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Spatially aggressive peyssonnelid algal crusts (PAC) constrain coral recruitment to *Diadema* grazing halos on a shallow Caribbean reef

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ABSTRACT

Peyssonnelid algal crusts (PAC) have rapidly spread on coral reefs throughout the Caribbean since 2010 and have become dominant space holders in multiple locations. In 2019, PAC covered 31–86% of the shallow reefs (< 6-m depth) at two sites in St. John, US Virgin Islands, but within halos around aggregates of the echinoid, *Diadema antillarum*, PAC was absent and small corals were common. To test the hypothesis that the density of small corals is greater in *Diadema* halos versus on adjacent substrata, and that this effect is accentuated by high coverage of PAC, the shallow reefs of St. John were surveyed in July/August 2019 and January 2020. Densities of small corals (pooled among taxa) in *Diadema* halos were equal to, or greater than, densities on adjacent substrata, and were highest in *Diadema* halos adjacent to areas with high coverage of PAC. Where the cover of PAC was ≥ ~10%, the mean (± SE) density of small corals was 23.3 ± 2.1 colonies m^{-2} in *Diadema* halos, but was 67% lower at 7.5 ± 1.2 colonies m^{-2} on adjacent substrata; where the cover of PAC was < ~10%, densities of small corals were nearly identical in *Diadema* halos (9.1 ± 0.9 colonies m^{-2}) and on adjacent substrata (9.0 ± 1.1 colonies m^{-2}). Similar results were obtained when the analyses were repeated for the common corals, *Porites* spp., *Siderastrea radians*, and *S. siderea*. As *Diadema* halos remained in the same location for at least 6 months, they may function as refuges for coral recruitment in locations where PAC is becoming spatially dominant.

1. Introduction

Space is a limiting resource in benthic marine communities (Jackson, 1977), and disturbances that clear patches of substratum affect community structure (Sousa, 1979, 1984). Disturbances prevent spatial dominance by individual taxa, shift communities to earlier successional stages, and promote diversity when they occur at intermediate intensities (Connell, 1978; Sousa, 1984). These principles are prominent on tropical coral reefs (Jackson and Buss, 1975; Rogers, 1993), where it once was common for corals to cover a high percentage of the benthos (Loya, 1972; Porter, 1974), and to rapidly recover from disturbances (Pearson, 1981). Since the early 1990s, a different paradigm emerged as wide-scale coral mortality resulted in functional dominance by fleshy macroalgae (Done, 1992; Hughes, 1994; Roff and Mumby, 2012), which can stabilize an alternative community state and make it more difficult for a coral community to recover (Dudgeon et al., 2010; Schmitt et al., 2019).

Although peyssonnelid algal crusts (PAC) have been reported on Caribbean reefs for nearly a century (Taylor and Arndt, 1929; James et al., 1988), they started to attract more attention around the start of the current millennium when they were reported to be increasing in cover and dominating hard substrata in shallow water in several locations (Pueschel and Saunders, 2009; Eckrich et al., 2011; Eckrich and Engel, 2013). In 2010, PAC was described growing in this mode in Lac Bay, Bonaire, where it covered ~19% of the shallow reef (< 3-m depth) and was growing over 46% of the colonies of scleractinians and octocorals (Eckrich and Engel, 2013). Over the last decade, extensive growths of PAC have been recorded on shallow reefs extending from Bonaire (Netherlands) to Roatan (Honduras) (Ballantine and Ruiz, 2011; Smith et al., 2018; Edmunds et al., 2019; Williams and García-Sais, 2020; Wilson et al., 2020), thereby expanding its historic distribution (Taylor and Arndt, 1929; Sammarco, 1980). Throughout the 20th Century, PAC was reported as covering generally trivial proportion of coral reef surfaces in the Caribbean (e.g., Sammarco, 1980; Littler et al., 1987), except in a few cryptic locations (Goreau and Goreau, 1973; Brawley and Adey, 1977). In the 21st Century, the recent rapid and extensive spread of PAC in the Caribbean appears to represent a niche expansion, but it is unclear whether contemporary PAC represents the

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same organism(s) found 40+ y ago, or whether new species are involved. Present-day expanses of PAC are composed of multiple taxa, including *Peyssonnelia* spp., *Metapeyssonnelia* spp., and *Ramicrusta* spp. (James et al., 1988; Antonius, 1999; Edmunds et al., 2019; Wilson et al., 2020), and depending on the geographic origin of *Ramicrusta* spp., an invasive origin from the Indo-Pacific has been hypothesized (Eckrich et al., 2011).

Regardless of the peyssonnelid species composing present-day PAC, there is evidence of high cover and rapid spread throughout the Caribbean (Ballantine and Ruiz, 2011; Eckrich and Engel, 2013; Smith et al., 2018; Edmunds et al., 2019; Williams and García-Sais, 2020). In St. John, for example, the mean cover of PAC at 5-m depth was 64% at one site in 2017 (Edmunds et al., 2019), and by 2019, areas of 100% PAC coverage were recorded in some quadrats (0.5 × 0.5 m) (PJ Edmunds, unpublished data). After a decade of spreading throughout the region, by July 2019, PAC had extended into deeper water to reach 3% cover at 14-m depth in St. John (PJ Edmunds, unpublished data), and was common (occurring in 75–100% of video clips) at one site at 30-m depth off St. Thomas (Smith et al., 2018). Contemporary growths of PAC appear to be spatially aggressive (Eckrich et al., 2011; Eckrich and Engel, 2013), as indicated by their occurrence on top of live stony corals, soft corals, and sponges (Eckrich and Engel, 2013; Bramanti et al., 2017; Edmunds et al., 2019). Moreover, PAC does not appear to be favored as a substratum for coral recruitment in St. John (Edmunds et al., 2019), although it is not an absolute deterrent to coral settlement (Suzuki and Hayashibara, 2011). Evidence that PAC may be able to deter coral settlement (e.g., Wilson et al., 2020) is cause for concern, because coral cover and coral recruitment have declined throughout the Caribbean in recent decades (Jackson et al., 2014; Price et al., 2019), and a bottleneck is deterring coral recruits from becoming adults (Arnold et al., 2010).

