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Removal of macroalgae from degraded reefs enhances coral recruitment

Running head: Macroalgae removal enhances coral recruitment

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Abstract

Declining coral cover on tropical coral reefs often results in a concomitant increase in macroalgae. When proliferation of macroalgae persists outside regular seasonal growth, it can shift the ecosystem dominance away from corals into a permanently altered system. Such an altered system is unlikely to recover naturally, despite ample supply of coral larvae, as coral settlement and survival is reduced by the presence of macroalgae. Physical removal of macroalgae has been proposed to overcome this biotic barrier to recovery, although empirical evidence demonstrating the effects of removal on phase-shifted reefs is lacking. Here, we manually removed macroalgae from twelve 25 m² experimental plots (88.5 ± 6.2 kg wet weight per plot; 90% benthic cover decrease) on a degraded reef prior to coral mass spawning across 2 years and recorded the number of coral recruits to settlement tiles and natural substrata. Four months after each spawning event, we found a threefold increase in coral recruits to tiles in plots where macroalgae had been removed (n = 12 plots; February 2019: mean 45.9 ± 12.7 recruits per tile; February 2020: mean 53.9 ± 5.9 recruits per tile) compared to control plots where macroalgae remained (n = 12 plots; February 2019 mean: 13.6 ± 2.8 recruits per tile; February 2020 mean: 17.5 ± 3.5 recruits per tile). These results suggest that, at small scales, macroalgae removal may be a useful intervention to boost recruitment on degraded reefs. Longer-term monitoring is needed to document if coral survivorship, growth, and subsequent reef recovery occurs.

Key words: citizen science, coral recruitment, Great Barrier Reef, macroalgae removal, phase shift, reef restoration

Implications for Practice

- Degraded coral reefs with high macroalgal abundance are unlikely to recover without intervention due to feedback loops reinforcing macroalgal cover and reducing coral fitness.
- Removal of macroalgae results in increased coral settlement and survival, and may reduce a biotic barrier to reef recovery.
- Macroalgae removal is an accessible, cost-effective reef management method, which can be transferred to reef practitioners, public community, or citizen science programs.
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Introduction

Coral reefs have become emblematic of global declines in ecosystem health brought about by anthropogenic influence. Increasing sea temperatures, decreasing pH, eutrophication, disease, coastal development, and overfishing combine synergistically leading to a severe loss of live corals on reefs worldwide (Eyre et al. 2018). The deterioration of coral cover and community health often coincides with a rise in macroalgae, which once established, can out-compete corals and lead to a shift in community structure and function (Hughes 1994; Ceccarelli et al. 2020). Biological, chemical, and physical feedback mechanisms reinforce the establishment and maintenance of this community shift (Johns et al. 2018), with macroalgae able to quickly gain dominance of reef ecosystems (Hughes 1994; Roff et al. 2015). A shift in

the dominant reef-building species from coral to macroalgae has been demonstrated on coral reefs in the Caribbean (Hughes 1994; Lapointe et al. 1997). For example, nutrient enrichment, repeated hurricanes, and coral bleaching, combined with the near-complete loss of the keystone seaweed-grazing urchins, *Diadema antillarum*, resulted in a 90% loss of coral cover and a concurrent rise in macroalgae on Jamaican reefs through the 1970s and 1980s (Hughes 1994; Lapointe et al. 1997). Although this example is presumed to typify a widespread ecological pattern, on Australia's Great Barrier Reef (GBR), large-scale shifts such as those seen in the Caribbean have yet to be realized. However, macroalgae have shown increasing dominance at the expense of corals in recent decades at smaller scales on the GBR, particularly on inshore fringing reefs (Done et al. 2007; De'ath et al. 2012; Ceccarelli et al. 2020), and such community shifts are predicted to become more common as anthropogenic impacts increase (Bellwood et al. 2004; Graham et al. 2015).

Macroalgae, particularly of the genus *Sargassum*, are aggressive competitors with reef-building scleractinian corals. Competitive interactions between coral and macroalgae have a range of negative outcomes for corals, including reduced coral fecundity (Foster et al. 2008; Monteil et al. 2020), settlement and recruitment inhibition (Diaz-Pulido et al. 2010; Webster et al. 2015), suppression of metamorphosis (Baird & Morse 2004), reduced juvenile growth and survival (Chong-Seng et al. 2014; Webster et al. 2015), and effects on colony health and fitness (Tanner 1995; van Woesik et al. 2018). Negative effects result from direct interactions (e.g. shading, space pre-emption, abrasion, pathogen transfer) as well as indirect mechanisms such as allelopathy (Morrow et al. 2011; Rasher et al. 2011), microbialization (Haas et al. 2016), or herbivory-related processes (Evensen et al. 2021). Combined, these impacts may serve as an effective barrier to coral recruitment, such that natural recovery is unlikely to occur even in systems with ample supply of coral larvae.

Despite these negative effects, macroalgae are an important component of tropical coral reefs, and provide positive services for corals and other reef biota (Fulton et al. 2019). For example, macroalgae can shade corals from harmful solar irradiance (Jompa & McCook 1998), provide food and shelter for diverse reef fishes (Fulton et al. 2020) and invertebrates (Tano et al. 2016), and serve as a sink for ocean carbon (Ortega et al. 2019). However, when in high abundance, macroalgae are generally regarded as a symptom of a degraded reef, particularly when their abundance persists outside of natural seasonal peaks (Morand & Briand 1996; McCook et al. 1997).

