect of the hurricanes on percent cover of sponges (Fig. 2a, Table 1). Sponge cover declined by an average of 24.9 ± 12.9% after the 2017 hurricanes, following a negligible increase of 7.6 ± 8.9% from 2015 to 2016 across all sites. In contrast, sponge density increased by an average of 43.9 ± 7.7% across all sites from 2015 to 2016 but did not change significantly post-hurricanes (− 8.5 ± 7.4%; Fig. 2b, Table 1). RM-ANOVA did not show significant temporal changes in sponge volume, likely due to high variability among individual quadrats (Fig. 2c, Table 1).

Sponge species richness increased over time across all sites (with the exception of Black Point, which was excluded from the analysis), with an increase of 16.6 ± 4.6% from 2015 to 2016 and 29.1 ± 6.4% from 2015 to 2017, although the increase following the hurricanes was not statistically significant (12.4 ± 5.9%; Fig. 3a, Table 1, Online Resource 3). Shannon index for sponges remained virtually unchanged between 2015 and 2016 but increased significantly post-hurricanes (Fig. 3b, Table 1). RM-ANOVA did not identify temporal changes in the inverse Simpson index for sponges, although there was a slight increase post storms (Fig. 3c, Table 1).

Overall, the sites in this study had low proportions of excavating and massive sponges, and there was no effect of year on these morphological categories (Fig. 4, Table 1). Encrusting sponges represented the highest proportion of the sponge community at all sites, and after remaining relatively stable from 2015 to 2016, this proportion increased

