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ARTICLE

Limitations to coral recovery along an environmental stress gradient

Christopher Doropoulos¹  | Luis A. Gómez-Lemos² | Kinam Salee¹ |
M. James McLaughlin¹ | Jan Tebben³ | Mark Van Koningsveld^{4,5} |
Ming Feng¹ | Russell C. Babcock¹

¹CSIRO Oceans and Atmosphere,
St Lucia, Queensland, Australia

²Universidad Nacional de Colombia -
Sede de La Paz - Escuela de Pregrados,
La Paz, Colombia

³Alfred Wegener Institute Helmholtz
Centre for Polar and Marine Research,
Bremerhaven, Germany

⁴Van Oord Dredging and Marine
Contractors B.V., Rotterdam,
The Netherlands

⁵Ports and Waterways, Delft University of
Technology, Delft, The Netherlands

Correspondence

Christopher Doropoulos

Email: christopher.doropoulos@csiro.au

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Abstract

Positive feedbacks driving habitat-forming species recovery and population growth are often lost as ecosystems degrade. For such systems, identifying mechanisms that limit the re-establishment of critical positive feedbacks is key to facilitating recovery. Theory predicts the primary drivers limiting system recovery shift from biological to physical as abiotic stress increases, but recent work has demonstrated that this seldom happens. We combined field and laboratory experiments to identify variation in limitations to coral recovery along an environmental stress gradient at Ningaloo Reef and Exmouth Gulf in north-west Australia. Many reefs in the region are coral depauperate due to recent cyclones and thermal stress. In general, recovery trajectories are prolonged due to limited coral recruitment. Consistent with theory, clearer water reefs under low thermal stress appear limited by biological interactions: competition with turf algae caused high mortality of newly settled corals and upright macroalgal stands drove mortality in transplanted juvenile corals. Laboratory experiments showed a positive relationship between crustose coralline algae cover and coral settlement, but only in the absence of sedimentation. Contrary to expectation, coral recovery does not appear limited by the survival or growth of recruits on turbid reefs under higher thermal stress, but to exceptionally low larval supply. Laboratory experiments showed that larval survival and settlement are unaffected by seawater quality across the study region. Rather, connectivity models predicted that many of the more turbid reefs in the Gulf are predominantly self seeded, receiving limited supply under degraded reef states. Overall, we find that the influence of oceanography can overwhelm the influences of physical and biological interactions on recovery potential at locations where environmental stressors are high, whereas populations in relatively benign physical conditions are predominantly structured by local ecological drivers. Such context-dependent information can help guide expectations and assist managers in optimizing strategies for spatial conservation planning for system recovery.

KEYWORDS

climate change, coral recruitment, disturbance, population recovery

INTRODUCTION

Habitat loss of marine ecosystems and stabilization into degraded states is becoming commonplace in coastal environments (Nyström et al., 2012). Acute disturbances such as marine heatwaves have deleterious impacts on habitat forming organisms through widespread mortality (Smale et al., 2019). Coupled with chronic stressors such as elevated sedimentation, the positive feedbacks required for population growth and recovery are often lost (Jones et al., 1997). For example, increased sedimentation can reduce the recruitment of coral larvae by deterring grazers from sediment-laden turf algae, which increases the cover and length of the turf algae and decreases the availability of colonizable space for the corals (Goatley et al., 2016; Wakwella et al., 2020). Once degraded, identifying and managing for the mechanisms that reverse unwanted feedbacks is therefore key to facilitating ecosystem recovery (Graham et al., 2014; Nyström et al., 2012).

Theory predicts that as environmental stressors transition from low to high, the main drivers of community structure shift from predation to competition to abiotic stress (Menge & Sutherland, 1987). In coral reefs, for example, competitive coral-algal interactions are often mediated by herbivore control in environments of low physical stress (Doropoulos, Roff, et al., 2017; Graham et al., 2015; Mumby et al., 2007), whereas light and temperature interact to limit coral abundances in marginal reefs (Howells et al., 2016; Sommer et al., 2018). Yet the set of factors that limit population growth is neither universal across study systems nor sites (Shears et al., 2008), and a recent meta-analysis has shown that predictability in how physical stress drives community structure remains largely unknown (Silliman & He, 2018). As the severity of environmental stressors under cumulative human impacts increases (Crain et al., 2008), identifying how environmental gradients influence the recovery of habitat forming species is central to conservation planning.

Population growth and recovery in disturbed environments are often driven by the recruitment of new propagules (Caley et al., 1996). Coral recruitment has three major phases that include propagule release and dispersal; substrate selection, attachment and metamorphosis (i.e., settlement); and early post-settlement survival and growth until establishment into the local population (Ritson-Williams et al., 2009). Each phase has unique attributes that can act independently as demographic bottlenecks during recruitment. These include broad-scale hydrodynamic drivers that affect larval dispersal (Boschetti et al., 2020; Feng et al., 2016; Hock et al., 2019), physical stress drivers such as temperature and sedimentation

(Humanes et al., 2017; Ricardo et al., 2017), and a range of ecological mechanisms such as competition, predation, and facilitation (e.g., Doropoulos et al., 2016).

Quantifying demographic bottlenecks at multiple scales along environmental gradients is a key challenge for predicting system recovery in degraded ecosystems. Recovery of habitat forming corals can be as rapid as 10–12 years (Edmunds, 2018b; Gouezo et al., 2019) and is related to abundant larval supply, high juvenile coral densities, and high structural complexity (Doropoulos et al., 2015; Graham et al., 2015; Mumby et al., 2007). For some degraded reefs, however, recovery to coral-dominated states may never occur and they can persist in low coral states with consequent reductions in ecological functions and services (Edmunds, 2018a; Graham et al., 2014; Williams & Graham, 2019).

Despite coral reef degradation under severe global change (e.g., Hughes et al., 2018; Knowlton, 2001), knowledge of recovery processes in degraded systems is relatively deficient (but see for example Edmunds, 2018a, Evans et al., 2020). To help fill this gap and provide strategies for conservation planning, we used disturbed reefs in northwestern Australia to identify whether recruitment bottlenecks and system recovery change along environmental gradients. The region is characterized by frequent cyclones and, in 1999, category-5 cyclone Vance passed from the north to south of Exmouth Gulf (Appendix S1: Figure S1), creating a 3.5-m storm surge that caused widespread mortality to corals across the region (Twigg & Collins, 2010). Coral bleaching events have also occurred on the reefs towards the northern end of the gulf, reducing live coral cover in 2011 from 79%–92% to 1%–6% (Depczynski et al., 2013). These stressors impacted major reef-building corals in the region, especially *Acropora* (Evans et al., 2020; Speed et al., 2013), that typically drive rapid recovery on reefs (e.g., Doropoulos et al., 2015; Gouezo et al., 2019). In relation to this recent disturbance, we specifically asked (1) Do environmental gradients alter the demographic rates and ecological interactions that drive coral recruitment? (2) How do the key limitations to system recovery change along environmental gradients?

METHODS**Study location**

Field work for this study took place from February 2016 to November 2017 at reefs in the UNESCO Ningaloo Marine Park and adjacent Exmouth Gulf, northwestern

Australia (Figure 1a). Field locations were stratified along the west coast of the Exmouth Gulf and on the west coast of the mainland at Coral Bay (Figure 1a) to incorporate a gradient of environmental (temperature, turbidity, sedimentation) and ecological (larval supply, settlement interactions, post-settlement competition, growth, and survival) drivers. There were two or more sites nested within each location, with each site measuring 400–625 m² and separated by 1 km or more. Coral Bay, NW Cape, and Bundegi each had two sites, and Exmouth had four sites, and Learmonth had three sites (Figure 1a). Coral Bay sites constitute clear water reefs under lower environmental stress compared to reefs within the Exmouth Gulf. Tidal ranges vary among the different locations: 1.62 m at Coral Bay, 2.29 m at North-West Cape and Bundegi, 2.66 m at Exmouth, and 2.84 m at Learmonth. All in situ observations and experiments were conducted on back-reefs at a range of 3–5 m depth at mid-tide.

Characterizing patterns of water quality and benthic community

Measurements of seawater temperature, water turbidity, sediment deposition rates, and sediment properties, as well as benthic, fish, and juvenile coral community structure were conducted to assess how physical and biological drivers may relate to recovery.

