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Research article

Sea-weeding enhances early coral survival on seeding devices, but benefits of seeding diminish after one year

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ABSTRACT

Borrowing from principles of aerial seeding in terrestrial reforestation, coral seeding utilises “devices” designed to increase coral spat survival. However, device-assisted coral survival has not been compared to natural survivorship, nor have devices been trialled in environments with strong competitors such as macroalgae. Herein, we deployed seeded devices alongside terracotta tiles, a proxy for natural coral recruitment dynamics. Tiles and devices were deployed to plots examining ongoing macroalgae removal (“sea-weeding”), and survival was monitored over two years. First-year coral survival was enhanced on devices compared to natural survival, and devices conferred the greatest survival benefit when deployed in areas where “sea-weeding” was undertaken. However, over the second year, the benefits of sea-weeding for device-assisted survival were lost, with no significant difference in survival on devices in control versus weeded plots. On average, devices retained 1.3 surviving colonies at two years, which was lower than naturally-occurring juvenile density in removal plots, but higher than control plots. Several factors influenced survival, including the starting spat density, orientation of deployment surface, and site. After two years, 50 % of devices yielded one live coral, but site-based survival varied between 37 % and 93 %. The estimated cost per surviving coral varied when accounting for site-based survival (high survival: \$334 coral^{-1}; low survival: \$577 coral^{-1}), which could be reduced via future efficiencies. The results of this study inform the potential outcomes of coral seeding on macroalgae dominated reefs, and highlight that assessing survival up to one year is not sufficient to measure long-term restoration goals.

1. Introduction

As coral reefs continue to degrade under the pressures of the Anthropocene (Hughes et al., 2017; Eyre et al., 2018; Heron et al., 2016), direct restoration and intervention strategies are rapidly being developed to assist their survival (Anthony et al., 2017; Bay et al., 2019; Knowlton et al., 2021). Large scale coral reef restoration efforts face many challenges, chief among them is overcoming high rates of early life stage mortality (Boström-Einarsson et al., 2020; McLeod et al., 2022; Knowlton et al., 2021). A type-III mortality curve (i.e., high early life stage mortality) is well established in corals (Hughes et al., 1992; Penin et al., 2010), with processes such as competition for benthic space and resources (Box and Mumby, 2007; Hughes et al., 2007; Vermeij and Sandin, 2008), sediment smothering (Babcock and Smith, 2000; Jones et al., 2015), and corallivory by fishes (Penin et al., 2010, 2011; Baria et al., 2010; Gallagher and Doropoulos, 2017) among the variables underpinning low survival rates.

Coral seeding, a reef restoration technique in development, mirrors a terrestrial method known as aerial reforestation or “seed-bombing.” In aerial reforestation, a mixture of organic material, plant seeds, and water bound together in a pod, sheath, or dart, are released from an aircraft over target restoration areas (Mohan et al., 2021; National Research Council, 1981). Optimisation of aerial reforestation considers aspects such as payload (size and number of seeds/seedlings (Novikov

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and Ersson, 2019)), addition of fertiliser (Wood, 2000), delivery strategy (type of aerial vehicle, altitude, speed (Ortolani et al., 2015; Novikov and Ersson, 2019)), and sheath characteristics (e.g. shape, biodegradable, (Cozens, 2019); self-burying (Luo et al., 2023)). While literature on the successes of aerial reforestation is limited (reviewed in Mohan et al., 2021; Castro et al., 2023), there have been some examples of aerial reforestation delivering ecologically relevant results. For example, aerially seeded forests of *Pinus massoniana* developed similar carbon stock levels to local natural forests (Xiao et al., 2015). Similarly, despite complex temporal patterns, aerial seeding of barren gravel flats in Iceland achieved an increase in plant cover and native plant diversity (Greipsson and El-Mayas, 1999), and aerially seeded sagebrush was successful in establishing sagebrush cover and limiting encroaching juniper growth (Davies et al., 2014).

The success of aerial reforestation in transforming some terrestrial ecosystems on an ecological-scale raises the opportunity to apply the same principles to analogous systems such as coral reefs (Reaka-Kudla, 1997; Knowlton et al., 2010). The considerations to increase survival of young plants in aerial reforestation are similar to those for juvenile corals, as these taxa share similar life history traits and early life-phase challenges (Darling et al., 2012). For example, like many species of plants' seeds are subject to wind patterns to disperse (Howe and Smallwood, 1982; Kuparinen, 2006), broadcast spawned coral larvae disperse through ocean currents and multi-scale hydrodynamic processes (Willis and Oliver, 1990; Thompson et al., 2018; Oliver et al., 1992). These passive dispersal modes can deliver seeds and larvae to areas with unfavourable substrata (Snyder, 2006; Jones et al., 2015), or to areas which lack the nutrients to induce germination (Soltani et al., 2022) or cues for settlement and metamorphosis (Whitman et al., 2020; Heyward and Negri, 1999). Once sprouted or metamorphosed, juvenile plants and corals are both subject to post-settlement stressors such as predation (Penin et al., 2011; Molofsky and Fisher, 1993), which makes reaching a size-escape threshold a critical point in early life for both corals and plants (Doropoulos et al., 2012, 2016).

Translating the principles of aerial reforestation to coral reefs, coral seeding involves the use of specially designed devices or seeding units populated with coral spat prior to field deployment to increase both delivery and survival post-deployment (Randall et al., 2020). Coral seeding via devices overcomes some of the challenges of delivering coral juveniles to reefs through direct larval cloud seeding (Edwards et al., 2015), such as a lack of suitable settlement substrate or settlement cues. After delivering juveniles to reefs, engineered refugia in devices may increase coral survival through protection from predators (Whitman et al., 2024; Randall et al., 2021) or other environmental influences (Page et al., 2024; McLeod et al., 2022; Randall et al., 2021). However, there has not been an explicit comparison of assisted survival (on seeded devices) compared to unassisted, natural settlement and survival, with studies instead focussed on comparing survival among device shapes/designs and environmental gradients (Whitman et al., 2024; Randall et al., 2023; Page et al., 2024). While measuring natural survival is a challenge, well-established proxies (e.g., settlement tiles; Edmunds, 2023) can help to fill critical knowledge gaps regarding how corals seeded on engineered devices perform relative to natural substrata. Furthermore, most coral seeding studies to date have been approximately 12 months or less in duration, partly based on the assumption that surviving the first year suggests the coral juvenile has escaped the major forces of early life stage mortality. Based on this assumption, one metric of seeding success is currently defined as having one live juvenile at one-year post-deployment. However, it remains unknown if coral seeding devices enhance longer-term coral survival, leaving a critical knowledge gap that underpins implementation of coral seeding at large scales.

For both aerial reforestation and coral seeding, additional challenges arise when the target environment is host to competitive species. It is difficult for plants to establish dominance where other plants are highly abundant; hence, aerial reforestation has often been tested in conjunction with the removal of unwanted dominant organisms through mowing, weeding, or prescribed burning (Knutson et al., 2014; Davies et al., 2014; Davies and Bates, 2014). Because the mechanisms of competition for corals and plants are similar (e.g. competition for light for photosynthesis; competition for space, etc.), we could expect that coral seeding will face similar difficulties on reefs with abundant competitors such as macroalgae. As coral reefs degrade, rapidly recruiting and growing macroalgae have a competitive advantage, with shifts from coral dominance to macroalgal dominance being observed on reefs worldwide (Souter et al., 2021). Macroalgae have well known competitive interactions with corals that generally favour macroalgal proliferation: macroalgae can reduce coral fecundity (Monteil et al., 2020; Tanner, 1995), inhibit or prevent coral settlement and metamorphosis through biochemical release (Evensen et al., 2019; Page et al., 2023; Fong et al., 2019) and/or space pre-emption (Smith et al., 2022a), and can harm corals directly through abrasion (Manikandan et al., 2021), allelopathy (Rasher et al., 2011), and alterations to associated microbiota (Morrow et al., 2011, 2016). Hence, on reefs where macroalgae dominate, corals are unlikely to regain dominance, and may require intervention. Indeed, removal of macroalgae can increase coral settlement (Smith et al., 2022a), with flow-on effects on coral cover (Smith et al., 2023). However, where significant degradation has occurred, sufficient coral larval supply does not exist, and post-settlement survival of corals is low, additional intervention strategies may be required. In these cases, coral seeding may be beneficial, but it is critical to understand how seeded corals perform in the presence of macroalgal competition, and to determine if there are positive synergistic interactions between removal of macroalgae and coral seeding.