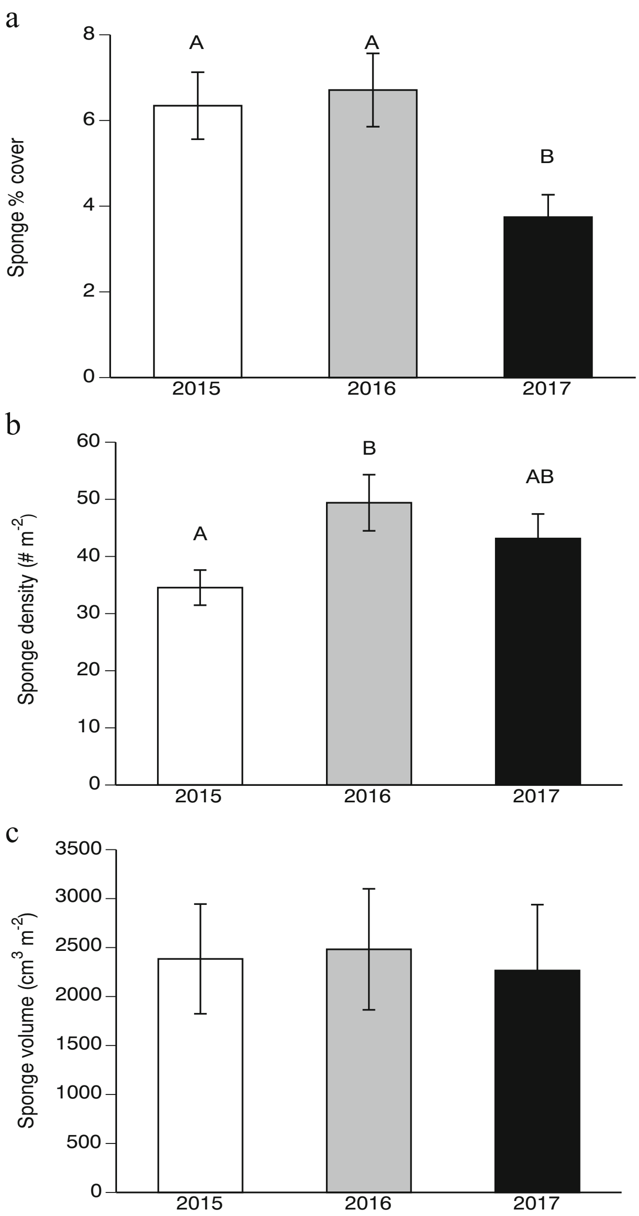

Fig. 2 Sponge abundance metrics for 3 years (pre hurricane: 2015 and 2016; post-hurricane: 2017) across six sites in St. Thomas. Histograms represent mean ± SE of **a** sponge percent cover along permanent transects ($n = 3$ per site), **b** sponge density (number of sponges m^{-2}) within permanent belt transects ($n = 3$ per site), and **c** sponge volume (cm^{3} m^{-2}) within permanent quadrats ($n = 3$–5 per site). For **a** and **b**, different letters denote significant differences between years as determined by post hoc comparisons using least square means (Online Resource 3). In **c**, there were no significant differences among years

significantly (+ 24.4 ± 9.8%) following the hurricanes in 2017 (Fig. 4, Table 1, Online Resource 3). In contrast, there was a significant decline in the proportion of upright sponges after the hurricanes (− 36.9 ± 8.8%; Fig. 4, Table 1, Online Resource 3), following no change between 2015 and 2016.

Effect of Hurricanes on the Overall Benthic Community

Whereas there was a significant effect of the hurricanes on percent cover of sponges, percent cover of other benthic community constituents showed variable responses to the hurricanes. Coral cover did not differ significantly across years (Fig. 5a, Table 1), although there was high variability among transects. However, while differences may have been relatively small, coral cover averaged 9.4 ± 1.4% across all sites pre storms and 7.8 ± 1.3% post storms. This absolute loss of 1.6% represents a 17.8 ± 6.7% decline in coral cover across all transects following the hurricanes. There was also no significant effect of the hurricanes on macroalgal cover at our study sites (Fig. 5b, Table 1). RM-ANOVA showed a significant effect of year on percent cover of EAC and non-living substrata, but these were due to increased cover of EAC and decreased cover of non-living substrata from 2015 to 2016, while there was no significant effect of the hurricanes on either of these parameters (Fig. 5c, d, Table 1).

Discussion

The effects of hurricanes on benthic coral reef organisms, including sponges, depend on the interaction of numerous factors, ranging from size and intensity of the storm to exposure of the reef, presence of other potential stressors, time since the last major storm event, and composition of the benthic community (Gardner et al. 2005; De'ath et al. 2012; Roff et al. 2015; Bell et al. 2017a). At the six sites studied, sponge cover declined after the 2017 hurricanes, despite stable or slightly increasing cover between 2015 and 2016. Although detailed data on sponge abundance were only collected at two pre-hurricane time points, sponge density in St. Thomas appeared to be increasing prior to the hurricanes, a pattern observed on reefs elsewhere, and potentially attributed to declines in corals due to disease, bleaching, and eutrophication (e.g., Ward-Paige et al. 2005; McMurray et al. 2010; Bell et al. 2013, 2018). Interestingly, only a minor decline in overall sponge density (− 8.5%) was observed after the hurricanes. This may reflect a loss of large individuals that was offset by fragmentation into a greater number of smaller sponges or the initiation of the recovery and/or regrowth process. Wulff (1995, 2006) found that sponges fragmented by Hurricane Joan in Panama and Hurricane Allen in Jamaica had a high probability of survival and recruitment into the community over 5 weeks to a year, with initial reattachment occurring as early as 1–3 weeks. Storms have also been shown to produce highly clonal populations of corals and gorgonians due to survival of fragments (Lirman and Fong 1997; Coffroth and Lasker 1998; Aranceta-Garza et al. 2012). Additionally, Fenner (1991) found that after Hurricane Gilbert, recovery

Table 1 Statistical results of repeated-measures ANOVA tests for the effect of year (pre hurricane: 2015 and 2016; post-hurricane: 2017), with site as a random factor, on sponge percent cover, density, volume, species richness, Shannon index, inverse Simpson index, and the four sponge morphological categories, as well as percent cover of other major constituents of the benthic community

