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RESEARCH ARTICLE

Sea-weeding: Manual removal of macroalgae facilitates rapid coral recovery

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Abstract

1. Coral reef ecosystems globally are under threat, leading to declining coral cover and macroalgal proliferation. Manually removing macroalgae (i.e. 'sea-weeding') may promote local-scale coral recovery by reducing a biological barrier, though the impact of removal on community composition of benthic reef organisms has not been quantified.
2. In this three-year study (2018–2021), fleshy macroalgae (predominantly *Sargassum* spp.) were periodically removed from 25 m^2 experimental plots on two inshore fringing reefs of Yunbenun (Magnetic Island) in the central Great Barrier Reef.
3. By the end of the study, coral cover in removal plots ($n = 12$ plots) assessed through in-field transects increased by at least 47% (2019 mean: 25.5%, 2021 mean: 37.4%), and macroalgal cover decreased by more than half. In contrast, in control plots ($n = 12$ plots), there was no change in macroalgal cover while coral cover remained stable (2019 mean: 16.4%, 2021 mean: 13.6%).
4. Changes in benthic cover were supported by photoquadrat data, with Bayesian probability modelling indicating a 100% likelihood that coral cover more than doubled in removal plots over the study period, compared to only a 29% chance of increased coral cover in control plots.
5. *Synthesis and applications*. Manual macroalgal removal can provide rapid benefits and enhance inshore coral reef recovery. Through involvement of community groups and citizen scientists, larger scale removal of macroalgae is a low-tech, high-impact, and achievable method for local reef management.

KEYWORDS
benthic community composition, citizen science, coral reefs, Great Barrier Reef, inshore reef, macroalgae, phase shift, reef restoration

Hillary A. Smith and Stella E. Fulton have contributed equally to this work and should be considered joint first authors.

1 | INTRODUCTION

Recent global reef assessments report persistent declines in scleractinian coral cover and simultaneous increases in macroalgal cover (Souter et al., 2021). On healthy reefs and at relatively low abundance, macroalgae fulfil important roles such as primary production (Schaffelke & Klumpp, 1997), food and habitat provision (Fulton et al., 2019), and reef framework consolidation (Diaz-Pulido & McCook, 2008). However, macroalgae compete directly with corals for space and light (reviewed in Birrell et al., 2008; Ceccarelli et al., 2018), and the proliferation of macroalgae can often be detrimental to corals through shading (Hauri et al., 2010), reducing coral fecundity (Monteil et al., 2020), decreasing available space for coral larval settlement and recruitment (Birrell et al., 2008), increasing juvenile coral mortality (Box & Mumby, 2007), direct allelopathic interactions (Bonaldo & Hay, 2014), and affecting surrounding water chemistry (Haas et al., 2016).

The causes of macroalgal proliferation are complex. Contributing factors can include increased nutrient loads (De'ath & Fabricius, 2010; Fabricius, 2005), reduced grazing intensity (Smith et al., 2010) and reduced competitive pressure from corals following coral mortality events (Cheal et al., 2010). These factors are increasingly present on reefs globally, particularly inshore coral reefs. In addition, feedback mechanisms can perpetuate high levels of macroalgae, preventing coral recovery and leading to a loss of reef resilience (Birrell et al., 2008; Fulton et al., 2019; Johns et al., 2018). As a result of these synergistic factors, many reefs worldwide have undergone shifts from coral to macroalgal dominance (Bruno et al., 2009; Ceccarelli et al., 2020; Hughes, 1994).

Inshore regions of Australia's Great Barrier Reef (GBR) are generally exposed to the factors that favour macroalgal growth (Fabricius et al., 2023), especially in comparison with mid- and outer-shelf reef regions. For example, inshore reefs experience elevated nutrient and sediment inputs resulting from erosion following land clearing, riverine run-off linked to agricultural development, port-associated dredging and other coastal development activities (De'ath & Fabricius, 2010; Williamson et al., 2019). Despite inshore reefs on the GBR exhibiting naturally higher levels of macroalgae relative to their offshore counterparts (Fabricius et al., 2023), over recent decades some inshore reefs have experienced substantial increases of macroalgal abundance, with concurrent declines in hard coral cover (Ceccarelli et al., 2020; De'ath et al., 2012; De'ath & Fabricius, 2010; Thompson et al., 2023). As the climate warms and anthropogenic pressures increase, macroalgae are expected to become more pervasive, thus threatening the resilience of coral reefs, particularly inshore reefs (Graham et al., 2015).

In response to the loss of live corals worldwide, there is an increased focus on evaluating approaches to restore damaged reef systems, and to prevent further coral loss (Anthony et al., 2020). Manual removal of macroalgae has been proposed as one such intervention to boost coral recovery by alleviating or eliminating the competitive pressure from dense macroalgal stands (Ceccarelli et al., 2018; Neilson et al., 2018). Indeed, adverse effects of macroalgae on coral growth are often density-dependent (Clements et al., 2018; van Woesik et al., 2018). Hence, manually reducing the density of macroalgae on degraded reefs may be an effective, low-cost strategy to reduce a biotic barrier to coral growth and recovery (Ceccarelli et al., 2018).

Experimental trials of macroalgal removal from various locations have shown positive impacts on coral reef habitats at small scales. For example, removal of native macroalgae species has led to increased growth and fecundity of *Acropora* spp. (Tanner, 1995), increased coral juvenile settlement and recruitment (Bulleri et al., 2018; Smith, Brown, et al., 2022), and increased herbivorous fish abundance (McClanahan et al., 1999, 2002). In Hawai'i, removal of invasive macroalgal species supplemented with urchin biocontrol was effective in shifting the reef community towards assemblages more conducive to coral recovery (Conklin & Smith, 2005; Hancock et al., 2017; Neilson et al., 2018). In contrast, experimental macroalgal reduction in Belize resulted in rapid algal regrowth and negligible coral recovery despite increased herbivore populations (McClanahan et al., 2001). The effectiveness of macroalgal removal is therefore likely dependent on complex interacting factors including how and when the removal effort is implemented. To date, most research on macroalgae removal has been limited in duration (ranging from 3 months to 2 years), scale (ranging from 0.5 m^2 to 11 ha), included only a single removal event, or targeted invasive rather than native macroalgal species (reviewed in Ceccarelli et al. (2018); summarised in Table S1).

