Strategies To Mitigate Predation by the Fireworm *Hermodice Carunculata* on Outplanted Colonies of *Acropora cervicornis*

MSc Thesis
MAE-80336

By Raf Verdaasdonk (1037911)

Supervised by dr. Ronald Osinga
Chairgroup: Marine Animal Ecology
Wageningen University and Research

31-3-2024

Abstract

The critically endangered status of the Caribbean reef-building coral *Acropora cervicornis* has increased the number of restoration efforts targeting this species. Restored colonies exhibit varying levels of mortality caused by multiple stressors, including corallivory. In this study, the four factors, elevation, coral preference, coral density, and natural predation were investigated to determine their influence on fireworm (*Hermodice carunculata*) predation on restored *A. cervicornis* patches. *Ex situ*, the effect of coral elevation on artificial structures was tested to determine coral accessibility by the fireworms. The structures varied in material type (rebar or PVC), height (0-30cm), and diameter (1.5-2.7cm). Additionally, to gain prey preference insights, a free-choice *ex situ* experiment was conducted exposing fireworms to fragment combinations of *A. cervicornis, Millepora complanata, or Agaricia sp*. Furthermore, corals were outplanted in densities of $1m^{-2}$ or $5m^{-2}$, either non-elevated or elevated (15cm), and monitored for 64 days to investigate the effects on fireworm corallivory. Lastly, to observe predation occurrence and to identify new fireworm predators, fireworms were tied up and scattered on three reefs.

The experiments indicated that elevation and using PVC significantly reduced fireworm accessibility. No difference was found among elevation heights. Prey preference for *A. cervicornis* over *M. complanata* and *Agaricia sp.* could not be demonstrated, with the latter being because of the low number of successful replicates. *M. complanata* was preferred over *Agaricia sp*. by the fireworms. Furthermore, prey-switching between *A. cervicornis* and *M. complanata* was observed. No significant differences could be found within the field outplacement treatments, due to the low number of fireworms observed. Additionally, a new fireworm predator, the squirrelfish *Holocentrus adscensionis*, was identified.

This study indicated that using PVC pipes to elevate *A. cervicornis* fragments from the seafloor is worth investigating to reduce fireworm predation. Such a positive effect could not yet be confirmed in the field. The long-term effects of the density and elevation treatments on outplacement success remain unknown and need further study. Additionally, the prey-switching behaviour should be further explored by looking at the effect of *M. complanata* as a neighbouring coral on *A. cervicornis* predation. Furthermore, the finding of an additional predator helps to select restoration sites with more top-down control.

Keywords: Coral restoration, Corallivory, Corallivory mitigation, *Acropora cervicornis, Hermodice carunculata*

Introduction

The continuous decrease of coral reef ecosystems since the 1950s has enhanced global awareness and active participation in conserving these systems for the socio-economic and ecological services they provide (Boström-Einarsson et al., 2020; Eddy et al., 2021; Hein et al., 2021; Woodhead et al., 2019). One previously dominant Caribbean reef-building coral, *Acropora cervicornis*, is critically endangered after initial population reduction by white-band disease was followed by disturbances such as bleaching, corallivory, and hurricanes (Aronson & Precht, 2001; Edmunds, 2019; IUCN, 2021; Rice et al., 2019; Sakai, 2019; Woesik et al., 2021). Reef-building corals are essential for reef growth (Perry et al., 2014). Current management of local anthropogenic disturbances (e.g., fisheries and pollution) protects the remaining wild endangered coral colonies and enhances their survival (Boström-Einarsson et al., 2020; van Oppen et al., 2017). The chance of natural recovery for endangered corals like *A. cervicornis* is improbable due to low population densities and frequent disturbance events (Boström-Einarsson et al., 2020). Therefore, appropriate conservation strategies are crucial to gain and maintain healthy *A. cervicornis* populations.

One common strategy for active conservation is maintaining nurseries that contain wild colony fragments to ensure a stable growing environment. After the nursery coral fragments reach the desired size, they are outplanted on reefs to enhance local population densities (Shaver et al., 2020). Proliferation of these outplants remains challenging in coral restoration practices as there is a high variability in success. A study by Ware et al. (2020) indicated varying *A. cervicornis* survival rates between 4% and 89% across seven 5-year projects from the same foundation. The high variability was accounted to various site-specific and time-specific factors (Ware et al., 2020). One potential site-specific difference influencing outplanting success is the density of coral predators. Predation directly harms coral health and increases susceptibility to other stressors, such as bleaching and diseases (Renzi et al., 2022; Rice et al., 2019). Despite this, the influence of coral predation related to coral restoration is a relatively understudied topic in coral conservation studies (Ladd & Shantz, 2020).

One widespread coral predator on the Carribean reefs is the bearded fireworm (*Hermodice carunculata). H. carunculata* is omnivorous, and its diet contains the endangered coral *A. cervicornis* (Wolf et al., 2014). By predating on the growing branch tips, *H. carunculata* actively disrupts the growth of *A. cervicornis* (Miller et al., 2014). Additionally, *H. carunculata* has a preference for consuming coral recruits, hindering the natural formation of new corals (Wolf & Nugues, 2013a). On some Caribbean reef sites, *H. carunculata* predation affected 53% of the *A. cervicornis* colonies (Miller et al., 2014). Furthermore, *H. carunculata* contributes to the spread of coral pathogens by acting as a vector (Sussman et al., 2003). Lastly, it has been indicated that *H. carunculata* can endure a broad range of temperatures and pollution (Schulze et al., 2017). These findings indicate that *H. carunculata* corallivory can be a long-lasting stressor for *Acropora* restoration. Therefore, sustainable methods should be investigated to reduce the impact of *H. carunculata* on *Acropora* restoration efforts.

Some of these methods can be directly related to the outplanting strategies of *A. cervicornis.* Decreasing the outplanting density of *A. cervicornis* benefits the colonies' survival, attributing it to less competition and predation (Ladd et al., 2016). For the predator, *Coralliophila abbreviata,* a decrease in prey coral density outplants resulted in a lower presence of the corallivore (Johnston & Miller, 2014*)*. It remains unknown whether the effect on predation of a lower coral colony density is similar for *H. carunculata.*

Additionally, knowledge of coral prey preferences of *H. carunculata* is helpful in designing outplanting strategies, but such knowledge is scarce. Only one study determined a coral preference for *A. cervicornis* over the two corals *Agaricia agaracities* and *Monstera annular* (Rylaarsdam, 1983). Broadening the knowledge of Caribbean coral preferences helps develop outplanting strategies that take the effect of neighbouring corals into account.

Outplanting techniques may also reduce risks for corallivory. It has been observed that *H. carunculata* presence in coral nurseries is low (R. Verdaasdonk, Pers. Observations). This leads to wonder if the nursery structures form a barrier for *H. carunculata.* One possibility is that the elevation of the nursery structures from the seabed hinders *H. carunculata* from reaching the corals. Therefore, outplanting corals in reefs elevated from the seabed might decrease *H. carunculata* predation.

Furthermore, natural predators can be helpful to in reducing the amount of *H. carunculata* predation through top-down control. There are only a few known natural predators of *H. carunculata*. Older studies indicated that the snails *Conus imperialis*, *Conus aurantius,* and *Conus cedonulli* feed on *H. carunculata* (Kohn et al., 1972; Vink, 1974; Vink & von Cosel, 1985). More recently, bluehead wrasses (*Thalassoma bifasciatum*), yellowhead wrasses (*Halichoeres garnoti*), white grunts (*Haemulon plumierii*), and sand tilefish (*Malacanthus plumieri*) have been observed to predate on *H. carunculata* (Wolf, 2012; Ladd & Shantz, 2016). These known predators were found by chance. No studies have actively tried to uncover other predators of *H. carunculata* to increase the knowledge of possible top-down control opportunities.

In this study, outplanting density, outplanting elevation, coral preference, and finding new natural predators were investigated to gain insights into new strategies to lower the predation pressure of *H. carunculata* on *A. cervicornis* outplants. *Ex situ* experiments were conducted to determine the effect of elevation and coral prey preferences. Furthermore, *in situ* experiments to uncover new fireworm predators, effects of outplanting density, and elevation of outplants above the seabed were conducted in the Portobelo Marine National Park in Panama, an area targeted for *A. cervicornis* restoration.

