Evaluating *Cittarium pica* for reef restoration: From grazing effects to post-release retention

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Cittarium pica; coral reef restoration; herbivory; turf algae; benthic community; retention; native herbivores

Abstract

Caribbean coral reefs have experienced extensive coral loss, accompanied by increased algal cover which inhibits coral recovery. Enhancing native herbivore populations is being explored as a means of controlling excessive algal growth. The gastropod *Cittarium pica* (*C. pica*) may represent an option, but its suitability for reef restoration is unknown. We therefore evaluated its grazing, survival, and behavior across depths, effects on benthic community composition, and retention after release on Saba, Caribbean Netherlands. *C. pica* remained active and grazed across the full 2–20 m experimental depth range, with algal height declining at all tested depths in enclosures with *C. pica*, whereas it generally increased in control enclosures. In enclosures on natural reefs, benthic community trajectories differed between enclosures with *C. pica* and control treatments. *C. pica* grazing reduced turf algae cover and increased crustose coralline algae (CCA) and bare substrate cover, while total macroalgal cover showed no consistent treatment-specific pattern. Retention after release declined rapidly in two separate experiments, reaching 7.3%

after 25 days following enclosure removal in one experiment and 1.2% after 43 days in the other. Migration and mortality contributed to low retention. Follow-up experiments showed that overturned *C. pica* were unable to right themselves on sand, potentially increasing their vulnerability to predation and starvation. Thus, despite beneficial benthic effects under enclosure conditions, the practical feasibility of *C. pica* for reef restoration remains uncertain and depends on achieving sufficient survival and retention under unrestricted reef conditions.

Introduction

Coral reefs are among the most productive and biodiverse ecosystems on Earth (Brandl et al., 2019; Hoegh-Guldberg, 2011). They provide essential ecosystem services such as coastal protection, tourism, recreation, and fisheries (Moberg & Folke, 1999; Cesar, 2002; Leenhardt et al., 2016; Eddy et al., 2021). However, anthropogenic stressors including pollution, climate change, and unsustainable fishing practices result in reef degradation and compromise the ecosystem services reefs provide (Woodhead et al., 2019; Moberg & Folke, 1999; Eddy et al., 2021). This is particularly evident in the Caribbean, where coral cover has declined substantially over recent decades (Wicquart et al., 2025).

As coral cover declines, available space is often occupied by turf and fleshy macroalgae (McCook et al., 2001; Precht et al., 2020). Algae can inhibit reef recovery by competing with coral recruits for space, light, and nutrients (McCook et al., 2001; Birrell et al., 2005; Box & Mumby, 2007). On Caribbean reefs, algal proliferation is further enhanced by reduced grazing pressure and increased nutrient availability (Roff & Mumby, 2012). Centuries of overfishing substantially reduced fish populations, including herbivorous fishes (Hay, 1984; Hughes, 1994, Pandolfi et al., 2003). Despite these declines, grazing pressure was maintained by high densities of the long-spined sea urchin, *Diadema antillarum*, until a mass mortality event in 1983–1984 decimated approximately 98% of the population throughout the Caribbean region (Lessios, 2016). The resulting reduction in herbivory facilitated increases in turf and macroalgae, which impaired coral recovery following other disturbances (de Ruyter van Steveninck & Bak, 1986; Hughes et al., 1987). At localities where *D. antillarum* recovered (Lessios, 2016), it was associated with reduced macroalgal cover and enhanced coral recruitment and survival (Edmunds & Carpenter, 2001; Idjadi et al., 2010).

Recent advances in aquaculture have enabled the cultivation and restocking of *D. antillarum* (Pilnick et al., 2021; Wijers et al., 2023). However, a second mass mortality event in 2022 demonstrated the continued vulnerability of this species to large-scale mortality (Hylkema et al., 2023; Hewson et al., 2023). Consequently, interest has grown in evaluating additional native herbivores, including crabs, other sea urchins, and gastropods, as

potential species for restoring grazing pressure on Caribbean reefs (Francis et al., 2019; Henry et al., 2019; Butler et al., 2024; Wilson et al., 2025).

One native Caribbean gastropod for which the potential for reef restoration has not been evaluated is *Cittarium pica* (*C. pica*), locally known as the West-Indian top shell or whelk. Ecologically, *C. pica* is one of the largest herbivorous gastropods in the Caribbean, with shells reaching up to 13 cm in diameter. The species is nocturnal, sheltering in crevices during the day, and primarily inhabits rocky intertidal and shallow subtidal habitats (Randall, 1964; Robertson, 2003). *C. pica* is considered strictly herbivorous, grazing on cyanobacteria, turf and macroalgae by scraping them from hard substrates (Randall, 1964). Its grazing behavior suggests that *C. pica* could contribute to reducing algae cover on Caribbean reefs, making it a potential candidate for reef restoration.

The effect of *C. pica* on subtidal benthic habitats such as coral reefs has not been investigated, but experimental studies on other species of herbivorous gastropods show that they can increase survival and growth of corals through algal removal (Toh et al., 2013; Villanueva et al., 2013; Watson et al., 2018; Neil et al., 2021; Lippens et al., 2024). In ex-situ mariculture, grazing by *Trochus maculatus* increased growth of juvenile *Pocillopora damicornis* by mitigating algal overgrowth (Toh et al., 2013), while under hatchery conditions, *Rochia nilotica* enhanced coral spat survival (Villanueva et al., 2013). These findings provide a basis for evaluating whether *C. pica*, a native Caribbean gastropod, can similarly contribute to reef restoration.

This study therefore evaluated the suitability of *C. pica* for reef restoration by assessing its behavior, survival, and grazing across a 2–20 m depth range, its effects on benthic community composition, and retention on reefs. Together, these experiments provide an initial evaluation of the suitability of using *C. pica* for reef restoration.