Rigorous investigation is needed to determine the effects of macroalgal removal on degraded reefs, and to assess the applicability of this approach to increase reef resilience at local scales (Ceccarelli et al., 2018). Recent field experiments suggest macroalgal removal can have a positive impact on coral larval settlement and recruitment (Smith, Brown, et al., 2022), as well as benefits to post-bleaching coral recovery (Smith, Prenzlau, et al., 2022). However, the longer term effects on reef benthic composition are yet to be assessed. To fill this knowledge gap, we conducted a field experiment on two macroalgal dominated fringing coral reefs of Yunbenun (Magnetic Island), in the central GBR. Macroalgae were removed from experimental plots and the resulting changes in benthic composition over 3 years were documented and compared with control plots.

2 | MATERIALS AND METHODS

2.1 | Study site and macroalgal removal experimental design

Accurate historic baselines of benthic composition of reefs surrounding Yunbenun are difficult to establish due to a lack of quantitative data prior to the 1980s. Currently, Yunbenun reefs are characterised as in ‘poor’ to ‘very poor’ health due to abundant macroalgae (Thompson et al., 2023), and repeat monitoring over the past two decades has identified a decrease in coral cover coinciding with increases in macroalgae cover (Ceccarelli et al., 2020; Thompson et al., 2023). Hence, despite a limited understanding of the long-term historical benthic baseline, the study sites at Yunbenun are an ideal location to test and implement macroalgal removal in the context of reef rehabilitation.

Twenty-four 25 m^2 (5 m × 5 m) experimental plots were established on fringing coral reefs of Arthur Bay (19.1291° S, 146.8776° E) and Florence Bay (19.1220° S, 146.8805° E) on the eastern coast of Yunbenun (central inshore region of the GBR; n = 12 plots per bay, Figure 1). Plots were established haphazardly at approximately 3 m depth after conducting visual surveys to ensure topographical consistency and representation of the wider reef ecosystem. Within each bay, six plots were randomly assigned as controls (referred to herein as 'control plots') while the remaining six treatment plots were periodically cleared of fleshy macroalgae (referred to herein as 'removal plots') (Figure 1). Macroalgae, predominantly *Sargassum* spp., were removed by hand from removal plots in October 2018, July and October 2019, July and October 2020, and April, July and October 2021. SCUBA divers removed macroalgae from the benthos by hand, assisted by snorkelers at the surface, and targeted holdfasts where possible, though no tools were used nor postremoval scrubbing undertaken to minimise time for removal. Minimising efforts to remove the holdfast ensures greater transferability to wider scale uptake, since removal will need to be implemented rapidly and with limited training. The removed macroalgae were collected into catch bags and taken to a support vessel by snorkelers, where wet weight of the biomass was recorded before disposal on land in a local school's organic compost. The July removal events were timed to coincide with the lowest *Sargassum* holdfast attachment strength during senescence (Xu et al., 2016), and October events were timed prior to mass coral spawning each year. All fieldwork was completed under permit G19/41693.1 granted by the Great Barrier Reef Marine Park Authority. Ethical approvals were not required.

2.2 | Collection of benthic community composition data

Changes in benthic community composition were documented using photographic surveys before (pre-removal surveys) and between 1

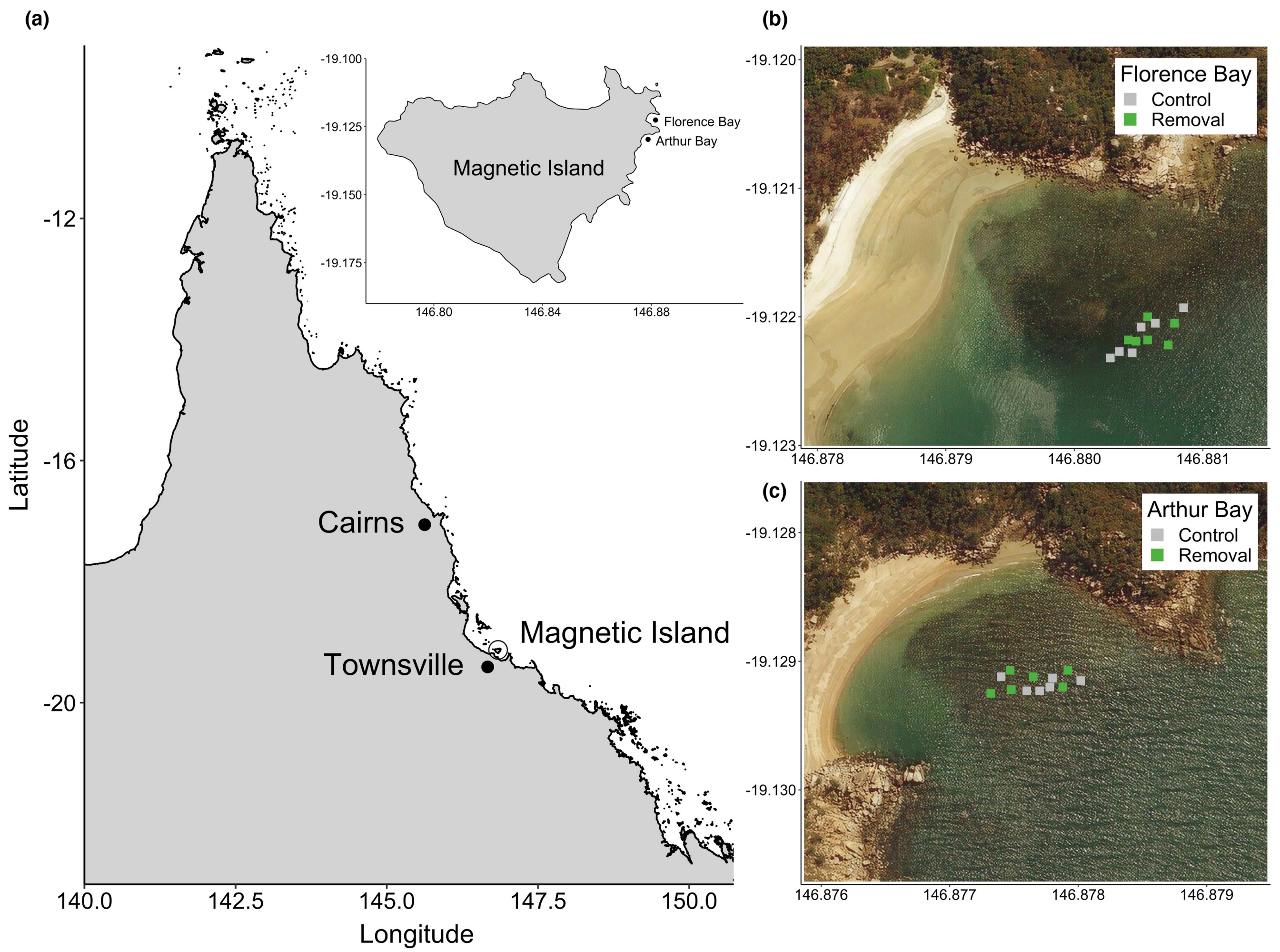

FIGURE 1 Location of study sites in (a) Queensland, Australia; and maps of (b) Florence Bay and (c) Arthur Bay showing experimental plot arrangement. In each bay, six 25 m^2 control plots (grey squares), and six 25 m^2 removal plots (green squares) were periodically cleared of macroalgae. Note plot icons are not to scale.

