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Combined impacts of natural recruitment and active propagation for coral population recovery on the Great Barrier Reef

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ABSTRACT: Coral populations on the Great Barrier Reef (GBR) are experiencing long-term shifts in size structure, including steep declines in small colonies, driving major concerns for recovery through the supply of new recruits. Whilst coral restoration began on the GBR in 2018, the combined influence of natural recruitment and outplanting for coral population recovery has not been evaluated. Here, we assessed 2 sites (Rayban and Mojo) at Opal Reef that were subject to intensive outplant efforts over a 3 yr period (2018–2021). Coral cover did not change significantly, with a baseline of 15% in 2018 and a cover of 28 and 25% in Rayban outplant and control areas, respectively, in 2021, while Mojo exhibited a coral cover of 38% in 2018 and 52% (outplant area) and 29% (control area) in 2021. Natural recruitment in 2021 did not vary by site and was characterised by a settlement rate of 5.5 and 3.7 recruits tile^{-1} at Rayban and Mojo, respectively. Juvenile coral abundance and diversity were similar for control and outplant areas at each site. Over the 3 yr period, coral cover as a metric did not identify differences between control and outplant areas; however, size–frequency distributions of key coral taxa revealed a higher frequency of small to mid-sized colonies in outplant communities compared to controls. Given that no differences were observed in recruitment rates or juvenile abundances, variations in population structure appear to be driven by planting efforts rather than natural recovery. Our results demonstrate the need for combined monitoring of natural versus intervention-based rehabilitation to understand the impact of coral propagation efforts for local site recovery.

KEY WORDS: Coral · Recruitment · Restoration · Outplant · Great Barrier Reef · Size–frequency · Population structure

1. INTRODUCTION

Coral reefs worldwide are facing unprecedented declines in health from local and global anthropogenic pressures including poor water quality, predatory corallivore outbreaks and climate-induced coral bleaching (Hoegh-Guldberg et al. 2017, Bruno et al. 2019, Donovan et al. 2021). Over the past 2 decades, global sea surface temperatures have warmed by an average of 0.9°C, with temperature increases of up to 3.3°C predicted by the end of the century (representative concentration pathway 8.5 scenario; IPCC 2022). Consequently, thermal stress events and coral bleaching — the breakdown in symbiosis between the coral host and its intracellular algae that drives wide-scale coral mortality (e.g. Suggett & Smith 2020) — will likely occur biannually on most coral reefs in the next 3 to 5 decades (van Hooidonk et al. 2016, Donner et al. 2018), further accelerating loss of reef system resilience, function and diversity (Lough & van Oppen 2018, van Woesik et al. 2018).

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Large-scale disturbances have the capacity to alter reef populations through community-wide losses in coral cover (often resulting in phase shifts from coral to algal-dominated reefs; Graham et al. 2015, Roff et al. 2015) or through taxa-specific impacts driven by differences in coral life-history strategies (Hughes et al. 2018). Such selective influences can cause drastic shifts in community composition and diversity, both of which underpin the effective function and resilience of a system (e.g. Mcleod et al. 2019). The capacity of a system to withstand change depends heavily on sufficient functional redundancy (i.e. species which provide similar ecological roles within the system) and response diversity (i.e. the range of responses produced among species within the same functional group), and thus the disproportionate loss of specific groups can have devastating effects on system function (Elmqvist et al. 2003, Nyström 2006, McWilliam et al. 2018). For coral reefs, functional traits are often linked to coral morphological structure due to the importance of reef architecture in determining habitat structure and, in turn, ecological functions (Zawada et al. 2019). For example, coral morphologies that are more top heavy such as tabular or plating corals are important refuges for large-bodied fishes in shallow reef environments (Kerry & Bellwood 2015) and provide indirect functions such as shading the benthos, thereby influencing understorey assemblages (Baird & Hughes 2000). However, many of these tabular species are also sensitive to environmental disturbance (Marshall & Baird 2000, Ortiz et al. 2021), and thus their loss not only reduces coral cover and alters community assemblage but also contributes to a decline within that functional group and, by extension, the ecological insurance for that population.

Disturbance can fundamentally impair community structure through selectively decreasing the relative abundance of particular coral size classes (e.g. Pisapia et al. 2019). Whilst declines in coral cover following disturbance events are well documented and often used as a proxy for reef health and resilience (De'ath et al. 2012, Jackson et al. 2014, Babcock et al. 2021), changes to population size structure are relatively rarely examined. However, population size structure dynamics can reveal important information about the underlying processes influencing communities, as well as long-term ecosystem function and viability (Bak & Meesters 1998, Álvarez-Noriega et al. 2016). This is particularly relevant to coral populations, as most life-history stages such as reproductive maturity, fecundity and mortality are linked to coral colony size (Meesters et al. 2001, Vermeij & Sandin 2008, Shlesinger & van Woesik 2021). For example, large coral colonies have been found to disproportionately affect population growth rates through pronounced contributions of survival and growth (Shlesinger & van Woesik 2021). Moreover, the loss of these adult colonies can have additional consequences through reduced fecundity, further impairing population trajectories (Dietzel et al. 2020). Accounting for such demographic processes — beyond coral cover — therefore has the capacity to yield greater understanding of shifts in coral community state and function over space and time.

The Great Barrier Reef (GBR) has experienced long-term shifts in the size structure of coral populations over the past 2.5 decades. Steep declines in the abundance of small colonies have been documented, likely due to high post-settlement mortality or the depleted supply of new recruits caused by the loss of large fecund colonies over time (Dietzel et al. 2020). Natural recruitment is crucial for rebuilding perturbed populations and maintaining system resilience, and recent studies have highlighted how coral communities may not have the capacity to recover unaided if stock–recruitment dynamics remain compromised from increasingly frequent stress events (dela Cruz & Harrison 2017, Hughes et al. 2019). Therefore, understanding the rates of larval production, successful settlement and establishment within a community provides vital information on the capacity of a reef to withstand pressures and rebuild functioning populations (Ritson-Williams et al. 2009, Doropoulos et al. 2015, Holbrook et al. 2018, Jonker et al. 2019). Yet, information on the abundance and assemblage of juvenile coral recruits (0–5 cm diameter) remains limited on the GBR, and thus the relative contribution of different life stages to overall community dynamics is not well understood.

In the wake of the recurrent mass bleaching events of 2016 and 2017, tourism operators in the northern GBR initiated propagation and planting of asexual coral fragments (>5 cm) as a means to aid local recovery at high-value sites (i.e. sites with disproportionately high ecological or economic value; Howlett et al. 2022). As such, this activity provided a unique opportunity to examine the concurrent impact of intervention-based coral restoration and natural recruitment on population structure and local site recovery. Changes to coral communities have been previously documented following occurrences of these processes in isolation; for example, Doropoulos et al. (2015) and Bramanti & Edmunds (2016) linked recruit demographics to recovery trajectories across reef habitats and coral taxa, whereas Williams et al.

(2019) and Shaish et al. (2010) assessed the impact of coral restoration approaches on community regeneration. However, the combined influence of natural recruitment and intervention-based rehabilitation for local site recovery is not well understood (but see Ladd et al. 2019), particularly on the GBR. Therefore, here, we evaluated 2 sites at Opal Reef (a northern GBR reef that has been subjected to substantial coral re-planting efforts; Howlett et al. 2022) that were differentially impacted by the 2016–2017 mass bleaching events and consequently subject to distinct outplanting effort: Rayban and Mojo. Changes in benthic composition between 2018 and 2021 were characterised to better understand shifts in mean coral cover and diversity over time. To quantify natural recovery at each site, the abundance and diversity of 2 recruitment stages were examined: coral spat that had settled on tiles (hereafter referred to as settled recruits) and juvenile colonies ≤5 cm diameter that had survived on the reef since settlement (hereafter referred to as juvenile corals). Size–frequency distributions of key coral taxa were then examined in outplant and control (unmanipulated) areas to evaluate the combined impact of natural recovery and coral outplanting on the population structure. We specifically hypothesised that populations subject to intensive outplanting would have greater coral cover and higher species richness compared to unmanipulated communities. Finally, we hypothesised that areas subject to intensive planting of coral propagules but low recruitment rates would have a greater frequency of small size classes (ca. 4–50 cm^2) compared to unmanipulated communities, resulting in a right-skewed distribution.

