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RESEARCH ARTICLE

Seeded *Acropora digitifera* corals survive best on wave-exposed reefs with grazing from small fishes

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Coral seeding is a restoration technique developed to replenish degraded reefs; however, grazing by herbivorous fish can impede coral survival post deployment. To investigate the impacts of hydrodynamics and fish grazing on seeded-coral survival, we deployed aquaria-reared *Acropora digitifera* spat on engineered-seeding devices across 10 sites spanning a wave-energy gradient at Moore Reef (Great Barrier Reef, Australia). Two devices were used to investigate the role of grazing: a fish-exclusion device and a featureless control. After 1 year, over 60% of devices had live corals. High-energy sites had 83–91% yield (i.e., device-level survival) and three times more survivors than low-energy sites. Exclusion devices significantly improved survival at moderate-to-low flow sites where excavating parrotfish were abundant. Survival was also influenced by the biological characteristics of the site, with more survivors at sites with Labrids (*Thalassoma*, *Gomphosus*), Acanthurids (*Acanthurus*, *Zebrasoma*), Blennids (*Cirripectes*), encrusting non-*Acropora* Scleractinian corals, coralline algae, and ascidians. Our study demonstrates that wave energy, fish activity, and benthic constituents all impact coral survival after seeding. Assessing potential sites for positive drivers of survival prior to deployment could improve the efficacy of coral seeding.

Key words: coral ecology, coral recruitment, coral restoration, fish ecology, reef hydrodynamics, wave energy

Implications for Practice

- Locations on the reef flank or front with high wave energy (annual median flow >0.28 ms^{-1}) should be selected for coral seeding of *Acropora digitifera*.
- Pre-deployment surveys to quantify the abundance of Labrids, Acanthurids, Blennids, and Balistids fish should be conducted to guide the selection of sites.
- Coral seeding devices with fish-exclusion features should be used, particularly in environments with low-to-moderate wave energy.
- The abundance of Scleractinian corals, crustose coralline algae, and ascidians should be considered when placing devices within sites.

Introduction

The increasing frequency of marine heatwaves has led to substantial losses in global coral cover (Souter et al. 2021) and, despite best-practice reef management, the Great Barrier Reef (GBR) in Australia has suffered from five major bleaching events in the last 8 years (Hughes et al. 2017; Henley et al. 2024). The current shift in reef composition and the observed decline of corals represent a window into our future, with more severe and catastrophic losses to populations and species predicted, even when full climate mitigation measures are employed (Kleypas et al. 2021; Condie 2022). Considering this, reef restoration has been proposed to accelerate adaptation and replenish corals on degraded reefs (Ladd et al. 2018; Bay et al. 2019; Rinkevich 2019). However, the restoration of corals at a population scale is challenging, and the experimental testing and implementation of novel techniques, particularly with sexually propagated corals, is in its infancy (Randall et al. 2020; Banaszak et al. 2023).

Coral seeding is a restoration technique currently being trialed at limited spatial scales (Chamberland et al. 2017; Randall et al. 2021, 2023) but has the potential to accelerate coral replenishment and promote adaptation as it is upscaled (Bay et al. 2019). One way to seed corals is to captively breed them, rear larvae, settle larvae onto engineered devices (herein coral-seeding devices) and then deploy the devices, housing newly settled corals (i.e., spat), to the reef. Coral-seeding devices are evolving, with the latest designs incorporating

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modularity, multidimensionality, and features for improved retention and coral protection (Page et al. 2024; Whitman et al. 2024), as well as ensuring compatibility with automated production processes and robotics. To date, coral mortality on seeded devices can be high, but eliminating fish predation pressure is one way to improve survival (Whitman et al. 2024).

The addition of fish-exclusion features (e.g., protrusions and microrefugia) on devices has shown clear benefits to coral survival. For example, microrefugia between 1 and 8 cm^3 on tiles increased the survival of *Pocillopora damicornis* and *Porites lobata* juveniles (Gallagher & Doropoulos 2017). Similarly, 2.5-cm grids on plates increased the survival of *Acropora* spat (Suzuki et al. 2011), while vertical grooves (approximately 4 mm) enhanced the survival of *Acropora tenuis* spat (Randall et al. 2021). Furthermore, fish-exclusion devices doubled the survival of *Acropora digitifera* spat over control devices on the offshore GBR (Whitman et al. 2024). Taken together, it is evident that coral spat can benefit from fish exclusion. However, fish grazing is often accidental, and grazing pressure can be strongly correlated to the biological and physical environment, causing site-specific coral mortality from grazing (Whitman et al. 2024).

Reef hydrodynamics play a crucial role in shaping coral-fish interactions. Wind, waves, currents, and bottom friction (herein wave energy) determine the geomorphic structure of coral reefs as they grow and change over extended geological timeframes (Storlazzi et al. 2004; Hearn 2011). Moreover, the seasonal and diel variability in wave energy influences fine-scale water movement (<2 m), temperature, dissolved nutrient content, and the delivery and resuspension of particulates on reefs (<100 m; Storlazzi & Jaffe 2008; Schlaefer et al. 2021). For instance, at high tide, wind-driven currents and waves can facilitate orbital motion in the water column, resuspending sediments. At low tide, water can become trapped on the reef flat, creating transient and stagnant pools of warm, nutrient-rich water. Over certain seasons, reefs with moderate-to-high wave energy experience turbulent waves, lasting 5–25 seconds, that swiftly sweep water off the flat at low tide (Van Dongeren et al. 2013). These turbulent flows differ from flows on lagoonal and sheltered reefs that take tens of minutes to move water (Van Dongeren et al. 2013). As a result, corals and fish show fine-scale variation in their abundance and behavior that is correlated with many of these hydrodynamic metrics.

Coral and herbivorous fish abundance often peaks on the reef crest and declines on the slope (Bellwood & Wainwright 2001; Bejarano et al. 2017; Fulton et al. 2017). For corals, rates of calcification, nutrient transfer, and heterotrophic feeding can increase with wave energy (Nakamura et al. 2005; Grottoli et al. 2006; Cacciapaglia & van Woesik 2016). For fish, adequate flow can enhance their swimming abilities and reduce predation risk (Hoey & Bellwood 2008). But extreme wave energy can limit coral larval movement (Hata et al. 2017; Reidenbach et al. 2021), increase the risk of overturning mature corals (Madin et al. 2014), and cause locomotive strain for some herbivorous fish (Hoey & Bellwood 2008). As a result, the abundances of corals and fish plateau at specific wave-energy optima, and these optima are likely to result from complex interactions that are taxon-specific. Tracking the interactions between seeded corals and grazing fishes along a gradient of wave energy could identify wave-energy optima to improve coral-seeding efficacy.

