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Management in Practice

Invasive corallimorpharians at Palmyra Atoll National Wildlife Refuge are no match for lye and heat

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Abstract

Invasive marine species are well documented but options to manage them are limited. At Palmyra Atoll National Wildlife Refuge (Central North Pacific), native invasive corallimorpharians, *Rhodactis howesii*, have smothered live native corals since 2007. Laboratory and field trials were conducted evaluating two control methods to remove *R. howesii* overgrowing the benthos at Palmyra Atoll (Palmyra): 1) paste mixed with chlorine, citric acid, or sodium hydroxide (NaOH), and 2) hot water. Paste mixed with NaOH had the most efficacious kill in mesocosm trials and resulted in > 90% kill over a 98 m^2 area three days after treatment. Hot water at 82°C was most effective in mesocosms; in the field hot water was less effective than paste but still resulted in a kill of ca. 75% over 100 m^2 three days after treatment. Costs of paste and heat (excluding capital equipment and costs of regulatory approval should this method be deployed large scale) were \$70/m^2 and \$59/m^2 respectively. Invasive *R. howesii* currently occupy ca 5,800,000 m^2 of reef at Palmyra with ca. 276,000 m^2 comprising heavily infested areas. Several potential management strategies are discussed based on costs of treatment, area covered, and the biology of the invasion. The methods described here expand the set of tools available to manage invasive species in complex marine habitats.

Key words: Cnidaria, *Rhodactis howesii*, control, coral reefs, sodium hydroxide, carboxymethylcellulose

Introduction

The term phase shift was introduced by Done (1992) to describe the process whereby a coral reef transitions from domination by corals to domination by another organism (typically algae). Phase shifts from corals to algae are considered indicators of coral reef degradation, typically as a result of eutrophication with nutrient loads leading to algal overgrowth (Done 1992). Whist coral-algae shifts are the most commonly reported for

coral reefs, coral dominated ecosystems can also transition to sponges, soft corals, or corallimorpharians as the dominant species (Norström et al. 2009). Phase shifts can also be caused by invasive species. For example, some species of introduced algae in Hawaii such as *Kappaphychus* sp. can overgrow live coral and become locally dominant (Smith et al. 2002).

In addition to algae, invasive cnidaria can have important ecological effects on coral reefs that can potentially lead to phase shifts. For instance, the azooxanthellate coral *Tubastrea* spp. was introduced from the Pacific to Brazil in the 1980s and is currently aggressively outcompeting native corals (Miranda et al. 2018). Attempts to control invasive *Tubastrea* have involved chiseling corals off the reef substrate (Creed et al. 2017, 2021) with mixed success including 2/3 of sites showing recolonization over 400 days observation post-treatment. Yet many species of cnidaria can regenerate from small living mm-sized fragments (Cary 1911; Luz et al. 2018), and physical removal methods that cause fragmentation could exacerbate invasions if not appropriately managed (Chen et al. 1995).

Invasive species are most effectively managed when infestations are detected early, a time when their distribution is limited and eradication is possible (Boudouresque and Verlaque 2012). Myers et al. (2000) outlined six criteria necessary for successful eradication of invasive species, including access to financial resources, clear lines of authority, known biology of the target, prevention of reinvasion, detectability at low densities, and habitat restoration. These criteria rarely align, and instances of successful eradications of invasive marine organisms are limited. Documented examples of successful eradications include the manual removal of the parasitic sabellid worm, *Terebrasabella heterouncinata*, in California (Culver and Kuris 2000), extirpation of the alga *Caulerpa taxifolia* from California using bleach and tarps (Anderson 2005), elimination of the invasive mussel, *Dreissena polymorpha,* in Darwin Australia using copper sulfate (Bax et al. 2002), removal of the invasive kelp, *Undaria pinnatifida*, from a ship's hull in New Zealand using heat (Wotton et al. 2004), and manual removal of the alga *Ascophyllum nodosum* in California (Whitman Miller et al. 2004). Of these, the mussels in Darwin were the only example of a successful eradication on a tropical coral reef (Supplementary material Table S1).

When eradication of invasive marine organisms is desired but seemingly not feasible, population suppression by physical means and/or regulation of environmental drivers is a management alternative. Controlling invasive marine species depends on reducing their populations to levels sufficient to mitigate their adverse effects in a given management area (Green and Grosholz 2021). For the marine biome, population control of invasive species outbreaks is still in its infancy when compared to terrestrial systems and suffers from additional logistical and socio-economic constraints. Marine-specific challenges include difficulty getting support and funding due to the perception of oceans as pristine habitats, the "openness and

connectivity" of oceans making containment difficult, no clear lines of responsibility for controlling marine invasives, limited information on the biology and management options for many marine invasives, and higher costs compared to terrestrial ecosystems (Booy et al. 2017; Thresher and Kuris 2004). Other obstacles preventing the successful control of invasive outbreaks (both marine and terrestrial) include geographic scale of invasions, limited access to effective tools, lack of information on costs, and difficulty in obtaining necessary permits. For example, a review of literature on control of invasive terrestrial and aquatic plants showed that most trials involve treatments using herbicides at scales less than 30 m^2, and only 29% of efforts actually enumerated costs of control (Kettenring and Adams 2011). Arthur et al. (2015) calculated the costs of controlling marine invasives and estimated that for infestations covering > 1 ha, costs could range from $AU 5–20 million, an amount that is unlikely to be available in most cases. An overview of the literature on the topic shows realized costs of controlling marine invasives in 2021 US dollars ranging from $200 to > $9 million with most efforts centered on invasive algae (Table S1). Finally, most research on marine invasives focuses on documenting effects or spread with relatively fewer efforts dedicated to development of viable management or control techniques (Hulme 2003).

Rhodactis howesii is a corallimorpharian that has demonstrated invasiveness within its native range, overgrowing live corals within Palmyra Atoll National Wildlife Refuge (NWR) located in the North Central Pacific (Work et al. 2008). Although recent genetic studies makes the identity of the invasive corallimorpharian uncertain (Jacobs et al. 2021), we are labelling it *Rhodactis howesii* to maintain continuity with current literature on this topic. Palmyra Atoll is situated at the northernmost portion of the Line Islands and is managed by the U.S. Fish & Wildlife Service (USFWS) in partnership with The Nature Conservancy (TNC). Emergent land of the atoll was substantially altered during WWII. The lagoon was extensively dredged, and the spoils used to enlarge or merge existing islands or create new islands connected by causeways for easy road access. These changes substantially altered lagoonal flows and killed large numbers of invertebrates such as corals and giant clams (Collen et al. 2009). Despite substantial physical disturbance, the atoll harbors a unique array of terrestrial ecosystems (*Pisonia* forests) and coral reef resources (McCauley et al. 2013).

Rhodactis howesii was first documented in large numbers at Palmyra in the early 2000s around a wrecked longline vessel, and subsequent systematic surveys in 2007 confirmed the infestation to be centered around the vessel (Work et al. 2008). In the initial 2007 survey, the infestation covered ca. one km^2. In follow up surveys in 2011, the infestation covered ca. 3.3 km^2. Small scale (9 m^2) trials were completed in 2011 to evaluate methods to manage the infestation using bleach and tarps to locally eradicate *R. howesii*.

This method was partially successful, and plots remained clear of *R. howesii* for one year post-treatment, but it was considered unwieldy and not deemed scalable to larger areas (Work et al. 2018). In 2013, the USFWS, the lead management agency responsible for the National Wildlife Refuge, removed the shipwreck. Subsequent surveys in 2016 showed large reductions of *R. howesii* around the wreck site but an overall increase in atoll-wide coverage to 3.6 km^2 (Work et al. 2018). Other methods used to control marine invasives such as dredging, scraping, or manual removal were judged unsuitable for *R. howesii* because they could generate viable reproductive fragments that could lead to further infestations (Chen et al. 1995).

