Insights into *Coralliophila spp.* predation mitigation on *Acropora spp.*

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Abstract

Coralliophila spp. snails are known to interfere with restoration efforts of *Acropora cervicornis* and *A. palmata*, both threatened reef-building coral species. Mitigating the negative effects of these coral predators has been labour intensive, unsustainable or just ineffective. Mitigation measures building on ecological dynamics are needed to restore resilient coral populations. In this study, possibilities for mitigation of corallivory by *Coralliophila* snails were explored experimentally. An *ex situ* experiment was performed to study if elevating coral fragments, *A. cervicornis*, by placing it onto rebar or PVC structures would mitigate predation by these snails. The potential effect of elevation was also tested by outplanting *A. cervicornis* fragments with masonry nails (0cm) and elevated on rebar (15cm) on a natural reef. In this *in situ* experiment, the effect of outplant density on snail colonization was also tested by comparing low and high densities of 1 and 5 corals per m^2. To gain insight into the role of possible *Coralliophila* snail predators, snails were exposed on concrete blocks and filmed to record any predation. Concurrent surveys on wild colonies showed that snail abundance per coral colony and reef can differ greatly and that the presumed snail predators, *Thais deltoidae*, do occur on these corals. Predation occurred in all *ex situ* experiment treatments. Only juvenile snails were observed on the coral fragments in situ, therefore no conclusions could be made for adult predation. Higher coral density lowered snail colonization per coral, while elevation showed no effect. Snail colonization per plot was similar, suggesting that settlement from planktonic larvae could be similar per area. Therefore, having a higher density of corals could decrease snail settlement per coral. No predation occurred on video recordings, but damselfish did show attempts to remove the snails, which could indicate the possibility of damselfish mitigating *Coralliophila* predation pressure. Further research on snail distribution and behaviour is recommended to develop effective mitigation strategies, including understanding adult and juvenile colonization and prey switching between existing and outplanted colonies. Current insights advocate for low-density outplanting on reefs with *T. deltoidei* presence and minimal *Coralliophila* abundance, with manual removal efforts annually, after storms, or snail spawning events to prevent and mitigate damage.

Keywords:

Corallivory/coral predation, *Coralliophila spp*., *Acropora spp*., outplanting methods

Contents

Introduction

Coral reefs systems have declined worldwide, along with the social-economic and ecological services they provide (Hein et al., 2021; Woodhead et al., 2019). There is need for appropriate and effective conservation strategies that include active restoration, as natural recovery is often improbable because of the progression of disturbance events (Boström-Einarsson et al., 2020), macro-algae competition (Souter et al., 2020) and climate change (van Oppen et al., 2017). Fragmenting corals and outplanting them in reefs could bring back wild populations and restore coral reefs (Boström-Einarsson et al., 2020; Omori, 2019).

Worldwide, these reef restoration efforts have been hindered by coral predation (Ladd et al., 2018; Shaver & Silliman, 2017; Villanueva et al., 2010). Besides the loss of coral tissue, coral predation can also increase the hosts susceptibility to thermal stress, bleaching and infections (Renzi et al., 2022; Rice et al., 2019). With more intense storms, macroalgal cover and increased water temperature, the adverse effects of coral predators will likely worsen (Shaver et al., 2020). Despite, coral predation and possible implications for restoration practices have been relatively understudied (Ladd & Shantz, 2020).

Coralliophila spp. snails represent a genus of obligate coral predators. In healthy coral reef, these corallivores mediate coral-coral competition and transfer energy from corals to higher trophic levels as prey (Rice et al., 2019). However, these snails are known to inhibit the recovery of coral populations (Gautrand et al., 2023; NOAA, 2015; Schopmeyer et al., 2017). They feed on a large variety corals (Hayes, 1990a), among which *Acropora spp.*, an endangered coral genus commonly used in restoration projects in the Caribbean (Johnson et al., 2011; Schopmeyer et al., 2017). *Acropora* corals, already suffering from increased water temperatures, have been shown to be more susceptible to predation when stressed (Bright et al., 2015) or mechanically damaged (Bright et al., 2016; Williams & Miller, 2012). As these snails tend to feed in aggregations, damage can reach significant amounts, since one snail can consume about 1 cm^2 of coral tissue per day (Baums et al., 2003). The manual removal of snails from nurseries and outplants have become a common practice (Johnson, 2011; Shaver et al., 2020). Although removal could provide a short-term effective solution (Miller, 2000), it is not permanent and only affects targeted corals (Williams et al., 2014). With the aim to increase coral restoration efforts, the need for removal will accumulate to ensure survival of outplanted corals. Conservation and restoration should incorporate ecological feedbacks into their strategies to ensure sustainable restored coral populations (Ladd et al., 2018; Ware et al., 2020). However, there is limited knowledge towards implementing ecological-based solutions to mitigate predation by *Coralliophila* snails on *Acropora spp.* (Knoester et al., 2023).

A study by Johnston & Miller (2014) showed that outplanting less preferred prey corals, or none at all, around *A. cervicornis* reduces snail colonization. Additionally, placing *A. cervicornis* in lower densities (0.75 to 3 coral per m^2) can increase survival and growth (Ladd et al., 2016). Besides, lowering outplant densities could also lower snail densities. As the snails are attracted to stressed or damaged corals, which is often the case with newly outplanted fragments. Furthermore, top-down control could be an ecological factor mitigating *Coralliophila* predation. Little is known about the predation pressure on these snails and what species predate on them. The Caribbean spiny lobster (*Panulirus argus*) is a confirmed predator in controlled aquaria, however, evidence for wild predation is lacking (Kamerman, 2023). Surveyed areas where this lobster was found showed to be negatively correlated with snail abundance; a similar observation was made for the black margate (*Anisotremus surinamensis;* Shaver et al., 2020). Other possible predators are the snapping shrimp (*Synalpheus fritzmuelleri*), pufferfish, hogfish, filefish, and octopi (Baums et al., 2003). A confirmed predator is the carnivorous gastropod *Thais deltoidei*, that showed predation on *Coralliophila* both *ex situ* and *in situ* when these snails were placed near *A. cervicornis* outplants. Despite predation pressure being low, *T. deltoidei* could trigger an escape response in *Coralliophila* snails, thus reducing their feeding rate on corals (Delgado & Sharp, 2020). However, these finding were based on experiments with repositioned predator snails over a two week period and long term efficiency remains unclear. Relying solely on this species to mitigate *Coralliophila* predation may be insufficient because natural occurring predation rates are unknown. Therefore, additional predators should be identified to aid management towards ecological mitigation of coral predation by *Coralliophila* snails.