Variable	Transformed	Factor	*DF*	*F*	*p* value
Sponge community					
Sponge cover (%)	No	Year	2	9.5557	*0.000*
Sponge density (no. per m^2)	Yes (sqrt)	Year	2	6.9266	*0.002*
Sponge volume (cm^3)	Yes (sqrt)	Year	2	1.97	0.151
Species richness (*S*)	Yes (log)	Year	2	12.047	*8.9e−05*
Shannon index (*H*′)	No	Year	2	4.2276	*0.022*
Inverse Simpson index ($1/\lambda$)	No	Year	2	2.7132	0.079
Morphological category					
Excavating	Yes (arcsin)	Year	2	1.92	0.16
Encrusting	Yes (arcsin)	Year	2	15.90	*5.6e−06*
Massive	Yes (arcsin)	Year	2	1.21	0.31
Upright	Yes (arcsin)	Year	2	11.91	*6.8e−05*
Other benthic constituents					
Coral cover (%)	Yes (log)	Year	2	1.61	0.211
Macroalgal cover (%)	No	Year	2	1.99	0.148
EAC cover (%)	Yes (sqrt)	Year	2	9.69	*0.000*
Non-living cover (%)	Yes (sqrt)	Year	2	8.89	*0.000*

DF = degrees of freedom; *F* = F statistic. Italic indicates significant effect ($p < 0.05$). Post hoc tests are shown in Online Resource 3. Analyses of sponge species richness, Shannon index, and inverse Simpson index exclude Black Point; all other analyses include all six sites

of the sponge community in Cozumel was well underway after 4 months and largely complete by 21 months. Thus, our initial post-hurricane survey at 10 weeks after Hurricane Maria may represent a community that was already in the early stages of recovery. Sponge volume did not change significantly through time. The absence of a hurricane effect on sponge volume was confounded by high variability among quadrats. For example, some quadrats were dominated by encrusting sponges, which typically represent small volumes individually. However, their increase in numbers after the storms, whether due to recruitment of new individuals, fragmentation of larger individuals, or damage to upright sponges leaving only the point of attachment behind, may have offset any loss of volume in upright sponges, at least in part.

There are over 650 described sponge species on Caribbean reefs, and many remain undescribed (van Soest et al. 2012). To date, we have recorded over 100 sponge species on St. Thomas' reefs. Sponge species richness increased by 29.1% from 2015 to 2017, although the post-storm increase was moderate. On any given 5-m^2 transect, richness ranged from 19 to 40 sponge species. This is substantially higher than the 12 to 24 species per 20-m^2 transect reported by Easson et al. (2015) in Panama and the 18 to 21 species per 60-m^2 transect reported by Villamizar et al. (2013) in Belize. Likewise, sponge density at these sites in St. Thomas (34.5–49.4 sponges per m^2) is an order of magnitude higher than that in Belize (0.98–1.17 per m^2; Villamizar et al. 2013), but within the range found in Panama (38.1–90.7 per m^2; Gochfeld et al. 2007). Shannon index for sponges in St. Thomas increased significantly post-hurricanes while there was a minor increase in the inverse Simpson index post storms. Disturbances, such as hurricanes, may provide an opportunity for previously rare species to proliferate and, at least, temporarily increase diversity (Hughes and Connell 1999); future surveys will evaluate whether changes in sponge assemblages persist or merely represent early successional communities.

Sponges represent a tremendous diversity of shapes, sizes, and consistencies that affect their relative susceptibility to intense wave action. In general, upright or ropy sponges are most susceptible to breakage during storms, as compared to massive, encrusting, and cryptic sponges (Woodley et al. 1981; Blair et al. 1994; Wulff 2006; Stevely et al. 2011; Easson et al. 2013). Secondary to gross morphology, susceptibility to breakage is also affected by more fine-scale characteristics, such as branch diameter, the ratio of spicules to spongin fibers (Wulff 1995), or disease (Easson et al. 2013). Easson et al. (2013) reported a dramatic decline (16–23%) in the volume of the upright sponge *Aplysina cauliformis* on Bahamian reefs following Hurricane Irene (Category 3), which was accompanied by a slight increase (6%) in the number of *A. cauliformis* at one site, possibly due to fragmentation. In this study, physical damage from Hurricanes Irma and Maria disproportionately affected upright sponges. Loose fragments of storm-detached upright sponges were seen at many sites, and these can eventually become lodged on hard substrate to which they can reattach (Wulff 1991, 2006), and any remaining sponge tissue has the potential to recover and grow (Easson et al. 2013). Upright sponges play particularly

