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RESEARCH

Site-specific variability in recovery of Caribbean sponge communities following two category-5 hurricanes

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Abstract Coral reefs worldwide are increasingly subjected to multiple disturbances, including storm events, thermal anomalies, disease outbreaks and more localized stressors. Climate change is predicted to increase the frequency and severity of tropical cyclones. In 2017, an unprecedented event of two Category 5 hurricanes in rapid succession occurred on St. Thomas, United States Virgin Islands. Short-term monitoring (2.5 months after the hurricanes) enabled us to characterize the impacts of these extreme events on coral reef sponge communities. In addition, to understand how coral reefs recover after disturbance, we evaluated changes in the sponge communities from pre-hurricane surveys in 2016 to two years post-storms in 2019. We identified 148 distinct sponge taxa within permanent transects at six sites around St. Thomas. Sponge communities varied across sites pre-storms, and exhibited different degrees of resilience. By two years post-storms, sponge cover did not return. Sponge volume increased overall, but was highly variable among sites. However, after two years, sponge densities increased by 42.3% over pre-storm densities, indicating the occurrence of sponge recruitment and fragmentation/reattachment. Sponge community richness increased at all sites over time, with an influx of rare species. Overall, succession of sponge communities was gradual and variable across sites and points to post-hurricane recovery requiring longer than two years. Although none of the sites returned to their pre-storm assemblages, recovery was greater at some sites at two years post-storms. Our data suggest that sponge recovery may occur on USVI reefs, but requires a longer timeframe and an absence of subsequent disturbances.

Keywords Porifera · Coral reef community structure · Storm damage · Resilience · Disturbance · Climate change

Introduction

Resilience of coral reef communities to stressors is crucial for the maintenance of the ecosystem services they provide (Hughes et al. 2017). Extreme storm events can cause physical damage to coral reefs, affecting their ability to provide coastline protection and reducing the three-dimensional structure necessary to create habitat for diverse reef species (Harmelin-Vivien 1994; Pascoe et al. 2021). These disturbances also stir up sediment that scours the substrata, and associated rainfall increases freshwater and land-based runoff of sediments, nutrients, toxins and terrestrial pathogens onto nearshore reefs (Rogers 1990; Fabricius 2005). Increased turbidity can reduce sunlight penetration, with negative effects on many reef organisms that rely on photosynthesis (Bessell-Browne et al. 2017; Edmunds et al.

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2019a). Disturbance-induced changes to ecosystem biodiversity can result in alterations in the abundance of individual species, both numerically dominant and rare, impacting community and ecosystem functions (Hughes et al. 2010; Walker et al. 2008).

Extreme storm events are predicted to increase in frequency and intensity as climate change escalates (Emanuel 2005, 2013). Future tropical storms, including Atlantic hurricanes, are expected to be characterized by increased wind velocities and precipitation, as well as changes to traditional storm paths (Balaguru et al. 2023), potentially affecting regions that have rarely been affected by storms in the past. These changes may also result in storms following similar paths in close temporal proximity. Responses of coral reef communities to hurricanes have been well studied (e.g., Woodley et al. 1981; Rogers 1993; Harmelin-Vivien 1994). However, most of the research on impacts, recovery and resilience to storms has focused on corals (e.g., Gardner et al. 2005; Edmunds 2019a; Pascoe et al. 2021; Madden et al. 2023), with fewer studies dedicated to other benthic coral reef taxa (sponges: Battershill and Bergquist 1990; Wulff 1995, 2006; Edmunds et al. 2020; Gochfeld et al. 2020; gorgonians: Lasker et al. 2020).

In September 2017, St. Thomas (U.S. Virgin Islands: USVI) was devastated by two Category 5 hurricanes within two weeks of each other (Gochfeld et al. 2020). Although similar, the storm paths differed slightly, affecting all of St. Thomas' coastal areas to at least some degree. At the time, this was an unprecedented event, both spatially and temporally, although more recent events (i.e., Hurricanes Helene and Milton in 2024) support this trend. Coral reefs in the USVI have been affected by numerous hurricanes since monitoring of reef sites began in the 1970s, with varying levels of damage to coral communities (e.g., Rogers et al. 1991; Tsounis and Edmunds 2017; Edmunds 2019a,b), yet the increasing frequency and intensity of storm events suggests that information on the response of the entire benthic community is needed to better understand the true extent of the impacts.

Historically, hurricanes caused acute disturbances from which some reefs recovered relatively rapidly, while others recovered more slowly or not at all (e.g., Fenner 1991; Gardner et al. 2005). Caribbean coral reefs are generally thought to have lost their ability to recover from hurricane-induced damage due to persistent multiple disturbances (Jackson et al. 2014), with stony coral communities not showing evidence of recovery to pre-storm states for at least eight years after the impact (Gardner et al. 2005). In the USVI, a combination of historical hurricanes with more recent bleaching, disease and runoff, has resulted in depauperate coral communities consisting predominantly of taxa resistant to hurricane impacts and other stressors (Edmunds 2019b). Octocorals also declined dramatically following extreme events on Caribbean reefs, but they have exhibited several years of consistent recovery (Lasker et al. 2020), enabling them to dominate some reefs (Tsounis and Edmunds 2017; Edmunds 2020; Lasker et al. 2020). In addition, many Caribbean reefs have undergone phase shifts from coral- to macroalgal-dominated communities following disturbances, including hurricanes (e.g., Hughes 1994; Norström et al. 2009; Dudgeon et al. 2010; Hernández-Delgado et al. 2024). However, less is known about resilience, recovery, recruitment and early successional stages of sponge communities in response to extreme events (Wulff 1995; 2013; Gochfeld et al. 2020; Segura-García et al. 2024).

Sponges are among the most diverse coral reef taxa, representing at least 676 named species on Caribbean reefs (van Soest et al. 2012), and are predicted to become "winners" on coral reefs in response to losses of corals (Norström et al. 2009; Dudgeon et al. 2010; Bell et al. 2013, 2018), although evidence that sponges are proliferating widely on reefs is limited (Wulff 2016; Lesser and Slattery 2020; Bell et al. 2022). Two studies suggest that sponges have increased on reefs in the USVI. Gochfeld et al. (2020) observed an increase in sponge density on repeatedly surveyed transects at six reefs in St. Thomas from 2015 to 2016, and Edmunds et al. (2020) reported an increase in sponge density on reefs in St. John from 1992 to July 2017 based on analysis of historical images. The enormous biodiversity that sponges represent provides important ecosystem services to coral reefs, by producing three-dimensional structure, food and habitat for other species, and through biogeochemical nutrient cycling (see recent reviews by Maldonado et al. 2012; Bell et al. 2023). However, sponges are susceptible to many of the same stressors that affect corals, including hurricanes (Wulff 1995; 2006; Edmunds et al. 2020; Gochfeld et al. 2020), diseases (e.g., Olson et al. 2006; Webster 2007; Easson et al. 2013; Luter and Webster 2017), and climate change (Carballo and Bell 2017), and it is clear that the loss of these critical taxa will have further negative implications for Caribbean reef structure and function. Associated with this remarkable biodiversity is tremendous morphological diversity, which contributes to the ability of some sponges to tolerate hurricane-associated damage, such as significant wave action, scour, and turbidity, while others, particularly upright branching morphs, are severely impacted (e.g., Wulff 2006; Gochfeld et al. 2020). Even within the same depth contour and ocean basin, sponge assemblages vary across spatial scales ranging from millimeters to hundreds of kilometers (Gochfeld et al. 2007; Wulff 2012), indicating that responses to stressors may also be site specific.

The goal of this study was to evaluate post-storm recovery and succession to assess potential resilience of the sponge community following two Category 5 hurricanes. By leveraging pre-hurricane data on sponge assemblages from six sites around the island of St. Thomas, USVI, we

previously reported the overall short-term (i.e., 2.5 months) impacts of Hurricanes Irma and Maria on St. Thomas' coral reefs, including its sponges (Gochfeld et al. 2020). Ten weeks after the hurricanes, we recorded significant overall decreases in sponge cover and volume, and an increase in sponge diversity, although there was no change in sponge density. Upright sponges were most impacted, exhibiting significant declines, while encrusting sponges increased in abundance (Gochfeld et al. 2020). Here, species- and site-specific responses to the storms were evaluated at four time-points during two years after the storms to evaluate potential resilience (i.e., the ability to recover to pre-disturbance conditions; Grimm and Wissel 1997) of the sponge assemblages on these reefs. Understanding how sponge assemblages respond to extreme storm events is important to characterize early effects of storm disturbance and to identify species that are resilient. Ultimately, this information will help fill gaps in our understanding of reef resilience under changing environmental conditions and provide a much-needed step towards being able to predict what Caribbean reefs will look like under future climate scenarios.

