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Effect of marine reserve status on coral seeding in the inshore Great Barrier Reef

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ABSTRACT: Highly connected marine reserves and assisted coral restoration are promising strategies to support coral reefs amidst rapid climate change. However, their effects on coral—fish interactions and thereby coral recovery processes via recruitment remain poorly understood. Coral seeding offers a valuable approach to investigate the ecological dynamics shaping reef communities within marine reserves. To investigate the impacts of reserve status and fish predation on coral recruitment, we deployed *Acropora millepora* spat on coral seeding devices to 6 sites in the Keppel Islands, Great Barrier Reef, Australia. Sites were selected from marine park zones open or closed to fishing, and 2 devices with fish-exclusion features were tested against a control. After 11 mo, >60% of devices had live corals. Coral yield was site-specific, with little variation across reserve zones. Reefs abundant with damselfish (60—200 individuals in 39.25 m^2) and *Pocillopora* corals (>15% cover) supported higher survival than those with parrotfish, macroalgae, and sediments. Only the fish exclusion star device yielded more corals than the featureless control, and this result was strongest at Home Reef where feeding by scraping parrotfish was high (20 bites min^{-1} in 0.25 m^2). Our study demonstrates that while marine reserve status is not a good predictor of coral seeding success, ecological characteristics can be used to guide site selection to maximise benefits for reef restoration.

KEY WORDS: Coral ecology · Fish ecology · Coral recruitment · Marine conservation · Coral restoration

1. INTRODUCTION

Marine reserve networks are a globally utilised conservation strategy. The reserve networks incorporate no-take, partially protected, and less- or un-restricted zones (Gell & Roberts 2003, Roberts et al. 2005, Hall et al. 2021), designed to manage fish stocks through sustainable fishing practices and thereby enhance ecosystem resilience (McCook et al. 2010, Emslie et al. 2015). However, as climate change accelerates, marine ecosystems are suffering increasingly frequent and severe disturbances, leading to substantial biodiversity loss, even in areas under best-practice management and protection (Bruno et al. 2019, Graham et al. 2020, Emslie et al. 2024, Henley et al. 2024). While highly connected reserves have the potential to support reefs into the future (Harrison et al. 2020, Kleypas et al. 2021, Benedetti-Cecchi et al. 2024), our current understanding of their role in coral community succession and in natural and assisted coral recovery processes is limited.

The effectiveness of no-take reserves in maintaining fish stocks is well documented (Roberts et al. 2005, 2017, Russ et al. 2008). No-take reserves positively influence the species targeted by fishing (e.g. meso-predators, large herbivores, and demersal taxa) and their prey, with direct increases in biomass, abundance, and richness (Williamson et al. 2004, 2014, Russ et al. 2008, Bode et al. 2025). A positive and cas-

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cading effect of no-take zones on neighbouring habitats has also been observed (Roberts et al. 2001, Gell & Roberts 2003, Babcock et al. 2010). Moreover, significant and beneficial regime shifts have occurred on coral reefs damaged by destructive fishing (i.e. dynamite, cyanide, overfishing; McManus et al. 1997) after reserve establishment (Russ & Alcala 2003, Russ et al. 2008, Stockwell et al. 2009, Babcock et al. 2010).

While no-take reserves can increase coral cover (Mumby & Harborne 2010, Selig & Bruno 2010, Mellin et al. 2016, Strain et al. 2019), the rates of coral recovery are often variable (Graham et al. 2011, Strain et al. 2019). The benefits of reserves can also diminish following severe disturbances and regardless of longstanding protection (Graham et al. 2020). The processes that underly an increase in coral cover, such as survival from settlement through recruitment, are also often overlooked in traditional monitoring (Edmunds 2023). Indeed, post-settlement survival is a major bottleneck to reef recovery (Randall et al. 2020, Banaszak et al. 2023). Thus, tracking coral spat survival and growth presents an alternative way to assess the effects of no-take reserves on coral recovery processes, which can be done using coral seeding devices (Chamberland et al. 2017, Randall et al. 2021, Page et al. 2024, Jurriaans et al. 2025). Seeding experiments also offer valuable opportunities to disentangle the complex relationships amongst corals and herbivorous fish (Baria et al. 2010, Trapon et al. 2013, Whitman et al. 2024, 2025), which may be influenced by reserve status.

Managing herbivore populations using no-take zones is considered important for resilience-based reef conservation (Mumby et al. 2007, Steneck et al. 2018), but a role of herbivores in maintaining coral-dominated states remains debated (Stockwell et al. 2009, Carassou et al. 2013, Russ et al. 2015). Herbivory mediates competition between algae and other space-occupying organisms (Lubchenco & Gaines 1981, Steneck 1983, Hughes et al. 2007). While the dynamics of this balance vary spatially and temporally (Roff & Mumby 2012, Smith et al. 2016), herbivorous fish broadly facilitate coral dominance by removing up to 50% of algal biomass (Bellwood et al. 2004, 2018, Holbrook et al. 2016). Although this algal removal is often necessary for successful coral recruitment (Kuffner et al. 2006), the broad guild of herbivorous reef fish includes multiple functional groups with distinct feeding modes (Holbrook et al. 2016, Clements & Choat 2018), exerting unique pressures on young corals.

Many fish graze on tufted and complex macroalgae (Carpenter 1986, Ceccarelli et al. 2001, Bellwood et al. 2018); some inadvertently remove juvenile corals during feeding (Baria et al. 2010, Doropoulos et al. 2012, Trapon et al. 2013). For example, territorial damselfish (Pomacentridae) guard and 'farm' turf algal patches, cropping algae and promoting its growth by removing competing organisms (Ceccarelli et al. 2001). Moreover, scraping and excavating parrotfish (Labridae, Scarinae) remove substrata, including coral spat (Doropoulos et al. 2012, Trapon et al. 2013, Whitman et al. 2024), to target protein-rich microscopic phototrophs (Clements & Choat 2018). Offering protection to corals from parrotfish is one way to maximise recruitment success (Baria et al. 2010, Trapon et al. 2013, Whitman et al. 2024); whether this technique is necessary on reefs already influenced by marine reserves that alter herbivorous fish abundance remains untested.

Although no-take reserves are no panacea for coral reef resilience (Williams et al. 2019), those with free space for coral settlement and diverse herbivores to control algae may be ideal for direct restoration. Yet, within these reserves, interactions between recruiting corals, fish, and algae are often complex (Gell & Roberts 2003, Mumby et al. 2007, Babcock et al. 2010, Carassou et al. 2013). To guide restoration strategies, we assessed interactions between herbivorous fish, coral spat, and their environment during a coral seeding experiment in the southern Great Barrier Reef Marine Park (GBRMP). Fished and no-take reserves were selected as deployment sites. Two fish-exclusion devices that housed coral spat were tested against a control. Three questions were of interest: (1) Does the yield of seeded coral spat differ between fished and no-take reserves? (2) Does device type interact with reserve status and fish community composition to influence coral yield? (3) Do fish abundance, fish feeding, and benthic community composition predict seeded-coral yield? Our findings provide new insights into the ecological processes shaping coral reefs within and outside no-take reserves, informing the potential for marine reserves to improve restoration efficacy.