At each site, two HOBO temperature loggers (Onset HOBO Pendant[®] Temperature logger, USA) were attached to star pickets 30 cm above the benthos on February 2016 and recorded seawater temperature (°C) at hourly intervals until October 2017. The error margin of these loggers is 0.53°C. Daily averages were calculated, averaged for each location, and trends fit for each location using the generalized additive model (GAM) function within *stat_smooth* in *ggplot2* (Wickham, 2009) in R (R Development Core Team, 2018). Water turbidity was quantified using daily images from the MODIS-aqua product diffuse attenuation coefficient (K_d 490 m⁻¹) for the same period. Following processing (Appendix S1: Section S1), data were averaged for each location and trends fitted using the same approach as for seawater temperature.

Sediment deposition was measured with two replicate sediment traps at each site in February 2016, and periodically collecting and installing new traps until October 2017 (see Figure 1d for exact sampling times). Ventilation caps on the traps had mesh openings ~10 × 30 mm. Following processing (Appendix S1: Section S1), data were converted to g deposited cm⁻² day⁻¹. A linear mixed effects model (LMER) was used to compare sediment deposition among time periods × locations, with sites random and nested within locations, using the *lme4* package (Bates et al., 2015) in R. Data were fourth root

transformed to conform to model assumptions. Multiple comparisons were investigated on significant effects using Tukey contrasts with adjusted *P* values using *emmeans* (Lenth & Lenth, 2018) in R. Additionally, sediment particle size distributions from May and August 2016 were visualized with the skew and kurtosis quantified for comparison among locations.

Benthic surveys were conducted in May and August 2016 and May and October 2017. Only one of the sites nested within each location was used. At each fixed site, 17–31 (mean = 24) replicate 0.5 × 0.5 m quadrats were haphazardly placed on hard substrate at every time point and photographed. Images were analyzed by identifying the substrate under 20 random points in Coral Net (Beijbom et al., 2012), classifying coral and algae to genus where possible. Benthic community cover was visualized using principal coordinate analysis (PCO) based on a Bray-Curtis similarity matrix. Statistical analysis compared locations, years, and seasons, using a fixed effects PERMANOVA and a Bray-Curtis similarity matrix with 999 permutations to generate *p* values in Primer-E v6 (Clarke & Gorley, 2006) with the PERMANOVA add-on (Anderson et al., 2008).

Juvenile corals <40 mm maximum diameter are an indicator of recovery potential and were surveyed at all sites in August 2016 by a single observer (C. Doropoulos). Fifteen replicate 0.25 × 0.25 m quadrats were haphazardly placed on hard substrate and the number, size using maximum diameter, and taxonomic identity of all juvenile corals recorded. A generalized linear mixed effect model (GLMM) was used to compare total juvenile coral abundance among locations, with sites random and nested within locations, using the *lme4* package in R. Poisson variance structure was used to account for overdispersion of the count data. Multiple comparisons were investigated on significant effects using Tukey contrasts with adjusted *p* values using *emmeans*.

Fish community structure was assessed in October 2016 by a single observer (RCB). Two sites were surveyed at both Coral Bay and Learmonth, whereas only one site was surveyed within NW Cape, Bundegi, and Exmouth (Appendix S1: Figure S2). Surveys were conducted using three randomly placed 25 × 5 m belt transects. All fish were identified to species and their sizes recorded in 5-cm bins. Biomass was estimated using standard allometric length-weight conversions with constants obtained from FishBase (Froese & Pauly, 2015) and visualized using PCO.

Spatial-temporal and environmental drivers to coral larvae supply and settlement

To quantify the natural supply of coral larvae, 15 replicate tiles (flat terracotta tiles measuring 11.4 × 11.4 × 1.2 cm)

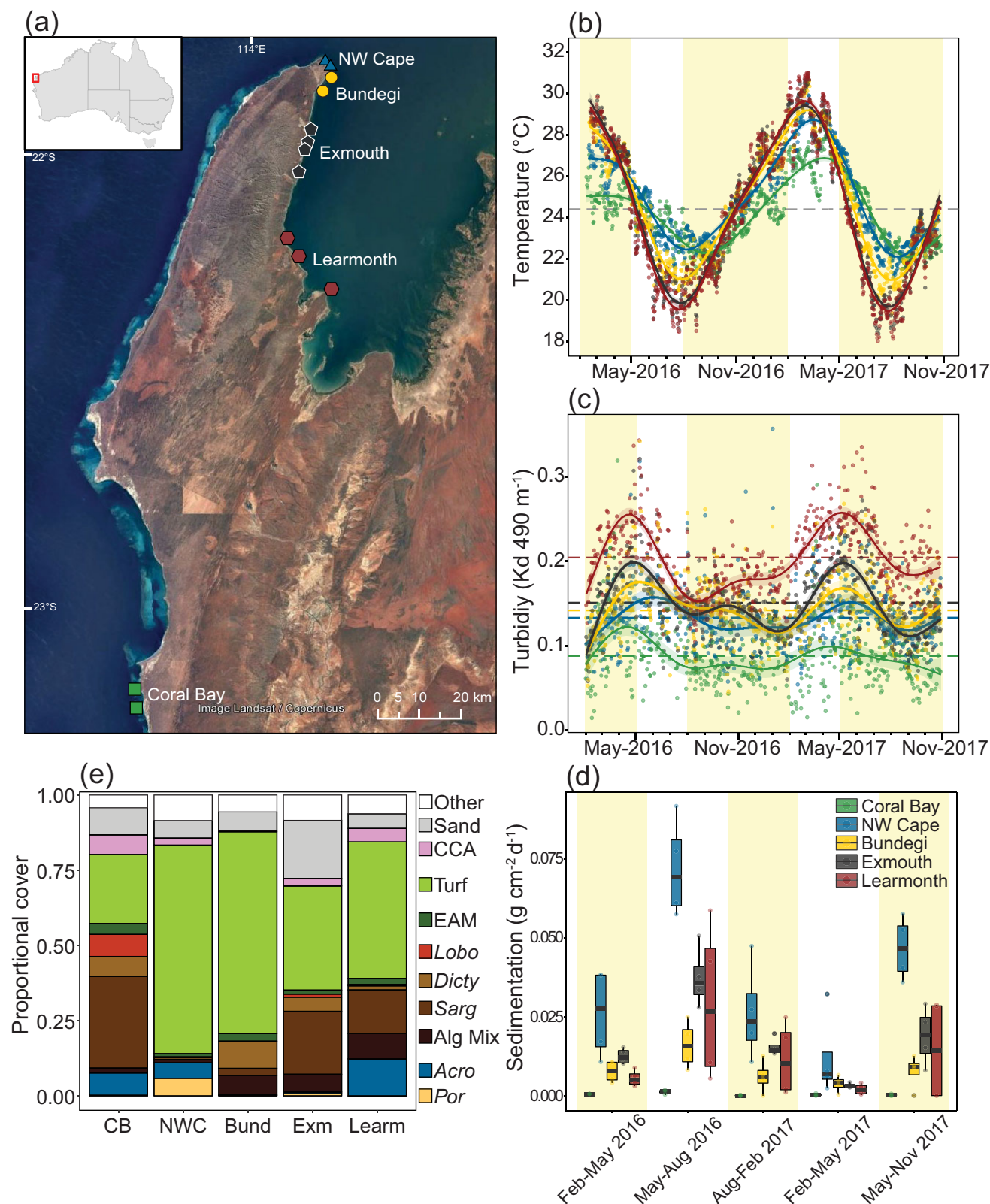


FIGURE 1 (a) Satellite map of the reef sites along the west coast of the Exmouth Gulf and on the west coast of the Ningaloo Marine Park, Australia. (b) Seawater temperature, (c) turbidity, (d) sediment deposition, and (e) proportional benthic cover are shown from throughout the study region. Individual data points are shown in panels (b–d), with smoothed trends ($\pm$ SE) for each location in panels (b) and (c). Yellow shaded areas in panels (b–d) represent monitoring sampling points. For panel (d) the middle line of each boxplot indicates the median value, upper and lower hinges indicate the 75 and 25% quantiles, upper and lower whiskers represent the maximum and minimum observations $+1.5 \times$ the inter-quartile range, and individual dots represent outliers. For panel (e) CB, Coral Bay; NWC, NW Cape; Bund, Bundegi; Exm, Exmouth; Learn, Learmonth; CCA, crustose coralline algae; EAM, epilithic algal matrix; Lobo, Lobophora; Dicty, Dictyota; Sarg, Sargassum; Alg Mix, algal assemblage; Acro, Acropora; Por, Porites