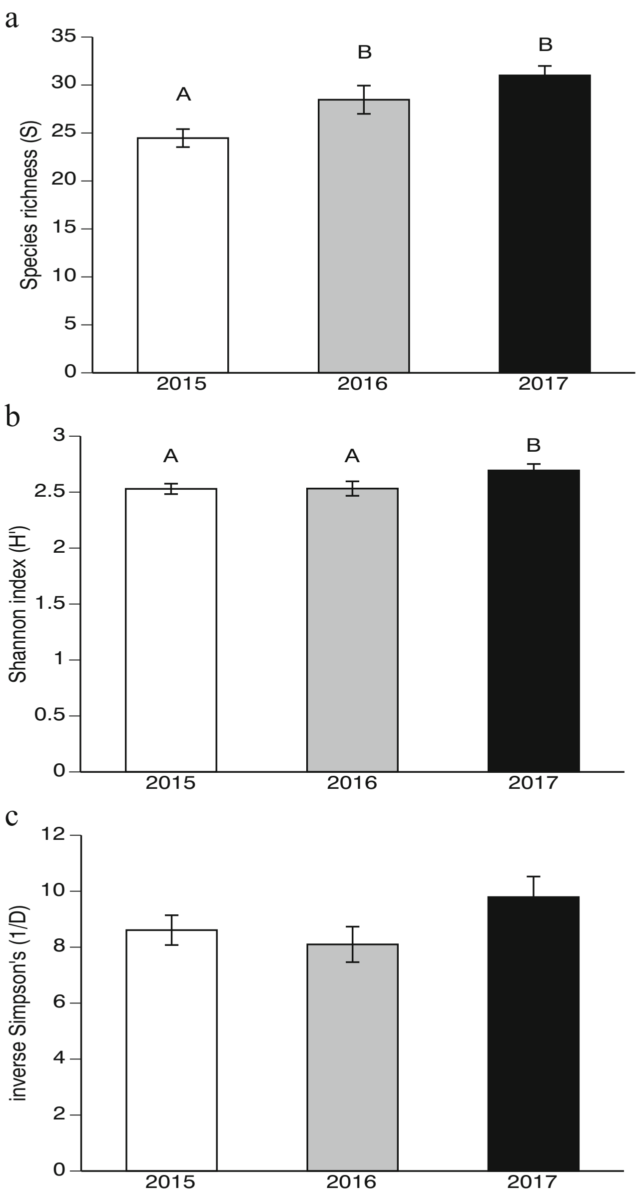

Fig. 3 Sponge diversity indices for 3 years (pre hurricane: 2015 and 2016; post-hurricane: 2017) from permanent belt transects ($n = 3$ per site) across five sites in St. Thomas (Black Point excluded; see "Methods"). Histograms represent mean ± SE of **a** species richness, **b** Shannon index, and **c** inverse Simpson index. For **a** and **b**, different letters denote significant differences between years as determined by post hoc comparisons using least square means (Online Resource 3). In **c**, there were no significant differences among years

