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RESEARCH ARTICLE

A comparison of in situ and on-vessel larval rearing for coral seeding

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Coral sexual recruitment is critical to reef recovery yet often fails on degraded reefs. Coral seeding is one approach to artificially increase the densities of coral settlers on reefs and can be applied in many ways. A thorough comparison of seeding-method performance is needed to inform restoration decisions yet is difficult to undertake given the cost and complexities around employing multiple methods simultaneously. Here, we first designed a vessel-based coral-spawning aquaculture system. Then we undertook an experimental comparison of the performance of larvae reared in the on-vessel system with those reared in in situ rearing pools (SECORE coral rearing in situ basins [CRIBs]). We parameterized survival estimates and assessed post-deployment survival of spat generated using each method. We also quantified survival of spat reared in situ and deployed across six sites on an inshore reef system of the Great Barrier Reef. Larval survival was lower when rearing in situ than on the vessel (3.8 vs. 66.1%, respectively), but settlement behavior and post-settlement survival were comparable between rearing treatments, with yield averaging 66 and 72% after 3 months of deployment, from CRIBs and culture tanks, respectively. Spat survival was also comparable across treatments, averaging 5 ± 8%. On-vessel rearing was more costly but supported higher survival, increased portability, and enabled more control and manipulation of rearing conditions. By contrast, in situ methods were low-cost, deployable from shore, and low-maintenance. Armed with this information, managers and practitioners can determine the most appropriate method(s) for a given restoration project.

Key words: coral larval rearing, density, restoration, settlement, survival

Implications for Practice

- Both high and low-tech larval rearing methods are feasible, and their use should be guided by situational requirements, including cost and target larval yield.
- The benthic cover of cyanobacteria and *Lobophora* was negatively associated with coral yield, suggesting that sites with high cover of these groups should either be avoided or that higher densities of corals may be needed to compensate for lower survival.
- An on-vessel rearing system design is presented for use in future applications.

Introduction

Coral replenishment through sexual recruitment is critical to maintaining the genetic and species diversity that underpins the value of reef ecosystems (Gouezo et al. 2019; McManus et al. 2021; Edmunds 2023). Yet sexual recruitment is often inhibited on reefs degraded by climate-change-driven disturbances like marine heatwaves (Webster et al. 2013; Fabricius et al. 2017; Kenyon et al. 2023), which can directly and indirectly reduce reproductive output and larval supply (Hughes et al. 2019; Briggs et al. 2024; Mumby et al. 2024). Thus, techniques that artificially enhance the settlement and recruitment of sexually produced corals at scale are urgently needed (Anthony et al. 2017; Randall et al. 2020; Knowlton et al. 2021).

Coral seeding is one way to artificially increase the density of coral settlers on reefs and can be done by directed larval seeding, where high densities of competent, ready-to-settle, larvae are released to the seafloor (Heyward et al. 2002; Suzuki et al. 2012; dela Cruz & Harrison 2017), or by using seeding devices that house newly settled corals (Chamberland et al. 2015; Randall et al. 2021,

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2022). Gametes, embryos, and/or larvae for seeding can be sourced from wild spawn slicks (Oliver & Willis 1987; Doropoulos et al. 2019), from the in situ collection of spawn via nets or cradles (Suzuki et al. 2020; Miller et al. 2021), or from the ex situ collection of spawn in an aquaculture facility (Severati et al. 2024). These varied approaches to seeding range from cheap and low-tech larval rearing in floating basins or pools (Suzuki et al. 2020; Miller et al. 2021) to expensive and high-tech aquaculture facility production (Severati et al. 2024) that applies layered interventions like inoculation with heat-evolved symbionts (Nitschke et al. 2024), climate hardening, and selective breeding (van Oppen et al. 2015; Mead et al. 2019).

Which collection and larval rearing methods are best suited to a given restoration site will depend on weather and oceanographic conditions (for larval slick collection), cost (i.e. pools may be best suited for locations with limited financial and capital resources), access (i.e. is the site nearshore or offshore?, sheltered or exposed?, large or small?), regulatory requirements (i.e. can corals be temporarily removed from the reef?), ecological knowledge of the species, communities, and sites of collection (i.e. known spawning time, slick formation locations, etc.), and the goals of the restoration activities. Similarly, once larvae are reared, determining which seeding methods are best suited to a restoration site will depend on cost (devices are more expensive), the drivers of mortality at that site (i.e. is there a strong post-settlement survival bottleneck?), and whether additional treatments and protection are needed to support early post-deployment survival (Whitman et al. 2024).

In situ rearing methods can also be applied by community or Indigenous groups and volunteers, requiring minimal training (Miller et al. 2021; Sellares-Blasco et al. 2021; Banaszak et al. 2023). The main limitations of in situ rearing include scalability and control in rearing conditions (i.e. temperature, turbidity, and microbial loads) that restrict the application of layered interventions, precision, and quality control. On the other hand, high-tech aquaculture-produced corals allow for automated and scaled production of large numbers of corals in controlled environments (Craggs et al. 2017; Severati et al. 2024), but require costly capital investments in technology and equipment, infrastructure and industry, and live-coral transport. Ultimately, optimizing both methods and selecting the method(s) that is(are) best suited to the situation at hand will form part of reef management decisions. In the future, a combination of both approaches is likely to be required and applied simultaneously or sequentially; thus, developing methods that are standardized, reproducible, and efficient is a key goal of restoration research.

Objectives

An essential step toward reaching these goals for coral seeding is to compare culture methods and assess settlement success across techniques. Larval survival rates are often the least well parameterized in models that are needed to predict intervention performance and provide decision support (i.e. which method to apply when and where), and as such, it is critical to estimate survival throughout this period and to compare these rates across methods. To address these research questions, we first designed a vessel-based aquaculture system to enable a direct comparison of in situ and ex situ rearing. We then undertook an experimental comparison of larval rearing in in situ pools/basins (coral rearing in situ basins, hereafter CRIBs) and in the ex situ culture system by (1) tracking embryo and larval density through time, as a proxy for survival, (2) comparing larval buoyancy and settlement behavior, and (3) assessing the post-deployment survival of spat generated under each rearing condition.

Methods

Vessel-Based Aquaculture System

In October 2022, a 34.9 m passenger ferry was re-purposed as a research vessel with an aquaculture system designed for the sexual propagation of corals (Figs. 1 & S1). The system was modeled after the National Sea Simulator (SeaSim, Townsville, Australia) coral spawning and culturing systems, providing flow-through seawater and multiple-use configurations for all stages of the coral propagation process (Figs. 1 & S1). Modularity of the design and flexible hoses connecting system components enabled optionality of water delivery and is briefly described here.

Magnetic drive metal-free pumps (Iwaki MX-403) supplied seawater for filtration and temperature manipulation. A heat pump (TAC 300 SSD) manipulated the temperature of a semi-recirculating loop (chilled seawater, hereafter CSW), in which experimental tanks sat, for temperature regulation. Baths were either deep tanks (approximately 2000 L, 700 mm deep) or tabled troughs (1200 L, 500 mm deep, and 300 L, 120 mm deep). Titanium coils submerged in the CSW baths in-line of ultrafiltered flow-through seawater (hereafter FSW) supplied experimental tanks, moderating the temperature of the FSW. Filtration was achieved via two parallel series of three increasingly fine bag filters (50 or 25, 5, and 1 μm), followed by a single ultrafilter (<0.1 μm). A tank (150 L) and pump (IWAKI MD-70) were used to backflush the ultrafilter with freshwater. The experimental tanks overflowed into the baths, acting as top-up and exchange to the CSW, which in turn overflowed off-board.

Experimental tanks included (1) broodstock colony holding tubs (65 L), (2) shallow multi-use experimental and settlement tubs (30 L), (3) large and small larval culture tanks (70 and 20 L), and (4) a multi-use work trough. Additionally, raw water (i.e. unfiltered and non-temperature-controlled seawater) was delivered to flow-through tubs, achieving temperature moderation to ambient seawater via a high flow rate. Air hoses supplied aeration to culture tanks, while red light-emitting diode (LED) strips were installed around the broodstock holding area to support night-time spawning work. Refer to Fig. S1 for the detailed system design.