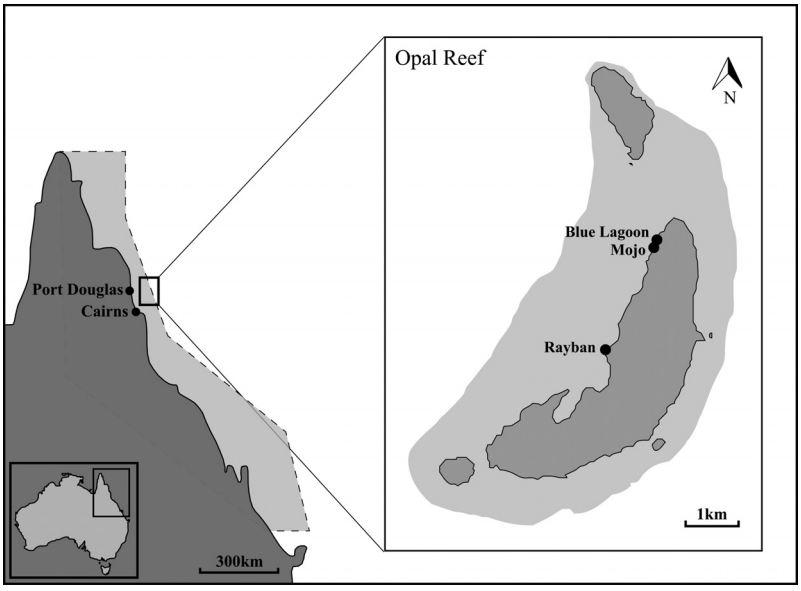

Fig. 1. Northern Queensland, Australia, and the Great Barrier Reef (dashed outline) showing the locations of the 2 study sites, Rayban and Mojo (including Blue Lagoon, the area of the 2018 baseline benthic surveys for Mojo), at Opal Reef (light grey)

2. MATERIALS AND METHODS

2.1. Study site and coral outplanting

The study was conducted at 2 sites on Opal Reef (16° 13′ S, 145° 53.5′ E), an offshore reef located 55 km northeast of Port Douglas, Queensland, Australia, on the northern GBR (Fig. 1). Rayban (16° 13′ 24.6″ S, 145° 53′ 24.7″ E), is located near the middle leeward side of Opal Reef and was heavily impacted by the 2016–2017 mass bleaching events (C. Roper & J. Edmondson pers. obs.). As such, Rayban has been subject to intensive coral outplanting since August 2018 (>14 050 corals planted as of February 2022). Conversely, Mojo (16° 12′ 23.8″ S, 145° 53′ 54.5″ E) was less impacted by the 2016–2017 thermal stress, possibly due to a slightly lower average sea surface temperature experienced over the summer months compared to Rayban (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m700p095_supp.pdf), and thus has been subject to a lower planting effort (>5700 corals planted) in the same time frame.

Coral outplanting was conducted from August 2018 to present by 1 local tourism operator using the Coralclip® (Suggett et al. 2020) to attach coral fragments to the substrate at each site: divers hammer Coralclip® into bare rock, brush the planting area free of algae or other debris, and position the coral fragment under the spring-loaded clip, ensuring adequate pressure to secure the fragment. Coral propagules were sourced from 2 locations: *in situ* fragments found naturally broken on the reef substrate (known as fragments of opportunity) or propagules grown on coral nurseries located within each site (Howlett et al. 2021). As such, planted fragments (typically 5–15 cm in length) generally represent those coral taxa already present within each site. Operators were responsible for reporting their planting activities, including number of outplants, coral taxonomy and source of fragments; however, the level of coral identification varied between genera (and mor-

phology) or species based on diver knowledge (see Howlett et al. 2022 for more detail). The operational planting area of each site was also determined through satellite imagery. The edge of the reef planting zone within each site was traced and the overall area (m^2) calculated using the measurement tool in Google Earth (version 9.164.0.0).

2.2. Benthic surveys

Benthic composition was determined via triplicate 30 m continuous line intercept video transects in 3 treatment areas: a baseline (measured in August 2018) and outplant and control (unmanipulated) areas (measured in November 2021) at each site (n = 9 at both Rayban and Mojo). Transect tapes were laid along the reef slope at 3 m (±0.5 m) depth, and a GoPro HERO 9® was used to record the substrate immediately below the tape. Substrate was classified into one of 8 categories: abiotic-hard (i.e. rock, rubble), abiotic-soft (i.e. sand), scleractinian corals, octocorals (i.e. soft corals), turf algae, calcifying algae, other macroalgae (i.e. any algae not included in the other 2 categories) and other invertebrates. Scleractinian corals were also taxonomically identified to species level. Whilst the August 2018 baseline survey for Mojo was conducted at the nearby mooring site known as Blue Lagoon located approximately 100 m north of Mojo (Fig. 1), Blue Lagoon and Mojo are a continuous reef habitat of similar coral species and community structure and only considered different sites by tourism operators due to access via 2 separate moorings. The 2018 baseline survey for Rayban was conducted in the same area which subsequently became the outplant area and was re-surveyed in November 2021. Control and outplant areas were approximately 100 m apart from one another at both sites.

Coral settlement rates were assessed for Rayban and Mojo during the mass spawning of November 2020. Six unglazed terracotta tiles (11 × 11 × 1 cm) were deployed randomly at each site (not specifically within outplant or control areas) approximately 3 wk prior to spawning to allow biofouling to occur (n = 6 at both Rayban and Mojo; permit no. G19/42292.1). Each tile had a 0.8 cm hole drilled in the centre and was fixed to a stainless steel plate which was secured onto bare limestone substrate via plastic plugs at approximately 4 m depth. Tiles were secured in a horizontal orientation 100 to 200 cm apart and approximately 2 cm from the substrate (Fig. 2). Tiles were collected from the reef in February 2021 via SCUBA by threading each tile onto a stainless steel rod to prevent dislodging recruits. Once above water, tiles were immediately placed in a 10% bleach solution for 24 h to remove organic material. Rinsed tiles were examined using an Olympus stereo microscope (model SZ61) at 2.5× magnification, and recruit abundance and diversity were recorded for each tile. Settled recruits were taxonomically identified to genus using Babcock et al. (2003), whereby any individuals unidentifiable due to location on the tile (e.g.

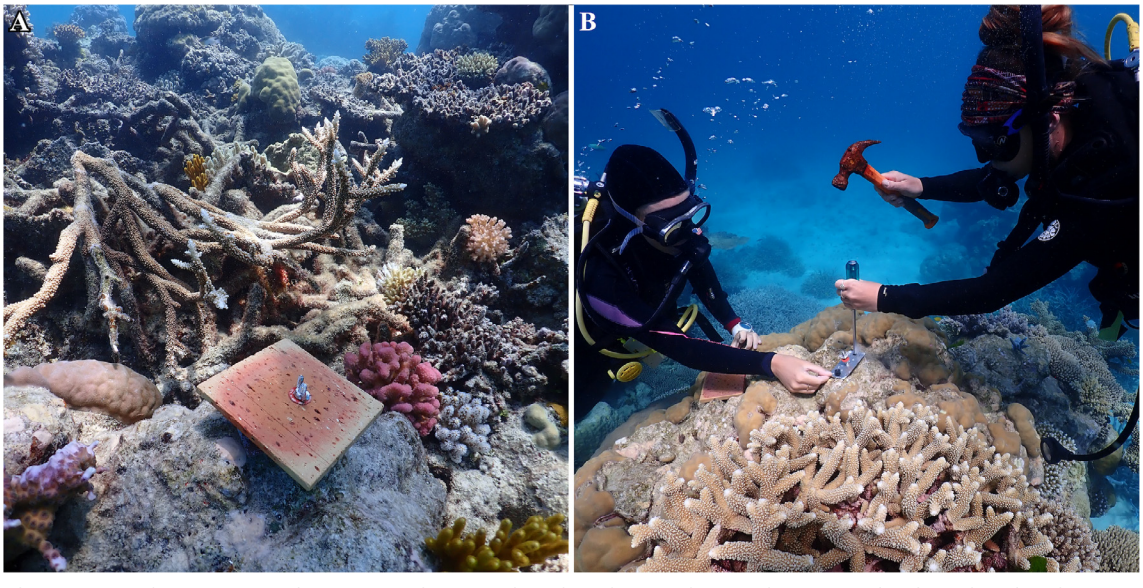

Fig. 2. Placement and orientation of recruit settlement tiles placed at Rayban and Mojo on Opal Reef in October 2020, 3 wk prior to the November 2020 mass spawning event. (A) Placement of tile on bare rock approximately 2 cm above the substrate; (B) divers attaching a stainless steel plate to bare substrate, which secured the tile in place via a mounted bolt

in a crevice) or damage to the skeleton were labelled as unknown.

The density of juvenile corals was examined in September 2021 at both sites within areas of the reef subject to long-term coral planting and control (unmanipulated) areas. Triplicate 30 m belt transects were laid at 3 m (±0.5 m) depth along the reef slope in each treatment area at both sites. Juvenile corals were counted and taxonomically identified 1 m either side of 2 randomly chosen 5 m sections of each 30 m transect (20 m^2 per transect). Any coral colony ≤5 cm at its longest diameter was considered a juvenile and was identified to the genus level.

Coral population size–frequency surveys were conducted along the same belt transects used for evaluating juvenile corals. Five coral species dominant at both sites were chosen, as they represented commonly outplanted fragments (Howlett et al. 2022; Table 1): *Acropora intermedia*, *A. millepora*, *A. muricata*, *A. spathulata* and *Pocillopora verrucosa.* However, due to the challenge of reliably differentiating similar species (within the same species complex) *in situ* (particularly for fragments of opportunity), *A. intermedia* and *A. muricata*, and *A. millepora* and *A. spathulata* were combined into 2 species groups, resulting in 3 distributions overall: *A. intermedia/muricata*, *A. millepora/spathulata* and *P. verrucosa*. Colonies 1 m either side of the 30 m transect tape (60 m^2 per transect) were measured for size (longest diameter and perpendicular width) using a measuring tape (to the nearest centimetre). To obtain a uniform sample size between treatments, colonies along 2 additional 30 m transects were also measured in each control area at both sites (n = 3 outplant transects, 180 m^2 total, and n = 5 control transects, 300 m^2 total).

