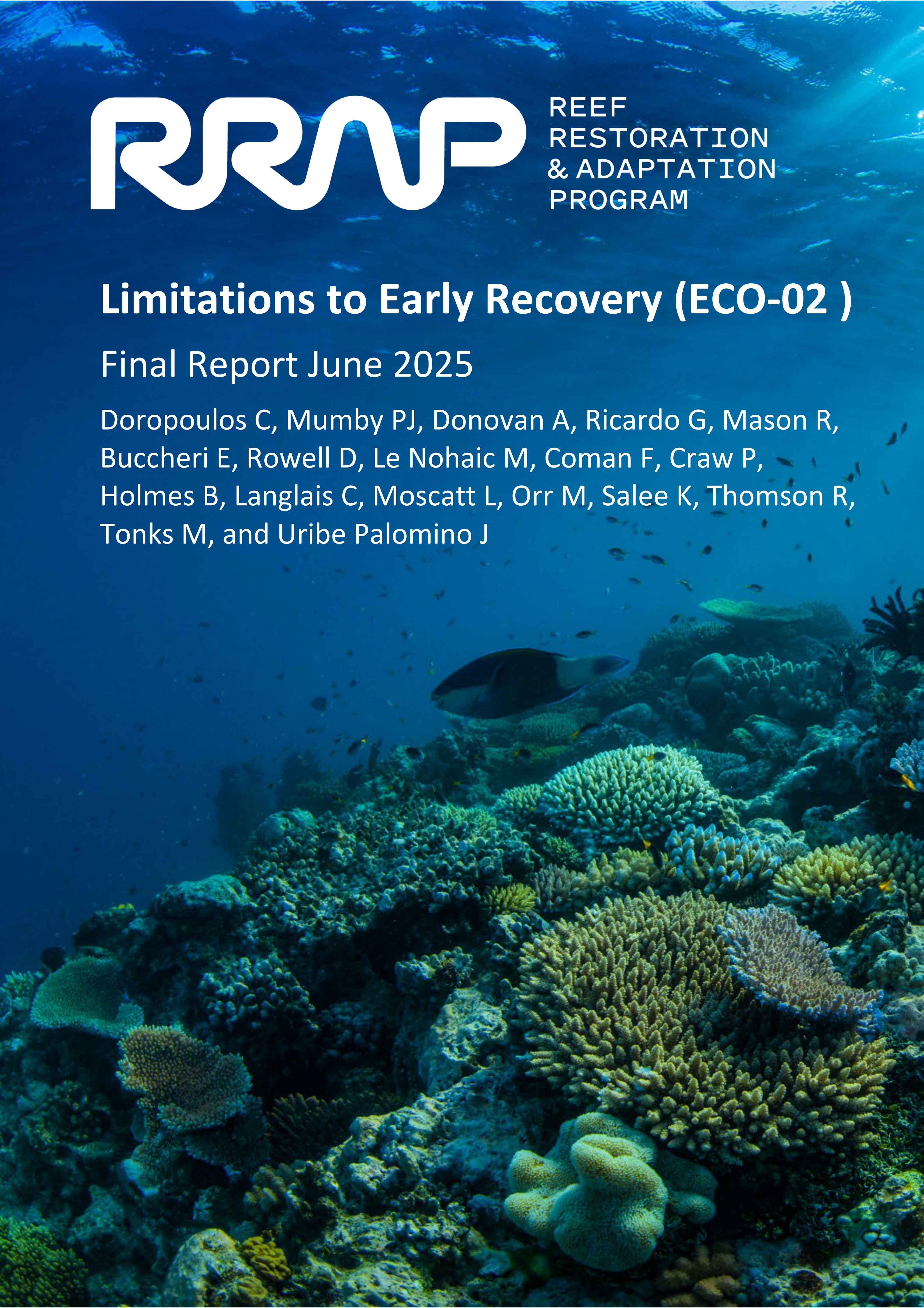

REEF
RESTORATION
& ADAPTATION
PROGRAM

Limitations to Early Recovery (ECO-02)

Final Report June 2025

Doropoulos C, Mumby PJ, Donovan A, Ricardo G, Mason R, Buccheri E, Rowell D, Le Nohaic M, Coman F, Craw P, Holmes B, Langlais C, Moscatt L, Orr M, Salee K, Thomson R, Tonks M, and Uribe Palomino J

RRAP Limitations to Early Recovery (ECO-02) Final Report June 2025

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Cover Page: Coral reef, Credit: Gary Cranitch, Queensland Museum

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This report summarises work undertaken under *Limitations to Early Recovery (ECO-02)* in accordance with the Reef Restoration and Adaptation Program's *Ecological Intelligence for Reef Restoration (EcoRRAP)* Project Agreements. It provides a summarised, point-in-time synopsis of activities, methods, findings and outcomes completed in accordance with the approved project scope up to 30 June 2025.

