ORIGINAL PAPER

A quarter-century of variation in sponge abundance and community structure on shallow reefs in St. John, US Virgin Islands

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Abstract

This study tested the hypothesis that sponge assemblages on the reefs of St. John, US Virgin Islands (18.315°N, 64.716°W), changed from 1992 to 2017. Sponges were identified to species or genus in photoquadrats and were quantified at 2–3 y intervals by density, with linear dimensions used to estimate volume as a proxy for biomass. From 1992 to July 2017, overall sponge density (pooled among taxa) increased, although trends varied among the most common species for which density increased (four species), decreased (one species), or showed no linear relationship with time (2 species). Hurricanes Irma and Maria caused a 51% decline in overall sponge density from July to November 2017, with density in November 2017 being 31% lower than in 1992. For the common sponges, densities of 6 declined by 82–100% between July and November 2017, but densities in November 2017 were 13–736% higher than in 1992 for four species, and 47–100% lower than in 1992 for 3 species. Sponge volume did not change linearly between 1992 and November 2017, but it was reduced by 54% following the hurricanes. Multivariate variation over time in benthic community structure was not strongly associated with sponge density alone, although a significant association with rainfall highlighted the potential roles of this environmental factor in directly, or indirectly, mediating changes in community structure. Overall, the mean density of sponges, as well as most of the common sponge species, trended upwards prior to the hurricanes, but these trends reversed following the storms.

Introduction

The plight of coral reefs continues to attract scientific (Hughes et al. 2010) and popular (Braverman 2018) attention as they transition from the condition in which they were described in the 1950s and 1960s (Goreau 1959; Loya 1972), to what may be their ecological demise (Veron et al. 2009; Pandolfi 2015). Many of their functional properties rely on the high abundance and rapid growth of the foundation taxon, scleractinian corals (Alvarez-Filip et al. 2011; Wild et al. 2011), which have remained the focus of time-series

analyses of benthic reef communities for decades (e.g., Jackson et al. 2014). This focus has left the population dynamics of many other animals understudied, making it challenging to evaluate the extent to which coral reef ecosystems are changing.

There is a rich history of describing the biodiversity of coral reefs (Connell 1978; Huston 1985), but apart from fishes, corals, and macroalgae (Bruno et al. 2009), many groups have not prominently featured in coral reef monitoring. There are exceptions to these trends, for example, including the Caribbean echinoid *Diadema antillarum* (Lessios 2016), the Indo-Pacific asteroid, *Acanthaster planci* (Moran 1986), macroalgae (McCook et al. 2001; Bruno et al. 2009), and in a few locations, Caribbean octocorals (Ruzicka et al. 2013; Lenz et al. 2015), sponges (Stevely et al. 2011; Wulff 2006a, 2013, 2016; Rovellini et al. 2019), and microbes (Glasl et al. 2017). A consequence of the taxonomic restriction of most analyses of coral reefs is a limited ability to place present-day reef communities in an historic context. The past is the key to understanding the future (Jackson 2007; Precht and Miller 2007), and for coral reefs, their historic community structure is critical to evaluating the ecological implications of their present condition

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Communicated by D. Gochfeld.

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(Jackson 1997; Cramer et al. 2012; McClenachan et al. 2017), their ecosystem functionality (Wild et al. 2011), and the capacity of contemporary species assemblages to persist over coming decades.

The issue of limited historic data is acute for sponges on Caribbean reefs. Although sponges were identified as functionally important with respect to filtering seawater in the earliest years of quantitative studies of coral reefs (Reiswig 1971a,b, 1972, 1973), and many additional functional roles have subsequently been identified (e.g., Wulff and Buss 1979; Wulff 1984; Diaz and Rützler 2001; Pawlik and McMurray 2020), sponges have been overlooked in most reef monitoring programs (Bell 2008; Wulff 2001, 2016). As a result, the historic context for present day patterns of variation in sponge abundance is sparsely populated with data (Wulff 2016). Lack of time-series information, use of ecological techniques that are appropriate to quantify corals or sea urchins, but poorly suited to evaluating the abundance of sponges, and a focus on a limited subset of sponge species, have encouraged interpretation of limited, and often equivocal, data as evidence that sponges are generally increasing in abundance on coral reefs (Bell et al. 2013; Pawlik and McMurray 2020).

In the Florida Keys, for example, the giant barrel sponge, *Xestospongia muta* increased in population density (numbers of individuals) from 2000 to 2006, yet the summed volume of this species ($cm^3 m^{-2}$) did not change (McMurray et al. 2010). In the same location, Maliao et al. (2008) reported a "phase-shift" to algal and sponge domination, but the cover of sponges was 2.2% at the start of their study, it dipped to 1.3–1.9% during the 4 years of monitoring, and then rose to 2.2% at the end of their study. The densities of 3 sponge species on the shallow coral reefs of St. John have also been reported to increase from 1992–2007 (Colvard and Edmunds 2011), but these taxa are branching or encrusting forms that readily fragment to produce new individuals without increasing biomass. In the central sector of the shelf lagoon of Belizean barrier reef, Aronson et al. (2012) described the rapid spread of *Chondrilla caribensis* over dead coral skeletons from 1999–2006, but the cover of this sponge declined > 50% from 2006–2009. On the fore reef of a portion of the Belizean barrier reef (at Carrie Bow Cay), Villamizar et al. (2014) reported "an expansion of the sponge community in 1995–2009", but the 2.6% cover of sponges measured in 2009 is within the range of sponge cover reported 15 y before in the same zone (i.e., 1.4–3.3%). In Curaçao and Bonaire, sponge cover at 20–40 m depth increased over 40 y (1973–2013), but the overall mean cover (at 10–40 m depth) increased from only 0.5% to 2.3% (de Bakker et al. 2017).

Not all long-term studies of sponge communities have concluded that sponges are increasing in abundance. In the few Caribbean locations where entire sponge faunas have been quantified with species resolution over lengthy periods, the results consistently have revealed fluctuations and declines in sponge biomass and diversity in the last 10–20 years, sometimes through mass mortality events. In the Florida Keys (Marathon and Long Keys) between 1991 and 1993, sponge abundances declined by 45–69%, and sponge biomass declined by 88–93% due to blooms of cyanobacteria (Stevely et al. 2011). In Kuna Yala, Panama, 44% of the sponge species and 41% of their summed volume were lost from 1984 to 1998 (Wulff 2006a). Finally, on a shallow Belizean reef that was surveyed over 6 years, 49% of the summed sponge volume was lost during a mortality event of unknown cause in 2008, and 3 years later, 27% of the sponge individuals, and 71% of their summed volume, were lost during a cyanobacteria bloom (Wulff 2013).

Relative to other taxa on Caribbean reefs, the difficulties of identifying and quantifying sponges have deterred their inclusion in monitoring projects. These difficulties arise from: (1) the challenges of identifying sponges to species, (2) the high species diversity of sponges, with 945 described species in the tropical western Atlantic (van Soest et al. 2012), (3) the huge variation in shape and size of sponges on all scales of investigation (within species, among species, over space, over time), and (4) the large amounts of time underwater required to measure the volume of individual sponges, the abundance metric by which most of their functional roles scale (Rützler 1978; Wulff 2001, 2009, 2013, 2016). The difficulties of enumerating sponges are intensified when the source of information is image-based, as is common in coral reef monitoring. Planar images provide an imperfect tool for reconstructing the abundance of taxonomically challenging and morphologically complex organisms, but they provide one of the few tools available for historic reconstruction of coral reef community structure (Lenz et al. 2015; Edmunds and Lasker 2016; Tsounis and Edmunds 2017). Many of these issues (e.g., challenges in identifying species by color, size, and shape, and limitations in evaluating abundance based on planar area) are unlikely to be resolved using planar photoquadrats of reef surfaces, but under standardized conditions including records of the same reef area, planar photoquadrats can serve as an assay for sponge abundance.

The present study focuses on the abundance of sponges on the shallow coral reefs of St. John, US Virgin Islands, which have been monitored for decades (Rogers et al. 2008; Edmunds 2000, 2019). On the benthos, one of the most comprehensive projects has focused on scleractinians, *Millepora* spp., macroalgae, and a combined category of crustose coralline algae, bare space, and algal turf (i.e., CTB) (Edmunds 2013, 2019), but starting in 2012, the study was expanded to include octocorals (Lenz et al. 2015). The decadal history of octocoral abundance in this location has been reconstructed using photoquadrats (Lenz et al. 2015; Edmunds and Lasker

2016; Tsounis and Edmunds 2017), and in-water surveys are supporting species resolution (Tsounis et al. 2018). These analyses suggest that the shallow reefs have undergone a cryptic regime change (sensu Hughes et al. 2010) favoring octocorals, with this transition associated with climate variation that includes changes in rainfall (Edmunds and Lasker 2016). Here, we expand the taxonomic breadth of previous analyses by focusing on sponges to address four objectives: (1) testing the hypothesis that sponges have changed in abundance since 1992 and, assuming this hypothesis is supported, (2) testing whether sponge taxa responded uniformly to environmental conditions, (3) re-evaluating the long-term trends in community structure on these reefs (e.g., Edmunds and Lasker 2016; Edmunds 2019) through an analysis combining sponges (this study), scleractinians, octocorals, macroalgae, and CTB (as in Edmunds and Lasker 2016), and (4) testing for statistical associations between environmental conditions and changes in sponge assemblages and holistic benthic community structure.