The larval culturing system used in this experimental comparison consisted of 16 × 70 L conical fiberglass larval rearing cones (Fig. 2F). The fiberglass cones received ultrafiltered seawater (<0.1 μm) at a rate of approximately 400 mL/min and aeration via a weighted acrylic rod, which bubbled across the surface of a wedge-shaped 106 μm filter on the outlet.

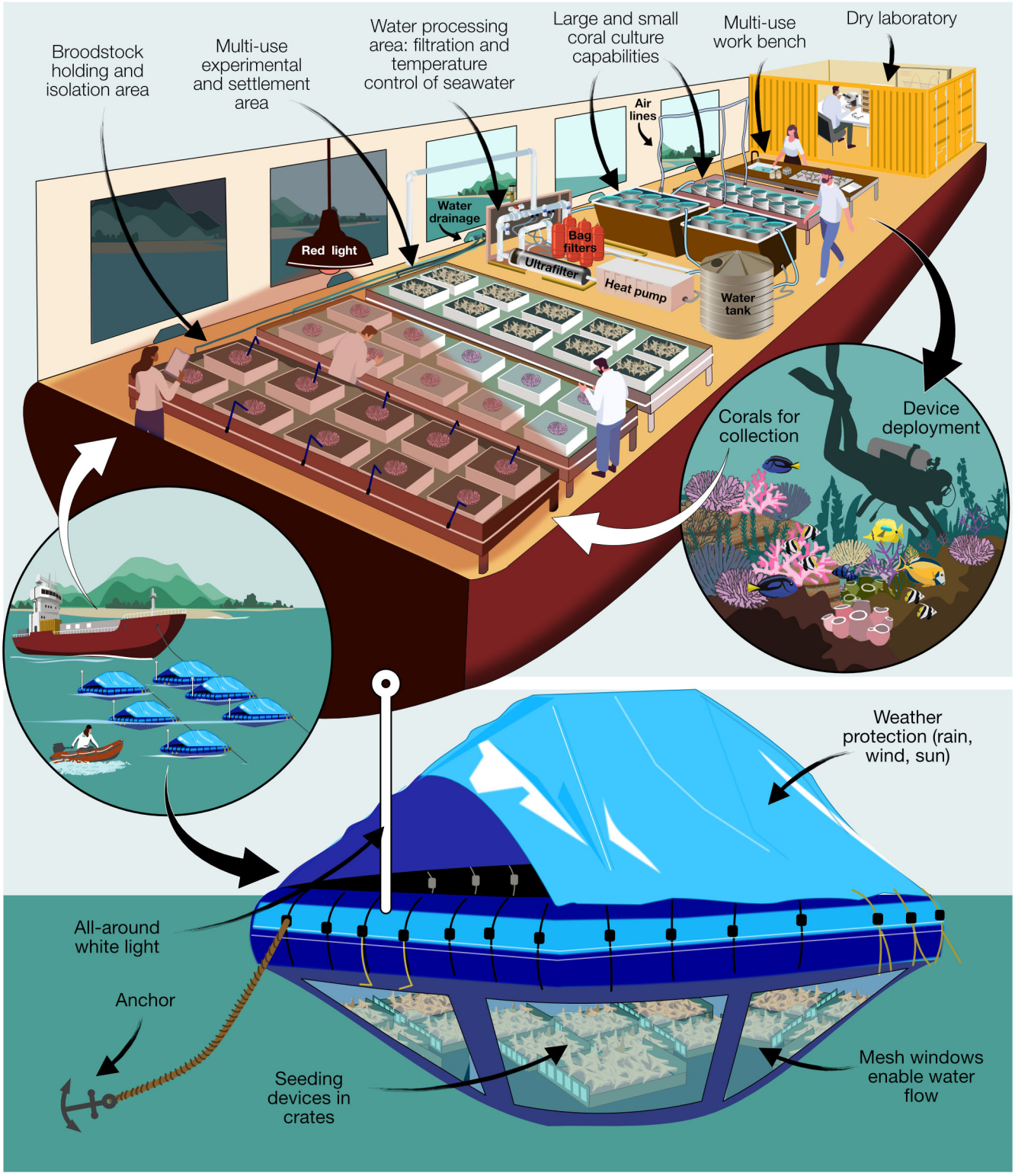

Figure 1. Schematic of two coral culturing methods: Vessel-based aquaculture system and SECORE's coral rearing in situ basins (CRIBs). See Figure S1 for a technical drawing of the on-vessel system.

The on-board aquaculture system functioned as intended and maintained all broodstock, larval cultures, and spat for the duration of the experiment and supported a dozen experimental investigations. Mechanical filters required maintenance on a 12-hourly basis, and steady temperature was maintained within culture tanks at 25.0 ± 0.64°C

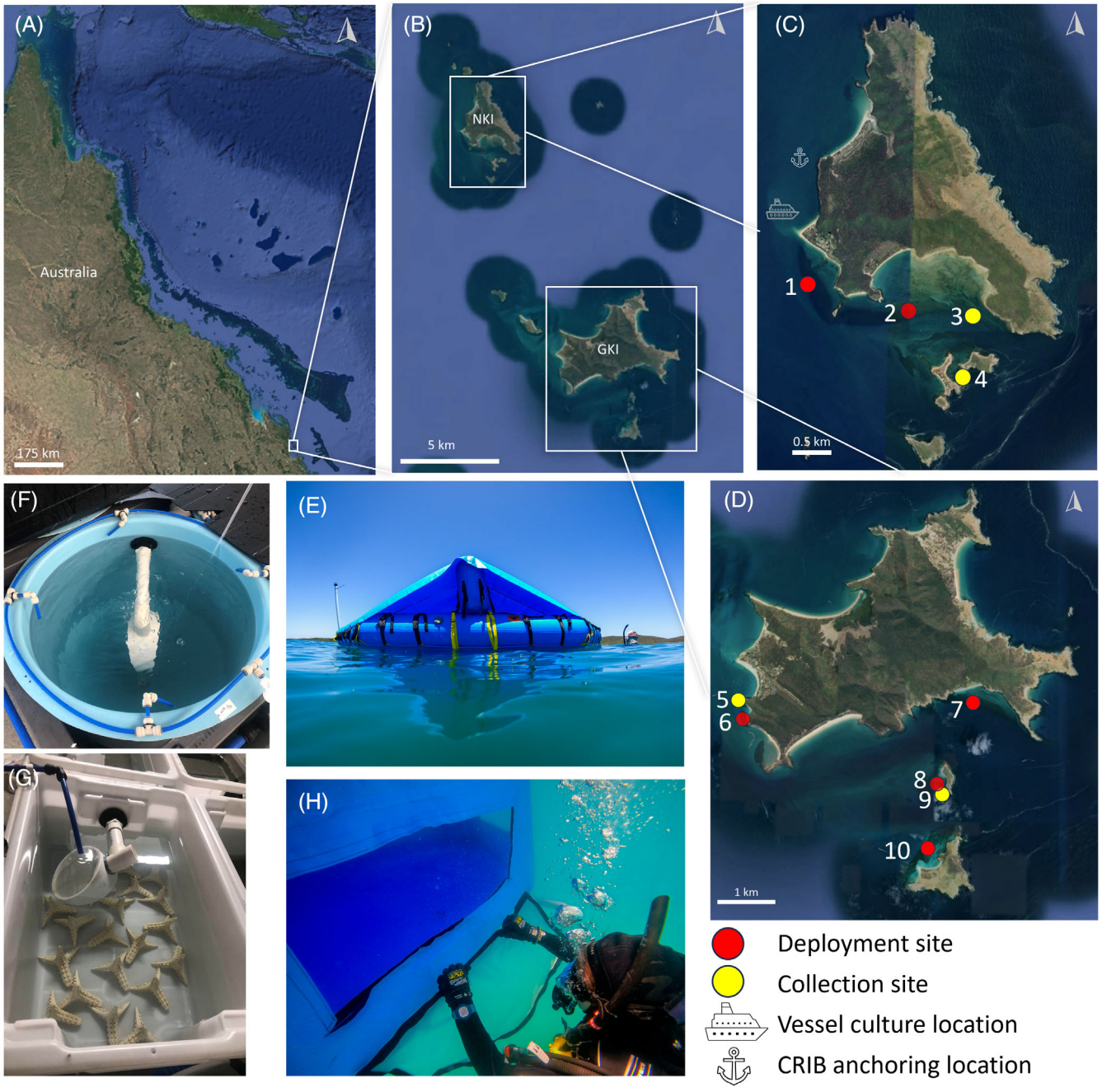

Figure 2. (A) Map of the Great Barrier Reef. (B) Map identifying the location of the southern inshore Keppel Islands region. (C) North Keppel Island (NKI; Konomie) and surrounds, with sites, vessel, and CRIB locations identified. (D) Great Keppel Island (GKI; Woppa) and surrounds, with sites identified. (E) Coral rearing in situ basin (CRIB) deployed with the shade canopy. (F) On-vessel larval culture tank. (G) On-vessel settlement tank with tetrapod seeding devices. (H) CRIB view from underwater showing a diver installing mesh windows. Sites in (C) and (D) are [1]Home reef, [2,3] Mazie Bay, [4]Pumpkin reef, [5,6]Shelving Bay, [7]Clam Bay, [8,9]Halfway Island [10]Humpy reef.