In this study, we deployed coral seeding devices populated with juvenile *Acropora kenti* corals to experimental field plots on two macroalgae-dominated reefs at Yunbenun (Magnetic Island), in the central Great Barrier Reef. Half of the plots have been cleared of macroalgae twice yearly since 2018, with the other half acting as controls. To test if devices enhance coral survival, we compared survival on devices with survival of natural, unassisted settlers on terracotta tiles over one year. To understand how devices perform over a longer term, we continued monitoring survival of corals on devices quarterly over approximately two years and compared survival between macroalgal-removal treatments. We also compared densities of surviving corals on seeded devices with naturally occurring juvenile densities in control and removal plots. Finally, the cost of seeding was estimated per-surviving-coral accounting for differences in survival between sites. The results of this study inform the potential success of coral seeding devices in rehabilitation of macroalgae-dominated nearshore reefs.

2. Methods

2.1. Field experimental design

Twelve 5 m × 5 m plots were established in each of two bays (Florence Bay, Arthur Bay) on the inshore fringing reefs of Yunbenun (total n = 24 plots). Half of these (n = 6 plots per bay) were randomly assigned as "control" plots, while the other half were assigned as "removal," where all fleshy macroalgae were removed by hand. Macroalgae were removed in October 2021, July and October 2022, May and July 2023. Site characteristics are described in Smith et al. (2023).

At multiple time points through the experiment (Supplementary Table 1), *in situ* surveys were conducted to quantify macroalgae density and height as previously described (Smith et al., 2022a,2022b). Briefly, within each 25 m^2 plot, *Sargassum* holdfast density and height were used to estimate biomass in each plot using the formula (Hoey, 2010):

$$\text{Wet weight } [\text{g m}^{-2}] = 0.5637\ [\text{g cm}^{-1}] \text{ x height } [\text{cm}] \text{ X density } [\text{num m}^{-2}]$$

2.2. Brood stock collections, coral spawning, and larval rearing

Approximately seven weeks prior to coral spawning (6 September 2021), 2 cm diameter circular aragonite plugs were placed in outdoor aquaria for "conditioning" – to develop biofilm and recruit crustose coralline algae (a settlement inducer; Whitman et al., 2020; Heyward and Negri, 1999) – in the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS). Filtered seawater (0.45 μm) was supplied to tanks at a constant temperature (28 °C) with low light (using shade cloths) and high flow rate.

Twenty adult colonies of *Acropora kenti* containing visibly pigmented oocytes were collected from Florence Bay (n = 9) and Arthur Bay (n = 11), Yunbenun, on 19 October 2021, and transported in 60 L containers of seawater to SeaSim (permit G19/42897.1, issued by the Great Barrier Reef Marine Park Authority). This species has some morphological deviations from the *A. kenti* voucher specimen and is therefore named *Acropora* sp. nov. aff. *kenti,* but abbreviated to *Acropora kenti* herein. Colonies were maintained in outdoor aquaria under ambient light, with water temperatures matched to seawater temperature from Geoffrey Bay, Yunbenun. At sunset each night after the full moon, and upon visual identification of setting, colonies were isolated into individual tanks for spawning. On the night of 24 October 2021, 4 nights after the full moon, 14 parent colonies spawned and their gametes were collected.

Gametes from each colony were kept separate, eggs were separated from sperm, and oocytes rinsed multiple times. Gametes from all colonies were then combined in a 60 L container for fertilisation. After 1 h, embryos were collected, rinsed, and split amongst three 500 L culture tanks, where they were maintained in filtered seawater at 28 °C until competent to settle. Competency was assessed using established methods (see Whitman et al., 2020), and $>$ 90 % competency was reached at a larval age of 7 days.

Approximately 2500 larvae were placed in each 48 L tank (n = 16 tanks) containing pre-conditioned aragonite plugs (n = 165 plugs per tank) fitted into unconditioned plug trays. After 48 h, twenty haphazardly selected plugs per tank were examined for successful larval settlement. All plug trays were then transferred to a 1000 L indoor tank, and supplied with filtered seawater matching the Geoffrey Bay seawater temperature profile. For the first week, the tank was exposed to a maximum of 33 PAR lighting, then ramped daily to a maximum of 300 PAR at deployment. Fragments of adult broodstock were placed in the tank to supply native Symbiodiniaceae to the developing spat (Nitschke et al., 2016).

Prior to deployment, plugs were inserted into triangular ceramic "devices" (Shanghai Gongtao Ceramics Co., Ltd; designed by AIMS), labelled with unique numbers to allow tracking of individual plugs through time. Devices were designed with protrusions intended to provide coral spat refuge from grazing/predation by herbivorous fishes (see Whitman et al., 2024 for full device design details). Three plugs (one with juveniles from each 500 L culture tank) were placed in the upward-facing ("top") position, and three in a side-facing ("side") position. Plugs with the highest number of individual spat were selected visually. All plugs were photographed in their device using a Nikon D810 camera prior to deployment.

The number of individuals per plug was counted from photographs using the manual class counting function in the microscopy software Capture (version 2.2). All individuals were counted and classified as aggregates or singletons, and if aggregates, the number of polyps were counted. Aggregates were defined as two or more polyps with shared tissue between them (Supplementary Fig. 1). At this life stage (approx. 2 weeks after settlement), it is likely that aggregates resulted from close settlement and fusion of distinct individual larvae, rather than growth of a single settler.

2.3. Deployment and monitoring

On 24 November 2021, seeded devices were transported to the field by boat in 100 L containers filled with seawater. Within each of the twelve 25 m^2 experimental plots per bay, five devices were haphazardly installed onto stainless steel threaded rod hammered into the benthos (total n = 60 devices per bay; under GBRMPA permit G21/45348.1). Devices were deployed as close to the reef substrate as possible, though not touching the substrate. Following deployment, the devices were censused approximately every three months for 21 months (for exact census dates see Supplementary Table 1). Censusing was completed visually by a SCUBA diver, whereby each device was unscrewed from its rod, each plug closely examined for live corals, and scored 1 for presence of any live, and 0 for no live *A. kenti* coral (Fig. 1). Wild recruits that had settled on the devices were also counted, determined visually as corals that did not match *A. kenti* morphology (Supplementary Fig. 2), acknowledging that wild *A. kenti* may also have settled on devices. Wild recruits were excluded from survival analyses.

At the final census (20 August 2023), devices were removed from experimental plots and transported to SeaSim in 100 L containers filled with seawater. Each device was photographed and closely inspected to count individual seeded *A. kenti* survivors. Individuals were identified as colonies that were homogenous in appearance and had a visible boundary between other colonies and/or an allogenic response could be visualised where boundaries were shared (Supplementary Fig. 2). Each individual was measured (maximum length, perpendicular width, height) in mm using digital callipers.

2.4. Assessment of natural recruitment and survival

To compare device-assisted coral survival to natural survival, we also deployed 11 cm × 11 cm × 1 cm terracotta tiles to the experimental field plots (n = 10 haphazardly placed tiles per plot, total 240 tiles). While terracotta tiles are not natural substrata, they are commonly used as a proxy to assess natural recruitment dynamics (Edmunds, 2023) and are used herein for that purpose. Tiles were deployed between 24–27 August 2021, and installed the same way as seeded devices (i.e., screwed onto a threaded stainless-steel rod hammered into the benthos). Tiles were labelled with unique numbers to enable tracking of individual tiles and retrieved for censusing three times within the first year of device deployment (Supplementary Table 1), at similar times as device censuses. At each census, the tiles were unscrewed from their rods, transported to land in 100 L bins of seawater, all live corals counted and photographed under a Nikon SMZ745 photomicroscope, then tiles were returned to their original position within each plot. All tiles were returned to their field locations within 24 h of being collected, and while on land were maintained at a constant temperature, with aeration from battery operated aquarium pumps. The tiles were removed for final census on 13 September 2022.