Methods

Study sites

For the purpose of this study, Hurricanes Irma (7 September 2017) and Maria (20 September 2017) are considered a single event, due to the brief (2 week) period between them during which no field research could be performed. Prior to these hurricanes, detailed surveys of sponge communities were performed at six sites around the island of St. Thomas, U.S. Virgin Islands (Table 1). These sites, previously described in Gochfeld et al. (2020) and Segura-García et al. (2024), represent a subset of shallow reefs from the Virgin Islands Territorial Coral Reef Monitoring Program's (TCRMP) permanent monitoring sites (Fig. 1). Black Point, Coculus Rock, and Magens Bay are nearshore sites in bays with developed watersheds. Botany Bay is also nearshore in a bay with recent coastal development activity, whereas Buck Island and Savana Island are undeveloped offshore islands. Direction and degree of exposure to wave action varies among the sites (Fig. 1). Among the

Table 1 Coordinates and general physical characteristics of the six study sites around St. Thomas, US Virgin Islands. Coordinates based on WGS84

Site	Latitude	Longitude	Nearshore/Offshore	Transect depth (m)
Black Point (BP)	N18° 20.665′	W64° 59.107′	Nearshore	8–13
Botany Bay (BB)	N18° 21.433′	W65° 02.071′	Nearshore	9–10
Buck Island (BI)	N18° 16.717′	W64° 53.925′	Offshore	9–18
Coculus Rock (CR)	N18° 18.734′	W64° 51.613′	Nearshore	7–8
Magens Bay (MB)	N18° 22.459′	W64° 56.077′	Nearshore	8–9
Savana Island (SI)	N18° 20.437′	W65° 04.939′	Offshore	9–12

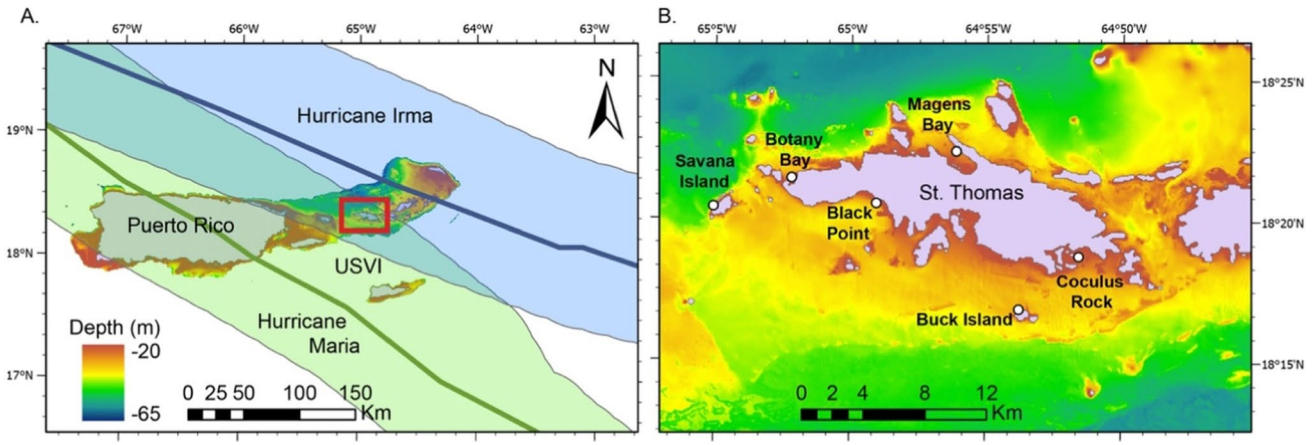

Fig. 1 Maps of the study region and storm paths. **A**: The U.S. Caribbean and Puerto Rican shelf, showing the central tracks and widths of hurricane force winds for Hurricane Irma (blue) and Hurricane Maria (green). Both storms tracked from southeast to northwest. Only seafloor depths less than 65 m shown. Red box indicates area shown in B. **B**: Locations of the study sites around St. Thomas, US Virgin Islands

nearshore sites, Magens Bay faces north, Botany Bay faces northwest, Coculus Rock faces southeast, and Black Point faces southwest. Of the offshore islands, the survey site on Savana Island faces west and the site on Buck Island faces north but is somewhat sheltered by the main island of St. Thomas. At each site, three of TCRMP's previously established permanent 10-m transects were repeatedly surveyed in August 2016 (the most recent pre-hurricane survey), early December 2017 (2.5 months after Hurricane Maria), March 2018 (6 months post-storms), November 2018 (14 months post-storms) and July 2019 (22 months post-storms). Percent cover of sponges and other benthic constituents were surveyed on the same schedule as the other sponge metrics, except in 2019, when percent cover surveys were performed in November (26 months post-storms).

Sponge community responses to hurricanes and recovery

To provide a more comprehensive picture of a diverse sponge community on topographically complex reefs like those in St. Thomas, several metrics were used, as described previously (Gochfeld et al. 2020). In addition to percent cover, which is widely reported but generally underrepresents cryptic and upright species, sponge density and volume were also quantified and are considered more ecologically relevant (Wulff 2012; Edmunds et al. 2020; Gochfeld et al. 2020; Reverter et al. 2021).

Percent cover of sponges was calculated from diver-held video surveys of the three transects at each site using established TCRMP methods (Smith et al. 2016, as described in Gochfeld et al. 2020). Briefly, independent photos were extracted from each video transect (~ 0.6 × 0.5 m; n = 21 per transect). Random points (n = 20) were superimposed on every photo, generating over 1200 points per site during each of the five sampling periods (Ennis et al. 2019). Benthic organisms under each point were classified to the lowest taxonomic level possible. For percent cover, we used the broader category of "sponge", which encompassed sponge taxa that could and could not be identified from the images. Rarefaction was accomplished by visual assessments of the running means. All benthic constituent means were stable at 17 points, indicating that our sampling approach represented an accurate estimate of percent cover (Gochfeld et al. 2020). To determine sponge density, every individual sponge or ramet was counted within 0.5 m on one side of each transect line. This resulted in 0.5 × 10 m belt transects for all sites except for Black Point in 2016, where 0.5 m on both sides of the transect lines were surveyed (resulting in 1 × 10 m belt transects). Density was calculated as the total number of sponges on each transect divided by the transect area, to yield sponges m^{-2}. Many sponges are cryptic and cannot be accurately quantified or identified from photos or videos, so these surveys were performed in situ by a diver. Sponge volume was determined within permanent 1-m^2 quadrats centered on the initial and/or final meter of each transect line (n = 3–5 quadrats per site). Due to the high density and diversity of sponges on these reefs, we used a standardized approach for measuring all sponges, as described in Gochfeld et al. (2020). Briefly, for each sponge, we used a flexible sewing tape to measure the longest dimension, followed by one or more width measurements, and one or more height measurements, as needed to adequately represent the shape of each sponge (Gochfeld et al. 2020). Multiple measurements in each dimension were averaged to calculate length × width × height, and for large tube and vase sponges, measurements of the interior cavity were subtracted from the exterior dimensions. This approach overestimated actual sponge volume by approximately 10.5% (Gochfeld et al. 2020).

Sponge diversity for each transect was calculated using the sponge density data. If sponges could not be identified in situ, voucher samples with associated photographs were collected for subsequent identification using a combination of gross morphology, spicule and skeletal structure. Those that could not be identified to the species level were differentiated to the lowest possible taxonomic level (i.e., genus, family, order, class). 148 distinct sponge taxa were used to calculate the diversity metrics. Species richness (S), Shannon Index (H′) and Pielou's Evenness Index (J′) were calculated in the PRIMER v6 software package (Clarke and Warwick 2001). Because transects were twice as large at Black Point in 2016, which could affect measures of sponge diversity, this site was omitted from diversity analyses in an earlier paper (Gochfeld et al. 2020). However, during the December 2017 surveys, the transects at Black Point were 1 m wide, with data recorded within 0.5 m on both left and right sides of the transect lines. In subsequent surveys, data were only collected within 0.5 m on the left side of each transect line. Therefore, for Black Point, the density data for 2016 were adjusted proportionally relative to the left side of the transect line used in subsequent surveys so that the 2016 Black Point data could be compared with those from other dates and sites. Sponges were distributed nearly evenly across both sides of the transect lines at Black Point in December 2017, with 51.2 ± 1.7% of sponges on the left sides of the transects, and 48.8 ± 1.7% on the right sides of the transects.

Since sponge morphologies can be differentially affected by hurricanes, each sponge taxon was assigned to a broad morphological category (sensu Wulff 2006; Zea et al. 2014). These morphotypes included excavating sponges ("excavating"); low relief (< 2 cm in depth) and encrusting sponges ("encrusting"); thicker cushions, massive, spheres, or other irregular shapes of medium relief ("massive"); and upright tube, vase, branching and rope sponges of high relief

("upright"). These categories differ slightly from those previously described in Gochfeld et al. (2020) and are now more representative of the typical (as opposed to locally observed) morphologies of the species found in our surveys. Morphotype assignments for each species are included in Supplemental Table 1. The proportional representation of each morphotype in the entire sponge community was calculated as the number of sponges in that category divided by the total number of sponges for each transect (Gochfeld et al. 2020).

Abundances of sponge species were categorized by frequency of occurrence in the study database. Rare species were defined as species that only occurred once or twice throughout the entire study, semi-rare species occurred 3–10 times across all transects, abundant species 11–100 times, and extremely abundant species > 100 times.