(mean ± SD), about 1°C cooler than ambient and less variable (Fig. S2).

Coral Rearing In Situ Basins

CRIBs were designed by SECORE International as an inexpensive, low-tech, coral culturing option that can be deployed from shore (Fig. 1) (Miller et al. 2021). CRIBs are constructed of a potable-water approved poly-vinyl chloride (PVC)-coated polyester and are approximately 2 × 4 × 1 m ($L \times W \times D$), enclosing a total ocean surface area of approximately 5.4 m^2 and an ocean volume of approximately 5.6 m^3. A pontoon ring provides flotation, to which a removable piece comprising the walls and floor is attached with quick-release straps. Sandwiched together, removable 100 and 200 μm mesh windows occupy much of the wall area, facilitating water exchange. Two zippered

hatches in the floor of each CRIB facilitate the removal of deposited sediments or debris. A PVC-pipe frame attached to the outside of the floor maintains the CRIB's shape against currents, while an inflatable support creates the structure of a gabled canopy to minimize rain, wind, and sun exposure. For details, refer to Miller et al. (2021).

Six replicate CRIBs were deployed near the anchored vessel, approximately 500 m northeast (Fig. 2C). This distance was close enough for visual monitoring and easy access of the CRIBs from the vessel. CRIBs were individually anchored with 22 m of rope bridled to the bow, with a 5 m chain and 22 kg anchor. They were anchored approximately 30 m apart in a 3×2 grid within an area of approximately 0.2 km^2 in approximately 3 m depth at the lowest astronomical tide. Each CRIB was marked with an all-around white light attached to a PVC post at the aft.

All CRIBs remained anchored, upright, and inflated throughout deployment. The all-round white anchor lights required battery replacement each evening. CRIB windows were cleaned once during the larval grow-out period (approximately 5 days) by divers using soft-bristled brushes. CRIB temperature averaged 26.1 ± 1.2°C (mean $\pm$ SD) throughout culturing and demonstrated a diurnal pattern. On two occasions during larval rearing, needlefish were observed in a CRIB and required removal.

Coral Collections and Experimental Treatments

Thirty-seven gravid *Acropora millepora* colonies were temporarily collected from Woppaburra Sea Country (Keppel Islands, southern inshore Great Barrier Reef [GBR]) approximately 8 days prior to the November 2022 mass spawning (Great Barrier Marine Park Authority [GBRMPA] Research Permit G19/43034.1). *Acropora millepora* was chosen because it is a common and widely distributed species on the GBR and because these particular colonies had been tracked previously through two heat-stress events and thus had known bleaching phenotypes, which was relevant for additional experiments not described here. Colonies were collected from four locations: Halfway Island ($n = 10$), North Keppel Island ($n = 12$), Great Keppel Island ($n = 9$), and Pumpkin Island ($n = 6$) (Table 1; Fig. 2C & 2D). Colonies were returned to the vessel, which was anchored southwest of North Keppel Island, and were placed in the onboard aquaculture facility in plastic holding tanks with filtered FSW. Colonies were maintained (up to 18 days), exposed to ambient indirect light until they were returned to their respective collection sites, post-spawning.

Coral Spawning and Larval Stocking

Colonies were monitored for spawning activity beginning on night 2 after the full moon. Using a red light, colonies were checked for bundle setting approximately every 30 minutes, from 30 to 180 minutes after sunset. When signs of bundle setting were observed, water flow was stopped to the holding tanks to isolate each colony's gametes in the event of their release.

Nine nights after the full moon (17 November 2022; noting there was a total lunar eclipse on the night of the full moon), mass spawning of the on-vessel corals was observed, and 27 *A. millepora* colonies partially or fully spawned. Gamete bundles were collected from each colony individually in clean 50 mL tubes or 500 mL jars, and were allowed to settle on the bench for a minimum of 10 minutes to record a packed egg volume. An estimated egg diameter of 560 µm (Babcock & Heyward 1986; Wallace 1999; Randall et al. 2024) was used to calculate the number of eggs along a 10 mm axis (17.9) and then converted to an estimate of packed eggs per mL (5694.24). Each colony's gametes were then gently poured simultaneously into a single large mass fertilization tub (100 L) to homogenize gametes and standardize the start time of fertilization among parent colonies. After approximately 10 minutes of gentle mixing, the culture was split across another 100 L tub to reduce gamete density and minimize the risk of polyspermy or anoxic conditions developing within the culture. After a fertilization period of approximately 30 minutes, embryos were collected to stock each replicate CRIB ($n = 6$) and on-vessel culture tank ($n = 8$). Due to the volumetric differences between CRIBs and culture tanks (CRIB = 5,600 L, culture tank = 70 L), it wasn't possible to standardize larval density across culture treatments to volume. Instead, we standardized to surface area (CRIB = 54,000 cm^2, culture tank = 2800 cm^2), aiming to stock each with an approximately equivalent surface density (approximately 12.5 larvae/cm^2) by controlling the number of packed eggs per mL during stocking (Table 2). Because *A. millepora* embryos are extremely buoyant during the first approximately 8 hours of development and form a single layer of embryos at the surface, standardizing to surface area during the period of highest mortality was deemed an acceptable comparison.

Density (Survival) Assessments

Embryo/larval density, as a proxy for survival, was assessed at the time of culture stocking and then daily for approximately 5 days post-spawning. To sample the CRIBs, two kayak paddles were used to gently homogenize the CRIB and mix embryos/larvae throughout the water column (i.e. push them down from the surface during the buoyant stages of early embryogenesis and up from the bottom during the bottom-seeking larval period). The resuspension of sediment and particulate organic material in the CRIB was used as a visual indicator that homogenization occurred. Then, three replicate samples of 450 mL were sampled from mid-water column in each CRIB by inverting the jar to a mid-point in the CRIB and then righting it to allow a known volume of water to be collected. Jars were then capped in the water column and brought to the surface. Jars were returned to the vessel, and the numbers of embryos/larvae within each sample were counted.

To sample the culture tanks, each tank was homogenized using a clean plastic bowl. Ten replicate 10-mL subsamples were then collected from each tank using a pipette, and the numbers of embryos/larvae present in each sample were counted.

Embryo/larval density was modeled through time for CRIBs and culture tanks separately because starting volumetric density was not comparable among treatments. Density was modeled against time using a generalized linear mixed effects model (GLMM) with the template model builder in the package

Table 1. Waypoints for each site, listed by activity or experiment. GKI = Great Keppel Island (Woppa); NKI = North Keppel Island (Konomie).