and 7 days after (post-removal surveys) each removal event. Surveys were also undertaken during summer when *Sargassum* spp. are at their peak abundance (Vuki & Price, 1994). A grid was laid out across each plot using transect tapes, and digital photographs were captured of each 1 m^2 square, totalling 25 photos per plot per timepoint. Photographs were edited using Lightroom (v5.1; Adobe Systems) to enhance image quality prior to analysis. Point count software, CPCe v4.1 (Kohler & Gill, 2006), was then used to generate per cent cover data from the photographs by overlaying 30 points randomly on each image and identifying the underlying benthic organism to genus level where possible. Abiotic substrata were identified as recently dead coral, rubble or sand. Per cent cover for each plot and time point was averaged across all 25 photos for statistical analysis. October 2019 surveys were excluded from the analysis due to poor image quality.

To supplement the photographic surveys and to combat canopy-effects, in situ surveys were conducted using a stratified transect method (detailed in Smith, Boström-Einarsson, et al., 2022), beginning in October 2019. Briefly, a transect tape was laid across the two diagonals of each 5 m × 5 m plot, for a total of a ~14 m transect per plot. At every 50 cm, a SCUBA diver recorded the organism at two levels, the first being if there was an obstructing, canopy-forming organism (e.g. canopy-forming macroalgae or plating coral) and the second being the benthic category occupying the benthos below. Where there was no obstructing canopy layer, only a benthic data point was recorded. Per cent cover data for each genus and broad category (i.e. hard coral, macroalgae, rock/rubble/sand and other invertebrate) were calculated based on the total number of data points (i.e. canopy plus benthic layers, up to 56 possible data points per plot).

2.3 | Statistical analysis

All analyses were conducted in the statistical and graphical software R (R Core Team, 2021). Per cent cover of all macroalgal genera (including crustose coralline algae and algal turfs) and per cent cover of all hard coral genera derived from photoquadrats and in situ surveys were modelled separately as a function of treatment (macroalgal removal) and survey timepoint using Bayesian generalised linear mixed effects models (BGLMMs) using the brms package (Bürkner, 2017). In all four models (i.e. macroalgal and hard coral models, photoquadrat and transect data), treatment and time point were fitted as interacting population effects and plot number was treated as a varying effect to account for the lack of spatial independence. All models used a Beta distribution with a logit link, and weakly informative priors (see Table S2 for prior details and chain specifications). A total of 20,000 Markov-chain Monte Carlo sampling iterations were performed across three chains, with a warmup of 10,000 and thinned to every fifth observation. For all models, diagnostics (trace plots, autocorrelation plots, r-hat plots, posterior predictive checks, effective sample sizes and residual plots) suggested model assumptions were met, chains were well mixed, and converged on a stable posterior (all r-hat values <1.05; Figure S1). Model validation did not reveal any patterns in the residuals.

Multivariate analyses were performed using the vegan package (Oksanen et al., 2020). Patterns in composition of macroalgal and coral communities across treatments and five timepoints (April surveys were omitted) were visualised using ordination plots generated using a nonmetric multidimensional scaling (NMDS) based on a Bray–Curtis matrix of Hellinger transformed per cent cover data (pre-removal photoquadrat data), separately for macroalgal and coral communities. Because transect data and photoquadrat data were strongly correlated (see Section 3), and since transect data collection commenced a year into the study, we chose to perform multivariate analyses on the photoquadrat data to capture the entire plot area and the entire time series. However, to combat potential issues with canopy effects in photoquadrat data, we removed taxa observed in less than 10% of surveys ($n = 35$ taxa) as these may be genera that were more likely concealed by the canopy. In removing these, we aimed to analyse more broad community patterns, hence avoiding detecting changes in diversity and community composition resulting from sampling artefacts. Following assessments of homogeneity of dispersion, statistical differences in both the macroalgal and coral community composition were assessed between the interacting factors of treatment (control vs. removal) and time point, using a permutational multivariate analysis of variance with 999 permutations and blocked by plot.

To further supplement the NMDS ordination plots, Shannon's diversity index, richness and evenness were calculated for both macroalgal and coral communities (photoquadrat data, with rare taxa excluded). The effect of treatment and time point on each of the diversity metrics was determined using generalised linear mixed effects models (GLMMs). For Shannon's diversity, a Gamma distribution with a log link, for richness a Poisson distribution with a log link, and for evenness a Beta distribution with a logit link were used. Treatment and time point were incorporated into all models as interacting fixed effects with bay (Florence and Arthur Bays) fitted as an additive fixed effect and plot number fitted as a random factor. Model selection was informed using second-order Akaike information criterion (AICc), and the most parsimonious model was selected for each of the diversity metrics (see Table S3 for model details). Model fits and assumptions were assessed via simulated residual plots, which were satisfactory in all cases. All models were fit using the glmmTMB package (Brooks et al., 2017). Significant differences among levels in the fixed factors (estimated marginal means) were distinguished via post hoc tests using the Tukey *p*-value adjustment method.

2.4 | Costing

The operational cost of implementing macroalgae removal was calculated following Iacona et al. (2018) including all materials, vessel and vehicle hire, fuel, dive equipment and SCUBA tank air fills, ferry costs and marina berths. The average cost for implementation per m^2 was estimated by dividing the total cost of the project by the total combined area of the removal plots (i.e. 300 m^2), acknowledging that field costs included monitoring of control plots, and costs varied based on the number of volunteer Earthwatch participants (i.e. additional cars were required for trips with higher number of participants). Staff salary costs were not included in the operational costings given the large contribution of students and volunteers to the macroalgae removal events and the high variation in staff salaries likely required for removal events in different coral reef regions. All costs were calculated in local currency (AUD), converted to U.S. dollars using the most recent (2019) exchange rate from the Penn World Table version 10.01 (Feenstra et al., 2015), then adjusted for inflation based on consumer price index to a base year of 2010 prices using the World Bank Development Indicators (The World Bank, 2023a), following Bayraktarov et al. (2019).

