Coral Reefs
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REPORT

Reconciling slow linear growth and equivocal competitive ability with rapid spread of peyssonnelid algae in the Caribbean

Megan K. Williams[1] · **Peter J. Edmunds**[1]

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Abstract Within the past decade, a functional group of encrusting red macroalgae defined as peyssonnelid algal crusts (PAC) has been rapidly spreading on shallow Caribbean reefs, frequently encrusting corals and sponges. This study focused on PAC growing on the reefs of St. John, US Virgin Islands, to (1) expand the monitoring of PAC abundance in this location, and (2) test two mechanisms, rapid linear growth and competitive dominance, by which PAC is hypothesized to enhance its capacity to spread. In August 2019, we found that the percentage coverage of PAC reached 46.6% at Tektite (3 m depth), and 63.8% at Cabritte Horn (3 m depth). Overall, the cover of PAC at these sites in 2019 was identical to, or up to 2.4-fold higher than in August 2017, and 2.1–3.7-fold higher than in November 2017, just after two category 5 storms impacted St. John. PAC was 1.8–29.1-fold more abundant at 3 m versus 9 m depth, and 1.4–22.0-fold more abundant at sites close to the tips of headlands than sites sheltered within bays. From August 2019 to January 2020, the rate of linear extension of PAC at each site and depth ranged from 26 to 43 µm d^{-1}, and of 80 PAC-coral interactions that were tagged in August 2019, none involved corals that had become completely overgrown by PAC by January 2020. The slow linear growth and absence of cases in which PAC completely overgrew coral colonies in 6 months are inconsistent with the high rate at which PAC has occupied space on Caribbean reefs over the past decade. One means to reconcile these observations is the possibility that recruitment of peyssonnelid spores to benthic surfaces facilitates the rapid spread of PAC.

Keywords Macroalgae · Scleractinian · Competition · Ecology

Introduction

Disturbances have long been recognized as a major determinant of community structure and function (Levin and Paine 1974; Connell 1997). Large scale changes in community structure can be followed by a phase shift to a different community state that persists under modified environmental conditions (Done 1992). Where hysteresis characterizes this response, alternative stable states can occur under identical conditions (Scheffer et al. 2001). In this situation, a reversal of the environmental conditions that initially caused the change in community structure does not result in the return to the previous stable state (Scheffer and Carpenter 2003). Spatial dominance by select community members can stabilize community states, and this in turn favors hysteresis in community structure as a function of environmental conditions (Scheffer et al. 2001). This phenomenon classically has been seen following clearance of trees in a patch of temperate forest. Once dominant trees have been cleared, the subordinate vegetation colonizes the vacant space and forms a dense cover that outcompetes the seedlings of the once dominant trees (Skutch 1929). In recent decades, most ecosystems have been exposed to numerous disturbances as a result of climate change (Hoegh-Guldberg et al. 2007), prompting resurgent interest in understanding the potential of communities to exhibit hysteresis after phase shift disturbances.

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✉ Peter J. Edmunds
peter.edmunds@csun.edu

[1] Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303, USA

Examples of community hysteresis often are equivocal because they require manipulative experiments to establish cause and effect (Scheffer and Carpenter 2003; Dudgeon et al. 2010). Some of the best examples that have experimentally demonstrated the presence of hysteresis can be found in marine ecosystems (Petraitis and Dudgeon 2004). On Caribbean reefs, transitions between spatial dominance by differing benthic taxa have often been described as examples of hysteresis (McManus and Polsenberg 2004; Norström et al. 2009), although experimental evidence has been absent (Dudgeon et al. 2010, but see Schmitt et al. 2019). In the 1980s, a widespread die-off of the sea urchin *Diadema antillarum* (Lessios 1988) was a critical event in contributing to many coral reefs transitioning to macroalgal dominance (Hughes 1994). The rapid growth and competitive capability of macroalgae resulted in this functional group preempting space on the reef, and with low population densities of herbivores, reversals in favor of scleractinians have been rare (Connell 1997; Hughes et al. 2010). Shallow reefs in the Caribbean continue to be densely populated by macroalgae, but in some cases peyssonnelid algal crusts (PAC) are involved (Edmunds et al. 2019; Williams and García-Sais 2020) as was first reported in Lac Bay, Bonaire, in 2010 (Eckrich et al. 2011).

PAC represents a functional group of macroalgae (sensu Steneck and Dethier 1994) that consists of multiple taxa within *Peyssoneliaceae*, and includes at least two genera, *Ramicrusta* and *Peyssonelia* (Pueschel and Saunders 2009; Ballantine and Ruiz 2011; Eckrich et al. 2011; Ballantine et al. 2016). While peyssonneliaceans have been described on Caribbean reefs for decades (James et al. 1988), the more recent reports include both unusually high coverage (Ballantine et al. 2011; Edmunds et al. 2019) and occurrence at multiple sites (Smith et al. 2018; Williams and García-Sais 2020). Over the last decade, PAC have spread throughout the Caribbean to include shallow reefs in Puerto Rico, Jamaica, and the US Virgin Islands (Pueschel and Saunders 2009; Ballantine et al. 2011; Smith et al. 2018; Edmunds et al. 2019). In St. John, US Virgin Islands, a high percentage cover of PAC became apparent in 2015 (Bramanti et al. 2017), and in the following two years, its cover increased three-fold at three sites, and at a quadrat scale, covered up to 100% of the benthos in 2018 (Edmunds et al. 2019). While evidence that PAC is rapidly spreading throughout the Caribbean is accumulating (Smith et al. 2018; Williams and García-Sais 2020), little is known about the mechanisms driving this trend. Given that PAC can rapidly preempt space (Ballantine et al. 2011) and has frequently been found overgrowing scleractinians and octocorals (Eckrich et al. 2011; Edmunds et al. 2019), its success may be associated with rapid linear growth (Bramanti et al. 2017) and strong competitive ability (Pueschel and Saunders 2009; Ballantine and Ruiz 2011; Eckrich and Engel 2013).