Site	*Latitude*	*Longitude*	*Activity/experiment*
Halfway Island	23°12.104′S	150°58.288′E	Coral broodstock collections
Mazie Bay, NKI	23°5.205′S	150°54.462′E	
Shelving Bay, GKI	23°11.446′S	150°56.118′E	
Pumpkin Island	23°5.517′S	150°54.155′E	
Mazie Bay, NKI	23°5.156′S	150°53.785′E	Coral deployments of CRIB- versus culture-reared spat
Halfway Island	23°12.048′S	150°58.193′E	Coral deployments of CRIB-reared spat for site comparisons
Shelving Bay, GKI	23°11.303′S	150°56.024′E	
Mazie Bay, NKI	23°5.133′S	150°54.190′E	
Humpy Island	23°12.678′S	150°57.970′E	
Home Reef, NKI	23°4.968′S	150°53.078′E	
Clam Bay, GKI	23°11.187′S	150°58.445′E	

Table 2. Size specifications for the two rearing conditions (CRIBs and culture tanks) and their corresponding target embryo/larval stocking densities. Calculations were made based on: a mean egg diameter for *Acropora millepora* (μm) = 560; the number of eggs packed along a 10 mm axis = 17.86; the number of eggs/mL = 5694.24.

Metric	*Coral rearing in situ basin (CRIB)*	*Culture tank*	*Difference*
Volume (L)	5600	70	80×
Surface area (cm^2)	54,000	2800	19×
Target number of larvae	665,000	35,000	19×
Target surface density (larva/cm^2)	12.3	12.5	1×
Target volumetric density (larva/mL)	0.12	0.5	0.24×
Realized volumetric density (larva/mL) (mean ± SD)	0.145 ± 0.08	0.684 ± 0.29	0.21×
Packed cell volume stocked (mL)	116.78	6.15	19×

"glmmTMB" (Brooks et al. 2017) in R (R Core Team 2023), with replicate CRIB/tank considered the random effect, using restricted maximum likelihood (REML) model fitting. CRIB densities were modeled using a Tweedie distribution with a log link function, due to overdispersion in the data, while culture tank densities were modeled using a Gaussian distribution. Model assumptions were assessed using "DHARMa" (Hartig 2020), and model results were visualized using "ggplot" (Wickham 2016).

Temperature was monitored throughout most of the larval rearing period in a haphazardly selected CRIB and culture tank (CRIB 2 and tank L), using a Hobo Temp Pro V2 weighted data logger set to record temperature every 10 minutes.

Behavioral Assays

The change in vertical positioning in the water column throughout embryogenesis and larval development was investigated using behavioral assays at four timepoints coinciding with density assessments from each of three replicate CRIBs and tanks. Following the counts, larvae from each CRIB and tank were placed in a 500 mL clear plastic graduated cylinder, topped up to 500 mL with FSW, and placed on a lab bench under fluorescent lighting. Larvae were left untouched for greater than 15 minutes to distribute in the water column before underwater paper was placed behind the cylinder to visualize larvae. The numbers of larvae in the beaker were then counted in ten 50-mL depth increments from the surface (0–50, 51–100, 101–150 mL, etc.) to track their distribution. For each assay, 119 ± 38 (SD) (min = 69, max = 196) larvae were counted. At later timepoints, larval densities were low, and thus additional larval samples were collected to ensure a minimum of 50 larvae were tested in each assay. The proportions of larvae distributed across depth increments were calculated for each replicate CRIB/tank and visually compared using stacked bar charts.

Settlement of CRIB- Versus Culture-Reared Larvae on Sloped Gear Shapes Deployed to Mazie Bay

To compare the settlement of larvae reared in CRIBs and culture tanks, a settlement trial was set-up on the vessel. CRIB 6 and Culture tank A were haphazardly chosen as the donor cultures for CRIB- and culture-reared larvae, respectively. On 22 November (5 days after fertilization [DAF]) approximately 5000 larvae were collected from each donor culture using a 200 μm mesh net. Approximately 2500 larvae were then distributed to duplicate tanks (32 L plastic tubs), each of which held 30 SECORE sloped gear shape (SGS; Fig. 3A) devices (approximately 80 larvae per device, 60 devices per treatment; Randall et al. 2022 for device design). Devices had been conditioned for approximately 4 weeks in a flow-through outdoor aquarium in the SeaSim under 70% shade before being placed in 70 L tubs receiving FSW with shade cloth on the vessel. A small black cable tie was added to each device with culture-tank spat as a treatment marker for field deployment.

After approximately 72 hours for settlement (8 DAF, 25 November), a subset of 15 devices from each tank (30 per

treatment) were assessed. Using blue light and yellow filter glasses to visualize spat fluorescence and enable spat detection, the numbers of settled spat on each device were recorded.

To compare settlement among CRIB and culture-reared larvae, a general linear model (GLM) was used to model the number of settlers by rearing treatment using a Gaussian distribution. Duplicate tanks were not recorded, so the variance associated with the tank could not be accounted for in the model. Model diagnostics were assessed, and outputs were visualized as above.

To compare spat survival on devices seeded with CRIB- and culture-reared larvae, a single 20-m long transect was established at Mazie Bay (Table 1; Fig. 2C). Every approximately 25 cm, pairs of SGS devices (i.e. one device each with culture- and CRIB-reared spat) were haphazardly deployed on either side of the transect line, for a total of 120 devices (60 each with CRIB- and culture-reared spat) (GBRMPA Research Permit G22/47664.1). Devices were deployed by divers and were gently placed on the reef substrate but were not attached to the reef. All devices with culture-reared spat were marked with a small black cable tie for visual identification, and half of all devices (30 per treatment) had yellow tags with numerical identifiers to track spat-level survival.

On 16 February 2023, 83 days after deployment, devices were retrieved and visually scored for survival under magnification lamps, onshore in a laboratory at the Konomie Island Environmental Education Centre. The total number of discrete live colonies on each device was recorded, and a yield (% of deployed devices harboring at least one live coral) was calculated for each rearing treatment. A Welch's two-sample *t* test was used to assess whether the log-transformed percentage survival differed between CRIB- and culture-reared spat. Data were log-transformed to improve normality, and a Welch's *t* test was applied to account for non-normal variances between groups.

Settlement of CRIB-Reared Larvae on Tetrapods for Deployment Across Six Sites

A second trial aimed to quantify the success of mass settlement within a CRIB, and to compare settlement preference between two device designs: tetrapods with indentations (TI) and tetrapods with protrusions (TP; Fig. 3B; see Randall et al. 2022 for device design). CRIB 5 was selected to receive devices due to a comparatively high density of larvae (Fig. 4A). On 22 November (5 DAF), a shelf of six plastic crates cable-tied together was placed in the CRIB and secured mid-water via six straps and weighted with dive weights. One hundred and sixty-six devices were haphazardly placed into each of the six crates for settlement. Tetrapods were conditioned as described above.

After approximately 48 hours for settlement (7 DAF, 24 November 2022), 20 devices were haphazardly retrieved from each of six replicate crates (120 tetrapods total). Devices were transported to the vessel in plastic tubs and held in flow-through FSW while each device was assessed. The number of spat settled on each device was counted using a blue light and yellow filter glasses, and the replicate crate and device type (TI or TP) were recorded. Devices with five or more discrete spats were retained for field deployment. Following this detailed quantification, the remaining devices were retrieved for a rapid assessment, and all devices with five or more spats were maintained on the vessel until deployment.

To statistically compare in-CRIB settlement among tetrapod types (TI vs. TP), a GLMM was used to model the number of settled spat by device type, with replicate crate as a random effect. A negative binomial distribution ("nbinom2") with a log link function was used, and model diagnostics and visualizations were done, as above.

On 25 November 2022 (8 DAF), 18 replicate tetrapods were deployed to each of six sites (Table 1) by divers (GBRMPA Permit G22/47664.1). Within each site, three devices were deployed around each of six replicate reo rods in plots. Devices were freely deployed (i.e. unattached), adjacent to another seeding experiment not described here. Between 12 and 17 February 2023 (79–84 days post-deployment), all devices were retrieved. Yield was recorded upon retrieval, noting each replicate plot and site.

To statistically compare survival (yield) among sites, a GLMM was used to model survival by site, with plot nested within site as a random effect, using REML model fitting. A binomial distribution with a logit link function was used; model diagnostics were assessed, and outputs were visualized, as above.