An increase in the total number of coral spat was observed between the first (November 2021) and second (February 2022) tile censuses, suggesting that an additional mass spawning event had occurred in December 2021 at Yunbenun. To allow a more meaningful comparison between tiles and devices, the tile dataset was filtered to include only tiles that had a live juvenile in November 2021 (n = 163 tiles), hence excluding tiles that had zero live juveniles in November, but $\geq$1 juvenile in February (n = 34) or September 2022 (n = 15).

We also conducted *in-situ* surveys to compare end-point survival on devices to juvenile densities on natural substrata in October 2023. Within each of the twenty-four 25 m^2 experimental field plots, the number of juvenile corals $\leq$4 cm diameter was counted within each of three, haphazardly thrown replicate 1m × 1m quadrats. This number was compared with the number of surviving individuals on devices after 21 months deployment (individuals defined as above; comparison assumes a deployment density of one device m^{-2}), and between control and removal plots.

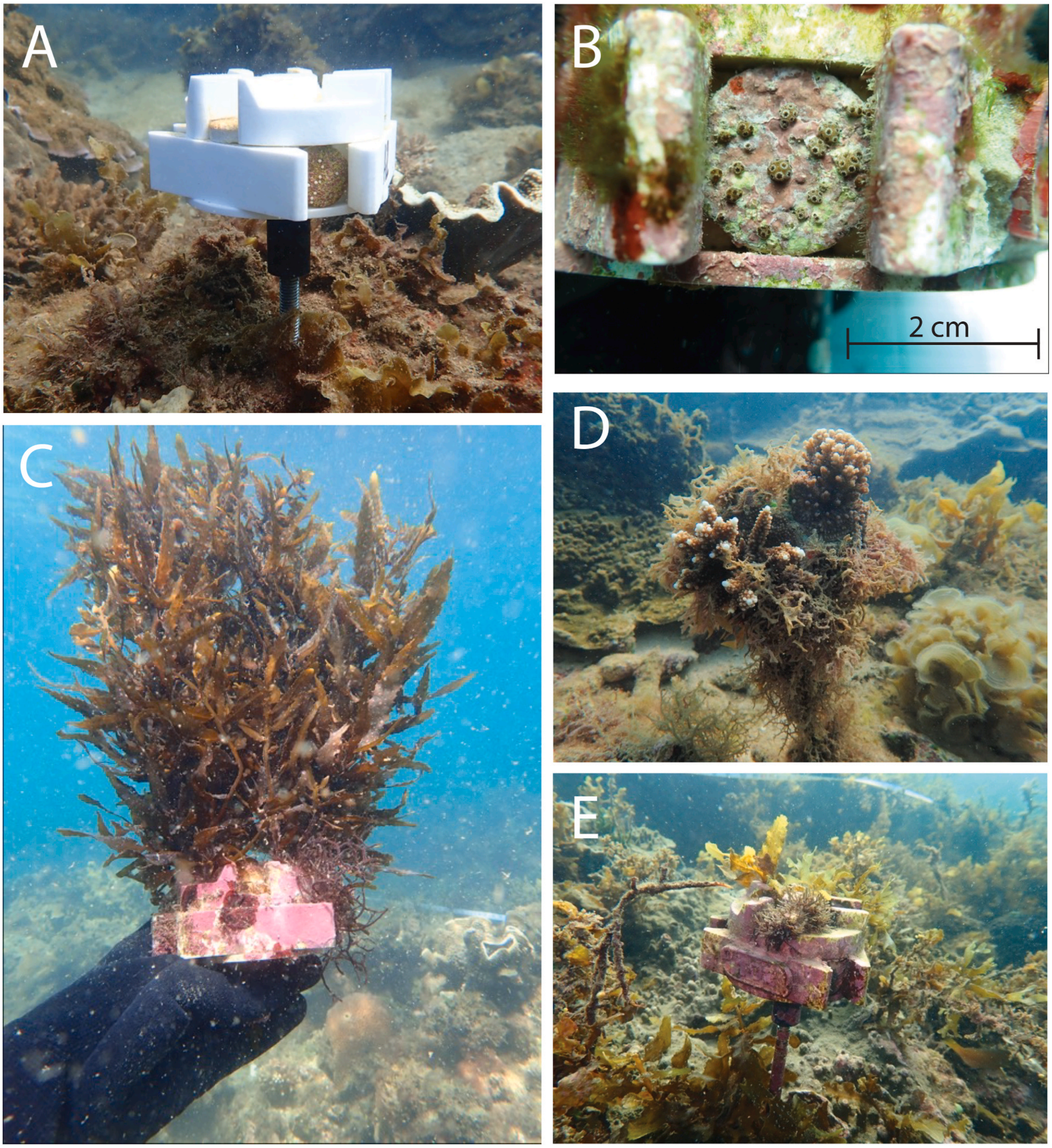

Fig. 1. *In situ* images of devices (containing inserted seeded plugs) showing A) deployment in November 2021. Diverse taxa colonising the device surfaces in B) February 2022, C) August 2022, and D) August 2023. E) May 2022. Censusing was completed visually for each plug by examining between the device grooves for presence of live coral juveniles, as shown in B. For detailed device design and composition details, see Fig. S1 in Page et al. (2024).

2.5. *Statistical analyses*

All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2021). Survival was quantified as a presence (1) or absence (0) of at least one live juvenile on each plug ("plug-level survival") or device ("device-level survival") at each time point. Plug- and device-level yield (% of plugs and devices, respectively, with at least one surviving coral) has been used in previous studies (Randall et al., 2021, 2023) and is used here given the challenges of counting the exact number of surviving juveniles *in-situ*, particularly where fusion of juveniles has occurred. Additionally, the end goal of coral seeding devices is to have a live coral survive to contribute to the existing coral population. Hence, if there remains at least one surviving coral, that end goal remains achievable.

Plug-level survival was modelled using generalised linear mixed effects models (GLMMs), where $y_{i,t}$ is the state (alive, dead) of plug i at time t. The probability of mortality p of plug i at time t is modelled using a Bernoulli distribution, where $p_{\mathrm{i,t}}$ is modelled as:

$$y_{i,t} \sim \mathit{Bernoulli}(p_{\mathrm{i,t}})$$

$$\mathrm{Logit}(p_{i,t}) = \beta_0 + \beta_1 \mathit{treatment}_i + \beta_2 \mathit{survey}_i + \beta_3 \mathit{bay}_i + z_i + N_t$$

Where z_i is a nested random effect to account for individual variation between plugs, devices, and plots; β is the coefficient of each predictor; and N is an offset for the number of plugs surveyed at time t to account for differences in device recovery (see Supplementary Fig. 6).

Device-level survival was modelled with the same formula, though $y_{i,t}$ denotes the state (alive, dead) of device i at time t; z_i is a nested random effect accounting for individual variation between devices and plots; and N is an offset for the number of devices surveyed at time t

(Supplementary Fig. 6). Model selection for both plug-level and device-level survival was informed using the Akaike Information Criterion, adjusted for small sample size. Selected models for both plug- and device-level survival were validated using simulated residuals plots, which were satisfactory in all cases.

Previous work has demonstrated that gregarious settlement of multiple polyps into aggregates can result in increased survival (Amar et al., 2008; Randall et al., 2021). To test if starting aggregate size increased endpoint survival probability, we modelled endpoint plug-level survival (0/1) as a function of the maximum aggregate size at deployment (i.e. the maximum number of polyps involved in a single aggregation per plug), using a binomial distribution and logit link. Model selection and validation were as described above.