Overall benthic community responses to hurricanes and recovery

Percent cover of other benthic constituents of the coral reef community was determined from the video transects described above, following Smith et al. (2016) and Gochfeld et al. (2020). In addition to sponges, hard corals, macroalgae, the epilithic algal community (EAC: i.e., diminutive turf and filamentous algal communities), and non-living substrata represented > 90% of overall benthic substrata, and percent cover of each of these constituents across sites and dates was analyzed.

Data analysis

To test for effects of the hurricanes (2016 vs. 2017) and subsequent recovery (2016–2019) on the sponge community, repeated-measures analyses of variance (RMANOVAs) were performed on percent cover of sponges and other major benthic constituents, sponge density, volume, species richness, Shannon Diversity and Pielou's Evenness indices, with site and date as fixed factors. These analyses were performed in JMP 17.0.0 (JMP Statistical Discovery LLC 2022). Prior to analyses, residuals were tested for normality using Shapiro–Wilk tests and for homogeneity of variance using Levene's tests. Transformations used for metrics that did not meet these assumptions are specified in Supplemental Table 2. For significant effects or interactions, Tukey's HSD post-hoc comparisons were performed using JMP. Post-hoc results for significant site x date interactions are presented in Supplemental Table 3. To characterize hurricane effects on sponges with differing morphologies, RMANOVAs were performed on arcsin-transformed proportions of each morphotype to test for the main effects of site and date, followed by Tukey's HSD post-hoc tests where warranted. For each metric, percent change between 2016 (pre-storm) and each post-storm survey date was calculated. All data are presented as means ± standard error (SE).

Sponge assemblages were visualized by site and date using nonmetric multidimensional scaling (nMDS) plots generated in the PRIMER software package (Plymouth Routines in Multivariate Ecological Research, version 7; Clarke and Warwick 2001) for all sites combined, and for each site separately, with trajectories showing changes by date for each transect within sites. A Bray–Curtis dissimilarity matrix was calculated for the ranked proportional abundance of each species and analyzed using a permutational ANOVA (PERMANOVA), with site and date as fixed factors, using the PERMANOVA function in PRIMER, followed by pairwise tests among site and dates. Transects within sites were compared using analyses of similarities (ANOSIM). Species contributing to dissimilarity among dates were identified using similarity of percentages (SIMPER) analyses in PRIMER. For the species identified as major contributors to dissimilarity among dates in the SIMPER analysis, patterns of change in abundance across sites and dates were analyzed using RMANOVA if residuals met assumptions of normality and homogeneity of variance. For those species that did not meet those assumptions, the transformations used are shown in Supplemental Table 2; alternatively, two-way ANOVAs were performed on rank-transformed data.

To determine whether rare species were more likely to be observed in later surveys, the number of rare species recorded during each survey was compared to an expected number of rare species using a Chi-squared test. Expected values were calculated as the total number of rare species observed during the study divided by the number of surveys (n = 5), assuming that rare species were equally likely to be observed at any time point. All sites were combined to provide enough rare species for analysis. For comparison with more common species, separate Chi-squared analyses were performed for semi-rare, abundant, and extremely abundant species.

Results

Effect of hurricanes on sponge percent cover, density, and volume

Percent cover of sponges varied significantly across sites and dates (RMANOVA, $P < 0.0001$ for both), and there was a significant site x date interaction ($P = 0.0002$; Fig. 2A, Supplemental Tables 2, 3). Although the absolute decline in sponge cover after the 2017 hurricanes was relatively minor (ranging from 1 to 5.4% across all sites), the decline relative to pre-hurricane sponge cover averaged 24.9 ± 12.9% and remained 28.2 ± 14.9% lower in 2019 compared with 2016 (Supplemental Fig. 1). Across the six sites, sponge cover

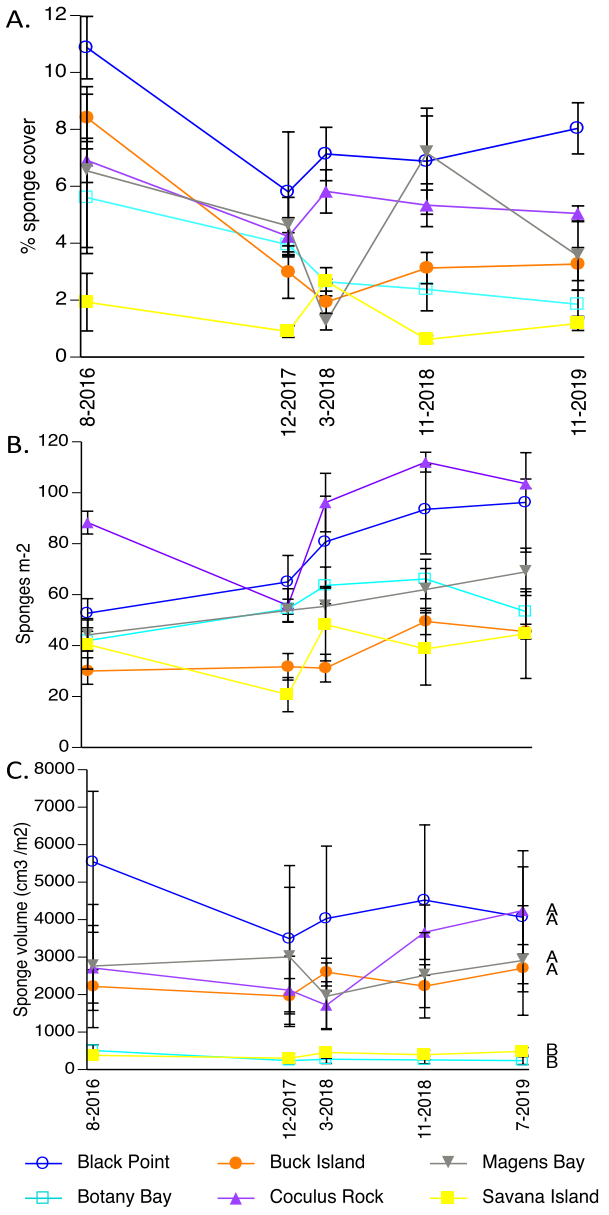

Fig. 2 Quantitative effects of storm damage and recovery on sponge communities in St. Thomas over time. Mean (±SE) **A**: percent cover and **B**: density of sponges across three transects, and **C**: volume of sponges in 3–5 quadrats at six sites on St. Thomas pre-hurricanes (2016) and at four dates post-hurricanes. In 2019, percent cover data from November; all other data from July. Letters on the right indicate significant differences among sites from Tukey's post-hoc tests where interaction term was not significant. Post-hoc tests for signfi-cant interaction terms in Supplemental Table 3

varied from ~ 2–11% pre-storms, and although the storms reduced sponge cover at all sites, the extent of recovery varied among sites, with some evidence of recovery at Black Point, but not at the other sites.

Sponge density also varied significantly across sites (RMANOVA, $P = 0.003$) and dates ($P < 0.0001$), and there was a significant site x date interaction ($P = 0.0015$; Fig. 2B, Supplemental Tables 2, 3). In contrast to sponge cover, overall sponge density was not negatively affected by the hurricanes (1.8 ± 9.3% increase in 2017), and increased by an average of 42.3 ± 9.3% across all sites from 2016 to 2019 (Supplemental Fig. 2). Coculus Rock and Savana Island experienced an immediate post-hurricane decline in sponge density, but density at all other sites either increased or did not change during that period. Overall, sponge density was highest and increased over time at Black Point and Coculus Rock (the two southern nearshore protected sites), and lowest at Buck Island and Savana Island, the two offshore exposed sites.

There was a significant effect of both site (RMANOVA, $P = 0.0205$) and date ($P = 0.0160$) on sponge volume, but no site x date interaction ($P = 0.0639$). Due to high variability, particularly among quadrats at Black Point, post-hoc tests only identified differences between sites, with significantly lower sponge volumes in quadrats at Botany Bay and Savana Island compared with the other four sites (Fig. 2C, Supplemental Tables 2, 3). At all sites combined, sponge volume declined by 23.9 ± 8.9% after the hurricanes (2016–2017), but increased over time, resulting in a 14.5 ± 13.2% increase from 2016 to 2019 (Supplemental Fig. 3).

Effect of hurricanes on sponge morphotypes

RMANOVAs indicated significant site x date interactions for all sponge morphs except for excavating sponges, which only varied significantly among sites ($P < 0.0001$; Fig. 3A; Supplemental Tables 2, 3). Across all dates, the sites in this study had low proportions of excavating and massive sponges (Supplemental Fig. 4). Excavating sponges may have been underreported due to the difficulty of seeing them under macroalgae. Encrusting sponges represented the highest proportion of the sponge community at all sites in 2016 (68.1 ± 3.8%) and increased significantly (+ 13.6 ± 4.9%) following the hurricanes in 2017 (Fig. 3B, Supplemental Figs. 4, 5A). Although less abundant overall, massive sponges also increased following the hurricanes (+ 49.6 ± 24.0% from 2016–2017; Supplemental Fig. 5B), specifically due to increases at Buck Island, Coculus Rock and Savana Island (Fig. 3C). In contrast, there was a significant decline in the proportion of upright sponges after the hurricanes (− 22.2 ± 11.8%; Fig. 3D, Supplemental Fig. 4, 5C), with the greatest losses at Buck Island (− 49.6 ± 6.3%) and Black Point (− 44.0 ± 8.4%), which had the highest proportion of upright sponges pre-storms (50.4 ± 1.9% and 26.8 ± 5.0%, respectively; Fig. 3D). By July 2019, 22 months post-storms, the proportion of upright sponges at all sites combined had increased over 2017 proportions but remained 16.6 ± 11.2% lower than pre-storm (2016) levels (Supplemental Figs. 4, 5C).