As a result of the combination of global and local threats, many coral reefs globally have degraded past the point of natural recovery, prompting active restoration attempts worldwide (Boström-Einarsson et al. 2020). Although the focus of most restoration initiatives to date has been on growing coral fragments in nurseries and "out-planting" them onto reefs, a toolbox of multiple interventions combined with strong action on reducing global greenhouse gas emissions and improved local management will be required to bring about ecologically relevant reef alterations (Anthony et al. 2017; Knowlton et al. 2021). Unfortunately, effective reef restoration techniques are still in the early stages of development, with a recent review highlighting a lack of scientific rigor and insufficient monitoring (in terms of metrics and longevity) for many rehabilitation activities (Boström-Einarsson et al. 2020). On the GBR, multiple recent mass bleaching events and impacts from cyclones and crown of thorns outbreaks have caused wide-scale reduction in live coral cover

(De'ath et al. 2012; Hughes et al. 2017), prompting investment in the research and development of strategies to mitigate reef degradation (Hardisty et al. 2019). Cutting-edge technologies are being harnessed to develop strategies to promote coral adaptation, protect reefs from further damage, and repair reefs where damage has already occurred (van Oppen et al. 2017; Bay et al. 2019). However, there is also value in harnessing low-cost, low-technology reef interventions, particularly those which can be transferred to community and industry action through citizen science programs, as these can effectively scale interventions to wider geographic areas (Hesley et al. 2017; Vardi et al. 2021).

Given the range of known negative effects of macroalgae on corals, it has been proposed that manual removal of algae may be one intervention to boost reef resilience (Ceccarelli et al. 2018). By increasing space for the growth of existing coral colonies and enhancing available benthic space for coral recruitment, removal of macroalgae has the potential to remove a biotic barrier to natural reef recovery. The method may be particularly relevant for reefs where management efforts are currently focused on improving the abiotic conditions (i.e. water quality) which may have led to the initial establishment of algal dominance (Waltham et al. 2021). Despite its potential, as well as some case studies showing evidence of positive effects following removal (human or herbivore mediated; reviewed in Ceccarelli et al. 2018), the removal of macroalgae has rarely been investigated as a reef intervention tactic. Indeed, most studies utilizing the technique have been short term, have not quantified the removal effort (i.e. used removal of macroalgae as a maintenance regime for coral transplantation), have targeted invasive rather than naturally occurring algal species, or have not been in the context of reef restoration (Ceccarelli et al. 2018). In this study, we assess the effects of removing macroalgae from a degraded inshore reef of the GBR on coral larval settlement and recruitment. Larval settlement and subsequent recruitment are primary drivers of recovery, and hence are key metrics to understand if macroalgae removal is a viable technique for reef restoration on similar reefs worldwide.

Methods

Study Site, Experimental Design, and Removal of Algae

Magnetic Island (Yunbenun) is situated in the central inshore region of the GBR (Fig. 1). The fringing reefs of Magnetic Island have endured repeated acute and chronic disturbances, leading to a demonstrated persistent shift in the dominant benthic community from corals to macroalgae (Ceccarelli et al. 2020). As such, these degraded reefs are considered an ideal location to examine the effects of manual removal of macroalgae on coral larval dynamics.

In October 2018, six 25 m² (5 × 5 m) experimental plots were established on the fringing reef of Florence Bay at Magnetic Island (Fig. 1). Visual surveys were conducted to ensure general topographic consistency between plots, avoiding large features such as sand patches and bommies. The six plots were randomly designated as “control” or “removal” plots, and initial surveys were conducted to characterize the baseline benthic composition (see below). Following initial surveys, snorkelers and SCUBA divers removed macroalgae by hand from the three removal plots prior to the predicted mass coral spawning event in October 2018. Removal of macroalgae was assisted by citizen science volunteers from Earthwatch Institute, and particular effort was focused on removing the algal holdfasts. The removed

macroalgae were retained in catch bags and the wet biomass was weighed per plot. Removal of macroalgae was repeated in July and October 2019 to maintain low algal biomass in treatment plots. In July 2019, the number of experimental plots was doubled, resulting in six replicate plots in each of the control and removal treatments.

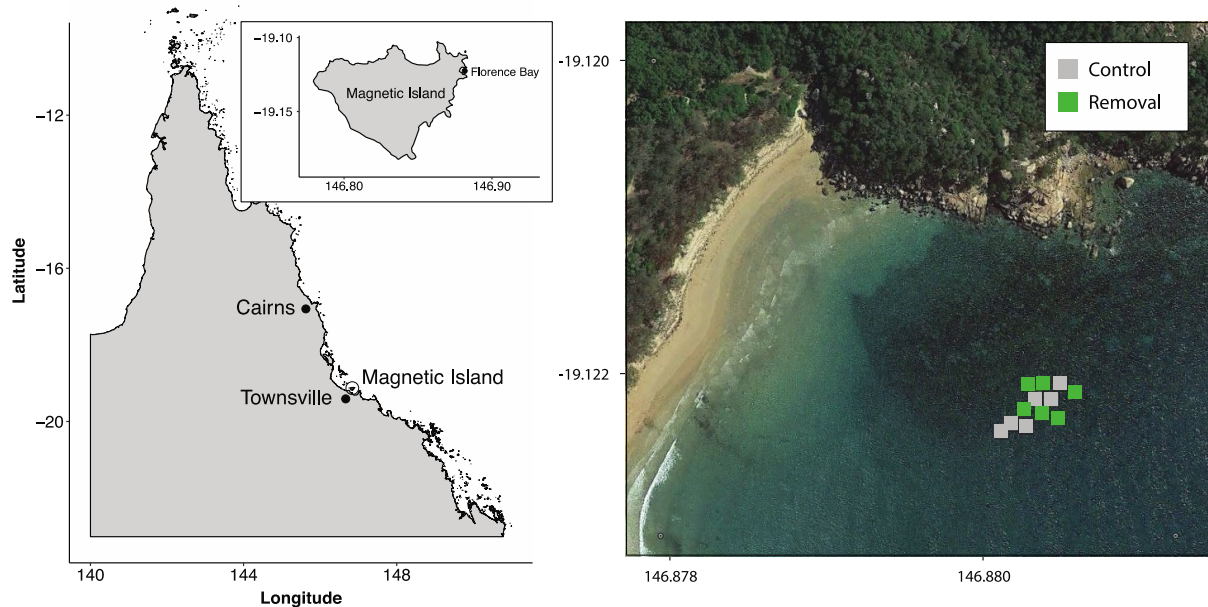


Figure 1. Study site and locations of experimental plots (note that 5 x 5 experimental plot icons are not to scale).