The objective of this study was to build from our previous work on PAC in St. John (Bramanti et al. 2017; Edmunds et al. 2019; Wilson et al. 2020) to explore the mechanisms by which it is changing reef communities. First, we measured the cover of PAC in 2019 to contextualize our process-oriented investigations, and to quantitatively evaluate its local population trajectory, relative to previous surveys (Edmunds et al. 2019). Second, experiments were used to test two hypotheses: (1) spatial heterogeneity between depths and sites in abundance of PAC (Bramanti et al. 2017; Edmunds et al. 2019) is driven by differential rates of growth on linear (µm d^{-1}) and planar (cm^2 $year^{-1}$) scales, and (2) PAC-coral encounters categorized as "PAC overgrowing corals", "neutral", or "coral overgrowing PAC" (after Edmunds et al. 2019) have equal mortality risks for the affected coral.

Materials and methods

Overview

This study took place on the south shore of St. John, and surveys were completed in August 2019 and January 2020 at Cabritte Horn and Tektite on the eastern side of Great Lameshur Bay. These sites were selected because the abundance of PAC has been measured in these locations since 2015 (Bramanti et al. 2017; Edmunds et al. 2019), and the high abundance of PAC created a tractable system to test for the outcomes of PAC-coral interactions. The coral community structure in St. John from 1987-present is described elsewhere (e.g., Edmunds 2018, 2019), but in brief, coral cover has been $< 4.5\%$ at six sites since 1992, but at two other sites, it has declined from 45 to 4% (Yawzi Point) and 32 to 27% (Tektite) from 1987 to 2019. Over the same period, the cover of macroalgae has increased, and the rest of the hard substratum has remained covered by crustose coralline algae, turf algae, and bare rock (combined as "CTB"). The high abundance of igneous rock on these reefs provides substratum suitable for growth of PAC (Pueschel and Saunders 2009). As PAC in St. John is more abundant in shallow (3–5 m) versus deep (5–9 m) water (Bramanti et al. 2017; Edmunds et al. 2019), surveys were designed to contrast PAC between depths. Sampling along a 15 m transect at each site and depth was used to evaluate PAC abundance, growth, and competitive encounters. An additional opportunity to evaluate PAC growth was provided by legacy settlement plates from adjacent areas upon which PAC was abundant during deployments extending from 2009 to 2019.

PAC abundance

PAC was surveyed in August 2019 in quadrats placed at random positions along transects positioned haphazardly along the 3 m and 9 m isobaths at Tektite and Cabritte Horn ($n = 20$ quadrats transect^{-1} with one transect at each site and depth). PAC abundance was determined by planar cover, which was evaluated using a quadrat (0.5 × 0.5 m) subdivided into 25 equal squares, each of which was categorically scored for planar dominance by "PAC" or benthic taxa considered together as "other". Other included octocorals, CTB, macroalgae (mostly *Halimeda, Dictyota*, and *Lobophora*), and scleractinians. With this approach, PAC abundance was resolved with 4% resolution.

Growth of PAC

Linear growth of PAC on natural substrata

Along the same transects used to quantify PAC cover, tags ($n = 20$ tags site^{-1}) were placed next to corals that were interacting with PAC, and they were used to measure both the growth rate of PAC and the outcome of the interactions (described below). Corals for tagging were selected haphazardly as encountered along the transect line, and in each case, the margin of PAC engaged in the coral-PAC encounter was marked with a numbered aluminum tag (32 mm diameter) epoxied (Z-Spar Splash Zone A-788) to nonliving substratum adjacent to the interaction. When the tags were deployed in August 2019, the shortest distance between the tag and the margin of the PAC was measured (± 0.1 mm) using calipers. In January 2020, the tags were located using a metal detector (Vibra-Probe 580, Treasure Products, Inc.), and for each coral, the tag was used as a fixed reference towards which the linear growth of PAC was recorded. The distance between the tag and PAC was measured again, and the growth of PAC recorded as the change in distance between the PAC and tag was expressed as $\mu m\ d^{-1}$. This method resolved the capacity of PAC to spread over rock, but it did not explicitly evaluate growth towards the coral.

Planar growth of PAC on settlement tiles

Unglazed terracotta tiles (15 × 15 × 1 cm) originally were deployed to measure coral recruitment (Edmunds 2018), and here photographs of the tiles were re-purposed to provide an additional measure of the planar growth of PAC. Tiles were seasoned for a year in seawater before use, and were deployed in July of each year at five sites along 5 km of the south shore of St. John at 5–6 m depth ($n = 15$ tiles site^{-1}) (Edmunds 2018). These sites were spread over the same area of coast over which PAC was studied herein. After one year, tiles were retrieved, soaked in bleach, rinsed, dried, and scored for coral recruits; new seasoned tiles then were deployed at each site. After scoring, tiles were photographed (at ~ 10 to 34 megapixels resolution), cleaned with dilute HCl, and replaced in seawater for seasoning. The orange coloration of PAC remained following bleaching, and this provided the opportunity to quantify the coverage of PAC on the upper surface of each tile. Photographs of complete sets of tiles were available for 2009, 2011, and from 2014 to 2019 ($n = 15$ tiles site^{-1} year^{-1}), but images of four additional tiles were opportunistically available from 2012. These additional tiles proved valuable in timing the potential arrival of PAC in St. John, but they were not used in the statistical analysis of the rate of growth of PAC on the tiles.