The sea urchin *Diadema antillarum* historically played an important role on Caribbean reefs by grazing macroalgae and promoting coral settlement (Lessios et al., 1984; Lessios, 2016). Following its widespread mortality in 1983 (Lessios et al., 1984), macroalgae greatly increased in abundance (Levitan, 1988; Hughes, 1994), and have remained abundant (Roff and Mumby, 2012; Jackson et al., 2014). Evidence that *D. antillarum* were increasing in density around 2000 in Jamaica (Edmunds and Carpenter, 2001) suggested a regional population recovery might have started (Carpenter and Edmunds, 2006). While this potential has not been realized (Levitan et al., 2014), the enhanced densities of *D. antillarum* recorded in 2000 underscored the capacity of this sea urchin to promote coral recruitment by removing macroalgae through grazing (Edmunds and Carpenter, 2001). While quantifying PAC in St. John over 2015–2019, we found halos (~ 50-cm wide) of cleared substratum around clusters of *D. antillarum* (hereafter, "*Diadema* halos"), within which PAC usually was entirely absent (Fig. 1). It is reasonable to infer that these halos were created by *D. antillarum* (Sammarco, 1982; Williams, 2018).

The presence of small (i.e., ≤ 4-cm diameter) scleractinian corals in *Diadema* halos suggested they recruited to these areas. In contrast, their rarity on PAC-dominated substrata indicates that coral larvae do not settle on this surface, or if they do, they do not survive (Eckrich and Engel, 2013). These observations raise the possibility that *Diadema* halos might play a role in facilitating coral recruitment on reefs that are becoming dominated by PAC (Edmunds et al., 2019; Williams and García-Sais, 2020). To explore this possibility, surveys were completed in St. John from July 2019 to January 2020 to test the hypothesis that the density of small corals (≤ 4-cm diameter) is higher in *Diadema* halos versus on adjacent substrata, with this effect accentuated by high cover of PAC. As *Diadema* halos can only promote coral recruitment if they remain in the same location long enough to allow corals to settle and survive within them, *Diadema* halos were evaluated for persistence over days-months. The study focused on corals that are described as small rather than as recruits, because the size range investigated included small colonies of *Favia fragum* and *Siderastrea radians* that are likely to sexually mature (Soong, 1993) and functionally are adults.

2. Methods

2.1. Overview

Research was completed at <7-m depth on shallow reefs in Great Lameshur Bay on the south shore of St. John, US Virgin Islands (18.316°N, −64.725°W). Surveys were completed in July and August of 2019 and continued in January 2020. The study sites are in the Virgin Islands National Park, where they have been protected since 1956 (Rogers et al., 2008). The density of small corals inside and outside of *Diadema* halos was measured along the shores of two headlands, Yawzi Point and Cabritte Horn, along which PAC differed in abundance. At the tips of the headlands, a zone of high PAC cover was found, within which in situ surveys using subdivided quadrats (described below) revealed that PAC cover was ≥ ~ 10%, with some areas of benthos fully covered by PAC. Northward of this zone at each headland, the cover of PAC was lower < ~10% (also surveyed using subdivided quadrats), and the distinction between the two zones was visible as a transitional area several meters in width. Surveys were completed along ~100 m of shore within each PAC zone, and the transitional area was avoided for sampling. The two PAC zones hereafter are referred to as "Low-PAC" (< ~10% cover) and "High-PAC" (≥ ~10% cover). The causes of this gradient in PAC distribution remain unclear, but extensive surveys in this location have demonstrated higher abundance at exposed sites (Edmunds et al., 2019), which suggests that growth and recruitment of PAC is promoted by water motion (Williams and Edmunds, 2021).

Within each PAC zone, *Diadema* clusters were identified based on the

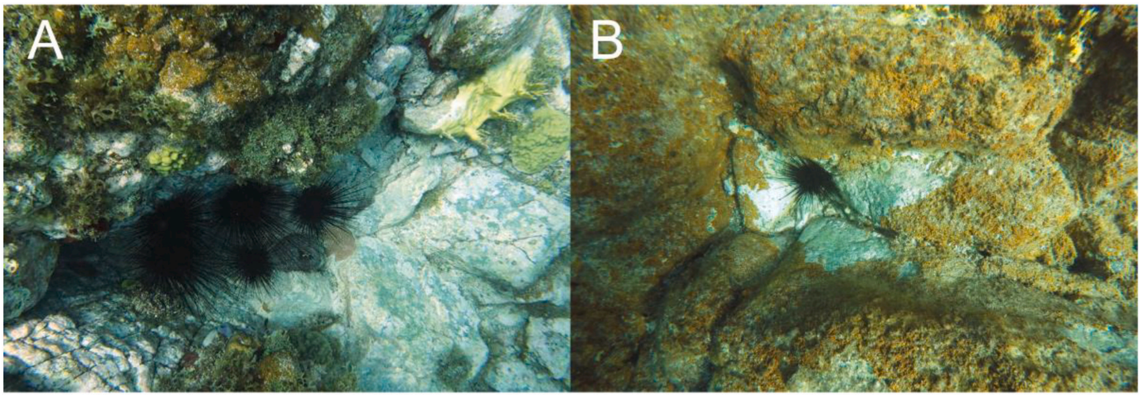

Fig. 1. Photographs taken in July 2019 showing examples of a *Diadema* cluster (A) and a *Diadema* halo (B) surrounded by dense cover of PAC. The reef in both images is at 3.0–4.5 m depth and is located in the High-PAC zone of Cabritte Horn. For scale, the *Diadema* are ~17–20 cm diameter (spine tip to spine tip).

presence of ≥4 sea urchins located ≤0.5 m from one another in shallow water (1.5–7.0 m depth), and they were haphazardly selected for the quantification of small corals in *Diadema* halos and on adjacent substrata. In this experimental design, each *Diadema* halo and the adjacent substrata were treated as plots nested within PAC zones, and they were sampled as encountered while working along each headland. Sampling initially was conducted along each headland to maintain a balanced design between zones, although fieldwork in January 2020 resulted in Cabritte Horn being sampled more extensively. Overall, 60 clusters of *Diadema* were sampled at Cabritte Horn (30 in each PAC zone), and 40 clusters at Yawzi Point (20 in each PAC zone), with each cluster sampled in a paired design with quadrats surveyed within the *Diadema* halo and on adjacent substrata.