Methods

Study area

This study comprised multiple experiments conducted at the Saba Research Center (SRC) and at field sites along the southwestern coast of Saba *(Fig. 1)*, which is a small (13 km^2), steep volcanic island in the northeastern Caribbean, forming part of the Caribbean Netherlands. Its coral reefs occur predominantly on volcanic outcrops and lava formations and are protected within the Saba National Marine Park, extending to a depth of 60 m. Over recent decades, coral cover has declined to under 3% in 2024, while benthic algal cover has increased to over 60% (Wicquart et al., 2025). These changes highlight the relevance of Saba

as a study site for evaluating the potential of *C. pica* as an additional native herbivore to reduce algal cover and support reef restoration.

Experiment 1 assessing *Grazing, survival and behavior* of *C. pica across depths* was conducted at the Mooring Field (1) and Fort Bay Harbour (2). Experiment 2 addressing *patch reef retention* was conducted at the dive sites of Hot Springs (4) and 50/50 (5), while Experiment 3, investigating *potential mechanisms influencing retention* were conducted at Fort Bay Harbour and the SRC (2). Finally, experiment 4 looking at the *effect of enclosed C. pica on the benthic community composition* and Experiment 5 examining *post-enclosure retention* were conducted at the Ladder Labyrinth dive site (6).

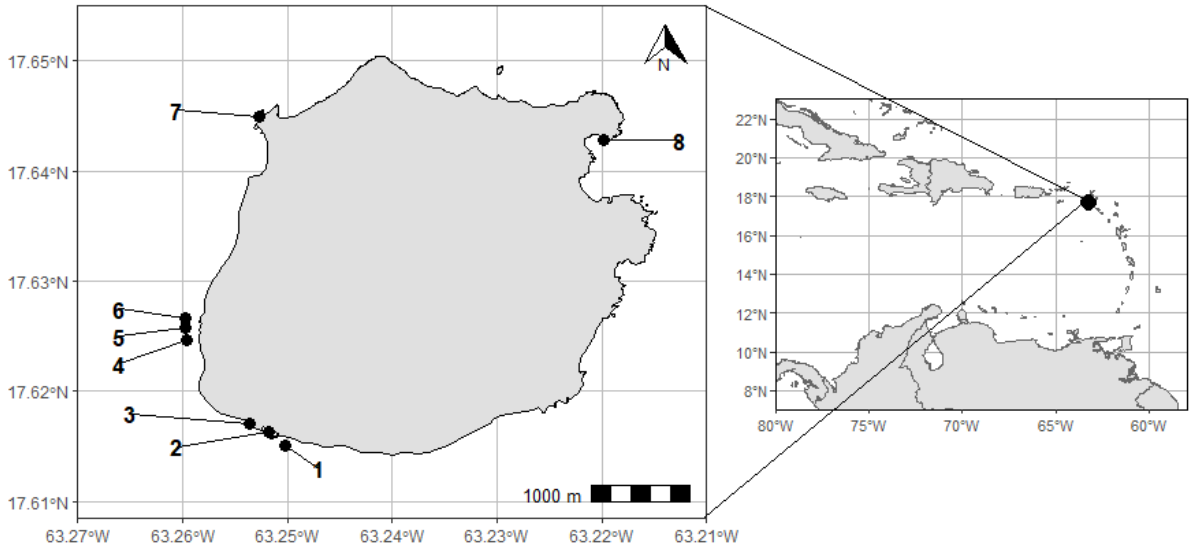


***Figure 1**: Experimental and C. pica collection sites on Saba, Caribbean Netherlands, with the island's location within the Northeastern Caribbean shown in the inset. Numbered locations indicate: (1) Mooring Field, (2) Fort Bay Harbour and SRC, (3) Tent Bay, (4) Hot Springs, (5) 50/50, (6) Ladder Labyrinth, (7) Torrens Point, and (8) Cove Bay.*

Animal collection and husbandry

All *C. pica* used in this study had a shell width between 60–97 mm. Individuals were collected at three locations on Saba (*Fig. 1*). At Tent Bay (3), 75 individuals were collected for Experiments 1 (n = 54) and 3 (n = 21). An additional 310 individuals were collected from Torrens Point (7) and Cove Bay (8) for Experiment 2 (n = 162) and Experiments 4 and 5 (n = 148). Before experimental use, individuals were held in lobster crates containing turf algae covered rocks within a mesocosm connected to an 11,000 L recirculating aquaculture system at the SRC. Salinity was maintained at 33–35 ppt and temperature at 27.5–30.2 °C. Waste was removed three times per week, and turf algae covered rocks were replaced weekly. Individuals were generally held for up to one week, except those used in Experiment 3 (four weeks) and reserve individuals for Experiment 4 (up to nine weeks). No mortality occurred during the holding period.

Experiment 1: Grazing, survival and behavior of *C. pica* across depth

To assess grazing, survival, and behavior of *C. pica* across depths, two sub-experiments (1a & 1b) were conducted. Experiment 1a was conducted at 2, 4, 6, 8, 10, and 12 m depth in March 2025, followed by Experiment 1b at 8, 12, 16, and 20 m depth in May 2025. At each depth, four 30 × 30 × 30 cm enclosures containing a 30 × 30 cm concrete artificial reef plate were deployed (*Fig. 2*). Enclosures consisted of black PVC-coated steel mesh secured with cable ties and were suspended approximately 75 cm above the seafloor on three 1.5 m rebar stakes. Three enclosures per depth contained three *C. pica* each, while one enclosure without *C. pica* served as a control. Enclosures were deployed four weeks before introducing *C. pica* to allow turf algae to develop on the plates. Over the following four weeks, individual position (*side*, *plate*, *bottom*, or *top*) and behavioral state (*moving*, *sitting*, *feeding*, *overturned with the soft body extended* or *retracted*, or *dead*) were recorded weekly. Algal height was measured with calipers (mm) at five fixed locations per plate. After the first survey, supplementary *Dictyota* was secured to the plate edge using steel mesh and cable ties to maintain food availability. Enclosure exteriors were cleaned weekly with a steel brush to remove fouling.



