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Ramicrosta invasive alga causes mortality in Caribbean coral larvae

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The settlement of coral larvae is an important process which contributes to the success and longevity of coral reefs. Coral larvae often recruit to benthic structures covered with crustose coralline algae (CCA) which produce cues that promote settlement and metamorphosis. The Peysonneliaceae *Ramicrosta* spp. are red-brown encrusting alga that have recently become abundant on shallow Caribbean reefs, replacing CCA habitat, overgrowing corals and potentially threatening coral recruitment. In order to assess the threat of *Ramicrosta* to coral recruitment, we compared the survival and settlement of *Porites astreoides* and *Favia fragum* larvae to 0.5 – 2 mg ml⁻¹ solutions of *Ramicrosta* sp. or CCA as well as sterile seawater (control). In all cases larval mortality was extremely high in the *Ramicrosta* treatments compared to the CCA and control treatments. We found 96% ($\pm$ 8.9% standard deviation, SD) mortality of *P. astreoides* larvae when exposed to solutions of *Ramicrosta* and 0 – 4% ($\pm$ 0 – 8.9% SD) mortality in the CCA treatments. We observed 100% *F. fragum* larval mortality when exposed to *Ramicrosta* and 5 – 10% ($\pm$ 10 – 20% SD) mortality in the CCA treatments. Settlement or surface interaction of larvae in the CCA treatments was 40 – 68% ($\pm$ 22 – 37% SD) for *P. astreoides* and 65 – 75% ($\pm$ 10 – 19% SD) for *F. fragum*. Two *P. astreoides* larva that survived *Ramicrosta* exposure did settle/surface interact, suggesting that some larvae may be tolerant to *Ramicrosta*. These results suggest that *Ramicrosta* is a lethal threat to Caribbean coral recruitment.

KEYWORDS

coral reef, ecology, USVI, coral larvae, settlement, recruitment, *Ramicrosta*, Peysonneliaceae

Introduction

Coral reefs are biodiverse ecosystems that provide coastal protection, food and other economic benefits to coastal and island communities. Scleractinia corals form the structural framework of this habitat. Key requirements for the success and longevity of reefs is for larval corals to settle onto reefs, grow into larger colonies and regularly reproduce.

Unfortunately, numbers of juvenile corals have recently decreased on many reefs (Edmunds et al., 2015; Hughes et al., 2019), suggesting that settlement and recruitment processes may be declining. Due to the small size of coral recruits and many possible stressors, specific factors attributing to this decline are challenging to document on reefs.

Ideal settlement substrates are one component contributing to successful coral recruitment. Some coral larvae preferentially settle on reef bedrock covered with crustose coralline algae (CCA; Rhodophyta family Corallinaceae). This relationship is related to chemical signals released by the CCA and/or associated microorganisms (Heyward and Negri, 1999; Negri et al., 2001; Sneed et al., 2014; Tebben et al., 2015). The presence of CCA is generally associated with high reef health or quality (Ritson-Williams et al., 2009). However, CCA has been replaced in some shallow reefs by encrusting red-brown colored algae of the Peyssonneliacean family, including *Ramircrusta* spp. (Pueschel and Saunders, 2009; Eckrich et al., 2011; Ballantine et al., 2016; Edmunds et al., 2019; Nieder et al., 2019). While *Ramircrusta* is known to have similar form and growth patterns as CCA, it behaves differently in that it frequently overgrows mature corals (Eckrich and Engel, 2013; Nieder et al., 2019). There is limited evidence of juvenile coral recruitment on *Ramircrusta*, with studies finding very limited (Edmunds et al., 2019) to no coral recruits on *Ramircrusta* coated surfaces (Eckrich and Engel, 2013). There are also differences in the microbial biofilms harbored by CCA and *Ramircrusta* which could additionally impact settlement (Wilson et al., 2020). *Ramircrusta* is considered invasive to shallow Caribbean reefs and studies suggest that the rapid spread of *Ramircrusta* may leave little suitable settlement substrate available for coral larvae (Eckrich and Engel, 2013; Edmunds et al., 2019).