Materials & Methods

Study sites

The experiments to identify new *H. carunculata* predators were performed at the reefs Drake Island (9°33'40.1"N 79°41'03.2"W), Huerta (9°33'39.5"N 79°40'51.6"W), and House Reef (9°32'09.3"N 79°40'21.1"W) of the Portobelo Marine National Park in the Caribbean. The experiment on the effect of density and elevation on outplanting was performed on the reef of Drake Island and started on the 30th of November 2023 lasting 64 days. The *ex situ* assays to determine the effect of elevation and coral preferences were performed at Scuba Portobelo. All *A. cervornis* fragments were retrieved from the coral nurseries (9°33'39.1"N 79°40'51.8"W) of Reef2Reef at a depth of 5m. All research activities (e.g., use of *A. cervicornis*) were conducted under the permit ARG-067-2023.

Fireworm collection

Fireworms were collected by hand during snorkelling and scuba diving at House Reef and Huerta between depths of 0-5m around noon. The fireworms were collected from the seabed or the corals *Acropora cervicornis*, *Agaricia sp.,* and *Millepora sp.,* with the latter species supplying most individuals. A total of 246 fireworms were used in this study, with an average length of 5.36(±1.61) cm.

Ex situ elevation experiment

An *ex situ* elevation experiment was performed to uncover the potential of height, diameter, and material as a barrier for fireworms' accessibility to outplanted corals (Fig. 1A). Five fireworms, not fed for at least 24 hours to induce hunger, were placed in PVC buckets (⌀ = 30cm) filled with newly collected seawater (n=3). Additionally, an *A. cervicornis* fragment was strung up in the bucket to either a centre-placed rebar (⌀ 1cm) or a PVC pole with a diameter of 1.5cm or 2.7cm.

The lowest part of the *A. cervicornis* fragment was placed at heights of 0cm (control), 10cm, 20cm, or 30cm. The fragments used had a total linear extension of 5 cm, with at least two cuts at the tips and some form of damage (mechanical or partially bleaching), to stimulate the fireworms' scavenging behaviour (Wolf et al., 2014). Observations were done 0.25, 1, 2, 3, 6, and 24 hours after start of the experiment. If any fireworms were observed to be predating on the coral at the mentioned time points, the time was noted, and these individuals were removed from the coral. Additionally, fireworm length was measured and compared to determine if fireworm length was a decisive factor for coral accessibility.

Ex situ coral preference experiment

An *ex situ* free-choice coral assay was performed to uncover preferences for distinct coral species by the fireworms (Fig. 1B). In total, 63 fireworms not fed for at least 24 hours were placed individually at the top left corner of an aluminum tray (32cm x 26.5cm) before being exposed to two coral fragments simultaneously. The fragments were placed 8cm from the edges in two consistent locations at the centre of the tray. For each trial, the placement of the coral fragments in the predetermined locations was randomized. In total, three choice treatments were presented for the fireworms: 1) *Acropora*

cervicornis vs *Agaricia sp.,* 2) *Acropora cervicornis* vs *Millepora complanata,* and *3) Agaricia sp., vs Millepora complanata.* The comparisons with *Agaricia sp.* and *M. complanata* were chosen because of their abundance at the House Reef. The *Agaricia sp.* and *M. complanata* fragments used were loose fragments found at the House Reef at depths from 0-3m.

The coral fragment sizes used in the treatments were between 10-20cm^2 and placed horizontally on the tray's surface. The coral surface was calculated by considering *Agaricia sp.,* and *M. complanata* fragments as a two-sided rectangle, and *A. cervicornis* as a cylinder. Observation time was six hours as fireworms have been indicated to detect even smaller-sized corals within this time limit (Wolf et al., 2014). A choice was considered to be made when a fireworm positioned its mouth on the coral and remained there for at least one minute. Predation within the mentioned time points could have occurred. However, since no clear distinction between bitemarks and standard coral decay could be made, these predation events went unnoticed. The aim was to receive at least ten successful trials per comparison. A trial was deemed successful if the fireworm made a choice. If no choice was made within six hours, the experiment was extended up to 24 hours to increase the total number of responses.

Outplanting predation mitigation experiment

In total, 96 *A. cervicornis* coral fragments with a total linear extension between 20-35 cm were collected and placed in two plastic buckets filled with seawater before being transported to Drake Island. The corals were never exposed to air during the transportation process. The corals were outplanted on Drake Island at depths between 3.8 – 7.5m. The fragments were divided over four treatments (n=8) to assess the influence of density and elevation from the seabed on predation pressure. The coral outplanting treatments (Fig. 1C) were low density (LD; 1 per m^2), high density (HD; 5 per m^2), low density 15cm elevation (LD+E), and high density 15cm elevation (HD+E). The different plots were located at least 5m apart. Furthermore, each treatment plot was chosen to minimize the presence of *Agaricia* sp. and *Millepora* sp. colonies to avoid competition and attraction of predators to other corals.

The LD and HD treatment outplanting was done by attaching the fragment to a 10cm flat steel masonry nail (~5cm in the seabed) with a cable tie, as this was proven to be an effective method (Goergen et al., 2018; Huang et al., 2023). The outplanting strategy for the LD+E and HD+E treatments was similar but rebar poles were used (⌀ 1cm) instead of masonry nails to elevate the corals approximately 15cm from the seabed, as no nails of this size were available.

After outplanting, the plots were monitored weekly for 64 days to count the number of fireworms in the plot and on the corals. Corals were also observed for bitemarks, bleaching, and diseases during each predation monitoring session. Three weeks after outplanting, a storm resulted in damage to the corals and a total loss of 20 corals (90% were non-elevated, 10% elevated). In week 5, all corals except one elevated coral (due to lack of material) were replaced.

Identification of natural predators of fireworms

In total, 89 fireworms were divided over 16 different predator trials (Fig. 1D) at the locations Scuba House Reef (n=5), Drake Island (n=6), and Huerta (n=5). Knoester et al. (2023) inspired the set-up for the predator trials. Fireworms were tied with a thread to a rebar pole stuck in a concrete disk (⌀ 20.5cm). A GoPro (Hero 7) was used to film the first hour after the placement of the disk on the reefs. After one hour, the number of surviving fireworms was counted. If all fireworms remained alive, an additional check was done after 1-7 days, depending on accessibility to the research area. Additionally, snorkelling sessions were performed at sites with regular fireworm sightings. In these snorkelling sessions fireworms were suspended individually to observe any predation on the exposed individual.

Statistics

R studio 4.2.2. was used to test significance ($p<0.05$) for the experimental results. Normality ($p>0.05$) and homogeneity of variances ($p>0.05$) of the data were tested with a Shapiro-Wilks- and Levene's-test, respectively. The *ex situ* elevation- and *in situ* outplanting data were not normally distributed. However, a two-way ANOVA was still performed to compare the treatments because of its robustness to type-1 errors (Blanca Mena et al., 2017). If significant, a Tukey's test was performed to determine further differences between treatments. An unpaired t-test was conducted for the fireworm length data of the *ex situ* elevation experiment. Coral preference choices were compared using the binomial test.