***Figure 2**: Experimental enclosures with artificial reef plates used to assess grazing, survival, and behavior of C. pica across depths of 2 -20 m.*

Experiment 2: Patch reef retention

To assess *C. pica* retention under natural reef conditions, 162 individuals were released across three isolated patch reefs surrounded by sand at 10–14 m depth, two at Hot Springs and one at 50/50 (*Fig. 3*). Reefs were selected for their similar surface areas (36.0–41.0 m^2) and relatively high structural complexity, including crevices and sheltered spaces. Each individual was marked with four Hallprint Glue-On Shellfish tags to minimize identification failure due to tag loss, and 54 individuals were released at the center of each reef. Surveys were conducted on days 6, 13, 21, and 43 after release, covering the experimental reefs, surrounding sand, and nearby reefs. Visibility allowed searches of the sand approximately 15–20 m from the release reefs. At Hot Springs, the facing side of one nearby reef was inspected, while at 50/50, the facing sides of multiple nearby reefs were surveyed. *Individual identity*, *location* (*release reef*, *other reef*, or *surrounding sand*), and *survival* were recorded.



***Figure 3**: Tagged C. pica after release on patch reefs.*

Following the unexpected discovery of alive, overturned individuals on sand, *orientation* (*upright* or *overturned*) was recorded systematically during subsequent surveys, although this information was not consistently recorded on one reef on day 6. After the day 21 survey, overturned individuals were returned to their original release reefs to assess subsequent retention.

Experiment 3: Potential mechanisms influencing retention

To investigate potential mechanisms underlying the observations from Experiment 2, three follow-up experiments were conducted using 21 *C. pica*. First, a drop experiment in Fort Bay Harbour assessed landing orientation (*upright* or *overturned*) after individuals were released upright from 25, 50, and 100 cm above the sandy seafloor. Second, righting ability was tested at the SRC by placing individuals overturned on sand, natural rock, and flat plastic overnight (16:00–08:00 h). Each individual was tested on all three substrates, with treatment order varying among individuals and a seven-day recovery period between trials. Finally, movement across sand and flat plastic was assessed by placing individuals upright at the center of each substrate and recording whether they had moved across it after three hours.

Experiment 4: Effect of enclosed *C. pica* on benthic community

To assess the effects of *C. pica* grazing on benthic community composition, a field experiment was conducted on three continuous reefs at 12–15 m depth at Ladder Labyrinth from 10 March to 20 May 2026 (*Fig. 4*). Three treatments were established: enclosures with 15 *C. pica*, enclosures without *C. pica*, and open controls (plots of equivalent size without enclosures or *C. pica*). Each treatment was replicated twice per reef (n = 6 per treatment), with plots positioned close together at similar depths and arranged in the same spatial pattern. Triangular enclosures (120 cm per side) consisted of rebar frames covered with 2 × 2 cm chicken mesh, secured to dead reef with nails. The reef surface area was approximately 0.6 m^2 per enclosure, corresponding to approximately 24 *C. pica* m^{-2}, excluding three-dimensional reef structure. Individuals were marked with four Hallprint



***Figure 4**: Experimental enclosures used to assess the effects of enclosed C. pica on the benthic community composition on natural reefs.*

Glue-On Shellfish tags each, and those that died or escaped were replaced during weekly inspections to maintain grazing density. Enclosure exteriors were cleaned weekly to remove fouling and repaired as needed. Benthic composition was assessed using three permanent 20 × 20 cm photo-quadrats per plot, photographed with an Olympus Tough TG-6 before *C. pica* introduction (10 March), during the experiment (6 May), and at the end (20 May 2026).

Experiment 5: Post-enclosure retention

Following Experiment 4, the six enclosures with *C. pica* were removed to determine retention. Each former enclosure center was marked with a nail and buoy, and retention was surveyed weekly for four weeks using a 3 m rope to define a circular search area of approximately 28.3 m^2. Alive individuals detected within 3 m of their original enclosure were considered retained. On day 12, adjacent sloping reef areas were additionally surveyed, and individuals found beyond the 3 m radius were recorded as outside the release area. For each individual encountered, *identity* was determined from the previously applied tags where possible, and *survival status*, *location*, and *orientation* (*upright* or *overturned*) were recorded. Individuals without identifiable tags were classified as *untagged*. Based on findings from Experiment 2, overturned individuals were returned to an upright position where they were found.

Data analysis

Experiment 1: Grazing, survival and behavior of *C. pica* across depth

Survival and behavior of *C. pica* were summarized descriptively. Algal height was averaged across five measurement points per enclosure, and treatment means ± standard error were calculated across enclosures at Weeks 0, 1 and 4 separately for Experiment 1a and 1b.

Experiment 2: Patch reef retention

Retention and individual *C. pica* status were summarized descriptively across the three patch reefs. Following Debrot (1990), observed retention was calculated as the percentage of 54 released individuals found alive on their original reef at each survey (mean ± SE across reefs). Tag-based retention also counted individuals subsequently re-identified alive on

their original reef as retained at earlier surveys. This was calculated only for days 6 and 13 due to the intervention following the day 21 survey. Individual status was classified by *location* (*release reef, other reef, sand*), *survival* and *orientation* (*upright* or *overturned*), including untagged individuals. Unknown survival or location was classified as *uncertain*, and missing orientation as *orientation unknown*. All 162 individuals were accounted for at each survey.

Experiment 3: Potential mechanisms influencing retention

Outcomes of the *drop* and *move across sand* experiments were summarized descriptively as the number and percentage of individuals exhibiting each response. Results of the *righting ability* experiment were compared across substrates using Cochran's Q test, followed by pairwise exact McNemar tests with Holm-adjusted p-values.