Recent observations indicate that *R. howesii* continues to spread at Palmyra Atoll (Carter et al. 2019; Work et al. 2018). Considering the negative effects further spread of *R. howesii* is likely to have on Palmyra's coral reefs, resource managers (USFWS and TNC) recently prioritized gaining additional data on atoll-wide distributions of *R. howesii* and developing control methods that could feasibly reduce or limit further spread of the organism. The aims of this study were to develop and test lethal control methods that were unlikely to produce live reproductive fragments of *R. howesii* and to undertake further distribution surveys. Specifically, we 1) evaluated the acute toxicity to *R. howesii* of chlorine, citric acid, or sodium hydroxide (NaOH) mixed with a biodegradable paste, 2) evaluated the acute lethality to *R. howesii* of hot water, and 3) undertook atoll-wide surveys to obtain current estimates of total infestation to support future management options for *R. howesii*. This study fills gaps identified in previous studies on marine invasive species control efforts by identifying and applying new technological approaches and estimating efficacy and cost per unit area for applying these new technologies. We also discuss various applications for the technologies tested depending on the species under management, location, funding, and management goals.

Materials and methods

The evaluation of methods to control *R. howesii* proceeded in two stages designed to assess several aspects related to toxicant type, dosage, and its application in the field including impact on non-target organisms. During Stage 1, we evaluated methods of control/toxicant type and dosage in mesocosms (Phase 1) and then tested our initial findings in small (1 m^2) field trials (Phase 2). Promising candidate methods identified in Stage 1 then proceeded to Stage 2 which were scaled up applications to treat larger areas (100 m^2) to assess the potential and feasibility of future large-scale use.

Stage 1: Mesocosm and small-scale field trials 2018

We pursued two options to control *R. howesii*: toxicants and hot water. The rationale for these approaches was to kill *R. howesii* in-situ without

causing fragmentation of living tissues thus reducing possibility of seeding new infestations. Stage 1 trials proceeded in three phases. Phase 1 (mesocosom trials) involved exposing wild-harvested *R. howesii* to varying levels of toxicant/hot water held in 11.3L buckets with aerated seawater and evaluating mortality the following day. Based on findings from Phase 1, Phase 2 trials treated small (< 1 m^2) field plots with either heat or toxicant at the dosage rate found to be the most effective during the mesocosm trials. We first tested these in areas comprising 100% *R. howesii* cover to minimize impact on non-target organisms. Phase 3 was a repeat of phase 2 applying heat or toxicant to *R. howesii* situated in mixed corallimorpharian/live coral cover to evaluate spillover effect on non-target organisms.

To apply the toxicant in situ, the base material (carrier) had to be negatively buoyant, able to adhere to *R. howesii* underwater, persist long enough to kill *R. howesii* (ca. 24 h), be compatible with the chosen toxicants, and, given the sensitive nature of Palmyra's coral reef ecosystems, be biodegradable. Candidate materials were tested on *R. howesii* in 11.3 L buckets and evaluated for good adhesive properties and lethality based on the level of toxicant used. We tested various materials used to make underwater adhesives (chitosan or alginate) (Cook and Khutoryanskiy 2015) or drilling muds (xanthan or guar gums) used for offshore oil rigs (Wang et al. 2015) to assess how they adhered to solid surfaces underwater. These materials failed to adhere to substrates or were too buoyant. We then modified a base recipe for toothpaste provided by Ashland Global (Wilmington, Delaware, USA) comprising 30–32% (w/v) glycerol (Univar Solutions, Downers Grove, Illinois, USA), 1% (w/v) sodium carboxymethycellulose (Aqualon CMC 7MF, Ashland), and 40–43% (w/v) calcium carbonate ($CaCO_3$) heavy powder (Univar Solutions, Dowers Grove, Illinois, USA) in fresh water. Toxicants chosen to mix into the paste included granules of chlorine (ClearView algae cure, Oreq, Temecula, California, USA), citric acid (Thermo Fisher, Waltham, Massachusetts, USA), or sodium hydroxide beads (Univar Solutions).

Sample sizes for Phase 1 and 2 trials were dictated by temporal and logistical constraints of operating at Palmyra. The field crew had only 3 weeks to achieve all objectives of Phases 1 and 2, and it was necessary to balance land-based activities with aspects like weather conditions and availability of boats that allowed us to carry out activities offshore for Phases 2 and 3. As such, the objectives of Phase 1 and 2 trials were not intended to be statistically rigorous but rather to provide empirical assessments of the formulation and concentration of potential control candidates for *R. howesii.* For paste in Phase 1 we exposed mesocosms of 5–10 individuals of *R. howesii* to one time applications of ca. 60 ml paste containing chlorine at various concentrations 0.1% (N = 1), 0.5% (N = 3), 1% (N = 1), 2% (N = 1); citric acid 6% (N = 1), 12% (N = 1); or NaOH 1% (N = 1), 3% (N = 2), 4% (N = 1), 5% (N = 2), 6% (N = 2), 12% (N = 1).

Rhodactis howesii in aerated seawater served as controls. Paste was dispensed onto individuals of *R. howesii* using 35 or 60-ml large-bore syringes. The paste was allowed to remain overnight (with no flushing or water changes), and live/dead *R. howesii* were evaluated the following day. Based on results from mesocosms, we then ran five Phase 2 field trials where individual clusters of 20–30 *R. howesii* were treated with paste applied by syringes containing the most successful dosage rates from the Phase 1 meoscosm trials: 1% (N = 2) or 2% (N = 1) chlorine or 6% NaOH (N = 2) (Figure S1A) followed by an additional three trials using a 1 m^2 quadrat divided into 25 squares measuring 20 cm^2 (Figure S1B). Three squares each randomly received paste mixed with 6%, 4%, 2%, 0% NaOH or no paste (controls). Patch trials from Phase 1 and quadrats from Phase 2 were monitored three days after application to determine percent survival of *R. howesii*. We judged that any method of control that required more than 3 days of contact to kill *R. howesii* would not be practical because the low likelihood of a control compound remaining on *R.howesii* for that long given oceanic currents at field site, hence our requirements that kill be effected within 24h in mesocosoms. For field monitoring, we chose three days, because that allowed for complete elimination of dead and dying *R. howesii* tissues post-treatment thereby facilitating photographic interpretation of results (e.g. providing maximum contrast between white bare rubble substrate and remaining live *R. howesii*). For Phase 3 trials in mixed *R. howesii*/coral habitat, we ran trials applying paste with syringes containing 5% NaOH for all trials. There, 17 small (100–200 cm^2) plots adjacent to live corals or clams were photographed, treated, and rephotographed 3 days later. The photographs were compared to assess the percent of treated polyps surviving as well as any damage to surrounding organisms.

To evaluate heat as a treatment, for Phase 1 mesocosom trials, seawater was heated to boiling, and allowed to cool while temperature was monitored with a glass thermometer. At the desired temperature, *R. howesii* were placed in a strainer, dipped into hot water for 1 s, immediately returned to aerated seawater buckets, and evaluated the following day for mortality. Control animals were dipped in ambient seawater. We ran 23 trials at 45 °C (N = 2), 49 °C (N = 2), 60 °C (N = 3), 66 °C (N = 2), 71 °C (N = 5), 76 °C (N = 4), 82 °C (N = 3) and 88 °C (N = 2). Based on results from mesocosms, we then moved to Phase 2 field trials. To deliver hot water to *R. howesii* in the field, we used a commercially available heater (Monkey Heater, Custom Design & Fabrication, Depford, New Jersey, USA) comprising of a large capacity electric pump that courses seawater through coils heated by diesel combustion dispensing hot seawater out of a hose. The heater and a E7000 generator (Honda, Tokyo, Japan) to run the electric pump were deployed on a surface vessel (Figure S1C). Heated water was applied directly to *R. howesii* for 1–5 s with a 30.5 m hose originating

from the unit with a funnel at the end of the hose to concentrate seawater onto the intended organisms (Figure S1D). Treatment plots comprised 1 m^2 quadrats divided in 25 squares placed on horizontal or vertical surfaces. Prior to applying heat, eight PVC pipe arrays each containing 5 temperature loggers (Hobotemp, Onset, Cape Cod, Massachusetts, USA) spaced at 0.25 m intervals recording every 60 s were deployed in a star pattern at the major azimuths (N, NE, E, SE, S, SW, W, NW) from the center (Figure S1E) or at the periphery (Figure S1F) of the quadrats to monitor for any residual heat that could potentially affect adjacent non-target areas. Outlet seawater temperature for the heater was measured both at the surface and underwater with glass thermometers. Plots were examined 3 days later to evaluate mortality.