Materials and methods

Sponge abundance was determined using photoquadrats recorded annually since 1992, but here they were sub-sampled by years scattered uniformly across the 26 year study (described below). These photoquadrats are part of a time-series that was designed to quantify the coral community (Edmunds 2013, 2019). The project consists of 6 sites on hard substrata at 7–9 m depth that was randomly selected in 1992, permanently marked and recorded using photo-quadrats (0.5 × 0.5 m) positioned randomly along a single transect at each site. Photoquadrats were recorded in May 1992, June 1993, August 1994, May 1995–1997, and July or August thereafter. Prior to 2000, ~ 18 photoquadrats site^{-1} were recorded annually using 35-mm film (Kodachrome 64), but from 2000, ~ 40 photoquadrats site^{-1} have been recorded using digital cameras ranging in resolution from 3.3 MP to 36.3 MP. Cameras were fitted with 2 strobes (Nikonos, SB 105), and color slides were scanned (4000 dpi) for analysis.

Definitive identification of Caribbean sponges requires analysis of spicules and other skeletal characteristics (Rützler 1978). As this was impossible with photoquadrats, a consensus set of 23 sponges was identified using expert opinion. This set resolved 19 species, 3 sets of congeners that could not be distinguished to species, and an unknown category (Table S1). Most sponges were identified to species (66%, n = 9608 pooled over the whole study), 4% were identified to genus, and 31% were assigned to the "unknown" category. Surveys on the adjacent island of St. Thomas suggested the total sponge diversity includes over 100 species (Gochfeld et al. 2020). Between 100 and 300 sponge species is typical for a localized area in which multiple sites

are combined (Wulff 2016), with individual Caribbean sites being characterized by 51–67 species (Villamizar et al. 2014; Wulff 2006b, 2013).
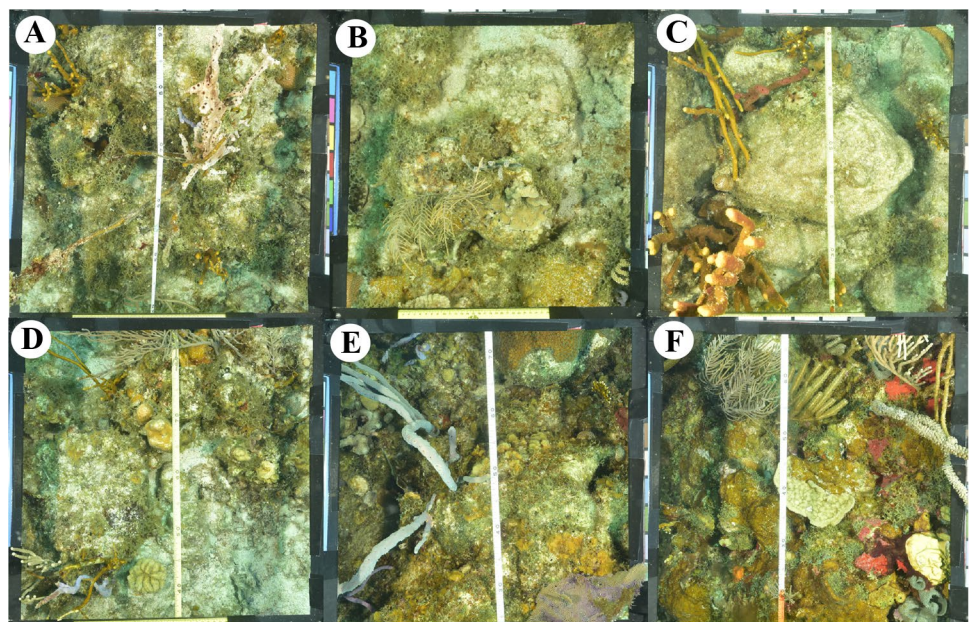
To evaluate sponge density, photoquadrats were opened in Adobe Photoshop CS5.1 software, and the number of sponges counted. Individuals were defined by their contiguous areas of sponge biomass, which were separated from other sponges of the same taxon. This method potentially overestimates sponge density where algae, other taxa, or topographically complex surfaces obscured connections among pieces of a contiguous sponge. The limitations of planar photographs in quantifying benthic communities have been inherent in the method since it was first used in modern ecology (Loya 1972). These issues are unavoidable with planar images, but their magnitude depends on the quantity of macroalgae and the rugosity of the benthic surfaces. With regard to rugosity, the study sites were located on carbonate pavement (RS11, 5), or igneous substrata (RS15, 2), or a combination of the 2 (RS9, 6) (Fig. 1), which provided relatively smooth surfaces with limited ability to obscure sponges (Fig. 2). Analyses of rugosity at Europa Bay (RS11) and East Cabritte (~ 500 m from RS2) in 2014 revealed that the mean (± SE) topographic complexity at ~ 8 m depth was 1.16 ± 0.02 and 1.22 ± 0.02, respectively (Tsounis et al. 2018). The values for topographic complexity from St. John describe relatively flat communities (Fig. 2) that correspond to 40 year minimal values across the Caribbean, where rugosity declined from ~ 2.5 in 1969 to 1.2 in 2008 (over a depth range from the surface to > 20 m) (Alvarez-Filip et al. 2009).

Evaluating the ecological importance of sponge density (i.e., sponges per area) requires measurements of sponge biomass (Wulff 2001, 2016), which are unobtainable from planar photographs. However, sponge biomass can be estimated from sponge volume calculated from linear dimensions and the volumetric formulae of geometric shapes matching those of the sponges (after Wulff 2001). We sought approximations of sponge volumes using photoquadrats, assuming that the shape of each sponge could be inferred from a planar image and volumetrically approximated by geometric shapes (i.e., rods, disks, and spheres). The volumes of these shapes were estimated using linear dimensions obtained from the photographs using ImageJ software (Abramoff et al. 2004). In the few cases where sponges were conical (e.g., *Ircinia campana*), it was not possible to accurately estimate their volume and they were excluded from the analysis. As *I. campana* accounted for only 1% of all sponges, the bias attributed to this affect was trivial. The volume of encrusting sponges was estimated assuming they were disks 1.7-mm thick (based on the mean thickness of 1.7 ± 0.2 mm (± SE, n = 23) of the encrusting sponges *Chondrilla caribensis* forma *hermatypica, Spirastrella coccinea, S. hartmani, Clathria venosa, Placospongia* cf. *intermedia, Acarnus nicoleae,* and *Cliona caribbaea* selected at random