Experiment 4: Effect of enclosed *C. pica* on benthic community

Photographs were analyzed in CoralNet using 50 random annotation points per image, classified to the lowest practical taxonomic level (Bouwmeester et al., 2022). Benthic cover was averaged across three photo-quadrats per plot and timepoint, and community composition was analyzed using Bray–Curtis dissimilarities (Bray & Curtis, 1957; Bouwmeester et al., 2022). Categories included corals, sponges, other invertebrates, macroalgae (*Amphiroa*, *Dictyota*, *Halimeda*, *Lobophora*, *Neomeris*, *Padina*, *Peyssonnelia*, and *Valonia ventricosa*), CCA, turf algae, cyanobacteria, and substrate (*bare substrate*, *sand*, and *rubble*). Unidentified cover (mean 2.52%) was excluded without rescaling the remaining percentage benthic cover. The treatment × timepoint interaction was tested using PERMANOVA (Anderson, 2001), with reef section included in the model and permutations restricted to whole plots within reef sections to preserve repeated measurements. Multivariate dispersion was assessed separately at each timepoint using PERMDISP (Anderson, 2005), with permutations restricted within reef sections and Holm-adjusted p-values across timepoints. Pairwise PERMANOVAs compared treatment trajectories using the same permutation restrictions and Holm-adjusted *p*-values (Holm, 1979). SIMPER analyses identified categories contributing most to dissimilarities between enclosures with *C. pica* and each control treatment at each timepoint. Categories contributing to 70% cumulative dissimilarity, including the category exceeding this threshold, were retained for descriptive interpretation (Sinner et al., 2023). Turf algae, CCA, and bare substrate were visualized based on SIMPER contributions, alongside total macroalgal cover to illustrate broader changes.

Experiment 5: Post-enclosure retention

Post-enclosure retention and individual *C. pica* status were summarized descriptively across six plots using the observed and tag-based methods described for Experiment 2, with retention defined as alive and remaining within 3 m of the original enclosure. Analyses included 73 identifiable individuals at enclosure removal, excluding 17 that had lost their tags during Experiment 4. Tag-based retention was calculated for days 5, 12, and 18. Individuals were classified as *uncertain*, *dead*, *outside the plot*, *inside the plot* (*upright* or *overturned*), or *inferred inside the plot* (tag-based retention).

R packages

All analyses were conducted in R v4.5.1 (R Core Team, 2025). Bray–Curtis dissimilarities, PERMANOVA, PERMDISP, and SIMPER were implemented using *vegan* (Oksanen et al., 2026), with restricted permutations specified using *permute* (Simpson, 2026). Data processing and visualization were performed using *dplyr* (Wickham et al., 2023) and *ggplot2* (Wickham, 2016).

Results

Experiment 1: Grazing, survival and behavior of *C. pica* across depth

All but one *C. pica*, which died at 12 m, survived the four-week experimental period of both sub-experiments. Moving, sitting, and feeding were observed, with individuals predominantly observed on the artificial reef plates. Algal height declined during the first week at all tested depths in enclosures with *C. pica* and remained low following the introduction of supplementary feeding after Week 1 (*Fig. 5*). In Experiment 1a, mean algal height in enclosures with *C. pica* decreased from 7.68 ± 0.63 mm at Week 0 to 0.17 ± 0.13 mm at Week 1 and 0.81 ± 0.48 mm at Week 4, compared with 8.92 ± 2.47, 12.20 ± 3.59, and 8.80 ± 1.57 mm in enclosures without *C. pica*. Similarly, in Experiment 1b, algal height decreased from 6.23 ± 0.98 to 0.85 ± 0.31 and 1.38 ± 0.54 mm in enclosures with *C. pica*, compared with 5.40 ± 0.90, 8.70 ± 1.76, and 14.80 ± 4.66 mm in enclosures without *C. pica* at Weeks 0, 1, and 4.



***Figure 5**: Artificial reef plate before the introduction of C. pica (left) and after one week of grazing by C. pica in the same enclosure (right), showing the reduction in algal cover.*

Experiment 2: Patch reef retention

Observed *C. pica* retention declined rapidly following release, from 100% at release to 27.8 ± 6.7% (mean ± SE) on day 6, 14.2 ± 1.6% on day 13, 11.1 ± 4.9% on day 21, and 1.2 ± 1.2% on day 43 (*Fig. 6*). Tag-based retention was higher but similarly declined, from 35.8 ± 8.0% on day 6 to 21.0 ± 3.8% on day 13. *C. pica* were also found alive on surrounding sand (33, 32, and 17 on days 6, 13, and 21) and other reefs (10, 3, and 4). Of those found on sand, 22 were overturned on day 6, with orientation unrecorded for the remaining 11, while all were overturned on days 13 and 21. In contrast, only 1, 1, and 3 individuals were overturned when found back on their original release reefs at these surveys. Cumulative recorded mortality increased from 6 individuals on day 6 to 22, 44, and 66 on days 13, 21, and 43 (40.7%), while the fate of 93 individuals (57.4%) remained uncertain.