The area of PAC (cm^2) on the tiles was measured using the Trainable Weka Segmentation plugin (Arganda-Carreras et al. 2017) for Fiji software (Schindelin et al. 2012). An image classifier (random forest model) was trained to segment out PAC using a subset of labeled tiles (10 tiles year^{-1}). The models were run across the remaining images in each year to segment out PAC and measure its area on each tile. The resulting areas for each tile were then manually reviewed to resolve any misclassifications of PAC in the image. Based on the year-long immersion times of the tiles, the area of PAC on their upper surfaces was used to provide a conservative estimate of the planar growth (cm^2 year^{-1}) of PAC on unglazed terracotta.

Coral-PAC interactions

As described above, coral-PAC interactions were haphazardly selected for tagging as encountered along the transect. These interactions were < 1 m from the transect, and represented cases where scleractinian tissue was contacting PAC, and included cases when PAC already was overtopping coral tissue. Interactions were tagged regardless of the species of coral or length of the contact zone with PAC. Therefore, coral species and their interactions with PAC were sampled according to the relative abundances of these interactions in the community. The tagging of coral-PAC interactions was restricted to coral colonies > 4 cm diameter in order to minimize the effects of high coral mortality attributed to small size alone (Bak and Engel 1979). Corals were identified to species, and interactions were categorized as: (a) "PAC overgrowing coral" when the PAC was on top of coral tissue, (b) "coral overgrowing PAC'' when coral tissue was over-topping PAC, or (c) "neutral" (sensu Chadwick and Morrow 2011) when the coral and PAC met, but neither was overgrowing the other (Fig. 1).

The scheme of categorical ranking of coral-PAC interactions was used to determine whether different interaction

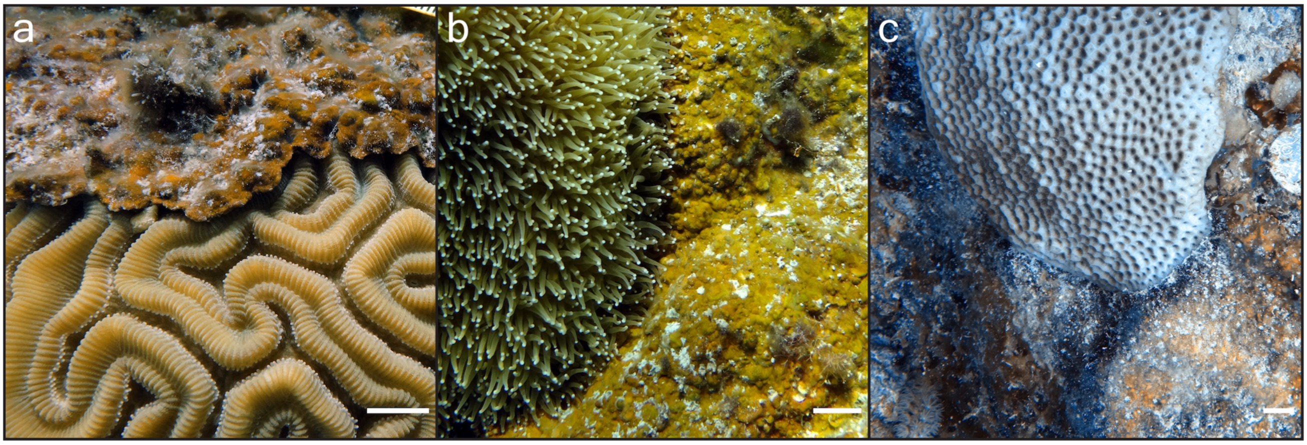

Fig. 1. An example of coral-PAC encounters that were tagged to evaluate the competitive capability of PAC. **a** PAC overgrowing *Diploria labyrinthiformis* at Cabritte Horn (3 m depth), **b** *Dendrogyra cylindrus* overgrowing PAC at Tektite (3 m depth), and **c** "neutral" where PAC and *Siderastrea siderea* are meeting at Cabritte Horn (9 m depth), but neither is overgrowing the other. Scale bars represent 1 cm.

types had equal chances for complete overgrowth of the coral by PAC. In January 2020, the tagged coral-PAC interactions were again located (described above) to evaluate their status. When the study began, we assumed from the threefold increase in PAC coverage recorded on these reefs over 2 years (Edmunds et al. 2019) that at least some of the tagged corals would be fully overgrown by PAC within 6 months. This assumption was incorrect with respect to our results and, therefore, it was not possible to score the tagged corals for the number that had become overgrown by PAC by January 2020. Instead, the corals were categorized on the same scale as used in August 2019 to test for changes in their relative rankings of interactions with PAC.

Statistical analyses

To test for variation in PAC abundance among sites and depths, a two-way fixed effects ANOVA was used in which site and depth were fixed effects, and percent cover of PAC (arcsine transformed) was the dependent variable. Differences in linear growth rate of PAC on natural substrata were analyzed using a two-way fixed effects ANOVA, with site and depth as fixed factors. As testing for an effect of depth was a primary objective of this study, growth rates were compared between depths using planned comparisons (after Sokal and Rohlf 2012). Differences among years in the growth rate of PAC on the tiles were analyzed using a two-way fixed effects ANOVA, with site and year as fixed factors, and the area of PAC covering each tile when they were recovered as the dependent variable (i.e., $cm^2\ y^{-1}$).

Assuming that the coral-PAC interactions encountered along the transects effectively were randomly selected, their frequency of occurrence in August 2019 was tested for independence among depths (3 m vs 9 m), sites (Tektite vs Cabritte Horn), and interaction type (described above) using log-linear analysis. This was used to determine whether the frequency of each interaction type could be compared between times (August 2019 vs January 2020) with a model simplified by pooling among depths and sites, with the rationale that these effects were not significant.