Finally, exploring outplanting techniques that impede the predators ability to reach is the coral is also worth investigating. Although this is not per se sustainable, it could offer an alternative that could be implemented directly. Outplanting corals on elevated structures such as iron poles have been shown to be successful (Zayasu & Shinzato, 2016). Nevertheless, there is no literature on using such structures to mitigate predation. Notably, in Portobelo (Panama), the NGO Reef Restoration Panama has lost numerous *A. cervicornis* outplants due to predation, but less to none in nearby nursery structures, suggesting that these nursery structures may act as a barrier for *Coralliophila* snails.

This research aims to give insights into various strategies for mitigating *Coralliophila* snail predation. Three approaches were addressed: 1) the potential of using structural barriers; 2) the application of different outplanting strategies; 3) the identification of corallivore predators and their predation pressure. First, we tested to what extent coral reachability is reduced when placing coral fragments of *A. cervicornis* elevated on a nursery-used material (rebar and PVC). Secondly, we outplanted *A. cervicornis* fragments *in situ,* both elevated onto rebar and at varying densities, and monitored snail abundance over time. Thirdly, an assessment was conducted to determine the extent of snail predation and identify the species responsible by exposing snails on the reef while they were attached to concrete blocks. Observations were conducted through video recordings and visual monitoring. Lastly, during the study period, a relatively heavy storm occurred, which gave the opportunity to survey the *Acropora spp.*, along with fragments, for snail abundance after disturbance. For the first approach it is hypothesized that that height can lower, but not likely stop the snails completely from reaching the corals. Corals elevated on PVC will likely experience higher snail predation than those elevated on rebar due to the smoother surface of PVC, which facilitates easier movement for the snails. It is expected that *in situ*, outplanting corals onto rebar and in lower densities will lower snail abundance. For the snail predator experiment, it is expected that the previously mentioned species, when observed, will predate on the *Coralliophila* snails.

Methodology

Study sites

The study was performed in Portobelo, Panama from 20th September 2023 till 5th January 2024. Five study sites were chosen; Scuba Panama House reef (9°32'09.3"N, 79°40'21.1"W), Huerta (9°56'08.1"N, 79°68'09.9"W), Drake island (9°56'13.9"N, 79°68'40.1"W), Tres Hermanas (9°59'56.6"N, 79°66'78.6"W) and Buenaventura (9°54'04.4"N, 79°68'31.9"W). Species collection for the *ex situ* experiments was performed at Scuba Panama House Reef. This was also one of the three locations for experiments on snail predation along with Huerta and Drake island. The NGO Reef Restoration Panama has several *Acropora cervicornis* nurseries situated in Huerta at 5 meters depth from which coral fragments for this study were taken. These nurseries were a combination of fixed roped nurseries with rebar and floating rope nurseries with PVC. The outplanting experiment was performed at Drake island. The west reef of Huerta was surveyed for *Coralliophila* snails after the storm along with Tres Hermanas and Buenaventura. All experiments were performed by at least two scuba divers.

Species collection

Coralliophila spp. collection was done in Scuba Panama House Reef. Adult snails (10 to 20 mm) were gathered and once back kept in a bucket with continuously aerated seawater. Water was changed every three days or when mortality occurred. Snails were first used in the structure experiment whereafter they were used in the snail predator experiment. All *A. cervicornis* fragments used in the experiments were taken from the aforementioned nurseries. Fragments were collected and transported in buckets with fresh sea water without exposing them to air.

Structure experiment

The structure experiment was performed to test if elevating the corals on different material could mitigate predation by *Coralliophila* snails. Collected snails were starved for at least a week, measured for maximum shell length (columella length, Monnet et al., 2009) and randomly assigned to a treatment. Adult snails of 10 to 20 mm length were used. Five snails were placed in a plastic bucket filled with fresh seawater. In the middle of the bucket a pole was placed of either rebar (1 cm Ø) or PVC (2.6 cm Ø). Snails showed to move relatively quick upwards along the side of the bucket after being measured and placed in the experimental bucket, therefore it was decided to acclimate them for 24h to lower this escape response. Then, a coral fragment of *A. cervicornis* of approximately 5 cm was tied to a pole at a height of either 30 cm, as elevation treatment, or at 0 cm, as control. Snails were then observed at 1, 3 , 6, 24 and 48 hours after the start of the experiment. If the snails would reach the upper side of the bucket they were placed back on the bottom. Snails on the bottom, pole or coral were left untouched till the experiment ended. Each treatment was done in triplicate, resulting in the use of 60 snails.