Benthic Ecological Surveys

Baseline benthic composition of the experimental plots was assessed using photo-quadrats. Each 25-m² plot was divided into twenty-five 1 m² and each grid-square was photographed at an angle parallel to the benthos, including the 1-m² boundary. Post-processing of the images was completed in the software CPCe (Kohler & Gill 2006), with 50 random points placed onto each image and benthic taxa identified to genus level where possible, and abiotic substrata identified as dead coral or grouped as rock, rubble, and sand. Community composition was calculated as the percent cover of each group. This process was repeated before and after algae removal for the removal plots. Because the number of plots was doubled in July 2019, and a difference in algal biomass is expected due to annual growth cycles with peak biomass in late summer prior to winter senescence (Vuki & Price 1994), the starting benthic composition of the original six plots and the six new plots were analyzed separately. In July 2019, post-removal photography could not be completed due to adverse weather, so benthic data are missing for this timepoint.

Within each 25 m² grid, three 1 m² grid-squares were haphazardly selected for SCUBA diver-conducted algae surveys. In each of the 3 replicate 1 m² quadrats, the total number of *Sargassum* holdfasts were counted (density), and 10 haphazardly selected thalli were

measured (to the nearest cm). These data were used to calculate biomass per plot using a length–weight relationship for *Sargassum polycystum* from Orpheus Island (Hoey 2010) (wet weight [g/m²] = 0.5637 [g/cm] height [cm] density [num/m²]).

Algal surveys were repeated periodically after the initial removal of macroalgae (Table S1). Surveys were repeated before and after removal of algal biomass in July and October 2019 to assess algal regrowth in the preceding period as well as the effectiveness of the removal technique. Surveys were not conducted in April 2020 upon completion of the experiment due to field restrictions associated with the COVID-19 pandemic (exemption was received for one field day, allowing enough time for the collection of settlement tiles only; see below).

Recruitment to Settlement Tiles

To assess the effect of macroalgae removal on recruitment success, we quantified the abundance of newly settled corals on experimental settlement tiles. Unglazed clay tiles (11 cm x 11 cm x 1 cm) were attached to the reef by a threaded metal rod hammered into the substratum with a locking nut above and below the tile. Tiles were attached horizontally, allowing approximately 5 cm space between the bottom of the tile and the seafloor. In 2018, five tiles per plot (n = 30 tiles) were installed after an initial 2-week conditioning period in unfiltered seawater at the Marine and Aquaculture Research Facilities Unit at James Cook University. The tiles were installed prior to the first spawning event of the year, which took place on 28 October 2018. The tiles were retrieved in two lots to examine short-term patterns in post-settlement mortality, with the first being removed 16 weeks after spawning (n = 3 tiles per plot), and the second being removed 21 weeks after spawning (n = 2 tiles per plot; Table S2).

The same process was repeated prior to the 2019 coral spawning event with some modifications. First, the number of tiles was doubled to n = 10 tiles per plot to buffer against loss or breakage of tiles, which was experienced in the first year of the experiment (Table S2). Second, the conditioning period was completed in situ, with tiles installed approximately 8 weeks prior to the initial predicted coral spawning period. The tiles were again retrieved in two lots with four tiles per plot retrieved approximately 20 weeks after the first spawning, and the remainder collected at approximately 24 weeks post-spawning (Table S2).

Retrieved tiles were soaked in a weak solution of sodium hypochlorite (bleach) to remove algae and soft-bodied invertebrates, leaving behind the calcium carbonate skeleton of coral recruits. All coral skeletons were counted and measured (in mm) under a Nikon SMX745T dissecting photomicroscope using the software Capture v2.1 (Nikon, Japan). The tile surface where the recruit settled was also recorded (i.e. top, bottom, and side of tile). Observers were “blind” to which tile came from which treatment to reduce bias in searching behavior.

In assessing coral recruitment between treatments and to account for unequal sample sizes between time points and plots (i.e. all tiles were not recovered at each time point, and the number of plots and tiles were doubled prior to the 2019 spawning), we report the number of recruits counted per tile, rather than using the tile as a pseudoreplicate and reporting per

plot. Previous studies have reported per-tile counts and hence this method is consistent to compare our data to historic recruitment studies (Mundy 2000; Baird et al. 2012; Hughes et al. 2019). For clarity, we refer to each recruitment census by the date of tile retrieval rather than the date of deployment or date of spawning (e.g. February 2020 rather than October 2019).

***In Situ* Recruitment**

In addition to the settlement tiles, coral recruits were counted on natural substrata. Within each 25-m² plot, three 1-m² quadrats were haphazardly placed and all visible coral juveniles <4 cm were counted, measured, and classified as branching or other morphology. Recruit surveys were completed periodically beginning in October 2019 and continued until July 2021 (Table S1). To ensure only those recruits that resulted from the 2018 and 2019 spawning were included in each census, only branching recruits were used for analysis as these are easily identifiable, have well-known growth rates, and most branching species participate in mass spawning events. For these reasons, branching recruits <4 cm can be confidently assigned as having arisen during the project period. Juvenile corals of massive and other morphologies often have slow growth rates or year-round reproduction (Babcock 1985; Dela Cruz et al. 2015), hence even a 1-cm massive morphology recruit cannot be confidently assigned as having recruited within the specified project period and were excluded from the analysis.

Statistical Analysis

To ensure differences in recruitment were not a result of benthic composition, differences in community composition between treatments at the start of the experiment were assessed. A Bray–Curtis matrix was calculated based on Wisconsin-standardized benthic cover data, which was then used to test for differences between treatments (i.e. control vs. pre-removal) using permutational multivariate analysis of variance (PERMANOVA) with 9,999 permutations and blocked by plot.

