Coral Reefs
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REPORT

# A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands

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**Abstract** In recent decades, many Caribbean reefs have experienced large declines in abundance of scleractinian corals, and blooms of fleshy macroalgae have often accompanied these trends. In 2010 a new macroalgal threat emerged in Lac Bay, Bonaire, where peyssonnelid algal crusts (PAC) rapidly spread in shallow water and overgrew corals and sponges. Similar growths have been reported in Puerto Rico and the Virgin Islands, and here, we describe the spread of PAC on the shallow reefs of St. John, US Virgin Islands, ~ 760 km northeast of Bonaire. In 2015, PAC covered 0.2–20.6% of hard benthic surfaces at $\leq$ 7 m depth. By August 2017, at the same sites, PAC had increased to 3.2–61.0% cover, at 5 m depth at 10 other sites along 5 km of shore, it covered 1.4–61.6% of reef surfaces, and at 9 m depth at five sites, it covered 0.8–41.0% of reef surfaces. At 5 m depth in August 2017, scleractinians and octocorals were frequently contacting PAC (42–47% of colonies), and more scleractinians (74%) than octocorals (39%) were overgrown by PAC. Following surveys in August 2017, St. John was hit by two Category 5 hurricanes, yet the shore-wide mean cover of PAC at 5 m depth was only reduced from 26 to 23%. Our results suggest PAC is poised to cause significant ecological change on the reefs of St. John and potentially will promote a community shift favoring octocorals over scleractinians. PAC constitutes an emerging regional threat on shallow Caribbean reefs to which researchers and resource managers will need to quickly respond.

**Keywords** Ecology · Scleractinia · Competition · Macroalgae · Community

## Introduction

Coral reefs are facing an ecological crisis (Bellwood et al. 2004; Hughes et al. 2010) characterized by declines in cover of scleractinian corals and increased abundances of other taxa, most frequently macroalgae (Roff and Mumby 2012), but sometimes corallimorpharians (Work et al. 2008), sponges (Loh and Pawlik 2014), or octocorals (Lenz et al. 2015). Given the foundational roles of scleractinians on coral reefs (Jones et al. 1994; Wild et al. 2011), these changes have substantial ecological and functional significance, and a great deal of effort has been spent addressing their causes (Hughes et al. 2007; Dudgeon et al. 2010; Edmunds and Lasker 2016). Blooms of macroalgae have been the focus of much of this work, as they are more abundant on many present-day reefs than in the 1970s and 1980s (McManus and Polsenberg 2004; Bruno et al. 2009; Jackson et al. 2014) and are functionally implicated in declining coral abundances (McCook et al. 2001). Macroalgal blooms represent a response to coral loss in a variety of circumstances, including situations where macroalgal growth is not well regulated by herbivory (Roff and Mumby 2012). The trend for increasing macroalgal

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cover on some coral reefs should not be construed to mean that macroalgae were rare on pristine coral reefs (Bruno et al. 2009) and, therefore, their increased abundance represents augmentation of the previous "normal" situation. Whether this trend can be reversed by a relaxation of the conditions favoring macroalgal growth (i.e., a change in phase), or whether a return to coral will be more difficult than the transition to macroalgae (i.e., an alternative stable state), remains uncertain (Dudgeon et al. 2010).

In 2010, calcareous algae in the rhodophyte family Peyssonneliaceae were found in high abundance on the shallow reefs ( $< 3$ m depth) of Lac Bay, Bonaire, where their high occupation of space was construed as a threat to Caribbean reefs (Eckrich et al. 2011; Eckrich and Engel 2013). In Lac Bay, Bonaire, peyssonnelid algal crusts (hereafter "PAC") covered 19% of the benthos in 2010 and were found overgrowing 46% ($n = 1374$ colonies) of the corals (consisting of 14 scleractinians, three octocorals, and *Millepora* spp.), two sponges, and crustose coralline algae and were identified as *Ramicrusta* spp. (Eckrich et al. 2011; Eckrich and Engel 2013). Previously, PAC have been described overgrowing corals in the 1980s in the Bahamas (*Peyssonnelia* spp. [James et al. 1988]), in 1997 in Belize and the Florida Keys (*Metapeyssonnelia corallepida* [Antonius and Ballesteros 1998; Antonius 1999]), and in 2003 in Jamaica (*R. textilus*), where they appeared to deter coral recruitment (Pueschel and Saunders 2009). Since 2010, examples of aggressive spatial occupancy by PAC have come from Puerto Rico (Ballantine and Ruiz 2011), the US Virgin Islands where it appears to have become established (Smith et al. 2016), including in St. John (Bramanti et al. 2017), and Honduras (B. Wilson pers. comm.). The sudden appearance of large areas of PAC on shallow Caribbean reefs, and in many locations with it overgrowing multiple benthic taxa, raises the possibility that they could accentuate macroalgal phase shifts. In St. John, an expansion of the space occupied by PAC might reinforce the cryptic regime shift favoring octocorals over scleractinians (Lenz et al. 2015; Edmunds and Lasker 2016), if PAC differentially impairs scleractinians versus octocorals.

While PAC on the present-day Caribbean reefs can be conspicuous (Eckrich et al. 2011; Bramanti et al. 2017), it has remained challenging to identify the taxa involved, or the mechanism(s) causing their abundance to increase. Peyssonnelids have been well known in the region for decades (Sammarco 1980; Littler et al. 1983; James et al. 1988) and usually have been identified as *Peyssonnelia* spp., although PAC described herein probably consists of multiple taxa. Using molecular genetic techniques, Pueschel and Saunders (2009) identified PAC in Jamaica as *Ramicrusta textilis*, thereby employing a genus erected in 1981 (Zhang and Zou 1981; Eckrich et al. 2011). In Lac Bay, Bonaire, Eckrich and Engel (2013) identified PAC as *Ramicrusta* spp., while Ballantine et al. (2016) found PAC to contain *R. monensis* in Puerto Rico, and *R. bonairensis* in Lac Bay, Bonaire, respectively. Samples of PAC collected from St. John in 2018 have been shown through molecular genetics to include *R. textilis* (B. Wilson pers. comm.). Based on morphology, PAC growing on Caribbean corals has been identified as *Peyssonnelia* spp. (James et al. 1988), and *Metapeyssonnelia corallepida* (Antonius 1999), with samples collected from St. John in 2015 identified as *P. stoechas* (R. Steneck, pers. comm.). The aforementioned results suggest for at least St. John that the recent growths of PAC include two genera (*Peyssonnelia* and *Ramicrusta*). While the novelty of the recent expansion of PAC in Lac Bay, Bonaire, and their assignment to *Ramicrusta* spp. encouraged Eckrich et al. (2011) to speculate that this taxon was invasive to the region, and Ballantine et al. (2016) to underscore that growths of PAC were a "recent phenomenon" (see also Pueschel and Saunders 2009), it is premature to conclude that the recent large growths of PAC in the Caribbean are driven by an invasive genus (i.e., *Ramicrusta*).