Outplant experiment

To test the effect of outplant density and elevation on *Coralliophila* snail predation of *A. cervicornis* an *in situ* experiment was performed at Drake island. This study site was chosen due to its proximity to the nurseries, availability of suitable substrate, and confirmed presence of *Coralliophila* snails. For the experiment, coral fragments of between 25 and 35 cm total linear extension were used. Corals were outplanted at 3.6 to 7.5 m depth on predefined plots of 1 m^2, which were located approximately 5 meters apart in a single direction. Plots were selected on lower coral cover to avoid competition and especially to avoid *Millipora spp.* and *Agaricia spp* to reduce coral predator attraction. Fragments were outplanted in two densities (1 or 5 per m^2) and either on ground level onto masonry nails or elevated (15cm) on rebar poles. Outplanting size and the use of masonry nails was based on Goergen & Gilliam (2018). This experiment resulted in four treatments (LN: low density – nails, HN: high density – nails, LR: low density – rebar, HR: high density – rebar), each treatment had 8 replicates resulting in 32 plots having a total of 96 corals fragments. Both masonry nail and rebar were hammered into the substrate, whereas the bottom rebar end was pred-cut in a point. Fragments were attached with cable ties. Plots were monitored weekly for snail abundance. The experiment lasted from week 48 of 2023 till week 5 of 2024 (9 weeks total). Three weeks after outplanting, no monitoring was possible because of a heavy storm. Out of the 96 corals, 21 corals from the nail treatment and 3 from the rebar treatment, were missing. Almost all corals showed signs of abrasion damage and/or broken branches. Five weeks after outplanting, all missing corals were replaced and all corals survived and showed healthy growth at the end of the experiment. Corals were not replaced directly as the coral nurseries were also damaged.

Snail predator experiment

To investigate which species, and to what extent, predate on *Coralliophila spp.*, snails were exposed on concrete blocks based on the experiment of Knoester et al. (2023). A small hole was drilled in aperture of the shell in order to attach a plastic monofilament line to a rebar pole. This pole was placed in the concrete block to prevent dislodgement. Per block, five snails were placed, whereafter a GoPro camera was placed to record the first hour of the experiment, or until depletion of the battery (40 to 50 minutes). Footage was later analysed for observed species and possible interactions. Snail survival was then monitored for days or some weeks, because it was logistically not possible to monitor for a fixed amount of time. This experiment was done at three locations, House reef, Huerta and Drake island, the outplanting site.

Wild colony survey

The storm at the end of 2023 gave the opportunity to survey wild colonies of *A. cervicornis & A. palmata*, including fragments, for *Coralliophila* snail and any associated species. Due to logistical constraints only four surveys were performed (Huerta 2, Tres Hermanas 1, Buenaventura 1). As *Acropora spp*. coverage is low in these areas it was decided to survey in locations were at least some colonies were known. However, nothing was known about the amount of predation in these sites and therefore comparison of snail predation before and after the storm was not possible. The surveys were done with the roving diver method, noting species, condition (fragment or base colony) and amount of *Coralliophila* snails whenever a colony was encountered. Due to time constraints, estimations of colony size were not possible for all colonies. Other species of interest residing on the colonies were noted as well.

Data analysis

Data was analysed in R Studio version 2023.12.1 Build 402 (R Studio Team, 2023). All tests were performed with p-value of 0.05 as significance level. The effect of material type and height on the amount of snails that could reach the coral fragments in the *ex situ* structure experiment was analysed using a Generalized linear mixed-effects model (GLMM) from the *glmmTMB* package (Brooks et al., 2017). The model had a poisson distribution, log link, non-zero inflated with the material type and elevation height as explanatory factor, bucket id as random factor and the amount of snails on the coral as response. From the *stats* package, AIC values were compared for different model fits. *DHARMa* (Badolo et al., 2018) diagnostic plots were visually inspected to validate the GLMM assumptions. The effect of outplanting method (nail and rebar) and coral density (1 and 5 per m^2) on the average amount of snails found per plot was tested with a two-way ANOVA. The same was tested for the average amount of snails per coral, where values of the high density plots were divided by 5. The distribution of the model residuals and data between groups was not normal. However, since the homogeneity of variance was sufficient and no fitting GLMM could be modelled it was decided to perform the two-way ANOVA as the model is robust for normality violation (Blanca et al., 2017). Snail counts per outplant monitoring were grouped as the primary focus was on assessment of overall predation pressure on the different treatment plots and not on trends over time. Footage of the snail predation experiment was analysed for species observed and if any interaction occurred. Monitoring the snail predation experiment frequently and consistently was not possible, therefore the raw results were visualized and analysed descriptively. This was similar for the wild coral survey, as the number of surveys was low (n = 4).

Results

Structure experiment

In all treatments, snails were able to reach the *A. cervicornis* fragments (material: PVC and rebar; elevation at height: 0 and 30cm). However, in no replicate did all 5 snails reach the coral by the end of the experiment at 48 hours. Material type did not affect snail colonization (GLMM; $\beta = -0.39$, SE = 0.30, $z = -1.31$, $p = 0.192$). Elevating the coral by 30cm decreased snail colonization by approximately 75% , when compared to the 0cm elevation (Figure 1; GLMM; $\beta = -1.44$, SE = 0.37, $z = -3.89$, $p < 0.001$). In the 30 cm elevation treatment, the first snails reached the coral after 24 hours, whereas in the control, colonization occurred after 1 hour (Appendix I).