3 | RESULTS

3.1 | Macroalgal removal events and site characteristics

Benthic communities across all time points consisted predominantly of canopy-forming macroalgae (*Sargassum spp.*) and corals from the genera *Montipora* and *Acropora* (see Table S4 for full list of genera and categories identified). Over the eight removal events from October 2018 through October 2021, a total of 2148 kg of macroalgae were removed, with an average of 23.1 ± 1.85 (mean ± SE) kg of wet biomass removed per 25 m^2 plot per removal event (Figure S2). Photoquadrat surveys conducted immediately following each macroalgal removal event showed that the average per cent cover of macroalgae was approximately halved (52.50 ± 3.01% (mean ± SE) reduction, Figure 2a). The removed macroalgae consisted predominantly of *Sargassum* spp., in addition to *Lobophora*, *Dictyota*, *Padina* and *Colpomenia*. Complete removal (100% reduction in per cent cover) of fleshy macroalgae was not feasible due to the difficulty in removing both noncanopy-forming genera (e.g. *Lobophora* spp.) and holdfasts of canopy-forming genera (e.g. *Sargassum* spp.), as well as time limitations in the field. Benthic cover of macroalgal and coral genera through time in control and removal plots are summarised in Figures S3 and S4.

3.2 | Patterns in macroalgal cover

The modelled relationship of photoquadrat-derived macroalgal per cent cover as a function of treatment and survey time point was strong, with population (treatment, timepoint) and varying (plot number) effects accounting for 90% of the variation in macroalgal per cent cover (conditional $r^2 = 0.90$). There was evidence for an interaction between treatment and survey time point, suggesting that the effect of macroalgal removal changed through time (Table S5a). In October 2018 when the study commenced, estimated average

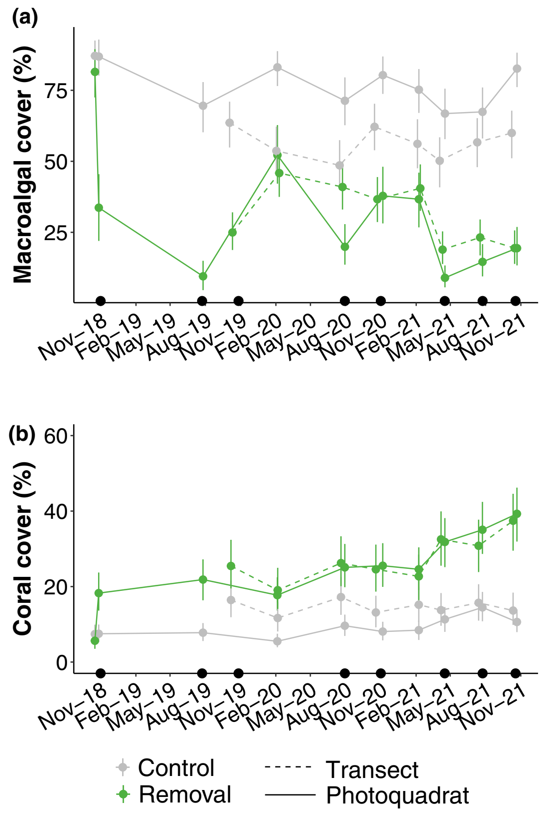

FIGURE 2 Per cent cover of (a) macroalgae and (b) corals within experimental plots in two bays (Arthur Bay, Florence Bay) of Magnetic Island, Australia. Points represent mean predicted fits of Bayesian generalised linear mixed effects models (Beta distribution with logit link) for photoquadrat data (solid line) and stratified transect data (dashed line), with predictions for control plots shown in grey and removal plots shown in green. Vertical lines represent 95% credibility intervals. For simplicity, only post-removal surveys are shown. Black dots along the *x*-axis indicate when macroalgae were cleared from removal plots. Note that macroalgae were removed in October 2019, however photoquadrat surveys from this timepoint were not used in statistical analyses due to low visibility and subsequent poor image quality.

macroalgal cover was similar in both the control and removal plots, with 87.04% mean cover (80.63, 92.74; lower and upper limits of 95% credibility interval) in control plots, and 81.35% mean cover (72.90, 88.86) in removal plots (Figure 2a). At the end of the study in October 2021, average macroalgal cover had decreased in removal plots to 37.84% (28.58, 47.79) pre-removal and 19.34% (12.85, 25.98) postremoval; in contrast to control plots with 83.39% (77.56, 89.05) macroalgal cover.

Calculated Bayesian probabilities demonstrate the effect of macroalgal removal through time. Macroalgal cover from photoquadrats in October 2021 (pre-removal) was less than half of October 2018 levels (pre-removal) in removal plots with 73% certainty, yet 0% certainty for the same change in control plots. In October 2018, the probability of macroalgae being the dominant benthic component (e.g. more than 50% cover, acknowledging that dominance could occur at lower levels) in both control and removal plots was 100%.

By October 2021, that probability remained at 100% for control plots but had dropped to 1% for removal plots.

While transect-derived estimates of mean macroalgae per cent cover were lower on average compared to the photoquadrat data, patterns remained similar. For example, at the end of the study in October 2021, transect-derived macroalgal cover in removal plots was 19.4% (13.8, 25.6; lower and upper limits of 95% credibility interval), and 60.0% (51.1, 67.8) in control plots. Similarly, Bayesian probabilities (Table S6) for transect data support the patterns observed in photoquadrats, with a 98% probability of macroalgae covering more than half the benthos in control plots, compared to a 0% probability in removal plots at the end of the study.

3.3 | Patterns in coral cover

Population and varying effects explained 95% of the variability (conditional $r^2=0.95$) in photoquadrat-derived coral cover modelled as a function of treatment and time point. In October 2018, there was no difference in estimated average coral cover between control (7.47% (5.21, 10.02); mean % (lower and upper limits of 95% credibility interval)) and removal plots (5.65% (3.80, 8.43); Figure 2b). Coral cover increased with greater than 99% certainty from October 2018 (pre-removal) to October 2021 (pre-removal) in both control and removal plots. Coral cover in control plots increased by approximately 40% between October 2018 and October 2021, rising to 10.39% (7.28, 13.22). Coral cover in removal plots increased substantially more, increasing six-fold to reach 35.09% (28.17, 42.11) cover in October 2021 (pre-removal), driven largely by the fast-growing genus *Acropora*. Coral cover in removal plots post-removal (October 2021) was 39.42% (32.01, 46.47), nearly a seven-fold increase since the start of the study. Bayesian probability calculations indicated that there was a 100% likelihood that coral cover more than doubled between October 2018 and October 2021 in removal plots, yet only a 29% likelihood in control plots, demonstrating that coral cover increased more in reef areas that had been cleared of macroalgae (see Table S6 for a full summary of Bayesian probabilities).