Stage 2: Landscape scale trials 2021

The objective for landscape scale trials was to treat 100 m^2 plots of benthos with paste or heat. To mix large amounts of paste, we used a 84L capacity grout mixer (CGMIX22ES, Chemgrout, Grange Park, IL, USA) (Figure S2A). To ensure smooth homogenous paste texture free of clumps of $CaCO_3$ (critical for adequate flow through dispenser head), we first added water to the mixer and with the mixer off, carefully added NaOH. The mixer was turned on until the NaOH was completely dissolved and the caustic solution was drained into buckets. We rinsed the mixer, added glycerol, started mixing in the polymer slowly and mixed for 15 minutes. The mixer was turned off and the NaOH solution was carefully added. The mixer was turned back on, and after 5 minutes, the $CaCO_3$ was sifted into the mixture at a slow steady pace using a large scoop. Mixing continued for another 30 minutes to ensure the paste had a smooth homogenous consistency, free of $CaCO_3$ clumps.

To deliver the paste, we used a shovel pump (Checkmate D60, Graco, Minneapolis, Minnesota, USA) powered by an air compressor (Quincy QT 14HP, Quincy, Bay Minette, Alabama, USA) (Figure S2B). The pump and compressor were deployed on a surface vessel and paste was delivered through a 30.5 m, 0.75 cm diameter hose (Figure 1A) attached to a multiport nozzle (Graco) (Figure 1B–D). To apply hot water, we used a custom designed Monkey Heater (Figure S2C described above) with coils that were twice the length as those used in the 2018 trials. Hot water was delivered through a 30.5 m, 0.75 cm hose wrapped in 2.5 cm thick foam insulation with PVC tape to minimize heat loss (Figure S2D). Flow rate and outlet water temperature were measured at the surface using a 2 L bucket and glass thermometers, respectively (Figure S2E) whilst outlet temperature at the benthos was measured with a glass thermometer. The end of the buoyant hose was weighted with 30 kg lead dive weights secured with rope (Figure 1E), and a custom designed threaded funnel at the end of the hose helped concentrate

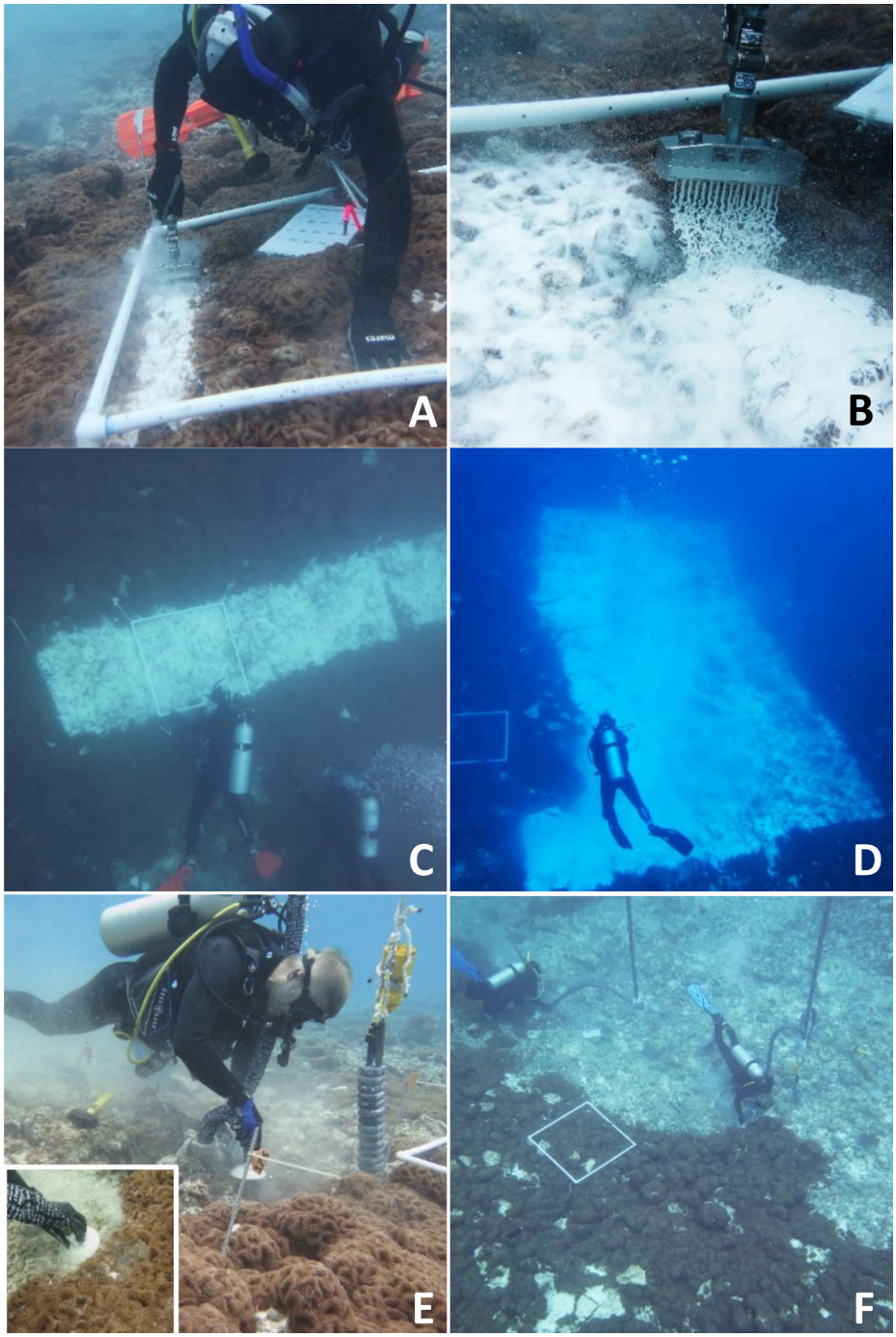

Figure 1. A) Deploying paste (white streak) on *R. howesii* (brown). B) Detail of C with multiport flow head. C) 5 m^2 paste deployed. D) ca. 30 m^2 paste deployed. E) Treating *R. howesii* with heat; note weights to right to keep buoyant hose submerged, live (foreground) and dead (background) *R. howesii*. Inset is detail of funnel to concentrate heat. F) Shark's eye view of two divers deploying heat to kill *R. howesii*. Photographs: A – Julia Rose, B-F – Thierry Work.

heat on *R. howesii* for 1–5 s (Figure 1E–F). Trials for paste and heat were done in areas of > 98% *R. howesii* cover. Two quadrats (1 each heat and paste) happened to contain a single large colony of non-target *Sarcophyton* spp., and attempts were made to treat around these organisms as a crude test of selectivity (non-target effects) of application during large scale trials.

To gauge costs and effort of paste and heat applications, we recorded personnel hours and costs of materials, fuel, and capital equipment. To gauge efficacy of treatment, 1 m^2 quadrats were individually marked with uniquely numbered stakes, photographed prior to and after treatment, and percent reduction of *R. howesii* cover calculated for each quadrat using Image J (Schneider et al. 2012). All trials were undertaken at depths ranging from 7–8 m in a total area not exceeding 250 m^2. Mean percent reduction in *R. howesii* cover vs treatment was compared using Wilcoxon rank sum test, and Kruskal-Wallis analysis of variance was used to compare percent *R. howesii* reduction vs person applying the treatment (applicator).

Atoll surveys

Atoll-wide surveys for *R. howesii* were undertaken as previously described (Work et al. 2008, 2018) with a further expansion of survey on portions of the western terrace visible from the water surface and south and north shore of the atoll in 2017 and 2018. Briefly, a snorkeler was towed behind a boat and every minute, a recorder on a boat captured a global positioning system location and noted the snorkeler's score of benthic cover of *R. howesii* (0–none, 1–1–30%, 2–33–66%, 3–>66%). Surveys in 2021 repeated the same approach as those of 2017–2018. Survey data were mapped, analyzed, and surface area of infestation calculated with R (R Core Team 2017) using packages rgeos, rgdal, and concaveman. Statistical comparisons between the two survey points (2017–2018, and 2021) were analyzed with Chi square tests using R (R Core Team 2017). Significance levels for all statistical tests was 0.05.