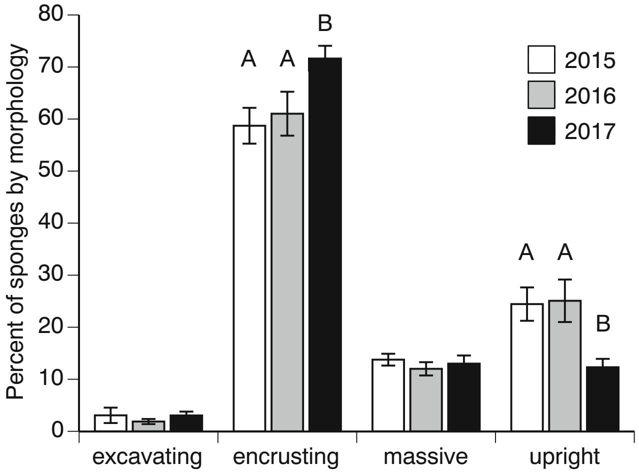

Fig. 4 Percent (mean ± SE) of the sponge community represented by each morphological category in 3 years (pre hurricane: 2015 and 2016; post-hurricane: 2017) from permanent belt transects ($n = 3$ per site) across six reef sites in St. Thomas. Morphological categories include **a** excavating, **b** encrusting, **c** massive, and **d** upright. For encrusting and upright sponges, different letters denote significant differences between years as determined by post hoc comparisons using least square means (Online Resource 3). For excavating and massive sponges, there were no significant differences among years

important roles in providing three-dimensional habitat for other organisms, as well as in consolidating loose pieces of rubble to provide stable substrata, while not preempting large areas of substratum on which coral larvae could otherwise recruit (Diaz and Rützler 2001; Bell 2008; Wulff 2012; Biggs 2013). Thus, their loss can have dramatic consequences to reef structure and function. Many tube and vase-shaped sponges (*massive*) were also observed rolling around in sand at the base of the reef where they are unlikely to find hard substratum on which to reattach and recover. The increase (+ 24.4%) in encrusting sponges, concomitant with the loss of upright and massive sponge species, limits the space available for recruitment of other sponges or benthic taxa, such as corals (Wulff 2013).

Intense wave action from hurricanes can cause significant damage to benthic reef organisms, and hurricanes are considered a major driver of coral cover (De'ath et al. 2012). Although earlier hurricanes affecting reefs in the Virgin Islands caused significant declines in coral cover (e.g., Edmunds and Witman 1991; Rogers et al. 2008), there was not a significant change in coral cover at these sites in St. Thomas following Hurricanes Irma and Maria. Likewise, Edmunds et al. (2019) did not observe a significant effect of these hurricanes on coral cover in St. John. Extensive physical damage to corals has been reported following numerous Atlantic hurricanes, typically to branching corals at very shallow depths, although massive corals can also be overturned and roll around, leaving further damage in their wake (e.g., Woodley et al. 1981; Edmunds and Witman 1991). While soft-bodied sponges are particularly susceptible to tissue damage, the absence of significant declines in coral cover may be due to a shift in coral species composition towards more wave-resistant communities (e.g., Smith et al. 2016b; Edmunds 2019), or to low overall coral cover (8.8% across all transects in all 3 years). Additionally, the sites in this study were fringing reefs, ranging from 8 to 15 m depth, which may have provided a partial refuge from damage due to wave action (Rogers et al. 2008). Nonetheless, coral cover prior to the hurricanes averaged 9.4% and declined to 7.8% post storms.