Statistical analyses were completed using the open-source software R ver. 3.5.1, with lme4 and Matrix packages for log-linear analysis, and DescTools for the *G*-test (R Core Team 2018). Statistical assumptions of ANOVA were tested using graphical analysis of the residuals.

Results

PAC abundance

In July 2019, some quadrats sampled many small (< 9 cm diameter) circular crusts of PAC, while others were nearly 100% covered by PAC. Quadrats that were almost fully occupied by PAC were common in shallow water (3–5 m) in exposed locations like Cabritte Horn. Anecdotally, across Great Lameshur Bay, numerous examples of octocorals and scleractinians interacting with PAC were observed. In these interactions, corals appeared to be losing their competitive encounters with PAC, based on the large extent to which they were covered by the crust. In July 2019, the mean cover of PAC was greatest at Cabritte Horn (3 m depth, 63.8 ± 3.7% ($n = 20$)) and lowest at Tektite (9 m depth, 1.6 ± 0.7% ($n = 20$)). PAC abundance differed between depths in a pattern that varied between sites ($F_{1,76} = 10.79$, $P = 0.002$), and while PAC always was more abundant in shallow water, the magnitude of this effect differed between Cabritte Horn (1.8-fold more abundant at 3 m versus 9 m) and Tektite (29.1-fold more abundant at 3 m versus 9 m) (Fig. 2a).

Growth of PAC

Linear growth of PAC on natural substrata

When the tagged corals were surveyed in January 2020, the tags typically were only covered by a thin layer of sediment or algal turf and remained < 2 cm from the PAC adjacent to which they had been placed. At Cabritte Horn (9 m depth) the PAC around one tag had retreated or been removed, thus exposing the underlying igneous rock, so that the nearest PAC was > 10 cm away. At Tektite and Cabritte Horn (3 m depth), two tags were located adjacent to areas grazed by sea urchins, and the PAC adjacent to these tags had been removed. For most other tags ($n = 73$), the PAC had grown towards the tag through positive linear growth.

Positive linear growth of PAC was greatest at 3 m depth at Cabritte Horn, where it averaged 43.0 ± 6.8 μm d^{-1}, and lowest at 9 m depth at Cabritte Horn (26.1 ± 3.8 μm d^{-1}); growth rates were similar at both depths at Tektite (33.1 ± 3.4 μm d^{-1} at 3 m and 31.8 ± 4.1 μm d^{-1} at 9 m). With no significant interaction between site and depth for linear growth ($F_{1,69} = 2.77$, $P = 0.10$), the main effects were interpreted. The linear growth of PAC was not affected by site ($F_{1,69} = 0.18$, $P = 0.67$), but there was a trend for it to differ between depths ($F_{1,69} = 3.90$, $P = 0.05$, Fig. 2b), with planned comparisons showing it was higher in shallow water at Cabritte Horn ($F_{1,69} = 6.64$, $P = 0.01$), but not at Tektite ($F_{1,69} = 0.04$, $P = 0.84$).

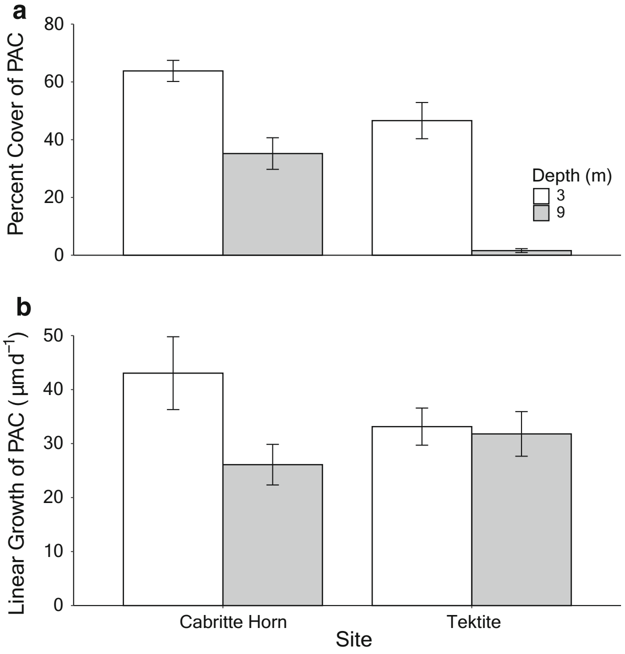

Fig. 2. **a** Percent coverage of PAC (± SE) along the shallow (3 m) and deep (9 m) isobaths at Cabritte Horn and Tektite in July 2019. $n = 20$ quadrats at each of the four reef areas. **b** Mean (± SE) linear growth of PAC on non-living substratum along the shallow (3 m) and deep (9 m) isobaths at Cabritte Horn and Tektite. $n = 18$ for both Cabritte Horn and Tektite 3 m, $n = 18$ for Tektite 9 m, and $n = 19$ for Cabritte Horn 9 m.

Planar growth of PAC on settlement tiles

The growth of PAC on settlement tiles varied widely across sites and years. Tiles with the greatest coverage of PAC consistently had PAC surrounding their perimeter, as well as circling the central hole where the tile was attached to the reef (Fig. 3). Planar coverage of PAC on the tiles was typically greatest at White Point, the headland to the west of Great Lameshur Bay, and in 2016, the highest mean growth rate of PAC on tiles was recorded in this location: 150.7 ± 6.4 cm^2 year^{-1} (Fig. 3). West Little Lameshur Bay, Yawzi Point, and Tektite had the lowest growth rate of PAC on tiles, with this trend well developed in 2009, 2011, 2018, and 2019. The lowest overall mean growth of PAC (0.5 ± 0.2 cm^2 year^{-1}) was recorded in 2009 at west Little Lameshur Bay. Growth of PAC differed among sites in a pattern that varied among years ($F_{28,521} = 8.07$, $P < 0.001$, Fig. 3).