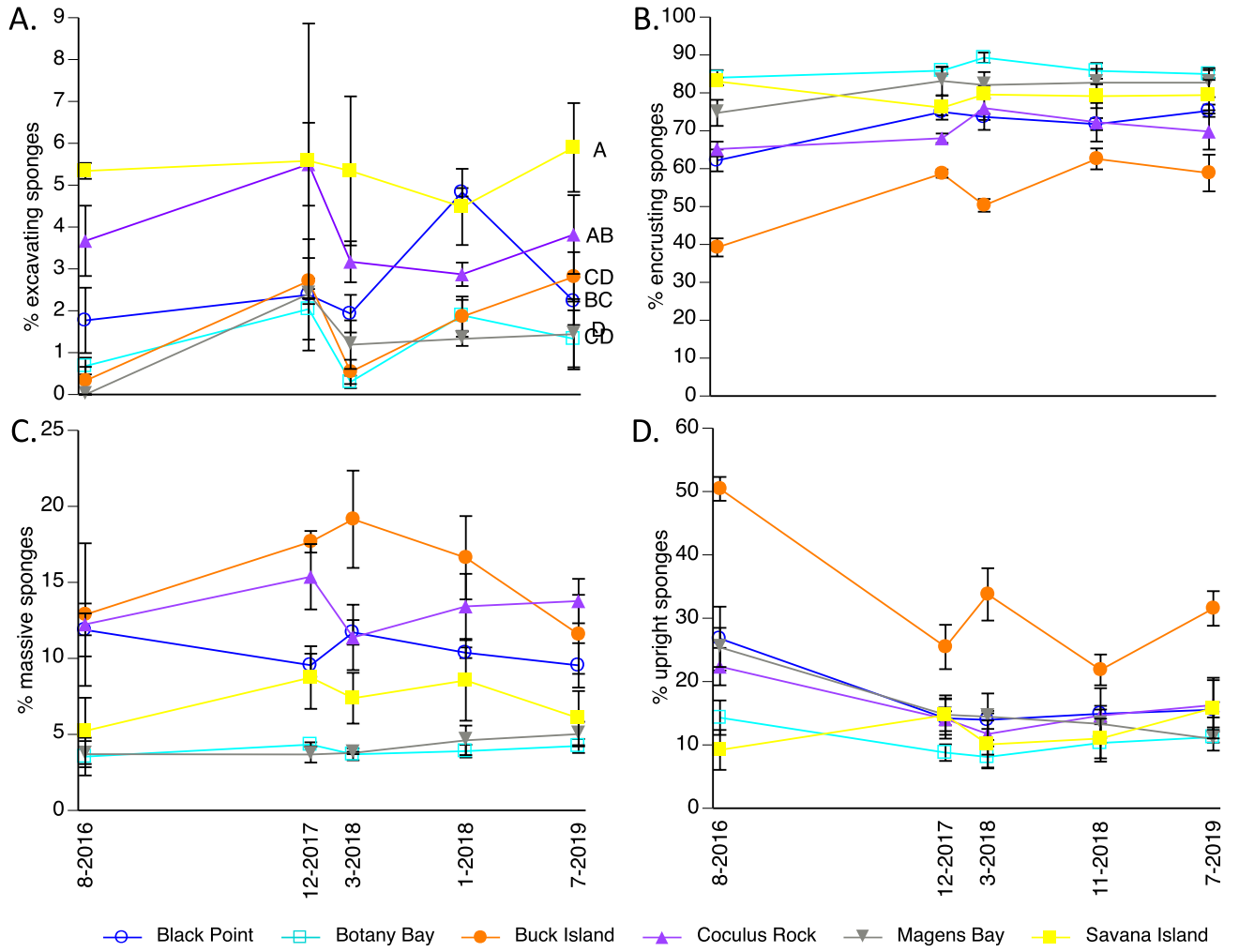

Fig. 3 Quantitative effects of storm damage and recovery on sponge morphotypes in St. Thomas over time**.** Percent (mean ± SE) of the sponge community at each site and date represented by **A**: excavating, **B**: encrusting, **C**: massive, and **D**: upright sponge morphotypes. Data based on three transects at each of six sites on St. Thomas pre-hurricanes (2016) and at four dates post-hurricanes. Note the different scale in each panel. Morphotype assigned to each species in Supplemental Table 1. Letters on the right indicate significant differences among sites from Tukey's post-hoc tests where interaction term was not significant. Post-hoc tests for significant interactions for all morphs except massives in Supplemental Table 3

Effect of hurricanes on sponge assemblages

Overall, 148 distinct taxa were identified, representing 31,158 sponges across 18 transects at 5 time points (Supplemental Table 1). Most sponges were distinguished and identified to the species level (99), whereas a few could only be identified to genus (23), family (6), order (7) or class (13). Species richness varied significantly across site (RMANOVA; $P = 0.004$) and date ($P < 0.0001$; Fig. 4, Supplemental Table 2), while the other two diversity indices (Shannon and Pielou's) showed significant effects of site ($P < 0.0001$ for both), date ($P < 0.0001$ for Shannon, $P = 0.001$ for Pielou's), and site × date interactions ($P = 0.0119$ for Shannon, $P = 0.014$ for Pielou's; Supplemental Table 2, 3, Supplemental Fig. 6). Although species richness across all sites was minimally affected by the hurricanes (increase of 7.5 ± 5.1% from 2016 to 2017), richness rose significantly from March to November 2018, resulting in an increase of 36.0 ± 5.4% from 2016 to 2019 (Supplemental Fig. 7). Overall, Black Point and Coculus Rock had higher species richness than the other four sites (Fig. 4). The Shannon Diversity Index was highest at Black Point, Buck Island and Coculus Rock, and lowest at Botany Bay. Diversity was relatively unaffected by the hurricanes, decreased at Botany Bay, Buck Island and Coculus Rock in March 2018, but by 2019 had increased overall by 7.0 ± 2.3% over 2016 (Supplemental Table 2, 3, Supplemental Fig. 6A). Pielou's Evenness Index was highest at Black Point, Buck Island and Savana Island, and lowest at Botany Bay. Evenness was relatively unaffected by the hurricanes, decreased at Botany

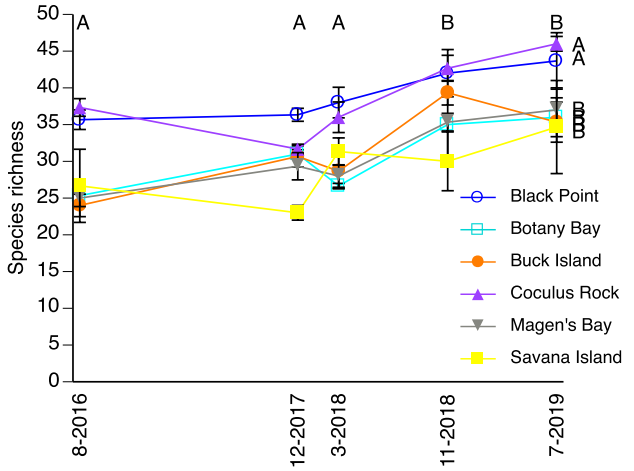

Fig. 4 Effects of storm damage and recovery on sponge species richness in St. Thomas over time**.** Mean (±SE) sponge species richness in three transects at each of six sites on St. Thomas pre-hurricanes (2016) and at four dates post-hurricanes. Letters at the right and top of the graph indicate significant differences among sites and dates from Tukey's post-hoc tests

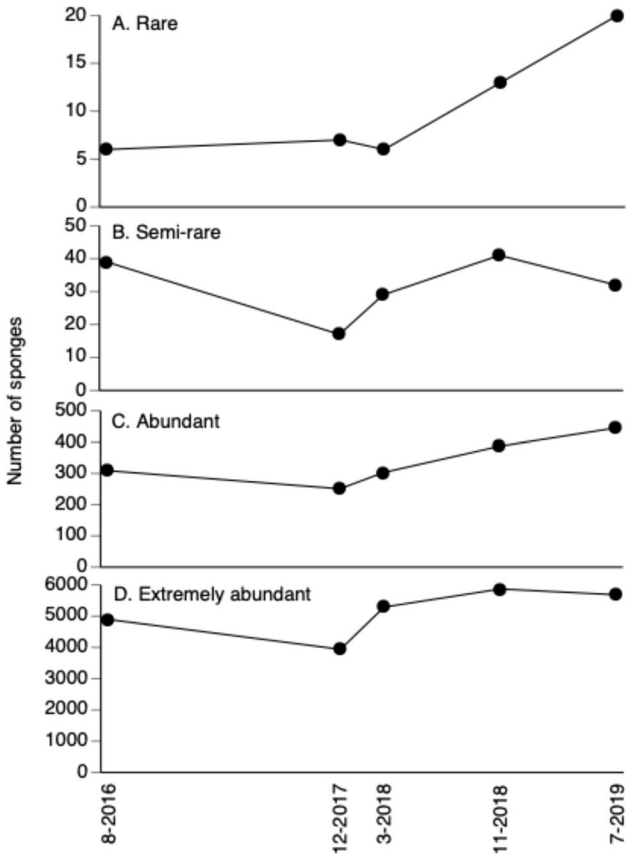

Fig. 5 Effects of storm damage and recovery on sponge abundance categories in St. Thomas over time**.** Number of sponges belonging to each abundance category based on three transects at each of six sites on St. Thomas pre-hurricanes (2016) and at four dates post-hurricanes. **A**: Rare (1–2 individuals per species over the entire study period; n = 41 species), **B**: semi-rare (3–10 individuals per species; n = 31 species), **C**: abundant (11–100 individuals per species; n = 40 species), **D**: extremely abundant (> 100 individuals per species; n = 36 species). Number of sponges within each category differed from random ($P \leq 0.0215$)

Bay, Coculus Rock and Savana Island in March 2018 and remained slightly lower than 2016 over the remainder of the study (Supplemental Table 2, 3, Supplemental Fig. 6B).