were deployed at each site 6 weeks prior to spawning and retrieved 6 and 8 weeks following spawning in 2016 and 2017, respectively. Coral spawning occurred on 2–3 April in 2016 and 20–22 March in 2017 (C. Doropoulos, L. A. Gómez-Lemos, R. C. Babcock, personal observations). Total replication per location within each year was therefore 30 tiles each for Coral Bay, NW Cape, and Bundegi, and 45 tiles each for Exmouth and Learmonth. Tiles were scored for coral settler location, abundance, and taxonomy by a single observer (C. Doropoulos; Appendix S1: Section S1). Total settlement was analyzed using an additive GLMM among years (two levels), locations (five levels), and orientation (three levels), with sites random and nested within locations, using *lme4* in R. Poisson variance structure was used to account for overdispersion of the count data. Interactions could not be included due to a lack of variance at multiplicative levels. Multiple comparisons were investigated on significant effects using Tukey contrasts with adjusted *p* values using *emmeans*.

Multiple regression analyses were then used to investigate biophysical effects on the settlement rates of *Acropora* spp. Physical predictors included seawater temperature ($^{\circ}\text{C}$), turbidity ($\text{Kd } 490 \text{ m}^{-1}$), sediment deposition ($\text{g day}^{-1} \text{ cm}^{-2}$), and self-recruitment potential. Water quality parameters were restricted to the 6 weeks following spawning. The connectivity model from Feng et al. (2016) was used to quantify a self-recruitment potential index for each site (Appendix S1: Section S1). Biological predictors incorporated the percent cover from the undersides and vertical edges of settlement tiles of the three facilitators (bare tile, crustose coralline algae [CCA], spiral worms) and four inhibitors (turf algae, encrusting fleshy algae, colonial invertebrates, macroalgae) of coral settlement (Appendix S1: Figure S3). Topsides were excluded because there was almost no settlement on that orientation. All predictors were scaled and centered by their mean. Model construction occurred using forward selection to compare a single added predictor to the null model using likelihood-ratio tests (LRT; Appendix S1: Table S4b). The final model for total coral settlement abundance used a GLMM with negative binomial variance structure and zero inflation, testing the combined effects of crustose coralline algae, self-recruitment potential, turbidity, and sedimentation with year, settlement orientation, and site nested in location incorporated as random effects. The analysis was conducted using the *glmmADMB* library (Bolker et al., 2012) in R.

Effects of water quality, sedimentation and biological interactions on coral larvae

Two laboratory experiments tested whether patterns of coral settlement observed throughout the study region were related to differences in water quality or differences

in benthic community interactions. Both experiments used competent larvae cultured from nine colonies of *Acropora millepora*. Colonies were collected from shallow reef flats in Coral Bay at a depth of 2–3 m, isolated in 60-L tubs each sunset, and spawned at 21:20–23:30 on 21 March 2017. Larval culturing and experiments took place at the Coral Bay Research Station.

The first experiment aimed to isolate any effects of seawater origin on larval survival and settlement (i.e., attachment and metamorphosis). Seawater was collected from Coral Bay, Bundegi, and Learmonth to capture the greatest range of environmental conditions. Immediately prior to the larval settlement assays, three replicate water samples were collected from the benthos within each location, stored on ice until return to the laboratory, and replicates within a location were homogenized prior to experiments. Unfiltered seawater was placed into 12 replicate 20-ml cell culture wells per location, half of which contained a settlement inducer (*Porolithon onkodes*) and every well contained 20 competent *A. millepora* larvae. After 48 h, the number of larvae swimming, dead, and settled were scored. The proportion of each response variable (larvae swimming, mortality, settled) was assessed among water location origin $\times$ inducer presence using separate GLMs. Binomial variance structure was used for larval mortality, whereas quasi-binomial variance structure was used for analysis of swimming and settled due to residual overdispersion (Zuur et al., 2009).

The second experiment aimed to isolate any effects of location specific early successional communities and sedimentation on coral settlement by preconditioning settlement tiles at Coral Bay, Bundegi, and Learmonth for 11 weeks. “Crevice tiles” made from a mix of calcium carbonate sand and cement at a ratio of 4:1 were used, and measured $10 \times 10 \text{ cm}$ and had 24 equally spaced crowns and crevices, where each crown measured $1.2 \text{ cm length} \times 1.2 \text{ cm width} \times 1.2 \text{ cm depth}$ (Doropoulos et al., 2016; Doropoulos, Evensen, et al., 2017; Doropoulos, Roff, et al., 2017). Tile preconditioning location was crossed with three levels of sedimentation, with sediment sources covarying with preconditioned locations. After the tiles were placed into the individual tanks, sediment was poured over the tile for an approximately evenly distributed deposition. Three levels of sediment were added to fall within the range measured during the study (see Figure 1d): 0.0 g cm^{-2} (control), 0.11 ± 0.04 (mean $\pm$ standard error) g cm^{-2} , and $0.4 (\pm 0.11) \text{ g cm}^{-2}$; covering approximately 0%, 10%–20%, and 80%–90% of the settlement surfaces, respectively (Appendix S1: Figure S4). There were seven tile replicates for every preconditioning location $\times$ sedimentation cross, and 100 competent *A. millepora* larvae were added to each 1.2-L tank 1 h after sediment addition. Seawater for this experiment was collected from Coral Bay and filtered through a sponge canister stack with UV sterilization (Odyssea CFS-1000 Canister Filter 2650lph + 9W UV Sterelizer, USA).

Larval settlement onto the tiles was quantified after 48 h, with a half water change at 24 h that incurred minimal resuspension. Following the settlement assays, proportional cover of the early successional communities was quantified (Appendix S1: Section S1).

Statistical analysis firstly analyzed the early successional community found on the settlement tiles comparing locations $\times$ sediment deposition using PERMANOVA (Anderson et al., 2008) based on a Bray-Curtis similarity matrix and 9999 permutations to generate p values. Data were $\log(x + 1)$ -transformed to meet assumptions of multivariate homogeneity, tested using PERMDISP. SIMPER analysis was used to characterize the contributions of the early successional groups to differences in community structure among locations.

Second, coral settlement was compared among tile preconditioning location $\times$ sediment deposition using a GLM with a negative binomial variance structure to account for overdispersion of count data using the MASS package (Venables & Ripley, 2002) in R. Pairwise analysis for significant effects were investigated using the Tukey contrasts with adjusted p values using *emmeans*.

Multiple regression analysis was then used to investigate the effects of the interactions between sediment deposition with the early successional groups on coral settlement. Correlations among early successional groups were initially tested using the *corrplot* package (Wei et al., 2017) and correlated variables removed. The full multiple regression model then included the cover of CCA, turf algae, macroalgae, and bryozoans, each crossed with sediment deposition and fit using backward selection, comparing full versus reduced models using LRT. The final model used a GLMM with tile preconditioning location treated as a random variable and a negative binomial variance structure to account for overdispersion of count data using the *glmmADMB* package (Bolker et al., 2012).