In St. John, PAC have been observed for decades on shallow reefs (PJ Edmunds, unpublished data), but prior to ~ 2009 they were trivial components (i.e., $< 1\%$ cover) of the benthic community (PJ Edmunds, unpublished data). At this level, the abundance of PAC was similar to that typically reported in early analyses of Caribbean reefs (i.e., from $< 1$–9% cover; van den Hoek et al. 1975; Sammarco 1983; Littler et al. 1987), although in the early 1980s (and before) areas of reef could be found with up to 50% cover of *Peyssonnelia* (James et al. 1988), and this algal group frequently "lined" walls and crevices in deep water on the north shore of Jamaica in the late 1950s (Goreau and Goreau 1973). Around 2010 in St. John, larger patches of PAC started to occur at $< 4$ m depth and, by 2015, had coalesced into spatially cohesive growths with mean coverage at 3-, 5-, and 7 m depth of $8.5 \pm 1.3\%$, $3.4 \pm 0.6\%$, and $1.0 \pm 0.2\%$, respectively (Bramanti et al. 2017). Anecdotal observations from Lac Bay, Bonaire, suggested the spread of PAC was facilitated by overgrowth of scleractinians, octocorals, and sponges (Eckrich and Engel 2013). In St. John, the spread of PAC continued to July 2017, when it covered large areas at $< 5$ m depth, and was common at 14 m depth on the Tektite reef (see Edmunds 2013). Two months later, the impact of two major hurricanes (Edmunds 2019) raised the possibility that storm damage might slow the advance of PAC.

The present study focused on PAC in St. John from 2015 to present and evaluated their potential to change benthic community structure through aggressive occupation of space. First, we expanded surveys conducted in 2015 (Bramanti et al. 2017) by sampling the same locations in July 2017 and November 2017 to test for variation in PAC abundance over time. Second, sampling was intensified in July and November 2017 by selecting 11 sites for analysis of community structure at 5 m and 9 m depth. Finally, surveys in 2017 were used to evaluate the capacity for PAC to overgrow scleractinians and octocorals. Because these surveys bracketed two hurricanes in September 2017 (Edmunds 2019), they were used to evaluate the role of physical disturbances in mediating the abundance of PAC.

## Materials and methods

### Overview

Shallow ( < 9 m depth) fringing coral reefs along ~ 5 km of the south shore of St. John were the focus of the present analysis, which utilized results from initial surveys in 2015 (Bramanti et al. 2017) and new surveys in 2017 (Fig. 1). The surveys in 2017 were conducted in July and August 2017 as part of time series analyses (Edmunds 2013), but the surveys were repeated as "event sampling" in response to Hurricanes Irma and Maria (Edmunds 2019), and were conducted from 18 to 26 November, 8 weeks after the second of the two hurricanes.

## PAC dynamics

To evaluate dynamics of PAC, the 2015 surveys (Bramanti et al. 2017) were repeated in August 2017 and November 2017. The 2015 surveys were completed at three sites that were haphazardly selected between White Point and

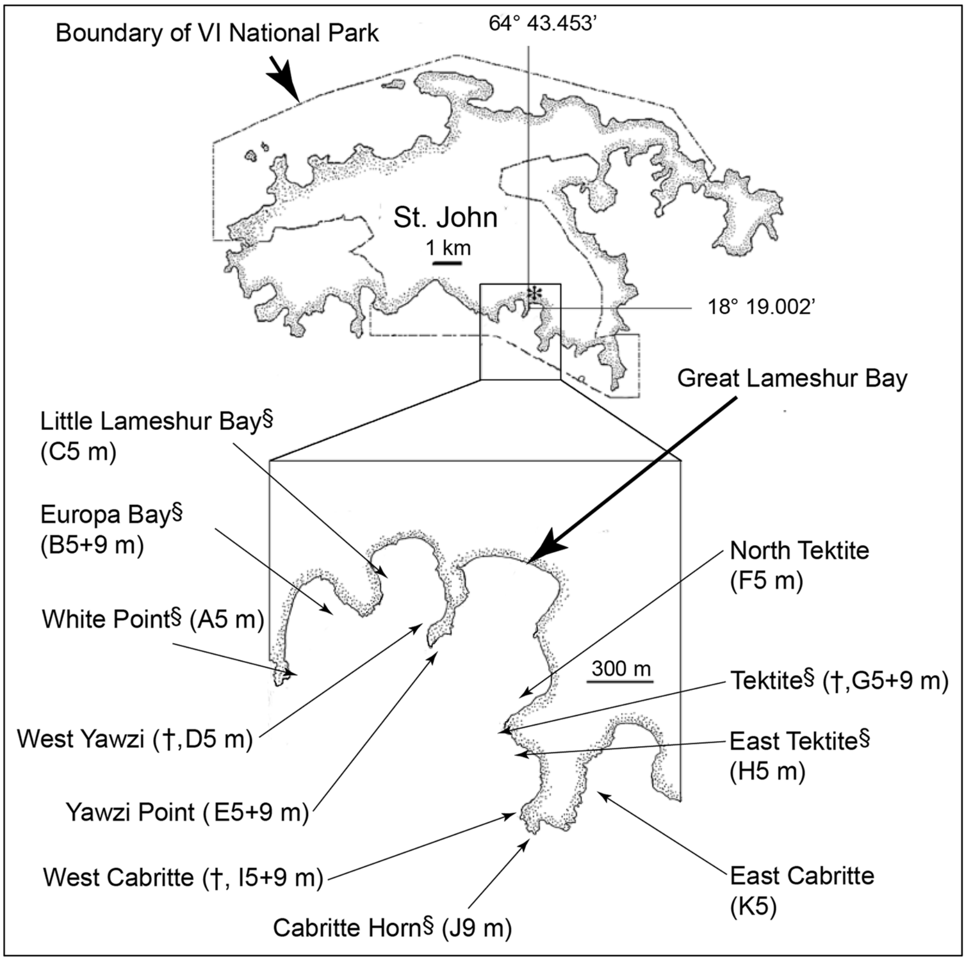

**Fig. 1** Map of St. John, US Virgin Islands, showing study sites between Cabritte Horn and White Point. Surveys were completed at eleven sites, first, to test for variation in abundance of PAC over time using video transects, and second, to quantify the distribution of PAC in 2017 using in situ surveys. Video transects (†, D, I and G) were completed at 3 m, 5 m, and 7 m depth on four occasions between August 2015 and November 2017 at west Yawzi Point (from November 2015), Tektite, and West Cabritte. In situ surveys were completed in August and November 2017 at 5 m and 9 m depth and were completed at the three sites used for video analyses and eight others; limited field time prevented both depths being sampled at all sites. Letters correspond to sites shown in Fig. 3. § = sites that have been sampled since 1992 (RS15, 11, 9, 2, 5, and 6 in Edmunds 2013), sites D–F, and I were randomly selected for the present study, and K was added based on field work for another purpose that suggested PAC was abundant in this location

Cabritte Horn and were conducted at 3 m, 5 m, and 7 m depth in August 2015 (West Cabritte and Tektite) and November 2015 (west Yawzi Point, West Cabritte, and Tektite) (Fig. 1). At each site and depth, PAC abundance was measured using 50 m transects that were recorded under ambient lighting using a GoPro Hero 3 camera held ∼ 1 m above the benthos. A monopod was used to standardize height above the reef, and a scale bar was included in the images. Transects were recorded along a constant isobath, and as they were not permanently marked, it was not possible to survey identical locations in 2017. Video transects in 2017 were recorded in the same manner and as close as possible to the initial locations based on GPS coordinates.