Differences in total recruitment (to natural substrata and to settlement tiles) between control and removal plots were assessed using generalized linear mixed models (GLMMs). Both models incorporated the interaction of treatment (control vs. removal) and tile removal date (February 2019, March 2019, February 2020, and April 2020) or in situ survey date (Table S1) as fixed factors, with plot and tile replicates as nested random factors. For the tiles, the response (number of recruits) was modeled according to a Poisson distribution with a log-link. For in situ recruits, to maintain the original data structure and account for pseudoreplication, the number of recruits for the three replicate quadrats was pooled, providing a total count of recruits across 3 m². A Poisson model was over-dispersed; hence, a negative binomial distribution (log-link) was used with all other model parameters the same. Model fit and assumptions were evaluated using simulated residual plots and tests of dispersion, which were satisfactory in all cases. Post hoc pairwise comparisons were made between treatments and time points based on estimated marginal means, and p values were significance adjusted using the Tukey method.

Spatial patterns in recruitment to tiles were similarly examined using a GLMM; however, the response (number of recruits) was calculated per cm^2 to account for differences in the size of each tile face (top/bottom = 121 cm^2 , side = 11 cm^2). As such, a Poisson distribution was inappropriate, as the area-standardized data were not integers. Instead, a Tweedie distribution with a log-link was used. The model selection process using Akaike's information criterion (AIC) indicated that time point (i.e., February, March 2019; February, and April 2020) did not improve the model, so all timepoints were pooled and the final model included only the additive effect of tile surface (bottom, top, and sides) and treatment (control, removal) with plot identity included as a random factor. Post hoc pairwise comparisons were made between tile surfaces and treatments based on estimated marginal means, and p values were significance adjusted using the Tukey method.

The size of coral recruits on tiles, measured as the longest diameter (mm), was compared between treatments and time points using a GLMM using a Gamma distribution and log-link. Post hoc pairwise comparisons were made between treatments within time points based on estimated marginal means, and p values were significance adjusted using the Tukey method.

Algal biomass in control and removal plots was compared at the post-removal survey time points closest to the mass coral spawning events in 2018 (closest survey December 2018) and 2019 (closest survey October 2019). Shapiro–Wilk tests and F tests were used to ensure data met assumptions of normality and equal variance. The 2018 data met these assumptions, and hence differences in biomass were tested via a two-sample t test. The 2019 data had unequal variance between treatments, thus differences in biomass were tested via a Welch's t test.

To investigate the relationship between algal biomass and recruitment, a GLMM was used to compare the number of recruits observed at each census (i.e., February, March 2019, February, and April 2020) to the biomass present at the relevant mass spawning event (December 2018 and October 2019 surveys, respectively). Model selection through AIC indicated that the best model included only biomass as a fixed factor, plot as a random factor, and did not include treatment nor census date. The number of recruits was modeled according to a negative binomial distribution with a log-link.

Results

Site Characteristics and Removal of Biomass

Prior to removing algae, 13 genera of corals and 9 genera of macroalgae were recorded in photo-quadrats across all plots and time points, in addition to crustose coralline algae, sponges, and turf algae (Table S3). There were no significant differences in the starting benthic composition between the six original control and removal plots (PERMANOVA, $F = 0.12$, degrees of freedom [df] = 1, $p > 0.05$), with macroalgae representing $89.1\% (\pm 6.45 \text{ standard error [SE]})$ and $86.8\% (\pm 4.2 \text{ SE})$ of mean benthic cover in control and removal plots, respectively (Fig. 2). Sand, rock, and rubble represented the second most abundant benthic category, representing $8.2 \pm 3.0\%$ of mean cover in control plots and $10.2 \pm 3.4\%$ of mean benthic cover in removal plots. Hard corals were detected in low abundance in both control ($1.2 \pm 0.7\%$) and removal plots ($2.5 \pm 0.8\%$; Fig. 2). The six additional plots that were

added in 2019 also showed no significant differences in starting benthic composition between control and removal plots (PERMANOVA, $F = 0.54$, $df = 1$, $p > 0.05$). Macroalgae were less abundant in July 2019 compared to the plots established in October 2018 due to seasonal senescence, though were still the benthic group with highest cover, representing 49.3% (± 4.2 SE) and 39.5% (± 3.7) of mean benthic cover in control and removal plots, respectively. Sand, rock, and rubble remained the second most abundant benthic category, covering 31.6% (± 5.4) and 41.3% (± 4.6) of the benthos in control and removal plots. Scleractinian corals occupied 10.0% (± 1.8) of mean cover of control plots, and 13.5% of removal plots. Initial removal of macroalgae from the experimental plots resulted in 88.5 kg (± 6.19) wet weight of algae per plot in October 2018 ($n = 3$ plots). Repeat removal yielded 39.8 kg (± 7.8) per plot and 15.4 kg (± 2.4) per plot in July and October 2019, respectively ($n = 6$ plots).

In 2018, manual removal achieved a 90% decrease in macroalgae, dropping to 8.8% ($\pm 2.2\%$) mean cover in removal plots (Fig. 2). Immediately after the removal of the macroalgal canopy, other benthic groups rose in apparent percent cover: sand, rock, and rubble increased 6-fold ($61 \pm 4.9\%$ cover), turf increased 46-fold (to $18.4 \pm 3.2\%$ cover) and hard coral quadrupled in cover, rising to 10.6% ($\pm 1.1\%$) benthic cover in removal plots (Fig. 2).