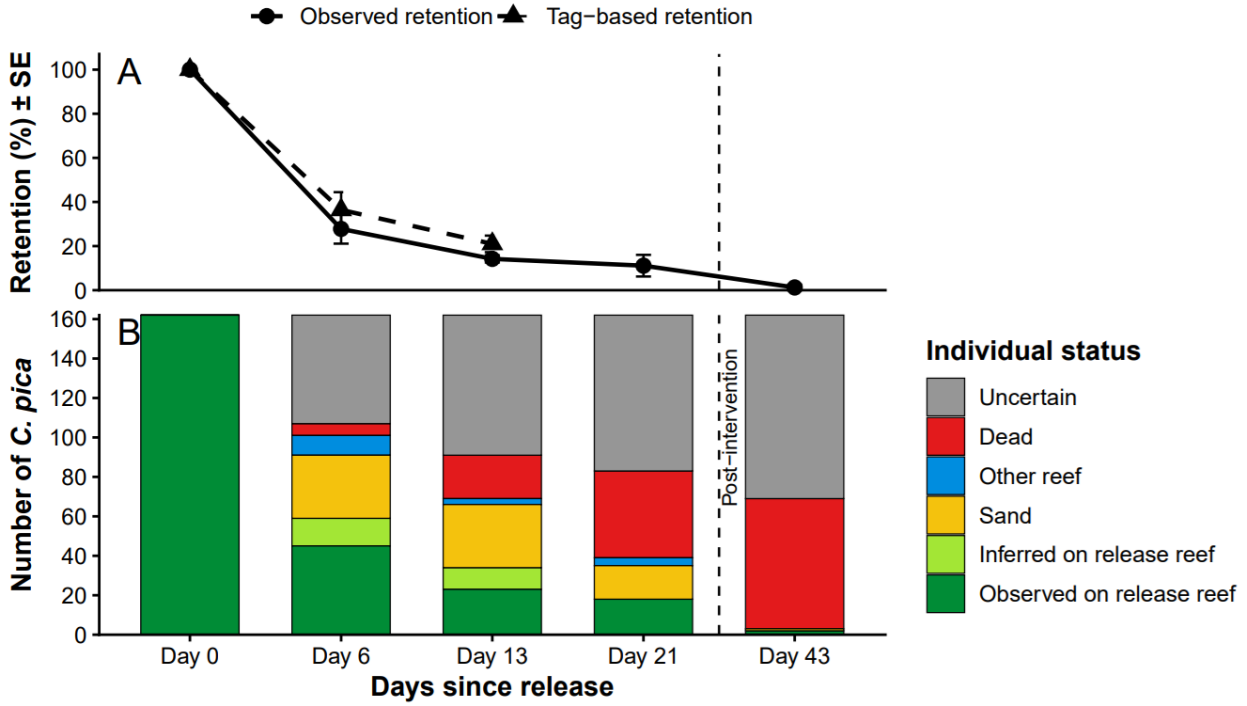


***Figure 6**: Retention and individual status of C. pica on three experimental patch reefs over 43 days. (A) Mean observed and tag-based retention (± SE) across the three reefs. (B) Status of the original cohort of 162 released individuals at each monitoring event, based on recorded location and survival. The vertical dashed line indicates the intervention on day 21, when overturned individuals from the sand were returned to their original release reefs.*

Experiment 3: Potential mechanisms influencing *C. pica* retention

Following drops onto sand, 20 of 21 *C. pica* (95.2%) landed overturned at each tested height (25, 50, and 100 cm). Righting success differed among substrates ($Q = 36.9$, $df = 2$, $p < 0.001$), with 21/21 individuals (100%) righting on rock, 18/21 (85.7%) on flat plastic, and none (0/21) on sand. Righting success was significantly lower on sand than on rock and plastic (both Holm-adjusted $p < 0.001$), but did not differ significantly between rock and plastic ($p = 0.250$).

Despite failing to right on sand, 20/21 upright individuals (95.2%) moved across it, compared with 21/21 (100%) on flat plastic.

Experiment 4: Effect of enclosed *C. pica* on benthic community

Benthic community trajectories differed among treatments over time (PERMANOVA: pseudo-$F_{4,43}$ = 1.76, R^2 = 0.084, p < 0.002). Multivariate dispersion (within-treatment variability) differed among treatments at T1 (PERMDISP: $F_{2,15}$ = 3.75, Holm-adjusted p = 0.044), but not significantly at T0 or T2. Holm-adjusted pairwise comparisons showed differences between the benthic community in enclosures with *C. pica* and enclosures without *C. pica* (p = 0.027) and open controls (p = 0.040), but not between the two controls (p = 0.512). SIMPER identified turf algae, CCA, bare substrate, *Dictyota*, and *Lobophora* among the main contributors to community dissimilarity at T1 and T2, with sand additionally contributing to the comparison with enclosures without *C. pica* at T1 and *Amphiroa* at T2. These patterns corresponded with declining turf algae and increasing CCA and bare substrate cover in enclosures with *C. pica*, while total macroalgal cover showed no consistent treatment-specific pattern (*Fig. 7*).