While there is evidence that *Ramircrusta* is a threat to adult corals, little is known about the effects of *Ramircrusta* on coral larvae and the settlement process. Here, we conducted a laboratory study using larvae from the Caribbean corals *Porites astreoides* and *Favia fragum* to investigate the impact of *Ramircrusta* and CCA solutions on larval mortality/survivorship and settlement. We show that *Ramircrusta* exposures cause high larval mortality compared to CCA.

Materials and methods

Sampling and coral spawning

Porites astreoides and *Favia fragum* adult colonies (12–20 of each species) were collected from 2–12 m using hammer and chisel from the southern shore of St. John, U.S. Virgin Islands several days before spawning. Corals were held in shaded seawater tables consisting of flowing, non-filtered seawater. During their respective spawning periods, corals were placed overnight in 63 μm mesh baskets and the seawater level was dropped in the sea table to contain the larvae. The baskets were checked for larvae the following morning and the water level was subsequently raised to allow the corals to feed. *P. astreoides* coral larvae collection began several days before the new moon of June (Goodbody-Gringley

et al., 2021) and *F. fragum* collection began 5–8 days after the new moon of July (Szamant-Froelich et al., 1985). Swimming larvae that were not exhibiting substratum searching behavior were collected and transferred into a container containing sterile seawater filtered using a 0.2 μm Supor filter (Millipore) under peristaltic pressure.

On the day of each experiment, igneous rocks containing pink coral crustose algae (CCA) or *Ramircrusta*, both identified based on morphology and coloration, were obtained from shallow 1–3 m southern shore St. John reefs. CCA was identified as a pink algal crust growing without the presence of *Ramircrusta*. *Ramircrusta* was consistently defined as a dark algal crust with mustard coloration (Ballantine et al., 2016).

Exposure experiments

To make the solutions, the *Ramircrusta* or CCA fragments were washed 5 times with filtered seawater and subsequently shaved off several rocks using a razor blade while carefully avoiding any substrate underneath. The shavings were weighed and ground into a powder using a mortar and pestle. Each powdered amount of *Ramircrusta* or CCA was added to a graduated cylinder with 60 ml of fresh 0.2 μm filtered sea water and stirred until a homogenous solution was formed. Each 60 ml solution was distributed into a 6-well plate, each well received 10 ml of a 0.5, 1, or 2 mg ml^{-1} solution of *Ramircrusta* or CCA. The concentrations were determined based on Pollock et al. (2017) who used a similar method to examine the optimal dosage of CCA for larvae settlement.

The *P. astreoides* and *F. fragum* experiments were conducted separately due to the differential spawning times. Each experiment used 6-well plates (16.8 ml well holding capacity, Costar, Corning Incorporated; Figure 1) and each plate was devoted to a separate treatment (5 wells per treatment, 10 ml sterile water or solution to each well).

In the first experiment *P. astreoides* larvae (5 wells each containing 5 larvae) were added to the following treatments: sterile seawater (control), 1 mg ml^{-1} of CCA, 2 mg ml^{-1} of CCA, 1 mg ml^{-1} of *Ramircrusta*, and 2 mg ml^{-1} of *Ramircrusta*. Due to the high larval mortality associated with *Ramircrusta* in the first experiment, concentrations of solutions were reduced for the second experiment to examine the impact of a lower dose. Therefore, in the second experiment *F. fragum* larvae (5 wells each containing 4 larvae) were exposed to the following treatments: sterile seawater (control), 0.5 mg ml^{-1} of CCA, 1 mg ml^{-1} of CCA, 0.5 mg ml^{-1} of *Ramircrusta*, and 1 mg ml^{-1} of *Ramircrusta*. Both experiments were conducted at indoor ambient laboratory temperature (approximately 26–28°C) with regular 12 h light/12 h dark room lighting (no aquarium lighting) for 48 hours. When the experiment ended, the 5 wells of each treatment were examined under a dissecting microscope at 10.5x magnification. The larvae were first examined for mortality as “alive” or “dead/unaccounted” and then quantified by categorizing each as “interacting with substrate”, “swimming”, or “dead/unaccounted” (Birrell et al., 2008). Percentage of larval mortality (or settlement/surface interaction) in each well were further examined using statistical approaches.