The videos were analyzed by randomly extracting still images ($n = 20$ transect$^{-1}$) using QuickTime Player (version 10.4) software. Each image recorded ∼ 0.25 m$^2$ of the benthos in which objects as small as 1–2 cm diameter could be resolved. Images were analyzed using Adobe Photoshop CC software (Adobe Systems Incorporated, San Jose, California, USA), in which a grid of 5 × 5 equal-size squares was super-imposed on the image, and each square was scored by eye for relative dominance by PAC to provide a resolution of 4%. In this analysis, each square was scored as dominated by PAC if this group was the single benthic category occupying the largest planar area in the square. Analyses were supervised by a single investigator, but images from 2015 and 2017 were analyzed by a different person, with informal cross-calibration used to ensure consistent scoring.

## PAC abundance in 2017

The analysis conducted at multiple times using video transects provided limited resolution due to the use of available light, and only three sites were sampled between White Point and Cabritte Horn. To broaden the spatial coverage and increase resolution, in August and November of 2017, surveys were completed in situ at 5 m and 9 m depth at 11 sites (Fig. 1), although logistics prevented sampling at both depths at all sites. The 11 sites included six that have been used for time series analyses since 1992 (Edmunds 2013) and were randomly established in the first year of that analysis, four that were randomly selected for the present analysis, and one (East Cabritte) that was selected based on anecdotal reports of high PAC abundance in 2016. Ten sites were surveyed at 5 m depth (Fig. 1: A–I, K), and five sites were surveyed at 9 m depth (Fig. 1).

At each site and depth, community structure was quantified using 10 quadrats (0.5 × 0.5 m) randomly positioned along 10 m transects placed haphazardly along the isobath. Depending on field logistics, 2–5 non-overlapping transects were surveyed to provide 20–50 quadrats at each site and depth. Each quadrat was divided into 25 equal sub-squares that were categorically scored by the dominant group covering the benthos to provide 4% resolution. Four functional groups were scored: "corals" (scleractinians, octocorals, and *Millepora*), macroalgae (mostly *Halimeda, Dictyota, Padina,* and *Lobophora*), PAC, and CTB (crustose coralline algae, algal turf, and bare hard surfaces combined). More categories were scored in this analysis than with the video transects as it was easier to discern benthic groups underwater. As described above for the analysis of the video transects, one of the functional groups needed to occupy the largest fraction of the planar area of each square for the square to be assigned as dominated by that group. With this approach, a square was scored as dominated by PAC in the same way regardless of whether surveys were completed in situ or with video transects. Surveys were repeated at all sites and depths in November 2017, but limited field time resulted in smaller sample sizes compared to August 2017.

## Overgrowth of corals by PAC

Anecdotal observations suggested that one mechanism by which PAC usurped space on the benthos was through aggressive spatial competition and overgrowth of other taxa (Eckrich and Engel 2013). To test this hypothesis, surveys were completed in which scleractinians and octocorals were categorically scored for interactions with PAC: (i) contact with PAC (yes or no), and if they were contacting PAC, as (ii) overgrown by PAC (iii) overgrowing PAC, or (iv) meeting with no signs of the coral being overgrown by PAC, or the PAC being overgrown by the coral. Meeting without signs of overgrowth may reflect a "stand-off" encounter (sensu Chornesky 1989), although sampling of the site of contact over time is required to evaluate this possibility; these interactions are described as "neutral" to reflect uncertainty in the dynamic status of the interaction. These analyses were completed at the same sites and depths (i.e., 5 m and 9 m) at which PAC was surveyed for abundance in 2017, and they were conducted in quadrats (0.5 × 0.5 m) randomly placed along 10 m transects ($n = 20$ quadrats for each site/depth combination). Analyses for PAC interactions were completed for adult colonies defined by a diameter > 4 cm for scleractinians (Edmunds 2013) and a height > 5 cm for octocorals (Tsounis et al. 2018).

## Analyses

Changes in percent cover of PAC from 2015 to 2017 were tested with a Model III, three-way ANOVA in which site was a random effect, and depth (3, 5, and 7 m) and time

(November 2015, August 2017, November 2017) were fixed effects; the August 2015 sampling was not included as only two sites were sampled. PAC abundance recorded in situ during 2017 was analyzed using two approaches, first with Model III, two-way ANOVAs contrasting time (fixed effect) and site (random effect) with separate analyses for 5 m (10 sites) and 9 m depths (5 sites), and second, with a Model III, three-way ANOVA contrasting time (fixed effect), site (random effect), and depth (fixed effect). The second analysis was restricted to the four sites that were sampled at both depths. These analyses were repeated for the three other components of community structure (corals, CTB, and macroalgae), but these results are presented in Supplementary Material as they were not the main focus of the present study.

Three-way contingency tables (Time × Depth × Interaction) were used to explore the interactions between scleractinians and PAC, and between octocorals and PAC, in which time (August and November) was contrasted with depth (5 m and 9 m) for interactions with PAC categorized as: (i) overgrown by PAC (ii) neutral, or (iii) overgrowing PAC. For octocorals, there were too few observations to include "overgrowing PAC" in the analysis. An additional analysis compared the frequency of contact with PAC between scleractinians and octocorals in August and November. Three-way tables were tested using log-linear models with the G-statistic evaluating goodness of fit (Sokal and Rohlf 2012).

Statistical analyses were completed using SYSTAT version 13 software (Systat Software Inc., Chicago, Illinois, USA). Percentage data were arcsine-transformed, and the statistical assumptions of ANOVA (normality and equal variance) were explored through graphical analyses of residuals.

## Results

### PAC dynamics

In 2015, small areas (typically ≤ 10 cm diameter) of benthos were found covered by PAC on almost every dive completed during a month of intensive field work. The patches of PAC were most prominent at 3 m versus 5 m and 7 m depth. In August 2015, mean cover of PAC ( ± SE, *n* = 20) varied from a low of 0.8 ± 0.5% at 7 m depth at Tektite, to a high of 20.6 ± 3.9% at 3 m depth at West Cabritte. Three months later (November 2015), the cover of PAC at three sites varied from low of 0.2 ± 0.2% at 5 m depth at Yawzi Point, to a high of 12.2 ± 3.0% at 3 m depth at West Cabritte. Nearly 2 yr later (August 2017), the cover of PAC at the same sites ranged from a low of 3.2 ± 1.2% at 5 m depth at west Yawzi Point, to a high of 61.0 ± 3.4% at 3 m depth at West Cabritte (Fig. 2). Examples of areas with very high cover of PAC and overgrowths of scleractinians and octocorals were common in the shallowest areas in August 2017. This also was true following two Category 5 hurricanes (in September 2017), and in November 2017, PAC cover still ranged from a low of 0.8 ± 0.6% (7 m depth at Yawzi Point) to a high of 30.4 ± 5.0% (5 m depth at West Cabritte) (Fig. 2). Statistical analysis revealed a Site × Time × Depth interaction (Table 1), which reflected a consistent trend for increasing abundance over time, which differed in magnitude among sites and depths (Fig. 2).