Table 1. Total number of coral fragments outplanted by species at each site from August 2018 to February 2022. The abbreviation spp. refers to any species within that genus which were not identified to species level. *Pocillopora* spp. refers specifically to *P. verrucosa* and *P. meandrina*, which were unable to be differentiated

Species	Rayban	Mojo
Acropora elseyi	60	0
Acropora florida	30	5
Acropora gemmifera	49	4
Acropora humilis	10	0
Acropora intermedia	560	322
Acropora loripes	82	0
Acropora millepora	337	371
Acropora muricata	131	85
Acropora pectinata	15	0
Acropora robusta	6	0
Acropora secale	4	0
Acropora spp.	10 060	3544
Acropora tenuis	52	4
Acropora valida	0	20
Echinopora horrida	9	0
Echinopora spp.	147	51
Montipora spp.	81	56
Montipora spumosa	56	0
Pocillopora damicornis	288	276
Pocillopora spp.	1398	792
Pocillopora verrucosa	136	0
Porites cylindrica	236	53
Turbinaria reniformis	56	0
Turbinaria spp.	81	53
Unrecorded	203	136

2.3. Statistical analysis

Four steps were used to statistically analyse the data. (1) The mean proportion of each benthic category was calculated by site and treatment and the categories visually compared using a principal components analysis (PCA). A 2-way ANOVA was used to compare the extracted ordination axes for principal component 1 (PC1) and principal component 2 (PC2) between sites, treatments and their combined interaction. (2) Differences in mean hard coral cover, species richness and diversity (Shannon-Wiener index) between treatments at each site were also assessed using a 1-way ANOVA and Tukey's post hoc test. All data met parametric assumptions of normality (Shapiro-Wilk) and homogeneity of variance (Bartlett's test) except for Mojo diversity data, which were transformed by raising to the third power to fit a normal distribution. (3) Settled recruits and juvenile corals were characterised by abundance, richness and diversity (Shannon-Wiener index), and settled recruits were analysed by site via a Welch 2-sample *t*-test. Settled recruit abundance was square root transformed to satisfy normality assumptions (Shapiro-Wilk), while diversity data contained ties (could not be ranked due to equal values) and were unable to fit a normal distribution; thus, a permutation test (with 10 000 permutations) was used to compare differences in diversity indices between sites. A 2-way ANOVA was used to assess juvenile coral characteristics (abundance, richness and diversity) by treatment, site and their interaction. (4) Size–frequency distributions of coral colonies were analysed for each species group by site and treatment by binning log-transformed colony area (length × width) into size classes and plotting against the count in each bin (15 bins were

used guided by dataset size). A 2-sample Kolmogorov-Smirnov test (with the alternative hypothesis specified as greater) was used to compare differences between distributions, but data were found to contain ties due to rounding of colony size (to the nearest centimetre) during data collection. Therefore, a small random perturbation was added to each measurement (±0.5 cm) and the validity of the method tested by repeating the process 10 000 times and observing how the test statistic varied. The test statistic (and hence p-value) never varied, confirming that the random perturbations were not affecting the test result, and thus the test was validated. For all tests, a p-value of less than alpha (α = 0.05) was considered significant. All data analyses were conducted in R (R Core Team 2021).

3. RESULTS

3.1. Changes in reef benthic composition

Since the initiation of coral propagation and planting in 2018, almost 3 times as many outplants were established at Rayban (>14 050 coral fragments) than at Mojo (>5700 coral fragments; Fig. 3). Accounting for the operational area of each planting site (Rayban ca. 6800 m^2, Mojo ca. 5500 m^2), Rayban ultimately received twice the density of coral outplants compared to Mojo, at 2.1 and 1.1 fragments m^{-2}, respectively. *Acropora* bushy/corymbose, *Acropora* branching and *Pocillopora* bushy have been the most commonly planted taxa and morphologies, collectively accounting for 90 and 89% of total outplants at Rayban and Mojo, respectively (Fig. 3).

PCA of benthic categories revealed distinct site-specific differences with minimal overlap (Fig. 4). Scleractinian corals and abiotic-hard substrate were responsible for the greatest variation along PC1 and were negatively correlated. Abiotic-soft substrate was responsible for the greatest influence along PC2. Regardless of treatment (baseline, control and outplant), Rayban and Mojo showed minimal overlap in benthic composition and were found to significantly differ for PC1 ($F_{1,12}$ = 70.327, p < 0.001) but not PC2 ($F_{1,12}$ = 0.024, p = 0.878; Table S1). Although outplant communities were characterised by higher scleractinian cover (Fig. 4), no significant differences were found between treatments within sites (PC1: $F_{2,12}$ = 1.655, p = 0.231; PC2: $F_{2,12}$ = 0.986, p = 0.402; Table S1).

Surveys revealed Rayban mean hard coral cover was 15.1 ± 2.9% (mean ± SE) in 2018 and went to 25.2 ± 2.1% in control areas (Tukey's post hoc, p = 0.489; Table S2) and to 27.8 ± 9.6% in outplant areas (Tukey's post hoc, p = 0.344; Table S2) in 2021 (Figs. 5 & S2, Table 2). In contrast, hard coral cover at Mojo went from a 2018 baseline of 38.2 ± 4.3 to 52.3 ± 5.2% (Tukey's post hoc, p = 0.118) and 28.7 ± 2.6% (Tukey's post hoc, p = 0.315) in outplant and control areas, respectively (Table S2, Figs. 5 & S2). Mean coral species richness significantly increased at Rayban from 11.33 ± 0.33 in 2018 to 20.7 ± 2.96 in outplant areas in 2021 (Tukey's post hoc, p = 0.024; Table S2). Similarly, diversity increased in both control and outplant areas from 2018 (Tukey's post hoc, p = 0.027 and p = 0.034, respectively; Table S2). Mean species richness also increased significantly at Mojo from 14.3 ± 1.67 in 2018 to 25.0 ± 2.52 in outplant areas in 2021 (Tukey's post hoc, p = 0.040; Table S2), as did diversity, with increases over time in both treatments (Table 2).

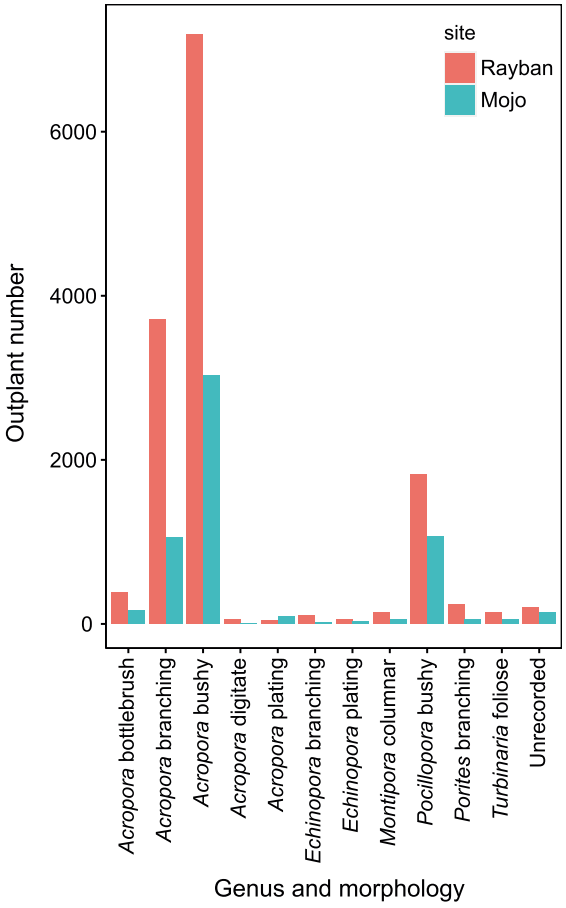

Fig. 3. Proportion of coral propagules planted at Rayban and Mojo from August 2018 to February 2022 by genus and morphology