Results

Stage 1: Mesocosm and small scale field trials September 2018

For Phase 1 paste trials in mesocosms, mortality from chlorine was 100% at concentrations ≥1% and ranged from 0–100% for < 1%. Mortality for 6% and 12% citric acid was 0 and 100%, respectively, however the acid dissolved the $CaCO_3$ in the base matrix leading to gas production, pressure-induced expulsion of the syringe plunger, and leakage of product, so this option was not pursued further. Sodium hydroxide yielded consistent 100% mortality at concentrations exceeding 3% and 0–100% mortality at lower concentrations. For phase 2 trials in individual plots, 1–2% chlorine treatment yielded reductions of corallimorpharian cover ranging from 71–100% measured after 3 days (Figure 2A), whereas reduction with 6% NaOH was 96–100% (Figure 2B). For quadrats treated with 2–6% NaOH, reductions ranged from 2 to 89%, in part because divers applied insufficient paste to completely smother *R. howesii* (Figure 2C). Chlorine-laden paste did not seem to adhere to *R. howesii* as well as NaOH-laden paste. For Phase 3 paste trials (mixed habitat), *R. howesii* was treated with paste containing 5% NaOH

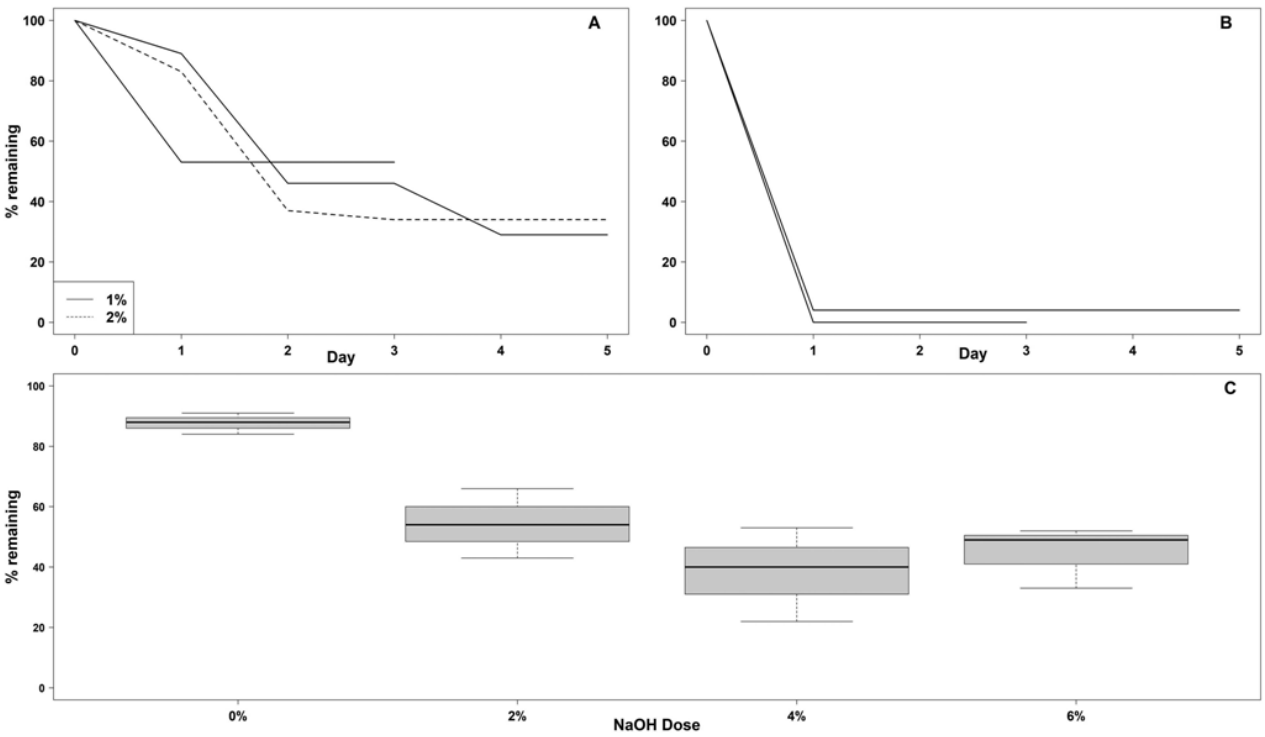

Figure 2. A) Percentage of *R. howesii* remaining over time after treatment with 1 (N = 2) or 2% chlorine (N = 1). B) As in A with 6% NaOH (N = 2). C) Boxplot (bold line is median, box is 25 and 75 percentile, whiskers are minimum and maximum minus outliers) of percent *R. howesii* remaining) in quadrats 3 days after treatment with 0, 2%, 4%, or 6% NaOH; each NaOH concentration represent 12 squares each covering 400 cm^2.

adjacent to 8 colonies of *Montipora* spp. (treating mean of 27 *R. howesii* polyps adjacent to each colony), 2 *Pocillopora* spp. (mean 19 *R. howesii* polyps adjacent to each colony), 1 each *Acropora* spp. (44 *R. howesii* polyps), *Astreopora* spp. (13 *R. howesii* polyps), *Favites* spp. (31 *R. howesii* polyps), *Fungia* spp. (48 *R. howesii* polyps), *Leptoria* spp. (36 *R. howesii* polyps), and 2 *Tridacna* spp. (mean of 30 *R. howesii* polyps adjacent to each clam). Mean ± standard deviation percent reduction of *R. howesii* polyps three days after treatment was 92 ± 10 with a range of 67–100% (Figure 3A–D). Proximity to the paste treatment did not result in any sign of harm to any non-target marine life unless the paste came into direct contact with non-targets. Partial damage to corals occurred in four coral colonies (all *Montipora* sp.) mainly due to their vertical orientation below the treatment area that led to the downward migration of paste onto the coral head (Figure 3C–D). Clams were unaffected (Figure 3E–F).

For Phase 1 heat trials (N = 21), mortality was 0% for < 49 °C, 0–88% for 54 °C, 0–80% for 60 °C, 43–50% for 66 °C, 0–100% for 71 °C, 50–100% for 77 °C, 100% for 82 °C, and 100% for 88 °C. Based on this, it appeared that immersion for 1 sec at temperatures > 82 °C were needed to effectively kill *R. howesii*. For Phase 2 trials, 42 plots of 20 × 20 cm were treated with eight plots as controls. Mean (SD) percent of *R. howesii* surviving after heat treatment 60% (30%) was significantly (t = 4.7848, p = 4.803e-05) lower than control 89% (11%). However, the percent reduction (ca. 30%) was deemed inadequate. A major issue with the heat set up was a combination