### PAC abundance in 2017

PAC were found at all sites and depths in August and November 2017, but their abundance varied among sites (Fig. 3). They were particularly abundant on igneous rock that occurs as boulders in shallow water ( < 5 m depth) and which forms large submerged cliffs at Cabritte Horn, Yawzi Point, and White Point. In August 2017, the mean cover of PAC ( ± SE) at 5 m depth varied from a low of 1.4 ± 0.5% (*n* = 40) at north Tektite to a high of 63.8 ± 1.9% (*n* = 50) at east Cabritte, and at 9 m depth, it varied from a low of 0.8 ± 0.3% (*n* = 40) at Yawzi Point to a high of 41.0 ± 3.4% (*n* = 40) at Cabritte Horn (Fig. 3). In November 2017, PAC remained abundant and showed few signs of retreat following the two hurricanes. The changes associated with Hurricanes Irma and Maria were most conspicuous for PAC on small ( ~ 30 cm length) igneous boulders, many of which at ~ 3 m depth at east Tektite were almost fully covered by PAC in August 2017, but were free of PAC in November 2017. The inferred effects of the hurricanes were seen at the rocky headlands where PAC had been chipped away from the substratum. Overall, mean ( ± SE) cover of PAC at 5 m depth in November 2017 varied from a low of 0.4 ± 0.4% (*n* = 20) at north Tektite, to a high of 60.6 ± 5.1% (*n* = 20) at west Cabritte, and at 9 m depth, it varied from a low of 0.3 ± 0.2% (*n* = 40) at Tektite, to a high 46.3 ± 4.0% (*n* = 40) at Cabritte Horn (Fig. 3). Within each depth (5 m and 9 m), PAC abundance differed among sites in ways that differed between times (i.e., there were Site × Time interactions, Table 1), and among the four sites at which surveys were completed at both times and depths, PAC abundance was affected by a Depth × Time × Site interaction (Table 1). These two- and three-way interactions are reflected in sites that differed greatly in PAC cover in inconsistent ways between depths, and cases where PAC cover did not change after the hurricanes (e.g., Site I, 5 m depth), and cases where PAC mostly

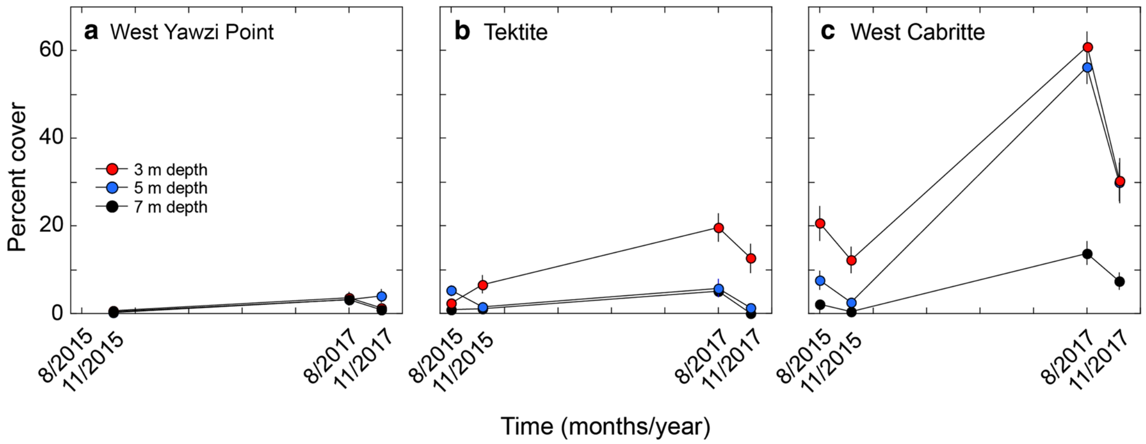

**Fig. 2** Line graph showing mean ( ± SE, $n$ = 20 quadrats along one video transects site$^{-1}$) percentage cover of PAC from August 2015 to November 2017 at 3 m, 5 m, and 7 m depth at west Yawzi Point (**a**), Tektite (**b**) and West Cabritte (**c**). Sampling began in August 2015 (Tektite and West Cabritte) or November 2015 (west Yawzi Point and second surveys of Tektite and West Cabritte) (see Bramanti et al. 2017) and was repeated in August 2017 and November 2017

disappeared (e.g., Site C, 5 m depth and Site G, 9 m depth) (Fig. 3).

Corals, CTB, and macroalgae also showed patterns of variation that differed among sites, depths, and times (Fig. 3, Table S1). As most macroalgae were growing on hard substrata, the combined cover of the four functional groups ( ≥ 75%) demonstrates that the benthos was dominated by hard substrata at all depths, sites, and times, and that a large percentage of the hard surfaces typically was occupied by PAC (22% averaged across all sites, depths, and times). Overall, Hurricanes Irma and Maria were associated with a reduction in mean ( ± SE) PAC cover from 25.8 ± 7.3% to 22.9 ± 7.3% at 5 m depth ($n$ = 10 sites), and from 13.6 ± 7.7% to 11.3 ± 8.9% at 9 m depth ($n$ = 5 sites). Additionally, mean (± SE) cover of coral (scleractinians + octocorals + *Millepora*) declined from 13.8 ± 2.3% to 10.5 ± 1.5% at 5 m depth, and from 20.4 ± 4.7% to 12.3 ± 3.0% at 9 m depth following the two hurricanes.

## Overgrowth of corals by PAC

In 2017, especially in shallow water ( ≤ 5 m depth), scleractinians and octocorals were frequently in contact with PAC, with many ( > 16%) being overgrown by this algal group (Figs. 4, 5). For scleractinians, at 5 m depth in August 2017, 47% of colonies ($n$ = 400) were in contact with PAC, with 35% of all colonies overgrown by PAC, 1% overgrowing PAC, and 11% in a neutral interaction with PAC. At 9 m depth, 23% of colonies ($n$ = 423) were in contact with PAC, with 14% of all colonies overgrown by PAC, 2% overgrowing PAC, and 7% in a neutral interaction with PAC. For octocorals in August 2017 (Figs. 4, 5), large numbers of colonies at 5 m depth (42%, $n$ = 405) were in contact with PAC, with 16% of all colonies overgrown by PAC, non-overgrowing PAC, and 25% in a neutral interaction. At 9 m depth, 18% of colonies ($n$ = 212) were in contact with PAC, with 7% of all colonies overgrown by PAC, non-overgrowing PAC, and 12% in a neutral interaction with PAC. At the same depths in November 2017, the results of the interactions between PAC and either scleractinians or octocorals largely were same (Fig. 5).