Survival on devices through time was compared to survival on tiles using only the overlapping census dates (i.e., November 2021, February and September 2022), and by filtering the tile dataset as described above. The model had the same structure as described above, with an additional additive predictor for "substrate type" (tile or device).

The number of survivors on devices was compared to juvenile densities on natural substrata using a GLMM, with the number of juveniles modelled as a function of treatment (control or removal) and substrate type (*in-situ* quadrat or device), using a Poisson distribution and log link. Comparison of these metrics assumes a deployment density of one device m^{-2}. Model selection and validation were as described above.

To determine if the number of initial settled spat influenced survival on tiles and devices, we modelled the probability of endpoint survival (0/1) as a function of starting number of juveniles, separately for tiles and devices. Both models implemented the number of starting spat and treatment as fixed factors, and a random factor for unit ID (tile/device) nested within plot, nested within bay. Both models used a binomial distribution and logit link, and were validated as described above.

To optimise future seeding efforts, we estimated the ideal number of spat needed for devices to have a 90 % chance of endpoint yield within control and treatment plots separately. We used lethal dose (LD) analysis, a measure common in toxicology that indicates the dose of a substance required to kill a given proportion of members of a tested population. For example, an LD_{50} is the dosage where the probability of death is 50 %. Here, we determined the point at which the probability of survival is 90 % (i.e., LD_{90}) given a starting "dose" (i.e., number of spat). In other words, we examined how many individual spat are required to be seeded prior to deployment to have a 90 % chance of survival at the device-level at the end of the study (August 2023; n = 101 devices). In this analysis, the number of individuals is defined as the number of polyps, regardless of whether the polyps form part of an aggregate, as this number most accurately reflects the number of settlers. Additionally, the number of individuals is summed across all six plugs per device. This analysis was not completed for tiles, as the number of natural settlers cannot be controlled.

Finally, the size of survivors was calculated and analysed in two ways. First, the volume of each individual was calculated using length, width and height measurements, and differences in size assessed using a GLMM. The best fit model chosen using AICc incorporated only treatment (control/removal) as a fixed effect. Secondly, the length and width across the colony were used to provide a 2-dimensional size estimate. We chose this method to correspond with often used planar-view monitoring techniques for measuring coral cover. The total coral cover increase over two years was estimated by pooling the 2-dimensional sizes of all survivors.

2.6. Costing

The cost of deploying coral seeding devices was calculated following Iacona et al. (2018) including minimum required materials, labour, and operational costs for larval production and deployment only (Supplementary Table 2). Monitoring costs were not included, as upscaled seeding is unlikely/unable to include a monitoring component. Labour costs were estimated using the minimum required personnel per task, with an assumed salary of AUD $30/hr. Shipping costs of devices from the manufacturer were not included, as local manufacturing of devices is encouraged in upscaled deployment. Cost is reported three ways: 1) cost of implementation per device, estimated by dividing the total project cost by the number of devices deployed (n = 120); 2) cost per coral yield, estimated by dividing the total project cost by the number of devices with at least one surviving juvenile at the end of the project (n = 60); and 3) cost per hectare restored, with estimates for 'high and 'low' survival sites based on Arthur and Florence Bay model-estimated survival rates, respectively. For the cost per hectare, we assume a density requirement of four live colonies per square meter, or 40,000 surviving devices per hectare (following Bayraktarov et al., 2019). Based on the model-estimated survival rates observed here (93 % Arthur Bay; 37 % Florence Bay; 50 % averaged across sites), between 43,000 and 109,000 devices (average 80,000) would be required to populate 1 ha (see Supplementary Table 2), noting that our costing assumes labour, operational, and consumable costs scale in linear proportion to that required in this study, which is unlikely. All costs were calculated in local currency (AUD), converted to U.S. dollars using the contemporary (2019) exchange rate from the Penn World Table version 10.01 (1 USD = 1.44 AUD; 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 (1 USD at 2019 = 0.83 USD at 2010; The World Bank, 2023), following Bayraktarov et al. (2019).

3. Results

3.1. Algae biomass varied between treatments

Algal biomass (as measured during *in-situ* surveys) varied through time in the control and macroalgal removal plots, with peaks in both treatments aligning with known seasonal cycles (Fig. 2A). Florence Bay had consistently higher biomass of macroalgae for both *in-situ* surveys and removed biomass. Averaged across all five removal events, 8.59 ± 0.79 SE kg $plot^{-1}$ were removed from Arthur Bay, compared to 16.5 ± 2.43 SE kg $plot^{-1}$ from Florence Bay (Supplementary Fig. 4).

3.2. Pre-deployment juvenile densities on plugs

Prior to deployment, densities of spat on plugs ranged from 2 to 103 with an average of 18.8 ± 0.7 SE individuals per plug (number of total polyps per plug, whether part of an aggregate or not; Supplementary Fig. 5). There were no significant differences in the number of individuals between treatments (Control: 20.7 ± 1.0 SE individuals $plug^{-1}$; Removal: 17.0 ± 0.9 SE individuals $plug^{-1}$; $\chi^2 = 0.37$, df = 1, $p = 0.54$) or between plug orientation (Top: 18.2 ± 0.9 individuals $plug^{-1}$; Side: 19.4 ± 1.0 individuals $plug^{-1}$; $\chi^2 = 0.04$, df = 1, $p = 0.84$).

3.3. Coral survival was higher in removal plots than controls, and on devices than terracotta tiles

In November 2021, 1390 corals had settled on terracotta tiles (mean 3.2 ± 0.4 SE individuals per tile) and of these, 162 (11.6 %) individuals survived the first year (September 2022). In September 2022, 60 % of tiles had at least one live coral across treatments and bays, compared to 68.3 % of devices for the same time frame. There was a significantly higher probability of coral survival in removal plots compared to controls regardless of substrate (i.e. across tiles and devices; $z = 3.79$, $p < 0.001$) and on devices compared to tiles regardless of plot treatment ($z = -5.43$, $p < 0.001$; Fig. 2B).