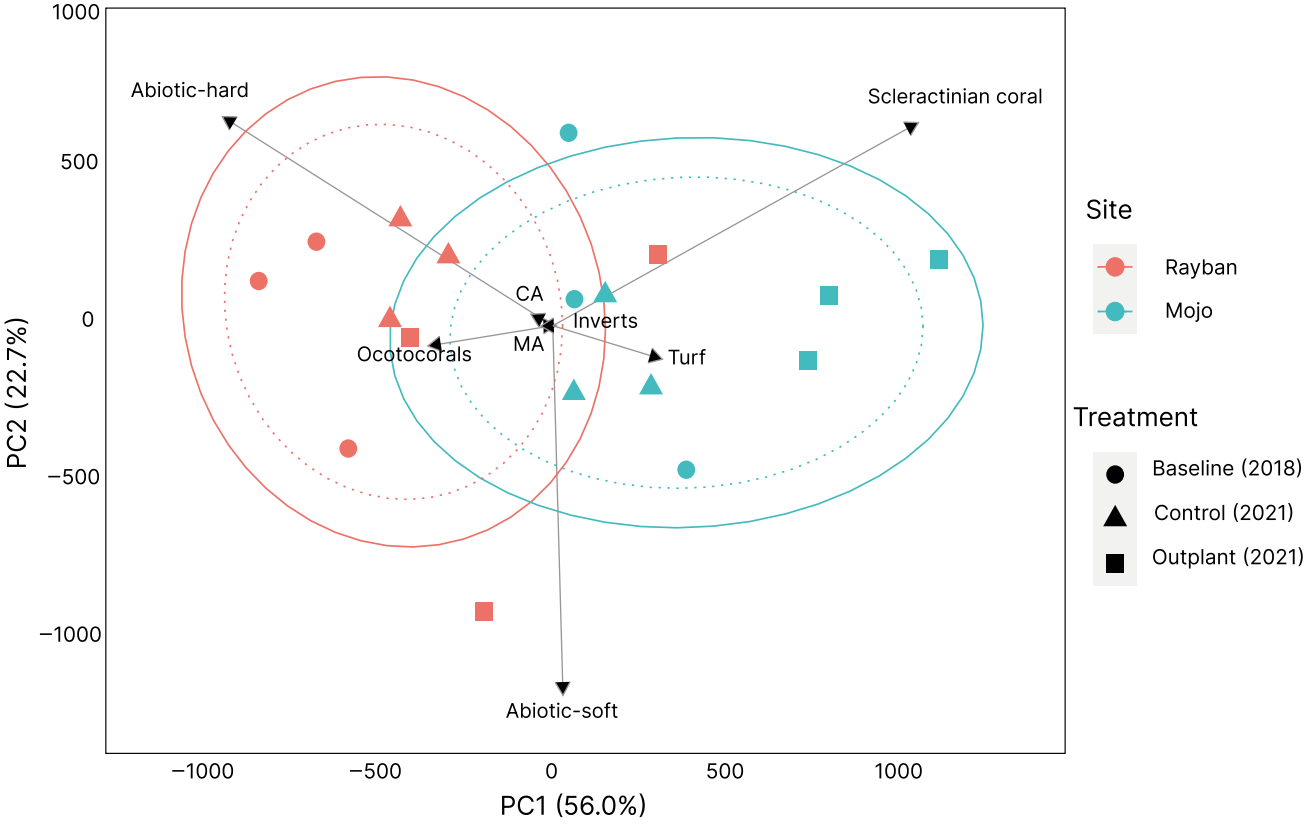

Fig. 4. Principal components analysis (PCA) of benthic categories grouped by site (Rayban and Mojo). Ellipses show 80% (dashed lines) and 90% (solid lines) CIs. PCA loadings of benthic categories (visualised as vectors) were scaled to PCA eigenvalues. Vector direction shows the relative contribution of each variable to the principal components (PCs); vector length indicates the strength of this contribution. CA: calcifying algae; MA: other macroalgae (i.e. any algae other than calcifying or turfing algae); Inverts: other invertebrates; Turf: turfing algae

3.2. Characteristics of settled recruits and juvenile corals

Abundance, richness and diversity (Shannon-Wiener index) of settled coral recruits on tiles — assessed in February 2021 following the November 2020 spawning — were similar between Rayban and Mojo, with no significant differences found between sites (Table S3). Although mean recruit count was almost twice as high at Rayban (5.5 ± 3.0 recruits tile^{-1}) compared to Mojo (3.7 ± 1.7 recruits tile^{-1}; Figs. 6 & S3), substantial variation in abundance was evident across tiles. *Acropora* sp. dominated the proportional diversity of settled recruits (Rayban = 55%, Mojo = 46%), followed by *Pocillopora* sp. and *Porites* sp. at Rayban (12 and 9%, respectively) and *Porites* sp. and *Pocillopora* sp. at Mojo (18 and 14%, respectively; Fig. 6).

Abundance, richness and diversity (Shannon-Wiener index) of juvenile corals on the reef (September 2021) did not significantly vary between control and outplant areas at either Rayban or Mojo (Tables 3 & S4). Although abundance was similar within sites ($F_{1,8}$ = 0.411, p = 0.539; Table S4), the number of juvenile corals between sites was significantly different, whereby Rayban exhibited 1.6 times more juveniles than Mojo ($F_{1,8}$ = 5.332, p = 0.050; Table S4, Fig. S4). Diversity was also significantly higher at Rayban, with an index of 2.10 ± 0.07 compared to 1.67 ± 0.09 at Mojo ($F_{1,8}$ = 14.147, p = 0.006; Table S4, Fig. 7). Juvenile corals at both sites were dominated by *Porites* (Rayban 38%, Mojo 57%) followed by *Acropora* sp. and *Pocillopora* sp. at Rayban (14 and 9%, respectively) and *Acropora* sp. and *Goniastrea* sp. at Mojo (each 6%; Fig. 7). Overall, juvenile coral patterns varied only between sites, not treatment (control versus outplant), but were not consistent for all characteristics (Table 3).

3.3. Population size structure

As expected, both Rayban and Mojo outplant communities were dominated by a higher frequency of

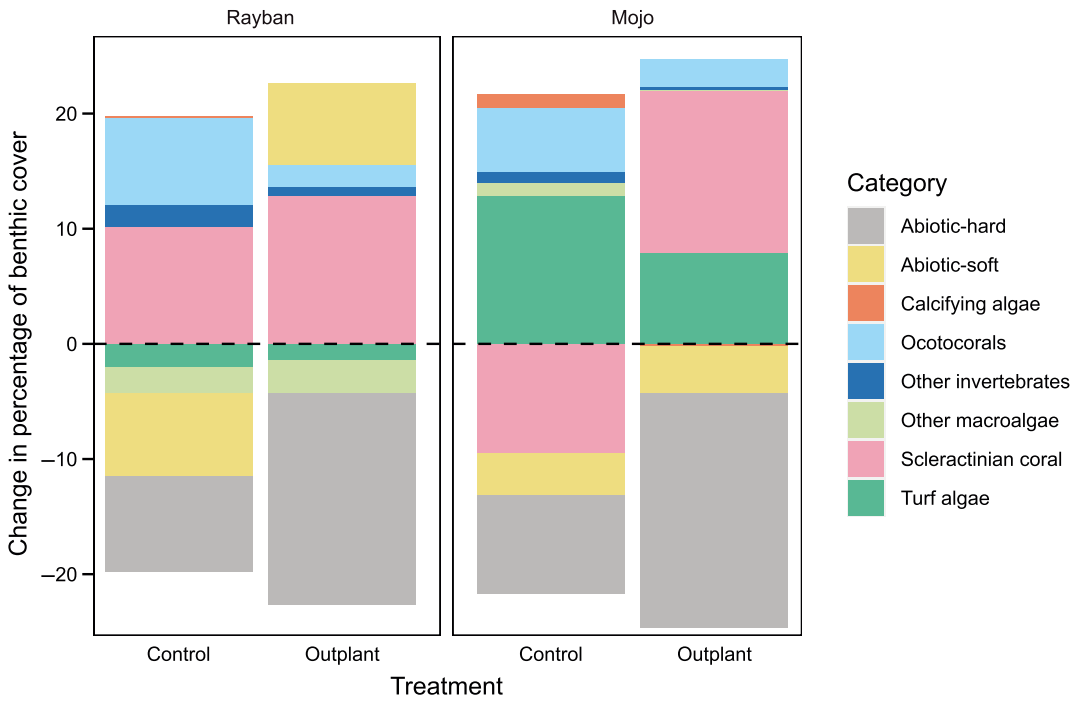

Fig. 5. Change in percentage of each benthic category in the control 2021 and outplant 2021 treatments compared to the 2018 baseline for Rayban and Mojo (n = 3 transects per treatment, 60 m^2 per transect). Benthic categories stacked above or below the dashed line indicate an increase or decrease from the baseline, respectively

Table 2. Summary of mean (±SE) hard coral cover, species richness and diversity (Shannon-Wiener index) by treatment (baseline 2018, control 2021 and outplant 2021) at Rayban and Mojo (n = 3 transects per treatment, 60 m^2 per transect). *Significant difference ($p < 0.05$) from baseline; ‡Significant difference ($p < 0.05$) between control and outplant (Table S2)

Site Treatment	Coral cover (%)	Species richness	Shannon-Wiener diversity index
Rayban			
Baseline	15.1 ± 2.9	11.33 ± 0.33	2.33 ± 0.07
Control	25.2 ± 2.1	18.67 ± 0.88	2.66 ± 0.08*
Outplant	27.8 ± 9.6	20.67 ± 2.96*	2.64 ± 0.06*
Mojo			
Baseline	38.2 ± 4.3	14.33 ± 1.67	2.31 ± 0.14
Control	28.7 ± 2.6	24.00 ± 2.65	2.94 ± 0.13*
Outplant	52.3 ± 5.2‡	25.00 ± 2.52*	2.86 ± 0.11

small to mid-sized colonies, while control areas had a higher number of mid-sized to large colonies (Fig. 8). At Rayban, *Acropora intermedia/muricata* colonies within the small to mid-sized range and *Pocillopora verrucosa* colonies within the smallest size classes were significantly more frequent compared to the distribution of their population in control areas ($p = 0.005$ and $p = 0.038$, respectively; Table S5). Comparatively, Mojo was dominated by a significantly higher frequency of small to mid-sized colonies of *A. intermedia/muricata* and *A. millepora/spathulata* in outplant areas compared to control areas ($p = 0.046$ and $p = 0.038$, respectively; Table S5, Fig. 8D,E). Overall, areas subject to intensive outplanting had a greater frequency of small size classes, resulting in a right-skewed distribution compared to control areas.