Fig. 1 Map of St. John showing the location of the 6, randomly selected (RS) sites on the south shore between Cabritte Horn and White Point. RS15 = White Point, RS11 = Europa Bay, RS9 = West Little Lameshur Bay, RS5 = Neptune's Table, RS6 = East Tektite, RS2 = Cabritte Horn, and *= location of the Virgin Islands Environmental Research Station
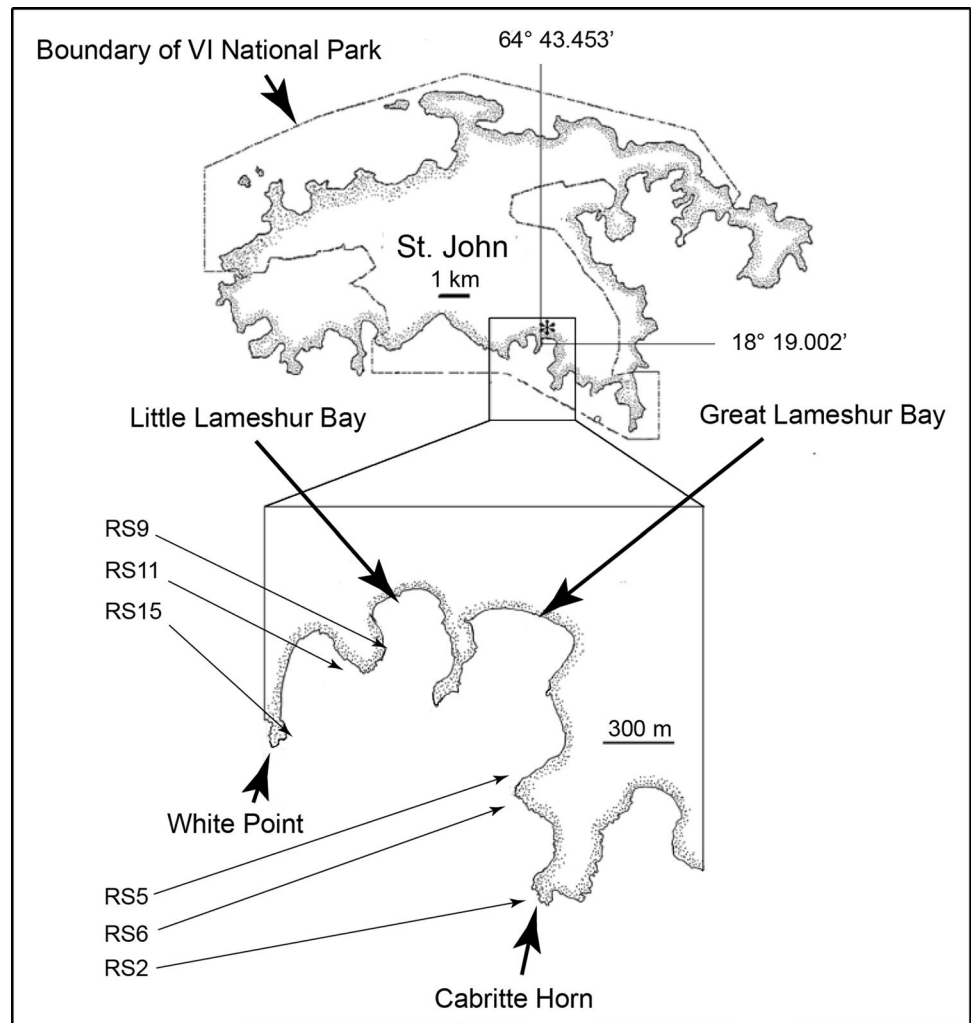
Fig. 2 Representative photoquadrats from the 6 sites (Fig. 1) in July 2017. **a** RS15, **b** RS 11, **c** RS9, **d** RS5, **e** RS6, and **f** RS2. Quadrat framer in all images is 0.5 × 0.5 m. Images show the low topographic complexity of the study reefs, with mean values of 1.16 at RS11 and 1.22 on the eastern side of Cabritte Horn (similar to RS2) (Tsounis et al. 2018)

for measurement in shallow water on the reefs of Belize during May 2019). Sponge volumes were summed by genus within each quadrat to provide a single replicate measure.

To measure sponge density and volume in the ~ 5000 photoquadrats from 1992 to 2017, the 26 year record was analyzed in 2–3 year intervals. All 6 sites were analyzed for sponge density, but 3 sites (White Point, Cabritte Horn, and Europa Bay) were selected to estimate sponge volume. The sites for volume estimates were selected to span the range of sponge abundances observed along this shore and to provide a tractable task commensurate with the limited capacity to estimate organism volume from planar images.

Physical environmental conditions

As part of the ecological monitoring in this location (Edmunds 2013; Edmunds and Lasker 2016), seawater temperature and rainfall have been recorded since 1989. The records from 1990 to 2017 were used to explore their capacity to account for variation in multivariate sponge assemblage structure, as well as the multivariate community structure defined by sponges, scleractinians, octocorals, macroalgae, and CTB. Seawater temperature was recorded at ~ 9–14 m depth at Yawzi Point using Hobo loggers [± 0.2 °C (U22-001, Onset Computer Co., MA)] that sampled every 10–15 min. Records were collapsed by day and used to calculate annual summaries of mean temperature, minimum temperature, maximum temperature, the number of hot days (i.e., > 29.3 °C), and the number of cold days (i.e., ≤ 26.0 °C). From 1992 to 2011, rainfall (cm y^{-1}) was obtained from the Southeastern Regional Climate Center (https://www.sercc.com), which compiled data from a rain gauge in Cruz Bay (Station 671980). Where this record was incomplete, values were obtained from Catherinburg (Station 671348), East End (Station 672551), or a mean value for the missing months calculated from all other values for that same month (in Edmunds and Gray 2014). From 2012, rainfall was measured using a Standard Rain Gauge (NOAA, National Weather Service) deployed on the north shore of St. John (18° 21′ 20.95 N, 64° 45′ 57.53 W). Temporal variation in the regional-scale physical environment was evaluated through a de-trended index reflecting the effect of the Atlantic Multidecadal Oscillation (AMO) as reported in Kajtar et al. (2019) and provided courtesy of the first author. Hurricane effects were evaluated on a categorical scale assigning impact values to storms of 0 (no storm), 0.5 (minor impacts), and 1 (major impacts), and summing impacts within each year (after Gross and Edmunds 2015).

Statistical analysis

Statistical analyses were completed using sites as replicates, with each site characterized by a density of sponges (pooled among taxa and for each taxon) averaged among quadrats by year, and compared among years using ANOVA with n = 6 sites. Linear relationships between sponge density (pooled among taxa and for each taxon) and time (1992 to July 2017) were tested using least squares regression. The statistical analysis of sponge volume was restricted to an exploratory investigation in which volume (pooled among taxa) was compared among samplings using a one-way PERMANOVA with n = 3 sites. More comprehensive analyses of volume were not completed because of the limitations of estimating sponge volume from planar images.

Multivariate sponge assemblage structure was described using 2-D ordination prepared with non-metric multidimensional scaling (NMDS), in which densities averaged by taxon (Table S1) and site within each year provided the raw data. Densities were $\log(x + 1)$ transformed and prepared as a resemblance matrix using Bray–Curtis dissimilarities. Analyses were completed with 100 restarts until stress stabilized at < 1.0. The influence of each taxon in creating differences among years was evaluated from Spearman correlations of density against each NMDS axis, with the results displayed in a vector plot.

To place the dynamics of the sponge assemblages in a larger ecological context, sponge densities were combined with data from the same sites and quadrats that describe the abundance of scleractinians, octocorals, macroalgae, and CTB [see Edmunds (2013) and Edmunds and Lasker (2016)]. In brief, the cover of scleractinians, macroalgae and CTB was determined using CPCe (Kohler and Gill 2006) or CoralNet [with manual annotations (Beijbom et al. 2015)] in which 200 randomly-located dots were superimposed on each image, and the number falling on each substratum category was counted. Scleractinians were resolved to the lowest taxonomic level, which consisted of a combination of species and genera, and macroalgae and CTB were resolved as functional groups. Octocorals were counted by colony with genus resolution, with colonies scored if their holdfasts were visible in each quadrat. As with the sponge analysis, the densities of scleractinians, octocorals, macroalgae, and CTB were averaged by site and year, with years matched to the temporal regime sampled for sponges (described above). The compiled data were standardized to a common scale, and square-root transformed prior to preparing a resemblance matrix by Bray Curtis dissimilarities. The resemblance matrix was used to create a 2-D ordination by NMDS, and the influence of the dependent variables on the spatial clustering explored through Spearman correlations.

The BEST procedure in PRIMER (Clarke and Gorley 2006) was used to evaluate the extent to which community structure (for sponges alone, and the holistic community) was associated with physical environmental conditions. The BEST procedure is based on rank correlations (ρ) between the resemblance matrix defining the community structure

and a suite of resemblance matrices defining physical conditions. Where community structure included variables measured on multiple scales, values were standardized and square-root transformed. Environmental data were standardized and square-root transformed, and collinear variables excluded. Resemblance matrices were prepared using Bray Curtis dissimilarities (biotic data) or Euclidean Distances (physical conditions).

To evaluate associations between biotic and physical data, analyses were conducted first, with data obtained in the year of measurement, then with a phase lag of physical data relative to biological data. The phase lag allowed a test for a delay in the response of community structure to environmental conditions 1 y earlier, 2 y earlier, and averaged over the 3 y starting with the measurement year and extending back 2 y. Significance of ρ was determined within a permutational framework (999 permutations) as the probability of occurrence by chance alone (P_{perm}).

Statistical analyses were completed using PRIMER version 6 (Clarke and Gorley 2006), which was operated within a Windows 7 environment on a Mac PC.

Results

Overview

Sponges were common in the photoquadrats, but substantial numbers of photoquadrats (6–34% by year, n = 102–248 y^{-1}) contained no visible sponges in all years analyzed. Overall, 23 taxa were resolved, but species diversity was higher (see Gochfeld et al. 2020) because of the unidentified individuals that were combined in an "unknown" group (Table S1). Together, these taxa represented 19 species, and a group of seven species accounted for 54.6% of all sponges (n = 9608 sponges in 2344 quadrats pooled among sites and years): 14.6% were *Aplysina fulva*, 4.9% were *A. cauliformis,* 17.5%

were *Monanchora arbuscula,* 4.5% were *Aphimedon compressa,* 6.2% were *Niphates digitalis,* 4.6% were *N. erecta,* and 2.4% were *Cliona delitrix*. Sponges were absent in 34% (the highest incidence, n = 241) of photoquadrats in November 2017, and 6% (the lowest incidence, n = 239) of photoquadrats in 2014, but for photoquadrats in which sponges were present, densities ranged from 1–23 sponges 0.25 m^{-2} in 1992, and from 1–17 sponges 0.25 m^{-2} in July 2017, just before Hurricanes Maria and Irma. In 1992, 6% of the photoquadrats (n = 102) contained $\geq$ 10 sponges, and in July 2017, 7% of the photoquadrats (n = 234) contained $\geq$ 10 sponges.