To that end, we quantified the growth and survival of coral spat on devices, with and without protection from fish, that were seeded to sites across a predicted gradient of wave energy on Moore Reef (northern GBR). Our study aimed to address three knowledge gaps to guide coral-seeding efforts. First, we sought to identify wave-energy conditions that promote high survival of seeded *A. digitifera* spat. Second, we tested the effect of fish-exclusion features on devices designed to protect coral spat. Lastly, we aimed to identify the fish and benthic constituents that predict high coral survival post seeding.

Methods

Coral Collection and Rearing

Colonies of *A. digitifera* were collected (permit G21/45348.1, Reef Authority, Australia) from Moore Reef (Fig. 1A) prior to February 2022 coral spawning. Colonies were transported via boat to outdoor, flow-through, and temperature-controlled aquaria at the National Sea Simulator in the Australian Institute of Marine Science (AIMS, Townsville, Queensland) and maintained until spawning. The timing of spawning and the numbers of colonies that contributed to mass cultures are reported in Table S1. Gamete bundles were collected, separated, washed, and fertilized following Whitman et al. (2024). Embryos were then transferred to indoor larval rearing tanks where they remained until they reached settlement competency after 5–6 days.

Conditioned concrete tabs (14 × 14 mm^2) were used as settlement substrates. Developed at AIMS under the Reef Restoration and Adaptation Program (RRAP), these tabs are cheap, small, and modular, designed to fit into coral-seeding devices (Fig. 2B & 2C). Tabs were created in sheets (1 sheet = 400 tabs; Fig. 2A) and conditioned in aquaria for 1 month to develop a biofilm known to induce larval settlement (Heyward & Negri 1999). The sheets were placed in individual tanks for mass larval settlement, with larvae settling over 72 hours at target densities of approximately 10–20 spat per tab.

The settled spat were maintained on sheets in aquaria with no light (similar to Ramsby et al. 2024 that used low light treatments) until seeding. At 1-week pre-deployment (2 months post spawning), 1,500 tabs with live spat were cut from the sheets and distributed (3 per device) to 500 devices (Fig. 2A–C). All corals were healthy and free from visual benthic competition at the time of deployment (Fig. 2D). See Supplement S1 for details regarding coral settlement and grow out.

Experimental Design

Corals were seeded to 10 sites on Moore Reef (Fig. 1D) in May 2022. The field deployment followed a hierarchical design (Fig. 2C). Devices were deployed to the reef crest (3–5 m depth,

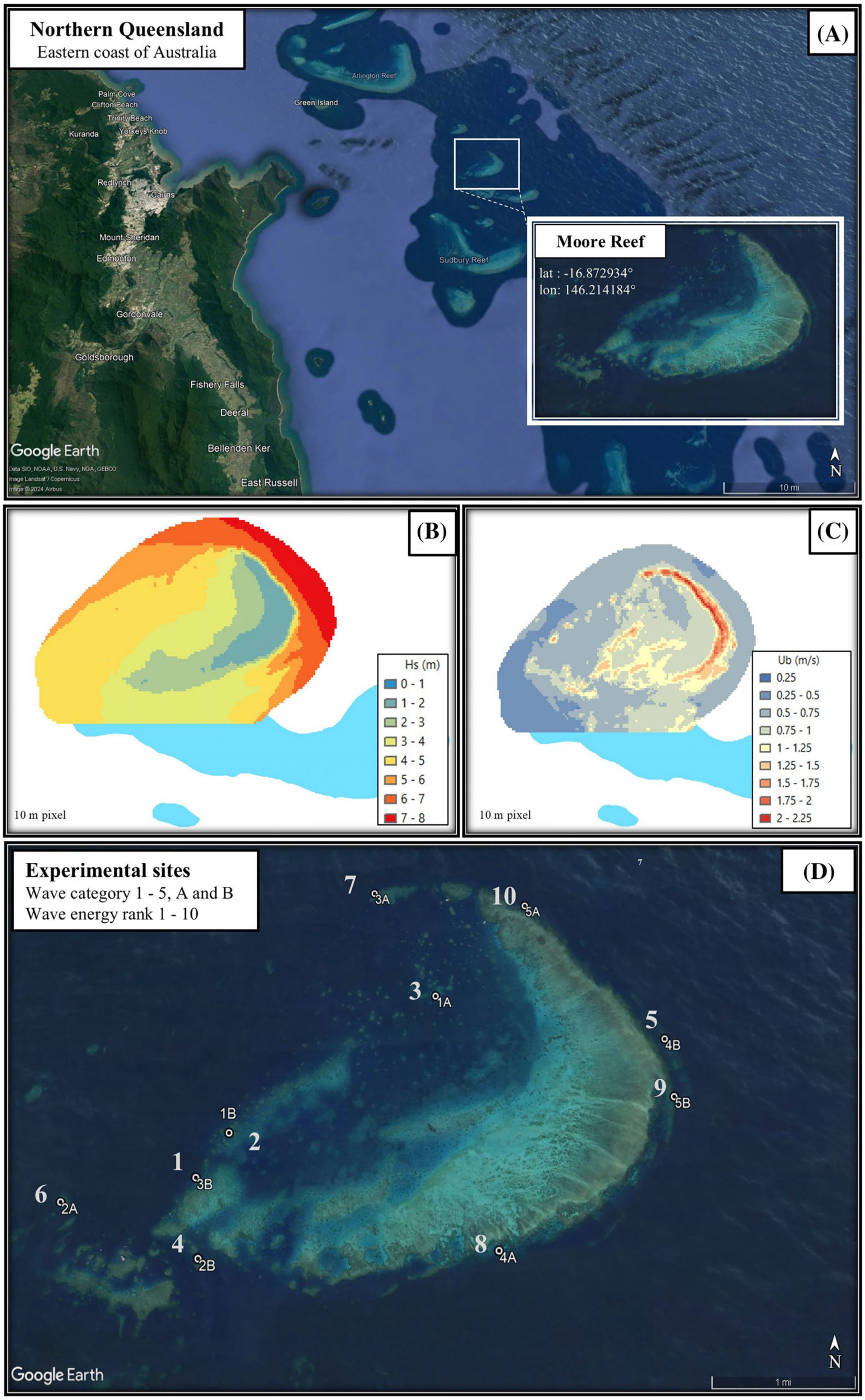

Figure 1. Experimental location and the site-selection process. (A) Geographic location of Moore Reef off the Queensland coast in Australia. (B) Significant wave height (Hs [m]) and (C) bottom stress (Ub [m/second]) modeled for Moore Reef. (D) Ten sites used in the coral-seeding experiment.