2. MATERIALS AND METHODS

2.1. Coral spawning and larval settlement

Gravid *Acropora millepora* colonies were collected for transport and holding on the research vessel (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/meps15069_supp.pdf) (Randall et al. 2025) prior to use in experiments. Colonies were isolated in individual tanks until mass spawning occurred on November 16, 2022 (for more information, refer to Text S1 and Table S1).

Following spawning, gametes were collected, rinsed, fertilised, and then transferred to rearing tanks (1 larva ml^{-1}; Fig. S1c) following standard procedures (Whitman et al. 2024, 2025). After 5 d, larvae were free swimming and competent to settle (>80 % settlement), as determined by standard settlement assays (Heyward & Negri 1999; our Text S1).

Concrete tabs (196 mm^2; 80:20 concrete:mortar) produced in sheets (Fig. S1e) were conditioned in aquaria at the Australian Institute of Marine Science (AIMS, Townsville) National Sea Simulator and used as settlement substrates (Text S1). After ~1 mo, sheets supported an early biofilm community of crustose coralline algae (CCA) and bacteria known to induce coral settlement (Heyward & Negri 1999). Substrates were moved to tanks on the vessel for transport and holding (Fig. S1d).

For mass settlement, sheets were placed horizontally with their biofilm surface facing upwards in tanks with small glass beads (sterile, <2 mm Ø) filling the spaces between sheets (Fig. S1e). Beads limited larval access to sheet undersides, constraining settlement to the upward-facing surface. Approximately 9000 larvae were seeded to each sheet (22 per tab).

2.2. Coral seeding devices

After settlement (24 to 48 h), individual tabs were cut from sheets and those with live coral (~12 ± 0.6 spat, range = 1−47; Text S2) were haphazardly placed into 1 of 3 coral seeding device types (Fig. 1a): (1) an exclusion star (hereafter 'exclusion device'), (2) an exclusion triangle (hereafter 'triangle device'), and (3) a featureless exclusion star with no protection (hereafter 'control device'). Tabs were vertically orientated in devices (Fig. 1b−f). The triangle device had 6 tabs (3 outward-facing, 3 inward-facing; Fig. 1e,f), with potentially different levels of protection, while the exclusion and control devices had 3 outward-facing tabs (Fig. 1c,d). The devices were made of 95% alumina ceramic (Shanghai Gongtao Ceramics). A ceramic cap (exclusion and control; Fig. 1b) or cyanoacrylate Gorilla Super Glue (Gorilla Glue®; triangle) secured the tabs. Adhesive glue was placed on the backside of the tab and left to cure overnight in aquaria prior to device deployment.

2.3. Experimental design and deployment

Devices with corals were deployed to 6 sites in the Keppel Islands (Woppaburra Sea Country, inshore, southern GBRMP; Fig. 2a, Table S2) from November

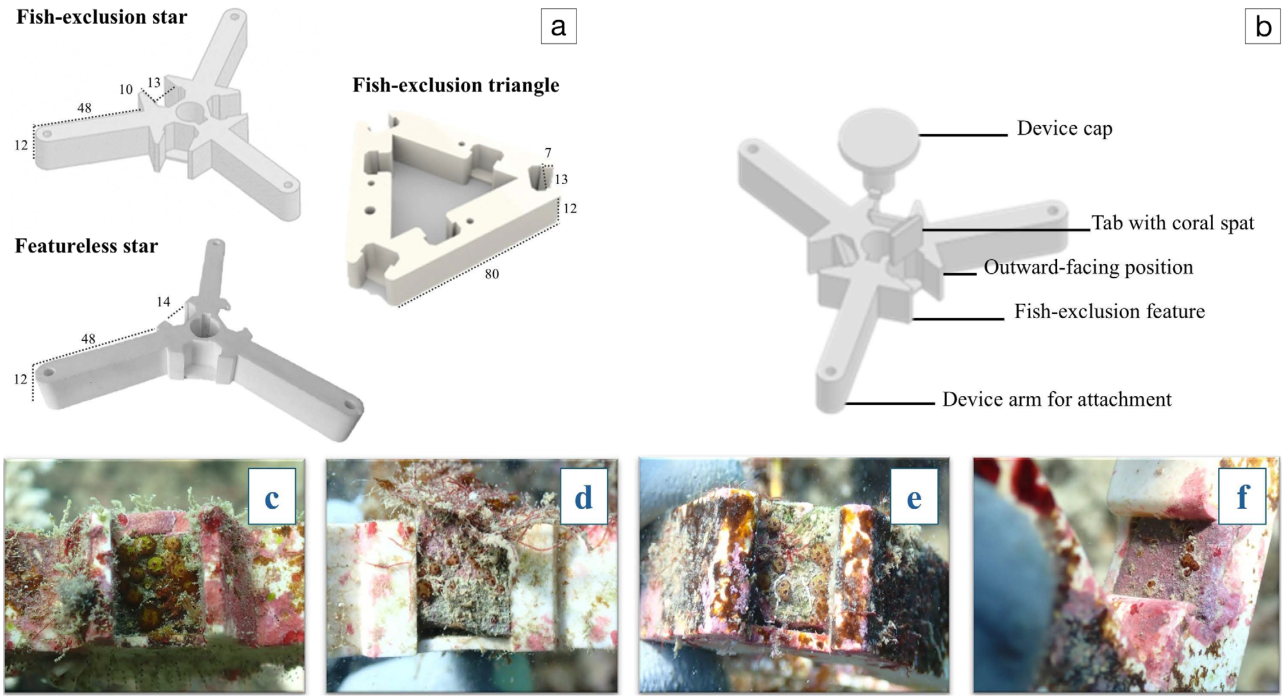

Fig. 1. Coral seeding device designs used in the experiment. (a) Three device types and their dimensions (mm). (b) The components of the fish-exclusion star device. Deployed (c) fish-exclusion star, (d) featureless-control star, (e) outer triangle, and (f) inner triangle, with live corals on the device tabs