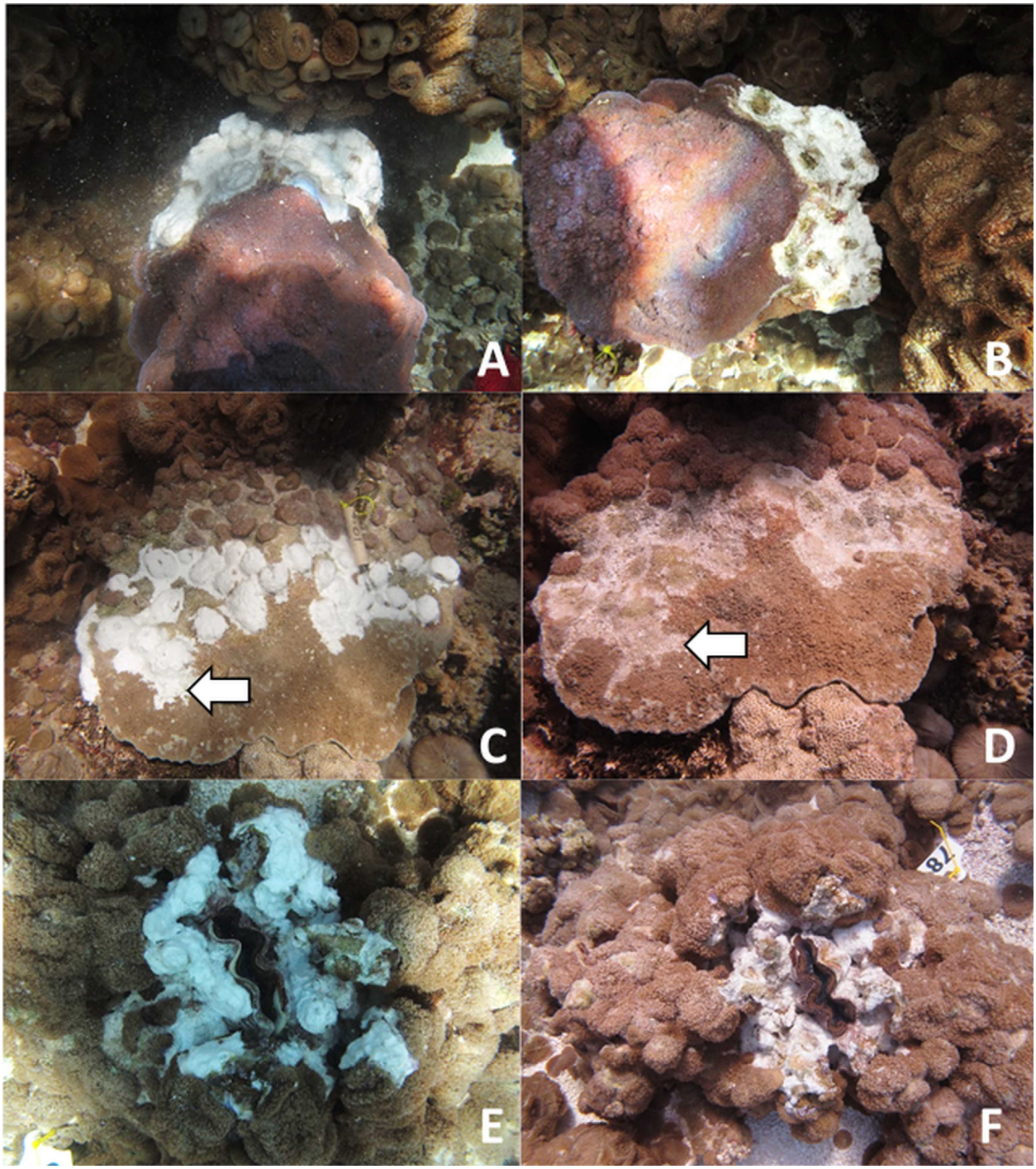

Figure 3. Mixed habitat treatment with 5%NaOH paste. A) *R. howesii* treated adjacent to *Montipora* sp. B) Same as (A) 3 days later. C) *R. howesii* treated adjacent to *Montipora* sp.; note overflow of paste onto coral polyps (arrow). D) Same as (C) with arrow pointing to dead coral. E) *R. howesii* treated adjacent to giant clam. F) Same as E 3 days later; note uninjured clam. Photographs by Thierry Work.

of heat loss from the uninsulated hose (ca. 10 °C) and inability of the existing machine to maintain temperatures experimentally deemed necessary to effectively kill (82 °C needed and maximum outlet temperature never exceeded 75 °C). Phase 3 trials (mixed habitat) were attempted but abandoned due to these limitations. Hobo temperature arrays only detected heat gain directly adjacent to the heat dispensing source (funnel) that rarely exceeded 6 °C above ambient for < 10 min (Figure S3).

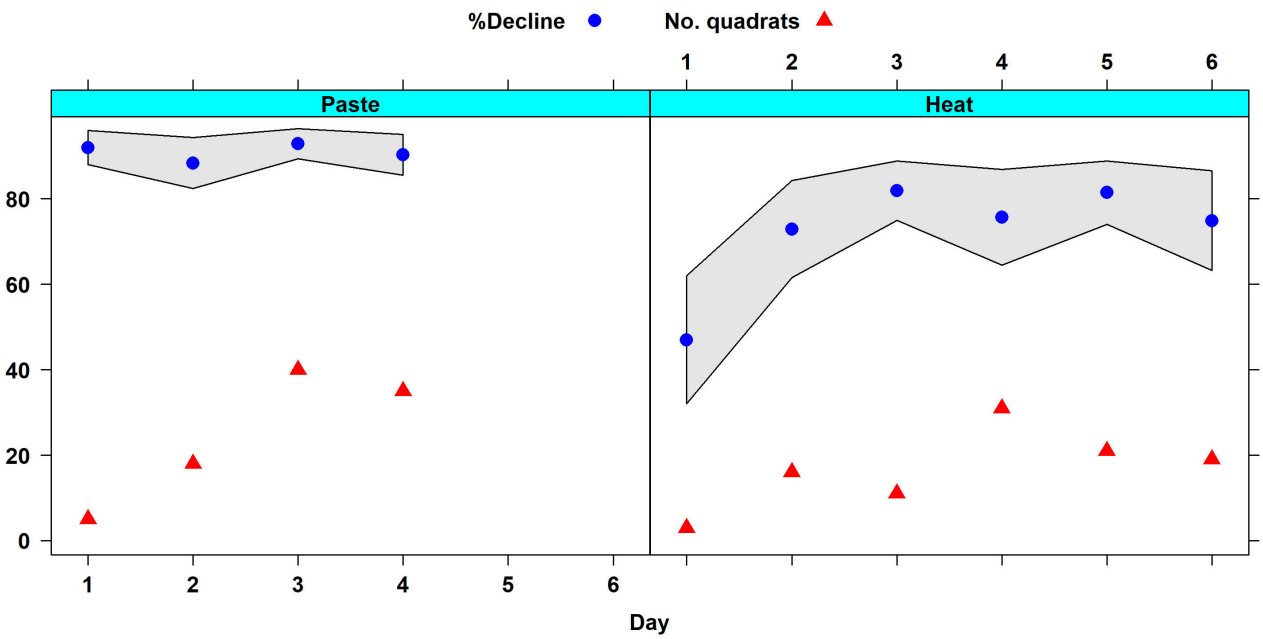

Figure 4. Number of 1 m^2 quadrats treated over time, mean percent decline of *R. howesii*, and standard deviation (grey area) for plots treated with paste and heat.

Stage 2: Landscape scale trials September–October 2021

The application of paste at larger scales occurred over four days. We treated 98 m^2 of benthos with sixty-five-22.7L buckets of paste (Figure 4). Mean (SD) percent cover of corallimorphs in quadrats treated with paste prior to treatment was 92% (7%) and 8% (4%) after treatment for a mean reduction of 91% (4%) (Figure 5). Heat treatment was applied over 6 days (Figure 4); mean ± SD percent cover of corallimorphs in quadrats treated with heat prior to treatment was 96 ± 5% and 23 ± 11% after treatment for a mean reduction of 76 ± 12% (Figure 5). The heater consistently delivered water to the benthos at 82 °C at flow rates of 100 ml/s with no measured loss of heat from surface to bottom. Percent *R. howesii* reduction for paste was significantly higher than for heat ($W = 943$, $p < 2.2e\text{-}16$). Five people applied paste or heat. For paste, there was a groupwise significant difference (chi-squared = 11.35, df = 4, $p = 0.02$) between person applying and percent reduction of *R. howesii*, but no pairwise significant differences were seen for post hoc assays. A groupwise significant difference (chi-squared = 16.643, df = 4, $p = 0.002$) in percent reduction of *R. howesii* cover between people applying heat was seen with the following applicators differing significantly between each other: 1 vs 4, $p = 0.0008$; 2 vs 4, $p = 0.05$, 3 vs 4, $p = 0.04$ (Figure S4). The two non-target *Sarcophyton* spp. in quadrats treated with paste or heat remained unaffected (Figure 6A–D), and notable numbers of reef fish invaded and consumed dead and dying corallimorphs during treatment (Figure 6E–F). Total costs for paste and heat operations (supplies, equipment, labor) for landscape scale trials were $US 38,140.78 and $US 27,215.67, respectively (Table 1). For paste, capital equipment consumed 82% of the costs followed by consumables (6%), labor (11%) and