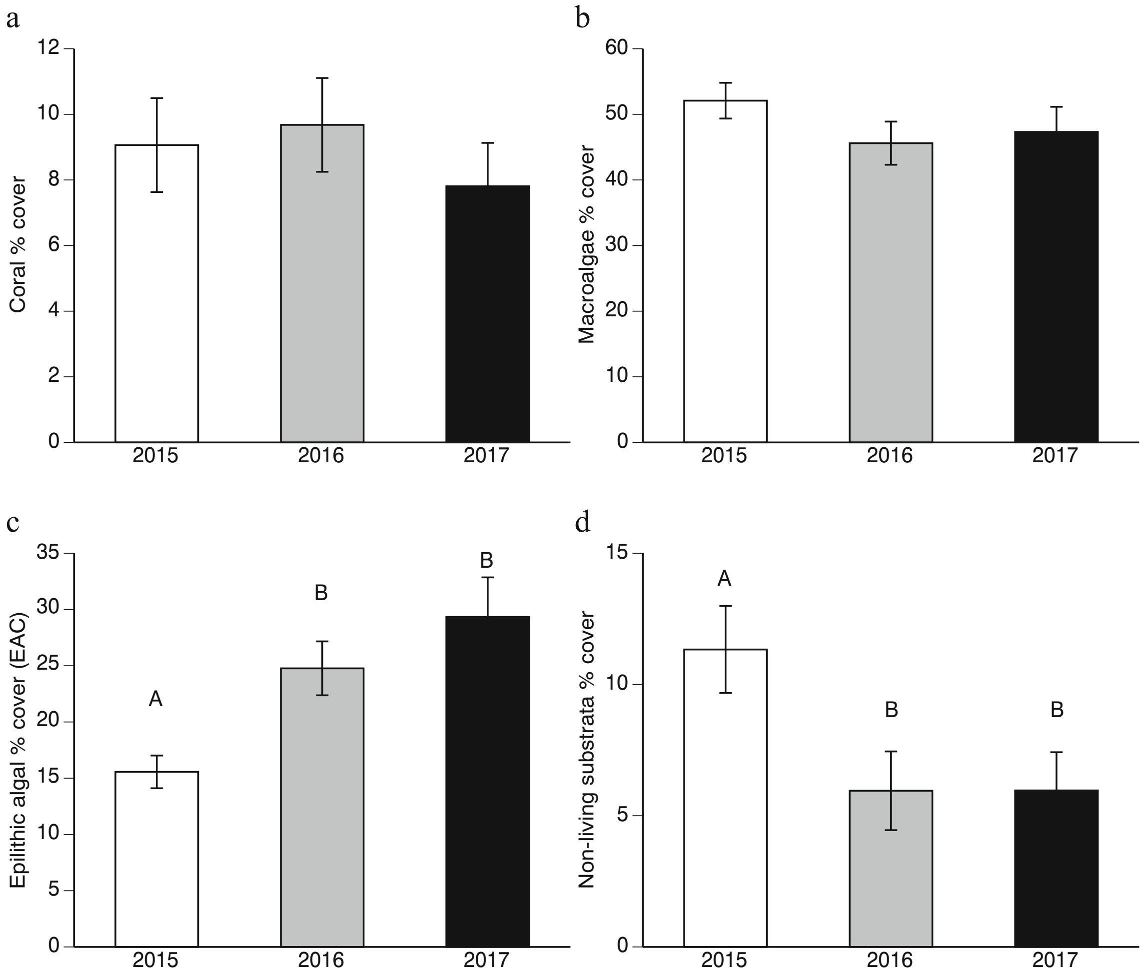

Fig. 5 Percent cover (mean ± SE) of major benthic community constituents in 3 years (pre hurricane: 2015 and 2016; post-hurricane: 2017) from permanent transects ($n = 3$ per site) across six reef sites in St. Thomas. Categories include **a** corals, **b** macroalgae, **c** epilithic algae community (EAC), and **d** non-living substrata. In **a** and **b**, there were no significant differences among years. For **c** and **d**, different letters denote significant differences between years as determined by post hoc comparisons using least square means (Online Resource 3)

Such a small numerical difference may be difficult to detect statistically, given natural variability, but this 17.8% decline in coral cover could have considerable repercussions, particularly with respect to reproductive potential and resilience of coral populations. Although percent cover of corals within transects did not change statistically, impacts to corals were observed at these sites. There were several overturned massive corals, some slumping of the reef structure, and most *Dendrogyra cylindrus* pillars were broken off and lying in the sand at the base of the reef. Many of the detached *D. cylindrus* pillars and remaining bases of the colonies were still partially alive 10 weeks post storms, but most of them exhibited signs of a plague-like coral disease.