Outcome of coral-PAC interactions

When tags were deployed in August 2019, corals interacting with PAC were common, and 17 species (10 genera) of corals in contact with PAC were tagged: *Agaricia* ($n = 5$), *Dendrogyra* ($n = 2$), *Dichocoenia* ($n = 2$), *Diploria* ($n = 6$), *Meandrina* ($n = 2$), *Montastraea* ($n = 5$), *Orbicella* ($n = 8$), *Porites* ($n = 16$), *Pseudodiploria* ($n = 15$), and *Siderastrea* ($n = 19$). All of the tagged coral-PAC interactions were found in January 2020, and most of the corals appeared unchanged relative to August 2019 with respect to the overall extent to which they were covered with PAC. A few small changes were observed along the margin of contact between the coral and PAC (e.g., "coral overgrowing PAC" changing to "PAC overgrowing coral"). Three of the corals surveyed in January 2020 were pale or white in color, with signs of tissue sloughing, and 4 were dead. At 3 m depth on Cabritte Horn, in one tagged coral-PAC interaction, a portion of the PAC covering a *Montastraea cavernosa* was inadvertently removed during scoring to reveal white, tissue-free skeleton beneath.

Log-linear analysis of the encounters categorized in August 2019 revealed independence (no three- or two-way interactions, $P \geq 0.05$) among depth, site, and encounter type (Table 1); depth and site therefore were dropped from

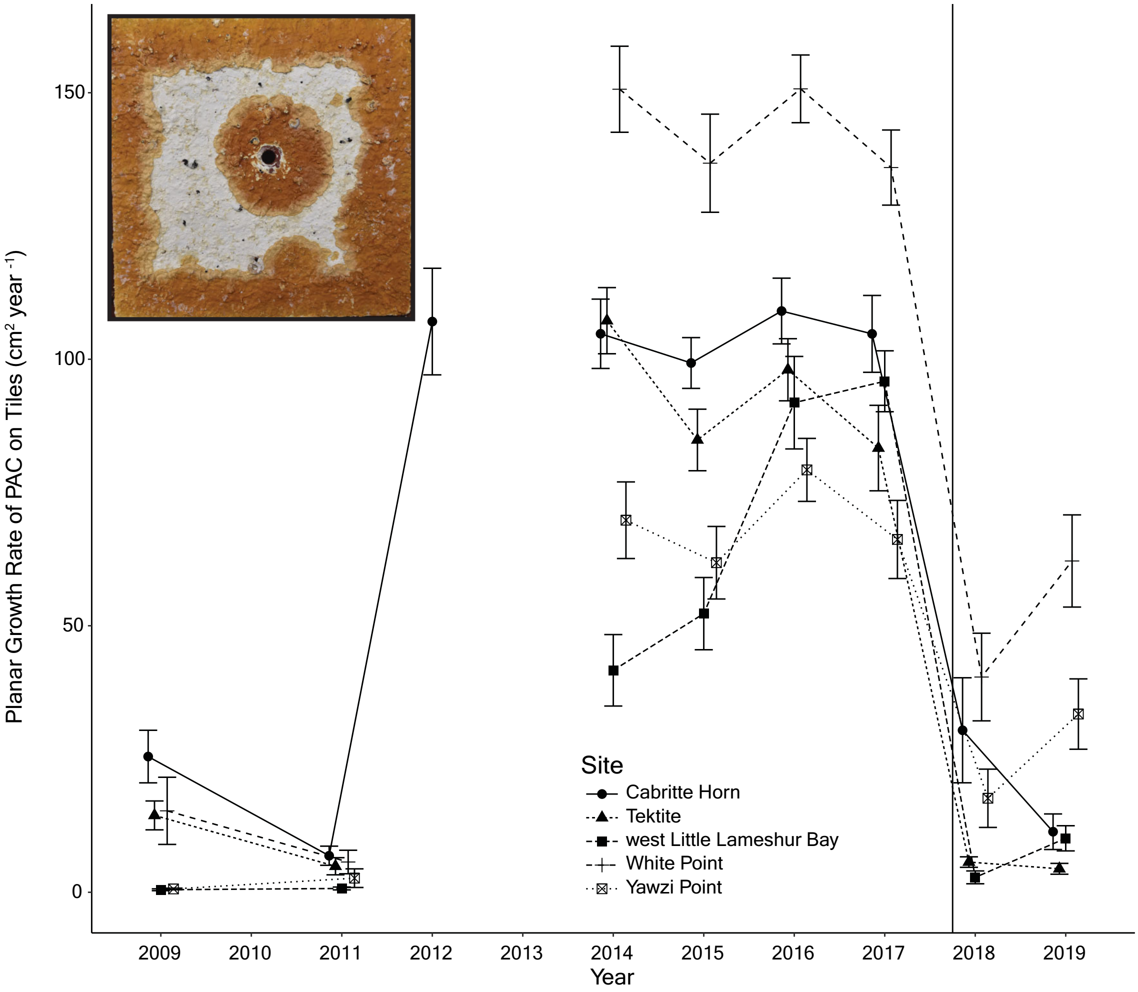

Fig. 3 Planar growth (cm^2 year^{-1}) of PAC (± SE, n = 15 tiles year^{-1}) on settlement tiles deployed at 5 sites around Great Lameshur Bay, St. John, from 2008 to 2009, 2010 to 2011, and 2013 to 2019. Four tiles were photographed from Cabritte Horn in 2012 and are included in the plot but not in the statistical analysis. Due to Hurricanes Irma and Maria hitting St. John in September 2017 (vertical line), tiles sampled in 2018 were incomplete for all five sites (n = 6–14 tiles site^{-1}), and tiles at Cabritte Horn were only deployed for 8 months. Photograph shows bleached and dried tile from Cabritte Horn in 2017, of which 70% is covered by PAC.