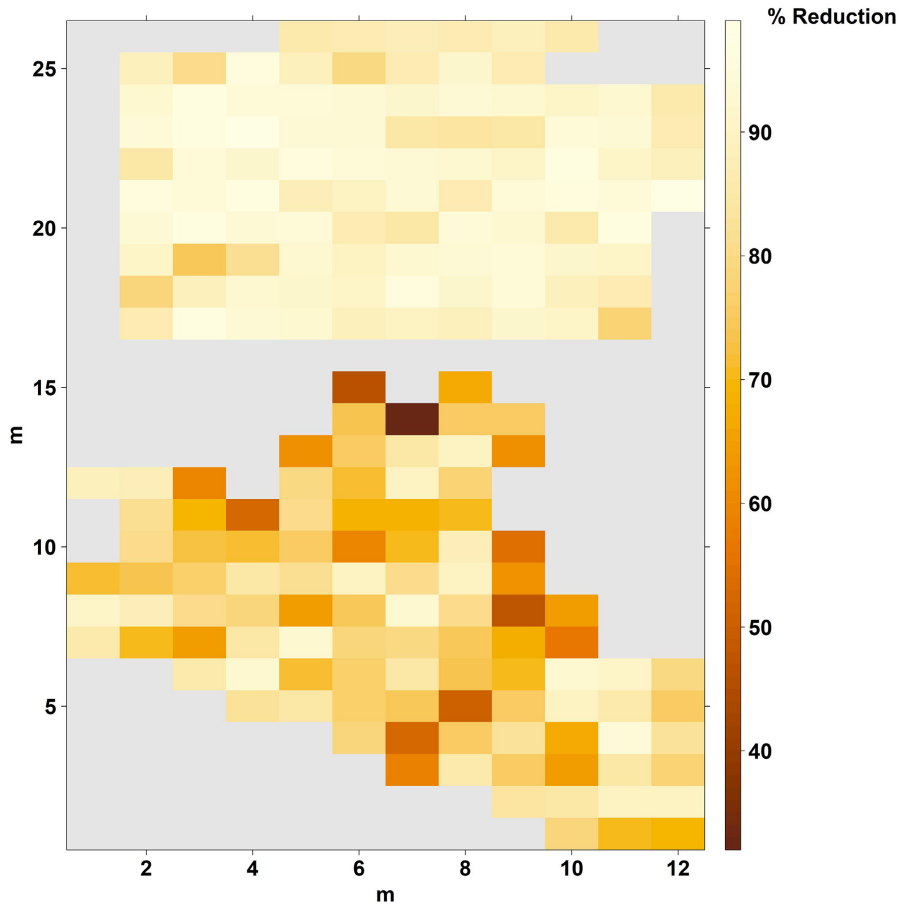

Figure 5. Physical layout of quadrats color coded by percent reduction in *R. howesii* cover after treatment. Paste is top and heat is bottom. Grey are untreated *R. howesii*.

fuel (1%). For heat, the proportions were 78% for capital equipment, 17% for labor, 3% for fuel, and 2% for consumables.

Atoll surveys

A total of 2377 GPS points were recorded in 2017–2018 of which 412 (17%), 736 (31%), and 190 (8%) scored as 1 (1–33% cover by *R. howesii*), 2 (34–66% cover) or 3 (> 66% cover), respectively (Figure 7A). For the 2017–2018 surveys, area coverage by *R. howesii* comprising Scores 1, 2, and 3 was 4,466,016 m^2, 597,560 m^2, and 990,479 m^2, respectively (Figure 7B). In 2021, 1977 points were recorded of which 349 (18%), 594 (30%), and 98 (5%) were scored as 1, 2, or 3, respectively (Figure 7C). In 2021 surveys, area coverage by *R. howesii* scoring 1, 2, or 3 comprised 5,028,389 m^2, 609,093 m^2, and 276,422 m^2, respectively (Figure 7D). Score 3 coverage between the two surveys significantly decreased with significantly more points recorded in 2017–2018 vs 2021 (18.546, df = 3, p-value = 0.0003).

Discussion

We present methods for applying corrosive paste and heat as two potential treatments for controlling invasive cnidaria on coral reefs. We have demonstrated successful treatment at a larger (> 30 m^2) scale than has

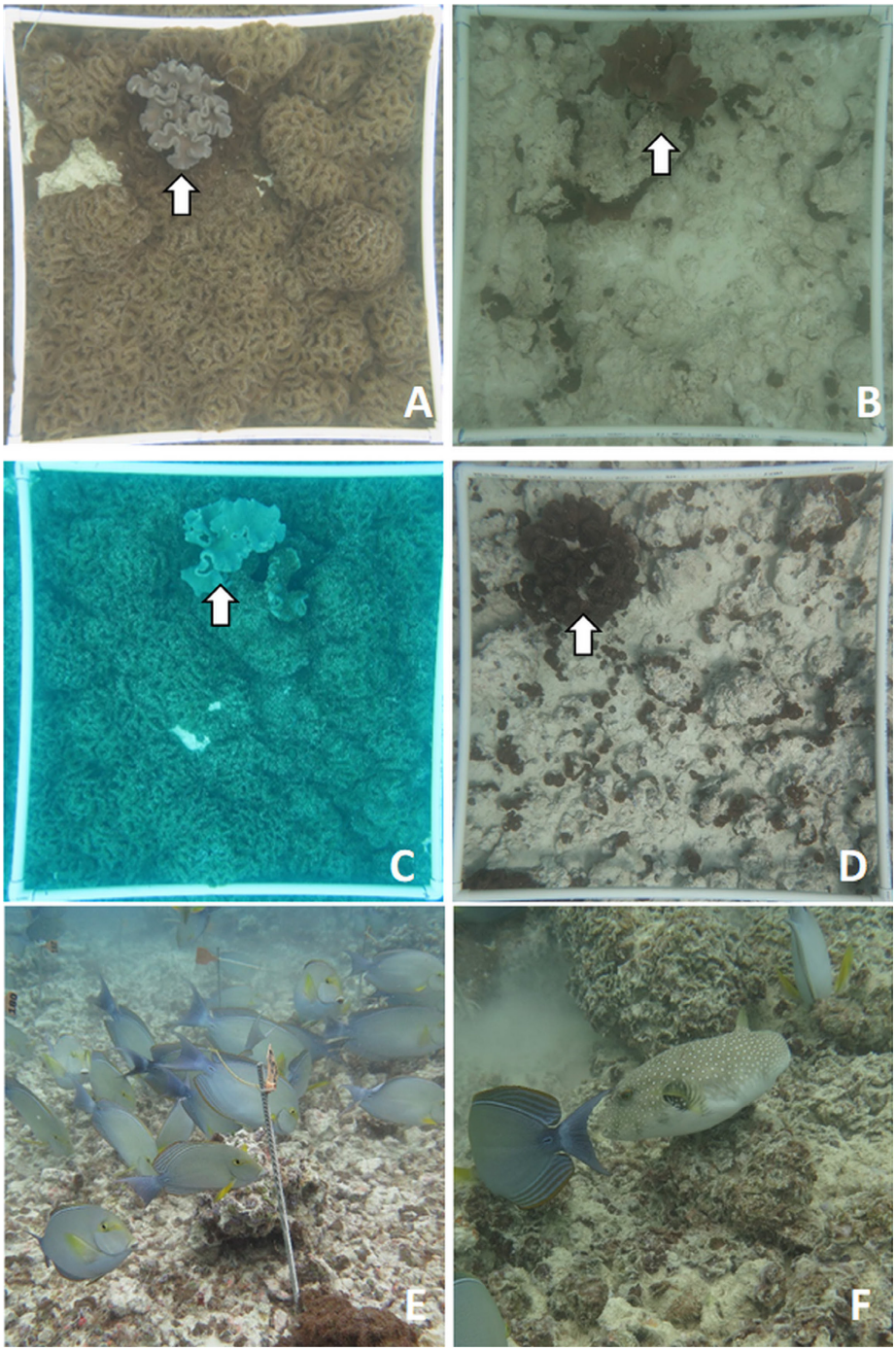

Figure 6. Examples of treatments sparing non-target organism. A) Paste plot prior to treatment; note *Sarcophyton* (arrow). B) same as A post treatment; note Sarcophyton (arrow). C) Heat plot prior to treatment; note Sarcophyton (arrow). D) Same as C post treatment; note *Sarcophyton* (arrow). E) Surgeonfish and F) pufferfish consuming dead and dying *R. howesii* immediately post-treatment. Photographs by Thierry Work.

previously been documented, indicating that these methods represent novel advancements in the tools available to protect coral reefs and other marine systems from sessile invasive species outbreaks. Crucially, these methods do not depend on scraping or fragmenting animals which can exacerbate invasions by seeding habitat with reproductive fragments (Chen et al. 1995). Slight modifications to the proposed methods could be used to control a wider variety of invasive species such as macroalgae.