Rare species (1–2 individuals per species over the entire study period) were recorded more frequently than random in the last two surveys ($X^2 = 14.346$, $P = 0.00627$; Fig. 5). These 41 species represented 28% of the overall community. Their frequency of sightings increased in Nov. 2018 and July 2019, with 20 (38.5%) sightings in July 2019, 13 (25.0%) in Nov. 2018, 6 (11.5%) in Mar. 2018, 7 (13.5%) in Dec. 2017, and 6 (11.5%) in 2016.

When the frequencies of semi-rare species (recorded 3–10 times), abundant species (recorded 11–100 times) and extremely abundant species (recorded > 100 times) were compared across dates, all distributions differed from random ($X^2 = 11.494$, $P = 0.0215$ for semi-rare (n = 31 species), $X^2 = 62.263$, $P < 0.0001$ for abundant (n = 40 species), and $X^2 = 457.947$, $P < 0.0001$ for extremely abundant groups (n = 36 species); Fig. 5). In all but the rarest group (1–2 individuals), frequencies of sighting declined after the hurricanes (Dec. 2017) and then increased over time (abundant) or increased until Nov. 2018 and then declined slightly (semi-rare, extremely abundant).

Significant differences in sponge community structure were found among the sites (PERMANOVA F = 23.743, df = 5, $P = 0.001$) and dates (F = 1.8038, df = 4, $P = 0.004$), but there was no significant site x date interaction (F = 0.67712, df = 20, $P = 1$). Pairwise post-hoc tests identified significant differences in the sponge communities in 2016 relative to all other dates ($P \leq 0.022$) except for July 2019 ($P = 0.083$), and between sponge communities in December 2017 and July 2019 ($P = 0.018$; Supplemental Table 4). All sites differed in pairwise comparisons ($P = 0.001$), but when visualized using a nonmetric multidimensional scaling plot, the nearshore sites of Black Point, Botany Bay, Coculus Rock, and Magens Bay clustered together, whereas the offshore sites of Buck Island and Savana Island were both distinct (Fig. 6, Supplemental Fig. 8). In addition, all transects differed within sites (ANOSIM, $P = 0.001$), except for transects 1 and 2 at Coculus Rock ($P = 0.079$).

Although there was no significant site x date interaction in sponge community structure based on the PERMANOVA results, trajectories by date within each site indicate a larger effect of the hurricanes (2016–2017) at Black Point, Buck Island, and Magens Bay, relative to any other time period, with sponge communities not returning to pre-storm

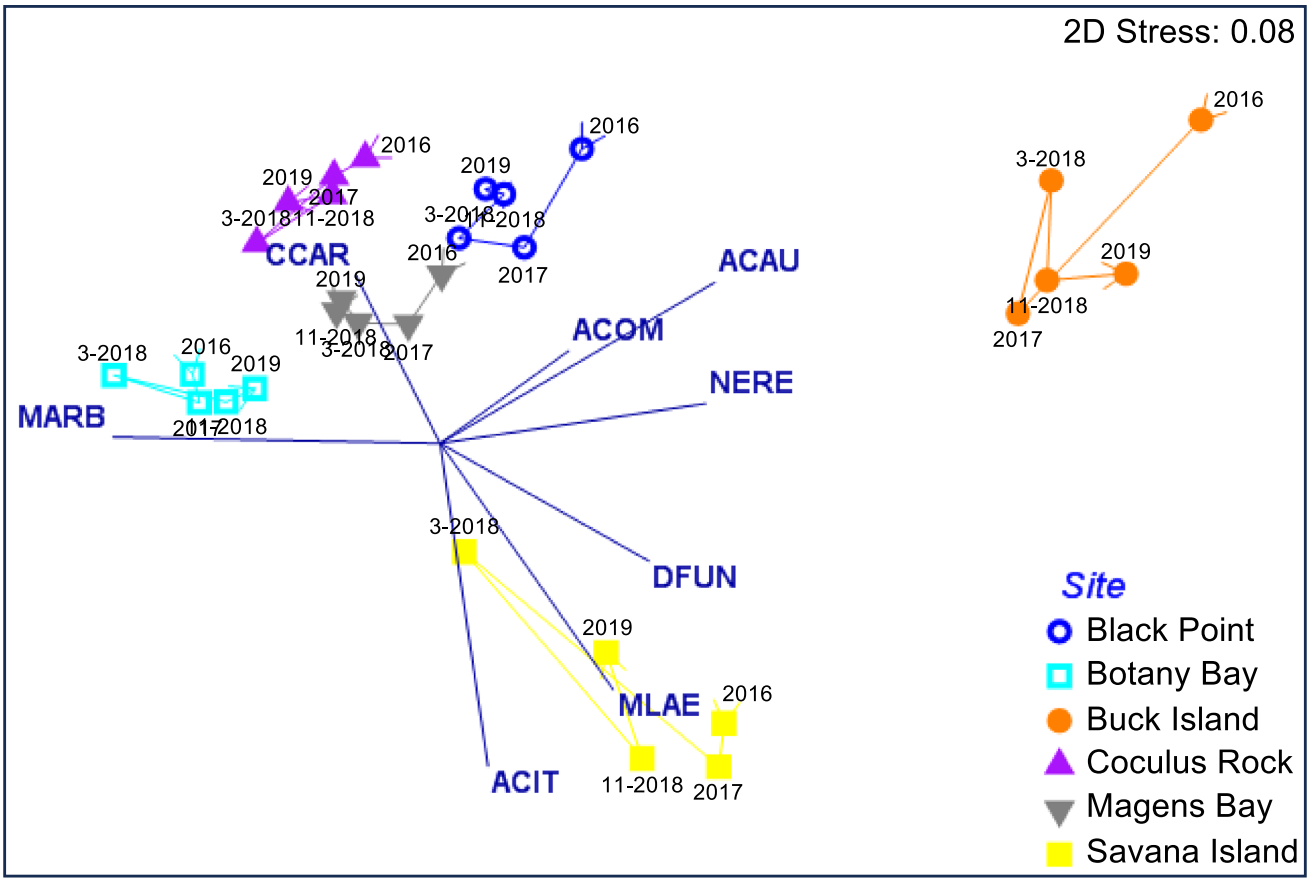

Fig. 6 Nonmetric multidimensional scaling (nMDS) plot of sponge assemblages in St. Thomas over time. Points represent all transects averaged within each site for each time point, with trajectories showing patterns of change within sites from one survey date to the next. Vector plot (blue lines) indicates relationships between densities of major sponge species contributing to dissimilarities among dates by SIMPER and each site x date assemblage. Species: ACIT = *Agelas citrina/sventres,* ACOM = *Amphimedon compressa,* ACAU = *Aplysina cauliformis*, CCAR = *Chondrilla caribensis*, DFUN = *Dictyonella funicularis*, MARB = *Monanchora arbuscula*, MLAE = *Mycale (Mycale) laevis*, NERE = *Niphates erecta*

assemblages (i.e., recovery) by 2019 (Fig. 6, Supplemental Fig. 9). In contrast, assemblages at Botany Bay, Coculus Rock, and Savana Island were more variable over time. The hurricane effects at Black Point, Buck Island and Magens Bay were largely due to losses of *Aplysina cauliformis* and, to a lesser extent, *Amphimedon compressa* (recently synonymized with *Amphimedon nodosa*; de Voogd et al. 2025), upright sponges that were most common at those sites pre-hurricanes.