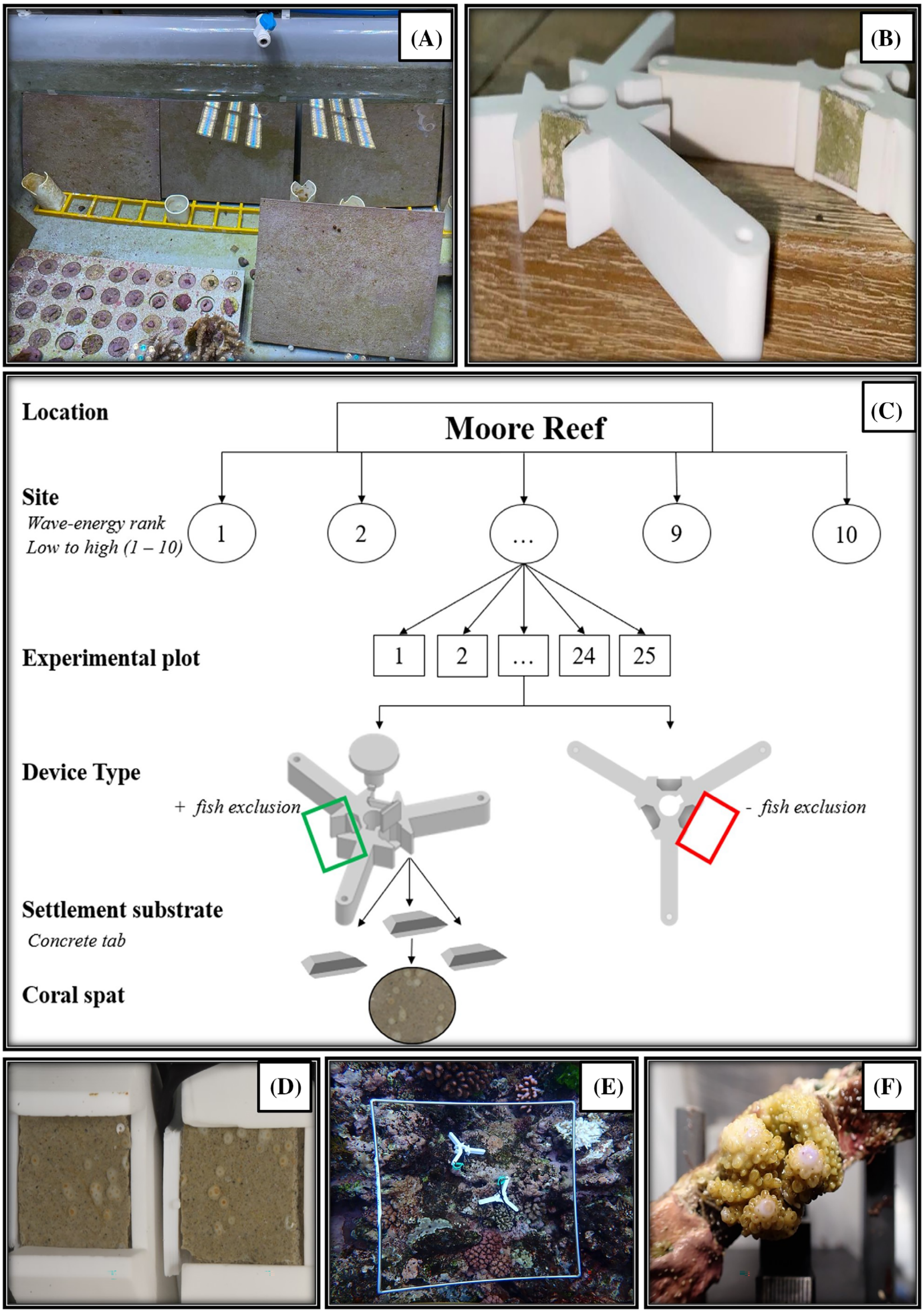

Figure 2. Methods used for the coral-seeding experiment. (A) Tab sheets conditioning in aquaria. (B) Coral-seeding device types: fish exclusion (left) and featureless control (right). (C) Experimental design. (D) Tabs with coral spat pre-deployment. (E) Plot with devices attached to the reef. (F) Sixteen-month-old coral post-deployment.

high tide) and fixed in experimental plots with a cable tie in an upright, horizontal position (Fig. 2E). Devices and their fixings were removed after 16 months.

Device Types. Two device types (Fig. 2B–C), made of 95% alumina ceramic (Shanghai Gongtao Ceramics Co., Ltd., People's Republic of China), were used to test the effect of grazing.

The control was a featureless device open to grazing, while the device of interest included side protrusions (1-cm length) around each tab to limit grazing from fishes with a gape >1 cm. Both designs maintained tabs in a vertical position (Whitman et al. 2024; Page et al. 2024).

Site Selection. High-resolution bathymetry maps (generated from Light Detection and Ranging and Sentinel 2 satellite products; Fig. 1B–C) were used to create a benthic-habitat prediction model for Moore Reef. A remote-sensing method, designed to identify habitat characteristics suitable for coral recruitment, was used following Radford et al. (2024). Bottom stress (Ub [$\mathrm{ms^{-1}}$]; Callaghan 2023; Callaghan et al. 2015; Fig. 1C) was overlaid on a constrained (2–8 m depth) habitat map and a generalized random tessellation stratified method (Stevens & Olsen 2004) was used to identify 10 sites (and 20 reserves) across 5 classes of equally and spatially balanced bottom-stress values. The sites were assessed by divers to confirm the presence of conspecifics or morphotaxa before deployment. Reserve sites were used when the initial site failed to meet selection criteria (e.g., depth, hard bottom, presence of conspecifics/morphotaxa). Initially, two sites, A and B, were selected in each wave class, 1–5 (Fig. 1D). Wave energy was validated using current meters (Marotte HS, Marine GeoPhysics Laboratory, James Cook University, Australia); sites were ranked from low to high flow (1–10), based on in situ measurements (Fig. 1D) and are hereafter referred to as sites 1–10.

Data Collection

Data were collected at six time points and included quantitative and qualitative assessments to determine the influence of biological (fish abundance and grazing, benthic composition) and environmental (wave energy) drivers on coral growth and survival. Assessments were categorized by spatial scale and are detailed below. See Table S2 and Supplement S1 for detailed protocols.