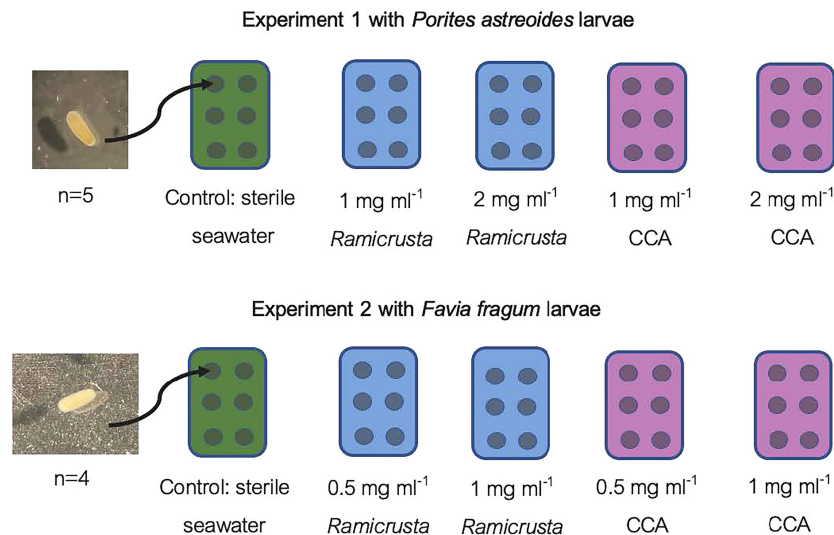


FIGURE 1

The experimental design for the larval exposure experiments. Each rectangle with six circles represents a 6-well plate and the circles represent 16.8 ml wells containing larvae and treatment. Green represents the sterile seawater, blue represents solutions containing *Ramicrusta*, and pink represents a solution containing CCA. Each well contained 10 ml of the solution or sterile seawater, and 5 wells each containing 4–5 larvae were examined per treatment.

The data were examined using SigmaPlot software (version 13, SYSTAT Software) using a Shapiro-Wilk test to determine if data were normally distributed. Based on the non-normality of our data distribution, we used a Kruskal-Wallis One-Way Analysis-of-Variance-on-Ranks (H test), and a Tukey *post-hoc* all pairwise multiple comparisons procedures with a significance level of $p < 0.05$ to examine pairwise trends.

Results

For both species of coral, larval mortality was the highest in the *Ramicrusta* treatments and there was a significant effect of treatment on larval mortality (H test, $p < 0.003$, [Supplementary Table 1](#)). For *P. astreoides*, mean larval mortality was 96% ($\pm 8.9\%$ standard deviation, SD) for both the 1 and 2 mg ml⁻¹ *Ramicrusta* treatments ([Figure 2A](#)). Mortality in the 1 mg ml⁻¹ CCA treatment was 4% ($\pm 8.9\%$ SD) and there was no mortality in the 2 mg ml⁻¹ CCA or sterile seawater treatments. Significantly more *P. astreoides* larvae survived in the control and 2 mg ml⁻¹ CCA compared to the *Ramicrusta* treatments ($p = 0.031$, H test with Tukey comparison), but the other *post-hoc* comparisons were either not significant ($p > 0.05$) or non-testable due to the lack of significant difference between the rank sums ([Supplementary Table 1](#)). There was 100% mortality in the *F. fragum* treatments with *Ramicrusta* and 10% ($\pm 20\%$ SD) and 5% ($\pm 10\%$ SD) mortality in the 0.5 and 1 mg ml⁻¹ CCA treatments, respectively with complete survival of larvae in the sterile seawater ([Figure 2B](#)). *Post-hoc* statistical comparisons were either not significant ($p > 0.05$) or non-testable due to no significant difference between the rank sums ([Supplementary Table 1](#)).