Spatial-temporal and environmental drivers to post-settlement coral growth and survival

Field experiments tested whether biophysical drivers throughout the study region influenced post-settlement coral growth and survival using three cohorts of *Acropora* recruits: newly settled *A. millepora*, 18-month old *A. digitifera*, and juvenile *Acropora* spp. tagged on the reef benthos. Larval culturing, settling, and deployment approaches are fully detailed in Appendix S1: Section S1, and follow those of Doropoulos, Evensen, et al. (2017). *Acropora millepora* were settled and mapped onto preconditioned tiles in April 2016. Five replicate tiles were deployed per site within each location and had 28–

154 newly settled colonies per tile, with initial size ranging from 1.0–7.2 mm (mean = 2.4 mm) maximum diameter. Eighteen-month old *A. digitifera* were initially settled onto aragonite plugs in April 2015 and developed in racks in a vertical orientation in the shallow lagoons of Coral Bay and Tantabiddi (ca. 140 km north of Coral Bay), with survival monitored for 15 months (van Koningsveld et al., 2017). Following the final monitoring period, they were left in situ in Coral Bay until retrieval and use in this study in October 2016. Upon retrieval, colonies were measured and randomly assigned and out planted to the same sites as the newly settled *A. millepora* recruits. The initial number of juvenile 18-month-old *A. digitifera* colonies ranged from 24–31 colonies per site, with initial sizes ranging from 6–40 mm (mean = 21.1 mm) maximum diameter. The third cohort of *Acropora* were juveniles tagged on the benthos located at the study sites in February 2016 and are independent to those surveyed in August 2016. There were 4–17 colonies tagged per site, with initial sizes ranging from 5–38 mm (mean = 19.8 mm) maximum diameter. Juvenile *Acropora* spp. colonies were only tagged at Coral Bay ($n = 17$), NW Cape ($n = 4$), and Bundegi ($n = 4$), with no juvenile colonies found at Exmouth or Learmonth. Periodic monitoring for growth and survival occurred every 1–5 months for 20 months.

Kaplan-Meier analysis was used to compare differences in the rates of coral recruit survival among locations $\times$ cohorts using the *survival* package (Therneau, 2014) in R. Exponential and Weibull variance structures were initially compared, with exponential providing a better fit. Differences in the size (maximum diameter) of the coral recruits was compared within each of the three cohorts due to differences in original starting sizes. For each cohort, a linear mixed effects model compared the maximum diameter of surviving colonies among location $\times$ time, incorporating colony ID as a random effect to account for the repeated sampling, using the *lme4* package in R. For both survival and size analyses, pairwise analyses for significant effects were investigated using the Tukey contrasts with adjusted p values using *emmeans*.

Multiple regression analyses then investigated biophysical effects on colony survival and growth. Colony size was converted into linear growth rates (mm d^{-1}), by subtracting the maximum diameter of a surviving colony at time 2 by its size at time 1 and dividing by the number of days between measurements. Correlations among environmental and biological parameters were initially tested and correlated variables removed. Physical predictors included seawater temperature, turbidity, and sediment deposition. Biological predictors incorporated the cover of the dominant algal competitor groups, turf, *Lobophora*, *Dictyota*, and *Sargassum* (Appendix S1: Figure S5b), as well as the biomass of herbivorous acanthurids, scarids, and siganids (Appendix S1: Figure S2b) as a proxy for top-

down control. All predictors were scaled and centered by their mean. Models were fit using backward selection, comparing full versus reduced models using LRT. Following backwards selection, the final model for colony survival across cohorts used a GLMM with binomial variance structure, testing the effects of temperature, turbidity, sedimentation, and turf algae (Appendix S1: Table S8b). The final model for colony growth across cohorts tested the effects of temperature, turbidity, and scarid abundance using a LMM (Appendix S1: Table S9b). Both models incorporated location, cohort, and colony ID as random effects to account for spatial, size, and temporal autocorrelation structure, respectively. All analyses were conducted using *lme4*.

RESULTS

Clear environmental gradients were apparent, with higher abiotic stress environments found in the mid-southern part of Exmouth Gulf and Learmonth, becoming milder towards the north of the gulf at Bundegi and NW Cape, and then to the west coast of the mainland at Coral Bay. Seawater temperature averaged 24.4°C during the study period, but seasonal ranges were higher towards the mid-south of the gulf, followed by the north of the gulf, while the west coast had the mildest range (Figure 1b). Turbidity followed a similar pattern, with the most turbid water found at the southern end of the gulf, gradually becoming clearer towards the north of the gulf, and most clear along the west coast (Figure 1c). On the other hand, sedimentation was generally highest at the northern end of the gulf at NW Cape in May–August, was always lowest at Coral Bay on the west coast, and generally low in February–May (Figure 1d; Appendix S1: Table S1). The type of sediment deposited did however, follow the environmental gradient. The southern part of the gulf was dominated by fine clays and silt, with the relative amounts of carbonate sand increasing towards the northern end of the gulf and along the west coast (Appendix S1: Figure S6).

Benthic communities at all study sites are coral depauperate (Figure 1e). Coral cover ranges from 1%–20% along the mid-southern gulf at Exmouth and Learmonth, 1%–16% along the north of the gulf at NW Cape and Bundegi, and 3%–13% at Coral Bay (Appendix S1: Figure S5b). Turf algae and foliose algae, including *Sargassum*, *Dictyota*, and *Lobophora*, dominated algal assemblages, driving seasonal changes in multivariate benthic community cover at Coral Bay, Exmouth, and Learmonth in particular (Appendix S1: Figure S5; Appendix S1: Table S2). Distinct fish communities were found at each location, with some overlap between sites along the northern gulf, and between sites along the southern gulf (Appendix S1: Figure S2).

Differences in juvenile coral densities on the reef benthos were evident among study locations (Figure 2a;

Appendix S1: Table S3), following a pattern similar to the temperature and turbidity gradients. Juvenile corals were most abundant in the clear waters of Coral Bay at 15.4 ± 3.1 individuals/m² (mean $\pm$ SE), declined by 55% at NW Cape (6.9 ± 1.6) and 69% at Bundegi (4.8 ± 1.9) in the northern the gulf, with negligible densities in the mid-southern gulf at Exmouth and Learmonth (1.6 ± 1.0). *Acropora* made up 40% of the juvenile coral community, followed by Merulinidae (31%) and *Porites* (16%; Appendix S1: Figure S7).

A clear distinction in coral settlement rates that did not match juvenile coral densities was observed between two major groupings among the study locations (Figure 2b,c; Appendix S1: Table S4a). Reefs along the west coast and northern gulf appear open to external larval supply, with settlement densities ranging from 0.40 ± 0.09 to 0.95 ± 0.19 individuals/tile. In contrast, reefs in the mid-southern gulf had negligible settlement rates that were reduced by more than an order of magnitude, with densities ranging from an average of 0.03 ± 0.02 to 0.07 ± 0.03 individuals/tile. Settlers were predominantly found on tile undersides and vertical surfaces (Appendix S1: Figure S8; Appendix S1: Table S4a). An increase of 32% total settlement was observed from 2016 to 2017, although the contribution to the model was minor relative to location and orientation effects (Appendix S1: Table S4a). *Acropora* made up 61% of settlers, followed by Pocilloporidae (34%) and *Porites* (5%).

Acropora spp. settlement rates from the region were significantly correlated with three bio-physical drivers following an initial selection of 11 (Appendix S1: Table S4b). Settlement had nonlinear, negative relationships with both increasing proportional self-recruitment potential (Figure 2d) and increasing seawater turbidity (Figure 2e), noting that these two predictor variables were also highly correlated (Appendix S1: Table S4). A weak negative relationship was also found between decreasing spiral worm cover and settlement (Figure 2f).

Even though negative correlations were found between *Acropora* spp. settlement and turbidity from the field observations, laboratory experiments show that the seawater turbidity from three of the study locations along the environmental gradient (Coral Bay, Bundegi, Learmonth) did not affect the proportion of *Acropora* larvae swimming, settled, or dead after 48-h assays (Appendix S1: Figure S9; Appendix S1: Table S5). Regardless of seawater origin, larval mortality averaged 5%, whereas those swimming averaged 93% and 68% in the absence and presence of CCA, respectively. Settlement was 12 times higher in assays when CCA chips were added.