2.2. *Densities of small corals in Diadema halos*

To test the hypothesis that *Diadema* halos provide a refuge for small corals in habitats dominated by PAC, clusters of *D. antillarum* were haphazardly selected in the Low-PAC and High-PAC zones of each headland. For each cluster, the abundance of small corals was quantified in the *Diadema* halo, and also on adjacent substrata outside the *Diadema* halo. PAC cover was quantified adjacent to the *Diadema* halo using the same quadrats used to determine the abundance of small corals. Although the sizes of the *D. antillarum* were not quantified, the clusters were created by adult sea urchins estimated to have test diameters > ~ 2 cm. Each cluster was surrounded by a halo (~ 50-cm width) of cleared substratum that was conspicuous in locations with high cover of PAC and other macroalgae (Fig. 1).

Clusters of *Diadema* were common at Yawzi Point and Cabritte Horn, and were composed of 4–28 sea urchins. Twenty clusters of *Diadema* (and their halos) were surveyed in the Low-PAC and High-PAC zones at Yawzi Point and Cabritte Horn in July and August 2019. At Cabritte Horn, 10 additional *Diadema* clusters in each PAC zone were surveyed in January 2020, with these surveys were completed in areas differing from those surveyed in the previous summer. Summer and winter samplings at Cabritte Horn were considered a single sampling, based on the assumption that the 5 months between them was not ecologically meaningful in terms of changes in density of small corals.

The density of small corals was measured using quadrats (0.25 × 0.25 m) that were haphazardly placed on the substratum, either within the *Diadema* halo, or on adjacent substrata outside of the halo ($n = 5$ within the *Diadema* halo, $n = 5$ on adjacent substrata). Haphazard placement was ensured by deploying the quadrat without looking at the substratum, and in the halos, haphazard placement was modified with the restriction that one side of the quadrat was in contact with the tips of the spines of the sea urchins; this ensured the quadrats were within the halos. Outside the halo, quadrats were randomly located <5 m from the halo margin. Small corals were counted when ≥50% of their area was within each quadrat, and their densities were expressed per square meter, which assumes that the density in the 0.25 × 0.25 m quadrats is 1/16th of that recorded in 1 × 1 m areas. In each quadrat, the density of small corals (≤ 4-cm diameter) was recorded by genus or species depending on the capacity to identify each taxon based on morphology. The percentage cover of PAC outside the halo was quantified using the same quadrats, which were subdivided into 25 sub-squares (each 5 × 5 cm). Sub-squares were scored for dominance of PAC, thereby allowing this substratum category to be quantified with 4% resolution.

2.3. *Temporal stability of D. antillarum clusters*

Testing of the hypothesis that *Diadema* halos provided refuges for small corals in PAC-dominated seascapes relies on *Diadema* clusters (and their halos) remaining in the same location long enough for corals to recruit to this microhabitat. To quantify the persistence of *Diadema* halos (hereafter "cluster stability"), the positions of haphazardly selected clusters were recorded over 9 days in January 2020 at Yawzi Point, and over 6 months at Cabritte Horn. At Yawzi Point, the positions of *Diadema* clusters ($n = 6$) were temporarily recorded with markers to allow subsequent relocation; their positions were evaluated every few days using photographs, and at the end of the 9 day period. Longer-term cluster stability was evaluated at Cabritte Horn where two *Diadema* clusters were photographed in July 2019 so that physical features of the benthos could be used to identify the same locations in January 2020. Over both time scales, it was not possible to determine whether the clusters of *D. antillarum* were composed of the same individuals, but this possibility was not relevant to evaluating whether the product of clustering (i.e., *Diadema* halos) remained in the same location.

2.4. *Statistical analyses*

The densities of small corals were analyzed with two approaches. First, densities pooled among taxa were analyzed by site with a split-plot ANOVA with model III sum of squares, in which PAC cover (high versus low) and location in *Diadema* halo (in versus out) were fixed effects, *Diadema* cluster was a randomized plot nested within PAC zones, and each quadrat was a statistical replicate. Each plot corresponded to a pairing of coral densities in a *Diadema* halo and on the adjacent substrata. Densities were square-root ($x + 3/8$) transformed (Zar, 2010), and the statistical assumptions of ANOVA were tested through graphical analyses of residuals. Analyses were completed using Systat 13.0 software.

Second, densities of small corals were analyzed separately for the three most common taxa, *Porites* spp., *Siderastrea siderea,* and *S. radians.* Subsampling of the data by taxon created multiple null records that were not amenable to parametric procedures and, therefore, a two way, fixed effects PERMANOVA was used to test for effects of PAC zones and *Diadema* halos on the density of small corals by taxon. In these analyses, the densities of small corals for each of the three taxa (separately) were averaged among quadrats within each halo, and also among quadrats on the adjacent substrata, to provide measurements of the density of small corals, one inside the halo and one outside the halo. Densities were square-root transformed, and resemblance matrices were prepared using a dummy variable (Anderson et al., 2008) for use in the PERMANOVA that was conducted using PERMANOVA+ for Primer v6 (Clarke and Gorley, 2006; Anderson et al., 2008).

3. Results

3.1. *Overview*

In July 2019, some of the areas studied at the tip of the headlands that were categorized as High-PAC zones were almost completely covered by PAC, and they included numerous *Diadema* clusters surrounded by halos that were free of PAC. The diagnostic dark-colored growths of PAC were absent within *Diadema* halos, within which carbonate and igneous rocks were exposed and sometimes were covered by growths of crustose coralline algae (Fig. 1). *D. antillarum* was not seen grazing PAC within their halos, but they crossed the halos to forage on adjacent substrata at night (L. Stockton, personal observation). During July and August 2019, and also January 2020, the majority of the small corals encountered were *Porites* spp. (31%, $n = 754$ colonies), *Siderastrea siderea* (25%), and *S. radians* (23%). The remainder was *Favia fragum* (11%) and *Agaricia* spp. (8%), with *Pseudodiploria* spp. and unidentified taxa accounting for 2% of the small corals. In High-PAC zones, 25% of the small corals (pooled between summer and winter sampling, $n = 467$ colonies) were on substrata adjacent to *Diadema* halos, and 75% were in *Diadema* halos. The distribution of *Diadema* halos along the headlands, and the occurrence of higher densities of small corals in *Diadema* halos versus on adjacent substrata, was similar at Yawzi Point and Cabritte Horn, and also between summer and winter at Cabritte Horn.