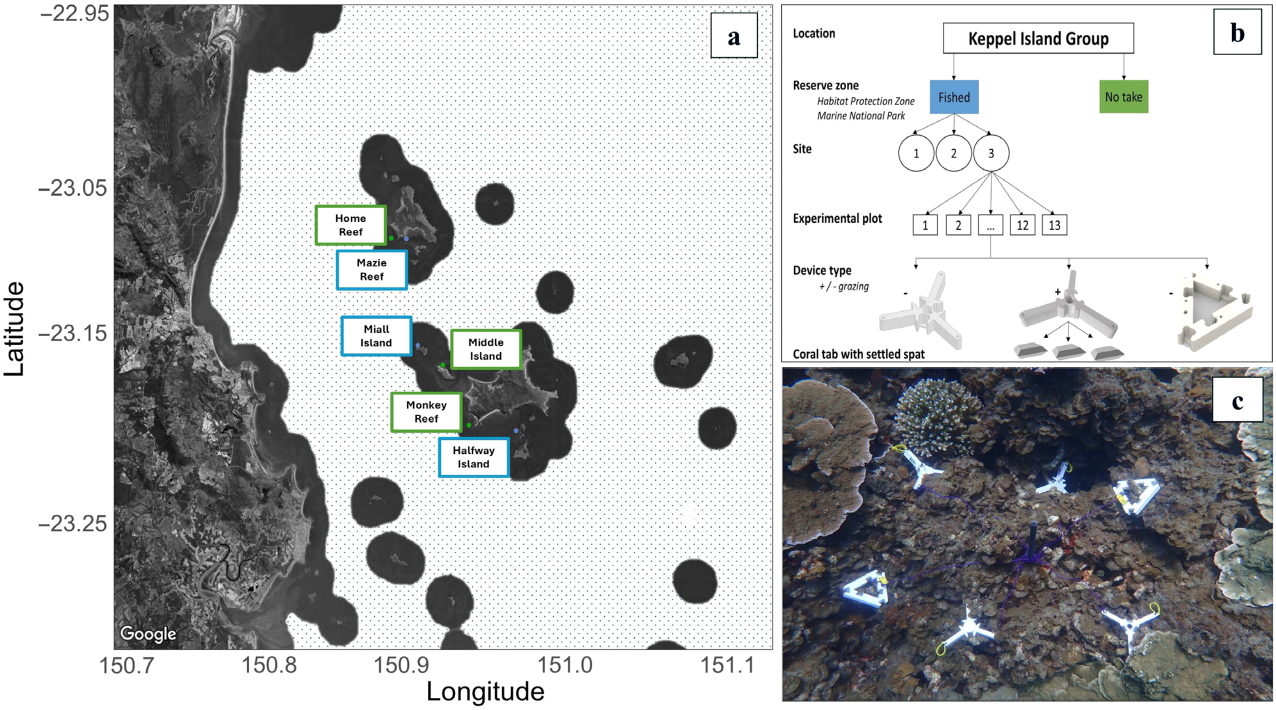

Fig. 2. Coral seeding methodology. (a) Six experimental sites, 3 green 'no-take' and 3 blue 'fished' marine reserves. (b) Hierarchical experimental design. (c) Experimental plot layout showing a central rod with 6 tethered seeding devices

23 to 27, 2022. The deployment followed a hierarchical design with replication at multiple scales (Fig. 2b). Fished reserves (Habitat Protection Zones, sites in blue in Fig. 2a) allowed recreational spear and line fishing, and no-take reserves (Marine National Park Zones, sites in green in Fig. 2a) prohibited fishing. The Great Barrier Reef (GBR) was designated as a Marine Park in 1975, and the Mackay/Capricorn section was added by 1989, with no-take zones in effect from 2004 (Great Barrier Reef Marine Park Authority 2004).

Each site had 75 devices deployed in 13 replicate plots (Fig. 2c) at ~4 to 6 m depth (lowest astronomical tide level, LAT). A fiberglass-reinforced polymer rebar (Beyond Materials Group, 12 mm Ø, 800 to 1500 mm length), hammered into the seafloor every ~2 m, constituted plot centres. Devices were tethered to the rebar with nylon rope (1 m length) and placed by divers to avoid sand and coral, but were not attached to the substrate so had the potential to move. We minimised device attachment to closely mimic the free deployment of devices that will be used in large-scale seeding trails in Australia (Pilot Deployment Program, AIMS). Twelve plots had 6 devices (2 replicate devices per plot) and 1 plot had 3 devices (1 replicate device per plot). Corals were deployed under the Reef Authority permit G22/47664.1; devices were removed after 11 mo.

2.4. Biological and environmental data collection

Data collection occurred 4 times (November 2022, February 2023, May 2023, October 2023; Table S2) over 11 mo to determine the influence of ecological drivers (fish abundance, fish feeding, benthic composition, and sedimentation) on coral survival and size. Data were categorised by spatial scale (tab [mm], plot [m], or site [10s m]); the data for each scale is described in the following sections.

2.4.1. Tab-level assessments. Coral yield and size were assessed at the final timepoint following removal. Yield (binary; 0 indicates no survivors, 1 indicates ≥1 survivors) was scored by a single observer. Maximum linear and perpendicular lengths of the largest surviving coral were measured using digital callipers. Size was expressed as a volume (mm^3, $V = \frac{2}{3}\pi r^3$) from the average of the 2 measurements.

2.4.2. Plot-level assessments. The benthic communities within each plot (1 m^2) were imaged (1 m height) at deployment (see Text S3 for further details) and assessed using the ReefCloud platform (https://reefcloud.ai/). Points (25) were uniformly overlaid on images in a 5 × 5 grid and labelled by a single observer, to estimate the percent cover of 72 potential benthic categories from 8 classes (Table S3). Sediments (herein 'sediment-laden surfaces') and other abiotic variables were accounted for in our plot-level assessment.

2.4.3. Site-level assessments. Fish stationary point-count surveys (39.25 m^2, 5 min, 3 replicates per site) were completed by a single observer at 3 timepoints (Table S2). Count data for herbivorous fish from the families Pomacentridae (damselfish), Labridae (Scarinae, parrotfish), Siganidae (rabbitfish), and Acanthuridae (surgeonfish) were collected (Table S4).

Fish feeding was recorded (GoPro HERO 9) at 2 timepoints (November 2022, February 2023). Cameras were stationed on the benthos in 2 haphazardly selected plots per site. The feeding area was initially marked by a quadrat (0.25 m^2). Footage (1 to 2 h), in the absence of quadrats and divers, was obtained for each survey. A single observer quantified feeding activity (VLC media player; Text S4, Table S5). An equal amount of footage was assessed per site, and the species bite rates (bites min^{-1}) were extracted. Direct bites on devices contributed to the rate but were also analysed separately. Aggressive behaviour towards another fish (binary) was also recorded.

Sediment collection pods were deployed at each site to quantify sediment deposition. 'SedPods' and 'TurfPods' were created following standard techniques (Field et al. 2013). Pods (3 replicates per type) were deployed to each site during coral deployment and collected after 5 d. The pods were rinsed (reverse osmosis [RO] water) to release sediments and the samples were stored (−20°C) until processing (Text S5). To determine average mass, samples were defrosted, homogenised, topped up to 500 ml (RO water), and three 50 ml aliquots were filtered and then oven-dried at 105°C (24 h). To measure organic content, samples were combusted (550°C, 1 h), cooled (5 h), dried (1 h), and then weighed.

2.5. Statistical analyses

2.5.1. Coral metrics. Bayesian hierarchical mixed-effects regression models (brms, R statistical software; Bürkner 2021, R Core Team 2022) were used to investigate the effects of site, reserve status, and device type on coral yield (binary, per tab and per device) and coral size (continuous, mm^3). The models were specified using the Bernoulli family (logit-link function) for yield and a Gaussian family (identity-link function) for size. The interactive effects of device type and site, and device type and reserve were explored. The random effect of device number nested within plot nested within site and reserve was included. Normal priors (mean = 0, SD = 1.7) for the intercept and the regression coefficients and Student's *t* priors (3 degrees of freedom = 3, mean = 0, scale of 1.7) for random effects were used for yield. An informative prior, calculated from qualitative data for the intercept (4.54, 1.55), slope (0, 2.5), and random effects (3, 0, 2.5), was used for size. Models were fit using Hamiltonian Monte Carlo sampling (HMC; Tables S6−S8). Posterior-predictive checks and the leave-one-out cross-validation information criterion (LOOIC) were used for model selection. Parameters were considered to have a credible effect when the 95% credible interval did not include 1 on the odds ratio scale. Outputs were visualised with 'ggplot2' (Wickham 2016).