Following the 11-week conditioning period of tiles to be used in the laboratory settlement assays, the early successional community differed ($p < 0.001$) among locations (Appendix S1: Figure S10). SIMPER analysis shows

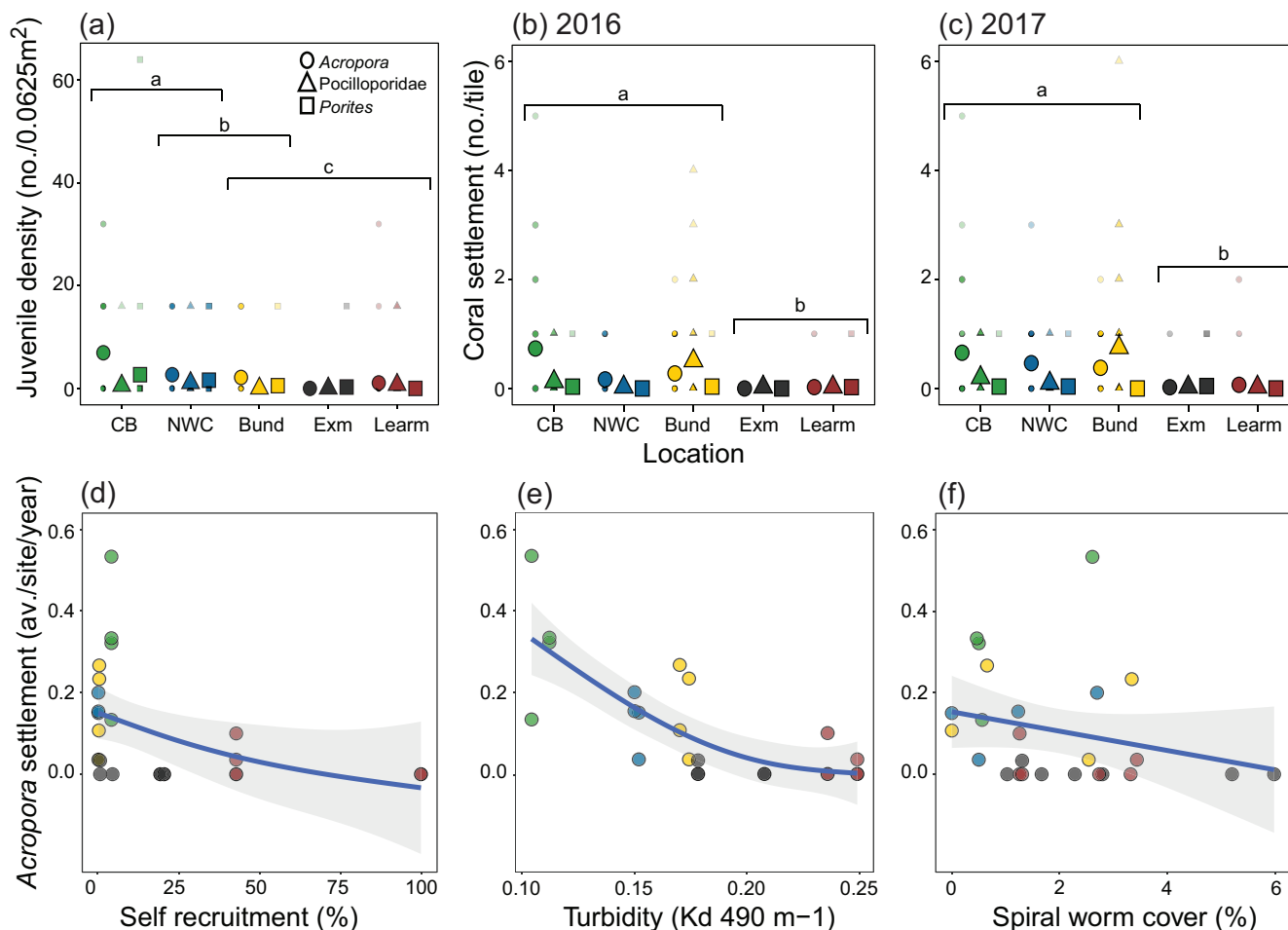


FIGURE 2 (a) Juvenile (<40 mm maximum diameter) coral densities across the study reefs, coral settlement rates from the study reefs in (b) 2016 and (c) 2017, and the relationship of *Acropora* spp. settlement with (d) proportional self-recruitment potential, (e) seawater turbidity, and (f) spiral worm cover. For panels (a–c) the small translucent shapes represent individual replicates and the large opaque shapes represent the mean. Groups with different letters above them are significantly different. For panels (d–f) circle colors refer to the corresponding locations in panels (a–c) and represent averaged data points from each year × site, with the solid blue lines representing significant model fits (±SE) following multiple regression

higher abundances of encrusting fleshy algae and CCA on tiles from Coral Bay, higher abundance of turf on tiles from Bundegi, and higher abundance of spiral worms on tiles from Learmonth (Appendix S1: Table S6). *Acropora* settlement on those tiles show significant differences due to preconditioning location and sediment deposition, but not their interaction (Appendix S1: Table S7a). Settlement rates were equal on tiles conditioned at Coral Bay and Learmonth, but 35% less on tiles conditioned at Bundegi (Figure 3a). Across locations, sediment deposition at the highest concentration (0.4 g/cm²) significantly reduced coral settlement by 37% compared to lower concentrations (0.0 and 0.1 g/cm²; Figure 3b) by reducing the available settlement space for the coral larvae. The interaction of sediment deposition and CCA cover also had a significant effect on settlement (Appendix S1: Table S7b). A positive relationship was found between

CCA cover and larval settlement at control sediment concentrations, which was progressively lost at low and high sediment concentrations (Figure 3c).

Patterns of newly settled to juvenile coral survival differed among cohorts × locations (LRT $\chi^2 = 93.2$, $p < 0.001$; Figure 4a–c; Appendix S1: Table S8a). Survival of newly settled *Acropora* colonies followed a Type III curve, with 22%–53% surviving the first 30 days and 2%–35% surviving until 138 days following deployment. By 563 days, newly settled recruits had the highest survival in the mid-southern gulf at Exmouth and Learmonth (22%–29% survival), followed by Coral Bay (18% survival) on the west coast, and Bundegi and NW Cape (2%–5% survival) at the northern end of the gulf. Survival of 18-month-old *Acropora* recruits was much higher, averaging from 70%–90% at all locations throughout the entire gulf after 364 days, but just 24% survival at Coral Bay. Seasonal *Sargassum* blooms from 0% to 84% cover at

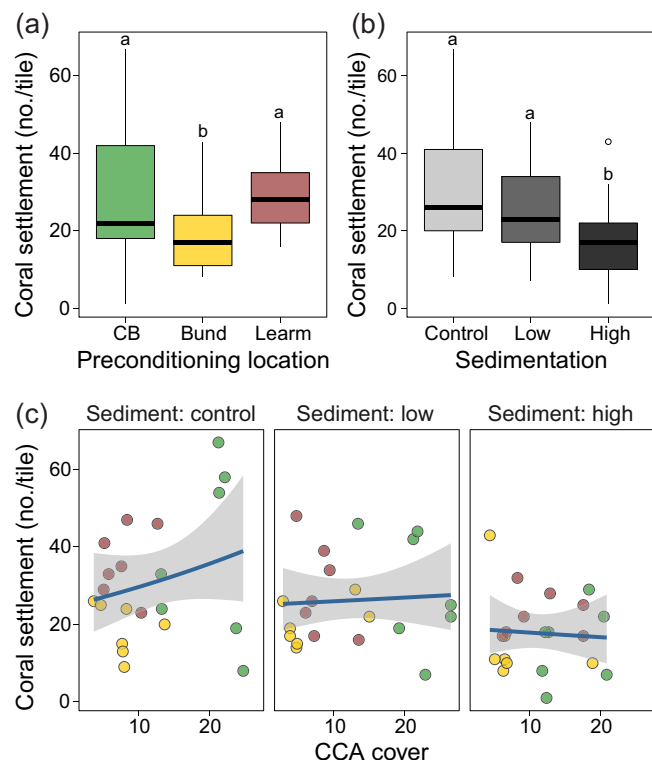


FIGURE 3 *Acropora* settlement rates in controlled laboratory assays on (a) substrates preconditioned at three of the study locations, (b) under control (0.0 g/cm²), low (0.1 g/cm²), and high (0.4 g/cm²) sedimentation treatments, (c) relationships with crustose coralline algal (CCA) cover under those sedimentation treatments. For panels (a) and (b) groups with different letters above them are significantly different. For panel (c) circle colors refer to the corresponding location colors in panel (a), with the solid blue lines representing model trends and gray bands the standard error of the significant sedimentation × crustose coralline algae cover interaction

Coral Bay (Appendix S1: Figure S5b) and was correlated with low survival (Appendix S1: Figure S11). Survival of juvenile *Acropora* spp. tagged on the benthos at Coral Bay, NW Cape, and Bundegi was >78% over 623 days.