Overall, the number of corals interacting with PAC (yes vs no, pooled between depths) was independent of taxon (scleractinia vs octocorallia), or date ($G$ = 3.246, df = 1, $P$ = 0.072). For scleractinians, the outcome of interactions with PAC (overgrowth vs neutral vs overgrown) was independent of depth and time ($G$ = 0.168, df = 2, $P$ = 0.916), but the outcome of interactions with PAC depended on depth, regardless of date ($G$ = 17.294, df = 4, $P$ = 0.002) (no other two-way interactions were significant, $P \geq 0.061$). For octocorals, the outcome of interactions with PAC (overgrowth vs neutral) was independent of depth and time ($G$ = 0.015, df = 1, $P$ = 0.903), but the outcome of interactions with PAC depended on date, regardless of depth ($G$ = 16.440, df = 2, $P < 0.001$) (no other two-way interactions were significant, $P \geq 0.862$). For scleractinians, colonies touching PAC were more likely to be overgrown by PAC at 5 m (70% of these colonies) versus 9 m depth (57% of colonies), regardless of time (i.e., pooled between August and November 2017). For octocorals, colonies touching PAC were more likely to be overgrown by PAC in August (39% of colonies) than November (19% of colonies), regardless of depth (i.e., pooled between 5 and 9 m depth).

**Table 1** Results of statistical analysis of percentage cover (arcsine-transformed) of PAC from (A) video surveys conducted in November 2015, August 2017, and August 2017 at three sites (Figs. 1, 2), and (B) in-water surveys conducted in August 2017 and November 2017 at multiple sites at 5 m and 9 m depth (Figs. 1, 4)

| Effect | SS | df | MS | *F* | *P* |
|---|---|---|---|---|---|
| *(A) Video surveys* | | | | | |
| Site | 12.100 | 2 | 6.050 | 213.672 | **< 0.001** |
| Depth | 3.795 | 2 | 1.898 | 2.540 | 0.194 |
| Time | 6.780 | 2 | 3.390 | 3.386 | 0.138 |
| Site × time | 4.002 | 4 | 1.001 | 35.337 | **< 0.001** |
| Time × depth | 0.450 | 4 | 0.113 | 1.051 | 0.439 |
| Depth × site | 2.988 | 4 | 0.747 | 26.381 | **< 0.001** |
| Site × time × depth | 0.856 | 8 | 0.107 | 3.779 | **< 0.001** |
| Error | 14.519 | 513 | 0.028 | | |
| *(B) In-water surveys* | | | | | |
| 5 m depth | | | | | |
| Site | 55.576 | 9 | 6.175 | 69.917 | **< 0.001** |
| Time | 0.281 | 1 | 0.281 | 6.084 | **0.014** |
| Site × time | 0.795 | 9 | 0.088 | 1.910 | **0.048** |
| Error | 28.908 | 625 | 0.046 | | |
| 9 m depth | | | | | |
| Site | 25.880 | 4 | 6.470 | 34.649 | **0.002** |
| Time | 0.494 | 1 | 0.494 | 18.572 | **< 0.001** |
| Site × time | 0.747 | 4 | 0.187 | 7.021 | **< 0.001** |
| Error | 9.520 | 358 | 0.027 | | |
| 5 m + 9 m depth | | | | | |
| Site | 17.006 | 3 | 5.669 | 151.745 | **< 0.001** |
| Time | 0.748 | 1 | 0.748 | 8.130 | 0.065 |
| Depth | 14.421 | 1 | 14.421 | 9.864 | 0.052 |
| Time × site | 0.277 | 3 | 0.092 | 2.468 | 0.061 |
| Depth × site | 4.386 | 3 | 1.462 | 39.136 | **< 0.001** |
| Time × depth | 0.063 | 1 | 0.063 | 0.396 | 0.574 |
| Depth × time × site | 0.476 | 3 | 0.159 | 4.249 | **0.006** |
| Error | 19.985 | 535 | 0.037 | | |

Two-factor analyses were conducted as Model II ANOVAs with site as random effect and time as fixed effect; three-factor analysis was conducted as a Model III ANOVA with site as random effect, and both time and depth fixed effects. Significant effects in bold. Refer to Supplementary Material for statistic analyses of coral, CTB, and Macroalgae from in-water surveys

## Discussion

### Overview

The role of macroalgae in the coral reef crisis has been addressed in detail (McCook et al. 2001; Bruno et al. 2009; Roff and Mumby 2012), and it is common for the situation to be presented as a dichotomy between numerical or function dominance by scleractinians versus macroalgae (Bruno et al. 2009, 2014; Graham et al. 2015). This construct has proved effective in communicating the severity of the problem facing coral reefs (Hughes 1994; Pandolfi et al. 2005; Graham et al. 2015), but it is inadequate to capture the complexity of ecological processes affecting coral reef community structure (Glynn and Enoch 2011; Mumby 2017). With so much coral reef science focusing on the cover of scleractinians and macroalgae, there is the potential to overlook the early stages of ecologically meaningful changes in abundance of other functional groups or taxa. PAC provide one example of a functional group that may be in the initial phase of an upward shift in abundance in the Caribbean (e.g., Eckrich et al. 2011; Eckrich and Engel 2013; Smith et al. 2016; Bramanti et al. 2017), and this trend has the potential to substantially affect benthic community structure in the region. The present study focused on the south shore of St. John, where PAC were studied over 3 yr, ~ 760 km northeast of the putative locus [i.e., Lac Bay, Bonaire (Eckrich and Engel 2013)] of the current expansion of this functional group. In St. John, PAC increased in abundance at three sites between November 2015 and August 2017, with increases as high as 35-fold (e.g., at 7 m depth at west Cabritte) that persisted after two hurricanes. Sampling in 2017 showed that PAC were common at multiple sites, although their abundance varied among sites and depths, and through abundant contact with corals that more frequently resulted in overgrowth of scleractinians versus octocorals, showed the capacity to alter community structure in favor of octocorals. Together with reports of abundant PAC throughout the US Virgin Islands since at least 2003 (Smith et al. 2016) and within the Caribbean (Pueschel and Saunders 2009; Ballantine and Ruiz 2011; Eckrich and Engel 2013; Vázquez-Machorro et al. 2016), PAC could be poised to make a large and negative contribution to the unfolding coral reef crisis.