Tab-Level Assessments (cm). Coral survival (alive or dead) on tabs (i.e., tab yield) was assessed by divers in situ. Pre- and post-deployment images (Olympus TG6; Fig. 2F) were used to assess coral survival and/or size ex situ. Maximum linear and maximum perpendicular lengths of the largest surviving coral on each tab were measured. ImageJ was used for the pre-deployment measurements, and calipers were used post-deployment. Coral growth was calculated as the change in surface area ($3\pi r^2$) over time, expressed in millimeters per year, using the average of the two lengths for the radius.

Plot-Level Assessments (m). Benthic composition was assessed at deployment. Quadrats (0.25 $\mathrm{m^2}$) were placed centrally around device pairs and imaged. The percent cover of benthic constituents (Table S3) was estimated for each plot using ReefCloud (https://reefcloud.ai/). Points ($n = 15$) were randomly overlaid on images ($n = 25$ per site) and labeled by an observer.

Site-Level Assessments (Tens of Meters). Divers conducted stationary-point-count surveys (39.25 $\mathrm{m^2}$, 5-minute intervals, 3 replicates $\mathrm{site^{-1}}$ survey $\mathrm{time^{-1}}$) to count fish of interest: Acanthuridae (surgeonfish), Balistidae (triggerfish), Chaetodontidae (butterflyfish), Labridae (Odacinae; wrasse), Labridae (Scarinae; parrotfish), Pomacentridae (damselfish), and Siganidae (rabbitfish). The time, depth, tide, sea state, visibility, and reef complexity were also recorded.

Fish grazing was quantified from video surveillance (GoPro HERO 9). Cameras were deployed to two haphazardly selected plots per site capturing 1–2 hours of footage per plot. Cameras were deployed at the sites on the same day, within 1 hour of each other. A quadrat (0.25 $\mathrm{m^2}$) marked the plot at the start of the recording and then was removed. The hours of footage were standardized (i.e., same duration measured) and assessed for feeding activity (i.e., total bites divided by the duration, bites per minute; Table S4). Fish feeding in the plots were imaged, time stamped, and identified to species by a single observer.

A Marotte current meter was deployed at each site for up to 16 months. Due to extreme weather, several meters were lost or damaged, resulting in nine sites with data (Table S2). Current data were obtained in 1-minute intervals and expressed as mean water flow ($\mathrm{ms^{-1}}$) over time.

Statistical Analyses

Coral Survival. To investigate the effects of device type and site on coral survival over time, a Bayesian hierarchical logistic mixed-effects regression model ("brms," R software; Bürkner 2017) with a Bernoulli distribution (logit-link function) was used. A random effect of device nested within plot nested within site was included for repeated observations. Normal priors (0, 1.7) were assigned to the intercept and regression coefficients. Student *t* priors (0, 3, 1.7) were used for random effects. The model was fit using Hamiltonian Monte Carlo (HMC) sampling (Table S5) and selected by comparing Leave-One-Out Information Criterion. Diagnostic tests (posterior predictive checks and hypothesis testing) were conducted to assess model fit and ensure validity. The model predictions and credible intervals were visualized using "ggplot2" (Wickham 2016).

Coral Growth. The effect of site, device type, and their interaction on coral growth was modeled as above, using a Gaussian distribution (identity-link function). A normal prior (0, 10) for the intercept, normal priors (0, 2.5) for the slopes of site and device-type effects, and a Student *t* prior (3, 0, 1) for the site-plot-device random effect were used. HMC sampling (Table S6), diagnostic checks, and visualizations were performed as above.

Fish Counts and Feeding. Principal component analyses (PCAs, "factoextra"; Kassambara & Mundt 2017) and redundancy analyses (RDA, "vegan"; Dixon 2003) with backward-stepwise models were used to deduce significant predictors of survival and growth from the fish count and bite data. Survival and growth were modeled against the interactive effects of device type and fish count or bites. Separate models were run for survival and growth, and for the species- and family-level classification for each dataset (counts and bites). Multiplicative models were fit (Tables S8–S10) and checked for accuracy as above. Site-related variation in fish counts and bites were investigated using a zero-inflated Poisson (identity-link function) and Gamma (log-link function) distribution model, respectively. Family-level classifications and sites were used as predictors, with time-site-replicate as the random effect. Normal priors were used for the intercept (1.7, 1.25 for count data and 0, 5 for bite data) and for the regression coefficients (0, 5). The bite model included an exponential prior (rate parameter = 1) for the standard deviation of the random effects. Models were fit (Table S7), checked for accuracy, and visualizations were performed as above.

Benthic Constituents. PCAs, RDAs, and backward-stepwise models were used to reveal significant predictors in the benthic dataset. Brms models were used to predict survival and growth by device type, the benthic variables, and their interaction. Multiplicative models, including the interaction with device type and the random effect of device-plot-site, were fit (Table S11), checked for accuracy, and figures created as above.

Results

After 16 months, >50% of devices and >25% of tabs had at least one live *Acropora digitifera* coral (Fig. 3A). The 10 sites captured a wave energy gradient spanning an average flow of 0.06–0.28 ms^{-1} (Fig. S1). The spread of sites across the gradient was fairly even, with slightly more sites with lower current speeds. Sites characterized by high wave energy on the reef front and flank had up to 90% of devices and >50% of tabs with live corals; this was three times higher than that of sheltered sites on the back reef.

Coral Survival

Tab-level coral survival (hereafter survival) declined through time (Fig. 3A). Nearly 50% of corals suffered mortality within 9 months, and the odds of survival declined further after 12 and 16 months (Table S5). Survival increased with increasing wave energy (Figs. 3B & S1). The odds of survival were twice as high at the highest-flow site (10) than at the lowest-flow site (1), and up to 18 times lower at the moderate-flow site (6; Table S5). More corals survived on fish-exclusion devices than on control devices, and this was consistent through time (Fig. 3A), although the best-performing device varied by site (Fig. 3B). Fish-exclusion devices outperformed controls at 60% of sites (Fig. 3B) but were only 1.25 times better than controls, on average (Table S5). The fish-exclusion device improved survival most at low wave-energy sites (Fig. 3B; Table S5).