Patterns of coral size across study locations varied between the newly settled *Acropora* and the other two cohorts (Figure 4d–f; Appendix S1: Table S9a). For the newly settled *Acropora*, corals were larger at Coral Bay (average of 4.1 mm maximum diameter) compared to NW Cape, Bundegi, and Exmouth (1–2.6 mm) by 138 days following settlement. By 563 days following settlement, however, the largest were found at Learmonth in the very south of the gulf (15.9 mm), followed by Exmouth and Coral Bay (10.5 mm), and the smallest at NW Cape and Bundegi at the northern end of the gulf (5.3 mm). In contrast, while the sizes of 18-month-old *Acropora* cohort averaged 21.1 mm upon deployment across locations, by 364 days, they were largest at NW Cape at the north of the

gulf (55.3 mm), smallest at Coral Bay (24.0 mm), and averaged 36.2, 35.4, and 43.8 mm at Bundegi, Learmonth, and Exmouth, respectively. Sizes of juvenile *Acropora* spp. tagged on the benthos after 623 days of monitoring were similarly largest at NW Cape (74.7 mm), followed by Bundegi (66.6 mm), and smallest at Coral Bay (60.3 mm).

The survival and growth of the newly settled to juvenile *Acropora* were significantly correlated with four biophysical drivers across the study locations. Survival was negatively related to increasing seawater temperature, turbidity, sedimentation, and turf algae (Figure 5a–d). Turbidity and sedimentation had the most severe effects on survival, followed by turf algae, whereas the effect of temperature was minor (Appendix S1: Table S8b). Growth rates showed a unimodal response to seawater temperature and was highest at warmer temperatures. In contrast, growth rates were similar from low to mid-range turbidity, but significantly declined at higher turbidity levels (Figure 5e,f; Appendix S1: Table S9b).

DISCUSSION

Insights into coral recovery have defined recruitment bottlenecks relating to microhabitat refugia, facilitation and competition, and trophic cascades (Arnold & Steneck, 2011; Doropoulos et al., 2016; Mumby et al., 2007), all of which are critical mechanisms of population recovery driven by ecological interactions at localized scales. Yet recent research assessing the effectiveness of resilience-based management on coral reefs has suggested the impacts of local stressors are overwhelmed by regional impacts (Bruno et al., 2019) that break down ecological interactions and dampen recovery, although other recent global studies show that local conditions do matter (Donovan et al., 2021). Here, we find that the combination of both regional and local factors influenced the recovery potential of coral populations throughout our study region, with the strength of the relationships changing across 60 km. Negligible propagule supply in the mid-southern Exmouth Gulf appears to be the main limiting factor of recovery, where residence times are prolonged and connectivity to external sources low (this study; Feng et al., 2016; Boschetti et al., 2020). In this part of the system, any influences of wide seawater temperature ranges and elevated turbidity on coral growth and survival appear to be largely overwhelmed by limited propagule supply. In contrast, clearer water reefs towards the northern gulf and on the west coast appear more open to propagule supply. However, localized competition with turf algae intensified early post-settlement mortality to limit recruitment at NW Cape and Bundegi, and seasonally high cover of *Sargassum* stands at Coral Bay

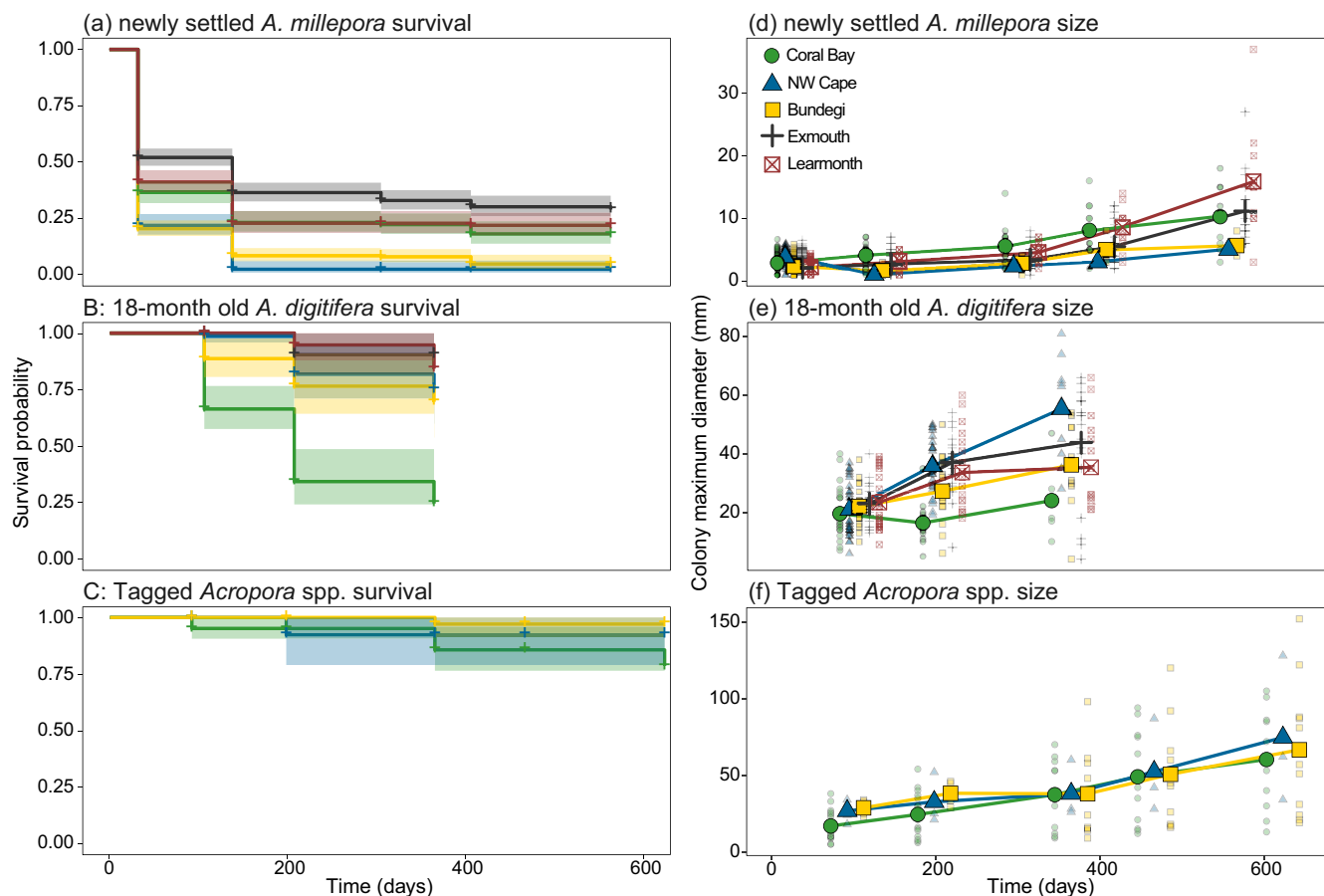


FIGURE 4 (a–c) Survival and (d–f) size of *Acropora* across the study locations and cohorts—that is, newly settled, 18 months old, or tagged on the benthos. Survival was modeled using Kaplan-Meier log-rank analysis, with the solid lines indicating the mean fit and shading the 95% confidence intervals. For growth plots, small translucent shapes represent individual colonies and the large opaque shapes represent the mean

intensified transplanted juvenile coral mortality. Across our study system, we suggest that the influence of oceanography on high residence times and low larval connectivity to external sources overwhelms the influences of both physical and biological interactions on recovery potential at locations where environmental stressors are higher (sensu Navarrete et al., 2005); whereas populations in relatively benign physical conditions appear proximally structured by local ecological drivers (sensu Doropoulos et al., 2016) and distally structured by global bleaching and cyclone disturbances that have generally depressed brood stock in the region (sensu Hughes et al., 2019). Such context-specific understandings of natural ecosystems provide the basis for management strategies to plan for the recovery of degraded coral reefs found along natural or human-induced environmental gradients.