Macroalgal blooms are widely known to follow hurricanes, likely due to increased nutrients in the water column from runoff and/or resuspension, or to their ability to recruit and/or spread rapidly to occupy newly opened substrata. There was no significant change in macroalgal cover at our sites, although algal volume might have been another relevant metric to assess. *Dictyota* spp. are particularly capable of asexual propagation due to fragmentation after hurricanes (Vroom et al. 2005), and while there was extensive coverage of *Dictyota* spp. on these reefs post-hurricanes, *Dictyota* cover was already high prior to the hurricanes. In the past, early macroalgal colonizers following hurricanes were often ephemeral (Edmunds and Witman 1991; Hughes 1994; Roff et al. 2015), and in the presence of healthy herbivore populations, these macroalgae were likely consumed, opening up substrata for coral recruitment (Hughes 1994). More recently, these early colonizers were often succeeded by more recalcitrant macroalgal species, particularly *Dictyota* spp. (Rogers and Miller 2006), rather than corals. Whereas macroalgal cover did not change over time at our sites in St. Thomas, there was a significant increase in EAC cover between 2015 and 2016, although there was no subsequent effect of the hurricanes. Macroalgae and EAC are the major benthic constituents on shallow reefs in St. Thomas and likely occupy space or produce allelochemicals that inhibit invertebrate larval recruitment (Ritson-Williams et al. 2009; Paul et al. 2011). In a 2015–2016 study, coral recruitment on these reefs was low relative to earlier studies in the USVI (Brandt et al. 2019).

Historically, one of the main effects of hurricanes on coral reefs was to provide open space for invertebrate, particularly coral, recruitment (Hughes and Connell 1999). In St. Thomas, non-living substratum consists of a combination of sand, rubble, and boulders but is often predominantly sand, and it is a relatively minor component of the benthos. There was a significant decline in non-living substrata from 2015 to 2016, but there was no further change following the hurricanes. Between the absence of open substrata and dominance of the substrata by algae, there appear to be limited opportunities for coral larval recruitment to the open reef (Kuffner et al. 2006). Unlike hermatypic corals, which need light, many sponges occupy cryptic habitats, such as the reef's interstices (Wulff 2006; de Goeij et al. 2013; Rützler et al. 2014). These habitats are largely occupied by encrusting sponges but may also represent locations where detached sponge fragments can become lodged or where sponge larvae may settle and grow, enhancing potential sponge resilience. There is also evidence that the presence of sponges may facilitate (Biggs 2013) or inhibit (Brandt et al. 2019) coral recruitment.

This unprecedented event, in which two Category 5 hurricanes occurred in rapid succession, generating significant wave action from multiple directions, significantly impacted the cover, richness, and composition of sponge communities in St. Thomas. Resuspended sediments due to this wave action, combined with land-based sources of pollutants and sediment from run-off following excessive rainfall, can damage sponges directly by clogging their filtration apparatus, reducing feeding and respiration rates, and inhibiting growth and reproduction, or indirectly by reducing light acquisition by photosynthetic symbionts and encouraging growth of macroalgae (Van Woesik et al. 1995; Gochfeld et al. 2007; Arias-Gonzalez et al. 2017; Biggerstaff et al. 2017; Edmunds et al. 2019). Mechanical damage from these storms disproportionately affected upright sponges, which are increasingly visible and important components of coral reef ecosystems, particularly where corals have declined in recent decades. The sponge assemblages varied among the study sites prior to the hurricanes, likely as a result of differing levels of anthropogenic impact and exposure to wave action, and ongoing studies will determine whether these shallow reefs are sufficiently resilient to return to their pre-hurricane states or whether alternate stable states develop. Losses or changes in sponge assemblages can reduce structural complexity, nutrient production, and consolidation of reef substrata. However, sponges have a remarkable capacity for recovery, through both regrowth and recruitment of new individuals through sexual and asexual propagation, and by 10 weeks post storms, the presence of new recruits and healed lesions indicate that sponge recovery was already underway on these reefs. As sponges are more resilient than corals in the face of multiple stressors, these extreme events may accelerate a regime shift towards sponge dominance on affected Caribbean reefs.

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