### PAC dynamics

Our analyses over time show that PAC increased in abundance from August 2015 to August 2017. While the cover of PAC at 5 m and 7 m depth was reduced in association with Hurricanes Irma and Maria at two of three sites, relative to the cover recorded in 2015, it remained high (i.e., 1.5- to 5.3-fold increases) at all other sites and depths. Surveys conducted in situ during November 2017 showed that large areas of PAC survived the storms at 5 m and 9 m depth (Fig. 3), and at 5 m, that the mean cover (across 10 sites) of PAC was reduced less (11% from 25.8 to 22.9%) than the mean cover of coral (24% from 13.8 to 10.5%) by the storms. The storms appeared not to alter interactions between scleractinians and PAC (i.e., to favor

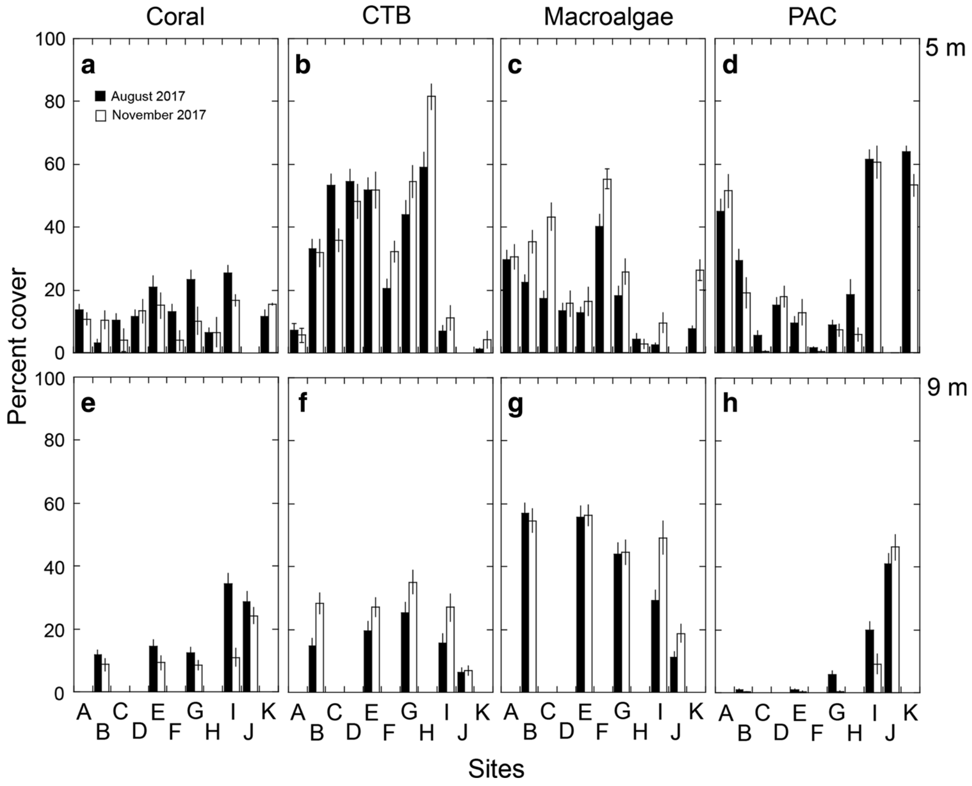

**Fig. 3** Community structure of shallow reefs at 5 m and 9 m depth for 11 sites (A–K, Fig. 1) along the south coast of St. John in August 2017 and November 2017. Values display means ± SE for four functional groups: corals (scleractinians, octocorals, and *Millepora*), crustose coralline algae, algal turf, and bare space (CTB), macroalgae (mostly), and peyssonnelid algal crust (PAC). Sample sizes (no. of quadrats): 5 m August 2017, *n* = 40, except K = 50; 5 m November 2017, *n* = 20 except C,*G* = 40; 9 m August 2017, *n* = 40; and 9 m November 2017, *n* = 40 (H,J), 20 (I), 39 (B), 32 (E)

PAC), although they were associated with a slight reduction in the extent to which octocorals were overgrown by PAC. These trends provide little reason to expect that two Category 5 hurricanes have appreciably altered the ecological processes favoring the spread of PAC in St. John. Anecdotal observations (i.e., pictures provided to PJ Edmunds by HE Clifton and C Birkeland) underscore the ecological novelty of these events, as shallow substrata near Cabritte Horn in these pictures show no signs of being occupied by PAC from 1968 and 1970 (cf. Fig. 4a).

When placed in a decadal context, the cover of PAC on the reefs of St. John in 2017 is unprecedented relative to 27 yr of photoquadrats recorded since 1992 at permanently marked sites (Edmunds 2013). Photoquadrats from May 1992 at Cabritte Horn, the site most extensively covered by PAC from 2015 to 2017, contained only traces of PAC (PJ Edmunds unpublished data), and in 2009, PAC covered only 4.3 ± 1.0% of the benthos at this site (cf 28.6 ± 3.2% in August 2017). Likewise at 9 m depth at White Point, PAC covered 2.8 ± 0.8% of the reef in July 2017, 1.2 ± 0.4% in 2015, and 0.2 ± 0.1% in 2009. At 14 m depth at Tektite, a reef dominated by the coral *Orbicella annularis* (Edmunds 2013, 2015), PAC was scarce prior to 2017 (e.g., 1.5 ± 0.3% cover in 2015), but in July 2017, it covered 3.3 ± 0.6% of the reef and was overgrowing many live colonies of *O. annularis* (PJ Edmunds personal observations). Elsewhere in the US Virgin Islands, PAC has increased in abundance in the last few years, and in 2016, it covered > 25% of reef surfaces at 8 sites around St. Thomas, St. John, and St. Croix, with a cover of 0–25% at 23 other sites (Smith et al. 2016). The most striking example of increasing abundance of PAC was recorded at 9 m depth at Savana Island ( ~ 4 km west of St. Thomas), where *Ramicrusta* spp. (inferred to be the main component of PAC in this location) increased from ~ 3% cover in 2003 to 60% in 2016 (Smith et al. 2016).

Although PAC historically have not prominently featured in ecological time series of Caribbean coral reefs, there is evidence that > 40 yr ago it occurred at low cover in many habitats (Sammarco 1980; Littler et al. 1987), although exceptions were found in some locations (e.g., James et al. 1988), particularly in shaded and deep water habitats (Goreau et al. 1973; Brawley and Adey 1977). The evidence presented here contrasts with most historical records in which PAC is mentioned, and together with records from elsewhere in the US Virgin Islands (Smith et al. 2016) and Lac Bay, Bonaire (Eckrich and Engel 2013), provides a compelling case that this algal group has increased in abundance throughout the region over the last 10–15 yrs. As discussed below, it is uncertain whether this represents a range expansion by members of a formerly inconspicuous functional group (e.g., *Peyssonnelia* spp.), or an invasion by *Ramicrusta* spp. (sensu Eckrich et al. 2011).