2.5.2. Ecological data and coral yield. Principal component analyses (PCAs) and redundancy analyses (RDAs; Dixon 2003) were used to visualise patterns and reduce dimensionality in the ecological data. Backwards-stepwise model selection was applied to candidate generalised linear models using Akaike's information criterion (AIC) to identify the most parsimonious predictors of coral yield. These variables were retained as predictors of tab-level survival and used in brms models (Table S10). Separate models were run for fish, benthic, and sediment deposition data since these predictors were highly correlated. The random effect of device nested within plot nested within site and reserve was included. Group-level data (fish family and benthic categories) were analysed separately from species-level (fish) and lowest taxonomic-level data (benthic). Total mass was used for the sediment deposition model. Diagnostic tests were performed and significant outcomes were plotted, as described in Section 2.5.1.

2.5.3. Biotic and abiotic community composition by site. Brms models were used to compare fish counts, fish bites, benthic cover, and sediment deposition across sites. For fish, the models included the species- or family-level identification, site, and reserve as predictors. The random effect of replicate nested within site nested within reserve and timepoint was included. A zero-inflated Poisson distribution (log-link function) was used for fish counts (Table S9); a Gamma distribution (log-link function) was used for bites (Table S11). For the intercept, the count data had normal priors (0, 5), while the bite data had informed priors (0.58, 1.18). The same regression coefficient (0, 5) was used. An exponential prior (1) for the SD of the random effects was included for the bite model. For benthic data, the lowest-level identification was the response, site and reserve were predictors, and the random effect included plots nested within sites and reserves. A zero-inflated Beta distribution (logit-link function) with informed intercept priors (0.48, 1.09) and regression coefficients (0, 5) were used (Table S12). For sediment, total mass was modelled against the predictors (pod, site, and reserve) and the random effect of pod nested within site and reserve (Table S13). A Gamma distribution and normal intercept priors (0, 1), regression coefficients (0, 1), and Student's *t* priors for random effects (3, 0, 1) were used. Models were fit and checked for accuracy before plotting.

3. RESULTS

3.1. Coral yield

3.1.1. Device yield. After 11 mo, approximately 50% of devices had at least 1 live coral (Fig. 3a–d), with no strong evidence for a difference between fished and no-take reserves (Fig. 3a, Table S6). Device yield was highest at Miall Island (64%, CI: 12–96%) and lowest at Home Reef (26%, CI: 3–76%), with substantial variation amongst sites (Fig. 3b, Table S6). The device types performed similarly across reserve type; however, protective devices generally yielded slightly higher survival (49%) than controls (41%; Fig. 3c). The top-performing device varied by site (Fig. 3d). At Miall Island and Home Reef, the exclusion-device yield was 3- and 12-fold higher than the control, respectively (Table S6). Yield of the exclusion device varied least by site, with 41 to 63% of devices containing live corals; this was 1.4 to 2 times more consistent than the inner triangle (17–47%), outer triangle (17–61%), and control (12–52%; Fig. 3c,d).

3.1.2. Tab yield. The average (±SE) number of spat on each tab prior to deployment, as estimated from a subset of tabs (n = 214), was 12 ± 0.6. Tab-level yield was similar to device yield, varying across sites, but only averaged up to 25% of tabs with live coral (Fig. 3e). Tab yield was highest at Miall Island (33%, CI: 4–79), twice that of the lowest at Home Reef (Fig. 3e, Table S7). Reserve status had no substantial effect on tab yield, but the device type (Fig. 3e) and deployment plot (Fig. S2) did. The exclusion device showed the least site-related variation in yield (29–39%, CI: 2–89, 4–82), while the control device had the most (14–34%, CI: 1–82; Fig. 3e). Device performance had credible variation at Home Reef only (Fig. 3e), where the exclusion device had twice the tab-level yield of other device types (Table S7). At Mazie Reef, tab yield was 13 times higher in Plot 5 than Plot 8, indicating high within-site variability (Table S7, Fig. S2). Similarly, at Middle Island, yield was 8 times higher in Plot 13 than Plot 5 (Table S7, Fig. S2).

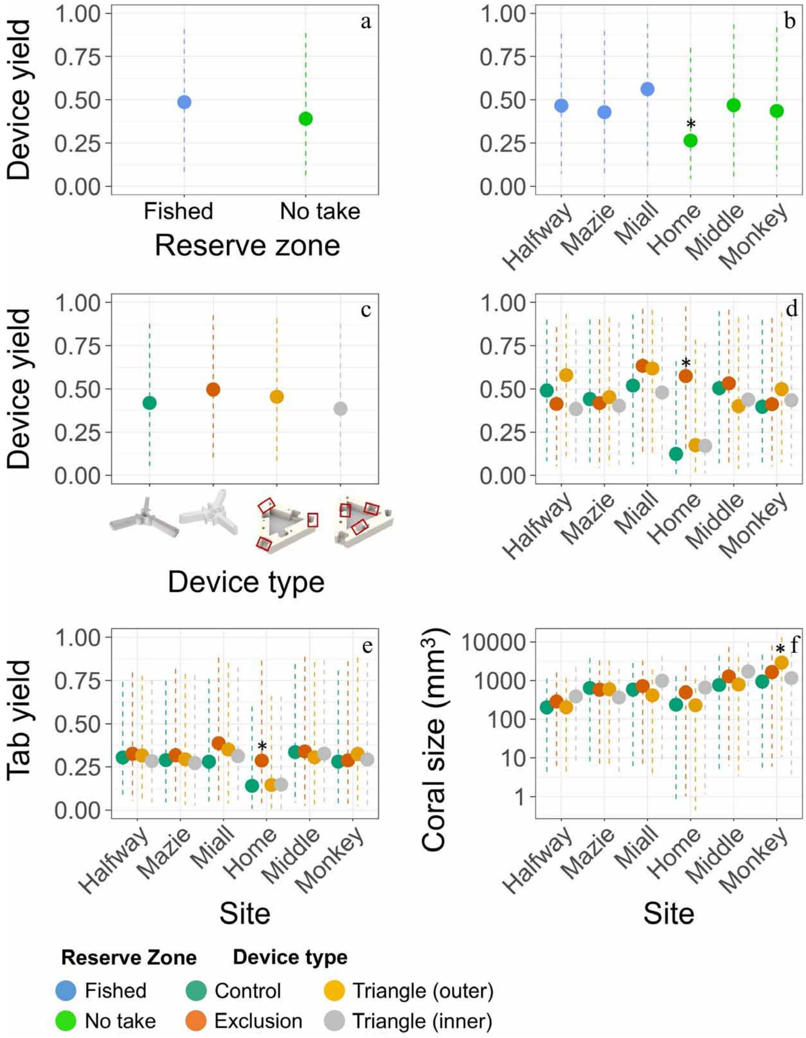

Fig. 3. Proportional device yield by (a) reserve zone, (b) site, (c) device type, and (d) device type by site. (e) Tab-level proportional yield by device type and site. (f) Coral size by device type and site (log scale). Mean estimates with 95% CI are displayed. (d–f) Data are jittered along the *x*-axis for ease of visualisation. *Result with credible variation (Tables S6–S8). The statistical comparison for (b) is to Mazie and Middle Island, (d) and (e) compare device types within Home Reef, and (f) compares them to the inward-facing tab of the exclusion triangle at Monkey Reef

3.2. Coral size

Coral size averaged 750 mm^3 (CI: 5–3839, range: 0.03–5610 mm^3; Fig. 3f). Reserve zone had no substantial effect on size but there were effects of device type on size at certain sites (Fig. 3f). At Monkey Reef, outer-facing corals in the triangle device were credibly larger than those in the control (Fig. 3f, Table S8).