Table 1. Items, unit cost in $US, and total cost for landscape scale paste and heat operations.

	Item	Paste			Heat		
		Units	Cost/unit	Total	Units	Cost/unit	Total
Personnel	Person hours mixing	64	$25.00	$1,600.00	NA		
	Person hours surface support	71	$25.00	$1,775.00	134	$25.00	$3,350.00
	Person hours diving	25	$25.00	$625.00	52	$25.00	$1,300.00
Fuel	Gasoline (L)	239	$1.14	$272.46	570	$1.14	$649.80
	Diesel (L)	NA	NA	NA	228	$1.14	$259.92
Equipment	Buckets	28	$15.80	$442.40	NA	NA	NA
	Mixer	1	$6,107.87	$6,107.87	NA	NA	NA
	Shovel pump	1	$21,860.15	$21,860.15	NA	NA	NA
	Compressor	1	$3,011.46	$3,011.46	NA	NA	NA
	Insulated hose	NA	NA	NA	2	$204.50	$409.00
	Pump	NA	NA	NA	1	$1,120.00	$1,120.00
	Generator	NA	NA	NA	1	$5,069.95	$5,069.95
	Heater	NA	NA	NA	1	$14,677.60	$14,677.60
Consumables*	Descaler (L)	NA	NA	NA	70	$5.42	$379.40
	CaCO3 (kg)	608	$1.52	$924.16	NA	NA	NA
	NaOH (kg)	76	$2.75	$209.00	NA	NA	NA
	Glycerin (L)	456	$2.88	$1,313.28	NA	NA	NA
	Water (L)	350	$0.00	$0.00	NA	NA	NA
	Total cost			$38,140.78			$27,215.67

* Carboxymethylcellulose was donated by Ashland.

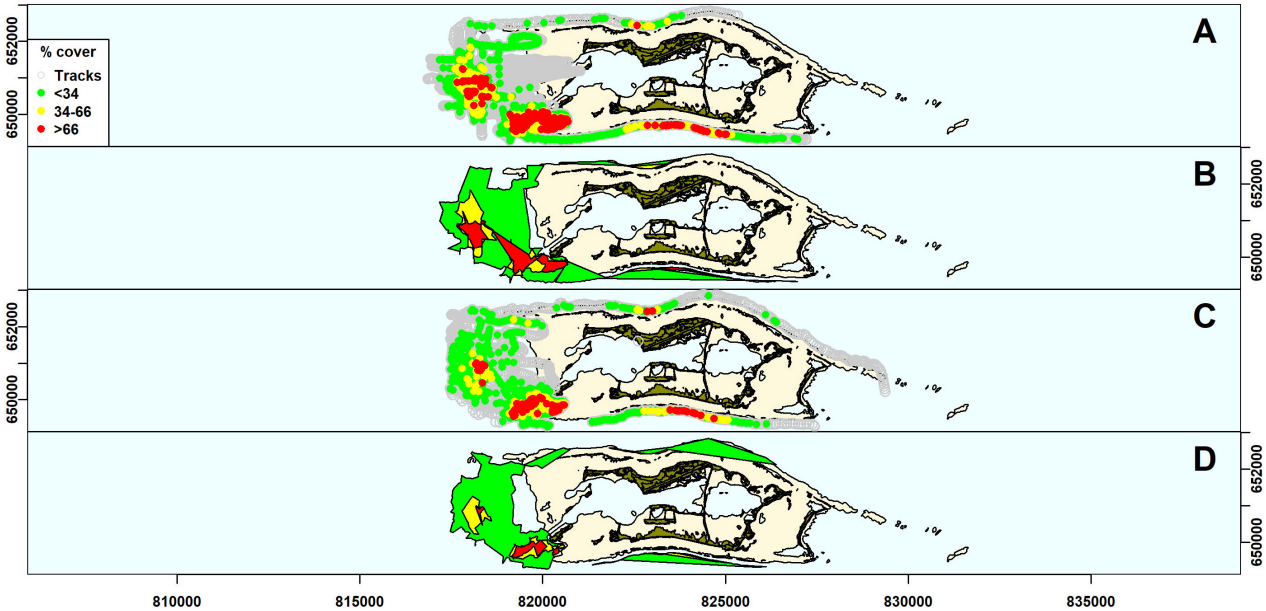

Figure 7. GPS points of towed surveys (A, C) and concave hull polygons (B, D) for *Rhodactis howesii* infestations color coded by percent cover (green: < 34%, yellow (34–66%), red (> 66%) for 2017–2018 surveys (A, B) and 2021 surveys (C, D). X and Y axes are UTM latitude and longitude, respectively, for all plots. Reef is colored tan and emergent land dark green.

In our trials, paste killed *R. howesii* more effectively than heat, particularly in horizontal substrate where the negative buoyancy of the $CaCO_3$ coupled with glycerin allowed the toxicant (NaOH) to reach the target in holes and depressions. In contrast, efficacy of heat depended on close contact between hose outflow and target, so this was less effective in rugose substrates with variably sized cavities (rubble). Heat might prove more effective in treating invasives attached to vertical or smooth substrates such as flat natural surfaces, or ships' hulls or pier pilings (Hewitt et al.

2005; Wotton et al. 2004), structures that often serve as stepping stones facilitating the spread of marine invasive species (Hulme 2006). For rugged vertical surfaces, heat may be preferable because it is not prone to forces of gravity, whereas paste tends to settle downwards, potentially having less effect on targets and more potential adverse effects on non-target organisms (Figure 3C–D). It is likely that some modifications of the funnels used to concentrate hot water such as designs allowing funnel to seal to substrates, could improve efficacy of heat delivery to targets in more rugose environments and enhance the application of hot water to control cnidaria. Increased time in contact with hot water or increased flow might also improve efficacy with heat but would need to be balanced against efficiency (i.e. time and effort required to treat an area).

Importantly, both methods are relatively safe to use and have minimal effect on non-target species. Neither method had lethal effect on neighboring biota located outside of the treated area or in the water column above the benthos. However, non-target organisms (e.g. small fishes and invertebrates) sheltering in low areas of the benthos could be affected in treated areas or in instance of paste spillover. Neither method left residual material on the reefs other than small amounts of calcium carbonate from the paste which dissipated within 3 days. Applying heat had no substantial residual thermal effects on surrounding seawater or biota. As such, both methods show promise in treating invasives in mixed invasive/natural habitat as exemplified by coral colonies and clams that were unaffected by adjacent application of paste (Figure 3). The methods can also be selectively applied on a larger scale to spare non-target organisms as evidenced by the surviving colonies of *Sarcophyton* in the paste and heat quadrats (Figure 6).

Applying heat or paste could complement or replace other methods to control or eradicate invasives (Table S1). For example, in Hawaii, a suction dredge was used to remove invasive algae from reefs (Neilson et al. 2018), however such removal methods often leave reproductive propagules behind that grow into new algae (Smith et al. 2004). This problem could be remedied by treating such areas with paste or heat after algal removal to kill propagules remaining on the substrate. Heat treatments required substantially fewer raw materials (seawater and fuel) compared to paste.

The costs we outlined in Table 1 were partitioned into categories that can be useful to managers contemplating this technique for broader scale control. We did this to be as transparent as possible given that some of the expenditures can be substantial. Costs/m^2 to treat *R. howesii* excluding capital expenditures were \$70/m^2 for paste and \$59/m^2 for heat. Using our cost estimates, the total investment required to treat the most heavily infested (Score 3) areas at Palmyra (276,422 m^2) would cost \$US 19.3 million for paste and \$US 16.3 million for heat which is lower than the upper limit of \$US 26 million estimated by Arthur et al. (2015) to treat invasive marine species at scale. This illustrates how costs of containment and control of

invasives can balloon with an increase of the surface area infested and provides further evidence for the cost-effectiveness of early interventions (Hulme 2006). For instance, the costs for paste and heat to treat the infestation immediately around the wreck apparent in 2005 (ca. 900 m^2) would have been $US 77,000 and $US 67,000, respectively. A substantial portion of our cost estimates involve labor priced at US labor costs. Looking at actual hours of labor, paste and heat were essentially equivalent. For instance, it took 186 hours of labor to treat with heat vs 96 hours for paste, but adding the time needed to prepare the paste would bring that tally to 160 h. Economies of scale might be gained, for instance by pre-packaging buckets of paste commercially. Our costs do not include those incurred to get regulatory approval for broad scale use of heat or paste, because estimating these was beyond the purview of this study.