the model. Due to low frequencies (i.e., < 12) of interactions categorized as "coral overgrowing PAC" and "neutral" at each time, these categories were pooled as "other." A test for independence of the two-way contingency table (interaction type × time) indicated that the frequencies of each encounter type ("PAC overgrowing coral" vs "other") were independent of time (August 2019 vs January 2020) (G = 1.98, df = 1, P = 0.16). Even though the small number of some interaction types necessitated pooling, and the frequency of interaction types was independent of time, there were trends for the number of each interaction type to vary over time. By January 2020, more interactions had transitioned to "PAC overgrowing corals" than between any other pair of interaction types. For interactions scored as "PAC overgrowing coral" in August 2019 (n = 62), 95.2% remained as "PAC overgrowing coral" in January 2020; for interactions scored as "coral overgrowing PAC" (n = 6) in August 2019, 50.0% changed to "PAC overgrowing coral"; and for interactions scored as "neutral" (n = 12) in August 2019, 58.3% changed to "PAC overgrowing coral" (Table 2).

Discussion

Overview

Alternative stable states have been a focus of studies addressing changes in benthic community structure on coral reefs (Mumby et al. 2007; Dudgeon et al. 2010), and in most cases, have been presented as a dichotomy between scleractinian- versus macroalgal- dominated states (McCook et al. 2001; McManus and Polsenberg 2004; Bruno et al. 2009). The ongoing rise in abundance of PAC

Table 1. Results of Site × Depth × Encounter Type contingency table using log-linear analysis. Data collected in August 2019. Depth was 3 m and 9 m, site consisted of Cabritte Horn and Tektite, and encounter types were "PAC overgrowing coral," "coral overgrowing PAC," or "neutral."

Term	*G*	df	*P*
Three-way interaction			
Site × Depth × Encounter type	4.18	2	0.12
Conditional independence			
Site × Depth	4.20	3	0.24
Site × Encounter type	7.92	4	0.10
Depth × Encounter type	5.21	4	0.27
Independence			
Site	7.92	5	0.16
Depth	5.21	5	0.39
Encounter type	8.93	6	0.18
Complete independence	8.93	7	0.26

Table 2. Percent of PAC-coral encounters that were scored in the same category in August 2019 and January 2020, versus those that changed category when scored in January 2020.

August 2019	January 2020	Percent	*n*
PAC overgrowing coral	PAC overgrowing coral	95.2	59
PAC overgrowing coral	Coral overgrowing PAC	1.6	1
PAC overgrowing coral	Neutral	3.2	2
Coral overgrowing PAC	PAC overgrowing coral	50.0	3
Coral overgrowing PAC	Coral overgrowing PAC	33.3	2
Coral overgrowing PAC	Neutral	16.7	1
Neutral	PAC overgrowing coral	58.3	7
Neutral	Coral overgrowing PAC	8.4	1
Neutral	Neutral	33.3	4

on Caribbean reefs (Smith et al. 2018; Edmunds et al. 2019; Williams and García-Sais 2020) suggests PAC could accentuate the dominance of macroalgae as an alternative community state. The present study focused on two sites in St. John, where PAC has been studied since 2015, and it addressed mechanisms that are hypothesized to contribute to the increasing cover of PAC (Eckrich and Engel 2013; Bramanti et al. 2017; Edmunds et al. 2019). Although the spread of PAC in St. John was slowed by Hurricanes Irma and Maria in 2017 (Edmunds et al. 2019), by 2019 the dynamics of PAC appear to have returned to the trends observed prior to these storms. In 2019, PAC again was increasing in cover, it was more abundant in shallow versus deep water, and it varied spatially in abundance on a scale of 0.5 km. However, the present results from the shallow reefs of St. John are inconsistent with the notion that the recent rapid spread of PAC is associated with rapid linear growth and strong competitive ability. These results suggest that while PAC continues to increase in cover on the reefs of St. John, the mechanisms promoting its spread are more complex than rapid growth over hard surfaces (Eckrich and Engel 2013; Bramanti et al. 2017; Edmunds et al. 2019).

PAC abundance

Based on four surveys conducted over the 47 months prior to the present study, PAC on the south shore of St. John differed in abundance among sites and was more common in shallow water (Bramanti et al. 2017; Edmunds et al. 2019). Overall, the cover of PAC increased threefold from 2015 to August 2017, when it reached 19.6% at Tektite (3 m depth), and 61.0% at Cabritte Horn (3 m depth) (Edmunds et al. 2019). Three months later and following Hurricanes Irma and Maria, mean PAC cover had declined to 12.6% and 30.4% at the same sites and depths, respectively. The present results show that PAC cover at Tektite and Cabritte Horn in 2019 was 2.1–3.7-fold higher than in November 2017, and 1.0–2.4-fold higher than in August 2017. This resurgence of increasing cover of PAC also has re-emphasized the contrast in PAC abundance between depths, with PAC cover in August 2019 being 1.8–29.1-fold greater at 3 m versus 9 m depth. Since the cover of PAC in August 2019 was higher than in November and August 2017, it is reasonable to infer that the region-wide trend for increasing PAC abundance (Smith et al. 2018) has resumed following a short-lived set-back in St. John (Edmunds et al. 2019).