The volume of most sponges was estimated assuming they were disks (54%, summed over all sites and years, n = 5913 sponges), 27% as spheres, and 19% as rods (Table S1). Summed sponge volumes averaged by site and year ranged from 17 cm^3 0.25 m^{-2} (RS11 in November 2017) to 528 cm^3 0.25 m^{-2} (RS15 in 2009) (mean = 233 $\pm$ 25 cm^3 0.25 m^{-2}, n = 36).

Sponge abundance

Mean sponge density (pooled among taxa, $\pm$ SE, n = 6 sites) in 1992 was 3.23 $\pm$ 0.99 sponges 0.25 m^{-2}, it reached 4.52 $\pm$ 0.53 in July 2017 (just before Hurricanes Irma and Maria), and between these dates the minimum density was 2.80 $\pm$ 0.67 sponges 0.25 m^{-2} (2002), and the greatest density was 6.49 $\pm$ 0.85 sponges 0.25 m^{-2} (Fig. 3). Sponge density in July 2017 was higher than in seven of the previous 10 years that were analyzed, but four months later and 2 months after Hurricanes Irma and Maria hit St. John (September 2017), density had declined to 2.19 $\pm$ 0.66 sponges 0.25 m^{-2}. The density of all sponges (pooled among taxa) significantly differed among years, as did the densities of *Aplysina fulva*, *Aplysina* spp. *Cliona delitrix*, *Mycale laevis*, *Niphates erecta*, *Verongula rigida*, and *Verongula* spp. (Table 1, Fig. 4). The density of all sponges (pooled among taxa), as well as for seven taxa, were linearly related to time

Fig. 3 Mean ($\pm$ SE) sponge abundance in St. John between 1992 and 2017 based on density (left ordinate) and volume (right ordinate) for 6 sites (density) or 3 sites (volume, RS15, RS2, and RS11). Values are plotted against sampling month located on a continuously distributed time axis, separated by year; volume is offset on the abscissa for clarity. The annual photographic record from the study sites was analyzed in 2-3 year intervals. Grey bars show disturbances: *H* hurricanes, *B* bleaching, *S* storms
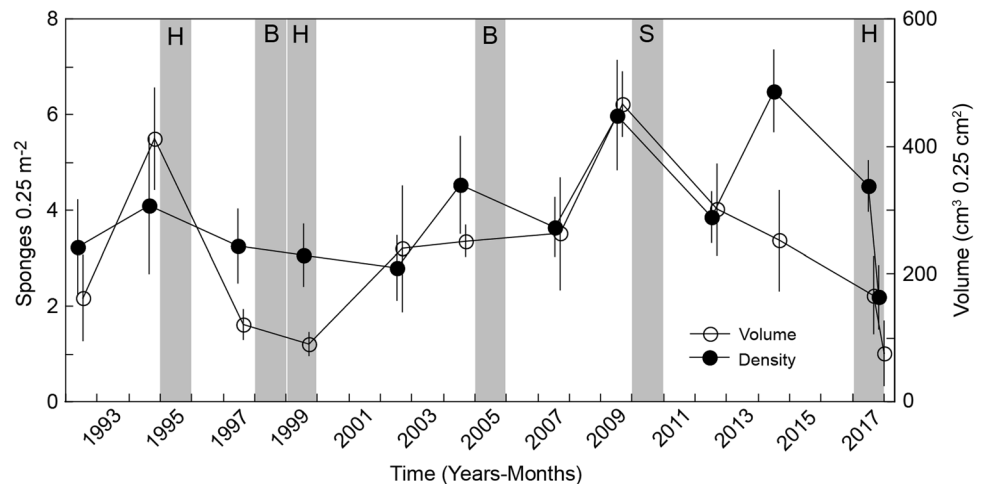
Table 1 Statistical contrasts of sponge abundances (sponges 0.25 m^{-2}) over time

Long-term trend	Taxon	Among years	Linear 1992–7/17	7/17 vs 11/17	1992 vs 11/17
Increasing	Pooled taxa	$F=2.160$, **$P=0.029$**	$F=5.311$, **$P=0.047$**	⇓ 51%	⇓ 31%
	Amphimedon compressa	$F=1.450$, $P=0.175$	$F=7.949$, **$P=0.020$**	⇓ 84%	⇑ 13%
	Aplysina cauliformis	$F=1.859$, $P=0.064$	$F=22.612$, **$P=0.001$**	⇓ 70%	⇑ 22%
	Aplysina fulva	$F=3.603$, **$P=0.001$**	$F=112.423$, **$P<0.001$**	⇓ 82%	⇑ 736%
	Aplysina spp.	$F=2.757$, **$P=0.006$**	$F=7.954$, **$P=0.020$**	⇓ 69%	n/a
	Niphates digitalis	$F=1.087$, $P=0.387$	$F=7.973$, **$P=0.020$**	⇓ 36%	⇑ 21%
Decreasing	*Cliona delitrix*	$F=6.481$, **$P<0.001$**	$F=12.665$, **$P=0.006$**	⇓ 100%	⇓ 100%
	Ircinia strobilina	$F=1.691$, $P=0.097$	$F=10.467$, **$P=0.010$**	⇓ 24%	⇓ 64%
No Trend	*Aiolochroia crassa*	$F=0.947$, $P=0.503$	$F=1.146$, $P=0.312$	⇓ 92%	⇓ 86%
	Callyspongia fallax	$F=0.839$, $P=0.603$	$F=0.069$, $P=0.799$	⇓ 2%	n/a
	Chondrilla caribensis	$F=0.738$, $P=0.698$	$F=1.323$, $P=0.280$	n/a	⇓ 100%
	Desmapsamma anchorata	$F=1.787$, $P=0.076$	$F=1.522$, $P=0.249$	⇓ 93%	n/a
	Ectyoplasia ferox	$F=1.060$, $P=0.408$	$F=0.005$, $P=0.947$	n/a	⇓ 86%
	Ircinia campana	$F=0.646$, $P=0.782$	$F=0.267$, $P=0.618$	⇑ 65%	⇓ 29%
	Ircinia felix	$F=0.922$, $P=0.526$	$F=0.294$, $P=0.601$	⇓ 31%	⇓ 47%
	Ircinia spp.	$F=1.198$, $P=0.308$	$F=1.289$, $P=0.286$	⇑ 64%	⇓ 65%
	Monanchora arbuscula	$F=0.584$, $P=0.834$	$F=0.827$, $P=0.387$	⇑ 4%	⇓ 47%
	Mycale laevis	$F=2.081$, **$P=0.036$**	$F=0.001$, $P=0.981$	n/a	⇓ 58%
	Niphates erecta	$F=5.233$, **$P<0.001$**	$F=0.876$, $P=0.374$	⇓ 86%	⇓ 68%
	Smenospongia aurea	$F=0.799$, $P=0.641$	$F=0.225$, $P=0.647$	⇓ 81%	⇓ 58%
	Verongula rigida	$F=2.440$, **$P=0.014$**	$F=4.393$, $P=0.066$	⇓ 61%	⇑ 3%
	Verongula spp.	$F=2.503$, **$P=0.012$**	$F=1.905$, $P=0.201$	⇑ 248%	⇑ 166%
	Xestospongia muta	$F=0.843$, $P=0.599$	$F=1.491$, $P=0.253$	n/a	n/a
	Unknown	$F=1.220$, $P=0.294$	$F=0.945$, $P=0.356$	⇓ 30%	⇓ 34%

Among years contrasts shows the results of one way ANOVA comparing abundances among 12 years using sites as replicates. "Linear 1992–7/17" shows the results of least squares linear regressions testing for relationships between abundance and time using the years sampled from 1992 to July 2017. The last two columns show contrasts of mean abundances at two times only: "7/17 vs 11/17" shows the percentage change in abundance (averaged across sites) between July 2017 and two months after Hurricanes Irma and Maria (November 2017); and "1992 vs 11/17" shows the percentage change in abundance (averaged across sites) between November 2017 and 1992. Analyses completed for pooled taxa and for all resolved taxa (Table S1). F statistic and probability (P) shown for ANOVA contrasts among years ($df=1,11$) and linear regressions ($df=1,9$). Arrows show direction of change, significant effects in bold, and n/a = contrast not possible due to zero initial density

up until July 2017, with 6 cases showing increases and 2 cases showing decreases (Table 1). For these 8 cases, Hurricanes Irma and Maria caused declines in density (24–100% between July 2017 and November 2017), but nevertheless, mean densities in November 2017 were higher than mean densities in 1992 in 5 cases (13–736%) and lower in 3 cases (31–100%).