Our cost estimates to treat *R. howesii* on a large scale are crude figures that come with two assumptions: 1) That the optimal strategy to control *R. howesii* is to focus on the most heavily infested areas first and 2) That complete elimination of the organism and its propagules is necessary for habitat recovery. There is debate in the literature regarding the optimal strategy of controlling invasive species. Two main schools of thought are to treat heavily infested areas vs treating peripheral populations or establishing firebreaks. The preferred strategy depends on the reproductive capacity of the invasive organism, the process of invasion, and the region being treated. For example, if satellite populations are the main source of invasion, focusing on those areas might be the optimal treatment strategy. If one or few dense core populations are the main invasive source, treatment should be focused there (Hulme 2006). Efforts to identify and control sparse and peripheral invasive populations are proportionately more expensive (Epanchin-Niell and Hastings 2010). Invasion in more compact areas might also warrant greater efforts to control invasives because their spread is less constrained and could be more damaging to native biota (Epanchin-Niell and Wilen 2012). Palmyra as a whole represents a compact isolated area in that infestations of *R. howesii* are limited to shallower depths (< 30 m) and unlikely to spread across deep ocean barriers that surround the atoll (Work et al. 2018). Within available habitat at Palmyra, *R. howesii* outbreaks appear present in one primary area with several smaller densely populated areas. Nevertheless, the methods we have applied at Palmyra are applicable to centralized and peripheral populations. Given that most corals at Palmyra are at < 30 m, infestations are likely to impact more reef area there over time because live coral appear to be optimal habitat for colonization by *R. howesii*. Additional treatment of *R. howesii*, potentially including further scaling up of methods described here, could potentially benefit Palmyra reef ecosystems.

Total eradication of invasives may be neither desirable nor necessary (Simberloff 2009), particularly in the case of *R. howesii* which is considered

an example of a native invasive (Valery et al. 2009). Strategies to control invasives that do not involve complete eradication are known as "functional eradication" where one exerts a level of control sufficient to mitigate ecological effects of invasives to an acceptable level (Green and Grosholz 2021). Taking advantage of the Alee effect (positive relationship between individual fitness and population size) can aid in invasive species control. For instance, decreasing population size or fragmenting habitat to a level where organisms can no longer find mates or effectively spread can be a useful management strategy (Tobin et al. 2011). In the case of *R. howesii* at Palmyra, this could be a viable strategy. For instance, it has now been 8 years since the shipwreck was removed, and the area around the wreck has remained *R. howesii*-free, so perhaps decreasing the population to a certain level may suffice to minimize spread (Work et al. 2018).

A major element of this study was documenting the costs involved with the control effort, an exercise that is not often done when looking at management of invasive species (Januchowski-Hartley et al. 2011). Epanchin-Niell and Hastings (2010) identified three things to consider when contemplating management strategies for invasives: (1) invasion dynamics and the effect of control on those dynamics, (2) damages caused by the invasion, and (3) the financial costs associated with control. Understanding the costs of control requires knowledge of the marginal cost (e.g. the costs needed to treat an additional unit of control) and the benefits of that control. Benefits of control tend to decline in a linear manner with scale of area treated. This is in part due to proportionally high marginal costs required to treat small areas. At the same time, treating very large areas can be prohibitively expensive. The optimal scenario for treatment occurs where marginal costs and benefits intersect (Epanchin-Niell and Hastings 2010). In the case of Palmyra, we have reasonable data on the invasion dynamics of *R. howesii* and the marginal costs needed to treat with heat and paste. A significant (> 75%) proportion of costs for heat and paste involved outlay of capital equipment. The remaining costs (materials, labor) to treat *R. howesii* are directly proportional to area treated. Large capital expenditures of control methods justify treatment of larger areas to recoup investments (benefits of treatment) (Hulme 2006). Putting an actual dollar cost to damage caused by *R. howesii* is difficult; indeed Epanchin-Niell and Hastings (2010) acknowledged that assessing monetary values to ecological damage remains one of the more intractable aspects of calculating cost-benefits of invasive species management. In the case of Palmyra, the USFWS spent $US 6,000,000 to remove the shipwreck from Palmyra leading to an abatement of ca. 1 km^2 of moderately to severely infested reef habitat (Work et al. 2018) which would amount to a habitat value of about $US 6/$m^2$. This is likely an underestimate, because this price does not account for total expenditures to manage coral reefs at Palmyra to which two different organizations (USFWS and TNC) contribute substantial

sums. Considering our cost estimates for paste and heat are at the upper limit for what managers are likely willing to pay to treat invasive species, future development of these methods might consider how to improve logistical efficiencies to help lower costs. Considerations could include professionalizing the operation, engineering more creative or efficient ways to apply paste or heat, reformulating paste ingredients with cheaper alternatives, and buying consumables in bulk.

Surveys between 2017–2018 and 2021 show little change in coverage of *R. howesii* at Palmyra and some declines in heavily infested areas. The infestation now occupies > 5 km^2 with an increase of moderately infested areas. Given that surveys were done during similar time periods of the year in 2017–18 and 2021, we do not think seasonal factors are responsible for declines of heavily infested areas. The slow rate of spread of *R. howesii* could influence management decisions; for instance, high rate of spread leads to more damage more rapidly thereby justifying higher costs of control (Epanchin-Niell and Hastings 2010). On the other hand, the low rate of recolonization of *R. howesii* after extirpation as evidenced from its continued absence at the shipwreck site (Work et al. 2018) might be an argument for continued control efforts to limit or fragment remaining populations. The benefits of control or eradication are reduced when the chances of reinvasion are high (Epanchin-Niell and Hastings 2010). Further information and modelling on the drivers of infestation, such as growth and reproductive patterns, seasonality, and biophysical drivers, direction, and speed of *R. howesii* colonization would help managers consider where best to apply limited resources (e.g. at the most heavily infested areas versus the edges to achieve management goals) (Epanchin-Niell and Wilen 2012; Hulme 2003) and how much reduction of *R. howesii* is needed to abate their spread. This information coupled with effective and cost-effective control methods such as those tested in this study, and sustained control of the spread of *R. howesii*, would likely enable its long-term containment.

Consideration of biological control agents and options to influence predation and competition has received very little attention in marine environments (Table S1) despite these having a long, albeit checkered, history of success in terrestrial invasives (Atalah et al. 2015). Palmyra may provide an ideal location to identify potential indigenous biological control agents for *R. howesii,* considering the relatively healthy reef community can provide a diversity of potential candidates and where confounding anthropogenic factors are relatively controlled. For instance, we noted that after heat treatment, eyestriped surgeonfish; *Acanthurus dussumieri* (Figure 6E) and white-spotted pufferfish; *Arothron hispidus* (Figure 6F) aggressively fed on heat-treated *R. howesii*. Understanding why fish at Palmyra have not controlled the *R. howesii* outbreak and under what circumstances other species could predate or compete with *R. howesii*

could help identify whether indigenous biological control agents are a likely option to support the management of future outbreaks.

In closing, this paper provides evidence that heat and the application of NaOH in a paste form have merit to control marine invasive organisms. With appropriate modifications, these methods also have the potential for use at medium-large scale (100–1000s m^2) applications as well as in more limited areas such as treatment of pier pilings or ships' hulls. The techniques described herein add to the small but growing marine eradication "existing toolbox" (Table S1).

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Authors' contribution

TW – research conceptualization; sample design and methodology; investigation and data collection; data analysis and interpretation; ethics approval; funding provision; writing – original draft; writing – review and editing. RB, RAR, VB, TC, CG, JR – sample design and methodology; investigation and data collection; writing – original draft; writing – review and editing. AW, SK– funding provision; writing – original draft; writing – review and editing.

Ethics and Permits

All activities in this study were done under the Federal NOAA Permit PIR-2018-10406, I-PI-18-165 1-AG. Ethics clearance was not required for this study.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Phase 1 procedures.
Figure S2. Phase 2 procedures.
Figure S3. Water temperatures during heat treatment.
Figure S4. Applicator effect on treatments.
Table S1. Summary of methods used to treat marine invasives.