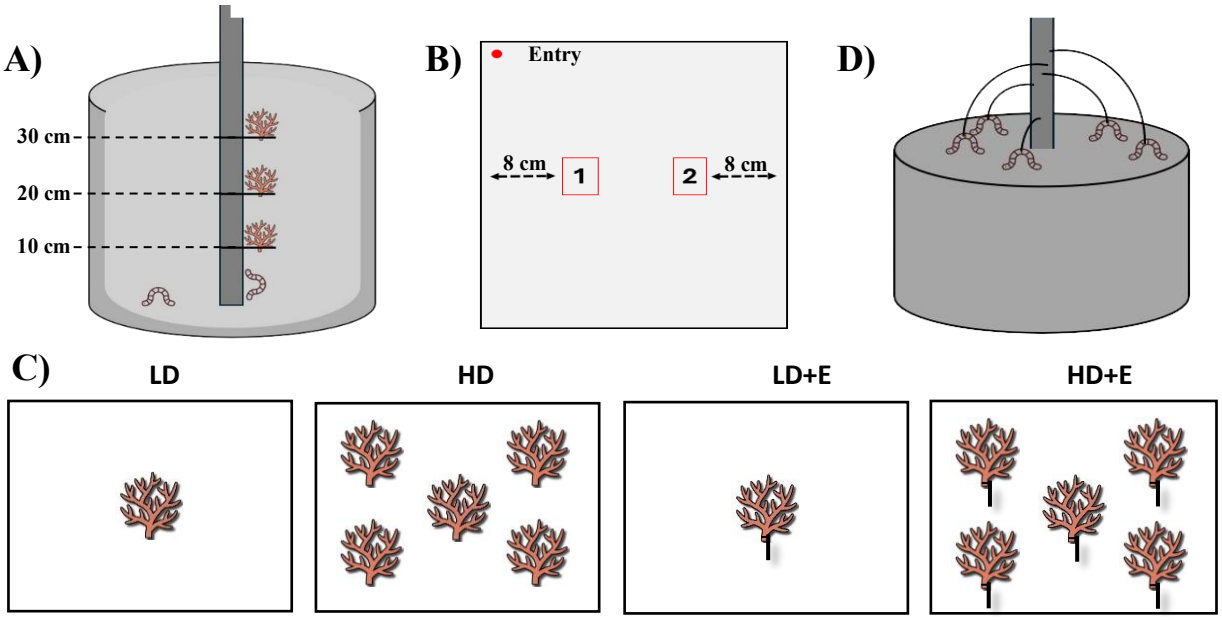


Fig. 1. Design of the four experiments. **A)** Overview of the elevation experimental set-up with the possible outplanting heights of the *A. cervicornis* fragments. **B)** Overview of the coral preference assay with the location of the two coral fragments indicated with '1' and '2'. The red circle indicates the entry point. **C)** Overview of the low density (LD; $1m^{-2}$), high density (HD; $5m^{-2}$), low density elevated (LD+E; $1m^{-2}$ + 15cm), and high density elevated (HD+E; $5m^{-2}$ +15cm) treatments used in the elevation and density experiment. **D)** Overview of how the worms were attached to the concrete disk in the natural predator experiment.

Results

Ex situ elevation experiment

The *ex situ* elevation experiment indicated that the maximum elevation tested of 30cm was still reachable by the fireworms. The overall coral reachability was lower for elevated corals in comparison to non-elevated ($p < 0.001$). There was no significant difference between the different elevations tested. However, when using rebar, more fireworms were able to reach the coral for the treatments tested in comparison to using PVC with a diameter of 1.5cm ($p < 0.001$) and 2.7cm ($p < 0.001$) (Fig. 2). Among the two PVC diameters, there was no significant difference. Nonetheless, for the PVC pole with a 1.5cm diameter no worms reached the coral at any of the elevations, despite an observed attempt to climb the pole (Supplementary Fig. 1; Supplementary Video 1). There was no significant difference in worm size for individuals that reached elevated corals in comparison to worms that did not. Lastly, it was observed that the worms in the treatments were able to climb the walls of the PVC buckets, in which the treatments were performed.

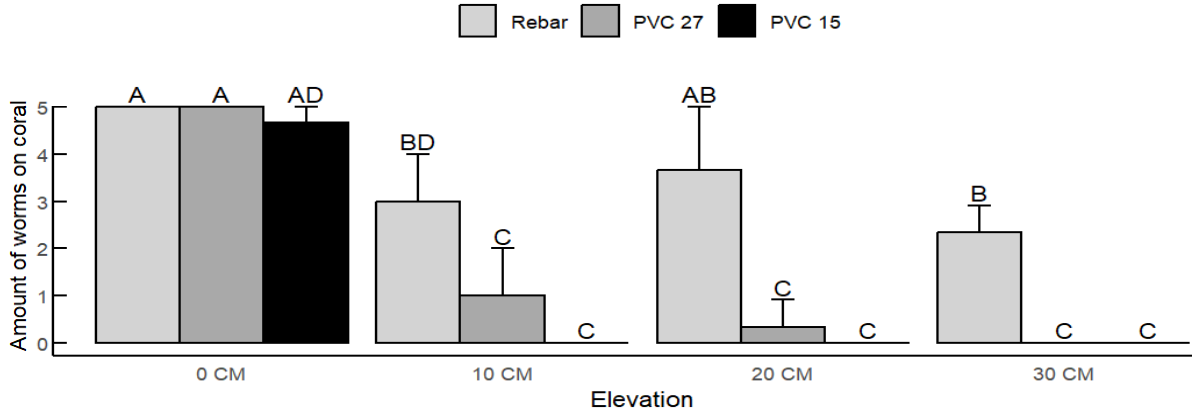


Fig. 2. Average amount of worms with their respective SD (n=3) being able to reach the coral at various elevations (0 – 30 cm), materials (Rebar + PVC), and diameter (PVC ⌀ 15mm, and PVC ⌀ 27mm) within 24 hours. Differing letters above bars indicate significant differences among the treatments.

Ex situ coral preference experiment

The success rates of the free choice experiments of *Acropora cervicornis* vs *Agaricia sp.*, (Ac vs Ag), *Acropora cervicronis* vs *Millepora complanata* (Ac vs Mc), and *Agaricia sp.* vs *Millepora complanata* (Ag vs Mc) were 12.5%, 34.5%, and 60% respectively. Because of these success rates and time constraints, the aim of 10 repetitions per coral preference trial (Fig. 3) were not always reached. Only *A. cervicornis* was chosen in the Ac vs Ag trial. However due to only having three successful replicates, it was not possible to determine if this observation was significant. The Ag vs Mc trial indicated that there was a preference ($p<0.05$) for *M. complanata* over *Agaricia sp.* A preference for *M. complanata* over *A. cervicornis* was not found in the Ac vs Mc trial. Despite this, prey-switching did occur in the Ac vs Mc trial. The worms shifted from their original coral choice (*A. cervicornis* or *M. complanata*) to the other coral fragment in 30% of the cases.

Outplanting predation mitigation experiment

The first fireworm predating on the outplanted corals was observed five weeks after the start of the experiment. A total of 6 fireworms were observed affecting 9.4% of the coral plots and averaging to a density of 0.02m^{-2} across all treatments over the two month period (Fig. 4). Neither the density treatment nor the elevation showed a significant effect on the amount of fireworms reaching the corals. However, the interaction effects of those two factors was significant ($p<0.05$). Three of the fireworms observed were present on two plots of the HD, and the remaining three on one plot of the LD+E treatment (Fig. 5). Re-occurrence of fireworms was observed on the LD+E plot and one HD plot. However the fireworms were never observed two consecutive weeks in a row. Furthermore, it was visibly apparent that the elevated treatments suffered more from mechanical damages (Fig. 5A) than the non-elevated treatments. Other organisms observed on the coral plots were coral crabs (on 13% of the plots), hermit crabs (38%), and coralliophilid snails (66%).

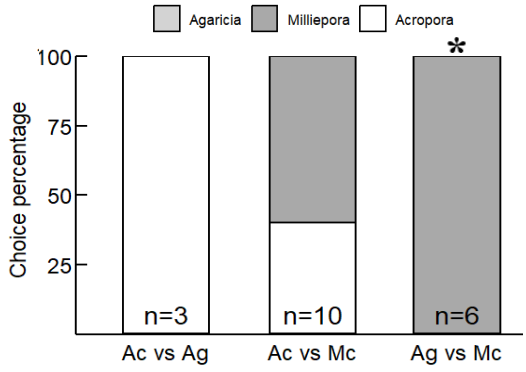


Fig. 3. Coral choice percentages for the *A. cervicornis* vs *Agaricia sp.,* (Ac vs Ag), the *A. cervicornis* vs *M. complanata* (Ac vs Mc), and the *Agaricia sp.,* vs *M. complanata* trials. Asterisk indicates a significant difference ($p<0.05$). Successful trials (n) are displayed in each bar.

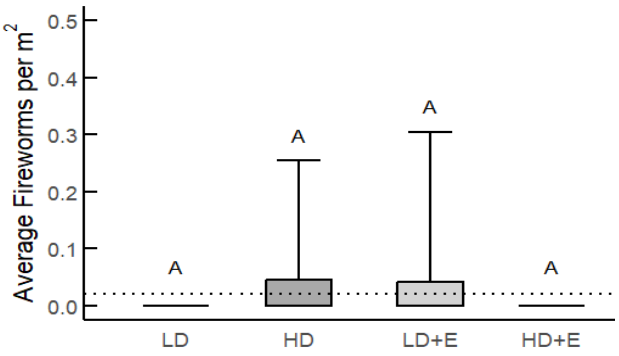


Fig. 4. Average number of worms observed for the low density (LD), high density (HD), low density elevated (LD+E), and the high density elevated (HD+E) treatments (n=8) with their respective SD. The dotted line indicates the average fireworm density across all treatments. Similar letters above bars indicate no significant difference.