3.2. *Densities of small corals in Diadema halos*

At Yawzi Point in July and August 2019, overall mean (± SE) densities of small corals (pooled by taxon and location in *Diadema* halos versus open reef substrata) ranged from 12.3 ± 1.7 colonies m^{-2} in the Low-PAC zone, to 22.0 ± 2.4 colonies m^{-2} in the High-PAC zone (both $n = 20$). PAC covered 36 ± 4% (mean ± SE, $n = 20$) of the benthos in the High-PAC zone, and reached 76% cover in some quadrats. The Low-PAC zone was qualitatively categorized while snorkeling as having $< \sim 10\%$ cover of PAC, but quantitative analyses showed that the mean cover was 2 ± 1% (± SE, $n = 20$). In the High-PAC zone, mean densities (± SE, $n = 20$) of small corals (pooled among taxa) were 30.9 ± 3.2 colonies m^{-2} within *Diadema* halos, and 13.1 ± 2.2 corals m^{-2} on adjacent substrata (i.e., 135% higher in *Diadema* halos) (Fig. 2). In the Low-PAC zone, mean densities of small corals were 13.4 ± 1.4 corals m^{-2} within *Diadema* halos and 12.2 ± 2.0 corals m^{-2} on adjacent substrata (i.e., 10% higher in *Diadema* halos) (Fig. 2). The density of small corals significantly differed between *Diadema* halos and adjacent substrata in ways that varied between PAC zones (i.e., the interaction was significant, $p = 0.001$, Table 1), with this effect resulting from an enhancement of density in *Diadema* halos in high PAC zones, but not in Low PAC zones (Fig. 2). Because the density of small corals was enhanced in *Diadema* halos, the density of small corals also significantly differed between PAC zones ($p = 0.001$, Table 1).

At Cabritte Horn in July and August 2019, densities of small corals ranged from 7.1 ± 1.0 colonies m^{-2} in the Low-PAC zone, to 8.8 ± 1.4 colonies m^{-2} in the High-PAC zone (both $n = 20$). In January 2020, the densities of small corals (pooled by taxon and location in *Diadema* halos versus open reef substrata) ranged from 5.4 ± 1.1 colonies m^{-2} in the Low-PAC zone, to 15.4 ± 3.8 colonies m^{-2} in the High-Pac zone (both $n = 10$). The benthos within some quadrats in the High-PAC zone was 100% covered by PAC, but mean cover of PAC on the substratum adjacent to *Diadema* halos was 81 ± 3% (± SE, $n = 30$); in the Low-PAC zone, mean PAC cover adjacent the *Diadema* halos was 2 ± 1% (± SE, $n = 30$). In the High-PAC zone, *Diadema* halos were striking in their absence of PAC (Fig. 1). Mean densities (± SE, $n = 30$) of small corals (pooled among taxa) in the High-PAC zone were 18.2 ± 2.4 corals m^{-2} within *Diadema* halos, and 3.7 ± 1.0 corals m^{-2} on adjacent substrata (i.e., 389% higher in *Diadema* halos). In the Low-PAC zone, the mean (± SE, $n = 30$) densities of small corals were virtually identical in *Diadema* halos (6.2 ± 0.9 corals m^{-2}) and on adjacent substrata (6.9 ± 1.2 corals m^{-2}) (Fig. 2). The density of small corals significantly differed between *Diadema* halos and adjacent substrata in ways that significantly differed between PAC zones (i.e., the interaction was significant, $p < 0.001$, Table 1), with this effect resulting from an enhancement of density of small corals in *Diadema* halos in High-PAC zones, but not in Low-PAC zones (Fig. 2). Because the density of small corals was enhanced in *Diadema* halos, again the density of small corals also significantly differed between PAC zones ($p = 0.012$, Table 1). At this site, there also was a significant interaction ($p = 0.037$) between clusters nested within zones and *Diadema* halos, which was caused by the relative effect of *Diadema* halos in accentuating the density of small corals differing among *Diadema* clusters.

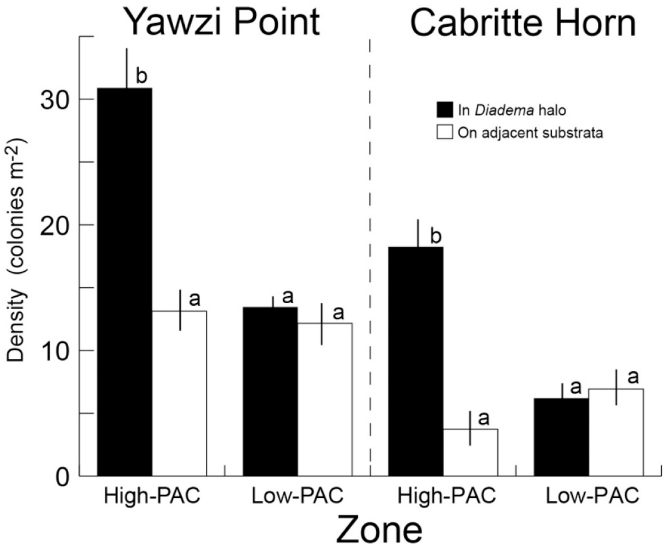

Fig. 2. Bar graphs showing mean densities (± SE) of small corals (pooled among taxa) in *Diadema* halos and on adjacent substrata at Yawzi Point ($n = 40$ clusters) and Cabritte Horn ($n = 60$ clusters) in High-PAC and Low-PAC zones. Letters above each bar show results of post-hoc analysis with common letters indicating no significant difference ($p < 0.05$).

Analyses of the distribution of small corals for the most common taxa produced more diverse results (Tables S1, Fig. S1) than for all corals together (Table 1). For *Porites* spp., *Siderastrea siderea,* and *S. radians* that accounted for 79% of the small corals ($n = 754$), four of the six interactions between PAC zones and *Diadema* halos were significant ($p \leq 0.022$, Table S1). These interactions reflected enhanced densities of small corals in *Diadema* halos versus on the adjacent substratum. Overall, in High-PAC zones, the mean densities of small colonies of each taxon were higher within *Diadema* halos compared to adjacent substrata, with these differences significant in four of six cases ($p \leq 0.004$, Fig. S1). In Low-PAC zones, densities of small colonies of each taxon were lower than in High-PAC zones (except for *S. radians* at Yawzi Point), and were similar between *Diadema* halos and adjacent substrata, with this contrast statistically indistinguishable in all six cases ($p \geq 0.05$, Fig. S1). For *Porites* spp. at Yawzi Point, the density of small corals was significantly greater in the High-PAC zone versus the Low-PAC zone ($p = 0.001$, and no other effects were significant, Table S1); for *Siderastrea radians*, the density of small corals significantly differed between PAC zones at Cabritte Horn ($p = 0.014$); and for *S. siderea*, densities of small corals were unaffected by the main effects or their interactions at Yawzi Point ($p \geq 0.169$) or the main effects at Cabritte Horn ($p \geq 0.132$) (Table S1, Fig. S1).