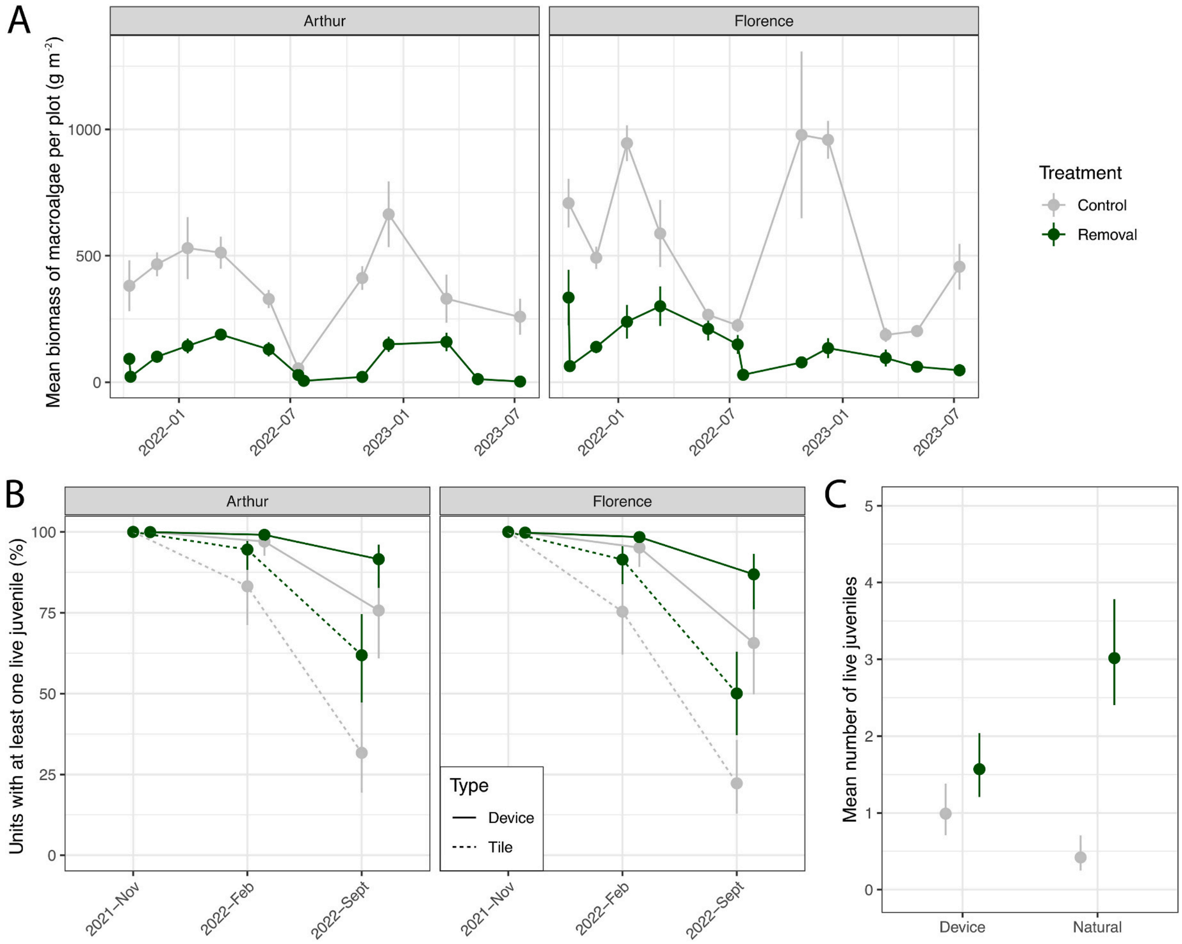

Fig. 2. A) Dynamics of macroalgae biomass through time. B) Dynamics of survival on devices (solid lines) and tiles (dashed lines) in Arthur and Florence Bays, in control (grey) and removal (green) plots. Points represent model estimated mean probability of survival, vertical lines represent 95 % confidence intervals. C) mean number of individuals at the final census on devices (left) and natural substrata (right), in control (grey) and removal (green) plots. Points represent model estimated mean number of individuals, vertical lines represent 95 % confidence intervals.

3.4. Devices enhanced in situ coral juvenile density in control plots but not removal plots

Of the 13,093 seeded individual coral juveniles on plugs, 114 (0.87 %) survived the duration of the 21-month experiment. Some survivors likely resulted from aggregated settlers, so the exact percent of individuals may be higher. A total of 101 wild-settled recruits across three genera (*Acropora, Montipora, Porites*) were observed on devices at the final census, with 75 of these occurring on devices from removal plots (Supplementary Fig. 2).

Notwithstanding differences in comparison metrics (i.e., number of individuals per device compared to number of individuals per m^2 of natural substrata), and assuming a deployment density of 1 device m^{-2} to substrata devoid of any naturally occurring juveniles, devices provided a significant increase in the density of juveniles in control plots compared to the natural substrate at the final census (1 juvenile per device compared to 0.5 juveniles m^{-2} on reef substrata in control plots; $t = 2.84$, $p = 0.026$; Fig. 2C). However, devices provided no additional increase to juvenile density in removal plots, with macroalgae removal alone resulting in a significantly higher density of naturally occurring juveniles (3.02 individuals m^{-2}) compared to survivors on devices (1.57 individuals device^{-1}; $t = -4.35$, $p < 0.001$; Fig. 2C).

3.5. Trends in seeded device survival: individual and plug-level survival was low and varied between top and side surfaces

At the final census, 121 plugs (16.8 %; combined total for both Arthur and Florence Bays) were populated by at least one surviving coral (Fig. 3A). While there was a similar endpoint survival across all surfaces (top vs side), treatments (control vs removal) and bays (Arthur vs Florence), the dynamics of survival were complex. For example, there was a rapid drop in survival on top-facing plugs at the first census following deployment (a 75.2 % reduction, across treatments and bays; Fig. 3A), but the same decrease in survival was not seen for side-facing plugs. At the final census, there was also a difference in survival dynamics between bays, with plugs in Florence Bay experiencing lower endpoint survival (11.4 ± 2.2 %) compared to Arthur Bay (28.4 ± 2.5 % averaged across treatments and surfaces). While there were few pairwise significant differences between treatments at selected timepoints, overall, there was no significant difference in plug-level survival between control and removal plots.

3.6. Trends in coral survival: device-level survival (yield) varied between bays

At the final survey, 60 devices (50 %) were populated by at least one surviving juvenile, across all bays and treatments (Fig. 3B). Devices in Florence Bay had significantly lower survival (37.4 ± 12.1 %, model estimated mean ± SE; averaged across treatments) compared to Arthur

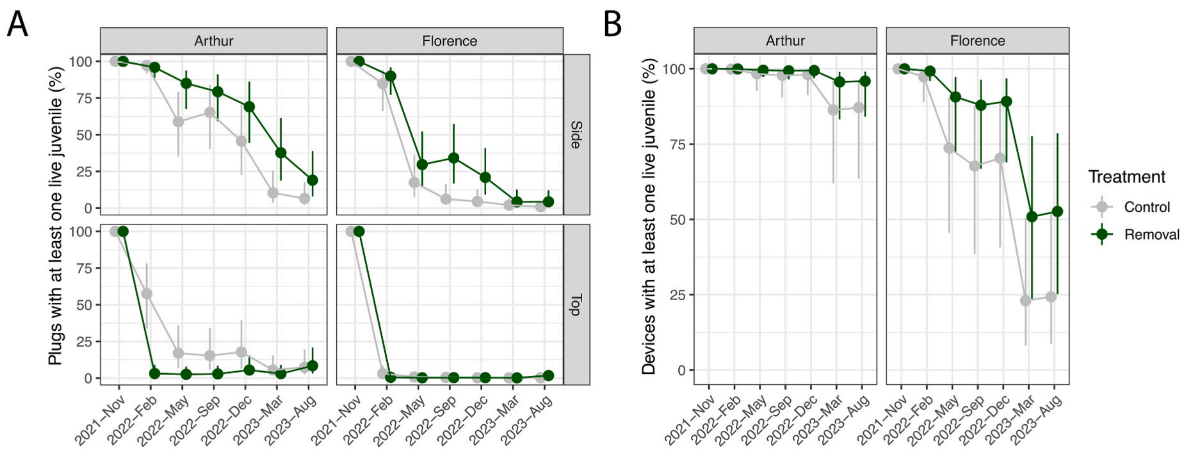

Fig. 3. A) plug-level survival on side- and top-facing plugs, and; B) device-level survival in Arthur and Florence Bays, in control (grey) and removal (green) plots. Points represent model estimated mean probability of survival, vertical lines represent 95 % confidence intervals.