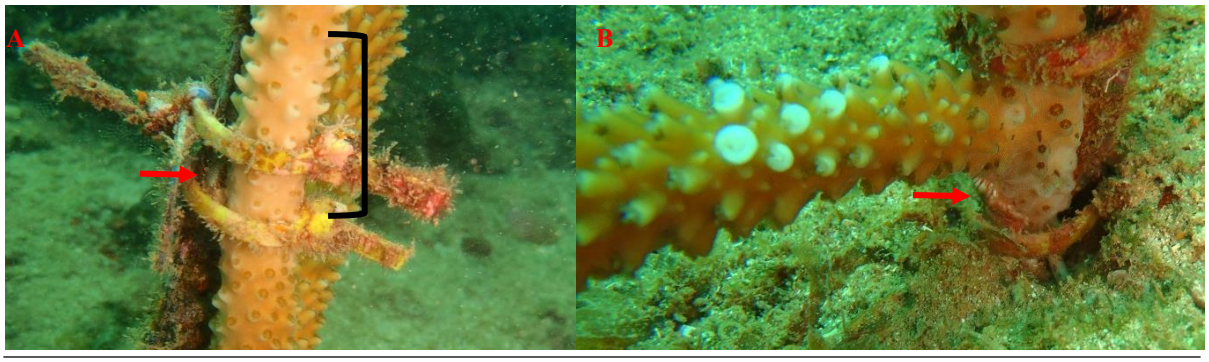


Fig. 5. Fireworms (indicated with red arrows) on the low density elevation treatment (**A**) and the high density no elevation treatment (**B**). The black bracket indicates the area affected by mechanical damage.

Identification of natural predators of fireworms

During the snorkeling trials predation events of the known fireworm predators *Haemulon plumierii* (Supplementary Fig. 2; Supplementary Video 2) and *Thalassoma bifasciatum* (Supplementary Fig. 3; Supplementary Video 3) were observed on manually suspended fireworms. These species as well as the other known predator *Halichoeres garnoti* were also observed in the disk trials, but did not predate on the worms during these trials.

For all disk trials, the fireworms were gone within seven days. In six instances survival checks were done within two days. For these instances all fireworms were absent. Furthermore, the squirrelfish (*Holocentrus adscensionis)* was shown to actively eat a fireworm tied to a thread (Fig. 6; Supplementary Video 4). After consuming the first worm, the squirrelfish was seen attempting to eat a second fireworm before being chased away by a porkfish (*Anisotremus virginicus*). Additionally, a table containing all observed species was created (Supplementary table 1).

Fig. 6. Time series of the squirrelfish (*Holocentrus adscensionis)* locating (**A**) the fireworm (indicated with a red arrow), to then orientating itself toward the worm (**B**), to eventually consume it (**C** and **D**).

Discussion

This study was designed to create new insights into the outplanting strategies of *Acropora cervicornis* to reduce the effect of predation by the bearded fireworm (*Hermodice carunculata*). No coral preference of *A. cervicornis* was found over *M. complanata*. Additionally, no preference could be determined between *A. cervicornis* and *Agaricia sp.,* due to the insufficient number of replicates. Furthermore, elevation and the use of PVC significantly decreased coral accessibility by the fireworms *ex situ*. A beneficial effect of elevation or density was not observed in the field, most likely due to a low predator density on the natural reef where the experiment occurred. Lastly, the squirrelfish (*Holocentrus adscensionis*) was observed as a new fireworm predator.

Ex situ elevation experiment

Corals at the highest tested elevation of 30cm were still accessible by *H. carunculata,* indicating that elevation cannot fully exclude predation. Nonetheless, elevation did significantly decrease fireworm coral accessibility in this study, but these results should be taken with caution. The first response of the worms after being placed into the container was a fleeing response to find a potential hideout (R. Verdaasdonk Pers. observations). This fleeing response is likely attributed to the cryptic nature of fireworms (Wolf et al., 2014). During the study, the non-elevated coral could have been seen as a suitable hiding spot, resulting in a higher coral reachability for the non-elevated treatments.

Furthermore, *H. carunculata* only leave their hideouts to feed (Ramos & Schizas, 2023). Although, the fireworms were not fed for at least 24h, this duration was probably insufficient to trigger a scavenging response. Fireworms can survive for over a week without being fed (R. Verdaasdonk Pers. observations), therefore extending the non-feeding period is possible to further stimulate *H. carunculata's* scavenging behaviour. Additionally, the duration time of the experiment can be increased. Wolf et al. (2014) observed a peak in fireworm abundance between 24h and 48h for an *in situ* prey preference study. Therefore, future studies can consider extending the non-fed period and the monitoring time up to 48h to gain more accurate results on the effect of elevation.

Despite this, the materialistic difference found between elevations through using a PVC or a rebar pole remains a significant result. The rebar's surface contained ridges that could have served as support ridges for the fireworms to climb upon the material. The surface of the PVC pole used was smooth. Indicating that a smooth material surface texture negatively influences the ability of fireworms to climb towards elevated corals. Furthermore, since fireworms use parapodia with lateral-orientated chaetae for their locomotion (Verdonschot, 2015), the curvature of the structure can also influence the ability of the parapodia placement on the structure. Although, there was no significant difference among the PVC diameters tested, it is noteworthy to mention that no worms reached the coral fragment for the 15mm diameter treatment. As a decrease in diameter increases the curvature angle, it is possible that the worm's parapodia could not find adequate support to climb the pole. In contrast, the large diameter, and thereby lack of curvature of the bucket walls, could explain why the fireworms were frequently observed to climb the bucket walls. These observations indicate that an optimal combination of material surface and diameter of the elevation structure can be found that maximally reduces the ability of *H. carunculata* to reach the coral. Based upon this research, the best option is to elevate the corals at least 10cm with PVC pipes that have a diameter of 15mm to reduce *H. carunculata* predation

<u>*Ex situ* coral preference experiment</u>

The coral preference study provided insights into the fireworm's predatory behaviour when exposed to two corals simultaneously. Although not significant due to the low number of successful trials, the experiments suggest that fireworms prefer *A. cervicornis* over *Agaricia sp.* This is similar to an older coral prey selection study by Rylaarsdam (1983), which showed that 30 individuals chose *A. cervicornis* over *Agaricia agaricites* in a similar set-up. Additionally, since there was no difference in preference between *A. cervicornis* and *M. complanata* and that there was a preference for *M. complanata* over *Agaricia sp.,* it supports the idea of *A. cervicornis* being preferred over *Agaricia sp.* That *M. complanata* was significantly preferred over *Agaricia sp.,* complements the personal observations (R. Verdaasdonk) during the collection process where fireworms were mostly collected from *M. complanata*. Fireworms seemed also to be more abundant on reefs with more *M. complanata* coverage (R. Verdaasdonk, Pers. Observations). Indicating that there might be a correlation between fireworm density and *M. complanata* reef coverage.

Interestingly, there was no prey preference between *A. cervicornis* and *M. complanata*. Since fireworms engulf their buccal cavity over their food source to digest it (Miller et al., 2014), it was expected that *A. cervicornis* would be the preferred coral species because of its structural properties. However, since there was no difference in preference, prey-choice likely depends on other factors. Other possibilities are differences in feeding deterrents and olfactory attractants excreted by the corals (Wolf et al., 2014).

Since fireworms have shown to alternate food sources when being exposed *ex situ* to *M. complanata* and *A. cervicornis*, it is possible that a positive neighbouring effect of *M. complanata* can be provided to *A. cervicornis*. For example, when fireworms are exposed to an *A. cervicornis* colony surrounded by *M. complanata colonies*, it can be hypothesized that the overall damage to the *A. cervicornis* colony will decrease, as fireworms scatter their predation to the neighbouring corals. However, the exact opposite can be proposed by potentially attracting a higher density of fireworms by creating an area with highly preferred coral species. A potential experiment to test these hypothesises is to compare predation differences for *A. cervicornis* outplanted individually and with *A. cervicornis* outplants surrounded by *M. complanata,* or *Agaricia sp.*

Outplanting predation mitigation experiment

The fact that no significant difference was found among the density and elevation treatments in the field outplace treatments, indicates that on short-term, these factors do not influence *H. carunculata* predation pressure on outplanted fragments of *A. cervicornis* at the Drake Island reef in Portobelo. The interaction effects of the density and elevation on the amount of fireworms showed a significant result. However, the post processing of this result revealed no clear indication where such effects where present among the treatments. These results should be taken with caution as the low number of individuals observed resulted in a small sample size making it improbable to find a more reliable result. Interestingly, a low number of *H. carunculata* observations was also found by Lohr et al., (2017), where predation occurred on 15% of their outplanted colonies in the Cayman Islands after a 3-month period. Thereby, implying that *H. carunculata* predation possibly is not a strong determining factor for initial outplanting success. Nonetheless, the long-term effects of density and elevation on *H. carunculata* predation are unknown and should be studied further.