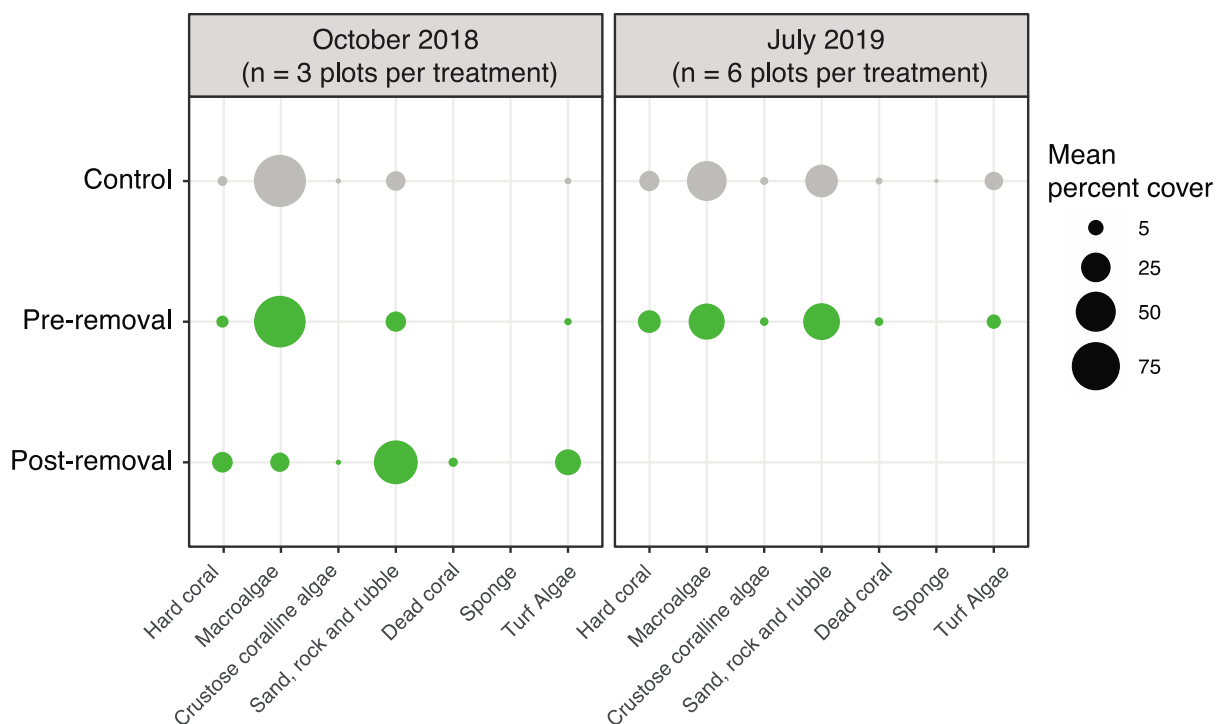


Figure 2. Baseline benthic community composition, where point size represents mean percent cover. Data are missing for post-removal benthic cover for July 2019.

Coral Recruitment Patterns on Settlement Tiles and to the Reef Benthos

A combined total of 3,772 recruits were counted across all settlement tiles and time points in Florence Bay. Recruitment of juvenile corals on tiles was significantly higher in removal plots compared to control plots in all measured time points (Fig. 3A). The pattern was

strongest on tiles from February 2019, when removal plots had over 3 times as many recruits per tile (45.9 ± 12.7 recruits, mean \pm SE) compared to control plots (13.6 ± 2.8 ; $t = 10.7$, $df = 127$, $p < 0.001$; Fig. 3A). In March 2019, removal plots had significantly more recruits than control plots (24 ± 7 and 22 ± 15.6 , respectively; $t = 3.1$, $df = 127$, $p = 0.048$), but the mean number of recruits dropped by 52% in removal plots since the previous census. In February 2020, again the mean number of recruits was threefold higher in removal plots compared to control plots (53.9 ± 5.9 and 17.5 ± 3.5 , respectively; $t = 9.1$, $df = 127$, $p < 0.001$). There was a significant decrease (56%) in the number of recruits between February 2020 to April 2020 in removal plots, but the number of recruits was still significantly higher in removal (30.6 ± 4.8) compared to control plots (18 ± 7.2 ; $t = 6.5$, $df = 127$, $p < 0.001$; Fig. 3A).

Recruitment to all tile surfaces (bottom, sides, and tops) was, on average, 2.9 times higher in removal plots compared to control plots ($z = 5.8$, $p < 0.001$; Fig. 3B). Within treatments, there were no significant differences between recruitment to the top and bottom of settlement tiles in either control (top: 0.05 ± 0.01 recruits cm^2 , mean \pm SE; bottom: 0.06 ± 0.02 ; $t = 0.98$, $df = 382$, $p = 0.93$) or removal plots (top: 0.11 ± 0.02 ; bottom: 0.13 ± 0.02 ; $t = 0.98$, $df = 382$, $p = 0.93$; Fig. 3B). However, there was a significant increase in recruitment to the sides of tiles across both treatments ($z = 13.9$, $p < 0.001$). Furthermore, recruitment to the sides of settlement tiles was significantly higher in removal compared to control plots (1.15 ± 0.16 and 0.41 ± 0.09 recruits, respectively; $t = 5.8$, $df = 382$, $p < 0.001$; Fig. 3B).

The size of coral recruits was similar between treatments and time points, with a mean diameter of approximately 1 mm across all groups. A significant difference between the diameter of recruits in control plots (1.27 ± 0.08 mm) versus removal plots (0.82 ± 0.03 mm) was only observed in the March 2019 census ($t = 6.60$, $df = 3,777$, $p < 0.001$; Fig. S1). This difference was likely driven by few large individuals skewing the mean size of recruits in control plots, and a left-skewed size distribution of recruits in removal plots. There were no strong patterns in recruit sizes for each tile surface (Fig. S2).