All information reflects project scope and outcomes as of May-June 2025. Subsequent updates, analyses, or scientific developments are not included. This report should be read alongside any associated and publicly available technical reports, datasets, and publications for full detail. This report does not provide scientific inferences, policy guidance or operational instructions beyond the project's defined scope and duration.

Acknowledgement

This work was undertaken for the Reef Restoration and Adaptation Program (RRAP). Funded by the partnership between the Australian Government's Reef Trust and the Great Barrier Reef Foundation, partners include: the Australian Institute of Marine Science, CSIRO, the Great Barrier Reef Foundation, Southern Cross University, the University of Queensland, Queensland University of Technology and James Cook University.

The RRAP partners acknowledge Aboriginal and Torres Strait Islander Peoples as the first marine scientists and carers of Country. We acknowledge the Traditional Owners of the places where RRAP works, both on land and in sea Country. We pay our respects to elders; past, present, and future; and their continuing culture, knowledge, beliefs, and spiritual connections to land and sea Country.

We specifically acknowledge and thank the following Traditional Owners of sea Country that this report relates to:

Location	**Traditional Owner Group**
Heron Island	Bailai, Gurang, Gooreng Gooreng, Taribelang Bunda
Palm Islands, Townsville	Manbarra, Bindal

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1 Executive Summary

The Ecological Intelligence for Reef Restoration (also known as the RRAP EcoRRAP Sub-program) project – Limitations to Early Recovery (ECO-02) – addresses critical ecological gaps necessary for effective, large-scale coral reef restoration by focusing on the limitations to early recovery —from reproduction through to larval development, settlement, and juvenile survival. The Great Barrier Reef (GBR), as well as reefs globally, are experiencing unprecedented levels of disturbance due to climate change, pollution, and overfishing. These pressures compromise natural recovery mechanisms, necessitating scientifically informed interventions for ecological resilience and long-term sustainability.

The research was designed around three key focal areas: (1) identifying the coral densities required to overcome reproduction bottlenecks; (2) understanding natural larval supply and validating models of larval connectivity; and (3) determining the survival thresholds for juvenile corals under varying reef conditions. These objectives were approached through empirical field studies, experimental manipulations, and model development and validation across diverse reef environments across the GBR.

Identifying coral densities to overcome reproduction bottlenecks involved determining the minimum densities needed for successful fertilisation, especially in areas with sparse coral populations. Field experiments manipulating adult coral densities under varying hydrodynamic conditions revealed critical thresholds to overcome the Allee effect, where low densities result in reproductive failure. Understanding these thresholds ensures restored populations reach self-sustaining levels and contribute to larval supply. These findings inform strategic placement and clustering of coral colonies to enhance fertilisation and long-term restoration outcomes. Based on field data and natural spawning observations, optimal colony spacing should not exceed five meters for common *Acropora* species. Further research is needed to determine appropriate spacing for other genera.

Larval connectivity studies revealed substantial variation in larval supply across locations and over time. Capricorn-Bunker reefs showed lower larval densities than the Palm Islands, which recorded up to ten larvae per cubic meter. Larval arrival correlated with settlement, though this varied by site. Innovations such as molecular techniques and the SaLP (Sampler of Larvae and Plankton) autosampler now enable high-resolution larval dispersal monitoring. However, hydrodynamic models often failed to predict larval arrival and settlement at fine spatial scales (<1 km²) relevant for practitioners. This underscores the need to validate models with ecological and site-specific data before use in restoration planning. Some reef areas consistently receive low larval input, highlighting the need for targeted enhancement.

Juvenile coral survival studies showed that survival improves with size, with individuals over 10 mm in diameter exhibiting a 50% annual survival probability. This trend varies by species, environment and location. For example, *Acropora* had better survival on cooler southern reefs, while *Porites* fared better in warmer northern areas. Coral cover influenced predation risk, and bleaching susceptibility increased with size. Selecting species and fragment sizes suited to site conditions can improve restoration outcomes. Larger juveniles generally survive better, but success depends on matching coral type, size, and habitat. Future work should identify local thresholds for coral survival and stress tolerance to refine strategies and reduce long-term intervention.