There was a significant effect of treatment on larval settlement and survivorship for both species of coral (H-test, $p < 0.005$,

[Supplementary Table 1](#)) and the highest settlement and surface interaction occurred in the CCA treatments. Mean *P. astreoides* settlement/surface interaction was 68% ($\pm 23\%$ SD) and 40% ($\pm 37\%$ SD) for the 1 and 2 mg ml⁻¹ CCA treatments, respectively ([Figure 2C](#)). One *P. astreoides* larva survived in each 1 mg ml⁻¹ and 2 mg ml⁻¹ *Ramicrusta* treatment. While both larvae showed evidence of settlement/surface interaction, the settlement/surface interactions in the *Ramicrusta* treatments were significantly lower than in the 1 mg ml⁻¹ CCA treatment ([Figure 2C](#), $p = 0.019$). Mean *F. fragum* settlement/surface interaction was 65% ($\pm 19.1\%$ SD) and 75% ($\pm 10\%$ SD) for the 0.5 and 1 mg ml⁻¹ CCA treatments, respectively ([Figure 2D](#)). Significantly more larvae interacted with the surface in the CCA 1 mg ml⁻¹ compared to each *Ramicrusta* treatments ($p = 0.021$), which is partially attributed to the complete mortality of *F. fragum* larvae exposed to *Ramicrusta*.

Discussion

Ramicrusta is a rapidly expanding encrusting algae that is especially prolific on shallow Caribbean reefs. Here we used exposure experiments to show that *Ramicrusta* causes mortality in larvae from two species of prominent brooding Caribbean corals, suggesting that *Ramicrusta* may be toxic to the larvae. We observed limited larval mortality ($< 10\%$) in our CCA exposure experiments, and 40–80% of these CCA-exposed larvae exhibited settlement or surface interactions, thus suggesting that the experimental conditions and solution concentrations were appropriate for the larvae. Notably, one *P. astreoides* in each *Ramicrusta* treatment (1 and 2 mg ml⁻¹) survived and showed evidence of settlement/substrate interaction, signifying that select coral larva may tolerate *Ramicrusta*, which could signify metamorphosis under stress ([Kitchen et al., 2022](#)).