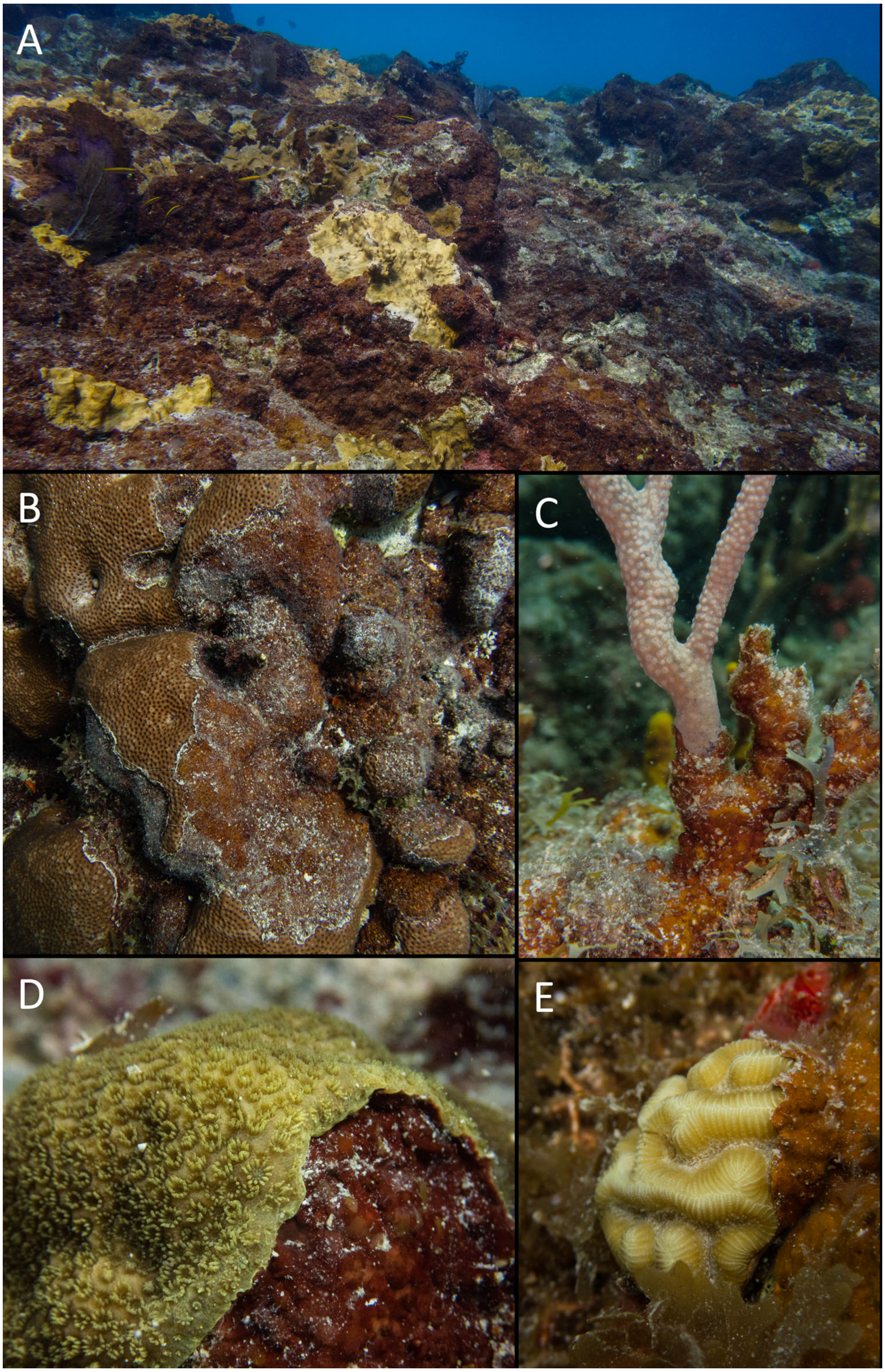

**Fig. 4** Photographs from the shallow reefs ( ~ 5 m depth) of St. John in August 2017 showing PAC interacting with a variety of taxa. **a** West Cabritte where PAC covered up to 62% of hard surfaces in July 2017, **b** PAC overgrowing *Siderastrea siderea*, **c** PAC overgrowing *Eunicea flexuosa*, **d** *Porites astreoides* overgrowing PAC, and **e** PAC overgrowing a juvenile ( < 4 cm diameter) *Pseudodiploria strigosa*

## PAC abundance in 2017

Surveys completed at 10 sites revealed large variation in community structure for four functional groups, with this variation well illustrated by PAC. Strong spatial variation in coral reef community structure is well known over scales of 10–20 km (e.g., Murdoch and Aronson 1999; Edmunds 2014; Williams et al. 2015), and even a few kilometers (Rogers 1993; Edmunds and Bruno 1996; Connell et al. 1997), with such effects often attributed to the mosaic nature of disturbance and recovery on coral reefs (Connell et al. 1997). It is consistent with these trends, therefore, to

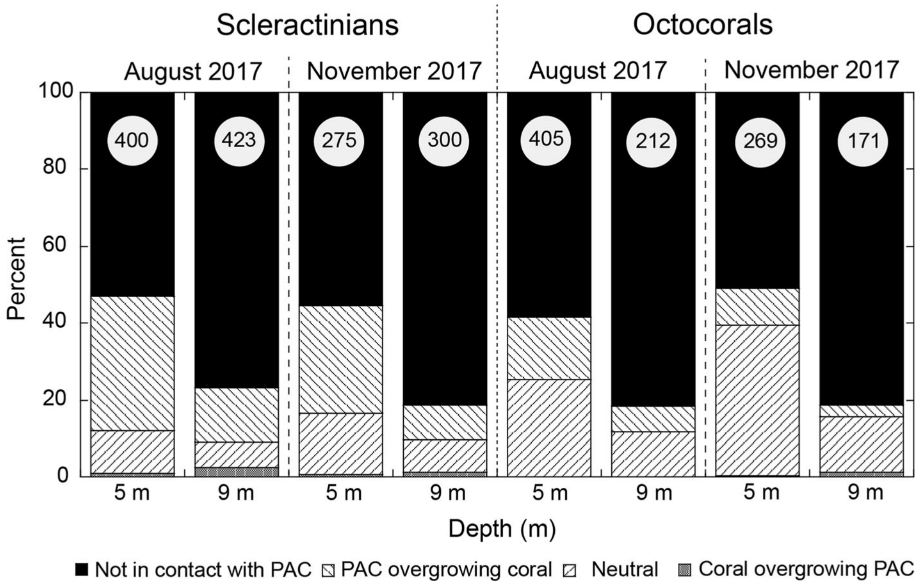

**Fig. 5** Summary of adult scleractinians (pooled among taxa, colonies > 4 cm diameter) and adult arborescent octocorals (pooled among taxa, colonies > 5 cm tall) scored for interactions with PAC at 5 m and 9 m depth. Surveys were repeated in August and November 2017 at the same sites at which PAC abundance was recorded in situ (Fig. 1), and corals were scored for: (1) independence of PAC (i.e., not in contact (2) overgrowth by PAC (as in Fig. 3) (3) neutral interaction with PAC (i.e., touching without signs of either partner overgrowing the other), or (4) overgrowth of PAC by the coral. Sample sizes (number of corals) shown in circles

have encountered such variation in the present analyses, particularly since PAC abundances varied among 31 sites around the US Virgin Islands in 2016 (Smith et al. 2016). For PAC in the present study, the causes of the spatial variation in abundance are unclear, although the preponderance of hard surfaces at 5 m depth (coral + CTB + PAC, > 65% except for north Tektite [35%]) suggests their abundance is not limited by suitable surfaces. It is possible, however, that the spread of PAC is promoted by water motion, as the highest cover of PAC was found near exposed headlands (e.g., Cabritte Horn and White Point), and the lowest cover was found in sheltered locations (e.g., Little Lameshur Bay and north Tektite). If PAC is spatially aggressive (described below, see also Eckrich and Engel 2013; Smith et al. 2016), then the among-site variability in PAC abundance on reefs in St. John might reflect the early stage of an ongoing expansion.