Our surveys, as well as longer term monitoring (Department of Biodiversity Conservation and Attractions, 2017), show that coral populations in the study region have hardly begun to re-establish in the period since the previous most recent major disturbance; severe coral bleaching that occurred in 2011 and reduced coral cover in

the north of the gulf from 85% to 3% (Depczynski et al., 2013). Currently there are no immediate signs of recovery through high rates of coral recruitment. Where larval settlement was observed, the actual rates of settlement are severely depressed to those expected to drive recovery. For example, coral settlement rates from Coral Bay, NW Cape, and Bundegi in this study averaged just 0.43 individuals/100 cm², compared to recovering reefs at the inshore and offshore Great Barrier Reef, and Mo'orea, that averaged 11.0, 1.75, and 2.22 individuals/100 cm², respectively (Davidson et al., 2019; Doropoulos et al., 2015; Edmunds, 2018b). Long-term monitoring from Ningaloo Reef shows a sharp reduction in coral settlement rates from 2009–2010 compared to 2011–2016, particularly for the Bundegi region where settlement rates declined from an average of 12 to 0.50 individuals/100 cm², respectively (Department of Biodiversity Conservation and Attractions, 2017), occurring immediately following the regional scale heat wave event of 2010–2011 and subsequent events (Gilmour et al., 2019). Similarly, evidence on the Great Barrier Reef shows an average decline of 89% in coral settlement from 2018 compared to 1996 following severe bleaching

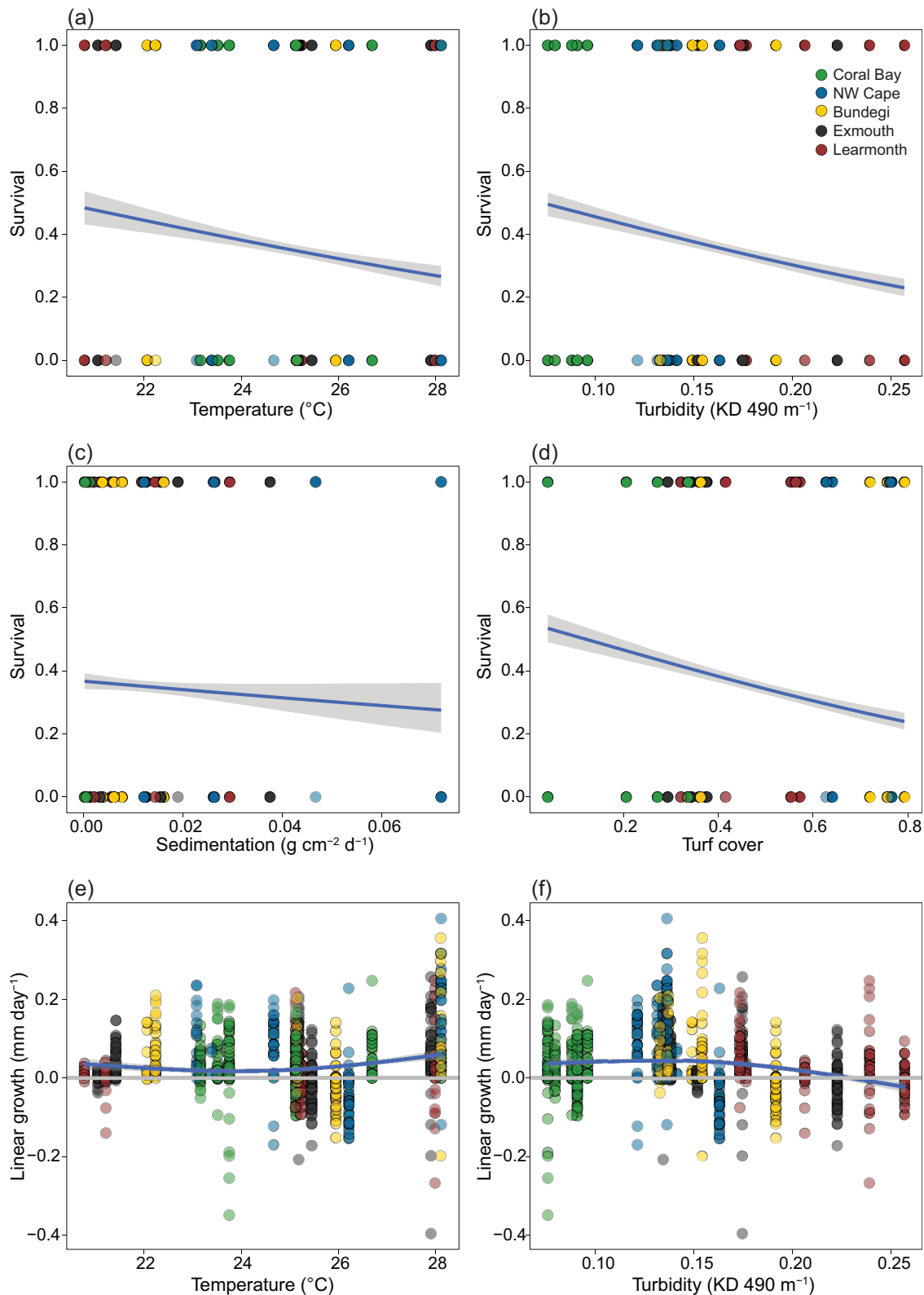


FIGURE 5 Partial regression plots showing the significant effects of (a) seawater temperature, (b) turbidity, (c) sedimentation, and (d) turf algae cover on rates of survival, and (e) seawater temperature and (f) turbidity on rates of growth of newly settled to juvenile *Acropora*. Circles represent individual data points, solid blue lines represent significant model fits, and gray bands represent the standard error

events in 2016 and 2017 (Hughes et al., 2019). Reductions in propagule supply show the extent to which regional disturbances can have long-lasting effects to ecosystem recovery at meta-population scales.

Juvenile coral densities are also well below thresholds expected for coral recovery in the southern two-thirds of the Exmouth Gulf, but within ranges of coral recovery for the other reefs in the Gulf and at Coral Bay. Rapid recovery on reefs in the Seychelles have required densities of >6.2 individuals/m² for all juvenile corals (Graham et al., 2015), or >1.5 individuals/m² for juvenile *Acropora* on reefs in Palau (Gouezo et al., 2019) and the Great Barrier Reef (Doropoulos et al., 2015). In this study, juvenile *Acropora* spp. densities ranged from 0–0.9 individuals/m² at Exmouth and Learmonth, but were 2.1–2.6 individuals/m² at Bundegi and North-West Cape, and 6.9 individuals/m² at Coral Bay, indicating clear differences in recovery potential across the environmental gradient.

Alternate hypotheses could be proposed to explain recruitment failure in the lower Gulf. For reefs in the mid-southern Exmouth Gulf with the largest temperature range and highest turbidity, larval mortality and/or settlement inhibition may act as major recruitment bottlenecks as opposed to supply limitation (Arnold & Steneck, 2011; Humanes et al., 2017). However, our laboratory experiments show equal proportions of coral larvae swimming or settled after 48 hours regardless of the regional source of water, suggesting that seawater properties such as potential differences in turbidity, dissolved organic or inorganic materials, or bacterial interactions, do not appear to explicitly stress the larvae or influence settlement rates. While we did not test the effects of seawater temperature on larval survival, laboratory studies using *Acropora tenuis* have shown that increasing seawater temperature reduces coral larvae survival, particularly for treatments $>29^{\circ}\text{C}$ (Graham et al., 2016). During the coral spawning and larval dispersal periods in the timeframe of our study, sites in the Gulf had average daily temperatures ranging from 25.7°C to 26.4°C on 1 April–14 May 2016 and between 27.8° and 28.2°C on 20 March–30 April 2017. Therefore, based on the information from Graham et al. (2016), we would not expect these temperatures to considerably affect coral larval survival onto those reefs during our study. Moreover, coral settlement densities were similarly equal on tiles preconditioned in the far south of the Exmouth Gulf to those conditioned at clear water reefs, suggesting that natural settlement rates were not altered by any variation in benthic-larval interactions. Recent work from Palau has also observed that the influence of interaction strengths of benthic communities with coral larvae can be overwhelmed by broader scale physical processes on limiting larval supply and settlement (Gouezo et al., 2020). Our experimental outcomes, the survival and growth information from the coral transplants, combined with modeled evidence showing these reefs have

high self-recruitment, suggest that the most likely explanation limiting the recovery of disturbed reefs in the mid-southern Exmouth Gulf is the limited and depressed rates of larval supply from internal or external sources.