3.3. *Temporal stability of D. antillarum clusters*

Along Yawzi Point and Cabritte Horn, *Diadema* clusters were common in the High-PAC and Low-PAC zones, and they remained in the same locations (as well as their halos) over multiple days and months. Over nine days in January 2020, the position of 6 *Diadema* clusters along Yawzi Point did not change (Fig. S2), although the position of individual sea urchins within each cluster differed among days. Over six months, photographs of two *Diadema* clusters at Cabritte Horn showed that the position of the clusters did not change between July 2019 and January 2020.

4. Discussion

Throughout the Caribbean and since about 2010, PAC has quickly occupied space on shallow reefs (< 10-m depth), overgrown corals and sponges, and deterred coral recruitment (Eckrich and Engel, 2013; Edmunds et al., 2019; Williams and García-Sais, 2020). More recently, PAC has started to be detected in high abundances at ~30 m depth (Smith et al., 2018), and in St. John, it is now found at 14-m depth (Wilson et al., 2020). It is of interest, therefore, to identify cases where the negative ecological consequences of spatial pre-emption by PAC are attenuated, and herbivory is one means by which this might be achieved. Although the sea urchin, *Diadema antillarum*, was recorded grazing on *Peyssonnelia* sp. in the early 1970s (Sammarco, 1982), only recently has this observation been revisited through studies of the capacity of *D. antillarum* to control high abundances of PAC (Williams, 2016, 2018). Evidence from 2019 that aggregates of *D. antillarum* in St. John were surrounded by halos in which PAC was absent, motivated

Table 1
Results of split-plot ANOVAs comparing the density of small corals (pooled among taxa) between *Diadema* halos and adjacent substrata ("*Diadema* halo"), in High-PAC and Low-PAC zones ("PAC"), at Yawzi Point and Cabritte Horn ("Site"). Site = study site, Type = between or within plots effect, Source = effects in the model (Clusters {PAC} = *Diadema* clusters nested in PAC zones), SS = sum of squares, df = degrees of freedom, MS = mean sum of squares, *F* = variance ratio, *p* = probability. Significant effects are in bold.

Site	Type	Source	SS	df	MS	*F*	*p*
Yawzi Point	Between	PAC	4.199	1	4.199	13.997	**0.001**
		Clusters{PAC}	11.399	38	0.300	1.301	0.119
	Within	*Diadema* halo	5.257	1	5.257	20.065	**< 0.001**
		PAC × *Diadema* halo	3.196	1	3.196	12.200	**0.001**
		Cluster{PAC} × *Diadema* halo	9.952	38	0.262	1.136	0.275
		Residual	73.767	320	0.231		
Cabritte Horn	Between	PAC	1.362	1	1.362	6.775	**0.012**
		Clusters{PAC}	11.678	58	0.201	1.375	**0.041**
	Within	*Diadema* halo	6.126	1	6.126	30.176	**< 0.001**
		PAC × *Diadema* halo	6.222	1	6.222	30.652	**< 0.001**
		Cluster{PAC} × *Diadema* halo	11.772	58	0.203	1.386	**0.037**
		Residual	70.273	480	0.146		

investigation of the role of these halos as refuges for scleractinian recruits on reefs where PAC is covering large areas of benthic surfaces. Our results show that small corals were concentrated in *Diadema* halos versus on open reef substrata in High-PAC zones, and in Low-PAC zones, they occurred at similar densities in *Diadema* halos and on adjacent substrata, or sometimes at higher densities in *Diadema* halos. Since, *Diadema* aggregates persisted in fixed locations for 6 months, it is reasonable to infer that *Diadema* halos serve as refuges for coral recruits on PAC-dominated reefs.

The crust-forming alga, *Ramicrusta textilus*, first was reported in the Caribbean from St. Ann's Bay, Jamaica, using samples collected as early as January 1997 (Pueschel and Saunders, 2009). These authors noted that "*this alga's ability to dominate substratum and contribute to the erosion of dead coral heads, thereby reducing the recruitment prospects for young corals, may have a greater ecological consequence than its overgrowth of living corals*". Realization of this potential was reported from shallow (< 3-m depth) reefs in Lac Bay, Bonaire, where surveys conducted from November 2009–January 2011 showed that *Ramicrusta* sp. covered 19% of the substratum and was growing over 46% of the corals (Eckrich et al., 2011; Eckrich and Engel, 2013). Extensive growths of *Ramicrusta* spp. have now been found around the US Virgin Islands (Smith et al., 2018; Wilson et al., 2020), Puerto Rico (Ballantine and Ruiz, 2011; Williams and García-Sais, 2020), and Honduras (Wilson et al., 2020), and multiple peyssonnelids are known to overgrow scleractinians (Pueschel and Saunders, 2009; Ballantine and Ruiz, 2011; Eckrich and Engel, 2013).

Around St. John, PAC emerged as an ecologically significant algal group around 2012 (Williams and Edmunds, 2021), with a mean coverage of 9% at 3-m depth in 2015 (Bramanti et al., 2017), 64% at one site at 5-m depth in August 2017 (Edmunds et al., 2019), and 64% and 47% at two sites at 3-m depth in 2019 (Williams and Edmunds, 2021). Even though these reefs were impacted by two Category 5 hurricanes in September 2017 (Edmunds, 2019), which depressed the cover of PAC by 23–26% at 5-m depth (Edmunds et al., 2019), by 2019 and 2020, the spread of PAC had resumed (Williams and Edmunds, 2021). Throughout the field seasons that supported the aforementioned research in St. John, only two scleractinian recruits were found on PAC (Edmunds et al., 2019), thus supporting the inference of Pueschel and Saunders (2009). Recently, Wilson et al. (2020) have suggested that depressed densities of *Pseuderoalteromonas* bacteria on the surface of PAC may play role in deterring the recruitment of invertebrates to its surface.