Additionally, since no distinctive predation scars were found, the results were solely based on *H. carunculata's* sightings. During the study, it became apparent during the collection of individuals that fireworm presence varies throughout the day. Despite being considered nocturnal (Schulze et al., 2017), personal observations during fireworm collection sessions showed that fireworm presence was highest between noon and afternoon and decreased approaching sunset. These times have also been recorded for the locations Barbados and Tenerife (Ott & Lewis, 1972; Schulze et al., 2017). However, for Ikaria, Greece, fireworm density increased as night time approached (Schulze et al., 2017). These findings suggests that the activity of *H. carunculata* is variable throughout the day but is also location dependent. Since the monitoring sessions were performed before noon, the peak in *H. carunculata* activity could have been missed. *H. carunculata* density also has a seasonal variety and tends to decrease between October and February (Toso et al., 2022). Therefore, by combining the study period and potentially missing peak fireworm activity at the outplanting site, the observed number *H. carunculata* can be lower than the actual value. Future studies should take these factors into account when trying to determine the effects elevation and density on *H. carunculata* predation in a similar matter.

Despite the experiment not providing significant results among treatments regarding to *H. carunculata* predation, the suitability for practical use of the treatments can be discussed. Firstly, the occurrence of a storm after three weeks led to a loss of 20 corals, of which 90% were non-elevated and 10% were elevated. The remaining elevated corals did slide down to the seabed but were not completely lost. Thereby, showing an unexpected positive factor of the poles used for elevation. Therefore, outplanting for areas with frequent storms can consider outplanting corals attached to ~20 cm poles to decrease the chance of losing corals due to weather conditions.

Secondly, using cable ties to attach the corals to the nails or rebar poles negatively influenced coral health. As cable ties were pulled tightly around the coral and nail, a strong current still slightly moved the cable tie over the nail or rebar, consequently loosening the coral from the rebar or nail. The loosening of the coral resulted into the fragment constantly moving over the surface of the nail or rebar with the coral. Although not quantified, attaching corals to rebar resulted in more mechanical damage (Fig. 5A), likely caused by the ridges visible on the rebar. Corallivores such as *H. carunculata* are attracted to damaged corals (Bright et al., 2015; Wolf et al., 2014), therefore the mechanical damage could lead to an increase of predation. Thus, when using similar methods, multiple monitoring sessions within the first week of outplanting to tighten loose corals to minimalize mechanical damage are recommended.

The viability of the treatments can also be discussed if there are no long-term effects on *H. carunculata* predation. An increase in *A. cervicornis* outplanting density can negatively influence coral growth and survival (Griffin et al., 2015; Goergen & Gilliam, 2018; Ladd et al., 2016). Factors suggested explaining these effects are increased competition, disease risk, and corallivore predation (Griffin et al., 2015; Goergen & Gilliam, 2018; Ladd et al., 2016). However, the downside of lower outplanting densities is that habitat complexity decreases simultaneously. As a result, the positive effects of reef complexity on marine life are postponed until colonies grow significantly (Béguinot, 2019). Despite this, with the initial goal of restoring corals, it is worth considering to outplant them in lower densities if practically possible, as Goergen & Gilliam (2018) suggested.

Alternatively, outplanting various coral species rather than solely conspecifics in higher densities can be considered. Using various species additionally decreases disease risk, as susceptibility to coral diseases is species specific (Rosenberg & Loya, 2004), while remaining habitat complexity. Also a reduction in coralliophila predation has been observed when using various coral species within the same colony aggregation (Johnston & Miller, 2014). However, if coral restoration is focused upon one species in a respective area, this can decrease outplanting productivity due to the increase in labour.

No studies were found that consider the effects of elevating corals. However, some artificial structures already have been proven effective for coral restoration (Lange et al., 2024), suggesting that appropriate elevation structures will not harm coral growth. Additionally, it can be considered that elevating corals at various heights within the same plot will distribute the colony's surface area across different parts of the water column. Thereby improving overall nutrient availability, gas exchange, and light distribution of the colony (Hoogenboom et al., 2008; Shakya et al., 2023). Further, alternating outplanting elevations within the same plot increases habitat complexity. Therefore, short-term elevation can be beneficial by minimalizing intraspecific competition and increasing habitat complexity.

Contrary to these benefits, the corals will depend on their elevation structure as an anchor to the seabed. As coral size and weight increase, the structure is more prone to break during harsh weather conditions. Consequently, resulting in mechanical coral damage suggesting that long-term elevation can be disadvantageous. However, if the structure holds until the colony inevitably reaches the seabed due to growth, these disadvantages can be minimized. Nevertheless, these effect of elevation considered are speculative, and the true effects on colony growth and survival need to be tested.

Natural predator experiment

In all instances the fireworms disappeared within seven days, revealing that there is a predation pressure for *H. carunculata* on the Portobelo reefs. However, whether the disappearance is exclusively due to predation cannot be certain. Other factors, such as the worms being able to segment themselves or strong currents removing the threads, also could have led to observing no individuals at the checks.

Furthermore, the fact that the known fireworm predators *Haemulon plumierii,* and *Thalassoma bifasciatum*, predated on *H. carunculata* during the snorkeling trials, but were not found to actively predate on *H. carunculata* during the disk trials, can indicate that *H. carunculata* is not a preferred prey species. However, it can also be that the experimental set-up negatively affected their predatory behaviour. Predation pressure studies, e.g., gut analysis of the predator species or *H. carunculata* density compared to predator abundance, can provide further detail of these predator-prey relationships.

The *H. carunculata* predation event recorded by the squirrelfish (*Holocentrus adscensionis*) might have revealed a previously unknown longstanding dynamic within the reef ecosystem. Although *H. adscensionis* and the other predators are not endangered globally, artisanal fisheries have shown to reduce local Caribbean reef fish populations (Hawkins & Roberts, 2004). A local decrease in corallivore predators results to less top-down control of corallivores (Ladd & Shantz, 2020), consequently leading to more corallivory. Therefore, local management can contemplate to temporarily protect reefs from fisheries where *H. carunculata* hinder *A. cervicornis* restoration.

Future implications

This study provided valuable insights that can be used for further studies aiming at reducing *H. carunculata* predation on *A. cervicornis*. Firstly, the potential of elevation, especially in combination with PVC, must be tested to see their long-term effects. The use of plastics can be controversial and negatively affect coral growth and disease risk (Hankins et al., 2021; Lamb et al., 2018). Therefore, one strategy can be to only use PVC elevation structures during a high expected *H. carunculata* density based on their seasonal variety. For example, a PVC pole can be placed over existing elevation structures during high *H. carunculata* density periods. This decreases coral accessibility by the worms and simultaneously minimizes the adverse effects of PVC on coral health.

One possible structure is the highly effective ‘reef star’ as used in the MARS restoration program. Restored reefs with these reef stars had as much carbonate production as healthy reefs within four years (Lange et al., 2024). The corals attached to the reef stars are elevated from the seabed by six independent

legs. By covering these legs partly with PVC tubes (e.g. 10 cm and ⌀ 15mm) they could potentially reduce fireworm predation. Thereby, the effectiveness of reef stars can become an important restoration tool for reefs suffering from high amounts of fireworm predation .

Furthermore, using PVC as a material for nursery structures can also be investigated for nurseries with re-occuring *H. carunculata* predatorion. Most nurseries use elevated structures to grow their fragments. These nurseries can test using PVC to (partly) cover the legs of their elevation structures to reduce fireworm predation simultaneously. If these structures reduce predation, it can further lower overall maintenance, which is a desired trait for nursery structures (Maurer et al., 2022).

Additionally, with more known predators *of H. carunculata*, more options become available for selecting sites with reduced predation risk. Sites with a healthy natural predator population can provide adequate top-down pressure on *H. carunculata,* thereby reducing the predation on *A. cervicornis*. However, with *H. carunculata* being tolerant to various environmental conditions and little knowledge about their life cycle (Schulze et al., 2017), reefs stay susceptible to unexpected increases in *H. carunculata* populations. Future studies should focus on uncovering the drivers of a sudden fireworm population increase. Additionally, another strategy should be investigated using the possible positive neighbouring effects of the widespread coral *M. complanata* to reduce predation on *A. cervicornis.*

Furthermore, studies must consider the whole reef system. For example, coralliophila snails were observed in 66% of the outplanted colonies of *A. cervicornis* in this study. Therefore, even if a practical methodology is found to decrease *H. carunculata* predation, it should not negatively affect total coral survivability through other factors. Additionally, the use of PVC and its potential long-term adverse effects on reef systems should be considered before large-scale application. Reef restoration should remain the key focus and should not be lost out of sight.