4. DISCUSSION

Natural regeneration and intervention-based coral restoration are 2 processes by which reef communities can recover following disturbance. Although changes to reef communities have been documented following these processes independently of one another (e.g. Doropoulos et al. 2015, Williams et al. 2019), the combined monitoring of natural recruitment and active rehabilitation for local site recovery on the GBR has not been examined. We aimed to systematically document the local recovery of 2 reef sites subject to 3 years (2018–2021) of intensive coral outplanting and natural recruitment since the last major disturbance. Despite differences in planting effort, coral cover in outplant communities was similar between sites. Coral species richness was greatest in outplant areas but not significantly different to control communities, while diversity remained relatively similar between treatment areas. Recruit set-

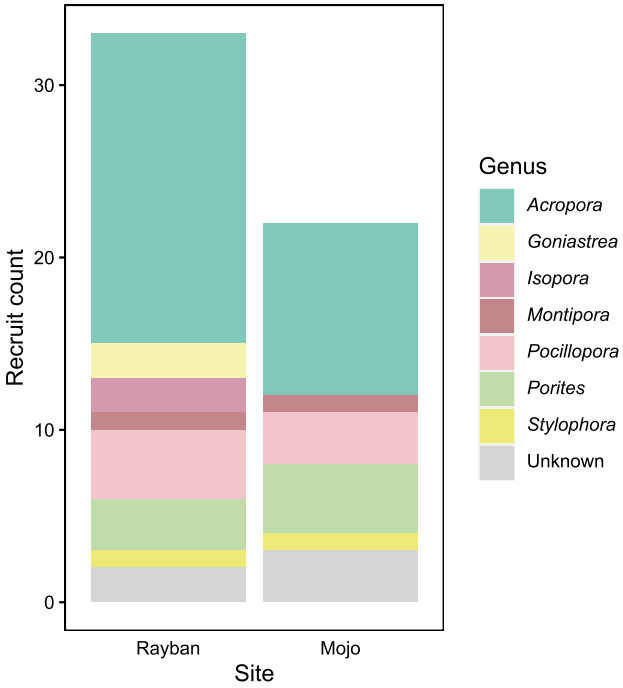

Fig. 6. Total count of coral recruits by genus settled on tiles (n = 6 per site) during the November 2020 spawning event at each site (Rayban and Mojo). Recruits that were unable to be identified were labelled unknown

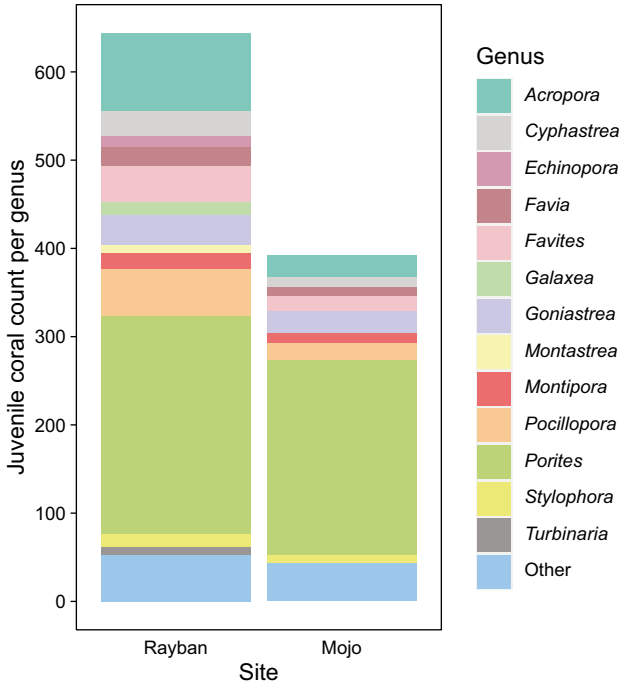

Fig. 7. Total number of juvenile corals per genera at Rayban and Mojo pooled across control 2021 and outplant 2021 treatments (n = 6 transects per site, 20 m^2 per transect)

Table 3. Summary of juvenile coral characteristics (mean ± SE) by site (Rayban and Mojo). *Significant difference ($p < 0.05$) between sites (Table S4)

Site	Abundance per 20 m^2	Genus richness	Shannon-Wiener diversity index
Rayban	107.3 ± 14.7*	17.83 ± 1.47	2.10 ± 0.07*
Mojo	65.3 ± 7.89*	13.17 ± 1.35	1.67 ± 0.09*

tlement rates were similar between sites, and juvenile coral characteristics (abundance, species richness and diversity) did not vary between control and outplant communities, suggesting that the higher frequency of small to mid-sized colonies of key coral taxa observed in outplant areas originated from active planting of small coral fragments rather than natural recruit-driven recovery.

4.1. Changes in reef benthic composition under natural and intervention-based recovery

Trajectories of reef recovery can be extremely variable, influenced by a range of factors and processes including the magnitude of the impact, site ecology, connectivity and management status (Graham et al. 2011). Moreover, reef recovery is often very slow, whereby the return of coral cover or assemblage to pre-disturbance levels frequently reaches or exceeds 10 yr (Gilmour et al. 2013, Graham et al. 2015, Guest et al. 2016, Gouezo et al. 2019). Recovery can be driven by a range of demographic processes, including the supply and survival of new recruits, as well as the survival and regrowth of any remnant adult colonies (Diaz-Pulido et al. 2009, Gilmour et al. 2013, Edmunds 2018). In circumstances where natural recruitment has been compromised, recovery dynamics of reef communities can be driven by the regeneration of small patch colonies which remain following the disturbance. For example, coral cover increased from 9 to 44% over a 12 yr period at an isolated reef in Western Australia following a bleaching event, whereby the influx of new recruits to the system was negligible for 6 yr post-disturbance; in this case, recovery was attributed to the regeneration of remnant colonies that were able to supply the population with pre-disturbance rates of recruitment once reaching maturity (Gilmour et al. 2013).

At Opal Reef, severe back-to-back bleaching in 2016 and 2017 resulted in the decline of mean hard coral cover from 20.9 to 11.3% from 2015 to 2021 (Australian Institute of Marine Science [AIMS] 2021). However, high spatial heterogeneity in coral abun-

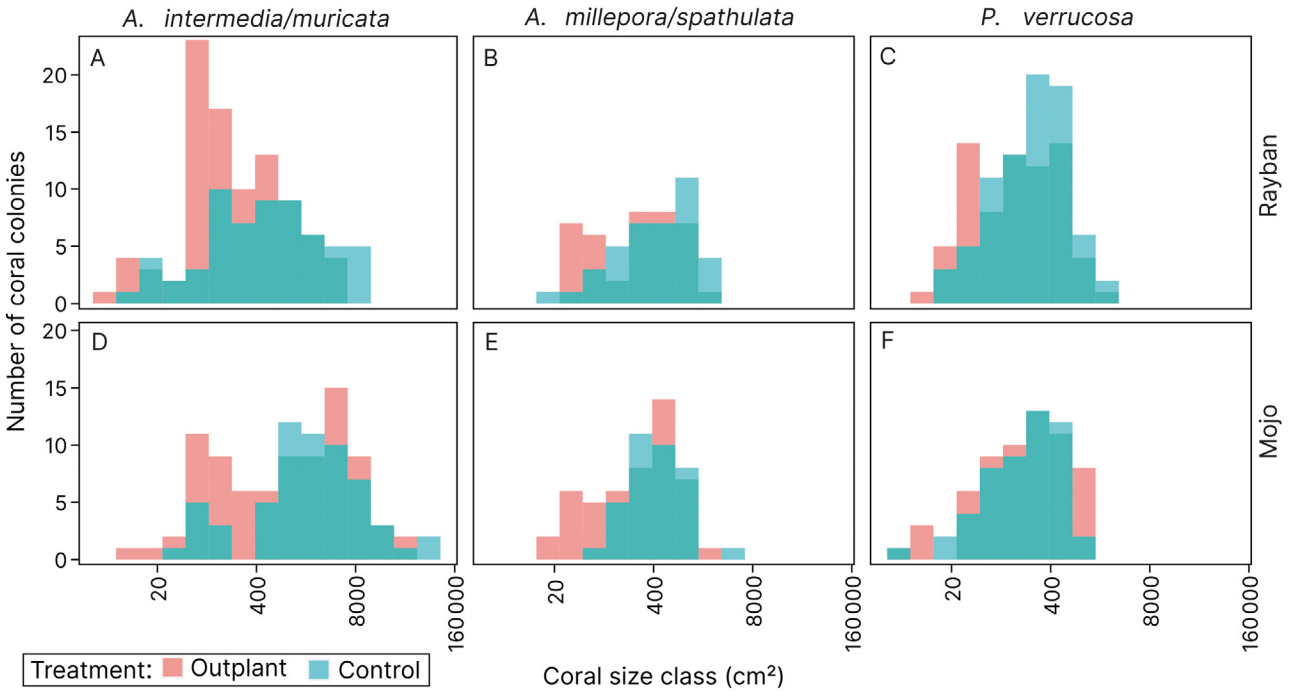

Fig. 8. Size–frequency distributions comparing coral colony sizes versus count (no. of coral colonies within each size class) at (A–C) Rayban and (D–F) Mojo between control and outplant areas for each species group. (A,D) *Acropora intermedia/muricata*; (B,E) *A. millepora/spathulata*; (C,F) *Pocillopora verrucosa*. Control and outplant histograms have been superimposed, with overlapping of the distributions depicted in a darker colour. Coral colonies were divided into bins according to the natural log of their area (length × width), and *x*-axis labels reflect true colony area (n = 5 control transects, n = 3 outplant transects, 60 m^2 per transect)