Mean densities of all sponges (pooled among taxa) increased from 3.20 sponges 0.25 m^{-2} in 1992 to 4.52 sponges 0.25 m^{-2} in July 2017, before decreasing to 2.19 sponges 0.25 m^{-2} in November 2017 (Fig. 3). The abundances of the seven most common species are shown in Fig. 4, and of these, four differed in density among times, one showed no variation among times, four increased linearly in density among sampled years from 1992 to July 2017, and one declined linearly in density over the same period (Table 1). Between 1992 and July 2017, the density of *Aplysina* spp. increased linearly, the density of *Ircinia*

strobilina decreased linearly, and 14 other taxa, as well as the "unknown" group, showed no linear trend with time (Table 1). Hurricanes Irma and Maria caused declines in mean abundance for 15 of 22 taxa (November 2017 vs July 2017), and the final densities were lower than initial densities for 13 of 22 taxa (November 2017 vs 1992) (Table 1).

The trajectories of change in sponge density differed among sites, with increases from 1992 to July 2017 at White Point, West Tektite, and East Tektite, and variable densities at Europa Bay, West Little Lameshur Bay, and Cabritte Horn (Fig. S1). Sponge densities declined at 5 of 6 sites (but not at Cabritte Horn) following Hurricanes Maria and Irma, with these declines representing losses of 39–93% of the sponges recorded in July 2017.

Overall, sponge volume (pooled among taxa) varied over time (Pseudo $F=2.259$, $df=11,24$, $P_{perm}=0.040$), and mean sponge volume ($\pm$ SE) (summed among taxa and averaged among sites) varied among years to a greater extent than

Fig. 4 Mean ($\pm$ SE, $n = 6$ sites) sponge density in St. John between 1992 and 2017 for the 8 most common taxa: **a** Unknown taxa, **b** *Monanchora arbuscula*, **c** *Aplysina fulva*, **d** *Niphates digitalis*, **e** *N. erecta*, **f** *A. cauliformis*, **g** *Amphimedon compressa*, and **h** *Cliona delitrix*. Chronology of disturbances shown in Fig. 3
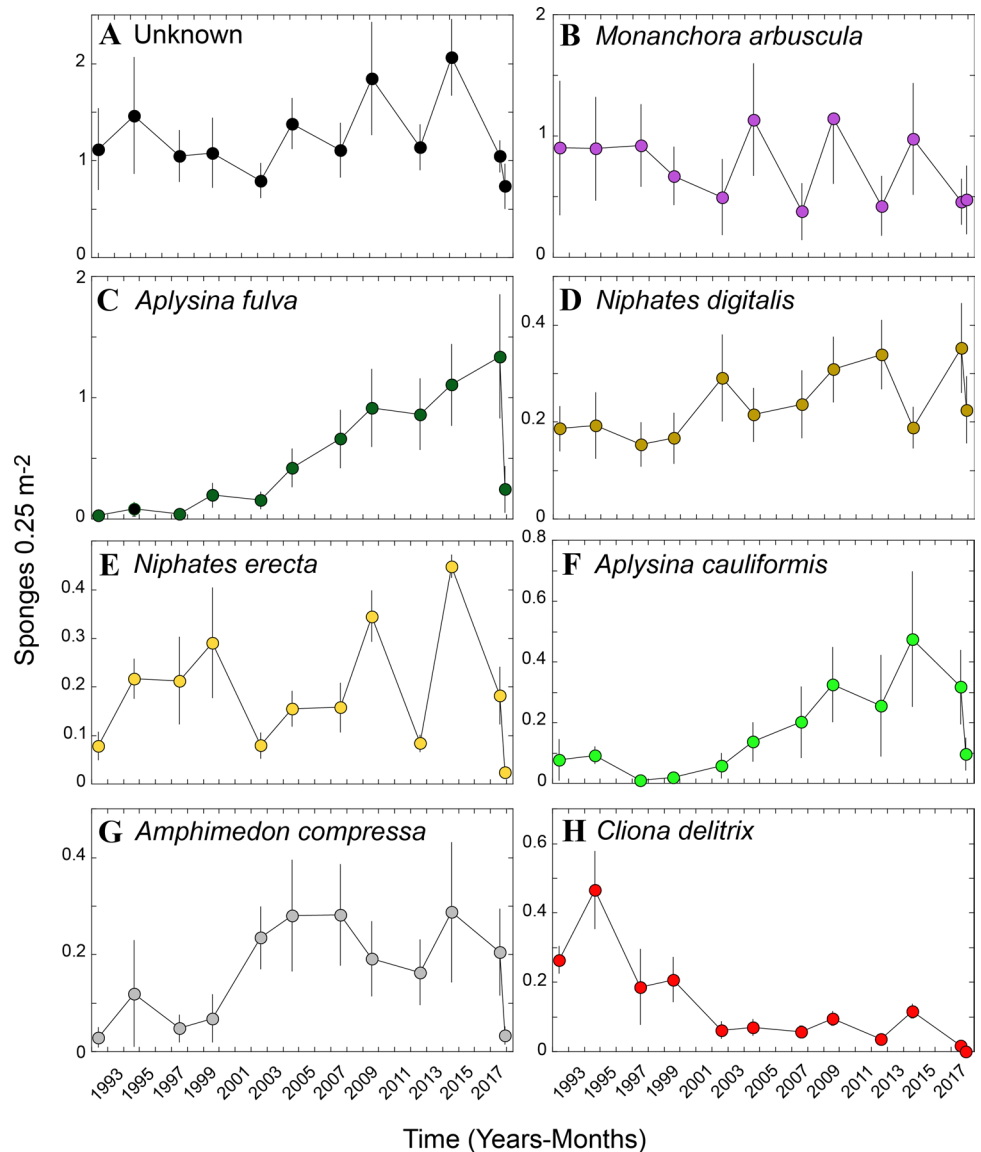
density (Fig. 3). Mean volume was 163 ± 67 cm^3 0.25 m^{-2} in 1992, 91 ± 19 cm^3 0.25 m^{-2} in 1999, 467 ± 51 cm^3 0.25 m^{-2} in 2009 (the maximum during the study), and then declined by 84% over 8 years to 77 ± 51 cm^3 0.25 m^{-2} in November 2017 (Fig. 3). Overall, sponge volume (pooled among taxa) was associated with density when averaged among sites ($P = 0.011$, Fig. S2).

Multivariate assemblage structure

Multivariate sponge assemblage structure based on the density of 23 taxa (Fig. 5) changed relatively little from 1992 to 1999, more from 1999 to 2007, and then entered a decade of variability from 2007 to July 2017. These trajectories identified four significant clusters of sampling years (SIMPROF, $P < 0.05$), the first defined by 1992 to 1999, the second by 2002, 2009, and 2014, the third by 2007, 2012, and July

2017, and the fourth by 2002 and November 2017 (Fig. 5). Over four months, Hurricanes Irma and Maria resulted in the largest change in sponge assemblages recorded over the study. As indicated in part by the univariate trends (Fig. 4, Table 1), the vector plot on the 2-D ordination revealed that the changes in multivariate assemblage structure were most strongly related to increasing densities of *Aplysina cauliformis*, *A. fulva*, and *Aplysina* spp. to July 2017, then their loss, together with reductions in density of *Cliona delitrix, Monanchora arbuscula,* and *Chondrilla caribensis* to November 2017 (Fig. 5).