3.3. Fish activity

3.3.1. Fish counts. A total of 5265 herbivorous Acanthuridae (surgeonfish), Labridae (wrasse and parrotfish), Pomacentridae (damselfish), and Siganidae (rabbitfish) were counted and identified. Fished reserves had slightly more fish than no-take zones (Fig. 4a); however, fish abundance varied most by site (Fig. 4b). Halfway Island had the most fish (2036 total, ~53 site^{-1} [39.25 m^2], CI: 17–121), while Home Reef had the least (327 total, ~8 site^{-1} CI: 2–19; Fig. 4a). The damselfish *Pomacentrus wardi* and *P. adelus* were abundant, particularly on fished reefs like Halfway Island, while surgeonfish were rare (Fig. 4c). The rabbitfish *Siganus argenteus* and *S. fuscescens* were most common at Mazie Reef, Middle Island, and Miall Island, with up to 8 times higher abundance than at other sites (Fig. 4d, Table S9). The parrotfish *Scarus rivulatus* was common at Middle Island, with abundance up to 20 times higher than at other sites (Fig. 4d, Table S9).

3.3.2. Fish bites. Twenty-eight fish species from 10 families were observed feeding in experimental plots. Feeding activity was similar across reserve status (Fig. 5a) but varied by site (Fig. 5b). Middle Island had the most activity (32 bites min^{-1} plot^{-1} [0.25 m^2], CI: 2–79), 6 times more than Monkey Reef, which had the least (Table S10). Damselfish (*P. wardi*) and wrasse (*Pseudolabrus guentheri*, *Stethojulis strigiventer*, *S. trilineata*, *Halichoeres melanurus*, and *Coris aurilineata*) commonly fed, while parrotfish (*Scarus ghobban* and *S. rivulatus*) fed less, with bites specific to no-take reserves (Fig. 5c). Notably, Home Reef had up to 20 times more parrotfish bites than other sites (Fig. 5d, Table S11). Damselfish were most active, taking substantially more bites at Middle Island and Miall Island than other sites (Table S11). Wrasse (*P. guentheri*, *C. aurilineata*, *H. melanurus*, and *S. strigiventer*) and damselfish (*P. wardi*, *P. australis*, and *Chromis nitida*) took 1253 total bites on devices. Device feeding was common at Miall Island (613 bites), with up to 56 times more bites than other sites (Fig. S3).

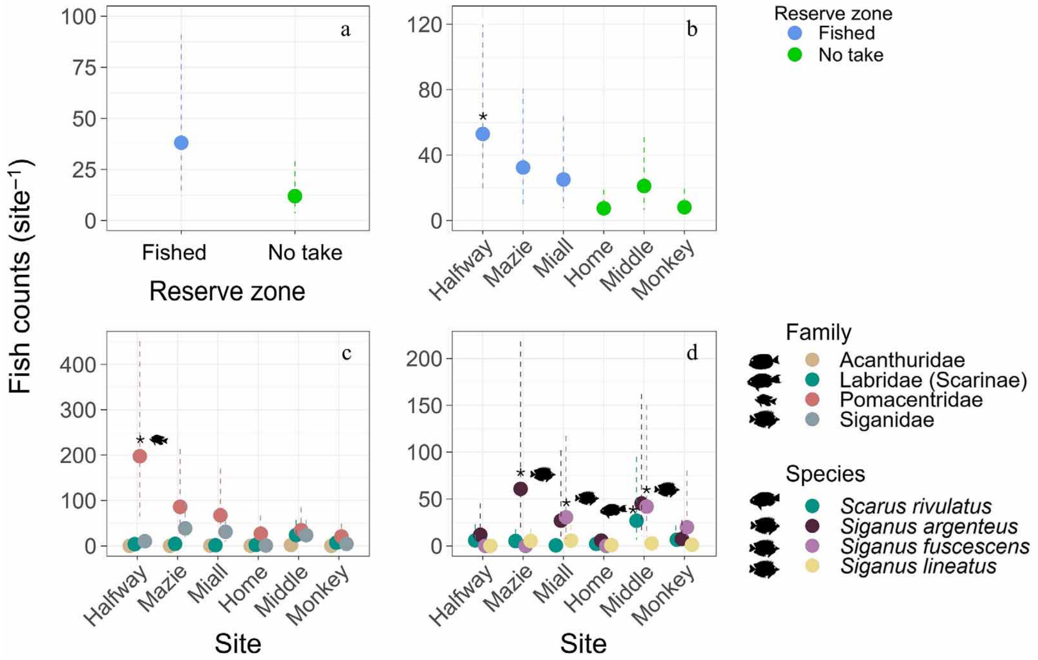

Fig. 4. Fish counts (in 39.25 m^2) by (a) reserve, (b) site, (c) family and site, and (d) species and site. Mean estimates per site (39.25 m^2) with 95% CI are displayed. Data in (c,d) are jittered along the *x*-axis for ease of visualisation. *Result with credible variation (Table S9), with the icon representing the fish group driving this response. The statistical comparison is to the site with the lowest recorded abundance for the identified fish group (c,d)