dance and assemblage is known to occur within the same reef (Brown et al. 2018, de Bakker et al. 2019), and as we observed for the 2 Opal Reef sites in our study, reef-scale averages are not expected at all sites. Despite a lower planting effort, Mojo exhibited a similar change in coral cover in outplant communities from 2018 to 2021 compared to Rayban, suggesting outplanting had a greater influence at Mojo. Conversely, these results indicate that outplanting had a minimal impact on benthic composition compared to natural recovery that yielded similar coral cover within control and outplant communities at Rayban. As rates of recruitment were relatively low at both sites (see Section 4.2 for further discussion), observed differences in coral cover may have been the result of the regrowth of remnant colonies. Indeed, as previous studies within the same sites have shown substantial growth of planted material over this time period (e.g. Howlett et al. 2022), presumably the same would be true for native colonies. Additionally, hard coral cover was significantly lower in control compared to outplant communities (but not the baseline) at Mojo, suggesting that fine-scale impacts to recovery may also be at play (e.g. potential differences in biological processes such as predation or competition, or small-scale differences in environmental conditions; Houk et al. 2014, Hernández-Fernández et al. 2019). Collectively, variations in the patterns of benthic composition between Opal reef sites suggest different processes may be guiding recovery, with Mojo more heavily influenced by outplanting with less impact from natural recruitment.

4.2. Contribution of settled recruits and juvenile corals to local population recovery

Settlement rates on tiles differed between Opal Reef sites but were also highly variable within sites (between individual tiles). Indeed, it is well documented that recruitment patterns can vary significantly in space and time as a result of various ecological and environmental factors (Connell et al. 1997, Bauman et al. 2015, Turner et al. 2018, Davidson et al. 2019), with variations of approximately 20 to 35% in settlement rates observed even on small spatial scales (i.e. 1–5 m; Hughes et al. 1999). Moreover, recruitment rates on the GBR have declined over a 20 yr period (Hughes et al. 2019). Specifically looking at sector 2 of the GBR (the sector which contains Opal Reef), a decline of 97% has occurred since 1996, with an average of 53.7 recruits $tile^{-1}$ pre-2016 versus 1.5

recruits tile^{-1} post-2016 (calculated from raw data in Hughes et al. 2019). These rates are comparable to densities observed at Rayban and Mojo (5.5 and 3.7 recruits tile^{-1}, respectively), suggesting recruit supply and survival over the past 2 to 3 yr has contributed little to local recovery. This is also supported by rates of population recovery documented in French Polynesia, whereby the density of settled recruits varied from 35 corals m^{-2} in highly recovered sites to <5 corals m^{-2} in sites with low levels of regeneration (Holbrook et al. 2018). Although a range of demographic processes may be necessary for the successful recovery of a population, sexual recruitment is crucial for providing genetic diversity and has been identified as critically important in the natural recovery and resilience of a population (McClanahan et al. 2012). For example, a recent study found a significant positive relationship between population recovery and cumulative recruitment over a 3 yr period, with recruitment rates accounting for 90% of the observed variation in site-level recovery rates (Holbrook et al. 2018). Given the limited recruitment rate observed at both sites, our observations suggest natural recruitment has not contributed substantially to the recovery of these Opal Reef populations, which could have consequences for the regeneration of this system through natural recruitment alone over the coming years.

Characteristics of juvenile corals (i.e. established colonies on the reef ≤5 cm diameter) did not vary between outplant or control communities at either site, suggesting recruitment contributed equally to natural recovery observed in both treatment areas. The abundance and assemblage of juvenile corals we observed are consistent with those reported previously at Opal Reef, whereby an average of 4.4 juveniles m^{-2} were recorded in 2021, a decline from 10.9 recruits m^{-2} in 2013 (AIMS 2021). In this AIMS survey, juvenile corals comprised primarily *Acropora*, *Pocillopora* and *Porites* species (accounting for 80 and 83% of juveniles observed in 2013 and 2021, respectively), indicating that recruit assemblage has likely remained stable over the past 9 yr (AIMS 2021). Given that 3 mass bleaching events occurred on the GBR between 2013 and 2021, the average of 5.4 and 3.3 juvenile corals m^{-2} found in our study at Rayban and Mojo, respectively, is not unexpected and likely an indication of impairment to stock–recruitment relationships following adult mortality during back-to-back bleaching events. Although coral settlement rates have been comprehensively examined over recent decades (Connell et al. 1997, Baird et al. 2012, Hughes et al. 2019), long-term studies investigating spatial patterns of juvenile corals (i.e. colonies ≤5 cm diameter) are much less common, despite the knowledge that spatial distributions of settled recruits are often not reflected by adult abundances (Hughes et al. 1999, but see Penin et al. 2010). Indeed, we observed that juvenile corals were more abundant and had greater species richness at Rayban, while the adult population at Mojo exhibited the highest coral cover, species richness and diversity of the 2 sites. As Rayban was characterised by benthic composition considered suitable for successful recruitment (i.e. high proportion of consolidated bare substrate, low proportion of turf algae), this disparity between adult and juvenile densities suggests post-recruitment mortality rates may be greater at Rayban or that recruit survival is higher at sites populated by fewer recruits. Density-dependent survival of corals has been documented as a consequence of greater competition for space, increased disease transmission or predation due to higher densities (Bruno et al. 2007, Chadwick & Morrow 2011, Ladd et al. 2016). In the Caribbean, adult coral density has also been found to positively influence settlement rates until coral cover reached approximately 10%, whereas the survival of young recruits (0 to 3 mo) decreased with increasing adult cover (Vermeij & Sandin 2008). Thus, the early life of scleractinian corals is highly dynamic, and patterns in abundance and assemblage may not be retained from one life stage to another. In the context of our study, while the observation of higher juvenile coral density and richness at Rayban could suggest a greater rate of recovery, the combined evaluation of settlement rates, juvenile corals and adult assemblages reveals that is not the case, with Mojo exhibiting population dynamics indicative of a more successful recovery trajectory.

4.3. Implications of natural recruitment and outplanting on community size structure

Juvenile coral densities were similar between outplant and control communities, indicating that natural regeneration was likely not responsible for the changes observed in community structure. Comparatively, the larger abundance of small to mid-sized colonies found only in outplant areas demonstrates that outplanting had a strong influence on population dynamics of key coral taxa. Knowledge of these population-level responses is valuable, particularly for impacted communities, as it can inform decision-making frameworks for more targeted recovery approaches. Recent studies have revealed a decrease

in the absolute abundance of small coral colonies on the GBR (Dietzel et al. 2020), as well as declining recruitment dynamics due to the acceleration of severe disturbance events (Hughes et al. 2019), causing major concerns for successful recruitment in future. As such, selective planting of small coral fragments in areas identified as being devoid of larval supply or experiencing low recruit survival could provide a cost-effective approach for population growth and local site rehabilitation, particularly where re-planted coral fragments exhibit high survivorship and growth (including Opal Reef, e.g. Howlett et al. 2022). As demographic rates of mortality tend to be extremely high for coral recruits (Wilson & Harrison 2005, Vermeij & Sandin 2008, Penin et al. 2010), bypassing the most sensitive and influential early life stages could increase the likelihood of survival in juvenile corals, thereby overcoming post-settlement bottlenecks to recovery. Furthermore, models have shown that 5 yr of outplanting not only has the ability to provide a boost in coral abundance of the dominant size class planted, but that community size class distributions can stabilise over time (in this case, 13 yr) despite the initial selection of size-specific fragments (Vardi et al. 2012). As a result, although coral propagation and planting practices are generally considered a short-term strategy, natural stochastic processes can eventually drive communities to a stable structure while also acquiring the ecological benefits provided by a range of size classes over time.