Since scleractinian recruitment has declined throughout the tropical western Atlantic over the last three decades (Price et al., 2019), including on the reefs of St. John (Edmunds, 2018), it is a cause for concern that the bottleneck restricting scleractinian recruitment (sensu Arnold and Steneck, 2011; Doropoulos et al., 2012; Chong-Seng et al., 2014) might be intensified by PAC. This possibility arises from the pre-emption of settlement surfaces by PAC (Eckrich et al., 2011; Eckrich and Engel, 2013), potentially active deterrence of settlement by coral larvae to its surface (Wilson et al., 2020), and reduction of the population size of reproductively mature corals through overgrowth by PAC (Edmunds et al., 2019). Since spatial pre-emption could be attenuated through herbivory, it was noteworthy to find narrow, PAC-free halos around *Diadema* in the PAC-dominated seascape characterizing the reefs of St. John in 2019.

The clustering of *Diadema antillarum* sea urchins in hollows and cracks is well-known (Pearse, 1972; Nelson and Vance, 1979; Carpenter, 1984) and is associated with avoidance of daytime predators (Nelson and Vance, 1979; Carpenter, 1984). On Caribbean reefs prior to the die-off of *D. antillarum* in 1983 (Lessios et al., 1984), this sea urchin sought refuge at night in cracks and crevices, where it showed strong (up to 84%) crevice fidelity (i.e., returning to the same refuge over multiple days) at densities of <5 sea urchins m^{-2} (Carpenter, 1984). At night, the *D. antillarum* left their refuges and foraged over <3.2 m before returning to the same refuge to avoid predators such as the Queen Trigger fish (*Balistes vetula*) and Black Margate (*Anisotremus surinamensis*) (Randall et al., 1964; Carpenter, 1984). Densities of *D. antillarum* were drastically reduced by disease in 1983 (Lessios et al., 1984; Levitan, 1988), and despite signs of population recovery around 2000 (Edmunds and Carpenter, 2001), densities have remained low for decades, and likely will remain low for centuries to come (Levitan et al., 2014). Nevertheless, as reported here (see also Lee, 2006), present-day populations of *D. antillarum* continue to cluster in refuges during the day, even though their predators (including *B. vetula*, *Anisotremus surinamensis*, *Biodianus rufus*, *Canthidermis sufflamen* [Randall et al., 1964; Carpenter, 1984]) are less common now than decades earlier (Garrison et al., 1998; Rogers and Beets, 2001).

Our analyses demonstrate that *D. antillarum* in St. John continue to form daytime clusters around which halos of bare substratum are found, even though the densities of *D. antillarum* are greatly reduced compared to before 1983 (Levitan et al., 2014). These narrow halos are associated with high densities of small corals in PAC-dominated seascapes, with this effect striking for corals pooled by taxon, and for three of the most common corals located in at least one study site. Together, the six taxa of coral found in the present analysis reflect the common species found in surveys of juvenile corals on these reefs (Edmunds, 2018), and the rarity of historically important species like *Orbicella* spp. and *Montastraea cavernosa* underscores both how much these reefs have changed in the last few decades, and the likely difficulty of reversing the recent trends affecting coral communities. The patterns of distribution of small corals are consistent with two hypotheses that currently cannot be distinguished. First, small corals may be found in *Diadema* halos because they preferentially recruit to these locations. This possibility is most likely for *Porites* spp., which recruits in high densities in this location (Edmunds, 2021), and displays relatively fast linear growth (i.e., ca 4–7 mm y^{-1} (Chornesky and Peters, 1987; Edmunds, 2007), which ensures that small corals (i.e., $\leq$ 4 cm diameter) are also young. In contrast, *Siderastrea* *radians* and *S. siderea* grow more slowly that *Porites* spp. (Edmunds, 2007; Elahi and Edmunds, 2007) and, therefore, small colonies are less likely to be recent sexual recruits. Second, small corals might appear concentrated in *Diadema* halos because small corals that settled on the adjacent substrata already had been overgrown by PAC. We consider this possibility as unlikely, however, because densities of small corals on open substrata in the low-PAC zones were greatly reduced compared to within *Diadema* halos in High-PAC zones (Fig. 2).

The present study underscores the potential importance of *Diadema* clusters in providing a spatial refuge for small corals on shallow reefs that are experiencing rapid increases in cover of PAC (e.g., Edmunds et al., 2019; Williams and García-Sais, 2020). It also draws attention to the ecological significance of "reef-flattening" (Newman et al., 2015) that is causing a loss of benthic rugosity and cryptic microhabitats that might otherwise serve a refuge in which *D. antillarum* might aggregate, ultimately leading to the formation of halos as discussed herein. Herbivory by *Diadema* is a requisite for the outcomes inferred in the present study, but this possibility cannot be construed to suggest that herbivory by *Diadema* is a feasible means to control the spread of PAC. Population densities of *D. antillarum* remain modest compared to historic densities (Lessios, 2016), without prospects of imminent increases (Levitan et al., 2014). It is unlikely that this sea urchin will be able to effect broad change in the coverage of PAC on present-day reefs.

Author statement

LS and PJE designed the study, LS conducted the fieldwork, LS and PJE wrote the first draft of the manuscript and contributed to revisions and edits.

Data accessibility

The data for this project are hosted at bco-dmo: https://www.bco-dmo.org/project/752508.

Declaration of Competing Interest

The authors declare they have no competing financial interests or personal relationships that could have influenced the outcome of the present study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2021.151569.

References

Anderson, M., Gorley, R.N., Clarke, K., 2008. PERMANOVA+ for Primer: Guide to Software and Statistical Methods.

Antonius, A., 1999. *Metapeyssonnelia corallepida*, a new coral-killing red alga on Caribbean reefs. Coral Reefs 18, 301. https://doi.org/10.1007/s003380050200.

Arnold, S.N., Steneck, R.S., 2011. Settling into an increasingly hostile world: the rapidly closing "recruitment window" for corals. PLoS One 6 (12), e28681. doi.org/10.1371/journal.pone.0028681.

Arnold, S.N., Steneck, R.S., Mumby, P.J., 2010. Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Mar. Ecol. Prog. Ser. 414, 91–105. https://doi.org/10.3354/meps08724.

Ballantine, D., Ruiz, H., 2011. *Metapeyssonnelia milleporoides*, a new species of coral-killing red alga (Peyssonneliaceae) from Puerto Rico. Caribbean Sea Botanica Marina. 54, 47–51.

Bramanti, L., Lasker, H., Edmunds, P., 2017. An encrusting peyssonnelid preempts vacant space and overgrows corals in St. John, US Virgin Islands. Reef Encounters. 32, 68–70.

Brawley, S.H., Adey, W.H., 1977. Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. Environ. Biol. Fish 2, 45–51. doi.org/10.1007/BF00001415.