SIMPER analyses identified the same eight major contributors to dissimilarities among sponge communities between 2016 and 2017 and between 2016 and 2019: *Monanchora arbuscula*, *Ap. cauliformis*, *Mycale (Mycale) laevis*, *Agelas citrina/sventres* (combined here because they tended to be cryptic and collected vouchers ultimately represented both species, which could not later be differentiated in field-collected data), *Chondrilla caribensis*, *Niphates erecta*, *Dictyonella funicularis* and *Am. compressa* (Supplemental Table 5). *Monanchora arbuscula* was by far the largest contributor to dissimilarities (> 18%) across both time periods. All of the major contributors varied across sites except for *My. laevis*, and all species except *Am. compressa* varied across dates, but only *N. erecta* and *D. funicularis* had significant site x date interactions (Supplemental Tables 2, 3). Patterns of change across sites and dates for these eight species are shown in Supplemental Fig. 10.

Across all dates, *Mo. arbuscula* was the most abundant species at the four nearshore sites, but its density remained low at the two offshore sites. The density of *C. caribensis* was highest at Black Point, where it increased over time, while remaining low at all other sites. The branching sponge *Ap. cauliformis* occurred at higher densities at Buck Island, Black Point, Magens Bay and Coculus Rock initially, but declined following the storms at Buck Island, Black Point and Coculus Rock, with recovery to pre-storm levels only occurring at Buck Island. In contrast, the branching species *Am. compressa* occurred at highest densities at Black Point and Botany Bay, and fluctuated little over time. *Niphates*

erecta and *My. laevis* were highly variable across sites and/or dates. *Agelas citrina/sventres* occurred almost exclusively at Botany Bay and Savana Island, and increased over time. Density of *D. funicularis* was highest at the offshore sites (Buck Island, Savana Island) initially, was dramatically reduced by the hurricanes, but eventually recovered to pre-storm levels. For *C. caribensis, Ap. cauliformis*, and *My. laevis,* it was not possible to differentiate statistically among dates even though the main effect of date was significant (Supplemental Table 2).

Overall benthic community responses to hurricanes and recovery

There was a significant effect of the hurricanes on percent cover of major benthic community constituents. Coral, macroalgal, EAC and non-living cover varied significantly across sites, dates and had significant site x date interactions (RMANOVA; Fig. 7, Supplemental Table 2, 3). While temporal differences were relatively small, coral cover averaged 9.7 ± 1.4% across all sites pre-storms (2016) and only 6.5 ± 1.5% in 2019. This absolute loss of 3.2% represents an overall 21.0 ± 5.8% decline in coral cover across all transects following the hurricanes (2017) and an overall 30.8 ± 8.0% decline in 2019 relative to 2016 (Supplemental Fig. 11A). Within sites, there was an absolute loss of 0.3–2.7% coral cover following the hurricanes (2017), with Buck Island least affected and Botany Bay most affected.

Overall, macroalgal cover increased by 10.6 ± 9.9% following the hurricanes (2017) and remained 15.2 ± 7.3% higher in 2019 relative to 2016 (Supplemental Fig. 11B). Within sites, there was an absolute change of 2–22%

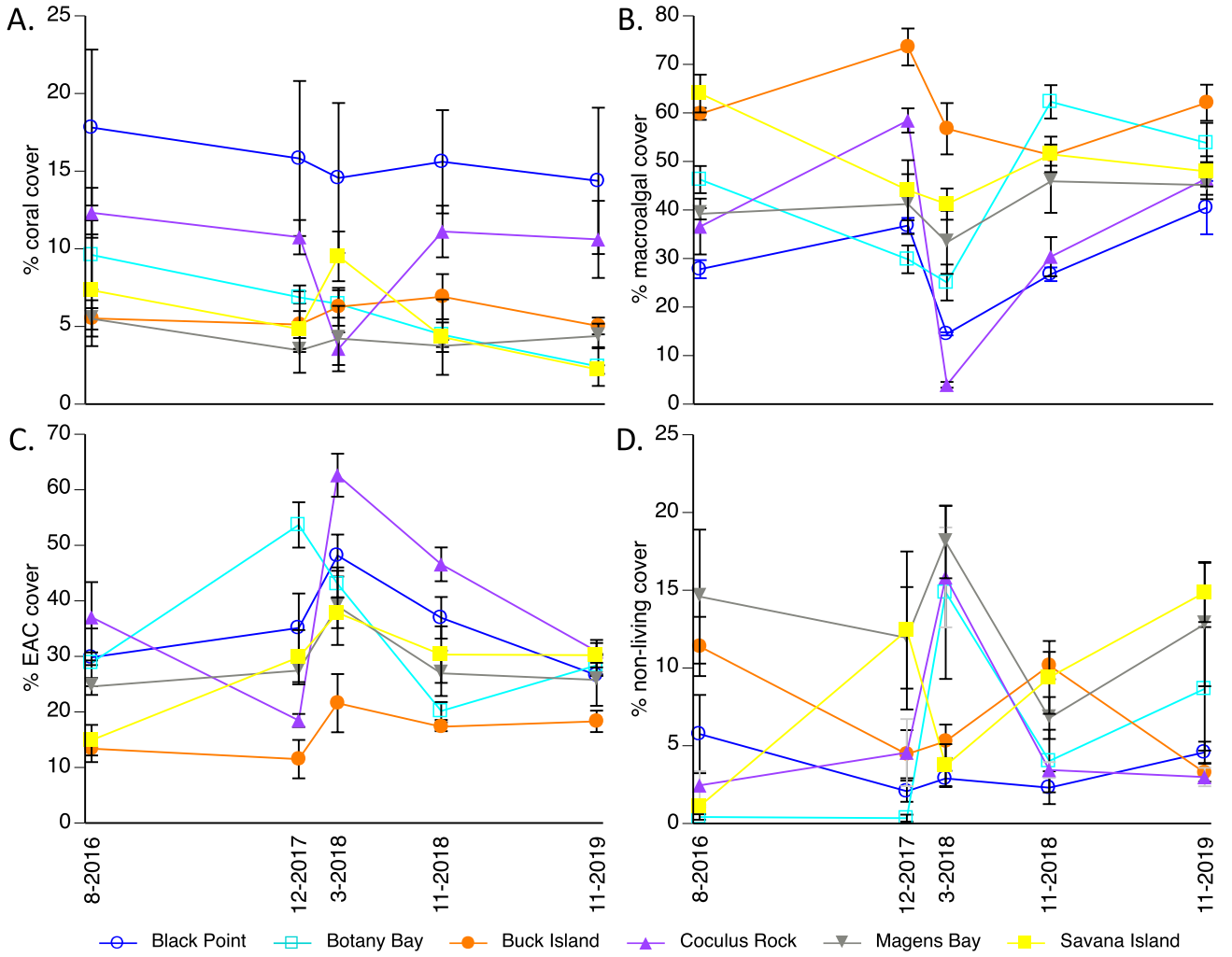

Fig. 7 Effects of storm damage and recovery on other major benthic categories in St. Thomas over time**.** Percent (±SE) cover at each site and date of benthic surveys in St. Thomas. **A**: corals, **B**: macoralgae, **C**: epilithic algae (EAC), and **D**: non-living substrata. Data based on three transects at each of six sites on St. Thomas pre-hurricanes (2016) and at four dates post-hurricanes. Post-hoc tests for interaction terms in Supplemental Table 3

macroalgal cover following the hurricanes (2017), with cover at some sites increasing (Black Point, Buck Island, Coculus Rock), decreasing (Botany Bay, Savana Island), or remaining nearly the same (Magens Bay). Across all sites combined, EAC cover increased by 25.8 ± 13.5% following the hurricanes (2017) and remained 22.7 ± 11.9% higher in 2019 relative to 2016 (Supplemental Fig. 11C). Within sites, there was an absolute change of 1.9–24.8% EAC cover following the hurricanes (2017), with cover at some sites increasing (Black Point, Botany Bay, Savana Island), decreasing (Coculus Rock), or remaining nearly the same (Buck Island, Magens Bay). Overall, the absolute cover of non-living substrata averaged 6.0 ± 1.5% across all sites pre-storms (2016) and 7.5 ± 0.7% post-storms (2017–2019). Due to low and variable initial values, this represents an increase of 164.6 ± 126.5% following the hurricanes (2017) and an expansion of 721.0 ± 378.9% in 2019 relative to 2016 (Supplemental Fig. 11D).

Discussion

Unprecedented extreme storm events, such as the back-to-back Category 5 hurricanes that impacted the U.S. Virgin Islands in September 2017, are becoming more likely under continuing climate change (Xi et al. 2023). Whereas several studies have evaluated the immediate, short-term impacts of hurricanes on coral reefs, few have monitored the same sites for recovery to pre-storm conditions over multiple years. Although sponges represent the most diverse coral reef phylum on Caribbean reefs (van Soest et al. 2012), many species are difficult to identify in the field, resulting in their frequent exclusion from reef surveys and monitoring programs (Schönberg 2015; Bell et al. 2017). Having pre-hurricane data on sponge communities at six sites around St. Thomas, USVI, provided us with the opportunity to examine both the short-term impacts of these storms on these communities, as well as evidence of recovery and early ecological succession over a two-year period. The sites exhibited different angles and degrees of wave action and different levels of embayment enclosure, providing different levels of protection and water flow that would affect storm impacts (Woodley et al. 1981), as well as larval availability, gene flow, species diversity and community composition.