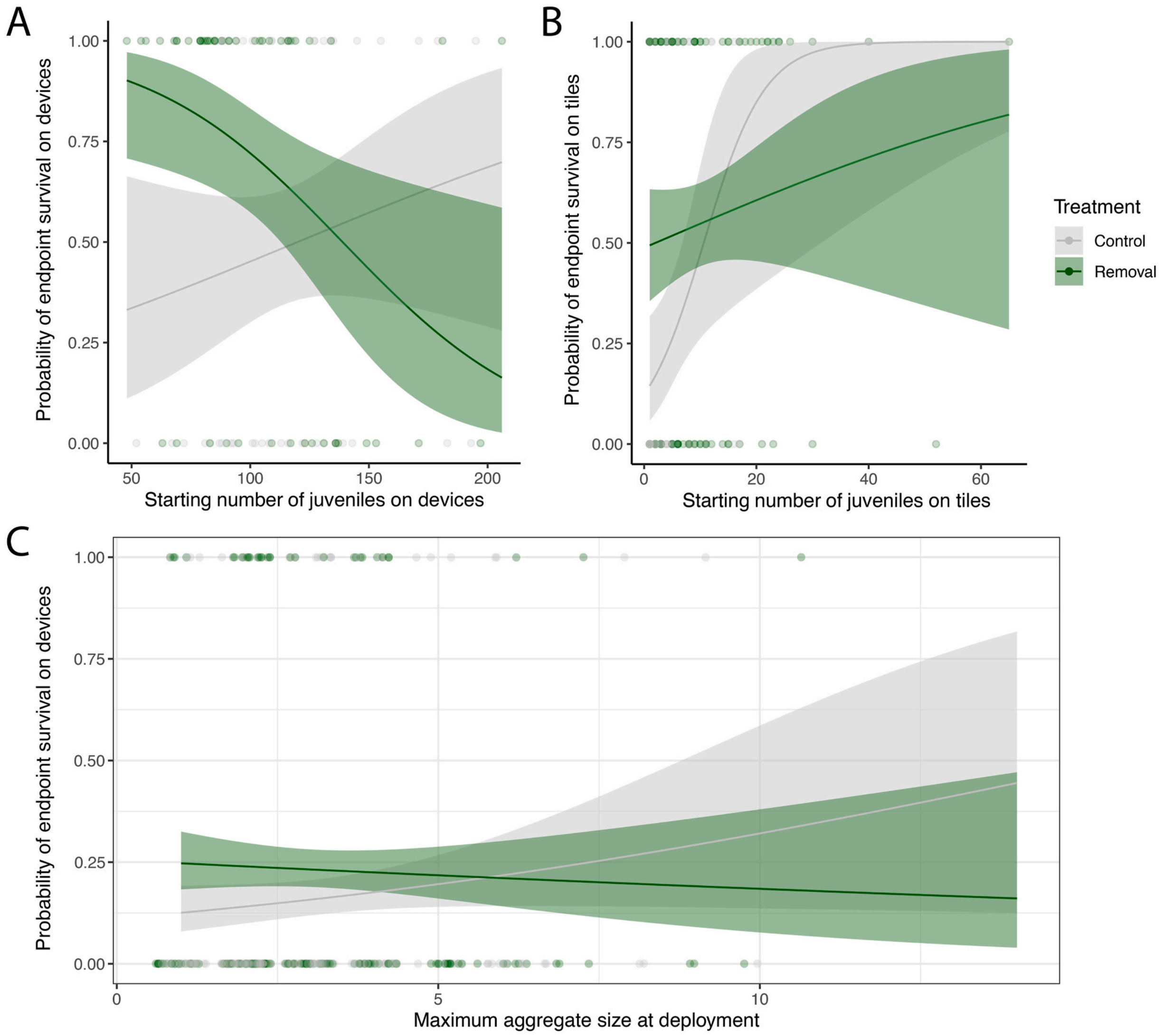

Fig. 4. A-B) The probability of endpoint survival varied significantly based on the interaction between the starting number of spat and treatment for A) devices (n = 101) and B) tiles (n = 148). C) The probability of having at least one surviving juvenile on devices did not vary based on the maximum aggregate size at deployment. Points are raw data, lines represent model estimated means, shaded ribbons represent 95 % confidence intervals. Control plots are shown in grey, removal plots shown in green. Note that x-axes differ between panels.

Bay (92.7 ± 4.4 %; $z = -4.16$, $p < 0.001$), and devices in removal plots had marginally higher survival (83.6 ± 8.0 %; averaged across bays) compared to control plots (59.6 ± 13.1 %; $z = 1.90$, $p = 0.058$). The greatest decline in survival was observed between December 2022 and March 2023 surveys, with a 56 % decrease in yield in Florence Bay. The fixed effects (treatment, survey date, bay) explained 85.9 % of the variability in yield (marginal $R^2 = 0.859$), with the random effects (plot) explaining an additional 8.9 % of variability (conditional $R^2 = 0.948$).

3.7. *Starting number of spat, but not aggregate size, influenced survival*

For both tiles and devices, the interaction between starting number of spat and treatment (control vs removal) had a significant effect on endpoint survival (tiles: $z = -2.08$, $p = 0.04$; devices: $z = -2.53$, $p = 0.01$; Fig. 4A and B), but the nature of the relationship was different. For tiles, both control and removal plots had positive slopes, and hence a greater number of starting spat was associated with a higher probability of survival in both treatments. For devices, there was a positive slope for control plot devices, and a negative slope for removal plot devices. This indicates a greater number of starting spat was associated with significantly increased survival probability in control plots, but a significantly decreased survival probability in removal plots. The number of spat needed for devices to have 90 % chance of endpoint yield (LD_{90}) was 7-fold higher (345.1 ± 222.0 spat per device) for devices deployed to control plots compared to removal plots (48.8 ± 27.2 spat per device). Plugs with a larger maximum aggregation size at deployment did not experience a significant increase in survival probability, irrespective of their deployment in removal or control plots ($z = 1.621$, $p = 0.105$, Fig. 4C).

3.8. *Corals grew larger in removal plots*

Based on 3-dimensional size measurements, there was a marginally significant difference in final colony size between control and removal plots ($z = 1.91$, $p = 0.056$; Supplementary Fig. 7), with removal plots harbouring larger individuals (49,468 ± 6897 mm^3, mean ± SE) than controls (31,131 ± 6258 mm^3). Based on 2-dimensional size measurements, devices added a cumulative 0.12 m^2 of coral cover to the reef over 21 months.

3.9. *Costing*

The total minimum cost of deploying settlement devices using SCUBA divers and manually securing devices to the benthos was calculated at $25,374.62, equating to $422.91 per coral yield, or close to $17 million per hectare (all USD at 2010 base rate; Supplementary Table 2) based on the average 50 % survival rate. The cost of deployment varied significantly depending on site-based survival rate, with costing based on ‘low-survival’ Florence Bay reaching $576.70 per coral yield or >$23 million per hectare, and ‘high-survival’ Arthur Bay costing $333.88 per coral yield or ~$9 million per hectare (USD at 2010 base rate; Supplementary Table 2).

4. Discussion

Coral seeding using settlement devices is proposed as a technique to enhance early coral survival and increase coral abundance, and could be used to maximum effect if deployed in conjunction with other management interventions. In this study, devices had a positive effect on first-year coral survival compared to natural survival (measured using terracotta tiles), and devices conferred the greatest chance of survival when deployed in areas where macroalgae removal (sea-weeding) was undertaken. However, the dynamics of coral survival on seeded devices were complex, with variations across scale, sites, time, micro-environments (deployment direction), and algae removal treatments. Additionally, longer-term (2-year) survival was low and costs high, highlighting the challenges of significantly reducing per-unit coral seeding costs and increasing survival prior to upscaling.

4.1. *Comparisons with natural survival*

An important prerequisite for the successful implementation of seeding devices as a restoration tool is evidence that they increase coral survival over and above natural levels. This study provides an explicit comparison of device-assisted survival with natural, unassisted coral settlement and survival on terracotta tiles, a comparison not previously included in other studies of coral seeding. In our study, devices conferred a significant increase in survival at one year, achieving among the highest yield (% of devices with at least one surviving juvenile) in coral seeding studies to date. Previous work has shown that larval cloud seeding can boost numbers of settlers in the short-term, but is ineffective long-term (>1 year) largely due to post settlement mortality (Edwards et al., 2015). The processes governing post-settlement survival could include macroalgal abrasion and fish grazing (Whitman et al., 2024), which the protective device design used here may have helped overcome, as evidenced by increased survival in control plots on devices relative to tiles.