In situ data generated by stratified transects produced similar patterns. When in situ surveys began in October 2019 (1 year into the study), there was no difference in estimated average coral cover between control (16.4%; 11.9, 21.6) and removal plots (25.5%; 19.5, 32.4). By the end of the study (October 2021), transect-derived coral cover had increased 1.5-fold, reaching 37.4% (29.5, 44.6) cover in removal plots, compared with 13.6% (9.8, 18.4) coral cover in control plots. Bayesian probabilities further supported this pattern, with a 0% likelihood that coral cover was equivalent within control and removal plots at the end of the study. Similarly, there was a 99% likelihood that coral cover increased in removal plots during this study, but only a 16% likelihood of an increase in control plots.

3.4 | Patterns in the composition of macroalgal and coral communities

Community composition of macroalgal genera varied significantly, driven by the interaction of treatment and time point (photoquadrat data; adonis: $F_{5,119}=2.8$, $r^2=0.04$, $p<0.01$; Table S7a). NMDS ordination plots visualised differences in community composition between control and removal plots through time (Figure 3a,c,e), with control plots dominated by *Sargassum*. Macroalgae communities in removal plots were similar to control plots in 2019, though by 2021, removal plot macroalgae communities had become characterised by taxa such as *Padina*, *Amphiroa*, *Hypnea* and *Colpomenia*.

Diversity metrics of macroalgal assemblages support the NMDS plots, with subtle changes in diversity, richness, and evenness through time (see Table S3a; Figure S5a). Throughout 2018 and 2019, the macroalgal communities across both control and removal plots were dominated by *Sargassum* and had low diversity and evenness (Figure S5a). Richness was consistent for both control and removal plots throughout the study period, with the total number of macroalgal genera unaffected by removal of the macroalgal canopy ($t=-0.37$, df = 119, $p=1.0$; Table S3a). However, by 2021, the macroalgal community in the removal plots was noticeably different to the control plots (Figure 3a,c,e), and this change was supported by the modelled diversity metrics: Shannon's diversity index and evenness both significantly increased in removal plots by the end of the study (Table S3a; Figure S5a).

The composition of non-macroalgal groups (11 scleractinian coral genera, two soft coral groups, one group for sponges) did not vary significantly between control and removal plots through time (photoquadrat data; adonis: $F_{5,119}=0.97$, $r^2=0.04$, $p=0.11$; Table S7b). NMDS plots (Figure 3b,d,e) showed that coral community composition remained stable in control plots across the study period, but removal plots were characterised by slightly higher cover of fast-growing taxa such as *Acropora* by the end of this study. Macroalgal removal had a significant positive effect on the endpoint diversity of coral genera in removal plots (October 2018–October 2021: $t=-5.80$, df = 116, $p<0.01$), driven by greater relative abundances of massive morphology corals (e.g. *Astreopora*, *Alveopora*, *Lobophyllia* and *Favites*; Figure S4), while there was no change in diversity in control plots (October 2018–October 2021: $t=-2.45$, $df=116$, $p=0.57$). Endpoint richness of coral communities also increased in removal plots ($t=-3.78$, df = 119, $p=0.01$), though there was no statistically significant change in evenness ($t=-0.99$, df = 116, $p=1.0$; Table S3b; Figure S5b).

3.5 | Costing

Over the 3 years of this study, 52 days of fieldwork were conducted, which encompassed all macroalgae removal events and monitoring. We spent a total of $20,763 (USD at base year 2010) on equipment and fees (vessel and car hire, fuel, dive gear and tank hire, marina