Coral Growth

The effect of fish exclusion on *A. digitifera* growth was generally positive (Fig. 3C). The exclusion device resulted in faster

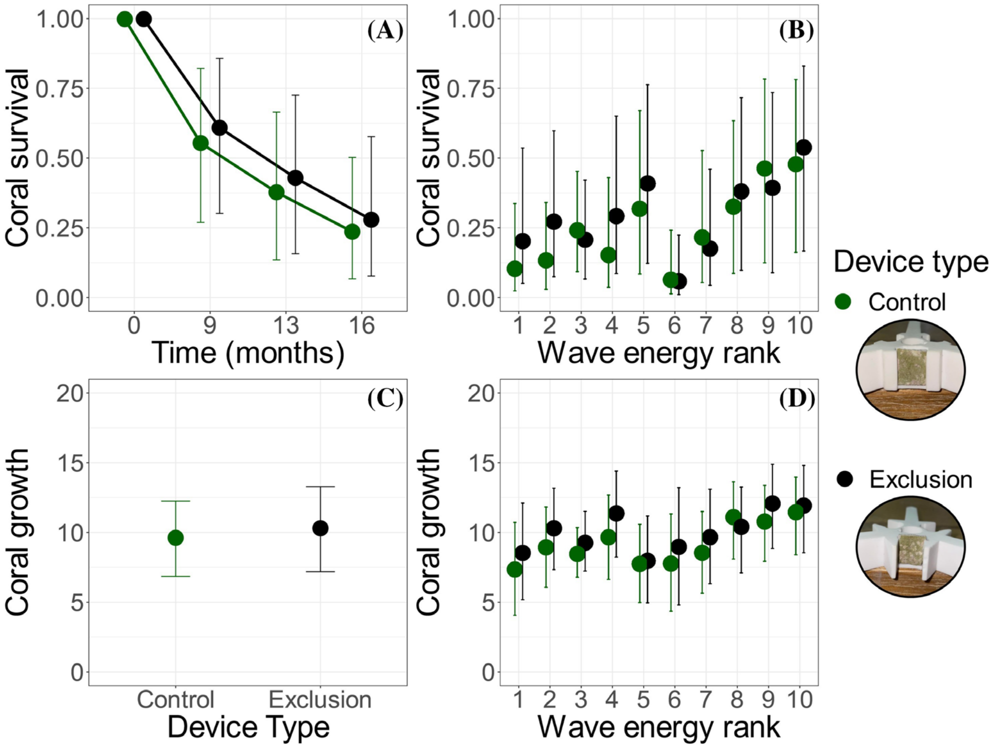

Figure 3. Tab-level coral survival after 16 months. (A) Survival by device type through time. (B) Final survival by wave-energy ranked sites. (C) Coral growth (mm/year) by device type and by (D) wave-energy ranked sites. Mean estimates with 95% CIs are displayed. The data in (A), (B), and (D) are jittered with respect to the x-axis for ease of visualization.

growth for corals at 70% of sites, while the control facilitated faster or similar growth at other sites (Table S6; Fig. 3D). Coral growth followed a similar trend to survival, irrespective of the device treatment (Fig. 3D). Sites 9 and 10 had the highest growth rate (>12 mm year^{-1}), while corals at sites 1, 5, and 6 were slow growing (<8 mm year^{-1}; Table S6; Fig. 3D). The greatest benefit of fish exclusion on growth was at site 4, with low-to-moderate flow, where growth was twice as fast in exclusion devices than in control devices (Table S6).

Fish Activity

Fish Counts. A total of 5,272 fish from five taxa were observed. Wrasse (*Thalassoma hardwicke*, *T. nigrofasciatum*, and *Gomphosus varius*) were the most abundant (>1,850 fish) and triggerfish (*Sufflamen chrysopterum*) were the least abundant (<30 fish). *Chlorurus microrhinos* and *C. spirulus* were common parrotfish, while *Ctenochaetus striatus* and *Acanthurus nigrofuscus* were common surgeonfish. *Chaetodon trifascialis* was the most common butterflyfish. Moderate-flow sites (5–6) had the most fish, while a low-flow site (3) had the least (Fig. 4A). Site 6 had the highest abundance of parrotfish and triggerfishes, and this was 3.5–10 times more fish than site 10 (Table S7; Fig. 4B). Site 7 (moderate flow) had double the number of butterflyfishes compared to other sites (Fig. 4B).

Coral survival increased with the abundance of *Thalassoma amblycephalum*, *Gomphosus varius*, and *Acanthurus lineatus*, but the result was not homogeneous across device types (Fig. 5A–C). *T. amblycephalum* and *G. varius* increased survival 2.6 times more for corals in controls than fish-exclusion devices (Table S8; Fig. 5A & 5B). *A. lineatus* increased survival 1.6 times more in exclusion devices than controls (Table S8; Fig. 5C). Survival decreased as *S. chrysopterum* and *C. microrhinos* abundance increased (Fig. 5D–E); these fishes were 3–4 times more detrimental to survival than *T. amblycephalum* (Table S8).

As *T. amblycephalum* and *G. varius* abundance increased, coral growth declined (Table S10; Fig. 4F–H). Coral growth increased with increasing abundance of *A. lineatus* (Fig. 5I) and decreasing abundance of *C. trifascialis* and *C. microrhinos* (Table S10; Fig. 5J–K).

Fish Feeding. A total of 20,818 bites from 72 species were recorded. Damselfish (*Pomacentrus* spp., 7,911 bites) and surgeonfish (*Ctenochaetus striatus* and *Acanthurus nigrofuscus*, 7,221 bites) fed frequently. Parrotfish, wrasse, and blennies were also feeding (Fig. 4D), with 910 bites taken by *Chlorurus spirulus*, *C. microrhinos*, and *Scarus* spp., 1,286 bites from *Thalassoma hardwicke*, *Gomphosus varius*, and *Halichoeres* spp., and 2033 bites from *Cirripectes* and *Ecsenius* spp. Threadfin breams (Nemipteridae) and hawkfishes (Cirrhitidae) were rarely feeding, with <5 bites recorded. Site 9 (high flow) had the most feeding activity, while site 3 (low flow) had the least (Fig. 4C). *C. spirulus* and *Ecsenius* spp. fed most at low-to-moderate flow sites, with 35 and 6 times more bites than high-flow sites, respectively (Table S7).