The holistic community structure included 23 sponge taxa, 12 octocoral taxa, 23 scleractinians, macroalgae, and CTB. The 6 most common scleractinians were *Siderastrea siderea* (1.1% cover averaged among all sites and years), *Porites astreoides* (0.6% cover), *Orbicella annularis* (0.5% cover), *Agaricia* spp. (0.2% cover), branching *Porites* (0.2%
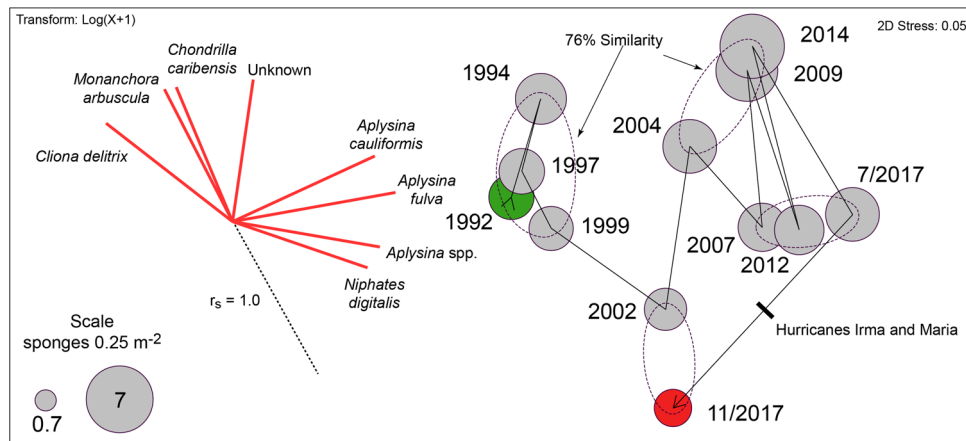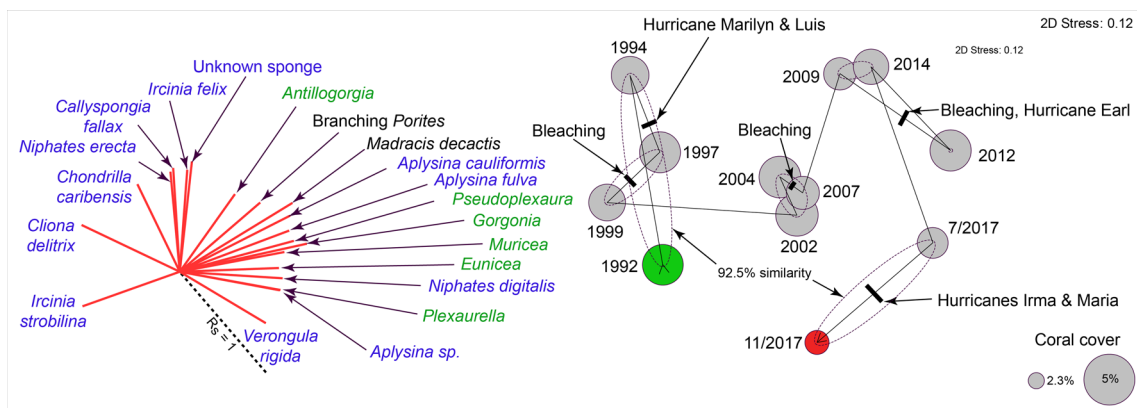
Fig. 5 Two-dimensional ordination prepared by NMDS showing multivariate sponge community structure in St. John between 1992 and 2017 (as in Figs. 3,4). Analysis is based on densities (taxa shown in Table S1) averaged among sites within years that were log(x + 1) transformed prior to preparing a resemblance matrix using Bray–Curtis dissimilarities. Dashed lines group sampling dates into significant clusters (SIMPROF, $P_{perm} = 0.05$) based on 76% similarity; green cover), and *Dendrogyra cylindrus* (0.1% cover). The four most common octocorals were *Erythropodium* (1.1 colonies 0.25 m^{-2} averaged among all sites and years), *Eunicea* (0.3 colonies 0.25 m^{-2}), *Antillogorgia* (0.3 colonies 0.25 m^{-2}), and *Gorgonia* (0.2 colonies 0.25 m^{-2}). Overall, the mean cover of macroalgae was 28%, and CTB was 43%. Two-dimensional ordination (Fig. 6) based on 60 taxa (i.e., sponges, scleractinians, macroalgae, octocorals, and CTB), revealed a progression of community structures from

shows first sampling, red shows last sampling, and dark bar marks the impact of Hurricanes Irma and Maria. Circles display overall sponge density (scale in lower left) and are linked by a vector among years. Vector plot (left) shows relationships (red lines) between sponge density and each NMDS axis as indicated by Spearman correlation coefficients screened to values > 0.8

1992 to November 2017 that grouped years into 5 clusters: 1992–1994, 1997–1999, 2002–2007, 2009 and 2014, and July 2017–November 2017 (SIMPROF, $P < 0.05$). The changes in community structure caused by major disturbances (i.e., bleaching and hurricanes) resulted in smaller changes (i.e., separation between sampling years before and after the events) than those between sampling years characterized by environmentally unremarkable conditions (e.g., 1992–1994, 1999–2000, 2014–July 2017). The largest

Fig. 6 Two-dimensional ordination prepared by NMDS showing multivariate benthic community structure as characterized by the abundances of sponges (density [sponges 0.25 m^{-2}] by 22 taxa and unknown), octocorals [density (colonies 0.25 m^{-2}) by 11 genera, and unknown], scleractinians (% cover by 23 taxa), macroalgae (% cover), and CTB (% cover). Analysis is based on abundances averaged among sites within years that were standardized prior to preparing a resemblance matrix using Bray–Curtis dissimilarities. Circles display overall scleractinian cover (green = first year, red = last year; scale in lower right), and are linked by a vector among years; black bars show the effects of major disturbances. Years are bounded by 92.5% similarity contours indicating significantly different clusters (by SIMPROF, $P_{perm} < 0.05$). Vector plot (left) shows relationships (red lines) between taxon abundance and each NMDS axis as indicated by Spearman correlation coefficients screened to values > 0.7; black = scleractinians, blue = sponges, and green = octocorals

differences in multivariate community structure from 1992 to July 2017 were associated with increasing abundances of *Madracis decactis, Alysina cauliformis*, and *Gorgonia*, together with declining abundances of *Cliona delitrix* and *Ircinia strobilina*. Hurricanes Irma and Maria reversed some of these trends so that the holistic community in November 2017 was more similar to the community in 1992 than in any sampling year following 2007 (Fig. 6).

Association with physical environmental conditions

Over 26 years, the physical environmental conditions were dissimilar (Table S2). Between 1992 and 2016, most years were characterized by the absence of hurricanes, although 2 major hurricanes occurred in 2017. Annual rainfall varied from 68 cm (1994) to 194 cm (2017), mean annual temperature varied from 27.3 °C to 28.3 °C, the maximum daily temperature each year reached as high as 30.6 °C (in 2005), and the lowest daily temperature was 24.9 °C (in 2009). The maximum temperature was collinear with several other environmental factors and was excluded from the BEST analyses.

Overall, the greatest capacity to account for the variation in the biotic community was obtained through consideration of the mean environmental conditions over 3 years, which included the year of community analysis, and 2 years before (Table 2). For both the sponge assemblages by density and the holistic community structure, the biotic data were best explained by rainfall averaged over 3 years ($\rho \geq 0.527$, $P_{perm} \leq 0.030$).

Discussion

Overview

Much is known about the ecological status of present day coral reefs, particularly with regard to the global decline in coral cover (Bellwood et al. 2004; Jackson et al. 2014; Hughes et al. 2017), and the high likelihood that coral abundance will be trivial on most coral reefs within a few decades (Hoegh-Guldberg et al. 2007; Hughes et al. 2017; Edmunds 2018). Yet, the taxonomic breadth of this knowledge remains restricted, and relatively little is known about the ways in which holistic benthic reef communities have changed, and in what form they will persist in the future.

Using 26 years of data from St. John, this study expands the existing understanding of changes in abundances of scleractinians, octocorals, macroalgae, and CTB (Edmunds 2013, 2019; Edmunds and Lasker 2016) by quantifying sponges over the same period for the same reefs. The study was approached with the premise that it would be valuable to learn something about sponge abundance over the past 26 years, rather to focus on the reasons why historic photographs are an imperfect tool for this task. While it was not possible to definitively address many aspects of sponge community dynamics that occurred over the study period, the analyses revealed changes over time in the abundance of many ubiquitous Caribbean reef sponges. They also allowed these changes to be placed in a broader context defined by the community dynamics of scleractinians and octocorals, as well as select physical environmental conditions that potentially drive these dynamics. Given the longevity of sampling, it is unsurprising that changes in abundance of sponges were detected (Objective 1), although it is striking that they defined 2 periods. One period extended from 1992 to 1999 and the other from 2002 to November 2017, with the 2 periods separating around the turn of the millennium. For the sponge fauna pooled among taxa, mean densities increased linearly (though noisily, $r^2 = 0.37$) from 1992 to July 2017, and were 40% higher in July 2017 than 1992. Hurricanes Irma and Maria caused a 51% reduction in these densities over four months, so that sponge density in November 2017 was 31% lower than in 1992.