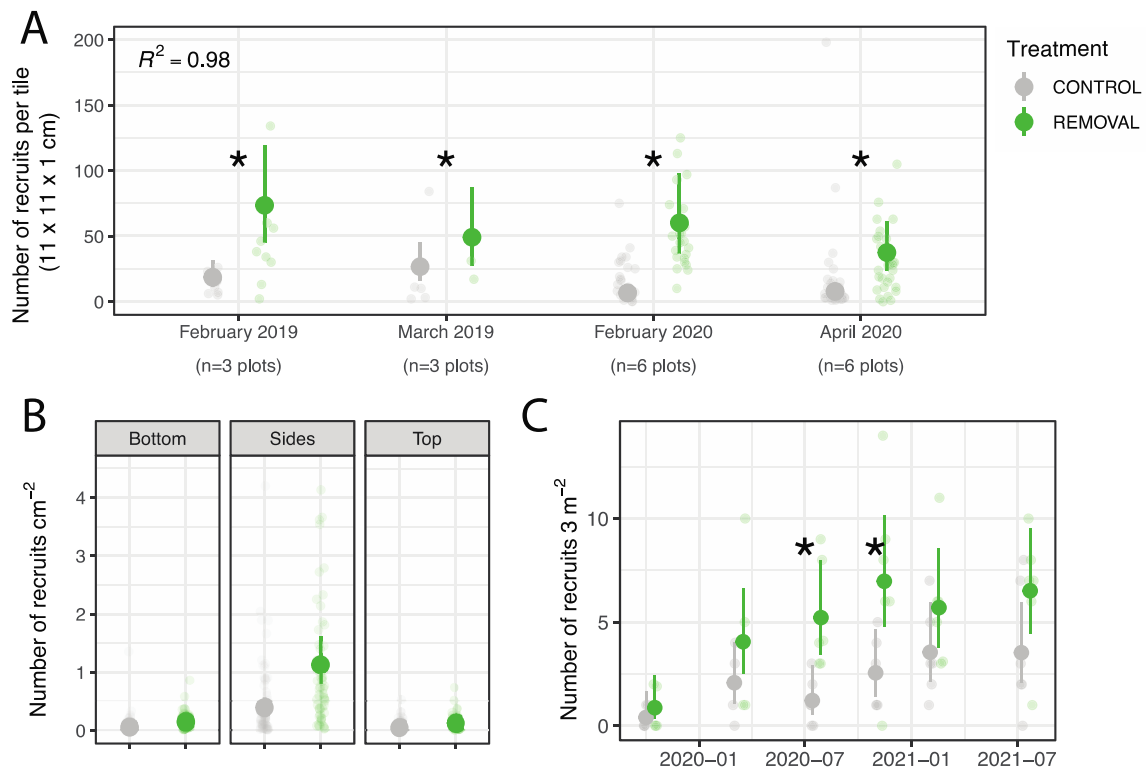


Figure 3. (A) Recruitment of corals to settlement tiles in experimental plots (i.e. sum of recruits per tile). Asterisks represent a significant difference in recruitment between treatments within time points. (B) Recruitment of corals to different tile surfaces in the two treatments (i.e. number of recruits per cm^2). (C) Recruitment of corals to natural substrata in experimental plots (i.e. number of recruits per 3 m^2). In all panels, transparent points are the raw data while opaque points are predictions based on the generalized linear mixed effects models. Bars represent 95% CI.

A combined total of 256 branching recruits were counted on the natural substrata within all experimental plots across the 5 survey time points between October 2019 and July 2021 in Florence Bay. Removal plots consistently had a higher number of recruits than control plots across all survey time points, whereas this difference was statistically significant at only two time points (July and November 2020). In July 2020, there were fivefold more recruits identified on substrata in removal plots compared to controls (5.2 ± 1.1 and 1.2 ± 0.5 recruits, respectively, mean \pm SE; $t = 3.03$, $p = 0.004$; Fig. 3C). Similarly, in November 2020, there were threefold more recruits in removal compared to control plots (7.2 ± 1.9 and 2.5 ± 0.7 recruits, respectively; $t = 2.82$, $p = 0.007$; Fig. 3C). Both control and removal plots demonstrated an increasing trend in the number of recruits through time (Fig. 3C).

Recruitment Correlates with Macroalgae Biomass at Previous Spawning

Algal biomass varied through time, and roughly followed the expected seasonal growth patterns (Vuki & Price 1994), noting that surveys were not conducted during the peak canopy period in the second year of the study (i.e. November 2019 to February 2020; Fig. S3). Immediately after each removal event, a considerable reduction in algal biomass was achieved relative to pre-removal biomass and control plot biomass (Fig. S3). Algal biomass

at the time of each annual coral spawning was significantly lower in removal compared to control plots in both 2018 (control: $1,030 \pm 25.8 \text{ g/m}^2$; removal: 257 ± 26.1 ; $t = 21.1$, $df = 4$, $p < 0.001$) and 2019 (control: $464 \pm 21.8 \text{ g/m}^2$; removal: 79 ± 6.1 ; $t = 17.0$, $df = 5.8$, $p < 0.001$; Fig. 4A). Increasing algal biomass at coral spawning had a clear and significant negative effect on coral recruitment to tiles ($z = 4.57$, $p < 0.001$; Fig. 4B).