Benthic Composition

The benthic community surrounding the devices deployed across six sites was captured during deployment by placing a 1 m^2 quadrat around each device and taking photographs (Olympus Tough TG-6). Images were analyzed using ReefCloud (Gonzalez-Rivero et al. 2020; https://reefcloud.ai/). A grid containing 20 points was overlaid on each image and classified by a trained observer into one of the following categories: *Acropora* branching and bottlebrush (AcroB), *Acropora* tabulate and corymbose (AcroT), *Montipora* (Monti), *Pocillopora* (Poc), *Porites* (Por), crustose coralline algae and *Peyssonnelia* (CA), *Lobophora* (Lobo), *Sargassum* (Sar), brown, green, and red macroalgae (Brown, Green, and Red), epilithic algal matrix (EAM), cyanobacteria (Cyano), and sand/sediment (Sed). At two sites, Home Reef and Mazie Bay, images of tetrapod devices were unavailable; we therefore used images of adjacent devices in the same plots for the analysis; these were reflective of the wider plot and site.

Point count data were transformed into percent cover. A principal component analysis (PCA) was then conducted to reduce data dimensionality and identify benthic groups that explained the most variance among sites. PCA results were visualized by site, using a biplot ("factoextra" package; Kassambara and Mundt 2020). A stacked bar chart was also created to visualize the benthic composition at each site ("ggplot2" package; Wickham 2016). A second PCA was used to investigate whether benthic community composition differed between plots with and without surviving corals.

To explore the relationships between coral survival and key benthic groups identified by the PCAs, GLMMs were used, with benthic data modeled as fixed effects and replicate plots within sites as the random effects. To assess the interaction between benthic groups, we fitted an interaction model while accounting for site as a random effect to control for site-level variability.

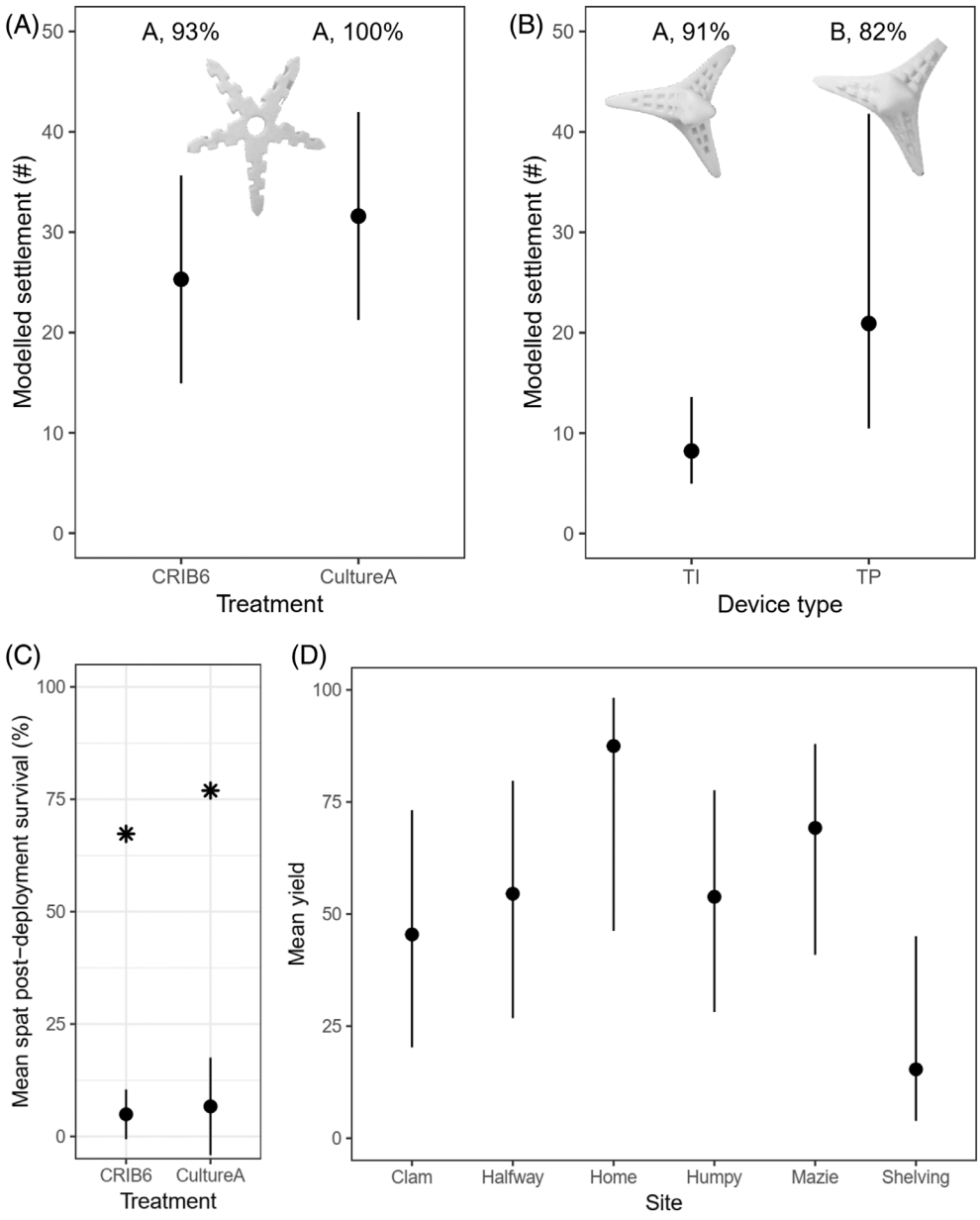

Figure 3. (A) Modeled number of spat settled per seeding unit, in on-vessel settlement trials, from CRIB 6 and Culture A. (B) Modeled number of spat from in situ CRIB settlement on tetrapods with indentations (TI) and tetrapods with protrusions (TP). Letters above each treatment in (A) and (B) indicate statistical significance; numbers above each bar indicate % settlement at the device level. (C) Modeled spat post-deployment survival from CRIB 6 and Culture A deployed to Mazie Bay. Asterisks indicate yield (i.e. survival at the device level) for each treatment. (D) Modeled yield of tetrapods deployed across six field sites. Points indicate estimated marginal means and bars represent ± CIs.

Models with the lowest Akaike Information Criterion (AIC) score were selected. Model diagnostics were checked, and outputs were visualized as above.

Results

Density (Survival) Assessments

Upon stocking, average larval densities were 0.14 and 0.68 larvae/mL in CRIBs and culture tanks, respectively, equating to surface densities of 14.7 and 17.1 larvae/cm^2 and total larval counts of approximately 784,000 and 47,600 per CRIB and culture tank, respectively (Fig. 4). In five of six CRIBs and in five of eight larval tanks, average larval densities increased between 1.5 and 17.5 hours after fertilisation (HAF); thereafter, there was a significant decrease in density through time in both treatments, but the magnitude of the decline was significantly greater in CRIBs (Fig. 4A). After 108 hours, average CRIB density had declined by 96% to 0.005 larvae/mL, while average culture density had