Key outputs of the project include empirical thresholds for reproductive density, larval arrival and settlement benchmarks, validation datasets for connectivity models, and detailed survival profiles for multiple coral taxa under varied environmental conditions. In total, we have contributed 10 published scientific publications, six scientific publications that are currently under review and deposited for open access on preprint servers, three scientific manuscripts in final stages, three reports to the Port Curtis Coral Coast (PCCC) Traditional Owner Native Title group, one technical report, three standard operating procedures (SOPs), and had three Masters and two PhD students complete their postgraduate training under our supervision.

Conclusions and recommendations underscore the need for restoration strategies tailored to site-specific ecological parameters. Effective reef restoration requires integrated planning that accounts for larval supply, hydrodynamics, coral traits, and habitat features. Restoration interventions should prioritise locations with low natural recruitment, use validated larval supply data and deploy coral juveniles at sizes and densities optimised for survival. These science-based guidelines offer a robust foundation for future coral restoration and adaptive management across the GBR.

2 Background and Justification for the Research

Habitat restoration on coral reefs is driven by the supply, colonisation and survival to sexual maturity of corals, which provide the structure and basis of all ecosystem services provided by corals reefs (Caley et al. 1996, Connell 1997). However, large-scale mortality events shift coral reefs into states in which natural recovery may be altered, reducing the capacity for reefs to return to pre-disturbance states (Mumby and Steneck 2008, Graham et al. 2015, Hughes et al. 2017). In the current Anthropocene, the scale and severity of disturbances on coral reefs require active interventions to promote immediate restoration for the activation of longer-term recovery processes in the face of global change (Anthony et al. 2017, van Oppen et al. 2017). Active interventions need to be applied at multiple scales, from individual genes to colonies to reefs to ecosystems, which all require fit-for-purpose ecological understanding for successful outcomes.

Ecological principles provide the platform for the long-term success of habitat restoration (Young et al. 2005). In terrestrial environments, these principles as well as new technologies have been incorporated to improve the success of large-scale restoration activities (Benayas et al. 2009, Perring et al. 2015). In coastal environments, incorporation of ecological principles into restoration activities have been advised (Halpern et al. 2007, Silliman et al. 2015) but often ignored, resulting in high cost to low success ratios from restoration projects—particularly notable in coral reefs (Bayraktarov et al. 2016). As such, determining key ecological rates and incorporating them into decision making processes is critical for effective large-scale coral reef restoration (Doropoulos and Babcock 2018, Ladd et al. 2018, Quigley et al. 2022, Shaver et al. 2022).

Underlying all ecological interactions are fundamental principles of population biology that include density-dependent thresholds (Courchamp et al. 1999), population connectivity (Hock et al. 2019), and functional trade-offs (Doropoulos et al. 2016). While many of these processes have been studied and even applied in small scale coral restoration projects (Ladd et al. 2018), many are practically unknown. These knowledge gaps are of fundamental importance to scaling reef restoration and adaptation as the optimisation of restoration interventions such as seeding larvae onto reefs (Heyward et al. 2002, Edwards et al. 2015, dela Cruz and Harrison 2017, Doropoulos et al. 2019), out-planting corals on settlement devices (Chamberland et al. 2017, Randall et al. 2021, Waters et al. 2025), and direct out-planting of coral fragments (Young et al. 2012, Page et al. 2018, Baria-Rodriguez et al. 2019), will rely on putting corals with appropriate phenotypes onto suitable substrata, in species-appropriate microhabitats, on the right part of a reef, and at the most effective densities (Silliman et al. 2015, Doropoulos and Babcock 2018, Ladd et al. 2018).

Coral recovery follows a cycle of reproduction, larval supply, early growth, and survival, with physical and biological interactions influencing each stage (Ritson-Williams et al. 2009, Doropoulos et al. 2016, Humanes et al. 2017, Ricardo et al. 2021). On the Great Barrier Reef (GBR), most corals reproduce through mass spawning, releasing eggs and sperm into the water (Harrison et al. 1984, Babcock et al. 1986). However, after bleaching, crown-of-thorns starfish (COTS) outbreaks, or cyclones, surviving corals may become reproductively isolated—a phenomenon known as the 'Allee effect' (Courchamp et al. 1999). Low coral densities can lead to fertilisation failure due to sperm limitation and egg dilution (Oliver and Babcock 1992). While theoretical thresholds for reproductive isolation exist (Teo and Todd 2018), empirical data are lacking. Targeted experiments are necessary to determine the coral densities required to sustain fertilisation under different hydrodynamic conditions. Findings will guide coral planting strategies for the restoration operations.