Carpenter, R.C., 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. Mar. Biol. 82, 101–108. https://doi.org/10.1007/BF00392768.

Carpenter, R.C., Edmunds, P.J., 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecol. Lett. 9, 271–280. https://doi.org/10.1111/j.1461-0248.2005.00866.x.

Chong-Seng, K.M., Graham, N.A.J., Pratchett, M.S., 2014. Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33, 449–461. https://doi.org/10.1007/s00338-014-1137-2.

Chornesky, E., Peters, E., 1987. Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. Biol. Bull. 172 (2), 161–177. https://doi.org/10.2307/1541790.

Clarke, K., Gorley, R.N., 2006. Primer v6: User Manual/Tutorial.

Connell, J., 1978. Diversity in tropical rain forests and coral reefs. Science 199 (4335), 1302–1310. https://doi.org/10.1126/science.199.4335.1302.

Done, T.J., 1992. Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247, 121–132. https://doi.org/10.1007/BF00008211.

Doropoulos, C., Ward, S., Marshell, A., Diaz-Pulido, G., Mumby, P.J., 2012. Interactions among chronic and acute impacts on coral recruits: the importance of size-escape thresholds. Ecology 93, 2131–2138. https://doi.org/10.1890/12-0495.1.

Dudgeon, S., Aronson, R., Bruno, J., Precht, W., 2010. Phase shifts and stable states on coral reefs. Mar. Ecol. Prog. Ser. 413, 201–216. https://doi.org/10.3354/meps08751.

Eckrich, C.E., Engel, M.S., 2013. Coral overgrowth by an encrusting red alga (*Ramicrusta* sp.): a threat to Caribbean reefs? Coral Reefs 32, 81–84. https://doi.org/10.1007/s00338-012-0961-5.

Eckrich, C.E., Engel, M.S., Peachey, R.B.J., 2011. Crustose, calcareous algal bloom (*Ramicrusta* sp.) overgrowing scleractinian corals, gorgonians, a hydrocoral, sponges, and other algae in Lac Bay, Bonaire, Dutch Caribbean. Coral Reefs 30, 131. https://doi.org/10.1007/s00338-010-0683-5.

Edmunds, P., 2007. Evidence for a decadal-scale decline in the growth rates of juvenile scleractinian corals. Mar. Ecol. Prog. Ser. 341, 1–13. https://doi.org/10.3354/meps341001.

Edmunds, P.J., 2018. The hidden dynamics of low coral cover communities. Hydrobiologia 818, 193–209. https://doi.org/10.1007/s10750-018-3609-9.

Edmunds, P.J., 2019. Three decades of degradation lead to diminished impacts of severe hurricanes on Caribbean reefs. Ecology 100 (3), e02587. doi.org/10.1002/ecy.2587.

Edmunds, P.J., 2021. Spatio-temporal variation in coral recruitment and its association with seawater temperature. Limnol. Oceanogr. https://doi.org/10.1002/lno.11693.

Edmunds, P.J., Carpenter, R.C., 2001. Recovery of *Diadema antilla*rum reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc. Natl. Acad. Sci. U. S. A. 98 (9), 5067–5071. https://doi.org/10.1073/pnas.071524598.

Edmunds, P.J., Zimmermann, S., Bramanti, L., 2019. A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands. Coral Reefs 38, 1329–1341. https://doi.org/10.1007/s00338-019-01846-0.

Elahi, R., Edmunds, P.J., 2007. Consequences of fission in the coral *Siderastrea siderea*: growth rates of small colonies and clonal input to population structure. Coral Reefs 26, 271–276. https://doi.org/10.1007/s00338-006-0190-x.

Garrison, V.H., Rogers, C., Beets, J., 1998. Of reef fishes, overfishing and *in situ* observations of fish traps in St. John, US Virgin Islands. Rev. Biol. Trop. 46 (Suppl. 5), 41–59.

Goreau, T., Goreau, N., 1973. Coral reef project—papers in memory of Dr. Thomas F. Goreau. 17.The ecology of Jamaican coral reefs. II. Geomorphology, zonation, and sedimentary phases. Bull. Mar. Sci. 23, 399–464.

Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265 (5178), 1547–1551. https://doi.org/10.1126/science.265.5178.1547.

Jackson, J., 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Am. Nat. 111 (980), 743–767.

Jackson, J.B.C., Buss, L.W., 1975. Allelopathy and spatial competition among coral-reef invertebrates. Proc. Natl. Acad. Sci. U. S. A. 72, 5160–5163. https://doi.org/10.1073/pnas.72.12.5160.

Jackson, J.B.C., Donovan, M., Cramer, K., Lam, V., 2014. Status and trends of Caribbean coral reefs: 1970-2012. GCRMN/ICRI/UNEP/IUCN 245.

James, N.P., Wray, J.L., Ginsburg, R.N., 1988. Calcification of encrusting aragonitic algae (Peyssonneliaceae); implications for the origin of late Paleozoic reefs and cements. J. Sediment. Res. 58 (2), 291–303. https://doi.org/10.1306/212F8D78-2B24-11D7-8648000102C1865D.

Lee, S.C., 2006. Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. Oikos 112 (2), 442–447. https://doi.org/10.1111/j.0030-1299.2006.14247.x.

Lessios, H.A., 2016. The great *Diadema antillarum* die-off: 30 years later. Annu. Rev. Mar. Sci. 8, 267–283. https://doi.org/10.1146/annurev-marine-122414-033857.

Lessios, H.A., Robertson, D.R., Cubit, J.D., 1984. Spread of *Diadema* mass mortality through the Caribbean. Science 226 (4672), 335–337. https://doi.org/10.1126/science.226.4672.335.

Levitan, D.R., 1988. Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at St. John, U.S. Virgin Islands. J. Exp. Mar. Biol. Ecol. 119, 167–178. https://doi.org/10.1016/0022-0981(88)90231-6.

Levitan, D.R., Edmunds, P.J., Levitan, K.E., 2014. What makes a species common? No evidence of density-dependent recruitment or mortality of the sea urchin *Diadema antillarum* after the 1983–1984 mass mortality. Oecologia 175, 117–128. https://doi.org/10.1007/s00442-013-2871-9.

Littler, M.M., Taylor, P.R., Littler, D.S., Sims, R.H., Norris, J.N., 1987. Dominant macrophyte standing stocks, productivity and community structure on a Belizean barrier reef. Atoll Res. Bull. 302, 1–24. https://doi.org/10.5479/si.00775630.302.1.