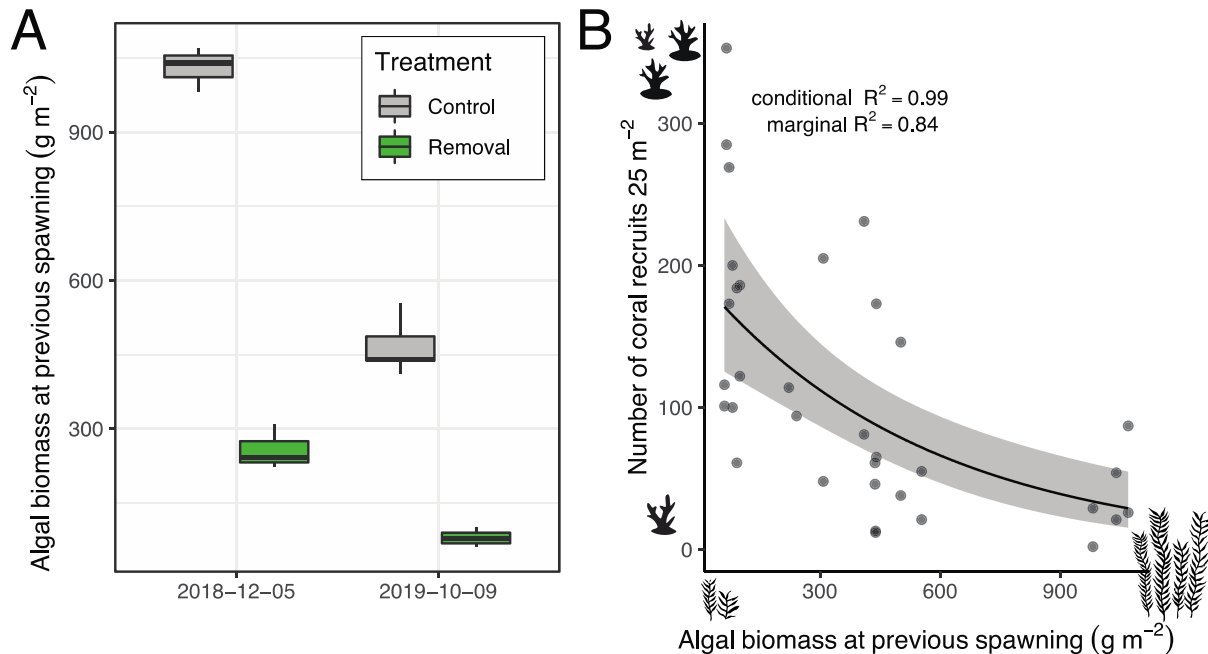


Figure 4. (A) Algal biomass was significantly higher in control plots compared to removal plots during both mass spawning events. (B) Algal biomass at spawning had a significant negative effect on coral recruitment patterns on tiles. Points represent raw data; the line represents predictions based on the generalized linear mixed model; ribbon is the 95% CI.

Discussion

Competitive interactions between coral and algae at early coral life stages can have critical flow-on effects on reef community structure, particularly following acute or chronic disturbance. By removing algae, the negative effects on coral survival can be diminished, and in this study, the effect of reduced benthic algae on recruitment was clear. A reduction in algal biomass (75 and 83% for each year) prior to the mass coral spawning event resulted in a threefold higher number of newly settled corals in manipulated plots in the February census across both years, suggesting that a major inhibitor to successful coral settlement had been removed. In the second census (approximately 4–5 months after spawning), the number of recruits dropped by approximately 50% in both years, a pattern consistent with the type III mortality curve characteristic of coral recruits (Hughes et al. 1992; Penin et al. 2010) but the treatment effect remained, with more recruits being observed on tiles in removal plots. Recruitment to natural substrata was also higher in macroalgae removal plots compared to controls across all surveys. These results provide strong support that removal of macroalgae could be a viable management strategy to enhance coral settlement to degraded reefs.

The number of recruits recorded on tiles deployed in Florence Bay was comparable to previous studies, with the settlement patterns observed in removal plots aligning with settlement levels for “healthy” reefs. For example, a recent study of coral recruitment on GBR reefs before and after the back-to-back bleaching events of 2016 and 2017 found that prior to bleaching (i.e. from 1996 to 2016), an average of 43 recruits per tile were observed at healthy reefs (Hughes et al. 2019). The tiles from removal plots in this study averaged 38 recruits per tile, suggesting that the reefs at Magnetic Island are connected to healthy larval source(s). Conversely, the number of recruits observed on tiles in control plots (average 17 recruits per tile across time points) aligned more closely with previous studies on reefs that had experienced significant disturbance, albeit with varying mechanisms of disturbance (e.g. 5 recruits per tile after 2016/2017 bleaching [Hughes et al. 2019], 15 recruits per tile after Cyclone Yasi [Lukoschek et al. 2013]). The difference between recruitment rates on tiles in control and removal plots suggests that larval supply may not be the key limiting factor to reef recovery at Magnetic Island. Instead, increased recruitment to removal plots indicates that competition for and availability of suitable substrate are driving forces in inshore coral recruitment dynamics. Algal biomass (holdfasts and canopy) appears to inhibit coral larvae, reducing successful settlement from the larval supply. Removal of macroalgae could alleviate one biological barrier to coral settlement, though high macroalgal abundance may still affect longer-term survival through physical abrasion (Manikandan et al. 2021), shading (Hauri et al. 2010), allelopathy (Rasher et al. 2011), or microbialization (Haas et al. 2016). Hence, management should continue to target factors enhancing macroalgal abundance, such as poor water quality.

The higher density of coral recruits on the sides of settlement tiles has been recorded in some previous studies (Babcock & Mundy 1996; Cameron & Harrison 2016) and suggests that, in addition to space availability, sediment deposition and light quality represent important drivers of mortality throughout the early ontogeny of corals (Ricardo et al. 2017). Indeed, Magnetic Island reefs are known to be subjected to high levels of turbidity and sedimentation due to their proximity to areas of coastal development and river outflow (Whinney et al. 2017). Although recruits may be more protected from herbivory on the bottoms of tiles, light penetration is low and could be insufficient for photosynthesis, calcification, and growth. Particularly where an algal canopy is dense, light penetration can be reduced by 97% (Critchley et al. 1990; Hauri et al. 2010), potentially further reducing survivability of corals in shaded habitats. In contrast, upward-facing surfaces receive more light for photosynthesis but are vulnerable to smothering by sediment deposition. Although it is not yet known how algal canopies affect sediment processes, sediments are known to play a key role in survival of juvenile corals (reviewed in Tuttle et al. 2020). For example, results of an experimental field study linked increased sedimentation with a 30% lower larval settlement rate and 60% lower recruit survival after 8 months (Babcock & Smith 2000). Overall, the higher recruitment to tile sides indicates a dynamic relationship of larval settlement interacting with substrate availability, light penetration, and sediment dynamics, and suggests that habitat complexity is likely important for recovery of Magnetic Island reefs. This information may be useful to inform the design of artificial reefs or coastal infrastructure to encourage coral recruitment and growth.