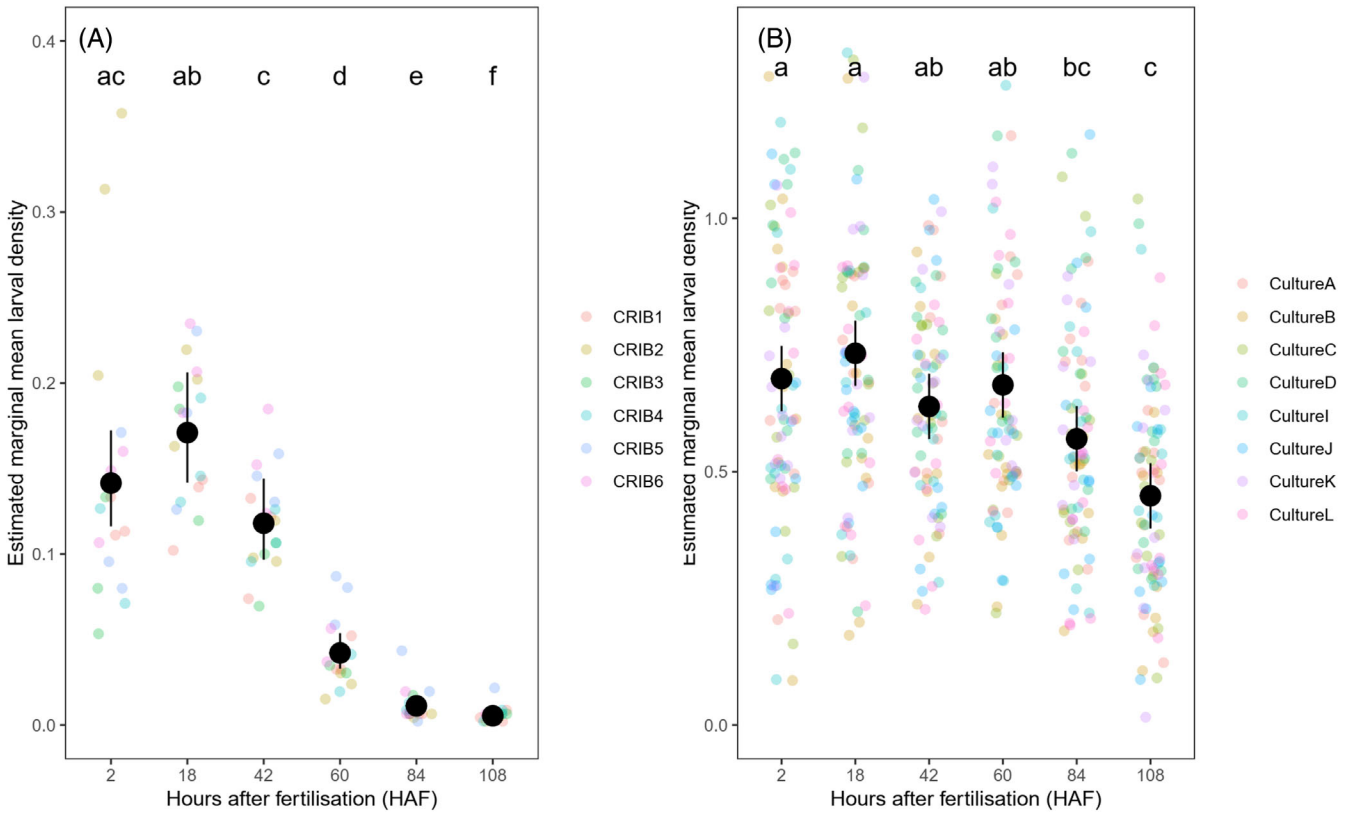

Figure 4. Modeled mean density (mL^{-1}) of *Acropora millepora* larvae in six replicate CRIBs (A) and eight replicate culture tanks (B) through time. Raw data for each CRIB and tank are plotted by colors, with modeled means and their confidence intervals in black. Letters above each time point represent results of pairwise statistical comparisons. Note that *y*-axes differ between (A) and (B).

declined by 34% to 0.45 larvae/mL; average survival was estimated at 3.8 and 66.1% for CRIBs and culture tanks, respectively, and temporal patterns were similar across replicates.

Behavioral Assays

The vertical distributions of larvae reared in CRIBs and culture tanks were similar but changed through time (Fig. 5). All embryos were positively buoyant following spawning (1.5 HAF). By 60 hours in culture, larvae from both treatments were distributed throughout the water column, with approximately equal proportions at the surface, on the benthos, and mid-water column. By 83 hours, most larvae (62%) from both rearing treatments were on or near the benthos, and the distribution was stable beyond that timepoint.

Settlement

On-vessel settlement of larvae from CRIB 6 and Culture A onto SGSs was not significantly different (estimate [Culture A] = 6.3, SE = 7.3, *z*-value = 0.861, $p = 0.389$), with an average of 25 ± 30 and 32 ± 27 spat settled to devices, from CRIB- and culture-reared larvae, respectively (Fig. 3A), with a maximum of 132 spat from CRIB-reared larvae on a single device. Settlement yield (i.e. percentage of devices that harbored at least one spat) totaled 93 and 100% for CRIB- and culture-reared larvae, respectively.

In situ settlement within CRIB 5 revealed a high average yield (89.1%), with a mean of 13.8 ± 28 spat settled per device (median = 5). Significantly more larvae settled on TP than TI (estimate [TP] = 0.94, std. error = 0.32, *z*-value = 2.91, $p = 0.004$), but settlement yield was higher on TI (91.2% yield) than TP (82.1%) (Fig. 3B).

Post-Deployment Survival

Of the 117 SGS that were deployed at Mazie Bay, 13 were not found (11%). Of the 104 retrieved, 75 had live corals (72% yield of those retrieved and 64% yield overall, with 67 and 77% yield for CRIB- and culture-settled spat, respectively). Average spat survival was 5 ± 8% and did not differ significantly between treatments (Welch's *t*-sample *t* test: $t = -0.552$, degrees of freedom [*df*] = 44.922, *p* value = 0.58; Fig. 3C).

Of the 105 tetrapods with CRIB-settled spat deployed across six replicate field sites, 69 were recovered (66%). Yield of recovered devices (i.e. excluding lost devices) was highly variable among plots within sites and among sites, ranging from an average of 15% at Shelving Bay to 88% at Home Reef. No significant differences in yield were observed among sites due to high variation.

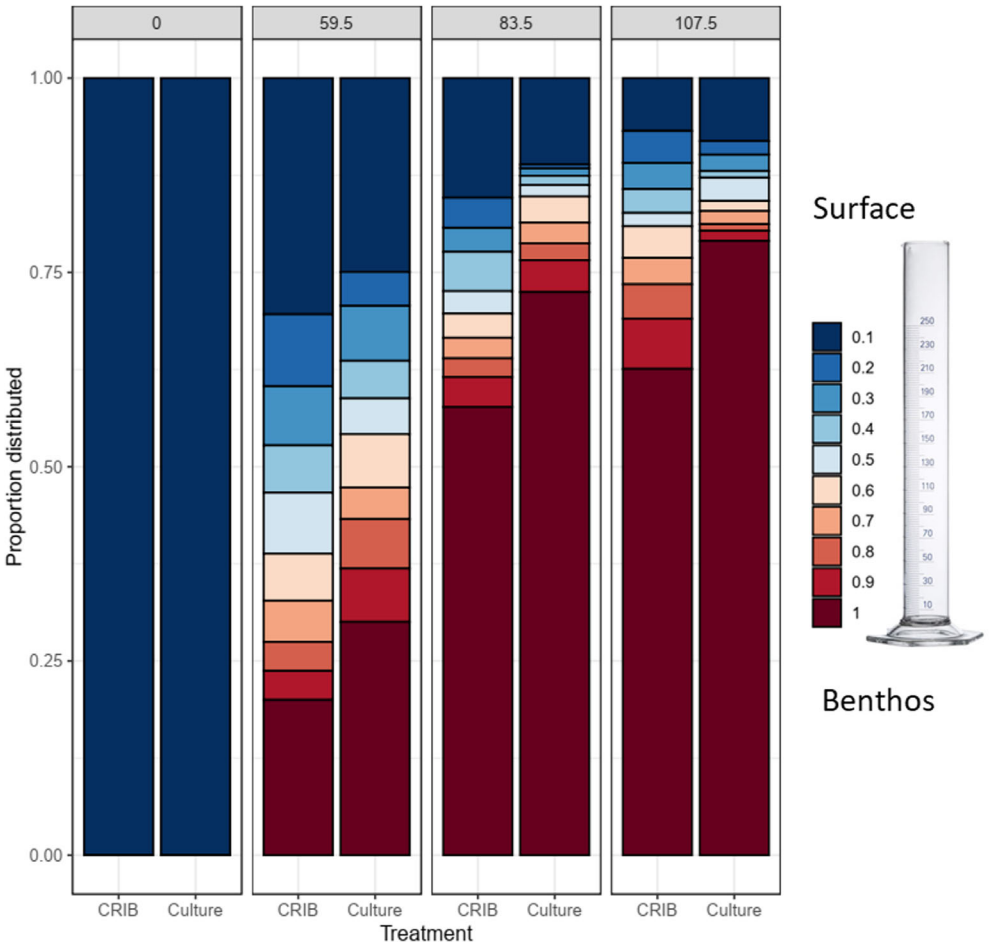

Figure 5. Average proportional distribution of *Acropora millepora* embryos/larvae in a static water column through time (hour after fertilization), from each of three replicate CRIBs and culture tanks. The color scale indicates the larval position in the water column in increments of 0.1, from 0 at the surface to 1 on the benthos. Panels represent hours after fertilization.