Temporal variation in sponge density from 1992 to July 2017 varied among taxa (Objective 2), with most (70%)

Table 2 Summary of BEST analysis testing for associations between environmental data (either sponge community structure defined by density, or holistic community [sponge density, octocorals, scleractinians, macroalgae, and CTB]) and environmental conditions either in the year of measurement of community structure (Year of measurement), with a lag of 1 year before (1 y before), a lag of 2 years before (2 y before), or averaged over 3 years beginning with the year of measurement and including two prior years

	Sponge assemblage	Holistic community
Year of measurement	$\rho = 0.371$, $p_{perm} = 0.080$	$\rho = 0.431$, $p_{perm} = 0.037$: 1,2,3,5
1 y before	$\rho = 0.250$, $p_{perm} = 0.260$	$\rho = 0.396$, $p_{perm} = 0.047$: 1,2,5,7
2 y before	$\rho = 0.278$, $p_{perm} = 0.230$	$\rho = 0.281$, $p_{perm} = 0.208$
Averaged over 3 y	$\rho = 0.527$, $p_{perm} = 0.030$: 2	$\rho = 0.578$, $p_{perm} = 0.002$: 2

For measurements in 2017, the Hurricane index was calculated with a value of 0 for the July 2017 sampling, and value of 2 for the November 2017 sampling. Statistics report the multivariate Spearman correlation (ρ), the probability of obtaining the value by chance alone through a permutational analysis (*P*-perm), and in the case of significance, the best variable or combination of variables for explaining variation in the community structure: 1 = Hurricane index, 2 = rainfall (cm), 3 = mean temperature (°C), 5 = number of hot days, and 7 = AMO

showing no statistically discernable linear trend, 9% declining in density, and 22% increasing in density. These trends differed for the seven most common taxa (as determined across the whole study, Fig. 4), of which four increased in density, one declined in density, and 2 showed no linear change; all but one of these experienced 36–100% declines in density following Hurricanes Irma and Maria. Summary statements regarding the long-term trends affecting sponge density in St. John, therefore, depend on the taxon and the time over which the changes are considered.

Combining the aforementioned trends to summarize the overall trajectory of change in the sponge communities of St. John is difficult, however, because it is not yet possible to balance the demographic implications of 26 years of noisy, but generally increasing abundances, with 4 months of precipitous declines associated with Hurricanes Irma and Maria. If the environmental conditions that favored increases in abundance from 1992 to July 2017 have not fundamentally changed with the hurricanes, and storms of similar intensity do not return more rapidly than predicted [i.e., within ~ 12 years (Gardner et al. 2005)], then is reasonable to speculate that growth of sponge populations is favored on these reefs and will resume following the storms. If severe storms return to St. John more frequently than suggested by historic records (Gardner et al. 2005), and future environmental conditions cease to favor sponge growth, then the weight of the evidence from St. John (from 1992 to November 2017) indicates an overall declining trend in sponge abundance.

As described in the introduction, evidence supporting impending widespread increases in sponge abundance on Caribbean reefs is limited and equivocal. Several studies have reported increases of sponge abundance for select species over a subset of years (e.g., McMurray et al. 2010; Colvard and Edmunds 2011; Aronson et al. 2012; de Bakker et al. 2017). Gochfeld et al. (2020) recently reported a significant 43.9% increase in sponge density from 2015 to 2016 in St. Thomas, and while density declined 8.5% after Hurricanes Irma and Maria, this effect was not significant. In the small number of studies conducted over numerous years, in which all sponge species were enumerated by both volume and number of individuals, declines in abundance have been documented. In the Florida Keys, San Blas Islands (Panama), and Carrie Bow Cay (Belize) where sponges have been monitored in great detail over 6–14 years, sponges have markedly declined in terms of both volume and density (Stevely et al. 2011; Wulff 2006a, 2013). In Belize, neither sponge densities nor volumes had recovered following a mortality event in 2008 before a second mortality event in 2011 depressed sponge abundances even lower (Wulff 2013).

Overall, it appears that sponges on shallow Caribbean reefs are showing a diversity of responses to contemporary environmental conditions. This observation underscores the importance of recognizing diversity in the possible outcomes of these trends, and in documenting them over decades (not just years). As reported here for St. John, sponge abundances can rapidly change (and in contrasting directions) between consecutive samplings, long-term trajectories differ markedly among taxa, and decadal-scale trends can be reversed by acute disturbances acting over a few months. Short-term studies over a few years are unable to detect the ecologically meaningful trends that become evident over decades, particularly when they are taxonomically restrictive. These effects are elegantly illustrated by, for example, contrasting 3 sampling years from 1994 to 1999 (indicating declining abundance) versus from 1999 to 2004 (indicating increasing abundance) (Fig. 3), and the different conclusions that would be reached by focusing only on *Cliona delitrix* (dramatic decrease followed by low density) versus *Aplysina fulva* (consistent increase until the hurricanes) and *Niphates digitalis* (noisy stasis) (Fig. 4).

Quantifying sponges in planar images

The challenges of quantifying the abundance of sponges on coral reefs are well known (Wulff 2001, 2016), and they arise from the difficulties in identifying sponge species, and reticence by researchers to use biomass (or volume as a proxy) to measure sponge abundance as has been recommended (Reiswig 1973; Rützler 1978; Wulff 2016). The difficulties of identifying sponges, especially in pictures, restricted the present study to resolving a limited number of taxa that is a subset of the sponge diversity on the shallow reefs of this region (Gochfeld et al. 2020). Initially, we sought to measure sponge abundance using density and volume (as a proxy for biomass), and we estimated volume by taxon using geometric approximations of shapes at 3 sites. This procedure had limited resolution by taxon and, therefore, volumes were pooled among sponges. Overall, the temporal trends for sponge volume were concordant with density (Figs. 3, S2), and volume statistically differed over the whole study. Sponge volume (and biomass) provides a clearer indication of the functional contribution of sponges to benthic communities than densities (Wulff 2001, 2016), and our coarse-grain analysis of volume suggest that our measures of density are not divorced from demographic properties with stronger ties to the functional biology of sponges (i.e., they are associated with sponge biomass). It is important to note, however, that the shape and strength of the association between sponge density and biomass is strongly affected by morphology, species, and mortality source, (Figs. 3 and 4 in Wulff 2009; Figs. 5 and 6 in Wulff 2013) and, therefore, that the functional implications of changes in sponge density cannot easily be predicted.

Although the results of our analyses can serve as inspiration for others to exploit legacy images from coral reef time-series to glean information on sponge abundance, the challenges we encountered in pursuit of this goal lead us to discourage reliance on 2-dimensional photographs in new monitoring programs designed to include sponges. Nevertheless, where planar images remain the most tractable means to monitor coral reef communities, efforts to use this format to quantify sponges should exploit "ground-truthing" to equate results from images to results obtained in the field where sponge can be identified to species, and accurately scored for abundance and volume. A limitation of planar images will remain their inability to record sponges on undersurfaces and sides of objects, or in cases where they are closely intertwined with other taxa such as arborescent octocorals.

Given the importance of sponge biomass in evaluating the ecological importance of sponges, there is a need to expand the capacity to measure this metric. While planar images are unlikely to be able to deliver this resolution, three-dimensional photogrammetry holds promise for this purpose (Olinger et al. 2019). This rapidly emerging approach might finally support the development of a rigorous description of the mathematical and functional relationship between sponge volume and density.

Long-term trends in community structure

The severity of the coral reef crisis (Hughes et al. 2010, 2017) encourages sweeping statements conveying the gravity of the event, but simplified descriptions overlook variability in the trends, and sometimes can be incorrect. Questioning whether US coral reefs are on a "slippery slope to slime" (Pandolfi et al. 2005) graphically captures the severity of the changes, but it overlooks exceptions to the common suite of events that are taking place (Jackson et al. 2014; Guest et al. 2018). Likewise, whereas assertions that sponges may be taking over coral reefs (Pawlik and McMurray 2020) have only equivocal support of empirical data, the few long-term records of sponge abundance reveal trajectories differing among sites, taxa, and abundance metrics (e.g., density, biomass, or cover).

Together, the studies describing sponge abundance over time in the Caribbean underscore how few data are available for this task (see also Wulff 2016), as well as the varied trends supported by sparse data. For the present study, interpreting the changes in sponge abundance requires consideration of the context provided by the decadal scale of the analysis. From 1992 to July 2017, the trends revealed examples of long-term increases in sponge density, although these trends were usually sustained with multiple setbacks between consecutive samplings. In 2017, Hurricanes Irma and Maria caused large declines in sponge abundance in four

months, so that interpretation of the trajectories of future change depends on the long-term impacts of the recent hurricanes on sponge populations. The nature of these impacts may not be revealed for years, but it is interesting to note that the upward trends for changing sponge abundance detected in St. John from 1992 to July 2017 were sustained over previous disturbances attributed to bleaching and storms (Fig. 3) and, moreover, that the recent hurricanes did not depress sponge density on St. Thomas (Gochfeld et al. 2020). Around St. Thomas, sponge recruits and healing of lesions on damaged sponges were observed within 10 weeks of the hurricanes (Gochfeld et al. 2020), and similar observations have been recorded after hurricanes in other locations (Wulff 1995, 2006b). These observations suggest that individual sponges can start to recover from hurricane damage relatively fast and that their populations might quickly begin to increase in size through recruitment. Regardless of these effects, the complete recovery of sponge communities damaged by hurricanes will likely take years to accomplish. This assertion is supported by the slow rates at which sponges grow, their normally slow rates of recruitment, the variety of responses to damage that extend from rapid wound healing to continued deterioration and death, and the diversity and complexity of sponge communities (Wulff 2006b, 2013).