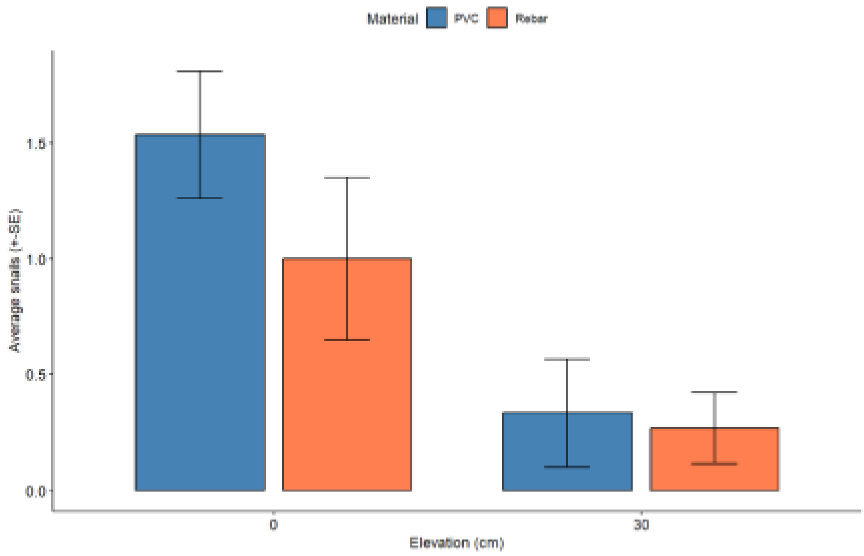

Figure 1. The average number of snails (+-SE) on the coral fragments per treatment.

Outplant experiment

Eight weeks after initial outplanting of the *A. cervicornis* fragments, the first *Coralliophila spp.* snails were sighted on the corals. Snails colonized fragments in all treatments and neither outplanting method nor density did affect snail colonization per plot (Anova: F(1, 266) = 0.530 & 0.542, p = 0.47 & 0. 462, Figure 2a). However, snail colonization per coral was affected by outplant density (Anova, F(1, 266) = 5.413, p = 0.021), outplanting fragments in high density (5 per m^2) lowered snail colonization per coral by approximately 73% compared to low density (1 per m^2). Yet, the method of outplanting had no affect (ANOVA, F(1, 266) = 0.200, p = 0.621). All snails observed were juveniles, having white shells of 1 to 5mm. They were often found between the coral and the outplanting material (Figure 2b.). Nine plots had no snail sightings throughout the monitoring period, and snail density varied for all treatments after snails were sighted (Appendix II). After the storm, the corals showed mechanical damage such as broken branches, sanded like texture and/or scratches from the rebar. By the end of the experiment, all coral fragments were alive with fragmentation wounds healed. No adults snails were seen on the experimental plot, however, one plot of five coral fragments outplanted with nails (0cm elevation) had 6 adult *Coralliophila* snails next to it. This aggregation of snails was residing on a *Montastraea sp.* colony and was observed for almost a month during monitoring and showed little to no movement.

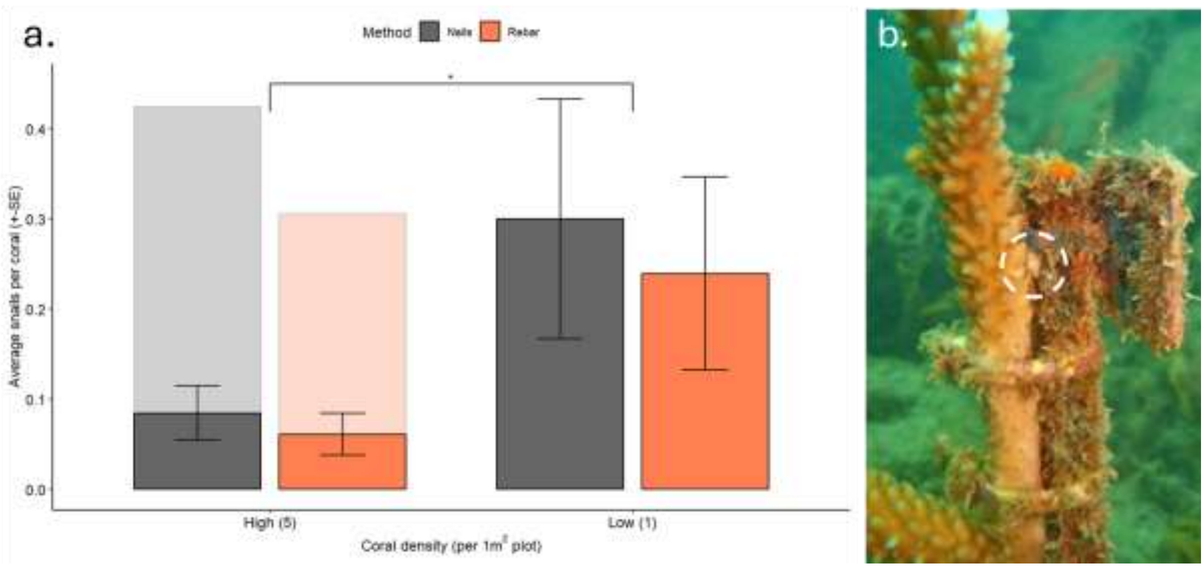

Figure 2. a; Average number of Coralliophila *snails found on a coral per treatment (+- SE). The x-axis shows the coral density and the different colours represent outplant method. The "*" shows the significant effect of coral density. Faded bars show snails per plot for the high density treatment, not correct for the amount of corals. b;* Acropora cervicornis *outplanted onto a rebar, white dashed circle shows the juvenile* Coralliophila *snail.*

Snail predator experiment

No predation on the *Coralliophila* snails was observed on the camera footage taken at the three locations (Drake island, Huerta, House reef). Damselfish (*Stegastes partitus* and *Stegastes diencaeus*) did show on two separate occasions to pick up the snails in an attempt to move them (Figure 3), but since they were attached, this was not possible. At the end of the exposure periods, 30 out of 45 exposed snails were not predated on. The remaining 15 snails and their shells went missing, empty or had the broken shells still attached to the lines; exposure time and observation intervals differed between sites and replicates (Figure 4). Almost all non-predated snails survived the experimental exposure time except for four individuals. One replicate showed survival up to 62 days. Snails were also placed in front of a group of spiny Caribbean lobsters (*Panulirus argus*) and all survived for 9 days until the set up was removed. Other species did not show any interaction with the exposed snails (Appendix III).