Two years after the hurricanes, sponge communities at the six sites displayed a gradient of responses, from no recovery to some resilience, but none of the assemblages had returned to their pre-storm states (Fig. 6; Supplemental Fig. 9). Sponge communities at the nearshore sites (e.g., Botany Bay, Black Point, Coculus Rock, Magens Bay) were most similar to each other and less variable overall, whereas the offshore sites (e.g., Buck Island, Savana Island) differed from the nearshore sites and from each other across all time points. Based on the assemblage trajectories (Supplemental Fig. 9), there was no recovery to pre-storm assemblages at some sites (e.g., Black Point, Magens Bay), while the other sites were more variable over time and showed some evidence of returning to 2016 assemblages. However, March 2018 was an outlier at some of the exposed sites (Botany Bay, Coculus Rock, Savana Island), likely due to a winter storm with strong swell, that appears to have added another layer of disturbance onto these already impacted communities, and points to the difficulty in characterizing long-term trajectories from a limited number of timepoints. Overall, the absence of complete recovery to pre-storm assemblages suggests that resilience was limited over this two-year time period, and that succession was ongoing but varied by site and species. These results differed from those for reefs in Cozumel where Hurricane Gilbert only minimally damaged sponges and recovery was complete after 21 months (Fenner 1991). In contrast, models of the growth rates of massive sponges after Hurricane Allen in Jamaica estimated that they would take a minimum of 4–6 years to recover biomass to pre-storm levels (Wilkinson and Cheshire 1988). Both our results and those of more recent studies of hurricane effects on coral reefs point to longer post-hurricane recovery times and less resilience overall (Gardner et al. 2005, Jackson et al. 2014).

Evaluation of multiple metrics of sponge abundance across the six sites and over time revealed different responses. As observed on many Caribbean reefs (e.g., Maliao et al. 2008; Villamizar et al. 2014; Gochfeld et al. 2020; Hernández-Delgado et al. 2024), the percent cover of sponges on reefs around St. Thomas is low (ranging from 2 to 11% across all sites pre-storms). In the immediate months after the hurricanes, we observed an approximately 25% decrease in sponge cover across the six study sites in St. Thomas (Gochfeld et al. 2020), with similar or even greater declines reported for nearby Puerto Rico (Hernández-Delgado et al. 2024) and St. John, USVI (Edmunds et al. 2020). In St. Thomas, the greatest declines were at sites with higher initial sponge cover (Black Point, Buck Island), and there was little evidence of recovery for this metric, with sponge cover remaining depressed or declining further at all sites over time. Whereas percent cover is commonly used to report sponge abundance, this metric tends to underrepresent cryptic and upright sponges, the latter of which dominate Caribbean sponge assemblages numerically and/or in terms of biomass, while contributing little to planar coverage of the substrate (Wulff 2001; Kornder et al. 2021; Reverter et al. 2021). Sponge percent cover is also inherently dependent upon cover of other benthic constituents (e.g., macroalgae, epilithic algae and nonliving substratum). The cover of other constituents varied considerably over time and affected the availability of new substrate for sponge recruitment and the presence of competitors for space, potentially

resulting in allelopathy or overgrowth (Cárdenas et al. 2016; Slattery and Lesser 2021).

Sponge densities exhibited a range of impacts after Hurricanes Irma and Maria. There was no overall change in sponge density between 2016 and December 2017 (Gochfeld et al. 2020), except for a short-term decline at Coculus Rock and Savana Island, two sites highly exposed to wave action. However, subsequent surveys identified an increase in sponge density of 42.3 ± 9.3% across all sites from 2016 to July 2019 (22 months post-storms). This suggests that in addition to sponges that survived the hurricanes, some fragments may have re-attached, and new sponges were able to successfully establish, although with considerable variability among sites. In contrast, sponge communities around St. John suffered a 51% decline in density two months after the hurricanes (Edmunds et al. 2020), indicating that different methods for generating the data (i.e., in situ surveys in St. Thomas vs. extrapolated from photoquadrats in St. John), coupled with variations in structural complexity of the reefs, need to be considered. Other studies have reported variable changes in densities of specific species after hurricanes, with Cropper and DiResta (1999) reporting recovery of commercial sponges to pre-hurricane densities three years after Hurricane Andrew, while others showed that populations of specific sponge species varied in their recovery times among sites (Easson et al. 2013; Wulff 2013).

Sponge volume measured in situ varied by orders of magnitude across sites and even within quadrats at individual sites both before and after the storms, making this metric challenging to use for meaningful comparisons both spatially and temporally. Sponge volume was very low at the highly exposed Botany Bay and Savana Island sites, where many sponges were cryptic. Volume also varied considerably within Black Point, where some quadrats lost many upright sponges (i.e., *Aplysina cauliformis*), while other quadrats had low topography with smaller encrusting or low relief sponges that were less affected by the storms. Sponge volume in St. Thomas declined by nearly 25% post-storms, but gradually increased over the subsequent two years (+ 14.5% in 2019 compared to 2016), largely due to an increase at Coculus Rock. In contrast, sponge volumes at sites dominated by cryptic sponges with low initial sponge volume remained low. Sponge volume has been proposed as the most relevant metric for scaling metabolic processes, particularly for large emergent sponges (Wulff 2016; Reverter et al. 2021; but see Bell et al. 2017), but is very time-consuming to measure in situ and requires many assumptions if attempting to measure from photoquadrats. Thus, as suggested by others (e.g., Bell et al. 2017; Gochfeld et al. 2020; Kornder et al. 2021), the use of several metrics provided a more complete picture of hurricane impacts on the diverse sponge communities found on topographically complex reefs around St. Thomas.

The sponge communities on the reefs of St. Thomas are comparable or more diverse compared to other reefs in the Caribbean (e.g., Gochfeld et al. 2007; Villamizar et al. 2014; Easson et al. 2015; Stubler et al. 2015) and western Atlantic (Monteiro and Muricy 2004; Morais et al. 2024) from which similar quantitative data are available. We identified 148 sponge taxa in our 18 transects across five survey dates on six reefs in St. Thomas, whereas Edmunds et al. (2020) was only able to identify 23 taxa (plus 19 unidentified taxa) at six sites monitored using photoquadrats across 26 years in neighboring St. John. In a more direct comparison, Gochfeld et al. (2007) found 51 species in 45 m^2 in Bocas del Toro, Panama, relative to the 148 species in the same total area surveyed in St. Thomas. In St. Thomas, species richness increased slightly after the hurricanes (+ 7.5%), but this change was negligible compared to the 36% increase across all sites from 2016 to 2019. This indicated that the storms created opportunities for species to establish on reefs where they had not been previously detected, possibly due to increased larval transport (Battershill and Bergquist 1990; Segura-García et al. 2024), newly available substrate, and/or release from competition (e.g., Slattery and Lesser 2021). However, species richness varied among sites, with Black Point and Coculus Rock exhibiting higher species richness throughout the study period. Wulff (2006) showed an inverse relationship between resistance to damage from storm events and recovery success in sponges, suggesting that more resistant species may be disproportionately lost with greater numbers and intensities of storms. Thus, determinations of the response of sponge communities to environmental stressors need to include species identifications, morphologies and estimates of diversity in assessing the potential outcomes, rather than focusing solely on metrics such as percent cover, density, or volume.

Sponge morphology plays an important role in determining its ability to resist or recover from physical damage (Woodley et al. 1981; Wulff 2006; Ávila et al. 2011). Although encrusting/low relief sponges were numerically dominant (68%) on all reefs initially, the most apparent short-term impact of the storms was the loss of upright sponges (-22%), which was most dramatic at Black Point and Buck Island, where upright sponges were dominant pre-storms, and virtually no effect at Savana Island, where upright sponges were nearly absent. Upright sponges are particularly susceptible to breakage due to wave action, as evidenced by large numbers of loose fragments following the storms (Gochfeld et al. 2020). The fragments of rope sponges have the potential to reattach, although this is species-specific (Woodley et al. 1981; Wulff 1995, 2006), and remaining basal portions may regenerate (e.g., Fenner 1991). Whereas upright sponges did not recover to pre-storm levels over the two years post-storms, there appeared to be an increasing trend in 2019, suggesting that recovery

was underway. Upright branching sponges tend to grow rapidly and have been found to recover quickly following disturbances in some cases (Easson et al. 2013) but not others (Wulff 2013). Although live fragments and recovering wounds on remnant sponges were observed 2.5 months post-storms (Gochfeld et al. 2020), the extreme nature of this storm event may have caused an excessive amount of damage, reducing fragment retention and survival, and limiting the ability of these sponges to recover rapidly. The loss of upright sponges was offset by an increase in encrusting and, to a lesser degree, massive sponges after the storms. Encrusting/low relief sponges remained most abundant at all sites. Wulff (2006) found that encrusting sponges on a Jamaican reef suffered the least damage following Hurricane Allen, and characterized the observed damage as "battered", which typically healed within a week.