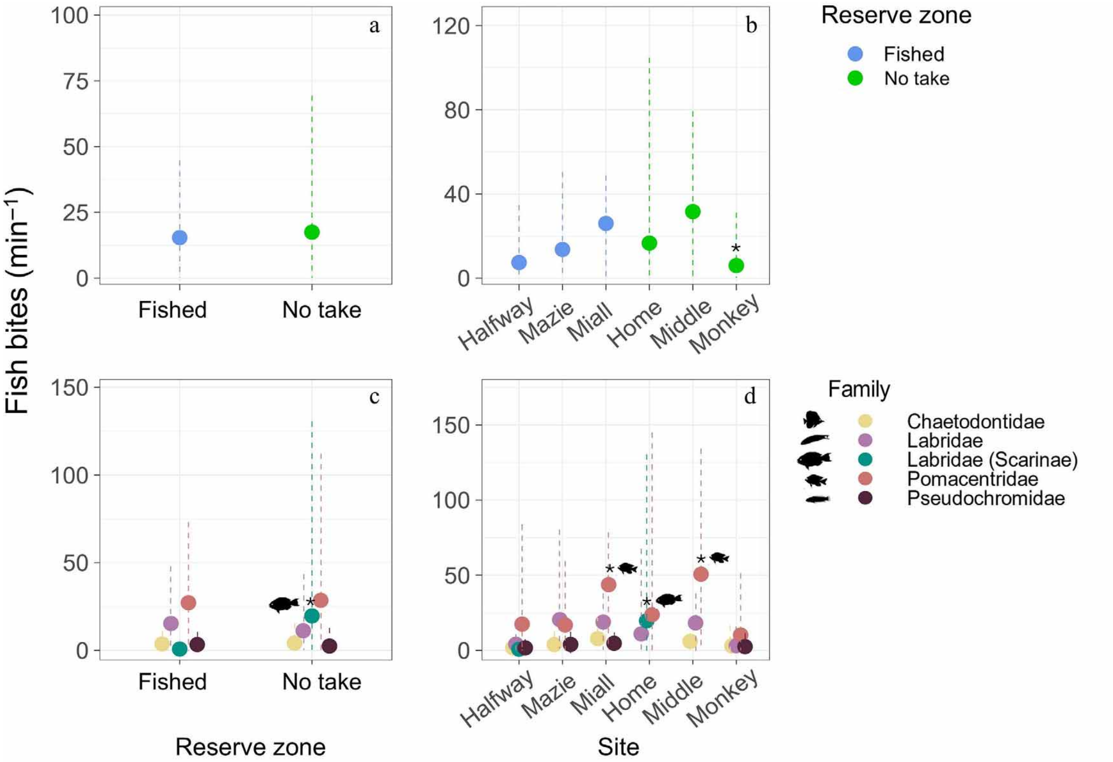

Fig. 5. Fish feeding by (a) reserve zone, (b) site, (c) fish family and reserve zone, and (d) fish family and site. Mean estimates per plot (0.25 m^2) with 95% CI are displayed. (c,d) Data are jittered along the *x*-axis for ease of visualisation. *Result with credible variation (Table S11). The statistical comparison is to the site with the most feeding (b), the opposing reserve zone (c), or to the site with the lowest recorded feeding of the identified fish group (d)

3.4. Biotic and abiotic community composition

Thirty benthic constituents were identified in the experimental plots (Table S3). Scleractinian corals (branching *Acropora*, encrusting *Montipora*) and low-lying macroalgae (*Lobophora*) were most abundant. No-take reefs had more macroalgae, sediment, and *Acropora* corals than fished reefs (Fig. 6a). Home Reef had the most erect macroalgae (*Sargassum*, *Padina*, *Colpomenia*, *Pseudochnoospora*) and branching *Acropora* (Fig. 6b).

Deposited sediments were primarily inorganic and averaged 0.019 and 0.048 g d^{-1} for SedPods and TurfPods, respectively. Sediment deposition showed minimal variation by site and reserve status (Fig. S4). Miall Island had the most deposition (1.37 g d^{-1}, CI: 0.11–7.51, TurfPods), while Halfway Island had the least (0.28 g d^{-1}, CI: 0.03–1.39; Table S13).

3.5. Coral yield by ecological drivers

3.5.1. Fish activity. Tab-level coral yield was positively correlated with the combined abundance of the damselfish *P. wardi* and *P. adelus* (Fig. 7a, Table S10), while parrotfish feeding was negatively correlated to yield (Fig. 7b,c, Table S10). Bites from the parrotfish *S. rivulatus* were more negative than bites from *S. ghobban*, particularly the initial phase variant of *S. rivulatus* (Fig. 7c, Table S10). Other notable but weak no-take reserve-specific results include a positive relationship between yield and damselfish *C. nitida* bites and a negative relationship with wrasse *P. guentheri* and *S. strigiventer* bites (Table S10). Bites from damselfish *P. wardi* substantially increased yield in exclusion devices only (Table S10). No other significant correlations were found with fish species or genera.

3.5.2. Benthic community composition. Tab yield was negatively related to the percentage cover of macroalgae and sediment-laden surfaces in experimental plots (Fig. 7d,e,g, Table S10). Erect brown macroalgae (*Sargassum*, *Colpomenia*) were negatively related to survival (Fig. 7d,e), but other erect (*Padina*) and low-lying (*Lobophora*) brown algae were not (Table S10). Adult coral abundance had mixed effects on yield. Increasing cover of *Pocillopora* (*P. damicornis*, *P. acuta*) was positively correlated with

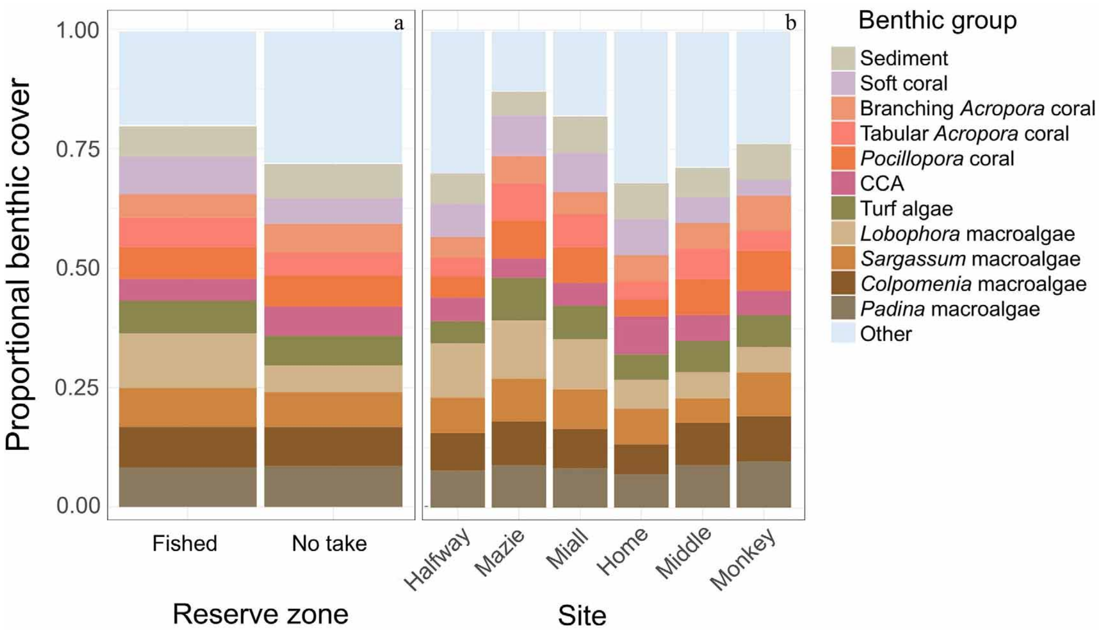

Fig. 6. Benthic community composition in experimental plots (1 m^2) by (a) reserve zone and (b) site. Dominant benthic groups are plotted individually, while rare groups are added together and plotted as 'other'. CCA: crustose coralline algae