Figure 3. Two species of damselfish in attempt to move the Coralliophila spp. *snails.* Stegastes partitus *at Drake siland (left) and ,* Stegastes diencaeus, *at house reef scuba (right). Snails that are being moved are marked with a red dashed circle.*

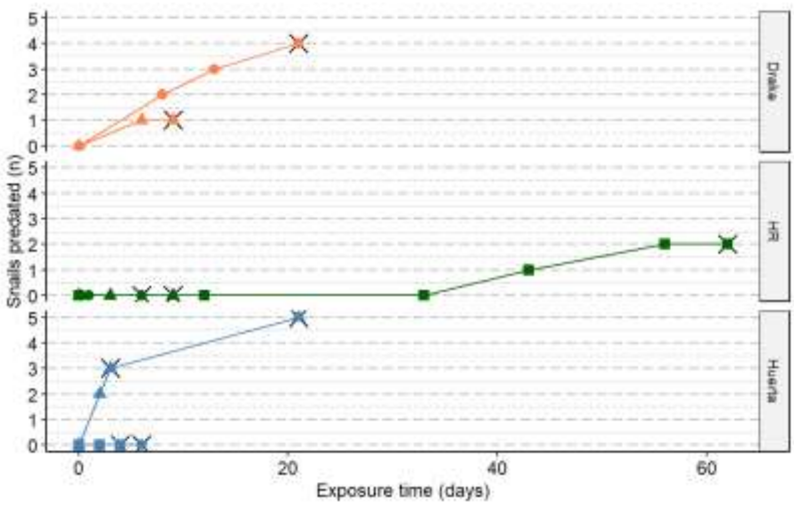

Figure 4. Amount of Coralliophila spp. *snails predated for each location per replicate assay (Drake n = 2, Huerta n = 4 and HR "house reef" n = 3). Each point is a check after an amount of days shown on the x -axis and replicates are divided by the different shapes. The black "X" shows the end of an replicate as the days of each replicate differed.*

Wild colony survey

Four surveys were performed, which did yield some interesting observations, although these are not statistically supported. Two *A. cervicornis* colonies surveyed in Huerta showed to host a total of 231 *Coralliophila spp.* snails (Table 1). Two species were identified as *C. salebrosa* and *C. abbreviata*. For *A. palmata* most snails were found in Tres Hermanas, these were mostly juveniles found on fragments. Some juveniles showed to aggregate on fragments and sometimes around adult individuals. Juvenile individuals were too small for determination, however the shells looked similar to *C. salebrosa's*. Also the snail predator *Thais deltoidea* was observed on *A. palmata* colonies in all locations. In Buenaventura no *Coralliophila* snails were found, though two *T. deltoidea* were found and multiple bearded fire worms (*Hermodice carunculate*) were found predating on *A. palmata*.

Table 1. The amount of A. cervicornis and A. palmata surveyed per location with the amount of Coralliophila spp. and T. deltoidea found on them. Locations are abbreviated (BU = Buenaventura, HU = Huerta, TH = Tres Hermanas).

	Acropora cervicornis			Acropora palmata		
Location	Corals surveyed	# snails	# T. deltoidea	Corals surveyed	# snails	# T. deltoidea
BU				10	0	2
HU	2	231		10	18	14
TH				9	126	2
TOTAL	**2**	**231**		**29**	**144**	**18**

Discussion

Structure experiment

In all structure experiment treatments at least one *Coralliophila* snails showed to be able to move on the structure and reach the *Acropora cervicornis* fragments. Therefore, elevating the corals with either material, PVC or rebar, cannot mitigate coral predation completely. Elevating the coral fragments did show to lower snail colonization, however the majority of the snails did not reach the fragments by the end of the experiment. The additional distance the snails had to move to the coral fragments could be an explanation for the lower amount of snails on the elevated corals. However, during the experiment acclimation period, the snails did show to be able to reach a height of 30 cm on either the pole or the side of the bucket within an hour. Since the experiment lasted up to 48 hours, with the first observation being done after one hour, the distance the snails had to move is unlikely the main explanatory factor.

Another reason could be behavioural, the snails being unwilling to expose themselves to reach a food source. These snails are normally observed on the corals surface and, depending on the coral structure, underneath or in crevices, likely to be safer from predators (Johnston & Miller, 2007; Potkamp et al., 2017; Shaver et al., 2020; Verboom & Hoeksema, 2023). Additionally, these snails form aggregations, creating positive feedback loops that influence their movement patterns (Hamman, 2018). Depending on where these aggregations form, they could either promote movement towards the coral fragments or discourage it. However, no clear aggregation formation was observed in the experiment. Studies have also shown that *Coralliophila* snails prefer coral fragments over other solitary snail (Bright et al., 2015). As snails in this experiment did not aggregate on the coral when an individual was on the fragment, these feedbacks might be less prominent as suggested. Nevertheless, larger aggregations should be minded as an increase in snail density increases tissue damage (Hamman, 2018).

Furthermore, it is known that other corallivorous gastropods, like *Drupella spp.*, are attracted by chemicals cues from the coral mucus (Kita et al., 2005). Since the current experiment was performed *ex situ* in stagnant water, it could be that these chemical cues had accumulated in the tank water. This could have caused the snails to be misdirected and not being able to find the coral. This could explain why more snails reached the coral sooner in the control, as chemical cues would accumulate in the bottom of the tank, closer to the snails. Chemical cues that promote the formation of aggregations or that can be used to find coral prey have not been described for *Coralliophila spp.* snails. Determining how they locate prey, for example through kinesis or odor-gated rheotaxis, could help understand and predict their movement (Yu et al., 2023). The fact that some snails moved over the coral fragments upwards suggests that feeding might have not been their priority. Other studies show that in prey exposure experiments, responses can be low (41 to 72%), which might explain this behaviour (Bright et al., 2015). As the water was fresh at the beginning of the experiment and since all snails survived the treatments, is unlikely that they tried to move to a location with better water quality rather than being interested in food.