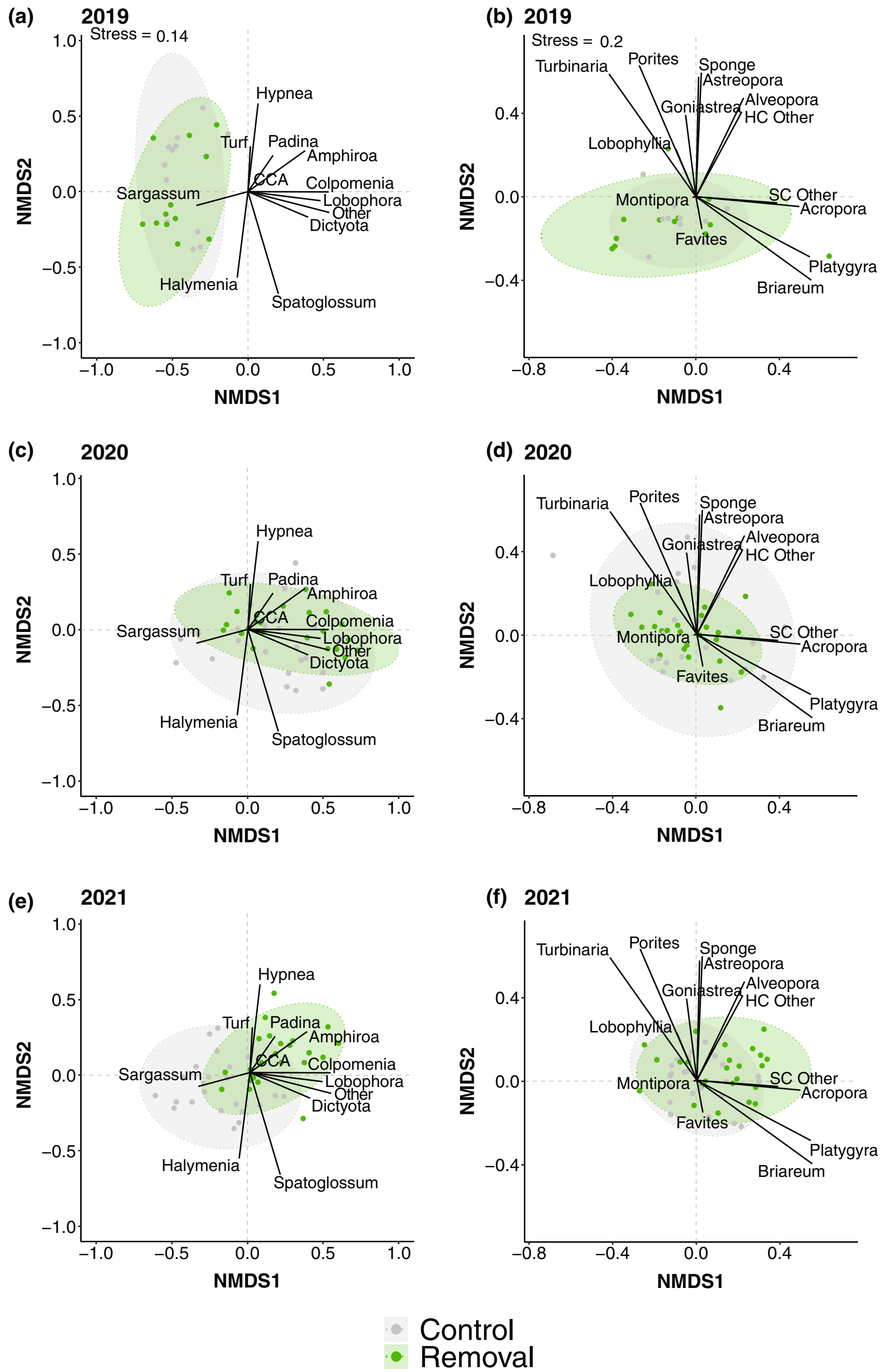

FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination of $N=120$ sampling units based on Bray–Curtis dissimilarity indices of Hellinger transformed per cent cover data in 2019, 2020, and 2021 of (a, c, e) $n=12$ macroalgal genera and (b, d, f) $n=14$ non-macroalgal genera (including hard coral, soft coral, sponges) around Yunbenun, Australia. Coloured points represent location of each survey in multivariate space with control plot surveys shown in grey and removal plot surveys (pre-removal surveys only) shown in green. 95% confidence ellipses are shown for treatment groupings in each year. Black lines represent loading vectors for (a, c, e) macroalgal genera (b, d, f) non-macroalgal genera.

berth and ferry ticket costs) over the course of the 3 years (Table S8). Start-up expenses, including the purchase of cameras, star pickets, transect tapes, data storage, and catch bags totalled $1964 (USD at base year 2010). Hence, the total project operational cost (not including labour) was approximately $23,000 (base year 2010) to double the coral cover in 300 m^2 of coral reef (i.e. removal plots only), equivalent to $77/m^2. Extrapolating costs per hectare and including cost of labour estimates, we estimate a total cost of $67,250 per hectare per removal event (Data S1). However, this cost will, of course, vary based on local labour costs, starting benthic composition and algal biomass, diving constraints, and other variables.

4 | DISCUSSION

Removing macroalgae from degraded inshore reefs facilitated rapid increases of scleractinian coral cover and simultaneous suppression of macroalgal regrowth. Macroalgal removal had a strong positive impact on hard coral cover, with the three-year intervention at least doubling coral cover. This is in stark contrast to control plots, which experienced little change in coral cover throughout the study. Furthermore, the coral cover observed in removal plots (38%) at the end of the study was considerably higher than the average live hard coral cover reported for Yunbenun reefs in 2016 (~22% cover, averaged across locations; Williamson et al., 2019) and 2021 (~27% cover, averaged across depths; Thompson et al., 2023). In removal plots, macroalgal cover was reduced to half the levels found in control plots, which remained at greater than 80% cover. These results suggest that this low-cost, low-technology intervention can achieve significant and rapid benefits for degraded, macroalgae-dominated inshore reefs, reversing declines in coral cover on reefs that were historically coral-dominated.

Both the existence of and definitions for phase shifts are hotly debated (Crisp et al., 2022; Dudgeon et al., 2010). While it is important to consider the long-term baseline of a reef prior to intervention, most reefs worldwide lack a robust, quantitative baseline that predates human influence (Knowlton & Jackson, 2008). A general trend of increasing macroalgae at the expense of corals has been reported for Yunbenun reefs over the recent past (Ceccarelli et al., 2020) and, while we make no claims to these reefs having experienced a "phase shift", it is nonetheless worth considering our results in this context. A recent review on coral reef phase shifts suggests a definition should require persistence of the dominant benthic component to occur for at least 3 years before and after the shift (Crisp et al., 2022). Hence, to reverse the current algal dominance on Yunbenun reefs, continued monitoring would need to show coral cover persisting at levels greater than macroalgal cover for at least 3 years. Our study achieved relatively rapid increases in coral cover, re-establishing coral dominance over macroalgae, without any alteration to underlying environmental conditions. These results suggest that coral dominance and macroalgal dominance may both be supported under the same underlying environmental conditions (i.e. poor water quality and high sediment load). Hence, these two divergent reef communities may represent alternative stable states (Fung et al., 2011) as opposed to a continuous phase shift (as defined by Dudgeon et al., 2010) driven by persistent environmental disturbance. If this is the case, macroalgal removal may be an effective way to re-establish an alternative, coral-dominated stable state on reefs where improving environmental conditions (e.g. water quality) may be difficult and/or slow to achieve.

The mechanisms underpinning the increase in coral cover in removal plots are likely to be multifaceted and complex. Previous work in the same experimental plots showed a threefold increase in coral recruitment in removal plots compared with controls (Smith, Brown, et al., 2022). Increased recruitment may lead to increased coral cover, dependent on post-settlement mortality (Cameron & Harrison, 2020; Coles & Brown, 2007). In addition to increased recruitment, the reduction in competitive interactions between corals and macroalgae likely allowed corals to redirect energetic resources from competition towards growth (Box & Mumby, 2007; Tanner, 1995; Vega Thurber et al., 2012). Other indirect mechanisms may also be at play. For example, declines in herbivorous fishes and invertebrates have been implicated in onsets of community shifts towards macroalgae (Briggs et al., 2018; Hughes, 1994). Similarly, natural or human-supplemented increases in herbivorous fishes and invertebrates can maintain low algal biomass in natural systems (Kuempel & Altieri, 2017), and after algal clearing (McClanahan et al., 2002; Neilson et al., 2018). On reefs such as those at Yunbenun where herbivorous fish exploitation is low (Ceccarelli et al., 2020), herbivory is unlikely to be the driver of initial macroalgae increases. However, healthy herbivore communities at these sites may contribute to the sustained decrease in macroalgae growth observed herein, and in particular may contribute post-removal to controlling algal genera that are unpalatable in their mature forms (Briggs et al., 2018; Paul & Hay, 1986). It is therefore unclear whether further supplementation of herbivores (e.g. Neilson et al., 2018) would benefit these reefs in maintaining low algal biomass. Nonetheless, it is likely that the mechanisms that supported the increased coral cover seen here are a combination of herbivory, increased coral larval settlement and recruitment, and enhanced adult colony growth.