Knowledge on growth rates of the species groups examined allows us to consider the potential contribution of outplanting to community structure across the 3 yr (2018–2021). At Rayban, *Acropora intermedia* fragments (ca. 40 cm^2 in size) have been found to grow an average of 328 ± 124 cm^2 yr^{-1} (Howlett et al. 2022). When considered alongside the high count of small size classes observed (ca. 4–70 cm^2), peaks in the outplant size–frequency distribution at 332 to 398 cm^2 and 661 to 727 cm^2 would coincide with 1 to 2 yr of growth following planting (i.e. planting from 2019 to 2020 and 2020 to 2021; Fig. 9A). Similar trends are also observed for *A. millepora/spathulata* and *Pocillopora verrucosa* distributions, whereby increases in the frequency of colonies within mid-sized categories correspond to fragment growth rates following 1 to 2 yr of growth (Fig. 9B,C). As these peaks do not align with 3 yr of growth (planting from 2018 to 2019), our observations suggest one of 3 processes (or a combination) may be occurring: (1) the lower planting intensity that took place in the first year (2018–2019) has resulted in lower increases in the frequency of those size classes compared to more intensive planting in years 2 to 3 (2019–2021); (2) survivorship of outplants may decrease over time, resulting in size structures of mid-sized to larger colonies

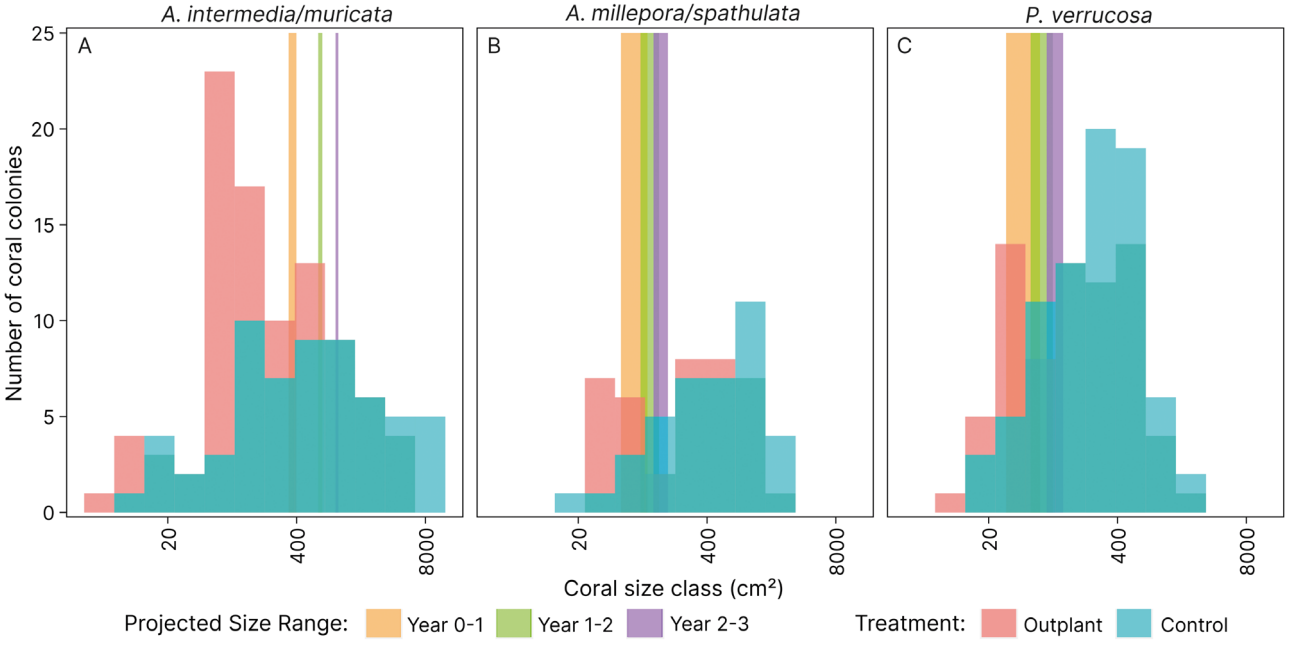

Fig. 9. Size–frequency distributions of control and outplant populations at Rayban superimposed with the projected colony size ranges of outplanted coral fragments following 0–1, 1–2 and 2–3 yr of growth. (A) *Acropora intermedia/muricata*; (B) *A. millepora/spathulata*; (C) *Pocillopora verrucosa*. Control and outplant histograms have been superimposed, with overlapping of the distributions depicted in a darker colour

that more closely resemble natural (control) community distributions; or (3) as growth rates decline with increasing colony size, this may result in a lower frequency of large size classes due to the majority of colonies not progressing beyond the mid-sized classes. As outplant numbers had a 3-fold increase from year 1 to year 3 (i.e. 2015 outplants from 2018 to 2019 versus 6928 outplants from 2020 to 2021), it is plausible the lower intensity in year 1 may not have contributed sufficiently to be captured by the size distribution. Furthermore, it is also likely that planting techniques have improved over time through optimised equipment and enhanced training of tourism operators, resulting in increased survivorship of outplants.

Finally, the disparities between findings from community cover and structure highlight differences in the sensitivity of monitoring methods used throughout this study. While small colonies would contribute insubstantially to the total proportion of hard coral cover, colony size–frequency distributions revealed a significantly higher frequency of small corals in outplant communities. Thus, demographic approaches including community structure are a more sensitive and valuable indicator of population change than coral cover alone and should therefore be considered for post-disturbance monitoring of reef recovery (Edmunds & Riegl 2020).

5. CONCLUSIONS

Understanding the concurrent effects of natural recruitment and intensive coral outplanting on population dynamics is critical for teasing apart the processes of reef recovery at sites subject to rehabilitation efforts (e.g. Hein et al. 2021). This is particularly important as coral restoration efforts continue to grow but where efficacy is rarely gauged against natural recovery rates. Our study at Opal Reef (northern GBR) revealed recruitment rates are sustained but relatively low and hence likely influence the speed of recovery of these sites. Conversely, observed differences in the size–frequency distributions of dominant coral taxa in outplant areas indicated that coral propagation and outplanting has the ability to shift population structure on impacted reefs to ultimately aid recovery. As declining recruitment dynamics are likely to continue with the persistence of severe disturbance events (Hughes et al. 2019), active approaches that can help augment the abundance of small community size classes could therefore provide some capacity to overcome recruitment limitations in future.

Examining changes in community demographics has provided a better understanding of the site-specific ecology unpinning the processes of recovery and thus how restoration activities can integrate with natural recovery at different sites. Our population-level perspective allows us to better tailor future restoration practices to compliment the local environment, thereby optimising our efforts and, in turn, the success of the restoration program. For example, monitoring of larval settlement and juvenile recruit abundance enables planting efforts to be focused on locations with low natural recruitment or as a means to increase the abundance of coral taxa that suffered a disproportionate decline post-disturbance (Gouezo et al. 2021). Moreover, broadening monitoring activities to include other site-specific factors that influence natural recovery (e.g. suitability of settlement substrate and cues, biological factors of mortality) would further compliment the integration of intervention-based approaches at sites with remnant coral populations or those which would benefit from accelerated recovery. As restoration initiatives continue on the GBR, future studies should therefore include a focus on understanding the differences in site ecologies and recovery processes among varying reef environments to optimise approaches through more informed practices. The benefits of understanding the concurrent contribution of natural and intervention-based processes to reef recovery should not be overlooked as reef restoration efforts continue to build worldwide.

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LITERATURE CITED

Álvarez-Noriega M, Baird AH, Dornelas M, Madin JS, Cumbo VR, Connolly SR (2016) Fecundity and the demographic strategies of coral morphologies. Ecology 97: 3485–3493

Australian Institute of Marine Science (AIMS) (2021) AIMS long-term monitoring program: crown-of-thorns starfish (*Acanthaster planci*) and benthos manta tow data (Great Barrier Reef). Australian Institute of Marine Science, Townsville. https://doi.org/10.25845/5c09b0abf315a

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool Stud 42:211–226

Babcock RC, Thomson DP, Haywood MDE, Vanderklift MA and others (2021) Recurrent coral bleaching in northwestern Australia and associated declines in coral cover. Mar Freshw Res 72:620–632

Baird AH, Hughes TP (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. J Exp Mar Biol Ecol 251:117–132

Baird AH, Emslie MJ, Lewis AR (2012) Extended periods of coral recruitment on the Great Barrier Reef. In: Yellowlees D, Hughes TP (eds) 12th International Coral Reef Symposium, Cairns, Australia, 9–13 July 2012. James Cook University, Cairns, p 5

Bak RPM, Meesters EH (1998) Coral population structure: the hidden information of colony size–frequency distributions. Mar Ecol Prog Ser 162:301–306

Bauman AG, Guest JR, Dunshea G, Low J, Todd PA, Steinberg PD (2015) Coral settlement on a highly disturbed equatorial reef system. PLOS ONE 10:e0127874

Bramanti L, Edmunds PJ (2016) Density-associated recruitment mediates coral population dynamics on a coral reef. Coral Reefs 35:543–553

Brown KT, Bender-Champ D, Kubicek A, van der Zande R, Achlatis M, Hoegh-Guldberg O, Dove SG (2018) The dynamics of coral-algal interactions in space and time on the southern Great Barrier Reef. Front Mar Sci 5:181

Bruno JF, Selig ER, Casey KS, Page CA and others (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. PLOS Biol 5:e124

Bruno JF, Côté IM, Toth LT (2019) Climate change, coral loss, and the curious case of the parrotfish paradigm: Why don't marine protected areas improve reef resilience? Annu Rev Mar Sci 11:307–334

Chadwick NE, Morrow KM (2011) Competition among sessile organisms on coral reefs. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition. Springer, Dordrecht, p 347–371