Juvenile corals observed on the natural reef substrata (not on settlement tiles) showed a positive trend through time in both control and removal plots, further supporting the

hypothesis that Magnetic Island is receiving larval supply, and that the Florence Bay reef is benefitting from a period of natural recovery (AIMS 2021). Although the difference was not statistically significant, recruits were consistently more abundant in removal plots compared to control plots. Importantly, however, the abundance of juveniles on natural substrata was a small fraction of the abundance observed on tiles. Although the artificial nature of settlement tiles may influence settlement patterns when compared to natural reef surfaces, the decline in numbers also reflects the type III mortality curve for corals (Penin et al. 2010; Doropoulos et al. 2016). The tile censuses took place approximately 4 months after spawning, with the in situ surveys commencing a full year after the 2018 spawning event. High levels of post-settlement mortality are experienced by coral juveniles across a range of environmental conditions and especially in high-sediment reefs (Gilmour 1999; Babcock & Smith 2000), so a significant decrease across the 8 months between the tile censuses and in situ surveys is expected. Longer-term monitoring is needed to determine if increased recruitment to removal plots is sustained, or if post-settlement mortality processes reduce or negate the positive effect seen during settlement phases (Edwards et al. 2015). Nevertheless, combined interventions to overcome post-settlement mortality bottlenecks, as well as improve long-term survival and health of corals could further boost the positive effects of macroalgae removal.

Increased early coral settlement is critical for reef recovery and persistence (Mumby 2009). However, while removal of algae appears to benefit coral settlement, removal could positively or negatively impact corals in other ways and in different life stages. For example, a macroalgal canopy could provide shading and protection from harmful solar irradiation, with removal potentially leading to increased ultraviolet penetration and bleaching susceptibility (Jompa & McCook 1998). Indeed, wide-scale coral bleaching was observed in Florence Bay in March 2020 (GBRMPA 2020) and may have driven increased mortality of recruits in removal plots. Further research is required to disentangle the effect of algal canopies on bleaching susceptibility and mortality of juvenile and adult corals. Alternately, competition with algae may decrease the fitness of corals, with one recent study finding macroalgae as a major predictor of post-bleaching mortality (Donovan et al. 2021). Nevertheless, long-term monitoring of a variety of reef health metrics is essential to determine how algal removal may alter key biological and ecological processes across reef organisms.

Changes in percent cover of dominant benthic organisms were not expected over the time span of this study, although the effects of macroalgae skewing estimates of benthic cover are interesting. Prior to macroalgae removal, photo-quadrats demonstrated 86–89% cover of macroalgae in the experimental plots. However, once the macroalgae canopy was removed, other benthic groups beneath the macroalgae increased in apparent cover, which is an artifact of the planar view employed by photographic techniques. Canopy effects have been discussed previously in the context of coral reefs, although most have centered on coral-dominated systems, highlighting how plating corals can obscure a more diverse benthos below (Goatley & Bellwood 2011). Limited discussion has focused on the potential for soft-bodied canopy-forming organisms (e.g. fleshy macroalgae) to affect survey outcomes. Although three-dimensional survey techniques are rapidly being adopted (e.g. photogrammetry) (Kornder et al. 2021), the suitability of these methods for algal-dominated reefs remains in question.

Removing macroalgae is labor-intensive though requires minimal technical training. In this study, citizen scientist volunteers from Earthwatch Institute assisted in the process of algae removal using snorkel and SCUBA, providing proof of concept that the method is transferable to the general public. Previous studies have shown that excision of the holdfast is needed to fully retard algal growth (Loffler & Hoey 2018). The manual removal process in this study did not achieve full elimination of holdfasts; however, positive benefits of reduced macroalgal biomass on coral settlement were still observed, and hence complete removal of the algal thallus may not be required to achieve benefits. Although the plots in this study were small scale, the results are encouraging and provide the scientific underpinning for larger-scale trials in the future on the GBR and at algal-dominated reefs in other regions. At larger scales, it is possible that other complementary interventions could be used to more extensively reduce benthic algae, for example, by adding grazers into the system (e.g. herbivorous crabs, urchins, fish). Manual and biological manipulations have been implemented to positive effect on Hawaiian reefs where invasive macroalgae were removed by divers, followed by an addition of herbivorous urchins (*Tripneustes gratilla*) to further control biomass (Neilson et al. 2018). However, on the GBR, the current regulatory environment may be restrictive for introducing biological manipulations (Fidelman et al. 2019), herbivore populations have complex links with the biocontrol of algae (Cheal et al. 2010), and *Sargassum* is not an invasive alga. There are also opportunities to increase removal efficiency through technology. For example, underwater pumps to remove algae have been trialed in Hawaii and in Australia (Neilson et al. 2018; McLeod et al. 2020). Combined with the potential for citizen science involvement, mass removal of algae remains a possibility, but robust science, technological innovations, and feasibility trials are needed to guide the type and timing of such interventions.

In summary, this study demonstrates that manual removal of macroalgae has positive effects on a degraded reef, with coral recruitment increased in areas where macroalgal biomass is reduced. These results have important implications for informing intervention approaches that may bolster reef resilience and rehabilitation. With many reefs around the world experiencing increased macroalgal abundance, this method is one that could be upscaled as part of conservation and restoration programs through harnessing the general populace. Longer-term monitoring is needed to determine if settlement patterns manifest as higher coral cover on the reef, and to examine if survival and other metrics of coral fitness (e.g. growth, fecundity) are affected. Although reversing anthropogenic damage across scales (i.e. global climate change and local impacts such as water quality) is the true solution to the reef crisis, the macroalgae removal approach has promising impacts for improving reef health.

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