Of the 148 sponge taxa, the same eight species were the major contributors to dissimilarity among sponge communities between 2016 and 2017 (pre- to 2.5- months post-storms) and 2016–2019 (pre- to 22 month post-storms). These species showed varying responses to the storms and in their return to pre-storm levels. The encrusting sponge *Monanchora arbuscula* had the largest impact on temporal comparisons and was the most abundant species on the four nearshore reefs, although it remained rare at the offshore sites. Whereas *Mo. arbuscula* can occur in both encrusting and upright morphologies (Esteves et al. 2018), only the encrusting morphology was observed on the study reefs. This species remained rare at Buck Island, possibly because over 50% of the substrate was covered by macroalgae across all dates. The density of *Mo. arbuscula* increased steadily from 2016 to 2019 at Black Point and Magens Bay, and showed a net increase at Botany Bay and Coculus Rock. Little is known about the ecology of *Mo. arbuscula,* but it has the characteristics of a typical weedy species, being able to recruit and grow rapidly to take advantage of available space, although it is not possible to rule out abrasion-driven separation of individuals into multiple remnants as contributing to the increased density. Another encrusting sponge, *Chondrilla caribensis*, was most abundant at Black Point and increased over time, while remaining low at other sites. *Dictyonella funicularis,* a small, thin and loosely attached encrusting sponge that occurred almost exclusively at the offshore sites (Buck Island, Savana Island) pre-storms, was reduced to near-zero after the storms although it recovered to nearly pre-storm levels by July 2019. This suggests that either tiny remnants remained after the storms that could not be seen and potentially reattached, or that recruitment occurred at the same sites where the sponge had occurred pre-storms. *Agelas citrina/sventres*, although massive at other Caribbean locations, was generally cryptic in St. Thomas, restricted to crevices and overhangs. These two species occurred almost exclusively at highly exposed Botany Bay and Savana Island, where they increased in abundance over time. At sites where the upright branching species *Ap. cauliformis* occurred at higher density pre-storms, it declined significantly post-storms and only recovered to pre-storm densities at Buck Island. Despite earlier studies purporting rapid recovery of this species, predominantly from fragmentation (Wulff 2006), this species recolonized St. Thomas' reefs largely via larval recruitment (Segura-García et al. 2024). This indicates that extreme storm events may enhance genetic diversity in some sponge species, although the intense losses experienced by these populations following this extreme storm event appear to require longer than two years for recovery. The loss of these upright branching sponges is particularly important ecologically, as it reduces stabilization of reef substrata and three-dimensional structure, which affects fish diversity and abundance (Wulff 2001; Bell et al. 2023). Life history information is lacking for many sponge species, making it difficult to determine how sponge communities will respond to perturbations of this magnitude, especially as we now understand that responses are largely species-specific and not broadly generalizable (e.g., Wulff 1995, 2006, 2013). Nonetheless, as previously noted (e.g., Wulff 2006), different upright branching sponges exhibit different levels of resilience to storm damage, as exemplified by *Am. compressa,* whose density did not change significantly over the course of the study, thereby showing a remarkable level of tolerance to these extreme events.

Large disturbances, including hurricanes, have the potential to provide rare sponge species with opportunities to colonize reefs, through increases in available space for larval settlement and/or removal of potential competitors (Hughes and Connell 1999; Arnold et al. 2010; Brandt et al. 2019). We predicted that rare species would become more abundant following the hurricanes, which could increase diversity in the community over time. Since this study only followed these communities for two years post-storms, it is not possible to determine whether these rare species will persist or eventually be lost to superior competitors or other disturbances. Although by definition uncommon, these rare species are thought to disproportionately contribute to the functional ecology of the species assemblage, particularly when undergoing rapid environmental transitions (Mouillot et al. 2013; Leitão et al. 2016). Thus, metrics such as sponge cover, density, or volume are unlikely to sufficiently represent the functionality of the sponge assemblage. By dividing the sponge community into four groups based on their abundance over the entire study period, we found that rare taxa (1–2 individuals per species over the five survey periods, n = 41 species) remained stable through March 2018, but were recorded much more frequently in the Nov. 2018 and July 2019 surveys (representing 25 and 38.5% of sightings on those dates, respectively). Semi-rare species

(3–10 individuals overall) increased in March and Nov. 2018 and then declined, whereas more abundant species increased over time. This suggests that rare sponge species were able to become established after the storms. However, due to the high spatial and temporal variability in cover of all benthic constituents, including nonliving substratum suitable for settlement, it is difficult to attribute this directly to space availability or release from competition following the storms. Competition and potential allelopathy from remaining sponges could prevent sponge (or coral) recovery or inhibit larval settlement and recruitment (Brandt et al. 2019; Slattery and Lesser 2021). However, the fact that recovery to pre-storm conditions had not been observed by two years post-storms implies that succession may have been ongoing. Variability among sites and species indicates that changes to the sponge community, including an increase in overall diversity and in rare species specifically, could preclude a return to pre-storm conditions.

In addition to the 2018 winter storm that particularly affected our exposed sites, other disturbances may have contributed to the low resilience at some of the study sites. In early 2019, stony coral tissue loss disease (SCTLD) was first reported in St. Thomas, and by our 2019 sampling dates, the disease was already affecting Black Point and Savana Island (Brandt et al. 2021). Coral cover on these reefs was already low (9.7% overall) prior to the 2017 storms, due to bleaching, disease and earlier storm events (Smith et al. 2016). However, coral cover declined by 21% overall post-storms, and continued to decline so that live coral cover was only 6.5% in 2019. The greatest overall loss of coral cover occurred at Botany Bay, a site unaffected by SCTLD at the time of our last survey, but with substantial overgrowth of macroalgae and a peyssonnelid alga crust (PAC) (i.e., PAC in Edmunds et al. 2019b; *Ramicrusta* spp. in Wilson et al. 2020; *Ramicrusta textilis* in Hollister et al. 2021). Particularly prevalent at Savana Island and Buck Island, PAC frequently overgrows corals, octocorals and sponges (Eckrich and Engel 2013, Edmunds et al. 2019b, Smith et al. 2020, Hollister et al. 2021). Coral losses have continued with the proliferation of PAC and as SCTLD has progressed around the entire island of St. Thomas and most of the Caribbean. Deterioration was further compounded by a severe bleaching event in 2023, so understanding the resilience of sponges, which provide many similar ecosystem services as corals (Bell et al. 2023), is vitally important.

We expected that nonliving substrate (i.e., boulder, pavement, rubble, sand) would increase after the hurricanes, providing opportunities for sponge growth and colonization and the proliferation of rare species. Nonliving substrate was relatively sparse overall and did not increase dramatically post-storms, possibly due to breakage and movement of reef structure away from transects due to high swell. A larger increase in nonliving substrate was noted starting in March 2018, when rare sponges also increased in abundance (Fig. 5). Macroalgal cover, particularly by *Dictyota* spp., was high pre-storms and increased (+ 10.6%) post-storms, as did the epilithic algal community, although there was variability among sites. Competition from algae with other benthic taxa (e.g., sponges, corals) due to shading, scour, and/or allelopathy could have prevented the recovery and growth of sponges and/or corals, or inhibited their larval settlement and recruitment (e.g., Hughes 1994; Kuffner et al. 2006; Cárdenas et al. 2016).

As climate change accelerates, increasing storm intensity and duration, associated precipitation and changes in traditional storm tracks are occurring (Balaguru et al. 2023), amplifying the likelihood of comparable events on Caribbean reefs in the future. Excessive storm precipitation increases runoff, turbidity, pollution and eutrophication (Browning et al. 2019; Edmunds et al. 2019a; Takesue et al. 2021), most heavily impacting nearshore sites. In addition, recurring mass coral bleaching events due to rapid ocean warming, along with widespread coral disease outbreaks, have continued to take their toll on Caribbean coral reefs. The effects of increased seawater temperature on sponges (e.g., Strano et al. 2022) have been less well studied than on corals, and while certain species can tolerate elevated temperatures, interspecific variability in both lethal and sublethal effects have been observed (reviewed in Carballo and Bell 2017). Diseases are well known to have reduced coral cover, but also affect sponges (reviewed in Webster 2007), and storms have the potential to reduce sponge disease by decreasing sponge biomass (e.g., *Aplysina* Red Band Syndrome in *Ap. cauliformis*.; Easson et al. 2013), but could also spread disease via the movement of affected fragments. In addition, the effect of SCTLD or other coral diseases on sponges or their assemblages remains unknown. Longer-term detailed studies of sponge assemblages are needed to evaluate resilience under changing environmental conditions. For coral reefs, it appears that as the frequency and intensity of storms and other environmental stressors increase, the potential for resilience and recovery is reduced.

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Author contributions Deborah J. Gochfeld (DJG), Julie. B. Olson (JBO), and Marilyn E. Brandt (MEB) conceptualized the study, obtained the funding, administrated and supervised the project, completed the visualization of the study and wrote the original manuscript. DJG, JBO, and Tyler B. Smith (TBS) established the methodology. DJG, JBO, Andia Chaves-Fonnegra (ACF), Rosmin Ennis (RE), and M. Cristina Diaz (MCD) conducted the investigation. DJG, JBO, MBE, TBS and RE performed the data curation. DJG, MEB, and ACF performed the data analysis. All authors reviewed the manuscript.

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Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Data availability All data with associated metadata are available at https://www.bco-dmo.org/project/749384 except for sponge species list and abundance by transect with assigned morphotypes (Supplemental Table 1).

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