Conclusions

This study indicated that in *ex situ* conditions, fireworm coral accessibility decreased with elevation and even further when using a smooth-surfaced material like PVC. Hence, it is worth investigating to use PVC pipes to elevate outplanted *A. cervicornis* fragments above the seafloor, since this likely reduces fireworm predation. No significant effect of elevation with rebar and density were found in the field, possibly attributed to the low fireworm density within the area. The long-term effect however remains unknown. Additionally, this study supports the known preference of *A. cervicornis* over *Agaricia sp.,* and gained new knowledge that there is no significant preference between *A. cervicornis* and *M. complanata*. Furthermore, the prey-switching behaviour observed between *A. cervicornis* and *M. complanata* can be useful in future neighbouring studies to decrease fireworm predation. Lastly, the finding of *Holocentrus adscensionis* as an additional *H. carunculata* predator helps to select suitable reefs with more top-down control on *H. carunculata* to increase *A. cervicornis* restoration efforts. Although the first indications for potential *H. carunculata* mitigation strategies are considered in this study, the influence of these strategies on reef systems is still unknown. Future studies focussing on the long-term effects of elevation, site selection based on neighbouring corals, and reef selection based on predator abundance will lead to more detailed insights into applying the mitigation strategies proposed in this study.

Acknowledgements

I want to thank dr. Ronald Osinga for providing me with the opportunity to perform research related to coral restoration. Additionally, I want to thank Jean Carlos Blanco and Luis Enrique Bernal from Reef2Reef for their help setting up the project and supporting me with practical insights. I also want to thank Lusmila from Scuba Portobelo, providing me with the feeling of being home during the months of field work. Lastly, I want to thank Valentijn Elsman for helping me with all the fieldwork and the joyful time in Panama.

References

Aronson, R. B., & Precht, W. F. (2001). White-band disease and the changing face of Caribbean coral reefs. In *Springer eBooks* (pp. 25–38). https://doi.org/10.1007/978-94-017-3284-0_2

Béguinot, J. (2019). Influence of Coral-reef Complexity on Species Richness and the Hierarchical Structuration of Species Abundances in Reef fish Communities: A Case Study in South-east Brazil. *Asian Journal of Environment & Ecology*, 1–20. https://doi.org/10.9734/ajee/2019/v9i330098

Blanca, M. J., Alarcón, R., Arnau, J., Bono, R., & Bendayan, R. (2017). Non-normal data: Is ANOVA still a valid option? *PubMed*, *29*(4), 552–557. https://doi.org/10.7334/psicothema2016.383

Boström-Einarsson, L., Babcock, R. C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S. C. A., Hancock, B., Harrison, P. L., Hein, M. Y., Shaver, E. C., Smith, A. K., Suggett, D. J., Stewart-Sinclair, P. J., Vardi, T., & McLeod, I. (2020). Coral restoration – A systematic review of current methods, successes, failures and future directions. *PLOS ONE*, *15*(1), e0226631. https://doi.org/10.1371/journal.pone.0226631

Bright, A. J., Cameron, C. M., & Miller, M. W. (2015). Enhanced susceptibility to predation in corals of compromised condition. *PeerJ*, *3*, e1239. https://doi.org/10.7717/peerj.1239

Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth*, *4*(9), 1278–1285. https://doi.org/10.1016/j.oneear.2021.08.016

Edmunds, P. J. (2019). Three decades of degradation lead to diminished impacts of severe hurricanes on Caribbean reefs. *Ecology*, *100*(3). https://doi.org/10.1002/ecy.2587

Goergen, E. A., & Gilliam, D. S. (2018). Outplanting technique, host genotype, and site affect the initial success of outplanted Acropora cervicornis. *PeerJ*, *6*, e4433. https://doi.org/10.7717/peerj.4433

Griffin, J. N., Schrack, E. C., Lewis, K. A., Baums, I. B., Soomdat, N. N., & Silliman, B. R. (2015). Density-dependent effects on initial growth of a branching coral under restoration. *Restoration Ecology*, *23*(3), 197–200. https://doi.org/10.1111/rec.12173

Hankins, C., Moso, E., & Lasseigne, D. (2021). Microplastics impair growth in two Atlantic scleractinian coral species, Pseudodiploria clivosa and Acropora cervicornis. *Environmental Pollution*, *275*, 116649. https://doi.org/10.1016/j.envpol.2021.116649

Hawkins, J. P., & Roberts, C. M. (2004). Effects of artisanal fishing on Caribbean coral reefs. *Conservation Biology*, *18*(1), 215-226. https://doi.org/10.1111/j.1523-1739.2004.00328.x

Hein, M. Y., Vardi, T., Shaver, E. C., Pioch, S., Boström-Einarsson, L., Ahmed, M., Grimsditch, G., & McLeod, I. (2021). Perspectives on the use of coral reef restoration as a strategy to support and improve reef ecosystem services. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.618303

Hoogenboom, M. O., Connolly, S. R., & Anthony, K. R. (2008). Interactions between morphological and physiological plasticity optimize energy acquisition in corals. Ecology, 89(4), 1144-1154. https://doi.org/10.1890/07-1272.1

Huang, L., Yu, X., Liu, C., Jiang, L., Chen, L., Ye, W., Zhang, P., Zhang, Y., & Huang, H. (2023). Actions to achieve rapid coral self-attachment: insights from outplanting nails, coral orientation, and substrate biological condition. *Restoration Ecology*, *31*(7). https://doi.org/10.1111/rec.13958

IUCN (2021, June 1). *IUCN Red List of Threatened Species: Acropora cervicornis*. IUCN Red List of Threatened Species. https://www.iucnredlist.org/species/133381/165860142

Johnston, L., & Miller, M. W. (2014). Negative indirect effects of neighbors on imperiled scleractinian corals. *Coral Reefs*, *33*(4), 1047–1056. https://doi.org/10.1007/s00338-014-1176-8

Knoester, E. G., Klerks, N., Vroege-Kolkman, S., Murk, A. J., Sande, S. O., & Osinga, R. (2023). Coral predation and implications for restoration of Kenyan reefs: The effects of site selection, coral species and fisheries management. *Journal of Experimental Marine Biology and Ecology*, *566*, 151924. https://doi.org/10.1016/j.jembe.2023.151924

Kohn, A. A., Nybakken, J. J., & Van Mol, J. J. (1972). Radula Tooth Structure of the Gastropod Conus

