Linear growth and competitive ability of Peyssonnelid Algal Crusts at St. John, USVI

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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 Peyssonnelid Algal Crusts (PAC) has been measured in these locations since 2015, 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, 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 1987–2019. 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. As PAC in St. John is more abundant in shallow (3–5 m) versus deep (5–9 m) water, 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 – 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"; octocorals, CTB, macroalgae (mostly *Halimeda, Dictyota*, and *Lobophora*), and scleractinians were scored as "other". 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 with corals (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 non-living 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 µm 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, 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 $site^{-1}$). 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 – 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 for Fiji software. 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 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. 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 and skeleton were over-topping PAC, or (c) “neutral” 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 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 3-fold increase in PAC coverage recorded on these reefs over 2 years 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. 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 transect lines 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. Statistical assumptions of ANOVA were tested using graphical analysis of the residuals.