For corals in the north of the Exmouth Gulf, in addition to low propagule supply, it appears that localized ecological interactions are limiting recovery. Laboratory settlement rates on tiles preconditioned in this region were depressed relative to those conditioned in the other regions, with tile communities preconditioned at Bundegi highly correlated with turf algae. Very high rates of early post-settlement mortality were also driven by competition with turf algae, and to a lesser extent from sediment smothering. Algal turf is a known agent of competition in both pre- and post-settlement phases of coral recruitment (Arnold et al., 2010; Doropoulos, Roff, et al., 2017), and its prevalence on degraded reefs is often related to positive relationships with sediment entrapment that reduces top-down control (Goatley et al., 2016; Tebbett & Bellwood, 2019). Results from our settlement assays using varying sediment deposition loads showed that coral larval settlement decreased at the highest load (0.4 g/cm^2) compared to the lower concentrations (0.0 and 0.1 g/cm^2). The highest sediment load would directly have reduced available settlement space on the tiles for the larvae to attach and metamorphose, as well as reducing the facilitative interaction between crustose coralline algae and coral larvae (Figure 3c). Suspended sediments during larval development can cause latent effects on larvae that reduce settlement rates (Humanes et al., 2017), while deposited sediments can directly and indirectly interfere with coral settlement rates by reducing preferred settlement space and altering settlement behavior (Ricardo et al., 2017; Wakwella et al., 2020). Even though the herbivorous fish community in this area is protected and abundant, the large-scale loss of corals would have relaxed grazing intensity by rapidly increasing grazable space (Scheffer et al., 2008). Intensified by interactions with high sediment deposition rates, optimal space for coral recruitment may currently be limited. Compounded by depressed rates of settlement, post-settlement bottlenecks are likely to be suppressing recovery in the north of the system.

Correlations between the survival and growth of the newly settled to juvenile corals with the biophysical parameters showed a complexity of interactions. For the larger cohorts of juveniles in our study, there were low sample sizes of tagged juvenile *Acropora* colonies located on the benthos at two of the three study sites (i.e., $n = 4$ at NW Cape and Bundegi vs. $n = 17$ at Coral Bay) where their growth and survival were tracked, and inferences from this data set in isolation should be made with caution. However, these data are supplemented with the higher sample sizes of 18-month-old *Acropora* that were transplanted across all sites ($n = 24$ – 31 per locations). Turbidity and sedimentation had the most negative effects on survival, followed by turf algae. Turf algae can

limit post-settlement survival of coral recruits by directly smothering them (Arnold et al., 2010), particularly when combined with increasing sediment loads (Birrell et al., 2005). It is well established that, as sediment deposition increases, corals can become smothered and mortality increases, accentuated in smaller sizes classes and having negative effects on coral recruitment (e.g., Erftemeijer et al., 2012; Jones et al., 2015; Wakwella et al., 2020). Negative relationships with turf algae were most prominent at the northern end of the Gulf where turf cover and sediment deposition were highest. The results of our study also show that coral survival and growth declined as turbidity increased, with the relationship most prominent at reefs in the southern two-thirds of the Exmouth Gulf where turbidity is highest. Suspended sediments increase turbidity, which can reduce the growth of coral recruits by reducing autotrophic pathways (Jones et al., 2015). Aquarium studies have mechanistically shown that low levels of light, particularly when interacting with suspended sediments can reduce coral growth and induce partial bleaching and mortality (Bessell-Browne et al., 2017). Combined, the effects of these multiple biophysical drivers explain the complexity of limiting effects to which coral recruits are exposed along environmental gradients.

Contrary to our expectation, the 18-month-old cohort of *Acropora* that were transplanted back into Coral Bay suffered the highest mortality rates (Figure 4b). Our analysis shows a significant correlation of mortality with high *Sargassum* cover at the Coral Bay sites, a macroalga that has been shown to reduce limit juvenile coral recruitment in previous studies at Ningaloo (Webster et al., 2015), the Great Barrier Reef (Hughes et al., 2007), and the Seychelles (Chong-Seng et al., 2014). The 18-month-old cohort of *Acropora* corals transplanted into Coral Bay may also have been targeted by fish, with fish predators often targeting larger transplants (Doropoulos et al., 2016; Miller & Hay, 1998).

Recent meta-analysis shows that transplant survival rates are the key driver of rapid population recovery for sessile marine invertebrates (Montero-Serra et al., 2018) and our results suggest that there is capacity for recovery even if corals originating from areas of more benign physical conditions are supplied to reefs of higher environmental stress. Transplanting two cohorts of corals originating from the clear waters of Coral Bay to the most turbid waters in the Exmouth Gulf did not reduce growth or survival. Once corals settle to the reef, surpass early post-settlement bottlenecks, and establish as juvenile coral colonies (usually ~6–12 months following settlement; e.g., Ritson-Williams et al., 2009; Doropoulos et al., 2016), the survival data from the 18-month old *Acropora digitifera* transplants and tagged *Acropora* spp. suggest that recovery is possible. Annual survival of those cohorts was >73%, which is slightly higher

than similarly sized juvenile *Acropora* found on reef slopes of the Great Barrier Reef and Mo'orea. For example, Doropoulos et al. (2015) found that the 6-monthly survival rates of juvenile *Acropora* at Heron reef slope, southern Great Barrier Reef, averaged between 85% and 90% for colonies <20 mm in maximum diameter. In contrast, Traçon et al. (2013) found annual survival rates of juvenile *Acropora* at Trunk reef slope, central Great Barrier Reef, averaged 48% and only 32% along reef slopes in Mo'orea. While juvenile coral densities and survival rates indicate potential for reef recovery across the study reefs, the recruitment of new corals is the first phase that needs to be overcome, and our data show recruitment is currently limited across all study reefs.

Overall, this study shows how coral reef recovery can be limited by local competitive interactions that drive high rates of early coral mortality when environmental stress is low but remain limited by low coral larvae supply under elevated environmental stress 10 years following large scale disturbance. Global stressors can have long-lasting effects that impact natural communities at meta-population scales (Boschetti et al., 2020; Gilmour et al., 2013; Hughes et al., 2019). Those meta-population impacts can severely depress natural recovery rates, which are further compounded by localized ecological interactions that may have previously been overcome when meta-population stress was not apparent. Coinciding with these global scale effects are the effects of more localized environmental stress gradients, with the level of environmental stress influencing how management approaches local recovery or rehabilitation planning.

The outcomes of this study provide key considerations for managers and suggest that approaches to managing coral reefs need to be context specific (Mumby & Steneck, 2008). For instance, direct coral propagation could be applied to reefs with low larval supply but high early survival, or by aiming to reduce competition where larval supply is sufficient but exogenous stress overwhelming. Recent work explicitly considers how to optimize coral reef recovery under context-specific management actions (Gouezo et al., 2021). Employing restoration as a tool to help maintain coral reefs in the face of global heating may rely on the success of intervention efforts (e.g., Anthony et al., 2017; van Oppen et al., 2017), but direct interventions are not always appropriate and consideration of all limiting factors found within any system require attention by decision makers (e.g., Gouezo et al., 2021; Saunders et al., 2020). While principles generally remain consistent, tendencies to generalize the processes limiting coral reef recovery appear inadequate in the context of global change. Context-specific observations and understanding of the entire set of relevant demographic processes are therefore required to manage reefs using case-by-case assessments.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Christopher Doropoulos and Russell C. Babcock conceived and designed the study; all authors collected and contributed data; Ming Feng conducted larval connectivity modeling; Christopher Doropoulos analyzed the data and led the writing; all authors gave their final approval for publication.

DATA AVAILABILITY STATEMENT

Data (Doropoulos, 2021) are available in the CSIRO Data Access Portal at <https://doi.org/10.25919/mvp4-t007>.

ORCID

Christopher Doropoulos  <https://orcid.org/0000-0001-8038-2771>

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