In St. John, the long-term trends for sponge density were taxonomically variable from 1992 to July 2017, and even for the most common seven species, examples of increases, declines, and stasis were recorded. Three of the sponges displaying linear trends for increasing density were "rope sponges" (*Amphimedon compressa*, *Aplysina cauliformis*, and *A. fulva*) (see also Colvard and Edmunds 2011), which are well known for their capacity to propagate through fragmentation (Wulff 1991). This life-history strategy probably contributed to their increase in density overtime in St. John. The common sponge that linearly declined in abundance, *Cliona delitrix*, is well known for its capacity to bioerode massive scleractinian corals, so its decline might reflect the low coral cover on the study reefs, as well as the paucity of carbonate substrata (Edmunds 2018). In the Florida Keys, where there is a greater availability of carbonate substrata and nutrient enrichment, *Cliona* spp. doubled in density from 1996 to 2001 (but remained at ~1% cover) (Ward-Paige et al. 2005), but on inshore reefs of the Great Barrier Reef, the cover of *Cliona* spp. did not change from 2005 to 2014 (Ramsby et al. 2017).

When considered as a multivariate sponge assemblage (Fig. 5), emergent effects were revealed that described gradual changes attributed to multiple taxa. While the sponge community changed, there were no clear "winning" species that dominated the communities. When the sponges were combined into a holistic community, 2-dimensional ordination (Fig. 6, Objective 3) revealed progressive changes mediated by multiple taxa and defining 2 periods, one from

1992–1999 and other from 2002–July 2017. This temporal structuring is similar to that identified for a subset of the community (i.e., scleractinians, octocorals, macroalgae, and CTB from 1992–2014) (Edmunds and Lasker 2016), with the structuring hypothesized to represent a cryptic regime shift (sensu Hughes et al. 2013) emerging around the new millennium in association with variation in rainfall and seawater temperature (Edmunds and Lasker 2016). The present results lend support to this hypothesis by broadening the taxonomic scope of the taxa involved, underscoring the separation in community structure around the new millennium, and again highlighting the association with rainfall (described below). The trends emerging from the multivariate community analyses do not suggest these reefs are becoming dominated by sponges. Such a trend would require a directional shift in community separation on the ordination plot, with the shift clearly and positively associated with rising sponge abundance. While the numbers of individuals of multiple sponge taxa increased in St. John, the absolute increases remained small.

Potential drivers of change in community structure

The coral reefs of St. John have been studied in more detail, for a longer period, and with the greater temporal resolution, than most coral reefs in the world. Until recently, the analyses have been restricted to scleractinians, *Millepora*, macroalgae, and CTB (Rogers et al. 2008; Edmunds 2013), and it was not until 2014 that octocorals were quantified (Lenz et al. 2015; Tsounis et al. 2018). The interpretation that has emerged from this work is that many of the reefs in St. John have transitioned to low stony coral abundance (Edmunds and Lasker 2016; Gross and Edmunds 2015; Edmunds 2018). In this condition, macroalgae occupy ~ 3–41% of benthic surfaces [in July 2017 (Edmunds 2019)] and octocorals create an "animal forest" of variable density and height (Edmunds and Lasker 2018), and with greater ecological resilience to contemporary disturbances than scleractinians (Tsounis and Edmunds 2017). Against this backdrop, it is timely to re-evaluate the role(s) of sponges on present-day reefs and determine whether they have been able to expand their population sizes under the environmental conditions favoring declines in abundance of scleractinians (Pawlik and McMurray 2020). Over 26 years from 1992 until July 2017, overall sponge density in St. John supported this possibility through a positive association with time, although just four months later (November 2017) these gains were erased. Interpreting the full complexity of the present results depends on the ecological implications of a 26 year trend, punctuated by an acute disturbance killing large numbers of sponges within 4 months (described above). Addressing this issue will require further long-term analyses of the sponge communities in St. John. With strong inter-annual variability

in sponge abundance from 1992–2017, and varying regimes of future disturbances, these studies will have to continue for years-decades to provide a robust interpretation of the status of sponge communities on present-day reefs.

In long-term analyses of community structure, the attribution of the process to patterns of change sheds light on the underlying mechanisms and strengthens the capacity to project population abundances into the future. Time-series cannot establish cause-and-effect without manipulation, or without observation before, during, and after an acute disturbance causing large changes in population size. Statistical associations between biotic features and environmental conditions can, however, be insightful to the processes that might give rise to the biotic features. These insights can include indications of the relative ecological importance of pulse disturbances, such as fires and storms, versus press disturbances, such as thermal challenges and chronic disease (Turner et al. 1997; Harris et al. 2018). For sponge communities that have been repeatedly surveyed, acute mortality has been associated with hurricanes (Woodley et al. 1981; Wulff 1995, 2006b,c; Gochfeld et al. 2020), phytoplankton blooms (e.g., of *Synechococcus*) (Butler et al. 1995; Stevely et al. 2011; Wulff 2013), and disease (Cowart et al. 2006; Webster 2007; Wulff 2006a; Easson et al. 2013), of which only hurricane-associated mortality has been observed on the shallow reefs of St. John (this study). Overall, however, sponge mortality historically has been underestimated on coral reefs, as sponges entirely vanish after they die and even traces of substantial partial mortality are rapidly erased as the surviving fragments regenerate. Coral reef monitoring programs often use the abundance of dead coral skeletons to evaluate mortality rates, but for sponges, unless individuals are mapped and measured before a mortality event, there is no way to know that they ever existed. Because reports of most sponge diseases rely on visual detection of aberrant coloration or structure (Webster 2007), they have been disproportionately reported in sponges that die slowly and may, therefore, be most likely to recover from the infection (Wulff 2006c).

Evaluating the proximal causes of the changes in sponge abundances in St. John was beyond the scope of the present study. Coincidence of contemporary sampling with Hurricanes Irma and Maria (Edmunds 2019) did, nevertheless, provide indirect evidence of the capacity of storms to damage sponge populations (Woodley et al. 1981; Wulff 1995) and depress sponge cover (Gochfeld et al. 2020). However, over multiple decades in St. John, neither hurricanes nor upward thermal anomalies (i.e., those causing coral bleaching) resulted in the largest changes in sponge communities. Instead, gradual changes that were spread over 26 years were best associated with annual rainfall averaged over 3 years (i.e., the result of addressing Objective 4). This outcome probably reflects the effects of press disturbances (e.g.,

sponge diseases [Wulff 2006c; Webster 2007]) compounded over decades for a diversity of taxa, as well as the capacity of rainfall to temporally integrate environmental conditions including variation in light, sedimentation, and nutrients (Fabricius 2005; Edmunds and Lasker 2016). Since rainfall in St. John increased at 1.6 cm y^{-1} between 1989 and 2013 (Edmunds and Lasker 2016), the association between rainfall and sponge community structure may reflect the effects of progressive reductions is light and increases in sediments and nutrients (i.e., effects functionally related to elevated rainfall and terrestrial runoff).

Summary

This study combines taxonomic breadth and study longevity to augment previous analyses (Edmunds 2013) that have revealed a regime change characterized by increasing abundances of octocorals (Edmunds and Lasker 2016). This regime change has culminated in 2 domains of sampling years that separate by benthic community structure around 2001–2002, with each characterized by distinct communities (Edmunds and Lasker 2016). By adding sponges to this analysis, the discrimination of temporal variation in benthic communities became more nuanced, but it did not reveal profound change (i.e., a phase change) as would be expected had sponge abundances dramatically changed. The role of scleractinians as foundation species on coral reefs (Jones et al. 1994; Wild et al. 2011) warrants close attention to trends in their abundance, but an objective evaluation of the future of coral reefs must include the diverse taxa—notably sponge—of which they are composed. Here, such an analysis highlights the community trajectories that remain hidden through a focus on scleractinians and macroalgae, but in so doing, the analysis clarifies the functional interpretation of changing abundances of scleractinians, octocorals, and macroalgae (as in Edmunds and Lasker 2016; Tsounis and Edmunds 2017). This holistic approach, and the test for association between community structure and environmental conditions, highlights a largely overlooked aspect of the physical environment (i.e., rainfall) with respect to the extent to which it can account for changes in coral reef biota. Association does not reflect cause-and-effect, but this approach underscores the importance of being able to match comprehensive ecological and environmental time-series from coral reef location to better understand why these systems are changing at a rapid rate.

Compliance with ethical standards

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