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461–488

Davidson J, Thompson A, Logan M, Schaffelke B (2019) High spatio-temporal variability in Acroporidae settlement to inshore reefs of the Great Barrier Reef. PLOS ONE 14:e0209771

de Bakker DM, van Duyl FC, Perry CT, Meesters EH (2019) Extreme spatial heterogeneity in carbonate accretion potential on a Caribbean fringing reef linked to local human disturbance gradients. Glob Change Biol 25: 4092–4104

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci USA 109:17995–17999

dela Cruz DW, Harrison PL (2017) Enhanced larval supply and recruitment can replenish reef corals on degraded reefs. Sci Rep 7:13985

Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R and others (2009) Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. PLOS ONE 4:e5239

Dietzel A, Bode M, Connolly SR, Hughes TP (2020) Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. Proc Biol Sci 287:20201432

Donner SD, Heron SF, Skirving WJ (2018) Future scenarios: a review of modelling efforts to predict the future of coral reefs in an era of climate change. In: van Oppen MJH, Lough JM (eds) Coral bleaching: patterns, processes, causes and consequences, 2nd edn. Springer, Cham, p 325–341

Donovan MK, Burkepile DE, Kratochwill C, Shlesinger T and others (2021) Local conditions magnify coral loss after marine heatwaves. Science 372:977–980

Doropoulos C, Ward S, Roff G, González-Rivero M, Mumby PJ (2015) Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. PLOS ONE 10:e0128535

Edmunds PJ (2018) Implications of high rates of sexual recruitment in driving rapid reef recovery in Mo'orea, French Polynesia. Sci Rep 8:16615

Edmunds PJ, Riegl B (2020) Urgent need for coral demography in a world where corals are disappearing. Mar Ecol Prog Ser 635:233–242

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Front Ecol Environ 1:488–494

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Gouezo M, Golbuu Y, Fabricius K, Olsudong D and others (2019) Drivers of recovery and reassembly of coral reef communities. Proc Biol Sci 286:20182908

Gouezo M, Fabricius K, Harrison P, Golbuu Y, Doropoulos C (2021) Optimizing coral reef recovery with context-specific management actions at prioritized reefs. J Environ Manage 295:113209

Graham NAJ, Nash KL, Kool JT (2011) Coral reef recovery dynamics in a changing world. Coral Reefs 30:283–294

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97

Guest JR, Tun K, Low J, Vergés A and others (2016) 27 years of benthic and coral community dynamics on turbid, highly urbanised reefs off Singapore. Sci Rep 6:36260

Hein MY, Vardi T, Shaver EC, Pioch S and others (2021) Perspectives on the use of coral reef restoration as a strategy to support and improve reef ecosystem services. Front Mar Sci 8:618303

Hernández-Fernández L, González de Zayas R, Weber L, Apprill A, Armenteros M (2019) Small-scale variability dominates benthic coverage and diversity across the Jardines de La Reina, Cuba coral reef system. Front Mar Sci 6:747

Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral reef ecosystems under climate change and ocean acidification. Front Mar Sci 4:158

Holbrook SJ, Adam TC, Edmunds PJ, Schmitt RJ and others (2018) Recruitment drives spatial variation in recovery rates of resilient coral reefs. Sci Rep 8:7338

Houk P, Benavente D, Iguel J, Johnson S, Okano R (2014) Coral reef disturbance and recovery dynamics differ across gradients of localized stressors in the Mariana Islands. PLOS ONE 9:e105731

Howlett L, Camp EF, Edmondson J, Henderson N, Suggett

DJ (2021) Coral growth, survivorship and return-on-effort within nurseries at high-value sites on the Great Barrier Reef. PLOS ONE 16:e0244961

Howlett L, Camp EF, Edmondson J, Edmondson J and others (2022) Adoption of coral propagation and outplanting via the tourism industry to advance site stewardship on the northern Great Barrier Reef. Ocean Coast Manage 225:106199

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:59–63

Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2018) Global warming transforms coral reef assemblages. Nature 556:492–496

Hughes TP, Kerry JT, Baird AH, Connolly SR and others (2019) Global warming impairs stock–recruitment dynamics of corals. Nature 568:387–390

IPCC (2022) Climate change (2022) Impacts, adaptation, and vulnerability. In: Pörtner HO, Roberts DC, Tignor M, Poloczanska ES and others (eds) Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge (in press)

Jackson JBC, Donovan MK, Cramer KL, Lam VV (eds) (2014) Status and trends of Caribbean coral reefs: 1970–2012. Global Coral Reef Monitoring Network, IUCN, Gland

Jonker MJ, Thompson AA, Menéndez P, Osborne K (2019) Cross-shelf variation among juvenile and adult coral assemblages on Australia's Great Barrier Reef. Diversity (Basel) 11:85

Kerry JT, Bellwood DR (2015) Do tabular corals constitute keystone structures for fishes on coral reefs? Coral Reefs 34:41–50

Ladd MC, Shantz AA, Nedimyer K, Burkepile DE (2016) Density dependence drives habitat production and survivorship of *Acropora cervicornis* used for restoration on a Caribbean coral reef. Front Mar Sci 3:261

Ladd MC, Burkepile DE, Shantz AA (2019) Near–term impacts of coral restoration on target species, coral reef community structure, and ecological processes. Restor Ecol 27(5):1166–1176

Lough JM, van Oppen MJH (2018) Synthesis: coral bleaching — patterns, processes, causes and consequences. In: van Oppen MJH, Lough JM (eds) Coral bleaching: patterns, processes, causes and consequences, 2nd edn. Springer, Cham, p 343–348

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

McClanahan TR, Donner SD, Maynard JA, MacNeil MA and others (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLOS ONE 7:e42884

Mcleod E, Anthony KRN, Mumby PJ, Maynard J and others (2019) The future of resilience-based management in coral reef ecosystems. J Environ Manage 233: 291–301

McWilliam M, Hoogenboom MO, Baird AH, Kuo CY, Madin JS, Hughes TP (2018) Biogeographical disparity in the functional diversity and redundancy of corals. Proc Natl Acad Sci USA 115:3084–3089

Meesters EH, Hilterman M, Kardinaal E, Keetman M, deVries M, Bak RPM (2001) Colony size–frequency distributions of scleractinian coral populations: spatial and interspecific variation. Mar Ecol Prog Ser 209:43–54

Nyström M (2006) Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. Ambio 35:30–35

Ortiz JC, Pears RJ, Beeden R, Dryden J, Wolff NH, Gomez Cabrera MDC, Mumby PJ (2021) Important ecosystem function, low redundancy and high vulnerability: the trifecta argument for protecting the Great Barrier Reef's tabular *Acropora.* Conserv Lett 14:e12817

Penin L, Michonneau F, Baird AH, Connolly SR, Pratchett MS, Kayal M, Adjeroud M (2010) Early post-settlement mortality and the structure of coral assemblages. Mar Ecol Prog Ser 408:55–64

Pisapia C, Burn D, Pratchett MS (2019) Changes in the population and community structure of corals during recent disturbances (February 2016–October 2017) on Maldivian coral reefs. Sci Rep 9:8402

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/

Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermeij MJA, Paul VJ (2009) New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithson Contrib Mar Sci 38:437

Roff G, Doropoulos C, Zupan M, Rogers A, Steneck RS, Golbuu Y, Mumby PJ (2015) Phase shift facilitation following cyclone disturbance on coral reefs. Oecologia 178: 1193–1203

Shaish L, Levy G, Katzir G, Rinkevich B (2010) Employing a highly fragmented, weedy coral species in reef restoration. Ecol Eng 36:1424–1432

Shlesinger T, van Woesik R (2021) Different population trajectories of 2 reef-building corals with similar life-history traits. J Anim Ecol 90:1379–1389

Suggett DJ, Smith DJ (2020) Coral bleaching patterns are the outcome of complex biological and environmental networking. Glob Change Biol 26:68–79

Suggett DJ, Edmondson J, Howlett L, Camp EF (2020) Coralclip®: a low-cost solution for rapid and targeted out-planting of coral at scale. Restor Ecol 28:289–296

Turner JA, Thomson DP, Cresswell AK, Trapon M, Babcock RC (2018) Depth-related patterns in coral recruitment across a shallow to mesophotic gradient. Coral Reefs 37: 711–722

van Hooidonk R, Maynard J, Tamelander J, Gove J and others (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. Sci Rep 6:39666

van Woesik R, Köksal S, Ünal A, Cacciapaglia CW, Randall CJ (2018) Predicting coral dynamics through climate change. Sci Rep 8:17997

Vardi T, Williams DE, Sandin SA (2012) Population dynamics of threatened elkhorn coral in the northern Florida Keys, USA. Endang Species Res 19:157–169

Vermeij MJA, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population. Ecology 89:1994–2004

Williams SL, Sur C, Janetski N, Hollarsmith JA and others (2019) Large-scale coral reef rehabilitation after blast fishing in Indonesia. Restor Ecol 27:447–456

Wilson J, Harrison P (2005) Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. Coral Reefs 24:418–421

Zawada KJA, Madin JS, Baird AH, Bridge TCL, Dornelas M (2019) Morphological traits can track coral reef responses to the Anthropocene. Funct Ecol 33:962–975

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