## Overgrowth by PAC

As spatial aggression with other taxa appears to be one means by which PAC acquires space on shallow coral reefs (Pueschel and Saunders 2009; Eckrich and Engel 2013; Smith et al. 2016; Bramanti et al. 2017), surveys were completed in St. John to quantify the frequency with which encounters between PAC and other taxa resulted in PAC growing over the adjacent organism. We reasoned that frequent occurrences of this outcome would provide insight into the potential for PAC to change benthic community structure through overgrowth and smothering. In August and November 2017 when these surveys were undertaken, 44% of corals (2455 colonies) were in contact with PAC, with contact inferred to elicit spatial competition. Although proximal mechanisms of competition were not observed, scleractinians are well known to compete for space through sweeper tentacles, sweeper polyps, mesenterial filaments, and rapid growth (Lang and Chornesky 1990), with octocorals using sweeper tentacles (Sebens and Miles 1988) thread-like tentacles (Lopez-Gonzalez et al. 2018), allelochemicals (Maida et al. 1995), and rapid growth (Gotelli 1988) for a similar purpose. In response, algae compete with corals through overgrowth, shading, abrasion, chemical interactions, space preemption, epithelial sloughing (McCook et al. 2001; Fong and Paul 2011; Rasher and Hay 2010), and bacteria associated with their surface (Nugues et al. 2004; Morrow et al. 2013). Although the mechanisms of spatial competition employed in encounters with corals (and other taxa) by PAC are unknown, their slimy surface, the unique microbial flora associated with this surface (B. Wilson pers. comm.), and the paucity of scleractinian recruits ($n$ = 2) found on the PAC-coated reefs of St. John suggest these features might contribute to the success of PAC in preempting space and growing over corals.

Overall, similar proportions of scleractinians and octocorals on the shallow reefs of St. John were in contact with PAC in 2017 (e.g., 69% vs. 60%, respectively, in August 2017), but the outcome of these interactions differed between taxa. Of the corals contacting PAC in 2017, approximately double the percentage of scleractinians versus octocorals were overgrown by PAC, and twice the percentage of octocorals versus scleractinians were engaged in neutral interactions with PAC. Potentially, our neutral interactions reflect stand-offs (sensu Connell 1976; Chornesky 1989), but sampling over time is required to accurately identify cases of temporally stable stand-off interactions. Very few corals were found overgrowing PAC, and most cases of this interaction type involved the scleractinian *Porites astreoides* (Fig. 4d), and occasionally *Acropora palmata* (PJ Edmunds personal observation) and *Agaricia agaricites* (S Zimmermann personal observation). Although the ultimate outcome of specific coral–PAC interactions are unknown since colonies were not surveyed over time, the numerous cases of complete enclosure of scleractinians and sponges observed in St. John during 2017 suggest that negative outcomes for scleractinians in coral–PAC encounters are common. Together, these observations indicate that coral–PAC encounters could promote the ongoing cryptic regime shift favoring octocorals over scleractinians (Edmunds and Lasker 2016). This possibility is further supported by the higher frequency with which PAC overgrew scleractinians (35% of contacts cases) versus octocorals (16% of contact cases), and the tendency for fewer octocorals in contact with PAC to be overgrown after the hurricanes (i.e., November 2017) versus before (i.e., July 2017). Such outcomes might arise from the rapid vertical growth of octocorals (versus scleractinians) providing escape from benthic competition with PAC, and from storm-induced flexing of octocorals causing encrusting PAC to break off the colony. As more scleractinians in contact with PAC were overgrown at 5 m versus 9 m depth, it is likely that PAC will continue to spread most aggressively in shallow water.

## Conclusion

Our results reveal the high coverage of PAC on shallow reefs in 2017, they document its capacity for rapid increases in cover and overgrowth of corals, and they show that PAC is not an ephemeral algal group that can be stripped from the reefs at a local scale by severe hurricanes (see Edmunds 2019). These trends might accentuate the coral reef crisis, both to further tip the ecological balance in favor of macroalgae (i.e., including PAC) by reducing the community resilience (sensu Gunderson 2000) of scleractinians and perhaps to reinforce a cryptic regime shift favoring octocorals over scleractinians (Lenz et al. 2015; Edmunds and Lasker 2016). A full evaluation of the ecological significance of these trends cannot be made until it is clear what taxa are driving the current spread of PAC and whether one or more is invasive to the Caribbean region.

Answers to these questions are not straightforward because the taxonomy of the peyssonnelid algae in PAC remains equivocal. *Peyssonnelia* and *Metapeyssonnelia* have been recorded at low cover on Caribbean reefs for decades (cited above), and it was not until 1981 that *Ramicrusta* (Peyssonneliaceae) was described from the region based on morphology (i.e., secondary pit connections) (Zhang and Zhou 1981); the type specimen (*R. nanhaiensis*) was described from the Paracel Islands in the South China Sea. Using molecular genetic approaches, this genus has been identified as a major contributor to PAC on the present-day Caribbean reefs (Pueschel and Saunders 2009; Eckrich et al. 2011). Three species have been described from the region (*R. textilis, R. bonairensis*, and *R. monensis* [Pueschel and Saunders 2009; Ballantine et al. 2016]), and based on their taxonomic novelty in the Caribbean (i.e., from 2009 [Ballantine et al. 2016]), and rapid expansion in one bay in Bonaire (Lac Bay), Eckrich et al. (2011) speculated that *Ramicrusta* spp. was invasive, and Ballantine et al. (2016) emphasized that their appearance was a "recent phenomenon."

Concluding that *Ramicrusta* is invasive in the Caribbean is premature, however, and definitive assignment of its biogeographic origin requires systematic sampling of PAC throughout the region. Analyses of a small area of PAC (at ~ 4 m depth) in St. John in 2017 revealed the presence of *R. textilis* using the marker genes 23S and psbA (B. Wilson pers. comm.), whereas a sample from 2015 was identified morphologically as *P. stoechas* (R. Steneck pers. comm.). Since many *Peyssonnelia* spp. have long been recognized as natural components of the algal flora of Caribbean reefs (e.g., Taylor and Arndt 1929), albeit based on morphological taxonomy, it is impossible to be certain that the PAC described herein does not contain peyssonnelids native to the region. Correctly identifying the functionally important taxon within the spreading PAC as invasive or native remains a critical research need in order to evaluate the possibility that PAC is a serious ecological threat to Caribbean reefs.

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**Compliance with ethical standards**

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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