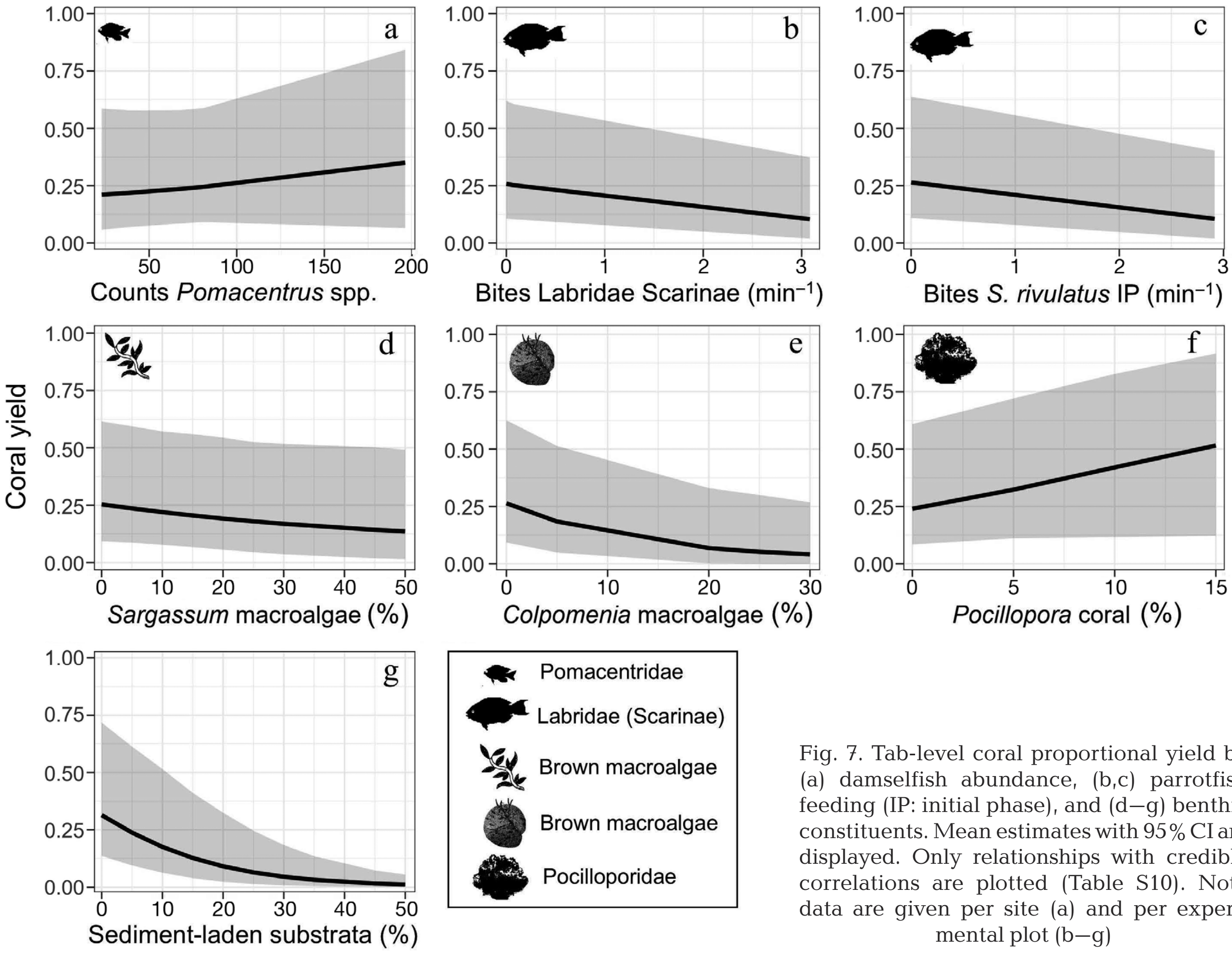

Fig. 7. Tab-level coral proportional yield by (a) damselfish abundance, (b,c) parrotfish feeding (IP: initial phase), and (d–g) benthic constituents. Mean estimates with 95% CI are displayed. Only relationships with credible correlations are plotted (Table S10). Note data are given per site (a) and per experimental plot (b–g)

yield, while branching and tabulate *Acropora* had weakly negative effects (Table S10). Tab yield was not correlated with site-level sediment deposition quantified from the deployed sediment collection pods (Fig. S4, Table S10).

4. DISCUSSION

After an 11 mo coral seeding trial, the yield of *Acropora millepora* spat varied within and among sites and was generally comparable to prior *Acropora* seeding experiments on the GBR (Randall et al. 2021, 2023, Page et al. 2024, Whitman et al. 2024, 2025, Jurriaans et al. 2025). We initially hypothesised that no-take reserves would influence spat survival; however, no consistent patterns related to reserve status were observed. Instead, site-specific and fine-scale interactions with fish and benthic constituents were the primary determinants of seeding success. Based on the emerging results, we propose 4 recommendations for coral seeding on reefs comparable to those examined here: (1) select both fished and unfished reserves for coral deployments; (2) within reserves, prioritise sites with moderate-to-high damselfish abundance (60 to 200 individuals in 39.25 m^2) and avoid those with intense scraping activity by parrotfish (>20 bites min^{-1} in 0.25 m^2); (3) within sites, avoid sediment-laden substrata and erect, fleshy macroalgae, and place devices adjacent to non-*Acropora* corals such as *Pocillopora* (>15% cover in 0.25 m^2); and (4) in the presence of parrotfish, employ seeding devices with protective features. Collectively, these recommendations underscore the importance of considering local fish assemblages and benthic structure when planning coral seeding interventions (Humanes et al. 2025). The ecological mechanisms underlying these guidelines are elaborated on in the following sections.

4.1. Coral yield and reserve status

The lack of a clear effect of marine reserve status on coral yield was generally consistent with other studies (McClanahan et al. 2005), suggesting both fished and unfished reefs may support future coral seeding initiatives. However, region- and site-specific factors warrant consideration. In Australia, coral groupers *Plectropomus* spp. and large snappers *Lutjanus* spp. are heavily fished, while key grazers, such as parrotfish and other herbivores, are comparatively less exploited (Russ & Alcala 2003, Williamson et al. 2004, Bode et al. 2025). Consistent with this, we observed minimal variation in parrotfish and rabbitfish abundance by reserve type, but a high prevalence of damselfish on fished reefs, potentially reflecting top-down predator removal (Sackley & Kaufman 1996, Ceccarelli et al. 2006). Moreover, no-take reserves, including those selected within our study region, sufficiently supply predatory fish biomass to neighbouring reefs, regardless of their reserve status (Bode et al. 2025). Consequently, seeded coral yield could change on reefs (1) where parrotfish and other grazers are heavily fished, and/or (2) when fished zones are not receiving flow-on benefits from no-take reserves. In support of this, line fishing on Kenyan reefs directly increased herbivorous urchin abundance, which then indirectly led to low coral recruit density via the reduction in settlement-inducing CCA (O'Leary et al. 2012). These results highlight the importance of investigating fish—benthic interactions by environment dynamics within reserves to better tailor our coral seeding efforts to sites.

4.2. Coral yield and herbivorous fish

Sites abundant with herbivorous damselfish yielded more corals than those with abundant and actively feeding parrotfish. Larger populations of herbivorous damselfish (*Pomacentrus wardi* and *P. adelus*) may support coral growth and survival through (1) mitigating coral competitors by cropping or removing macroalgae and turfs (Ceccarelli et al. 2001, Randazzo Eisemann et al. 2019), and (2) defending corals by excluding corallivorous, scraping, and excavating fish from their territories (Eurich et al. 2018, Tiddy et al. 2023, Stier et al. 2025). Observations of high feeding by damselfish at Miall Island and increased damselfish aggression at Mazie Reef support these hypotheses. However, *P. wardi* feeding was only positive for coral yield when the most protective fish-exclusion device was used. Seeding unprotected corals in proximity to herbivorous blennids *Ecenius* spp. was also negative to yield on the offshore GBR (Whitman et al. 2025). Developing devices that fully exclude small fish (Baria et al. 2010, Trapon et al. 2013, Whitman et al. 2024) and deploying them both inside and outside fish territories represents a logical next step to improve survival, particularly as these coral—fish dynamics are expected to shift under climate change (Doropoulos et al. 2012).