imperialis Elucidated by Scanning Electron Microscopy. *Science*, *176*(4030), 49–51. https://doi.org/10.1126/science.176.4030.49
Ladd, M.C. and Shantz, A.A. (2016). Novel enemies – previously unknown predators of the bearded fireworm. Frontiers in Ecology and the Environment 14, 342–343 https://doi.org/10.1002/fee.1305
Ladd, M. C., & Shantz, A. A. (2020). Trophic interactions in coral reef restoration: A review. *Food Webs*, *24*, e00149. https://doi.org/10.1016/j.fooweb.2020.e00149
Ladd, M. C., Shantz, A. A., Nedimyer, K., & Burkepile, D. E. (2016). Density Dependence Drives Habitat Production and Survivorship of Acropora cervicornis Used for Restoration on a Caribbean Coral Reef. *Frontiers in Marine Science*, *3*. https://doi.org/10.3389/fmars.2016.00261
Lamb, J. B., Willis, B. L., Fiorenza, E. A., Couch, C. S., Howard, R., Rader, D. N., True, J., Kelly, L. A., Ahmad, A., Jompa, J., & Harvell, C. D. (2018). Plastic waste associated with disease on coral reefs. *Science*, *359*(6374), 460–462. https://doi.org/10.1126/science.aar3320
Lange, I. D., Razak, T. B., Perry, C. T., Maulana, P. B., Prasetya, M. E., & Lamont, T. A. (2024). Coral restoration can drive rapid reef carbonate budget recovery. Current Biology. https://doi.org/10.1016/j.cub.2024.02.009
Lohr, K. E., McNab, A. a. C., Manfrino, C., & Patterson, J. T. (2017). Assessment of wild and restored staghorn coral Acropora cervicornis across three reef zones in the Cayman Islands. *Regional Studies in Marine Science*, *9*, 1–8. https://doi.org/10.1016/j.rsma.2016.11.003
Maurer, L., Puishys, L., Ho, N. K. P., Dahlgren, C. P., Kamerman, T. Y., Martin, S. E., & Stamper, M. A. (2022). Acropora cervicornis and Acropora palmata cultured on a low maintenance line nursery design in The Bahamas. *PLOS ONE*, *17*(4), e0267034. https://doi.org/10.1371/journal.pone.0267034
Miller, M. W., Marmet, C., Cameron, C. M., & Williams, D. E. (2014). Prevalence, consequences, and mitigation of fireworm predation on endangered staghorn coral. *Marine Ecology Progress Series*, *516*, 187–194. https://doi.org/10.3354/meps10996
NOAA (2016). Acropora coral propagation efforts in Puerto Rico and the U.S. Virgin Islands : 2016 annual report.
Ott, B., & Lewis, J. B. (1972). The importance of the gastropod Coralliophila abbreviata (Lamarck) and the polychaete Hermodice carunculata (Pallas) as coral reef predators. *Canadian Journal of Zoology*, *50*(12), 1651–1656. https://doi.org/10.1139/z72-217
Perry, C. T., Steneck, R. S., Murphy, G. N., Kench, P. S., Edinger, E., Smithers, S. G., & Mumby, P. J. (2014). Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Global Change Biology*, *21*(3), 1153–1164. https://doi.org/10.1111/gcb.12792
Ramos, M. a. C., & Schizas, N. V. (2023). Population structure of the fireworm Hermodice carunculata in the wider Caribbean, Atlantic and Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, *103*. https://doi.org/10.1017/s0025315422001114
Renzi, J. J., Shaver, E. C., Burkepile, D. E., & Silliman, B. R. (2022). The role of predators in coral disease dynamics. *Coral Reefs*, *41*(2), 405–422. https://doi.org/10.1007/s00338-022-02219-w
Rice, M. M., Ezzat, L., & Burkepile, D. E. (2019). Corallivory in the Anthropocene: Interactive effects of anthropogenic stressors and corallivory on coral reefs. *Frontiers in Marine Science*, *5*. https://doi.org/10.3389/fmars.2018.00525
Rylaarsdam, K. W. (1983). Life histories and abundance patterns of colonial corals on Jamaican reefs . *Marine Ecology Progress Series*, *13*, 249–260. https://doi.org/10.3354/meps013249
Sakai, K., Singh, T., & Iguchi, A. (2019). Bleaching and post-bleaching mortality of Acropora corals on a heat-susceptible reef in 2016. *PeerJ*, *7*, e8138. https://doi.org/10.7717/peerj.8138
Schulze, A., Grimes, C. J., & Rudek, T. E. (2017). Tough, armed and omnivorous: Hermodice carunculata (Annelida: Amphinomidae) is prepared for ecological challenges. *Journal of the Marine Biological Association of the United Kingdom*, *97*(5), 1075–1080. https://doi.org/10.1017/s0025315417000091
Shakya, A. W., & Allgeier, J. E. (2023). Water column contributions to coral reef productivity: overcoming challenges of context dependence. *Biological Reviews*, *98*(5), 1812–1828. https://doi.org/10.1111/brv.12984
Shaver E C, Courtney C A, West J M, Maynard J, Hein M, Wagner C, Philibotte J, MacGowan P,

McLeod I, Boström-Einarsson L, Bucchianeri K, Johnston L, Koss J. 2020. A Manager's Guide to Coral Reef Restoration Planning and Design. NOAA Coral Reef Conservation Program. NOAA Technical Memorandum CRCP 36, 128 pp

Sussman, M., Loya, Y., Fine, M., & Rosenberg, E. (2003). The marine fireworm Hermodice carunculata is a winter reservoir and spring-summer vector for the coral-bleaching pathogen Vibrio shiloi. *Environmental Microbiology*, *5*(4), 250–255. https://doi.org/10.1046/j.1462-2920.2003.00424.x

Toso, A., Furfaro, G., Fai, S., Giangrande, A., & Piraino, S. (2022). A sea of fireworms? New insights on ecology and seasonal density of Hermodice carunculata (Pallas, 1766) (Annelida) in the Ionian Sea (SE Italy). *The European Zoological Journal*, *89*(1), 1104–1114. https://doi.org/10.1080/24750263.2022.2113156

Van Oppen, M. J. H., Gates, R. D., Blackall, L. L., Cantin, N. E., Chakravarti, L. J., Chan, W. Y., Cormick, C., Crean, A. J., Damjanovic, K., Epstein, H. E., Harrison, P. L., Jones, T. A., Miller, M. W., Pears, R., Peplow, L. M., Raftos, D. A., Schaffelke, B., Stewart, K., Torda, G., . Putnam, H. M. (2017). Shifting paradigms in restoration of the world's coral reefs. *Global Change Biology*, *23*(9), 3437–3448. https://doi.org/10.1111/gcb.13647

Van Woesik, R., Banister, R. B., Bartels, E., Gilliam, D. S., Goergen, E. A., Lustic, C., Maxwell, K., Moura, A., Muller, E. M., Schopmeyer, S., Winters, R. W., & Lirman, D. (2020). Differential survival of nursery-reared Acropora cervicornis outplants along the Florida reef tract. *Restoration Ecology*, *29*(1). https://doi.org/10.1111/rec.13302

Verdonschot, P. (2015). Introduction to Annelida and the class Polychaeta. In *Elsevier eBooks* (pp. 509–528). https://doi.org/10.1016/b978-0-12-385026-3.00020-6

Vink D.L.N. (1974) A strange food preference of Conus aurantius. Hawaiian Shell News 12, 8.

Vink, D., & Von Cosel, R. (1985). The Conus cedonulli complex: Historical review, taxonomy and biological observations. *Revue Suisse De Zoologie*, *92*, 525–603. https://doi.org/10.5962/bhl.part.81894

Ware, M., Garfield, E. N., Nedimyer, K., Levy, J., Kaufman, L., Precht, W. F., Winters, R. W., & Miller, S. L. (2020). Survivorship and growth in staghorn coral (Acropora cervicornis) outplanting projects in the Florida Keys National Marine Sanctuary. *PLOS ONE*, *15*(5), e0231817. https://doi.org/10.1371/journal.pone.0231817

Wolf AT (2012) The Role of Macroalgae and the Corallivorous Fireworm Hermodice carunculata on Coral Reef Resilience in the Caribbean. PhD dissertation, Leibniz Center for Tropical Marine Ecology (ZMT).

Wolf, A. T., & Nugues, M. M. (2013). Predation on coral settlers by the corallivorous fireworm Hermodice carunculata. *Coral Reefs*, *32*(1), 227–231. https://doi.org/10.1007/s00338-012-0969-x

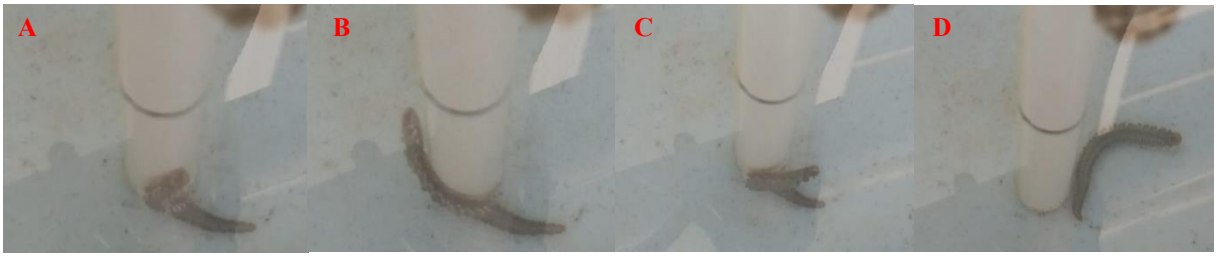
Wolf, A. T., Nugues, M. M., & Wild, C. (2014). Distribution, food preference, and trophic position of the corallivorous fireworm Hermodice carunculata in a Caribbean coral reef. *Coral Reefs*, *33*(4), 1153–1163. https://doi.org/10.1007/s00338-014-1184-8

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. a. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*(6), 1023–1034. https://doi.org/10.1111/1365-2435.13331