Macroalgal community composition changed through time in response to the removal effort, and these changes likely have varying effects on reef ecology. For example, a greater diversity of genera was observed in removal plots, including the corticated red algae *Hypnea*, the upright calcareous red alga *Amphiroa*, the common brown alga *Padina*, the ephemeral brown alga *Colpomenia*, and the mat-forming brown alga *Lobophora*. These algae dominated in the absence of canopy-forming *Sargassum* spp., and may pose varying levels of risk to corals based on their species-specific interactions (Jompa & McCook, 2003; Vieira, 2020). *Lobophora* spp., for example, can overgrow live corals (Antonius & Ballesteros, 1998) while also inhibiting coral settlement and recruitment (Box & Mumby, 2007; Evensen et al., 2019). Therefore, an increase in *Lobophora* spp. cover may reduce the potential benefits of canopy removal. Conversely, *Hypnea pannosa* has been found to have no effect on the tissue of a branching coral, and hence poses little threat to coral communities (Jompa & McCook, 2003). Further research on species specific coral-algal interactions is warranted to better understand the longer term outcomes of altering macroalgal community composition.

The change in coral community composition was less prominent, likely attributable to the slower growth and recruitment of corals compared with macroalgae. Coral communities in control plots consisted primarily of a few common genera, including encrusting *Montipora*, branching *Acropora*, and massive *Porites*. The coral communities in removal plots increased in diversity compared to control plots, characterised by higher relative proportions of massive coral genera including *Astreopora*, *Alveopora*, *Lobophyllia* and *Favites*. Importantly, there was no observed decline in coral diversity which can be viewed as a positive result since loss of coral biodiversity can instigate negative feedback loops that suppress reef resilience (Clements & Hay, 2019). Hence, manually reducing macroalgal cover on inshore reefs is unlikely to lead to negative changes in short-term coral community composition and diversity.

Survey methods used in macroalgal dominated areas can influence estimates of benthic cover, and can prejudice understanding of reef dynamics (Smith, Boström-Einarsson, et al., 2022). To counter these known issues, we quantified the change in benthic cover using two approaches, photoquadrats and in situ stratified transects (Smith, Boström-Einarsson, et al., 2022). While overall the two methods were strongly correlated, there were a few differences in the benthic community patterns detected. For example, the macroalgae cover detected by transects was consistently lower than photoquadrats for control plots. This observation is not surprising, however, as the algal thallus biomass is predominantly suspended in the water column, making it more detectable when assessed by photographs. In contrast, the encounter rate with the holdfast is far less frequent when employing transect methods. Similarly, coral cover detected by transects was generally higher than photoquadrats for both control and removal plots, and is representative of canopy effects affecting photoquadrat data. While the stratified transect data provide a better understanding of benthic community patterns in areas of high macroalgal biomass, the photoquadrats were highly valuable for assessing benthic communities across the entire survey area, rather than the subset sampled by the transects. Nonetheless, the overall patterns of change were consistent between the two methodologies.

Importantly, the effects of macroalgal removal on coral communities were not realised immediately. After 2 years of removal, changes in per cent cover and community composition were minimal between control and removal plots. After 3 years, the effects were clear, with Bayesian probability modelling showing a 4% chance that macroalgal cover had been reduced (by more than 50%) after 2 years, and a 99% chance after 3 years. Furthermore, the trends of decreasing macroalgal cover and increasing coral cover are yet to plateau, suggesting there is potential for further benefits with continued removal efforts. These findings suggest that with regular intervention, reef communities at Yunbenun, and likely other inshore reefs on the GBR, are capable of shifting towards less dominance of canopy-forming macroalgae, and increased dominance of hard corals. However, sporadic or one-off removal events are unlikely to achieve beneficial outcomes. Longer-term removal studies are required to determine whether there is a threshold beyond which macroalgal removal is no longer required to sustain coral cover recovery.

One challenge for all reef intervention approaches is the feasibility and cost of scaling up (Boström-Einarsson et al., 2018). To accomplish this study, volunteer citizen scientists engaged through Earthwatch Institute contributed to macroalgal removal with one team (two people) clearing 25 m^2 of reef benthos in approximately 30 min (removal only, not including monitoring tasks). Because the approach requires low-technology and minimal training, this manual macroalgae removal method may be feasible to scale up through volunteer citizen science initiatives, and would provide benefits not only to local reefs, but also to local tourism and community groups (Hesley et al., 2017; Suggett et al., 2023). The total actual operational cost of this study, which resulted in the doubling of coral cover over 300 m^2 of reef (i.e. removal plots only), was USD ~\$77 per m^2 or ~\$400 per day of field work (2010 base rate; Table S8). It should be noted that these costs included monitoring activities, and hence the operational cost for implementation (i.e. removal only; no monitoring) may be less. Extrapolating operational costs and including an estimate for labour costs, the total estimated cost is ~\$67,250 per hectare per removal event (Data S1). In comparison with other reef restoration projects, which have a median cost of \$400,000 USD/ha (range \$6000–\$4,000,000/ha, inclusion of labour costs not known; Bayraktarov et al., 2019), the sea-weeding method is reasonably cost-effective, requires little training or skill to implement and upscale, and importantly, is not coral species-specific in providing benefits (Hughes et al., 2023). Because the cost of materials and particularly labour varies significantly worldwide (The World Bank, 2023b), and the starting condition of the reef will dictate the magnitude of efforts required, it is difficult to extrapolate costs for other reef regions. Nonetheless, labour costs can be reduced and socio-ecological benefit maximised through the use of ecotourism, volunteers, citizen scientists and/or community action groups (Suggett et al., 2023), though some paid labour is likely required to provide initial training and ensure perverse impacts of removal events are avoided.

Disposal of the by-product algae can create opportunities for circular economies and carbon sequestration. In the Caribbean, episodic influxes of pelagic *Sargassum* are posing a management issue (Smetacek & Zingone, 2013), with a current focus on harnessing potential economic benefits (Davis et al., 2021; Milledge & Harvey, 2016), including use as biofuels (Orozco-González et al., 2022), bioplastics (Lim et al., 2021), agricultural fertilisers (Sembera et al., 2018) or in other ecosystem restoration programs (e.g. dune plants (Williams & Feagin, 2010), mangroves (Trench et al., 2022)). Additionally, sea-weeding has the potential to sequester carbon by removing a mature plant, the carbon being captured (Gouvêa et al., 2020) and redirected to alternate uses, rather than released through the natural senescence cycle. Future work would be valuable to determine region- and species-specific valorisation pathways, and to quantify the carbon sequestration potential of sea-weeding.