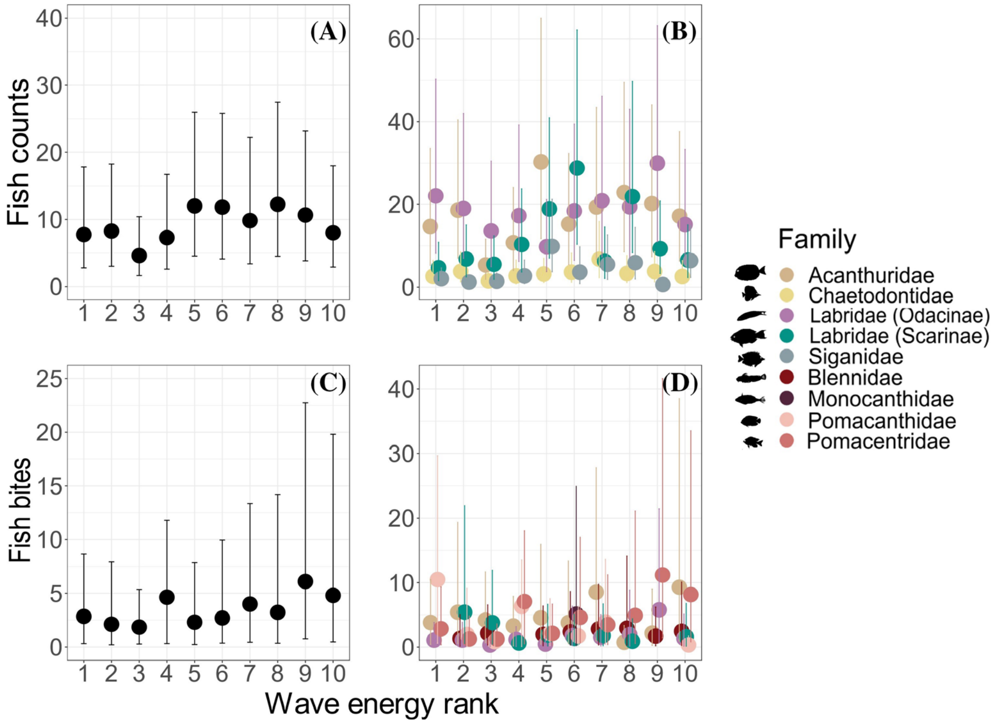

Figure 4. Fish activity during the deployment. (A) Fish counts (in 39.25 m^2) by wave-energy-ranked sites. (B) Fish counts by site and family. (C) Fish bites (per minute) by wave-energy-ranked sites. (D) Fish counts by site and family. Mean estimates with 95% credible intervals are displayed. The data in (B) and (D) are jittered with respect to the x-axis for ease of visualization.

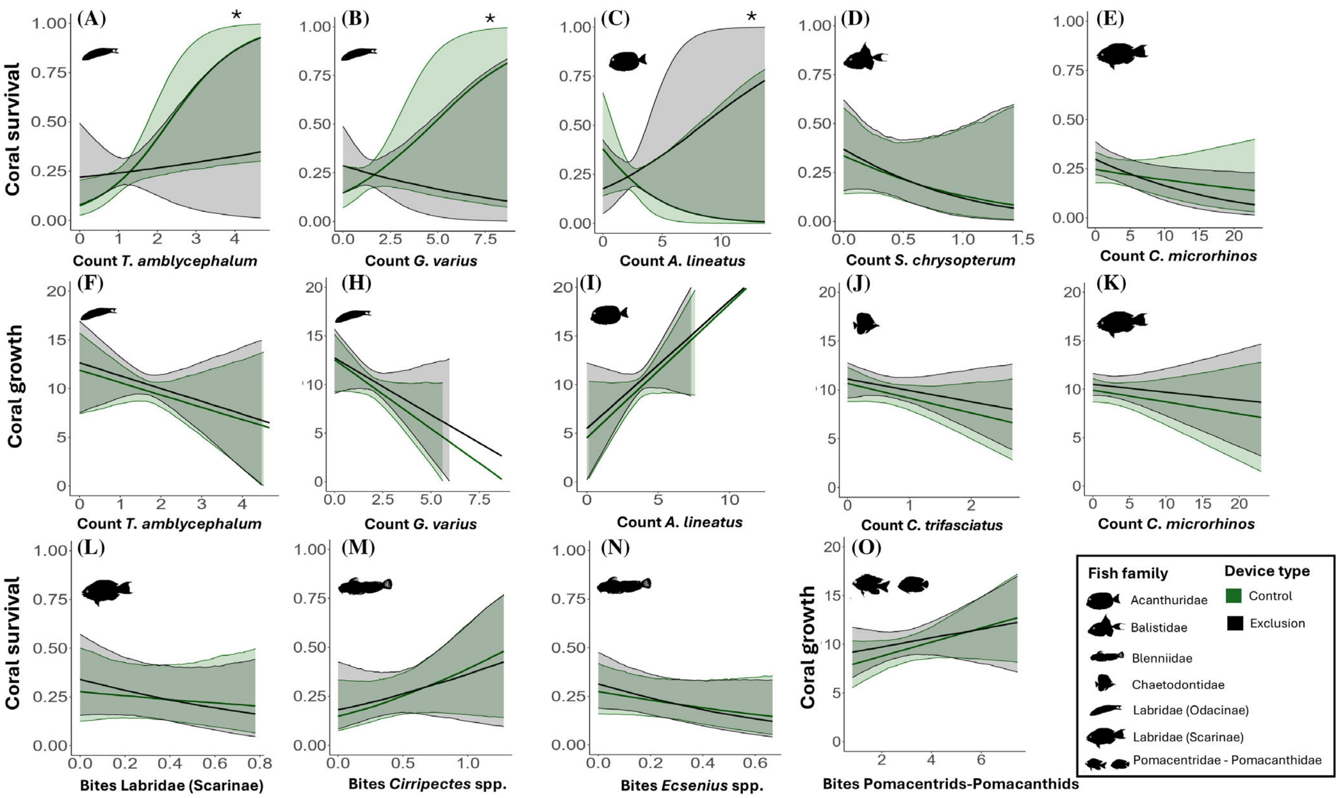

Figure 5. Tab-level coral survival and growth by fish activity and device type. (A–E) Survival by fish counts (in 39.25 m^2). (F–K) Growth (mm year^{-1}) by fish counts. (L–N) Survival by fish bites (per minute). (O) Growth by fish bites. The "*" denotes a difference in the response by device type. Mean estimates with 95% CIs are displayed.

Bites from parrotfish generally reduced survival (Fig. 5L), but this response was weak and species-specific (Table S9). The effects of feeding by blennies on survival were also heterogeneous. Survival was 11 times higher in plots with feeding from *Cirripectes* spp., but low in plots with feeding from *Ecsenius* spp. (Table S9; Fig. 5M & 5N). Other notable, yet weak relationships, include increasing survival with increased feeding from *Halichoeres* wrasse and the surgeonfish *Zebrasoma scopas* (for control devices only), and with decreased feeding from the angelfish *Centropyge vrolikii*. Parrotfish bites were more detrimental to survival than bites from wrasse (Table S9).

Coral growth increased with feeding by damselfishes and angelfishes (Fig. 5O) and the *Cirripectes* blennid but decreased with feeding from the *Ecsenius* blennid (Table S10).