In addition to PAC resuming its increase in cover in St. John (cf. Edmunds et al. 2019) following the hurricanes, spatial variation in PAC abundance was similar before and after these events. Determining the factors promoting both high and variable abundance of PAC was beyond the scope of this study, but there are at least two hypotheses to explain these patterns. First, because high flow promotes the growth of encrusting algae (Littler and Littler 1984), facilitates the delivery of algal spores to the benthos (Norton 1992), and deters fish herbivory (Bejarano et al. 2017; Karkarey et al. 2020), it is possible that high flow also promotes the growth and recruitment of PAC. On the south shore of St. John, the highest cover of PAC consistently has been recorded on exposed headlands (Bramanti et al. 2017; Edmunds et al. 2019). In 2019, the cover of PAC was highest at Cabritte Horn, which is exposed to waves (Witman 1992), and lower at Tektite, which is sheltered (Treml et al. 2002). This trend is supported by variation among sites in the cover of PAC on settlement tiles, as the tiles were more extensively covered by PAC at exposed (Cabritte Horn and White Point) versus sheltered

(West Little Lameshur and Tektite) sites over 5 years. While recent growths of PAC have been reported from a variety of habitats, including sheltered (Eckrich and Engel 2013) and deep locations (Smith et al. 2018), the present data, as well as reports from exposed locations like Vieques and Culebra (east of Puerto Rico (Williams and García-Sais 2020)), suggest high cover of PAC is promoted by water motion.

Second, high recruitment of PAC could facilitate rapid increases in cover (Santelices 1990). Although the recruitment of peyssonnelid spores was not recorded in the present study, the recruitment of small PAC individuals was assayed through their appearance on tiles deployed for a year and, anecdotally, through observation of small (i.e., ≤ 9 cm diameter) individuals of PAC on natural surfaces. Tiles similar to those deployed here are a well-established tool for measuring recruitment of encrusting algae (Kennedy et al. 2017), and here the analysis of settlement tiles supports two conclusions. First, the consistent appearance of PAC on tiles since at least 2014 (perhaps since 2012 (Fig. 3)) suggests that PAC recruitment has been ecologically meaningful in St. John for at least 6 years. Second, the differences among sites in coverage of the tiles by PAC agrees with the notion that recruitment also varies among sites. This interpretation is consistent with anecdotal observations of a high abundance of PAC individuals at some sites but not others. In August 2019, numerous small (≤ 9 cm diameter) PAC individuals were found at Tektite, and high densities (11 ± 2 individuals m^{-2}) of similar-sized crusts were counted at 3 m depth at Yawzi Point (M. Williams unpublished data). Yet at other sites, very few PAC individuals were found. Rhodophyta tetraspores can support high rates of recruitment (Ngan and Price 1983), and because they are non-motile (van den Hoek et al. 1995), the enhanced water motion in areas with high flow may accentuate the delivery of peyssonnelid tetraspores to the benthos, resulting in a higher abundance of PAC (Norton 1992).

Growth and competitive ability of PAC

To shed light on the mechanisms utilized by PAC to rapidly increase in cover, the growth rates of PAC were measured, and interactions between corals and PAC were monitored to determine their outcome. Evaluating the ecological implications of the empirical linear growth of PAC requires benchmarking against the growth rates of algae in a similar functional group (sensu Steneck and Dethier 1994), but such data remain sparse. One comparison is supported by the Caribbean macroalga *Lobophora variegata*, the encrusting form of which extended at ~200–600 µm d^{-1} in Curaçao (calculated from Nugues and Bak 2006), and another by the crustose coralline alga *Sporolithon durum* from New Caledonia, which extended at 1.6 µm d^{-1} (Darrenougue et al. 2013), both in shallow water (< 5 m depth). While the present growth rates of PAC (i.e., 26–43 µm d^{-1}) are at the low end of this range and are similar to growth rates of PAC reported from Bonaire (Eckrich and Engel 2013), they are incongruent with the speed with which the benthos has been covered by PAC in St. John. For example, Edmunds et al. (2019) reported a change in PAC cover corresponding to an increase of 1.7% $month^{-1}$ at 3 m depth at Cabritte Horn, which represents hard substratum being occupied at ~ 168 cm^2 $month^{-1}$.

The higher coverage of PAC in shallow versus deep water (Fig. 2a and Edmunds et al. 2019) is consistent with the 65% faster rate at which PAC extended at 3 m versus 9 m depth at Cabritte Horn. It is unclear why this effect was absent at Tektite, although the sea urchin *Diadema antillarum* was common in shallow water at this site, but uncommon across a wider depth range at Cabritte Horn. While *D. antillarum* were not observed grazing PAC in shallow water at Tektite, the advance of PAC adjacent to two tags (11% of the tags at this site/depth) was reduced by ~ 20% compared to other tagged locations at the same depth. Because clusters of *D. antillarum* were located < 0.5 m from the tagged interactions, it is likely that cases of reduced PAC advance were within the grazing ranges of *D. antillarum* (sensu Ogden et al. 1973), from which PAC could have been removed by *D. antillarum* grazing (Sammarco 1980; Williams and García-Sais 2020). More generally, therefore, *D. antillarum* may have contributed to similar mean extension rates of PAC at 3 m and 9 m depth at Tektite. Together, the slow growth rates of PAC (present study and Eckrich and Engel 2013), juxtaposed with the high rate at which PAC has occupied benthic space on some Caribbean reefs (Eckrich and Engel 2013; Bramanti et al. 2017; Edmunds et al. 2019), requires explanation.