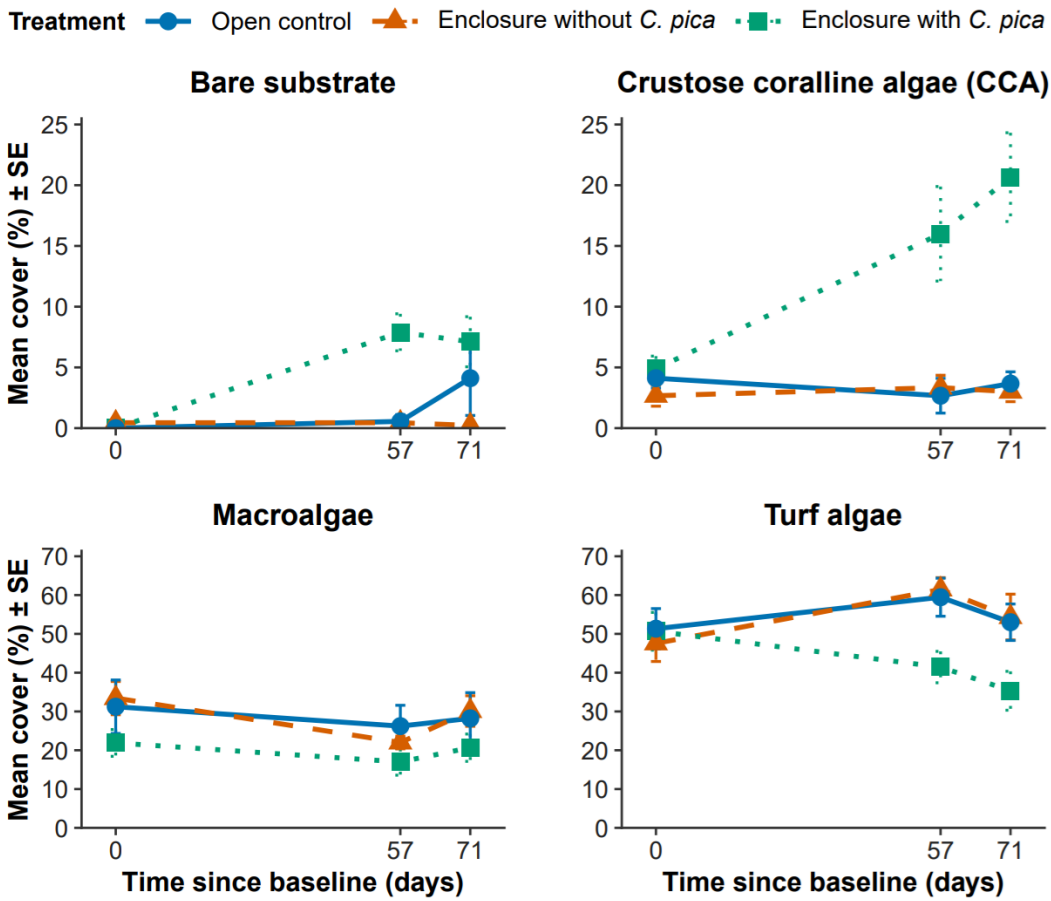


***Figure 7**: Changes in benthic cover across experimental treatments. Mean cover (± SE) of bare substrate, CCA, macroalgae, and turf algae is shown for enclosures with C. pica, enclosures without C. pica and open controls at day 0, 57 and 71 days*. Values represent plot-level benthic cover estimated from three permanent photo-quadrats per plot.

Experiment 5: Post-enclosure retention

Observed *C. pica* retention declined rapidly following enclosure removal, from 100% to 50.3 ± 2.6% (mean ± SE) on day 5, 22.3 ± 3.1% on day 12, 16.8 ± 5.2% on day 18, and 7.3 ± 3.6% on day 25 (*Fig. 8*). Tag-based retention was higher but similarly declined, from 61.0 ± 4.7% on day 5 to 31.2 ± 7.0% on day 12 and 19.7 ± 6.2% on day 18. Among retained individuals, 17/37 (45.9%), 9/16 (56.2%), 5/12 (41.7%), and 4/5 (80.0%) were overturned on days 5, 12, 18, and 25. Cumulative confirmed mortality increased from 11 individuals on day 5 to 28, 36, and 39 (53.4% on day 25), while the fate of 29 individuals (39.7%) remained uncertain.

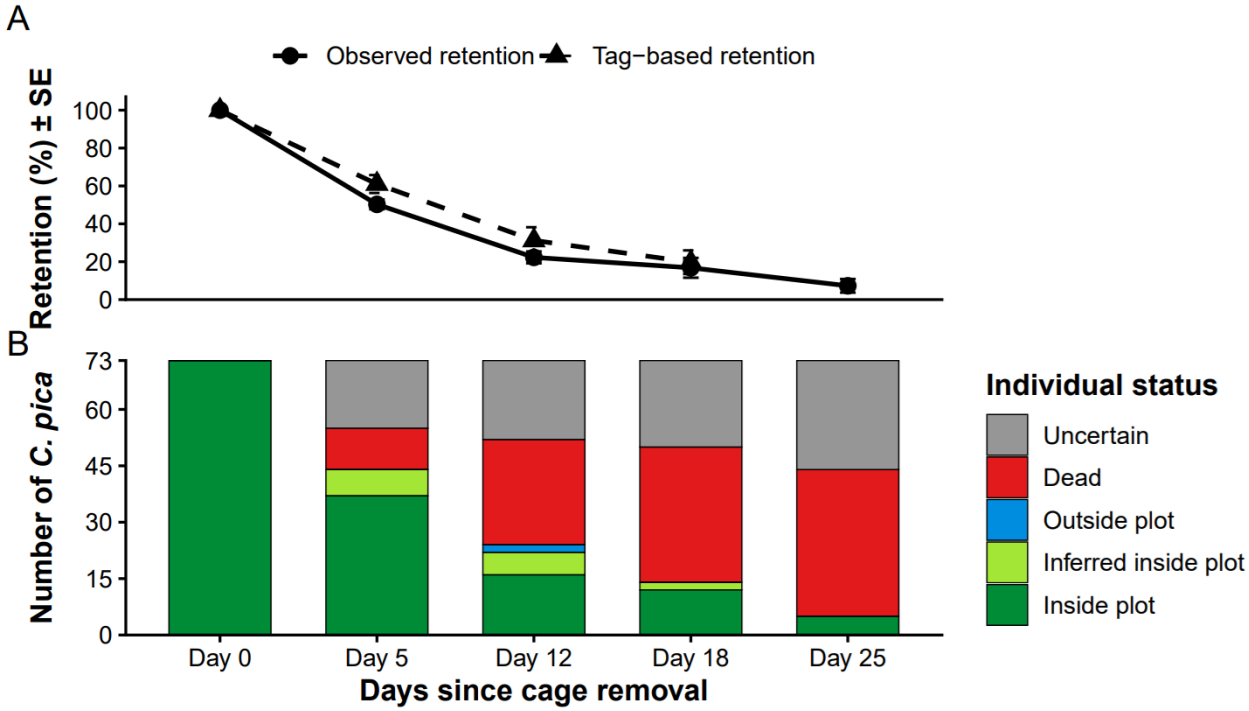


***Figure 8**: Post-enclosure retention and individual status of C. pica. (A) Mean observed and tag-based retention (± SE) across the six experimental plots over 25 days. (B) Status of the 73 individually identifiable C. pica at each monitoring event, based on survival and location.*