Benthic Community

Fifty-four benthic categories from 6 groups were identified in device plots. CCA were the most abundant, while sponges and hard corals *Goniopora* and *Mycedium* were rare. On average, plots contained >75% algae, >15% hard coral, and <10% other organisms.

Corals were more likely to survive with increasing cover of encrusting non-*Acropora* corals (>20% threshold), sessile invertebrates (>10%), and CCA (>75%; Table S11; Fig. 6A–C). *Acropora* coral and carbonate rubble (including mixed-algal biofilms) were negative for survival (Table S11; Fig. 6D–E). Encrusting *Porites* and *Platygyra* most significantly increased survival (Fig. 6F–G), while Ascidians were the most significant non-coral invertebrate (Table S11; Fig. 6H). Coral responses to the benthic community were generally similar between device treatments, but the error associated with the exclusion device was higher (Fig. 6).

Discussion

We investigated the effects of wave energy, fish grazing, and their interaction on coral-seeding efficacy and identified four criteria to achieve high survival of *A. digitifera* spat on the northern GBR. (1) Select seeding locations on the reef flank or front with high wave energy (annual median flow >0.28 ms^{-1}). (2) Use the abundance of small fish (Labrids, Acanthurids, Blennids, and Balistids) to guide the selection of sites. (3) Use devices with fish-exclusion features, particularly in environments with low-to-moderate wave energy. (4) Consider the abundance of Scleractinian corals, crustose algae, and ascidians when placing devices. These findings provide clear guidelines to improve the value of coral seeding as a tool for restoration.

Our study demonstrates the direct positive role of wave energy in supporting juvenile *A. digitifera* growth and survival;

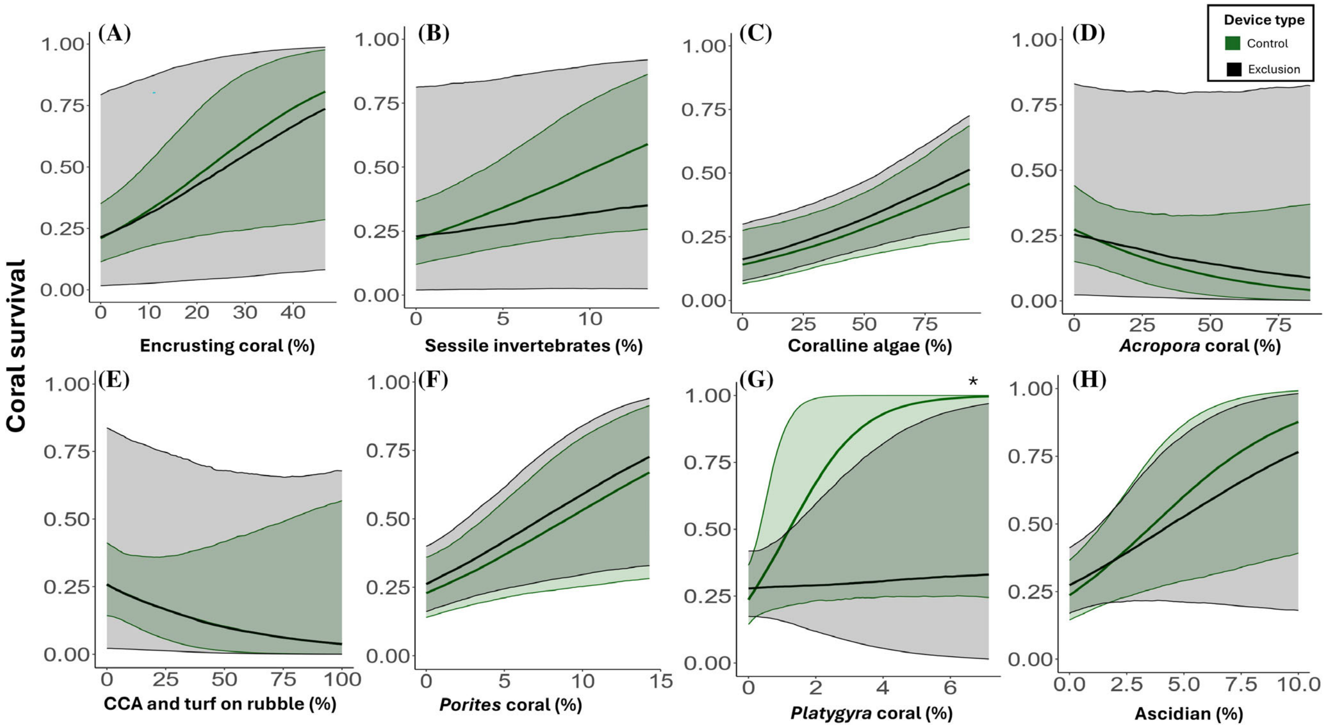

Figure 6. (A–H) Coral survival by benthic constituents (% cover in experimental plots) and device type. A difference in the response by device type is denoted by: "*." Mean estimates with 95% CIs are displayed.

coral response was site specific but peaked at wave-exposed sites on the reef flank and front. Similar studies have found that *Montipora* juveniles (Hancock et al. 2021) and adult *Montipora* (Hancock et al. 2021), *Acropora* (Nakamura & Van Woesik 2001), *Stylophora* (Nakamura et al. 2003), and *Galaxea* (Schutter et al. 2011) corals can grow two times faster in wave-exposed environments, and there are several mechanisms by which flow can increase survival. For example, wave-exposed reefs have high turbulence and more water mixing that introduce zooplankton (Robinson et al. 2013) and induce phytoplankton settlement (Ruiz et al. 2004); zooplankton and phytoplankton can be a potential food source for heterotrophic corals. Similarly, increased pigment concentrations, increased host tissue biomass, and up to 10 fold higher symbiont densities have been identified for *Porites* and *Diploastrea* corals in response to high wave energy (Roder et al. 2011); these increases can improve photosynthetic output and nutrition, resulting in faster growth. Overall, high wave energy equates to high nutrient acquisition, and this facilitates growth and survival. Seeding spat to wave-exposed sites could reduce the time required to reach coral size-escape thresholds (Doropoulos et al. 2016), avoiding mortality from fish predation and increasing recruitment success.