The material types tested (PVC and rebar) did not show to affect the capability of the snails to reach the corals. Although only two material types were tested, the surface textures are very different. If material and texture would have had some effect on snail colonization, this difference would have likely been observed. A more coarse and erosive texture could be a solution, as the snail might fall off such a structure in its attempt to reach the coral. Any option for a repellent surface might also harm other organisms and most importantly the coral itself, so such surfaces should be designed with care.

Outplant experiment

For the outplant experiment in Drake island, elevating *Acropora cervicornis* fragments by 15cm on rebar did not show to lower *Coralliophila* predation compared to fragments outplanted with masonry nails. The snails observed were all juveniles (1-5 mm in length approximately), which could explain why no difference between methods was observed. These snails could have settled on the fragments after their planktonic veliger larvae stage (Wells & Lalli, 1976) and may therefore not have been affected by the corals elevation at all. The planktonic origin of these juvenile snails could also explain why there was an unexpected difference in colonization between the outplant densities tested (1 and 5 per m^2). Experimental plots had similar colonization densities, yet low coral density plot had more snails per coral than high coral density plots. This suggests that snail settlement from planktonic larvae could be similar per area and thus having a higher density of corals would lower the amount of snails settling on a single coral fragment.

These results are contradicting with other studies, showing that higher coral outplant densities would increase snail predation (Johnston & Miller, 2014). Yet these studies were done with collected adult snails, which were placed on the study site and with all corals being outplanted fragments. Therefore, natural occurring colonization and predation on outplanted *A. cervicornis* was not studied, but prey selection behaviour. In this study, no adult snails were observed on the outplanting plots, although their presence was confirmed at the experimental site by surveying. It could be that the study period of two months is insufficient to observe snail colonization. Studies *in situ* showed that snail movement can highly vary, ranging from 0.13 to 32.43 meters in 192 days (Johnston, 2012). Besides, Hayes (1990a) reported that *Coralliophila abbreviata* could easily move from one colony to another in a single night, as their median nocturnal speed was 2.63m/h. This study of 8 weeks is therefore likely sufficient to observe at least one adult snail on the 32 experimental plots.

Some studies reported that snails in natural reefs were found more on non-acroporid corals (Baums et al., 2003; Hayes, 1990b; Miller, 1981), which suggests that *Coralliophila spp.* might be less attracted to *A. cervicornis* than suggested in the study of Johnston & Miller (2014). A lesser preference for acroporids is supported by the observation of the snail aggregation on the *Montastraea sp.* colony for several weeks and did not move to the *A. cervicornis* outplants at ground level. Being newly outplanted, and therefore somewhat damaged and stress, should make them a preferred prey, especially given their accessibility at ground level (Bright et al., 2015). However, snails consuming non-acroporid corals, including *Montastraea sp.* are more sedentary (Hayes, 1990a). Here *Coralliophila* snails act as ectoparasites that feeds on corals energy sink sites, areas where relatively more energy is translocated to because of growth, reproduction or defence. Maximizing efficiency of energy exploitation by predation on these sites and minimizing tissue damage to the coral (Oren et al., 1998). If the coral is weakened, it would be reasonable that this energy sink feeding cannot be supported and would cause the snail to move for healthier tissue, increasing tissue damage. It is likely this phenomenon also occurs on *A. cervicornis* as *Coralliophila spp.* snails have been reported to frequently move on and off colonies and cause lethal damage within days (Hayes, 1990a). Moreover, feeding rates on *Acropora spp.* are higher than on *Montastraea spp.* (Baums et al., 2003). Knowing how and when these snails change their hosts could help restoration strategies for *A. cervicornis*. This includes the early live stages such as veliger settlement and juveniles phenology.

Snail predator experiment

Since active predation from the Caribbean spiny lobsters (*Panulirus argus*) was not observed, it can be concluded that this species does not prey on *Coralliophila* snails, or at least is unlikely to aid in reducing coral predation, despite previous documentation (Gnanalingam & Butler, 2018; Shaver et al., 2020).

Moreover, two species of damsel fish (*Stegastes partitus* and *Stegastes diencaeus*) made and attempt to move the snails away from the concrete blocks. It is known that damselfish are able to remove herbivorous invertebrates from their territory (Hata & Kato, 2004) and *A. cervicornis* colonies with damselfishes have shown decreased predation by *Coralliophila* (Schopmeyer & Lirman, 2015). Yet, contradicting positive relationships have been observed also, as high damselfish abundance was found to coincide with high numbers of specifically *Coralliophila galea* (Kamerman, 2023). Damselfish could decrease *Coralliophila* predation by removing these snails or increase predation by attracting snails due coral damage following from their algae farming activities (Schopmeyer & Lirman, 2015). Lastly, damselfish were also observed to chase-off potential predators during the recording, which hints towards a negative relationship in mitigating coral predation.

Despite little predation occurred, the observed predation marks do show that as least some predators are active. Given the different states of the predated snail shells (missing, empty, or broken), there are potentially different predator species involved. The known predator *T. deltoidae*, for example, leaves empty prey shells after predating (Delgado & Sharp, 2020), which was also observed in this study. Additional predators are likely species that have the strength and physiology to crush a shell, like *Tetraodontidae*. Almost all replicates, aside from one, were not completely predated, indicating that the current predator species in Portobelo, Panama, are unlikely to effectively mitigate *Coralliophila* populations. These predators might be in low abundance, predate while roaming between reefs, or both, and therefore predate too little to mitigate predation by *Coralliophila* snails. Besides, predation on *A. cervicornis* colonies might even be lower than on the experimental assays, as the branching structures of the corals might limit some predators to reach the snails.