Discussion

Depth-related suitability of *C. pica* for reef restoration

Experiment 1 showed that *C. pica* survived, remained active, and grazed across 2–20 m, despite its predominantly intertidal and shallow subtidal distribution (Randall, 1964; Robertson, 2003). Natural densities found in previous studies were highest within 0.5 m of the air–sea interface (Debrot, 1990), with smaller individuals generally occurring higher on the shore and larger individuals lower in the intertidal and shallow subtidal (Randall, 1964; Debrot, 1990; Toller & Gordon, 2005). This pattern may partly reflect shallow recruitment, as 1–2 mm juveniles have been recorded between the low-tide bench and high-tide level (Bell, 1992), although very large individuals have also been reported from unquantified “deeper

water" (Robertson, 2003). Our observations suggest that the predominantly shallow natural distribution of *C. pica* cannot be explained solely by an inability of adults to survive and graze at greater depths.

Predation may also contribute to the natural shallow distribution. Vermeij (1972) proposed that shore-level size distributions of mobile gastropods may reflect differential mortality rather than physiological limits alone. Similarly, *Littorina littorea* survives and grows in subtidal enclosures but remains scarce there due to higher predation related mortality (Perez et al., 2009). For *C. pica*, Toller & Gordon (2005) reported infrequent predation in the intertidal, mainly on individuals 25–35 mm in shell width, with no observed predation above 62 mm. Size-dependent predation vulnerability may therefore contribute to its vertical distribution, although variation in predation pressure across depths remains unknown.

Effects of *C. pica* grazing on benthic communities

Experiment 1 demonstrated grazing by *C. pica* across 2–20 m, with algal height declining rapidly in enclosures with *C. pica* at all depths, while generally increasing in enclosures without *C. pica*. In Experiment 4, benthic community trajectories differed between enclosures with *C. pica* and both controls. These patterns corresponded with declining turf algae and increasing CCA and bare substrate cover, while total macroalgal cover showed no consistent treatment-specific response. The reduction in turf algae is consistent with the feeding ecology of *C. pica*, which primarily consumes filamentous and relatively soft algae (Randall, 1964). Increased CCA cover was also reported by Daza-Guerra et al. (2020) in enclosures with *C. pica*, although enclosure effects limited attribution to grazing and little control of algal assemblages was detected. Their study used smaller individuals (2–4 cm basal shell diameter) at 33.3 individuals m^{-2}, compared with individuals >6 cm at approximately 24 individuals m^{-2} in this study. Differences in body size, density, and substrate complexity may have contributed to the contrasting benthic responses. Lastly, bare substrate cover also increased in enclosures with *C. pica*, exposing dead coral and volcanic rock, with skeletal grooves becoming visible on dead coral after turf algae removal.

These benthic changes may benefit reef restoration by increasing suitable substrate for coral recruitment (Arnold & Steneck, 2011; Harrington et al., 2004). While turf algae can inhibit coral settlement, particularly through sediment retention, (Birrell et al., 2005; Speare et al., 2019), increased bare substrate and CCA cover could facilitate coral settlement, depending on CCA species identity (Harrington et al., 2004). Together, these changes may resemble the early-successional recruitment window described by Arnold and Steneck (2011), although coral settlement was not measured in this relatively short experimental period. These results suggest that the benthic effects of *C. pica* observed under experimental enclosure conditions may be relevant to the herbivore-restoration framework

discussed by Butler et al. (2024), particularly the reduction of turf algae and increase in exposed bare substrate. Where established macroalgae also require control, *C. pica* might have a complementary role alongside native herbivores such as *Diadema antillarum*, rather than serving as the sole grazer, although this potential complementarity has not been experimentally investigated.

Retention as a constraint for reef restoration using *C. pica*

Despite the observed benthic effects, *C. pica* retention declined rapidly in both retention experiments, partly due to mortality, with predation potentially contributing to these losses. Documented predators include bonefish (*Albula vulpes*), porcupinefish (*Diodon hystrix*), puddingwife wrasse (*Halichoeres radiatus*), rock hind (*Epinephelus adscensionis*), octopuses, and predatory gastropods (Randall, 1964; Robertson, 2003; Toller & Gordon, 2005). Although Toller & Gordon (2005) observed no predation on individuals exceeding 62 mm shell width, the present study documented predator interactions involving large *C. pica* (>60 mm). In Experiment 2, aggregations of live and dead individuals occurred near slipper lobsters, while empty shells in an octopus den were consistent with octopus predation, as also reported by Toller & Gordon (2005). Fireworms (*Hermodice carunculata*) were associated with overturned or dead individuals in Experiment 4 and were observed feeding on dead and, in one instance, living *C. pica* in Experiment 5 (*Fig. 9*). Fireworms can act as predators or scavengers and have been reported to overturn chitons to access their soft tissues (Simonini et al., 2018). A Caribbean spiny lobster (*Panulirus argus*) was also observed attempting to prey on an overturned individual. These observations suggest that predation may significantly contribute to mortality, although the principal predators and proportion of deaths attributable to predation remain unknown.