In summary, results of this study indicate regular macroalgal removal efforts are effective in reducing macroalgal cover, reducing a barrier to coral recovery, and can be used as a local-scale intervention to improve reef resilience. If the patterns observed in this study persist in response to continued removal events (even if only reducing macroalgal per cent cover by half), the trajectory of the reef community at Yunbenun has the potential to breach a theoretical biotic barrier to coral recovery, re-establishing the historical coral dominated state. Importantly, there was some natural recovery of coral cover observed in control plots (though not nearly the recovery observed in removal plots), which highlights the need for robust experimental design including long-term monitoring of intervention-free, control reef areas (Hughes et al., 2023). While the increases in coral cover achieved were rapid and significant, it remains unclear if these increases represent successfully 'restored' reef areas, since we did not explicitly set any restoration goal that would consistute 'success' of the method. Instead, we aimed to examine if the method of removal would be useful towards reef restoration or rehabilitation goals (potentially in combination with other methods). Future experiments with explicit socio-ecological goal-setting would be useful (Hein et al., 2019), and in particular would require monitoring and evaluation of other elements of reef health such as fish communities and structural complexity. Macroalgal removal trials in other reef regions are also needed to investigate how various environmental conditions influence the impact and benefit of macroalgal removal on coral recovery. Longer term studies will help to determine the persistence of the patterns observed herein, especially if predicted additional acute impacts such as tropical storms or bleaching affect these sites. Nonetheless, this low-cost, low-technology method provides an exciting advancement in the local management of inshore coral reefs in an era of rapid global declines in coral reef health.

AUTHOR CONTRIBUTIONS

David G. Bourne, Hillary A. Smith, and Ian M. McLeod conceived the ideas and designed methodology; Stella E. Fulton, Hillary A. Smith, David G. Bourne and Cathie A. Page collected the data; Stella E. Fulton and Hillary A. Smith analysed the data; Stella E. Fulton, Hillary A. Smith and David G. Bourne led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available via the Research Data JCU repository https://doi.org/10.25903/6zyt-yv37 (Smith et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Trace plots indicating level of chain mixing for Bayesian generalised linear mixed effects models for (a) macroalgal per cent cover from photoquadrats; (b) coral per cent cover from photoquadrats; (c) macroalgal per cent cover from transects; (d) coral per cent cover from transects.

Figure S2: Biomass ($kg\,m^{-2}$) of macroalgae removed from plots ($n=6$ plots per bay, each $25\,m^2$) in two bays of Magnetic Island, Australia, during each removal event from October 2018 to October 2021. Points represent mean mass removed with dashed line representing Arthur Bay and solid line representing Florence Bay; vertical lines represent standard error.

Figure S3: Photoquadrat-derived per cent cover of different macroalgal genera within experimental plots in two bays of Magnetic Island, Australia. Solid, coloured points represent the mean per cent cover averaged across all control plots (grey) and removal plots (green) with vertical lines representing the associated standard error. Vertical grey lines indicate when macroalgae were cleared from removal plots. Only pre-removal survey timepoints are shown here for simplicity.

Figure S4: Photoquadrat-derived per cent cover of different hard coral genera within experimental plots in two bays of Magnetic Island, Australia. Solid, coloured points represent the mean per cent cover averaged across all control plots (grey) and removal plots (green) with vertical lines representing the associated standard error. Vertical grey lines indicate when macroalgae were cleared from removal plots. Only pre-removal survey timepoints are shown here for simplicity.

Figure S5: Diversity metrics for (a) macroalgal and (b) coral communities from 2018 to 2021 in two bays of Magnetic Island, Australia. Coloured points are mean predicted fits of generalised linear mixed effects models (conditional r^2 shown in top left corner of each panel, except for evenness where r^2 values are not applicable), with predictions for control plots shown in grey and removal plots shown in green. Solid vertical lines represent 95% confidence intervals. Partialised observations (sum of fitted values and residuals) are shown as faint-coloured points. Asterisks represent statistically significant differences between control and removal plots.

Table S1: Summary of previous studies conducting removal of macroalgae.

Table S2: Bayesian generalised linear mixed effects model specifications detailing prior values (adjusted scale) and chain characteristics for models used to investigate the relationships through time between benthic cover and macroalgal removal (treatment) from photoquadrat and transect data in two bays of Magnetic Island, Australia, from 2018 to 2021.

Table S3: Summary of generalised linear mixed effects model results used to examine patterns in Shannon's diversity index, richness, and evenness of (a) macroalgal communities and (b) coral communities from photoquadrat data throughout 2018 to 2021, in two bays of Magnetic Island, Australia.

Table S4: Per cent cover from photoquadrat surveys, shown as mean and standard error, of benthic organisms observed within 24 experimental plots (each $25\,m^2$) in two bays of Magnetic Island, Australia, averaged across a three-year period (2018–2021). Genera are ordered from most common (highest mean per cent cover averaged across all plots and entire study period) to least common (lowest mean per cent cover) within each functional group. The category labelled 'OTHER' within each functional group was used when visibility was poor and genus level identification was not possible. Genera observed in less than 10% of photo-quadrat surveys were excluded from analyses and are not listed here.

Table S5: Summary table for Bayesian generalised linear mixed effects model used to investigate the relationship through time between (a) macroalgal cover, (b) coral cover and macroalgal removal (treatment) in two bays of Magnetic Island, Australia, throughout 2018 to 2021. Values are on the link scale; hence, 95% credibility intervals (CI) show an effect of the associated term when the interval does not include zero.

Table S6: Bayesian probabilities for a range of (a) photoquadrat per cent cover and (b) transect per cent cover values for both macroalgae and corals at selected timepoints throughout the study period in control plots (C) and removal plots (R) located in two bays of Magnetic Island, Australia (e.g., the probability that there was less than 70% macroalgal cover in control plots in July 2021 is 0.72). Light grey shading indicates probability greater than 0.5, and dark grey shading indicates probability of 1.

Table S7: Results from a three-factor permutational multivariate analysis of variance of (a) macroalgal and (b) coral community composition surveyed throughout 2018 to 2021 in two bays of Magnetic Island, Australia. Asterisks indicate significance at $p<0.05$.

Table S8: (a) Field operational expenses and (b) start-up expenses for implementation of macroalgae removal and monitoring at Magnetic Island, Australia, from 2018 to 2021. Values shown are Australian Dollars (AUD) unless otherwise specified.

Data S1: Calculation of estimated costs to implement macroalgae removal.

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