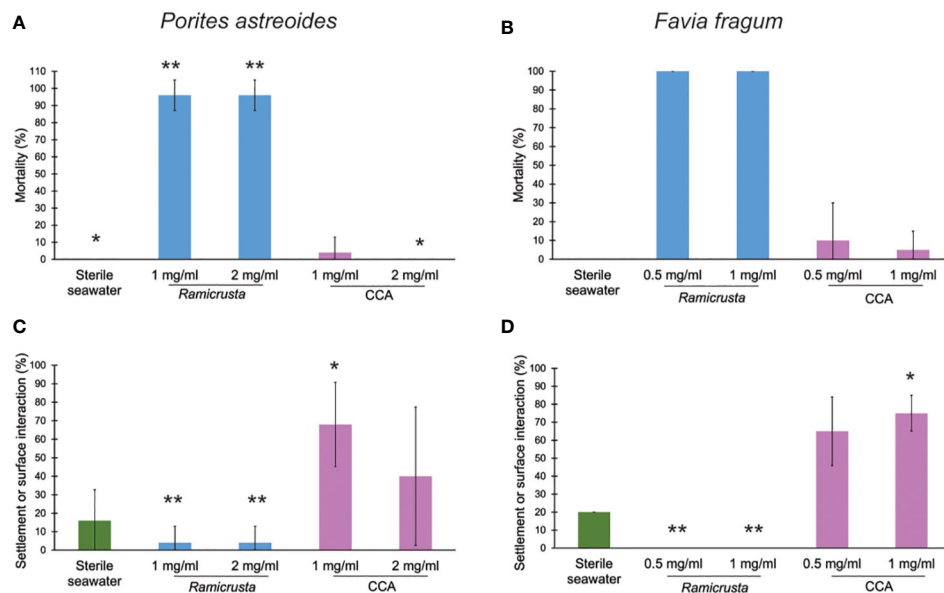


FIGURE 2

Ramircrusta exposure causes larval mortality and reduced settlement. The average percent ($\pm$ SD) of *P. astreoides* (A) and *F. fragum* (B) larval mortality in the treatments (5 wells each containing 4–5 larvae) and percent of *P. astreoides* (C) and *F. fragum* (D) larvae that settled or interacted with the well surface (5 wells each containing 4–5 larvae). There was no mortality in the sterile seawater treatment of either experiment. Significantly different treatments according to Kruskal-Wallis H-test and Tukey Test *post-hoc* test are denoted by different asterisks groups (e.g., * and ** are significantly distinct) and are distinct for each figure panel ($p < 0.05$).

Our data suggest that *Ramircrusta* may contain or produce metabolites toxic to coral larvae. A recent study showed that *Ramircrusta textilis* produced caffeine, among other metabolites (Weber et al., 2022). Caffeine is a common deterrent of herbivores and pathogens by land plants (Kim et al., 2010), and it has adverse growth impacts on insect larvae (Srinivasan and Kesavan, 1977; Maguire et al., 2017). The impact of caffeine, as well as other *Ramircrusta* producing metabolites, on coral larvae is an area for further investigation.

Our study exposed coral larvae to *Ramircrusta* that was dissolved in solution at specific concentrations. While our CCA exposure experiments at similar doses resulting in settlement suggests that these concentrations may be in-line with natural exposure and other larval studies (Pollock et al., 2017), future studies could expose larva to surfaces with encrusted with *Ramircrusta* (instead of solutions) to verify the impact of typical surface-type exposures on larval survival and settlement. Here we used solutions to achieve homogeneity in all replicates, which may be more inconsistent with *Ramircrusta* surfaces due to differential biofilms on the surfaces. Additionally, we only evaluated two concentrations of *Ramircrusta* solutions and response could be evaluated with lesser dilutions of *Ramircrusta*. However, our results are in line with prior observations of no to limited coral settlement on *Ramircrusta* coated surfaces (Eckrich and Engel, 2013; Edmunds et al., 2019). Our experiments used replicate wells within a plate for each treatment which may introduce a plate-type effect in our study. Future experiments should randomize treatments within each plate and/or use separate plates for each replicate within a treatment to strengthen the experimental design and resulting conclusions. It should also be noted that only two species of coral larvae were used in this experiment, and expansion to additional

species are warranted, as well as molecular genotyping to verify the species of *Ramircrusta*. Here we observed slightly elevated settlement in *F. fragum* compared to *P. astreoides* larvae which signifies species-related differences. Indeed, *F. fragum* typically settles within the first 24 hours (Goodbody-Gringley, 2010), and *P. astreoides* can maintain longer larval durations (Harrison and Wallace, 1990).

Overall, our results add to the growing knowledge that *Ramircrusta* is harmful to corals and is a potential threat to Caribbean reefs. Research that explores herbivory controls as well as other intervention mechanisms to remove or inhibit *Ramircrusta* spread on reefs is urgently needed to prevent further reef decline.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

Author contributions include study conception, design and funding (AA, TM), experimentation (KC, NA, SF), data analysis (KC, AA), writing (KC, AA), and editing (all authors). All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2023.1158947/full#supplementary-material>