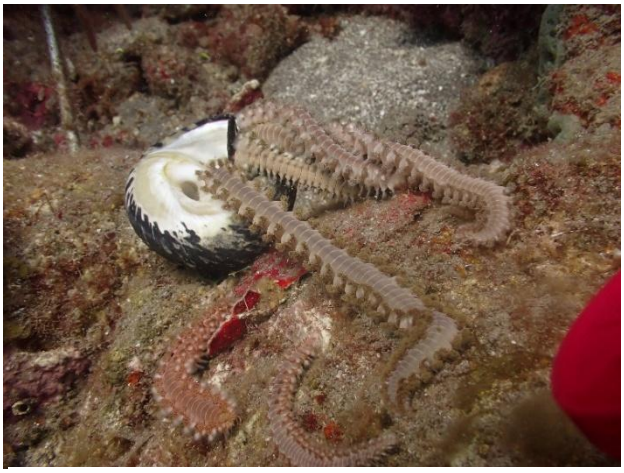


***Figure 9**: Fireworms feeding on overturned dead or alive C. pica during experiment 5.*

Migration beyond the release areas also contributed to declining observed retention, particularly in Experiment 2, where *C. pica* were repeatedly found on surrounding sand and reefs. In Experiment 5, few individuals were found outside the plots during the single additional search, suggesting that mortality may have contributed more strongly to declining retention, although migration could not be reliably quantified. Previous studies generally reported limited movement: Debrot (1990) found a median daily displacement of 0.3 m and a median displacement of 7.5 m after 255 days, while Randall (1964) reported that most

marked individuals remained near their release sites, although one large *C. pica* (60 mm) moved approximately 46 m. In contrast, *Littorina sitkana* and *L. scutulata* moved shoreward after transplantation to the lower intertidal, sometimes travelling 10–15 m within two to three days (Rochette & Dill, 2000). Similar movement towards shallower habitat may be possible for *C. pica*, but migration direction was not established in this study.

Habitat-mediated *C. pica* retention

Predator induced escape responses and displacement may contribute to low observed retention, as juvenile *C. pica* respond to chemical cues from predatory gastropods (Hoffman & Weldon, 1978), and individuals may detach from rocky substrates following predator disturbance (Osorno-Arango et al., 2009). Such displacement could explain the frequent overturning observed in Experiment 2, particularly on surrounding sand near edges of the experimental and bordering reefs (*Fig. 10*), where several individuals remained alive but overturned across consecutive surveys before dying. Experiment 3 showed that *C. pica* frequently landed overturned and could not right on sand, despite being able to cross it when upright, suggesting impaired righting rather than locomotion. Similarly, righting in *Haliotis discus hannai* depends on pedal adhesion, which was absent on sand (Zhang et al., 2020). Prolonged overturning may increase predation vulnerability: crabs consumed *Concholepas concholepas* experimentally prevented from righting, whereas upright individuals suffered no lethal attacks (Manríquez et al., 2013). Together with the predator interactions observed around overturned *C. pica*, these findings suggest that displacement onto sand may prevent righting and increase exposure to predation or starvation. Sand surrounding the patch reefs in Experiment 2 may therefore have contributed to mortality.



***Figure 10**: Overturned alive C. pica in sand next to patch reef.*

Overturning in Experiment 5 suggests that impaired righting may extend beyond sand, as many *C. pica* remained overturned on reef substrate despite successfully righting on clean rock and solid surfaces in Experiment 3. This contrasts with their strong attachment to bare rock through a muscular foot (Osorno-Arango et al., 2009; Forrester et al., 2016). Turf algae containing trapped sand was common on the experimental reefs and may have reduced foot contact with the substrate, potentially facilitating dislodgement and impairing righting, although this remains untested. Habitat characteristics may therefore influence retention. *C. pica* naturally occupies rocky habitats with holes and crevices (Robertson, 2003), while suitable adult habitat for the related *Rochia nilotica* is associated with low sand cover

(Seinor et al., 2020), and released individuals were mainly recaptured in crevices and holes (Purcell et al., 2004). Together, these observations suggest that retention may depend not only on the availability of hard substrate, but also on substrate surface characteristics, surrounding sand, and refuge availability. Selecting release sites that account for these habitat characteristics may therefore improve retention.

Research priorities

Further research is needed to evaluate the restoration suitability of *C. pica*. Priorities include identifying its principal predators and assessing how predation and retention vary with depth and body size, particularly for smaller individuals that may be more feasible to produce through aquaculture. Their post-release survival and effects on benthic communities also require evaluation. Further studies should also examine how (surrounding) sand, reef substrate characteristics, and shelter availability influence retention. Combining *C. pica* with complementary native herbivores, such as *D. antillarum*, also warrants investigation to determine whether their grazing is complementary. Finally, potential bioerosion requires assessment, as carbonate removal during grazing has been reported (McLean, 1967), but its extent at restoration densities and consequences for corals remain unknown.

Conclusion

Overall, this study evaluates the suitability of *C. pica* as a native herbivore for reef restoration and reveals a distinction between its effects on the benthic community and its practical feasibility. Under experimental enclosure conditions, *C. pica* reduced turf algae and increased bare substrate and CCA at depths greater than those typically occupied by natural populations. However, observed retention declined rapidly, with substantial mortality and migration beyond release areas, and predation potentially contributing to mortality. Field observations and righting experiments suggest that the selection of experimental reefs surrounded by sand may have contributed to mortality, as overturned individuals were unable to right themselves on sand, potentially increasing their vulnerability to predation and possible starvation. These findings highlight the importance of release site selection and habitat characteristics, particularly the presence of sand, alongside depth and body size, when evaluating the restoration potential of *C. pica*. Currently, its practical feasibility for reef restoration remains uncertain and will depend on whether sufficient survival and retention can be achieved under unrestricted reef conditions to sustain the benthic effects observed in this study.

Statements and Declarations

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AI disclaimer

Artificial intelligence tools were used in a supportive role during this research. ChatGPT was employed as a sparring partner during the development of the experimental design and discussion, and for assistance in identifying and resolving coding errors in RStudio for data analysis. All outputs generated by the AI were critically evaluated, verified, and edited by the authors. Final decisions regarding experimental design, data analysis, interpretation of results, and conclusions were made solely by the authors, who take full responsibility for the content of this work.

Ethics approval

Ethical approval was not required for this study involving the marine gastropod *C. pica*. Animals were handled with care throughout the experiments to minimize unnecessary harm.

Competing interests

The authors declare no conflicts of interest.

Data and code availability

The datasets, accompanying metadata, and R scripts supporting the findings of this study are available through Zenodo at https://doi.org/10.5281/zenodo.24082768.

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