Relationship Between Survival and Benthic Composition

Sites varied considerably in their benthic community composition; some sites, including Mazie Bay and Shelving Reef, were dominated by branching *Acropora* and *Lobophora* (Fig. 6A). Other sites, like Home and Humpy Reefs, were dominated by brown macroalgae and *Sargassum* (Fig. 6A). Benthic community composition did not significantly differ between plots with and without surviving corals (Fig. 6C; permutational multivariate analysis of variance [PERMANOVA] 2024, AIMS: $df = 1$, sum of squares $= 21.06$, $r^2 = 0.025$, $F = 1.635$, $p = 0.126$), although the percentage cover of two components of the benthic community, cyanobacteria and *Lobophora*, showed significant negative relationships with survival (Fig. 6B & 6D) (GLMM(Cyano): estimate $= -33.8676$, SE $= 14.22$, z-value $= -2.38$, $p = 0.017$; GLMM(Lobo): estimate $= -1.954$, SE $= 0.87$, z-value $= -2.25$, $p = 0.024$).

Discussion

Culturing *Acropora millepora* larvae was successful using both CRIBs and the on-vessel aquaculture system and allowed an experimental comparison of settlement and post-deployment survival of larvae and spat from each rearing environment.

While larvae were cultured under both rearing conditions, densities declined considerably faster in CRIBs than in culture tanks. The reason for this difference is unknown but could have several explanations, including both biological and physical/mechanical causes. Firstly, greater (a)biotic disturbances or pressures in situ may have resulted in higher mortality during embryogenesis and larval development. The inshore environment in the Keppel Islands is often turbid (Thompson et al. 2023) and suspended sediments were observed in and around the CRIBs. Gilmour (1999) found that *A. digitifera* larval survival declined at suspended sediment concentrations as low as 50 mg/L, although Ricardo et al. (2016) found no lasting negative effects of suspended sediment concentrations up to 800 mg/L on *A. millepora* larvae. While mesh windows (120 μm) largely excluded coarse grains from entering the CRIBs, fine-grained sediments may have entered, and sloshing could have carried in additional sediments. By contrast, negligible sediment was observed in the on-vessel culture tanks, which had robust mechanical

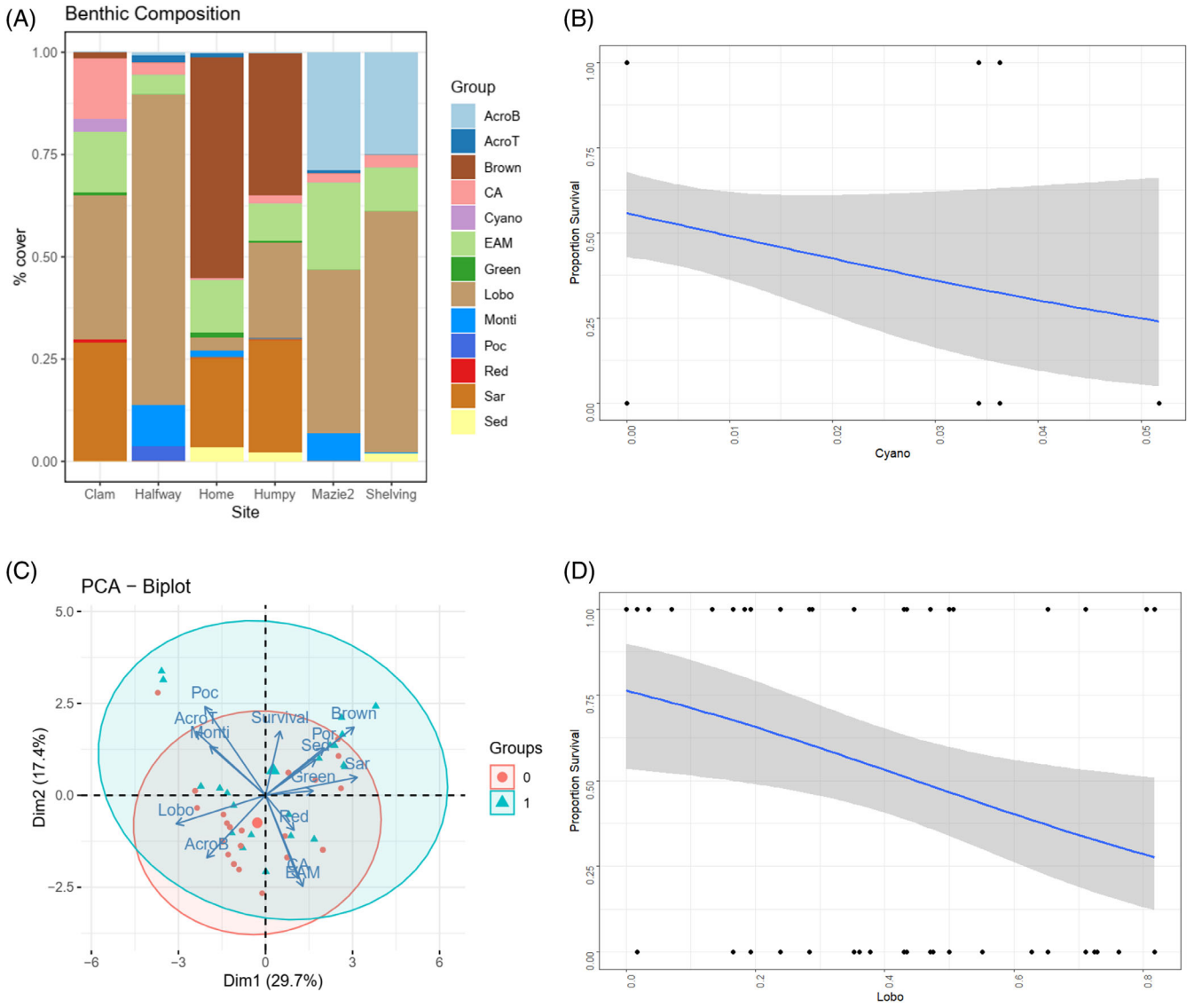

Figure 6. (A) Benthic community composition across six sites where tetrapods with CRIB-settled spat were deployed. (B) PCA of the benthic community composition grouped by pots with (1) and without (0) surviving devices. The community composition did not significantly differ between groups. Significant relationships were detected between survival and benthic cover of (C) cyanobacteria ("Cyano") and (D) *Lobophora* ("Lobo").

filtration (<0.1 μm). This differential turbidity could have resulted in higher mortality in CRIBs than in culture tanks.

Secondly, it is likely that the microbial and macrobial environments differed between CRIB and tank environments, both in composition and biomass. Biofilm developed on windows and other surfaces in the CRIBs (Witt et al. 2011), and alongside particulate organic matter from sediments and dissolved organic carbon from nearby benthic communities (Haas et al. 2011), likely fueled a growing bioload. It is possible that seawater within the CRIBs could have supported pathogens, altered the larval microbiome, or mediated the environment, although this was not tested here. By contrast, culture tanks received ultrafiltered (0.1 μm) seawater presumably exposing larvae to lower bioloads, which may have facilitated higher survival.

Finally, it is possible that CRIBs suffered higher rates of embryo/larval "escape" than culture tanks. Wind caused sloshing of water within the CRIBs that could have washed larvae out of the basins. By contrast, the stability of the vessel meant that conditions were calm in culture tanks, and larval retention was high. Similarly, sloshing of other organisms *into* the CRIBs could have resulted in some predation of embryos and larvae. Indeed, needlefish were observed on two occasions within the CRIBs and were removed, indicating that there were predator entry pathways. Small, potentially predatory invertebrates were also observed swimming near the CRIBs' surfaces, and small ciliates and other organisms (<120 μm) could have entered through the mesh windows. Planktonic coral predators are diverse and were likely present in the CRIBs during development.