Fish species associated with higher coral survival were more prevalent at wave-exposed reefs, while fishes that correlated with low survival were more common at sheltered sites. These results are in line with previous literature; but importantly, we provide foundational evidence for the underlying role that wave energy has on the coral-fish relationship. For example, *Thalassoma* wrasse can be 15 times more abundant in wave-swept habitats than those that are sheltered (Fulton et al. 2017), and sites abundant in small wrasse had more coral survivors in our study. Similarly, the parrotfish *Chlorurus microhinos* is highly associated with low-wave exposure (Bejarano et al. 2017); coral survival declined with increasing abundance of this species and other excavating parrotfish. Moreover, small-bodied blennies (*Ecsenius* spp.) dominate on reefs where larger-bodied blennies (*Cirripectes* spp.) are absent (Townsend & Tibbetts 2000); feeding from *Cirripectes* blennies was positively related to survival in our study, and they were most prevalent on wave-exposed reefs. We suspect that, at fine spatial scales, small herbivorous fishes are directly feeding on turfing and filamentous algae that grow near seeded corals (Choat et al. 2004), while carnivorous fishes could indirectly remove algae and deposited sediments as they detach prey. Indeed, *Zebrasoma* surgeonfish generate thrust while feeding, using a lateral head-flick and fin movement (Perevolotsky et al. 2020). Likewise, *Acanthurus* spp. engulf and use suction to draw algae into their mouths (Mihalitsis & Wainwright 2024). Together, these movements could reduce benthic competition and move sediments, helping to promote coral survival. But the influence of fish on these fine-scale variables is multifaceted and not necessarily consistent between seeding device types.

More corals survived when using fish-exclusion devices in our study, and these devices were most beneficial at sheltered sites with low-to-moderate wave energy. In a previous study, survival of 4-month-old *A. digitifera* spat doubled when fish-exclusion devices were used at sheltered sites (central, offshore, GBR; Whitman et al. 2024). Taken together, these results suggest there are clear benefits to using protective devices in coral-seeding trials on the offshore GBR. However, the protection provided by fish-exclusion devices likely extends beyond predation and includes the moderation of other coral stressors. For example, coral survival was lowest at a moderate-flow, rubble-dominated site, with a high abundance of excavating parrotfish. Under periods of moderate-to-high flow, reef rubble can become dislodged, move, and disturb sediments; these mechanisms can increase coral abrasion, scouring, and smothering (Kenyon et al. 2020), hindering spat survival (Heyward et al. 2024). Furthermore, excavating parrotfish can erode >25% of reef carbonate (Bellwood 1996) and this bioerosion is highest in habitats dominated by rubble, *Acropora* spp., and *Pocillopora* spp. (Yarlett et al. 2020, 2021). The reworking of coral rubble and sediments by parrotfish could produce a higher volume of small sediments that are easily mobilized by wave energy. Understanding how recruiting corals respond to increased bio-eroded sediments would provide new insights into the coral–fish relationship.

The abundance of encrusting Scleractinian corals was positively correlated with coral survival in our study, but branching, corymbose, and plating corals were negatively correlated. Similarly, Page et al. (2024) found that the survival of seeded *M. aequituberculata* spat declined in response to increasing branching-*Acropora* abundance. There are three plausible explanations for these findings. Firstly, corals with complex morphologies are vulnerable to high wave energy (Madin et al. 2014), which can increase rubble and sediments and negatively affect spat survival. Next, coarse obstructions like plating corals and large boulders might alter water movement and retain sediments within their Momentum Boundary Layer (MBL; Shashar et al. 1996), hindering spat survival. In support of this, corals with rough-textured branches (e.g., *Montipora*) have been shown to produce a thicker MBL than columnar and smooth corals (e.g., *Porites*; Shashar et al. 1996). Finally, overtopping and shading from complex corals can impact recruit growth and impede survival (Baird & Hughes 2000; Carlson et al. 2024). While these responses are likely species- and context-specific, there is growing evidence to avoid certain benthic communities when seeding coral spat to reefs.

We also found that some non-coral sessile organisms increased spat survival. Previously, two coral-seeding experiments on the GBR found that sites with more sponges, epilithic-algal communities, and cyanobacteria improved seeded *Acropora* survival (Randall et al. 2023; Whitman et al. 2024). Since sponges and ascidians can be proxies for water flow (Schönberg 2021), high spat survival in their presence could implicate wave energy as the underlying driver. Furthermore, sponges, ascidians, and cyanobacteria are also common on rubble reefs (Schönberg 2021; Wolfe et al. 2021), and although they could be fostering survival in this habitat, their effect is weakened due to negative effects from rubble and sediment abrasion. Equally, competitive macroalgae (*Lobophora* spp.) and bryozoans, commonly found on rubble reefs (Baird & Hughes 2000), were observed at our rubble-dominated site. We propose low-lying brown algae and bryozoans on tabs could be early indicators of *Acropora* coral mortality since their early-successional biofilms can impede *A. kenti* survival (Fong et al. 2024) and restrict growth in shaded habitats (Yarlett et al. 2020). Antifoulant coatings (Roepke et al. 2022) on seeding devices and tabs could be explored to buy time for corals to reach size-escape thresholds before competitive algae begin colonization. Site preparations, such as macroalgae removal (Smith et al. 2023) and rubble stabilization (Ceccarelli et al. 2020), may also be required on highly degraded reefs.

In this study, we initially reduced grazing pressure by raising corals in no-light conditions, therefore removing crustose algae, a critical food source for herbivorous fishes (Whitman et al. 2024). We then directly manipulated the odds of predation on seeded corals by deploying devices across a gradient of wave energy. While the relationship between recruiting corals, grazers, and their environment is often complex, this experimental research advances our fundamental understanding of coral reef ecology. Spatial-habitat models can be used in the site selection process with environmental and physical variables, but diver surveys will be required to ground truth in situ biological conditions. Restoration practitioners who plan to use coral seeding as a tool to repopulate reefs should consider applying the four criteria described in our study and holistically monitor the survival outcome on an annual basis to gauge the impact of the intervention. To combat the detrimental effects of climate change, we need to prioritize research into creating and deploying thermally tolerant corals and curb our carbon emissions on a global scale.

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Supporting Information

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

Supplement S1. Coral settlement and grow out.
Figure S1. Mean current speed (ms^{-1}) ranked by site, lowest to highest (wave energy rank 1–10).
Table S1. Coral spawning and settlement information, including relevant dates, times and colony contributions.
Table S2. Field survey successes and failures.
Table S3. Benthic classification label set.
Table S4. Detailed information from the GoPro video analysis to quantify grazing pressure.
Table S5. Coral survival (tab yield) model output.
Table S6. Coral growth rate model output.
Table S7. Fish counts and feeding by site model outputs.
Table S8. Coral survival by fish count model outputs.
Table S9. Coral survival by fish feeding model outputs.
Table S10. Coral growth by fish count and feeding model outputs.
Table S11. Coral survival and benthic composition model outputs.

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