Only 1 site, Home Reef, experienced high feeding pressure from the scraping parrotfish *Scarus rivulatus*, which coincided with the lowest coral yield. Three site-specific factors may explain this outcome. Firstly, leeward reefs like Home Reef typically have limited waterflow, supporting less parrotfish biomass (Bellwood & Wainwright 2001, Hoey & Bellwood 2008) and less diverse parrotfish foods (Clements & Choat 2018). Such food limitations can increase grazing-induced coral predation post seeding (Whitman et al. 2024, 2025) and are indicative of site-specific coral survival across reserves with variable fishing pressure (McClanahan et al. 2005). Secondly, Home Reef includes small patches of live reef separated by unconsolidated sediments and sand, potentially confining parrotfish herbivory to the consolidated area where devices were seeded. The low survival on control devices and the localised feeding behaviour typical of *S. rivulatus* (Bonaldo & Bellwood 2008, Welsh & Bellwood 2012) support these first 2 hypotheses.

However, thirdly, oceanographic conditions, such as waterflow, vary independently of reserve status (Wenger et al. 2015, Graham et al. 2020) and can strongly influence site-specific coral survival (Hancock et al. 2021, Whitman et al. 2025), fish assemblages (Benthuysen et al. 2022, Galbraith et al. 2023), and the environmental conditions produced from grazing. Parrotfish enhance bioerosion during feeding (Bellwood 1996, Welsh & Bellwood 2012), with the resulting sediments causing coral mortality via abrasion and smothering (Fabricius 2005, Heyward et al. 2024, Whitman et al. 2025). These rates of erosion are highest on patch reefs dominated by branching *Acropora* corals (Yarlett et al. 2021); these corals are common at Home Reef but are also broadly indicative of sites across the study region (Heyward et al. 2024, Page et al. 2024). Parrotfish-induced bioerosion may have thereby lowered coral yield at Home Reef, even when protective devices were employed. In support of this, the combined effects of feeding by excavating parrotfish *Chlorurus* spp., the suspected accumulation of bioeroded sediments, and limited water flow correlated to post-seeding mortality on the offshore GBR (Whitman et al. 2025). Further investigation into coral—fish by sediment—waterflow interactions could lead to improved seeding strategies for inshore, branching *Acropora*-dominated reefs.

4.3. Coral yield and benthic communities

Sediment-laden surfaces and those with erect macroalgae (*Sargassum* and *Colopomenia* spp.) yielded less corals than those with *Pocillopora* corals. Given the known harmful effects of sediments (Fabricius 2005, Jones et al. 2015, Ricardo et al. 2017) and macroalgae (Webster et al. 2015, Ritson-Williams et al. 2020) on recruiting corals, it is not surprising that these factors negatively impacted seeding. For example, the foliose macroalgae *Sargassum* and *Dictyota* spp. can abrade, release toxic chemicals, and block light, thereby hindering coral growth and survival (Jompa & McCook 2003, Kuffner et al. 2006, Paul et al. 2011). Seasonal and fast-growing *Colpomenia* can engulf small corals, increasing the likelihood of competition-driven mortality (McCook et al. 2001). And even low-lying *Lobophora* spp., that were less harmful to seeded corals in this study, can damage *Acropora* spat under direct contact (Fong et al. 2024). Macroalgal cover is also more harmful to coral recruits than seasonally induced sediment accumulation (Mwachireya et al. 2015), typical of inshore turbid reefs (Fabricius 2005, Jones & Berkelmans 2014). Consequently, seeding decisions that minimise contact with macroalgae are recommended. The manual removal of macroalgae (Smith et al. 2022, 2025) could also be trialled at seeding sites with significant coral—algal regime shifts.

Pocillopora corals were often found where *Acropora* corals were absent, which may help explain their positive association with seeded-coral yield. Emerging evidence suggests that non-*Acropora*-dominated reefs and those with low-relief morphologies (e.g. encrusting forms) may provide more favourable conditions for coral recruitment and seeding (Madin et al. 2014, Page et al. 2024, Whitman et al. 2025). More specifically, *Pocillopora* are more frequently targeted by corallivorous fish compared to *Acropora* (Rotjan & Lewis 2008, Bonaldo et al. 2012), and this could have reduced direct predation on the *Acropora* corals seeded in our study. Additionally, *Pocillopora*-dominated reefs are often associated with reduced fish functionality and richness (Richardson et al. 2018, Russ et al. 2021, González-Barrios et al. 2025). This may lessen coral predation via a reduction in corallivore diversity, thereby favouring the survival of recruiting spat. While the role of *Pocillopora* and other taxa in mediating coral recruitment requires further study, avoiding *Acropora*-dominated plots and targeting sites with greater taxonomic diversity may enhance seeding efficiency in the interim.

4.4. Coral yield and device design

Fish-exclusion devices only improved coral yield at 1 site in our study. However, we tested 2 variants of a fish-exclusion device, with the exclusion star facilitating twice the survival of the exclusion triangle at this site, and more consistent yield across sites and device types overall. In agreement with results obtained for other coral-seeding devices (Randall et al. 2021, Whitman et al. 2024, 2025, Smith et al. 2025), we believe the protective features of the exclusion star adequately reduced pressure from parrotfish grazing and macroalgal abrasion. But the lack of an effect with the exclusion triangle could suggest that larger features or, consequently, more protection is required to fully eliminate the negative effects of fish or other environmental variables. For example, deployed corals show increased survival when fully enclosed in a protective cage (Baria et al. 2010, Trapon et al. 2013, Whitman et al. 2024) and when longer protrusion features are used (van der Steeg et al. 2025). Further reducing the size of the exclusion aperture provides one example of how to mimic the benefits of a cage without the additional application of a secondary feature. Elevated device structures, such as metal frames (Vida et al. 2024) and rods (Page et al. 2024, Smith et al. 2025), could also be trialled to further reduce direct algal competition, sediment smothering, and/or abrasion. If tested in combination, these device modifications may improve our coral seeding efficacy.

5. CONCLUSIONS

These results improve our understanding of the fine-scale ecological drivers influencing coral survival and seeding efficacy. Foremost, the boundaries defined by marine reserves did not predict survival outcomes. Instead, when assessing a site for seeding, the fine-scale fish and benthic assemblages must be considered. The recommendations outlined in our study can be used as a part of our coral-seeding toolkit to establish sites, while helping to refine no-take reserve boundaries to protect fine-scale drivers that aid in coral reef recovery. While these findings are based on a single coral species and location, similar trends are emerging for different species and environments. Testing across new species, reef habitats, and locations is essential for advancing coral-seeding technologies for widespread reef restoration. Safeguarding coral futures requires not only ecology-driven restoration, but also the implementation of best-practice reef management alongside substantial cuts to global carbon emissions.

Data availability. Data are available through the Australian Institute of Marine Science online public repository: https://apps.aims.gov.au/metadata/view/bbf15cd5-3835-4b91-83c8-924908da6faf.

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