CRIBs demonstrated higher mortality during embryogenesis and larval development than culture tanks, and it is possible that this mortality was the result of differential selective pressure that could lead to increased fitness of the surviving larvae and spat in CRIBs. For example, while only 1°C warmer on average, there was higher variability in seawater temperature in the CRIBS (1.2 vs. 0.6°C standard deviation in CRIBs and culture tanks, respectively), which could have resulted in higher stress and mortality in the larvae in pools and increased fitness in surviving larvae (Randall & Szmant 2009). By contrast, the lack of mortality in culture tanks could indicate a relaxation of selective pressures, allowing less fit individuals to persist through deployment (Crates et al. 2023). Indeed, the relaxation of selective pressure in aquaculture has been demonstrated in hatchery-grown brown trout (Linløkken et al. 2021). Yet larval settlement and post-deployment survival were comparable between treatments, suggesting that the fitness of the surviving larvae and resulting spat was similar and indicating that the mortality seen in CRIBs may have been the result of stochastic processes rather than directional selection. Whether these processes were occurring in the CRIBs and cultures remains unknown and would require genetic sampling of the larval populations through time.

While larval densities differed among rearing treatments, behavior and developmental rates were similar in CRIB-reared and culture-reared larvae, reflecting pre-determined life histories (Okubo et al. 2016). Bottom-seeking behavior was observed in some larvae within 60 hours of fertilization, although most larvae in both rearing environments were not distributed low in the water column until the next sampling timepoint (approximately 84 hours post-fertilization). With rearing temperatures averaging 25.2 and 26.1°C in the culture tanks and CRIBs, respectively, this developmental rate was on par with expectations (Randall & Szmant 2009; Woolsey et al. 2013) and resulted in larval settlement competency beginning 5–6 DAF (Randall et al. 2024). Despite similar larval behavior across rearing environments, culture tanks always had a slightly higher proportion of bottom-seeking larvae than CRIBs, which was particularly surprising given that CRIBs were always approximately 1° warmer than culture tanks and coral larval development is faster at warmer temperatures (i.e. Bassim & Sammarco 2003; Randall & Szmant 2009). The reason for this pattern is unknown but could be the result of sampling bias, where the most negative (bottom-seeking) larvae from CRIBs were missed during homogenization. Regardless, this variation in distribution did not appear to affect settlement, and larvae in both treatments largely developed and behaved comparably.

Interestingly, in most CRIBs and culture tanks, larval densities increased between 1.5 and 17.5 hours. The reason for this increase is unknown but could be an artifact of sampling methodology or the result of embryo fragmenting that can occur in early morulae (Heyward & Negri 2012).

While data were limited to one site and a 3-month duration, post-deployment yield was high (>70%) and was similar for CRIB- and culture-reared spat. Average spat survival was 5%, in line with previous seeding experiments of devices directly on the benthos. For example, *Acropora* cf. *kenti* spat survival averaged 4–7.7% after 219 days deployed on a central mid-shelf reef, on similar seeding devices (Randall et al. 2021). As expected, yields were higher than previously recorded for spat deployed directly on the benthos to Keppel Island sites for a longer period (10 months; approximately 28.6% survival, C. Page unpublished data), but lower than those deployed above the substrate (Page et al. 2024), highlighting the importance of direct contact with the benthic environment in driving survival responses. Not surprisingly, some seeded devices were lost among the reef matrix and rubble, highlighting the need to identify approaches to decrease device loss at sites with high rugosity or unstable substrates.

While there were no clear differences in the benthic community composition that supported devices having live and dead spat, there were some significant relationships between survival and specific benthic groups. Firstly, as the cover of *Lobophora* increased, the likelihood of survival decreased. This is not surprising given the well-documented direct and indirect negative effects of *Lobophora* on coral larval settlement, survival, and growth (Morrow et al. 2016; Evensen et al. 2019; Page et al. 2023). Many devices were overgrown or overtopped by *Lobophora* at retrieval; therefore, spat may have been shaded, abraded, directly overgrown, or impacted indirectly via allelopathy. *Lobophora* often co-occurs with branching *Acropora* in the Keppel Islands, which appears to be a poor environment for natural recruitment (C.J. Randall, 2024, AIMS) and the survival of seeded corals (Page et al. 2024). Secondly, the cover of cyanobacteria was also negatively related to coral survival, consistent with previous studies of negative effects of cyanobacteria on coral settlement (Kuffner et al. 2006; Ritson-Williams et al. 2020), although only a small number of plots contained cyanobacteria, and most of these were located within a single site; thus, this result warrants further investigation.

A key outcome of this study was the demonstration of successful spawning, larval culturing, and mass settlement of corals on board a vessel. To date, there have been very few examples of vessel-based coral larval culturing (but see Doropoulos et al. 2019) and concerns regarding the effects of engine vibrations and noise, vessel lights, and other associated factors were mitigated or proved to be unfounded. The use of red lights and black plastic sheeting minimized light pollution while maintaining access to ambient sunlight and moonlight to cue spawning (Babcock et al. 1986) and indeed resulted in highly synchronized spawning behavior in the broodstock. While the environment in the Keppel Islands is turbid (Thompson et al. 2023), the on-board system provided filtration and supported a constant flow of clean water for coral culturing. Furthermore, the rocking motion of the vessel aided in distributing the embryos throughout the tanks during the buoyant stages of embryogenesis, essentially eliminating desiccation above the meniscus and reducing the formation of dense rafts of floating embryos after early mortality, both of which are common occurrences in aquaculture rearing. This unexpected benefit reduced maintenance and handling, which in turn reduced the risk of contamination or physical damage of delicate embryos. Despite generator- and engine-associated noise and vibrations, larvae settled on the vessel, corroborating a recent study demonstrating that larvae can settle directly onto moving substrates (Heyward et al. 2024). Overall, spawning, culturing, and settlement of corals

for seeding on board a vessel was effective and resulted in a high degree of control throughout the process, with high survival.

While larval survival was high, particularly in the culture tanks, post-deployment spat survival averaged only 5% and did not differ between rearing conditions. While 5% may seem low, some estimates of natural spat survival are below 0.5% (Babcock & Mundy 1996; Wilson & Harrison 2005), and this metric remains incredibly difficult to quantify due to the size and cryptic settlement behavior of spat and the highly stochastic nature of reef disturbances (Mumby 1999; Gouezo et al. 2023). For this reason, yield (device-level survival) has been recently adopted as a common metric for the comparison of restoration methods, with the aim to have at least 1 surviving adult coral per seeding device (Chamberland et al. 2017; Miller et al. 2021; Page et al. 2024). Using this metric, the greater than 70% yield seen here was considered high, noting that this only represents 3 months of deployment. Regardless, optimizing the spat density on seeding devices to manage density-dependent processes (i.e. Doropoulos et al. 2018) and improving the device design to support survival are areas for further development (Whitman et al. 2024).

The largest drawback to on-board culturing was the high cost, which included the vessel use, the culture system components, and the staff required to assemble and run the system. In situ rearing was cheaper and could be maintained from shore with fewer staff, making it a much more economical option. Yet the ability to manipulate rearing and settlement conditions on the vessel increased quality control, provided opportunities for additional research (not described here), and could enable restoration activities to take place in remote locations where land-based options are not available. Vessel-based rearing could also increase scalability by extending the duration of on-board rearing and the spatial extent of seeding (Doropoulos et al. 2019). Finally, the control of conditions provided by on-vessel rearing could enable future heat hardening, targeted symbiont inoculation, and controlled breeding, among other methods, to increase the resilience of deployed corals (Voolstra et al. 2021; McLeod et al. 2022; Nitschke et al. 2024). Regardless, both in situ and on-vessel rearing approaches were effective at generating larvae to use in coral seeding, and in situ rearing can likely be modified further to improve survival. Which rearing method should be applied when will be a consideration for managers and practitioners, and the data herein can be used to guide those decisions.

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Conflict of Interest Statement

The authors declare no competing interests exist.

Data Availability Statement

All data are freely available and housed on the AIMS data repository. Data can be accessed here: https://apps.aims.gov.au/metadata/view/cfc60d0b-8c0c-4bfd-a8a9-b7e6e7ebad49

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. AutoCAD drawing of the on-vessel aquaculture system.
Figure S2. In situ temperature data recorded by a Hobo logger placed in a haphazardly selected CRIB and culture tank, throughout the period of *Acropora millepora* embryogenesis.

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