Loya, Y., 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar. Biol. 13, 100–123. https://doi.org/10.1007/BF00366561.

Nelson, B.V., Vance, R.R., 1979. Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. Mar. Biol. 51, 251–258. https://doi.org/10.1007/BF00386805.

Newman, S.P., Meesters, E.H., Dryden, C.S., Williams, S.M., Sanchez, C., Mumby, P.J., Polunin, N.V.C., 2015. Reef flattening effects on total richness and species responses in the Caribbean. J. Anim. Ecol. 84, 1678–1689. https://doi.org/10.1111/1365-2656.12429.

Pearse, J.S., 1972. A monthly reproductive rhythm in the diadematid sea urchin *Centrostephanus coronatus*. J. Exp. Mar. Biol. Ecol. 8, 167–186. https://doi.org/10.1016/0022-0981(72)90018-4.

Pearson, R., 1981. Recovery and recolonization of coral reefs. Mar. Ecol. Prog. Ser. 4 (1), 105–122.

Porter, J.W., 1974. Community structure of coral reefs on opposite sides of the Isthmus of Panama. Science 186 (4163), 543–545. https://doi.org/10.1126/science.186.4163.543.

Price, N.N., Muko, S., Legendre, L., Steneck, R., Oppen, M.V., Albright, R., Ang, P.O., Carpenter, R., Chui, A., Fan, T., Gates, R., Harii, S., Kitano, H., Kurihara, H., Mitarai, S., Padilla-Gamiño, J., Sakai, K., Suzuki, G., Edmunds, P., 2019. Global biogeography of coral recruitment: tropical decline and subtropical increase. Mar. Ecol. Prog. Ser. 621, 1–17. https://doi.org/10.3354/meps12980.

Pueschel, C.M., Saunders, G.W., 2009. *Ramicrusta textilis* sp. nov. (Peyssonneliaceae, Rhodophyta), an anatomically complex Caribbean alga that overgrows corals. Phycologia 48 (6), 480–491. https://doi.org/10.2216/09-04.1.

Randall, J.E., Schroeder, R.E., Starck, W.A., 1964. Notes on the biology of the echinoid *Diadema antillarum*. Caribb. J. Sci. 4, 421–433.

Roff, G., Mumby, P.J., 2012. Global disparity in the resilience of coral reefs. Trends Ecol. Evol. 27 (7), 404–413. https://doi.org/10.1016/j.tree.2012.04.007.

Rogers, C.S., 1993. Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. Coral Reefs 12, 127–137. https://doi.org/10.1007/BF00334471.

Rogers, C., Beets, J., 2001. Degradation of marine ecosystems and decline of fishery resources in marine protected areas in the US Virgin Islands. Environ. Conserv. 28 (4), 312–322. https://doi.org/10.1017/S0376892901000340.

Rogers, C.S., Miller, J., Muller, E.M., Edmunds, P.J., Nemeth, R.S., Beets, J.P., Friedlander, A.M., Smith, T.B., Boulon, R., Jeffrey, C.F.G., Menza, C., Caldow, C., Idrisi, N., Kojis, B., Monaco, M.E., Spitzack, A., Gladfelter, E.H., Ogden, J.C., Hillis-Starr, Z., Lundgren, I., Bane Schill, W., Kuffner, I.B., Richardson, L.L., Devine, B.E., Voss, J.D., 2008. Ecology of coral reefs in the US Virgin Islands. In: Riegl, B.M., Dodge, R.E. (Eds.), Coral Reefs of the USA, 1st edn. Springer, Dordrecht, pp. 303–373.

Sammarco, P.W., 1980. *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. Exp. Mar. Biol. Ecol. 45 (2), 245–272. https://doi.org/10.1016/0022-0981(80)90061-1.

Sammarco, P.W., 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J. Exp. Mar. Biol. Ecol. 61 (1), 31–55. https://doi.org/10.1016/0022-0981(82)90020-X.

Schmitt, R., Holbrook, S., Davis, S., Brooks, A., Adam, T., 2019. Experimental support for alternative attractors on coral reefs. Proc. Natl. Acad. Sci. 116 (10), 4372–4381. https://doi.org/10.1073/pnas.1812412116.

Smith, T.B., Ennis, R., Kadison, E., Nemeth, R.S., Henderson, L., 2018. The United States Virgin Islands Territorial Coral Reef Monitoring Program. In: 2018 Annual Report. University of the Virgin Islands, United States Virgin Islands 289pp.

Soong, K., 1993. Colony size as a species character in massive reef corals. Coral Reefs 12, 77–83. https://doi.org/10.1007/BF00302106.

Sousa, W., 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49 (3), 228–254. https://doi.org/10.2307/1942484.

Sousa, W., 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Syst. 15, 353–391.

Suzuki, G., Hayashibara, T., 2011. Do epibenthic algae induce species-specific settlement of coral larvae? J. Mar. Biol. Assoc. U. K. 91 (3), 677–683. https://doi.org/10.1017/S0025315410000573.

Taylor, W., Arndt, C., 1929. The marine algae of the southwestern peninsula of Hispaniola. Am. J. Bot. 16 (9), 651–662.

Williams, S., 2016. A novel approach to the restoration of *Diadema antillarum* on coral reefs in the Caribbean. Reef Encounter. 44.

Williams, S., 2018. The control of algal abundance on coral reefs through the reintroduction of *Diadema antillarum*. https://doi.org/10.13140/RG.2.2.30050.17604.

Williams, M.K., Edmunds, P.J., 2021. Reconciling slow linear growth and equivocal competitive ability with rapid spread of peyssonnelid algae in the Caribbean. Coral Reefs 40, 473–483. https://doi.org/10.1007/s00338-021-02052-7.

Williams, S.M., García-Sais, J.R., 2020. A potential new threat on the coral reefs of Puerto Rico: the recent emergence of *Ramicrusta* spp. Mar. Ecol. 41, e12592. https://doi.org/10.1111/maec.12592.

Wilson, B., Fan, C.M., Edmunds, P.J., 2020. An unusual microbiome characterises a spatially-aggressive crustose alga rapidly overgrowing shallow Caribbean reefs. Sci. Rep. 10 (1), 20949. https://doi.org/10.1038/s41598-020-76204-0.

Zar, J.H., 2010. Biostatistical Analysis, 5th edition. Prentice-Hall/Pearson, Upper Saddle River, xiii. 944 p.