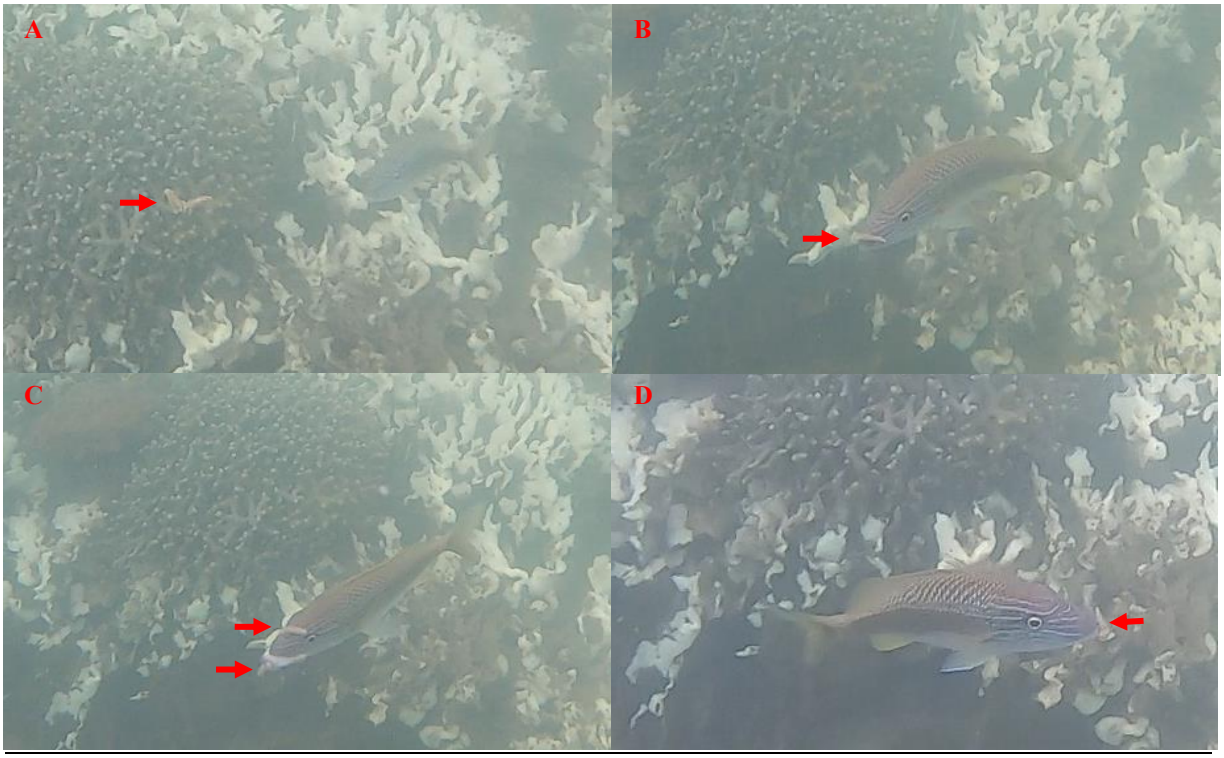
Zayasu, Y., Satoh, N., & Shinzato, C. (2018). Genetic diversity of farmed and wild populations of the reef-building coral, Acropora tenuis. *Restoration Ecology*, *26*(6), 1195–1202. https://doi.org/10.1111/rec.12687

Appendix

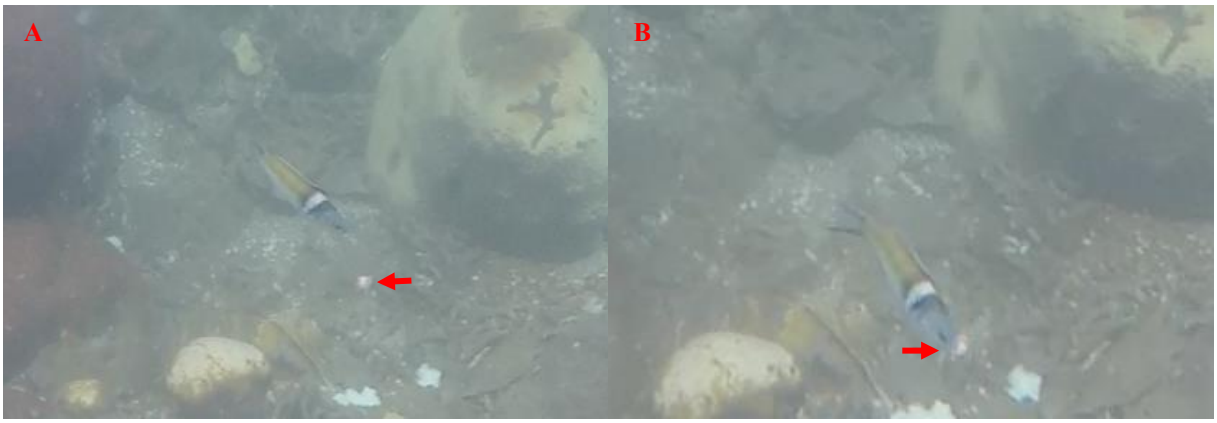
Supplementary figures



Supplementary Fig. 1. Time series of a fireworm trying to climb the PVC pole (⌀ 15 mm) vertically (A), or trying to fold around it via the left (B) or right side (C) before eventually giving up (D).



Supplementary Fig. 2. Time series of the white grunt (*Haemulon plumierii*) locating (A) the fireworm (indicated by red arrows), to approaching the worm (B), biting it in half and consuming the first half (C), to then coming back and eating the second half (D).



Supplementary Fig. 3. Time series of the bluehead wrasse (*Thalassoma bifasciatum*) locating (A) the fireworm (indicated by red arrows), to right before consuming the worm (B)

Supplementary Table. 1. List of mobile marine organisms observed during the natural predator experiments.

Scientific Name	Common Name	Scientific Name	Common Name
Abudefduf saxatilis	Sergeant major damselfish	*Holacanthus bermudensis*	Blue angelfish
Acanthurus chirurgus	Doctorfish	*Hypanus americanus*	Southern stingray
Acanthurus coeruleus	Blue Tang	*Kyphosus cinerascens*	topsail chub
Anisotremus virginicus	Porkfish	*Kyphosus vaigiensis*	Brassy Chub
Aulostomus maculatus	Trumpetfish	*Lactophrys triqueter*	Smooth trunkfish
Bodianus rufus	spanish hogfish	*Lutjanus apodus*	Schoolmaster snapper
Cantherhines pullus	Orangespotted filefish	*Lutjanus mahogoni*	Mahogany snapper
Canthigaster rostrata	Sharpnose Pufferfish (small)	*Lutjanus synagris*	Lane snapper
Carangoides bartholomaei	Yellow jack	*Mulloidichthys martinicus*	Yellow Goatfish
Caranx ruber	Bar jack	*Ocyurus chrysurus*	Yellowtail snapper
Cephalopholis cruentata	Graysby	*Panulirus argus*	Spiny Caribbean lobster
Chaetodon capistratus	Foureye Butterflyfish	*Pomacanthus paru*	French Angelfish
Chaetodon ocellatus	Spotfin butterflyfish	*Pseudupeneus maculatus*	Spotted goatfish
Chaetodon striatus	Banded butterfly fish	*Scarus iseri*	striped parrotfish
Chromis cyanea	Blue chromis	*Scarus taeniopterus*	Princess Parrotfish
Chromis multilineata	Brown Chromis	*Scarus vetula*	Queen parrotfish
Chrysiptera Parasema	yellowtail damselfish	*Sepioteuthis sepioidea*	Carribean Reaf squid
Diodogorgia nodulifera	Dog snapper	*Serranus tigrinus*	Harlequin Bass
Elacatinus evelynae	Cleaner Goby	*Sparisoma aurofrenatum*	Redband parrotfish
Haemulon flavolineatum	French grunt	*Sparisoma rubripinne*	Yellowtail Parrotfish
Haemulon macrostomum	Spanish grunt	*Sparisoma viride*	Stoplight Parrotfish
Haemulon plumierii	White grunt	*Stegastes diencaeus*	Longfin damselfish
Haemulon sciurus	Bluestriped Grunt	*Stegastes partitus*	bicolor damselfish
Halichoeres bivittatus	Slippery dick	*Stegastes planifrons*	Threespot damselfish
Halichoeres garnoti	yellowhead wrasse	*Synodus intermedius*	Common sand diver
Halichoeres pictus	Rainbow Wrasse	*Thalassoma bifasciatum*	Bluehead wrasse
Halichoeres poeyi	Blackear wrasse	*Urobatis jamaicensis*	Yellow stingray
Halichoeres radiatus	puddinwife		

Supplementary videos

Supplementary video 1: Climbing attempt PVC pole 1.5cm diameter
Supplementary video 2: White grunt eating fireworm
Supplementary video 3a: Bluehead wrasse eating fireworm, normal speed
Supplementary video 3b: Bluehead wrasse eating fireworm, 0.25x speed
Supplementary video 4: Squirrelfish eating fireworm