Based on positive first-year survival (68.3 % survival averaged across sites), we extended our monitoring and witnessed significant mortality in the second year of deployment. Without the comparison to tile-survival (tiles were removed after 1 year), we cannot affirm if endpoint device survival is elevated compared to wild settled juvenile survival over the same time frame. However,when comparing the number of individuals that survived on devices to the density of wild juveniles found on natural substrata, we found that devices resulted in a greater density of juveniles than naturally occurring juveniles in control plots. In removal plots, wild juvenile density was higher than that achieved by devices. This information is valuable to inform the density of device deployment required to match or exceed natural levels: in control plots, deployment densities as low as 0.5 devices m^{-2} would be required to meet or exceed natural survival rates. In removal plots, a minimum of 2 devices m^{-2} would be needed to match natural survival, demonstrating that the improved substrate qualities delivered through sea-weeding alone may be sufficient to tip the balance toward favouring corals without seeding. Sea-weeding, however, requires a local breeding population of corals to populate or adult corals to grow. Hence, seeding using devices may be most relevant on reefs that have suffered catastrophic and acute losses in adult populations and/or lack larval supply, and have a low biomass of macroalgae (naturally or through weeding). However, the longer-term benefits of device-assisted survival (e.g., up to reproductive age) are unclear, and a priority for future work should be to increase the duration of device deployments, with paired deployments alongside natural substrata, to assess the long-term efficacy of coral seeding in elevating juvenile coral survival. Nonetheless, the dynamics of device-assisted survival over the two-year study here provide valuable insights for future coral seeding trials.

4.2. *Coral survivorship varied at individual, plug, and device levels*

Many coral seeding studies to date considered only device-level coral survival (termed yield; Randall et al., 2023, 2021; Chamberland et al., 2017, 2015). At this level, while mismatches in deployment durations and coral species used preclude exact comparisons, device-level survival rates (yield) achieved in this study after one year (up to 93 % in Arthur Bay) were among the highest observed using seeding device technology, with survival in recent work reaching 90 % (Page et al., 2024). However, we found that measuring survival at different levels (e.g. individual-, plug-, and device-levels) is important for different restoration goals. For example, at the first year, we observed low plug-level survival (27.4 %). After two years, this difference was even more pronounced: we observed very low individual level survival (0.87 %) when compared with plug-level (17 %), and device level (50 %) survival. Low individual-level survival may indicate a genetic bottleneck, with only a few genotypes contributing to the population of surviving juveniles. Maintenance of genetic diversity has been highlighted as a critical goal of ecological restoration (Di Sacco et al., 2021; Coleman et al., 2020; Broadhurst et al., 2008; Mijangos et al., 2015) including for corals (Quigley et al., 2022; Vardi et al., 2021; Baums et al., 2022), and there are several examples where low individual survival in restoration programs introduces genetic issues such as bottlenecks (e.g. in conifers; Kettle et al., 2008), inbreeding depression (e.g. in mosquitofish; Leberg and Firmin, 2008), and potential maladaptation (e.g. in salmon; Bailey et al., 2010; in eucalypts; Gellie et al., 2016). To improve the low individual survival rates, managed breeding could produce corals with advantageous traits matched to the receiving environment (e.g. heat tolerance, rapid growth; Drury et al., 2022). Alternatively, low individual-level survival may simply be indicative of the innate life history strategy of corals, and one that restoration practices may not (and perhaps should not) be able to overcome. As mass spawners, corals produce widespread and abundant gametes leading to high genetic diversity among larvae, but it is inevitable that some proportion of offspring produced through this strategy are maladapted (Van Oppen et al., 2011; Robinson et al., 2023). Low individual survival in this study may reflect the selection processes occurring as part of the natural life history strategy of corals (Healy et al., 2023; Graham et al., 2008). Therefore, genetic studies would be a useful complement to future device seeding trials to examine genetic diversity in natural populations, spawn slicks, and throughout larval development, settlement, and survival. These varying survival metrics underscore the importance of clearly defining restoration goals and what counts as “success” against a set target (Boström-Einarsson et al., 2020), particularly given the variation in coral survival across individual, plug, and device levels was affected by various parameters.

4.3. Habitat conditions influenced survival on devices

There were variations in coral survival on devices according to a range of fine- and broad-scale habitat characteristics. On a fine scale, plug orientation (top-vs side-facing) strongly influenced survival, with top-facing plugs experiencing near complete mortality within the first year. It is likely that survival at this micro-environmental scale is driven by a combination of resource availability (i.e. light) and stressors (i.e. sedimentation). These results have important implications for future device designs: like aerial reforestation, the delivery sheath/device design is important in fastening the juvenile to the substrate in an orientation that maximises survival. Higher survival on side-facing surfaces, and near-zero survival on top-facing surfaces in this study and others (e.g. Smith et al., 2022a; Whitman et al., 2024; Page et al., 2024) suggest that the efficacy of device deployment will depend on the device’s final position on the benthos providing corals a favourable orientation that protects against sedimentation, particularly on turbid nearshore reefs. Surface-deployed device designs and delivery methods are in development (Gibbs et al., 2019), though automating surface-deployed delivery of devices to reefs in precise orientations (and long term retention in this orientation) remains a challenge. Nonetheless, future device designs and delivery strategies should maximise the probability of corals landing in a side-facing orientation.

At the macro-environmental scale, we found significant differences in survival between bays. Survival was consistently lower in Florence Bay compared to Arthur Bay. While we did not measure environmental characteristics, the bays do have contrasting topographic structures and hydrodynamic regimes (Fulton et al., 2024). Site-based differences have previously been identified as strong drivers of survival, with survival varying most between sites rather than between device designs (Randall et al., 2023), sometimes driven by availability of nutritious food sources for fish which reduces grazing on coral juveniles (Whitman et al., 2024). The strong influence of site identity on survival underscores the importance of continued efforts focussed on identifying environmental drivers of juvenile survival. Identifying characteristics of sites that favour coral juvenile survival (device-associated or otherwise) is critical to avoid misdirecting restoration efforts to reefs with sub-optimal conditions.

4.4. Substrate preparation through sea-weeding increased survival on devices

The algal removal treatment was positively associated with survival in the first year. For aerial reforestation, increased survival has been achieved when employed with weeding of the target environment (Knutson et al., 2014; Davies and Bates, 2014; Davies et al., 2014) in a similar way that macroalgae were removed here. There has been an abundance of research examining the multi-faceted ways in which macroalgae negatively affect coral juvenile health and survival (Monteil et al., 2020; Evensen et al., 2019; Bonaldo and Hay, 2014; Box and Mumby, 2007; Tanner, 1995), so it was not surprising to observe an increase in survival in removal plots. Interestingly, however, the benefit of sea-weeding for device-assisted coral survival was lost in the second year. The cause of reduced survival in year two versus year one is difficult to ascertain. Device-aided reductions in abrasion, shading and allelopathy from macroalgae in removal plots may all have contributed to higher survival in removal plots in the highly sensitive early life stage of coral juveniles. Devices were designed to provide protection from grazing fish, however, it is also possible that the devices provided protection from abrasion by macroalgal thalli, as abrasion has negative impacts on coral health (Manikandan et al., 2021; Jompa and McCook, 2003; Birrell et al., 2008), and would explain the increased survival in control plots relative to tiles. It may also be possible that thermal stress experienced during the study period was alleviated by competitor removal – indeed, previous research has found that acroporids benefit from a lack of canopy-forming macroalgae during both bleaching and recovery (Smith et al., 2022b), though the impact of algal canopies has not been examined for bleaching in juvenile stages. While further research could focus on the exact mechanism, our study has shown that substrate preparation may be an important step in future device deployments to maximise first-year survival, particularly where macroalgae are abundant. Just like aerial reforestation, identifying microhabitat suitability at a submeter scale (Page et al., 2024) to enhance survivability and cost efficiency (Castro et al., 2021) will be critical to the success of coral seeding projects. While this goal presents challenges for submerged aquatic habitats, technological advancements in remote sensing (Radford et al., 2024), automation, photogrammetry, and remotely operated vehicles could be harnessed for a precision-based approach to coral seeding.

4.5. Implications of size and number of deployed spat

Previous work has established that coral juveniles surviving one year are at reduced risk of mortality (Vermeij and Sandin, 2008). Hence, it was theorised that corals should have reached a size escape threshold over the two years of deployment and growth in this study. However, we documented a continuous decline in survival at the plug- and device-level over the study period, suggesting that the size-escape threshold had not yet been met. Indeed, corals in our study reached an average diameter of 23 mm after two years, and previous work highlights that most corals reach a size-escape threshold at 50 mm, depending on habitat characteristics (Doropoulos et al., 2015). Given that we have not identified when the size escape threshold occurs for *A. kenti*, it would be ideal to monitor survival on devices until mortality reaches an asymptote and/or corals reach sexual maturity (dependent on species; see Rapuano et al., 2023) and can contribute to the ongoing replenishment of the local reef.