Wild colony survey

Although the wild colony survey did not yield enough data for statistical analysis, it did show some interesting observations. Within one reef, Huerta, snail infection can differ a lot between *Acropora spp.* colonies, with two *A. cerviconis* colonies being colonized by over 220 snails and *A. palmata* on the same reef having no significant predation. Studies lack clear results of prey preference within this genus and between taxa (Hayes, 1990b; Johnston & Miller, 2014). Nevertheless, the observations emphasize the need to further study the distribution of these corallivores in the Portobelo area, as this quantity of snails will likely be lethal to the colonies as feeding rates differ between 0.44 and 3.28 cm^2 per day per individual (Baums et al., 2003). The presence of the *Thais deltoidae* snail predator on the inspected *A. palmata* colony could have caused the low presence of snails on that colony. Although, Delgado & Sharp (2020) found that placing the gastropods predators on *A. cervicornis* colonies did not trigger significant predation, but rather a flight response of *Coralliophila* snails. To what extent *T. deltoidae* predates on *Coralliophila* snails and effectively protects *Acropora spp.* colonies from predation is unknown.

Furthermore, large differences between reefs were observed, some reefs showed little to no *Coralliophila* snails on their *Acropora palmata* colonies, but did have fireworm, *Hermodice carunculate,* predation. On other reefs, like Tres Hermanas, both fireworms and *Coralliophila* snails, mostly juveniles but also adults, were observed on fragmented *A. palmata*. This again emphasizes to survey for both coral and snail predators, like *T. deltoidae*, on the reefs before and after outplanting to increase the success of *Acropora spp.* survival.

Conclusion & recommendations

To conclude, elevating corals with a simple pipe like structure cannot completely mitigate *Coralliophila* snails predation on *A. cervicornis*. Other materials will likely improve the observed delay in colonization, for example by forming another type of barrier, such as sharp edges or erosive material. Outplanting corals did not show predation by adult snails, but juveniles showed to colonize the plot independent of coral density, causing low density corals to have higher colonization of juveniles. As no adults were observed on the experimental plots, no effect on predation mitigation can be concluded yet from these preliminary results. However, the results from the structure experiment suggest that applying these methods in the field will not be likely to mitigate predation completely. Performing this study in more snail-dense reefs or with experimentally introduced individuals, along with longer monitoring, would provide final conclusions on the effectiveness of these structural mitigation measures. Outplanting on masonry nails or rebar also creates a surface between the material and the coral, which in this study was occupied by juvenile corallivores. Therefore stability of the outplant structure and facilitation of potential predators or parasite need to be weighted per location. It is highly suggested to further study snail distribution, prey choice and prey selection behaviour of the snails between outplanted corals and existing colonies, including the colonization of juveniles. Gaining knowledge about snail aggregations, prey switching, transitioning from a slower ectoparasitic feeding to causing significant damage to acroporid corals, could aid in mitigating predation on *A. cervicornis* outplants. Currently, it is recommended to outplant *A. cervicornis* in low densities, ideally on reefs with *T. deltoidei* presence and minimal *Coralliophila* spp. abundance. If the latter condition cannot be met, regular manual removal efforts should be performed, either annually, after storm events or spawning seasons, to mitigate damage by these corallivores gastropods.

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Appendix

Appendix I Structure experiment graph per observation

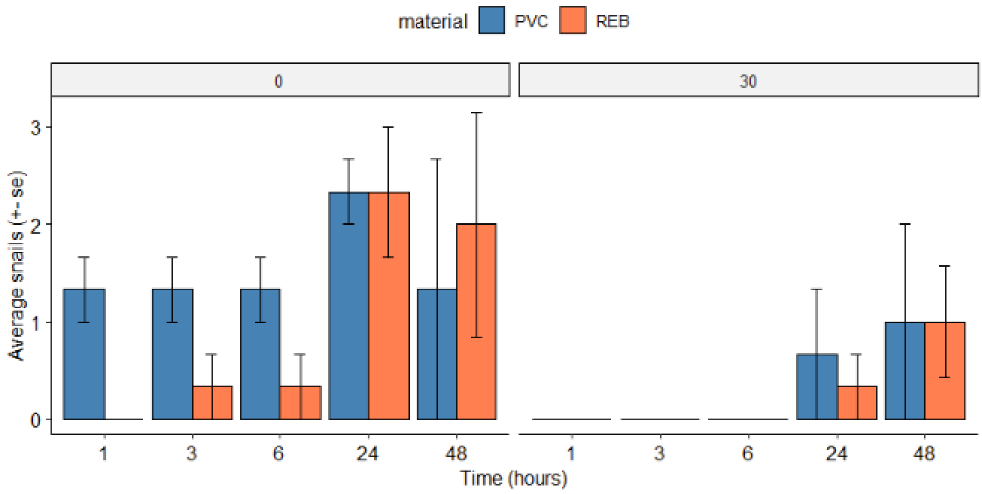

Figure 5. Average number of snails (+se) that reached the coral fragment (corals). Treatment 0 and 30 stands for the amount of cm elevation and time on the x-axis is hours from the start of the experiment. Error bars show the standard error.