Beginning with the initial reports of the recent spread of PAC in the Caribbean (Pueschel and Saunders 2009; Eckrich et al. 2011), several studies have alluded to the strong competitive ability of PAC when confronted by corals as a factor contributing to the spread of PAC (Ballantine and Ruiz 2011; Eckrich and Engel 2013; Edmunds et al. 2019). Eckrich and Engel (2013) reported that PAC (i.e., *Ramicrusta* sp.) grew over the scleractinians, *Porites astreoides* and *P. porites*, and the hydrocoral, *Millepora complanata*, at 60–80 µm d^{-1} over ~ 11 months, and after 18 months, had overgrown 10 of 27 monitored corals. While Eckrich and Engel (2013) demonstrated the potential for PAC to overgrow corals, the features of their shallow and sheltered study site in Bonaire warrants caution in extrapolating the outcomes to other reef habitats. To better understand how the competitive ability of PAC varies among depths and habitats, we completed our study in the exposed portions of Great Lameshur Bay, St. John, where the fringing reefs are characterized by large igneous features, depths extending to ~ 15 m, and flow speeds that are generally low but which can reach 19 cm s^{-1} (Horst and Edmunds 2010).

With 5 years of data showing that PAC has rapidly spread throughout Great Lameshur Bay, it was reasonable to expect that a 6 month analysis of coral-PAC encounters would reveal unambiguous outcomes. While our analysis did not show dominance of PAC in coral-PAC interactions, it revealed examples of encounters initially scored as "coral overgrowing PAC" and "neutral" shifting to cases of "PAC overgrowing coral." In contrast, most encounters initially scored as "PAC overgrowing coral" were unchanged 6 months later. These observations are consistent with the hypothesis that PAC ultimately would overgrow corals that they encounter given sufficient time, but further experimental analyses are required to test this possibility. It is important to note, however, that our results were obtained from coral-PAC interactions that did not include small corals (i.e., colonies < 4 cm diameter) because we expected these would exhibit high mortality regardless of PAC (e.g., Bak and Engel 1979). Ultimately, interactions between PAC and small corals (< 4 cm diameter) were rare in our surveys, which raises the possibility that they already had been overcome and smothered by PAC.

This slow progression of PAC over corals, and absence of definitive outcomes of such interactions, in part is a product of the slow growth rate of PAC. Through growth at 26–43 µm d^{-1}, PAC interacting with an adult coral (> 4 cm diameter) would require > 30 months to fully overgrow the colony. Further, the defenses that can be utilized by scleractinians engaged in competition with algae (Nugues et al. 2004; Vieira 2020) can prevent overgrowth of the coral for up to a year (De Ruyter van Steveninck et al. 1988; Nugues and Bak 2006), and might also deter PAC. Overall, contrary to expectations that coral-PAC interactions would turn into full overgrowth by PAC within 6 months (i.e., a competitive win (Chornesky 1989)), we found little-to-no change in the extent to which corals engaged in interactions with PAC were overgrown by PAC.

Reconciling slow linear growth with high coverage of PAC

Together, the present results and those of recent studies (Eckrich and Engel 2013; Edmunds et al. 2019; Williams and García-Sais 2020) present a challenge to reconciling evidence that PAC is rapidly spreading throughout the Caribbean, with evidence that its linear growth rates are slow, and it cannot achieve rapid competitive superiority over corals. Although the present growth rates of PAC recorded from the summer to winter leave open the possibility that growth is faster over the remainder of the year (i.e., winter–summer), this hypothesis is inconsistent with the similarity of the present growth rates with those of Eckrich and Engel (2013), who recorded growth over almost a year. However, populations grow through demographic events that include growth rates of individuals, recruitment, and mortality. In the case of PAC spreading in St. John and the wider Caribbean, it is challenging to account for these observations without evoking a role of PAC recruitment.

Neither reproduction nor dispersal of peyssonnelid algae is completely understood. The benthic crust of peyssonnelids consists of tetrasporophyte and gametophyte life stages, and sexual reproduction, although rare (Santelices 1990), occurs through syngamy of non-motile gametes to form an attached carposporophyte (van den Hoek et al. 1995). The carposporophyte produces carpospores that are released (Boney 1978), and while these are non-motile (van den Hoek et al. 1995) and probably negatively buoyant (Amsler and Searles 1980), they can disperse over scales of 1–10 m (Boney 1978; Kinlan and Gaines 2003). While such dispersal could sum to large distances in shallow water, it remains challenging to account for dispersal among islands separated by deep water, unless rafting is employed (Holmquist 1994; Fenner and Banks 2004). Settled carpospores develop into a tetrasporophyte crust which produce asexual tetraspores that also can undergo non-motile, local-scale dispersal (Fletcher and Callow 1992). When combined with the high likelihood that PAC can produce large numbers of tetraspores, like other red algae (Ngan and Price 1983), but has low rates of linear growth (this study, Eckrich and Engel 2013), a possibility that deserves attention is that the delivery of tetraspores is supporting rapid spread of PAC on present-day reefs throughout the Caribbean. Understanding of the reproduction of tropical peyssonnelids may, therefore, be the key to reconciling rapid spread over years and kilometers, with slow growth over months and centimeters. Before studies of these processes can begin, effective methods will be required to identify the multiple species (James et al. 1988; Pueschel and Saunders 2009; Ballantine et al. 2016) involved in the spread of PAC on present-day reefs.

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Data availability Data reported in this paper are available at https://www.bco-dmo.org/project/734983, https://doi.org/10.26008/1912/bco-dmo.836071.1, https://doi.org/10.26008/1912/bco-dmo.836097.1, https://doi.org/10.26008/1912/bco-dmo.836164.1, https://doi.org/10.26008/1912/bco-dmo.836304.1.

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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