Interestingly, maximum aggregate size at deployment was not associated with increased 2-year survival. Fusion of recruits has previously been implicated in increased survival, and has provided some justification for large-scale aquaculture facilities to grow out juveniles destined for deployment (Raymundo and Maypa, 2004). Other work has found that there is a "sweet spot" for aggregate size, with all aggregates over 3 spat experiencing increased survival, and aggregates of 6–9 spat displaying greatest survival (Ligson et al., 2022). However, these observations were made up to 21 weeks (Ligson et al., 2022) and 6 months (Raymundo and Maypa, 2004), and hence the benefit of fusion may be lost in later life stages, as our study found no association between large fused aggregate size and probability of survival at 2 years. However, explicit testing of long-term survival across different aggregate sizes would provide clarity to these dynamics.

Similarly, the starting number of spat at deployment provided no increase in device survival probability. There have been conflicting reports regarding how starting number of spat relate to survival, with some studies finding no relationship (Randall et al., 2020), and others suggesting greater spat numbers will increase survival (Whitman et al., 2024). We found that in removal plots, high numbers of spat were associated with lowest survival (with an optimum stocking density of 49 spat per device), likely due to coral-coral competition (Cameron and Harrison, 2020). However, in control plots, a greater number of starting spat increased survival (with an optimum stocking density of 345 spat per device), potentially due to competition with algae rather than competition with other corals. Hence, the processes of density dependent survival may interact with receiving environment, highlighting that more spat does not make more corals, and mass-deployment should not necessarily favour scaling up the number of spat deployed per device. This trend has also been seen in aerial reforestation, where more seeds do not equate to more trees (Castro et al., 2023), but instead require intricate assessment of the receiving environment, targeting delivery of propagules of the right species, to the right microenvironment, in the right density, based on these complex dynamics.

4.6. *Costs and challenges*

The total cost of deploying 120 seeding devices (excluding monitoring) was $25,374.62 (USD at 2010 base rate), which equates to a per-surviving-colony cost of $422.91. While direct extrapolation of costs may be overly simplistic, from our study we estimate deployment of seeded devices to cost between $9 million and $23 million per hectare, based on high and low survival, respectively (average $17 million; at a density of 4 surviving colonies m^{-2}). The cost was high compared to other reef restoration methods including transplantation, coral gardening, larval enhancement, and substrate enhancement, which have a median cost of $400,000 per hectare (Bayraktarov et al., 2019), or sea-weeding alone ($67,250 per hectare; (Smith et al., 2023). Per surviving device costs were higher than reported from previous deployments ($1 - $17.9 per surviving unit after 1-year), however, most previous costings excluded coral aquaculture costs (Chamberland et al., 2017), which can be significant (~$28,000 in this study; Schmidt-Roach et al., 2024). A large proportion of the deployment cost reflects the method's requirement for a large-scale, specialised aquaculture facility for larval rearing and settlement, with highly trained technical staff, which could potentially be reduced through automation of coral aquaculture (Severati et al., 2024), though automation may not be pragmatic nor feasible in low-income nations (Schmidt-Roach et al., 2024). Our costing assumed a salary of AUD $30/hr, noting that higher labour costs may be incurred where significant expertise is required, with recent work estimating over $579,000 USD per annum in labour costs required to operate land-based facilities in high wage economies (Schmidt-Roach et al., 2024). Labour costs vary significantly worldwide and will have a large effect on the cost of restoration implementation. While this study reduced some costs (e.g. transport distance, boat-time) by deploying to sites close to the aquaculture facility, the availability of such infrastructure may limit the feasibility of the approach, particularly for developing nations. Also, limiting the distance between the onshore aquaculture facility and deployment reef will not always be practicable, and the need for, or appropriateness of seeding should drive identification of target sites, not proximity to aquaculture facilities. Finally, while we utilised SCUBA divers to install devices on the benthos, aerial reforestation techniques could be more closely mirrored by using surface-deployment, and could reduce costs associated with *in-situ* installation. Considering the target maximum cost of $4.50 per seeding unit (Gibbs et al., 2019), significant reductions in the per seeding unit cost must be realised, driven by increased coral survival, but also potentially through other technologies such as automated aquaculture systems (Severati et al., 2024), floating larval rearing pools (Suzuki et al., 2020), heat-evolved corals and/or symbionts (McLeod et al., 2022), and surface deployments to increase cost-efficiency, to achieve these cost targets.

Over the two years of our study, we observed two noticeable drops in coral survival coinciding with summer periods. From February to May 2022, there was a mass bleaching event that affected reefs at Yunbenun, with degree heating weeks reaching >8 °C-weeks in the region (Skirving et al., 2019; coralreefwatch.noaa.gov; $0.05^{\circ} \approx 5$ km, daily resolution). Interestingly, during the following summer (December 2022–March 2023), corals on devices experienced an even greater drop in survival despite only experiencing ~ 2 °C-weeks of thermal stress. These dynamics accentuate the importance of longer-term monitoring, particularly through acute stress events, to understand if and how restoration strategies help "weather the storm" of climate change. We did not observe an asymptote in survival after two years, in contrast to previous work (Randall et al., 2021; Chamberland et al., 2015), and hence even longer time frames would be valuable to understand how seeding devices may contribute to reef recovery. Seeding with heat-adapted brood stock and symbionts could improve coral survival through heat stress events, however this is yet to be tested.

4.7. *Conclusions*

This study offers two major findings applicable to future coral seeding efforts. Firstly, we showed the importance of quantifying survival on coral seeding devices compared to natural survival, and preferably over multiple years, to confirm seeding is delivering enhanced coral survival. Secondly, we showed that substrate preparation through sea-weeding significantly enhances first-year coral survival (natural and device-assisted), though the benefit of sea-weeding for seeding success diminishes in the second year. Despite the loss of effect over longer timeframes, sea-weeding may be a key step for future restoration endeavours to maximise early survival, and further research in this area is encouraged. Overall, while devices initially increased coral survival, the approach is currently expensive and the ecological benefits, if achieved, are only likely to be realised over long time periods (e.g., 5–10 years), highlighting the need for research on longer-term deployments. We note that this area of research is rapidly developing, and it is possible that improved device designs and efficiencies in coral aquaculture, and therefore survival outcomes, could be achieved in the future to reduce the cost of coral seeding. The future viability of coral seeding as a restoration approach will depend on understanding device-assisted vs unassisted survival, long-term dynamics (including through acute stress events), the need for habitat preparation, drivers of site-specific survival, and an overall cost-benefit analysis, including carbon footprint estimates. One of first tenets of ecological restoration is considering a range of options, including the option of doing nothing (Hobbs and Cramer, 2008). On reefs where there is a sufficient supply of adults and evidence of juvenile recruitment, this option may be preferable, but the choice to intervene or not should follow a robust decision-making framework guided by the best available science (Streit et al., 2024), and accounting for the significant social, economic and ecological value afforded by coral reefs (Sing Wong et al., 2022).

CRediT authorship contribution statement

Hillary A. Smith: Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Genevieve Dallmeyer-Drennen:** Writing – review & editing, Data curation. **David G. Bourne:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Suhelen Egan:** Writing – review & editing, Supervision. **Cathie A. Page:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Cathie Page reports financial support was provided by BHP Group Ltd. Hillary Smith and David Bourne reports financial support was provided by Earthwatch Institute Australia. Hillary Smith reports a relationship with Society for Ecological Restoration Australasia that includes: board membership. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.125322.

Data availability

Data supporting this article have been uploaded to the Research Data JCU repository and are available at doi: 10.25903/ce1s-yf78.

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