Appendix II Outplant experiment graph per monitoring date

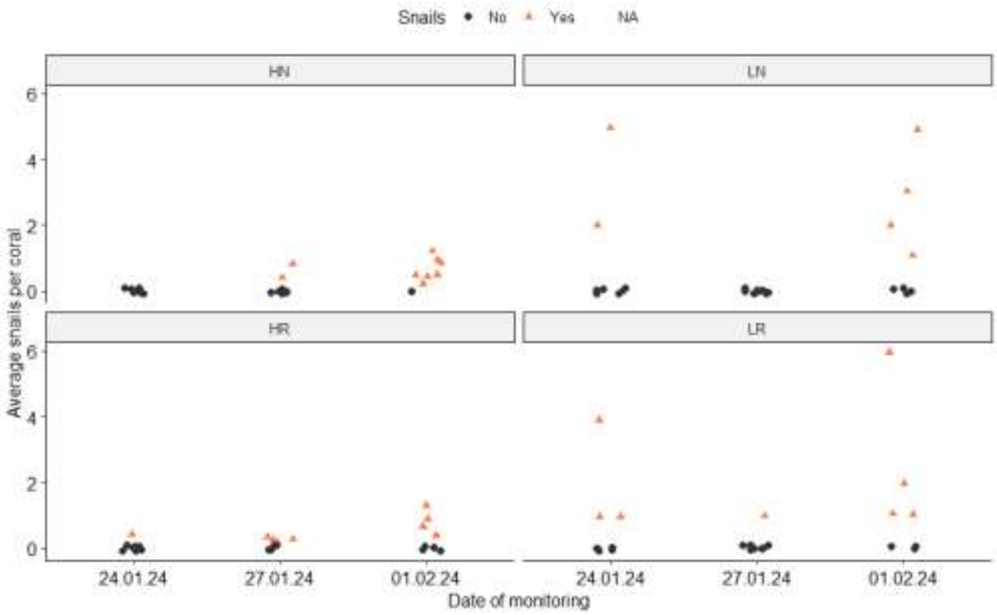

Figure 6. Average amount of Coralliophila snails per coral over the monitoring dates where snails were sighted. Different colours and shaped show if there were any snails or none at all. Facets show the different treatments (H = high coral density (5), L = low coral density (1), R = Rebar, N = Nail).

Appendix III Species observed

Table 2. Table of species observed from the camera footage in the buffet experiment. On the left the common species names and on the right scientific names. Not all observations could be determined to species level.

Common species	Scientific names
Banded butterfly fish	*Chaetodon striatus*
Bar jack	*Caranx ruber*
Bicolor Damselfish	*Stegastes partitus*
Blackear Wrasse	*Halichoeres poeyi*
Blue angelfish	*Holacanthus bermudensis*
Blue chromis	*Chromis cyanea*
Blue Tang	*Acanthurus coeruleus*
Bluehead Wrasse	*Thalassoma bifasciatum*
Bluestriped grunt	*Haemulon sciurus*
Brassy Chub	*Kyphosus vaigiensis*
Brown Chromis	*Chromis multilineata*
Carribean Reaf squid	*Sepioteuthis sepioidea*
Sharknose Goby	*Elacatinus evelynae*
Common sand diver	*Synodus intermedius*
Damselfish sp.	*Pomacentrinae*
Doctor fish	*Acanthurus chirurgus*
Doctorfish	*Acanthurus chirurgus*
Dog snapper	*Lutjanus jocu*
Filefish Sp.	*Monacanthidae sp.*
Foureye Butterfly fish	*Chaetodon capistratus*
Foureye butterflyfish	*Chaetodon capistratus*
French Angelfish	*Pomacanthus paru*
French Grunt	*Haemulon flavolineatum*
Goby sp.	*Gobiidae sp.*
Graysby	*Cephalopholis cruentata*
Grouper sp.	*Epinephelinae sp.*
Harlequin Bass	*Serranus tigrinus*
Juvenile Schoolmaster Snapper	*Lutjanus apodus*
Lane Snapper	*Lutjanus synagris*
Longfin damselfish	*Stegastes diencaeus*
Mahogany Snapper	*Lutjanus mahogoni*
Orangespotted filefish	*Cantherhines pullus*
Parrotfish Sp.	*Scaridae sp.*
Porkfish	*Anisotremus virginicus*
Princess Parrotfish	*Scarus taeniopterus*
Princess Parrotfish (Juvenile)	*Scarus taeniopterus*
Puddingwife (Wrasse)	*Halichoeres radiatus*
Queen Angelfish	*Holacanthus ciliaris*
Queen Parrotfish	*Scarus vetula*
Queen Parrotfish (initial phase)	*Scarus vetula*
Rainbow Wrasse	*Halichoeres pictus*
Redband parrotfish	*Sparisoma aurofrenatum*

Schoolmaster Snapper	*Lutjanus apodus*
Seabass	*Serranidae sp.*
Sergeant major	*Abudefduf saxatilis*
Sharpnose Puffer	*Canthigaster rostrata*
Slippery Dick	*Halichoeres bivittatus*
Smooth Trunkfish	*Lactophrys triqueter*
Southern stingray	*Dasyatis americana*
Spanish grunt	*Haemulon macrostomum*
Spanish Hogfish	*Bodianus rufus*
Spiny caribbean lobster	*Panulirus argus*
Spotfin Butterflyfish	*Chaetodon ocellatus*
Spotted Goatfish	*Pseudupeneus maculatus*
Squirrelfish	*Holocentrus adscensionis*
Stoplight Parrotfish	*Sparisoma viride*
Striped Parrotfish	*Scarus iseri*
Surgeonfish sp.	*Acanthuridae sp.*
Threespot damselfish	*Stegastes planifrons*
Topsail Chub	*Kyphosus cinerascens*
Trumpetfish	*Aulostomus maculatus*
White grunt	*Haemulon plumierii*
Yellow Goatfish	*Mulloidichthys martinicus*
Yellow Jack	*Carangoides bartholomaei*
Yellow Stingray	*Urobatis jamaicensis*
Yellowhead Wrasse	*Halichoeres garnoti*
Yellowtail Damselfish	*Microspathodon chrysurus*
Yellowtail Parrotfish	*Sparisoma rubripinne*
Yellowtail Snapper	*Ocyurus chrysurus*