Understanding reef hydrology and larval connectivity at multiple spatial scales is crucial for effective coral restoration (Treml and Halpin 2012, Doropoulos and Babcock 2018, Hock et al. 2019). While large-scale RRAP planning incorporates larval dispersal models (Condie et al. 2021, Ani et al. 2024, Cresswell et al. 2024, Bozec et al. 2025), their accuracy remains unvalidated. Fine-scale hydrodynamic influences on larval retention and transport are poorly integrated into these models, necessitating validation trials to ensure effective RRAP implementation at the spatial scales of sites within reefs that are relevant for restoration operations.

In the Caribbean, relationships between juvenile coral size, density, and restoration success are partially understood (Young et al. 2012, Ladd et al. 2016, Ladd et al. 2018), but similar data for GBR corals are insufficient (Trapon et al. 2013, Doropoulos et al. 2015). Identifying mortality thresholds that hinder juvenile coral growth into reproductive colonies is essential to optimise out-planting densities for restoration operations, particularly as reseeding corals utilising sexually produced recruits (Randall et al. 2020) or fragments (Boström-Einarsson et al. 2020) are the dominant intervention methods for repopulating reefs. Determining optimal juvenile coral sizes, densities, and deployment strategies—accounting for coral traits and environmental stressors—will provide practitioners with guidelines to improve restoration operations.

The RRAP Limits to Early Recovery (ECO-02) Project focuses on the early stages of coral recovery from reproduction to larval development and transport, recruitment onto the reef, and early growth and survival (Figure 1). It aims to empirically quantify critical gaps in ecological knowledge to improve the parameterisation of ecological models that support decision making and the design criteria for several interventions that involve placing corals in the field. Guidelines for the spatial distribution of how and where interventions can be optimised will provide the platform for effective decision-making strategies for optimal delivery, spread, and effectiveness.

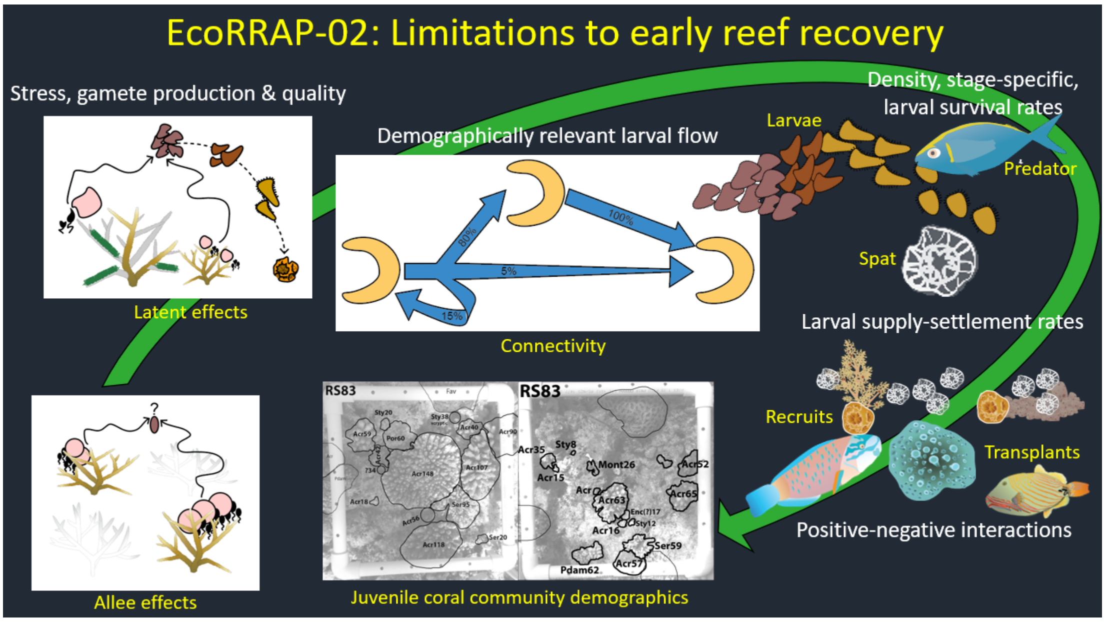


Figure 1: Major processes being assessed by the RRAP Project Limitations to Early Recovery (ECO-02) to characterise critical knowledge gaps needed for modelling and strategic restoration deployment activities.

Specifically, this project assessed:

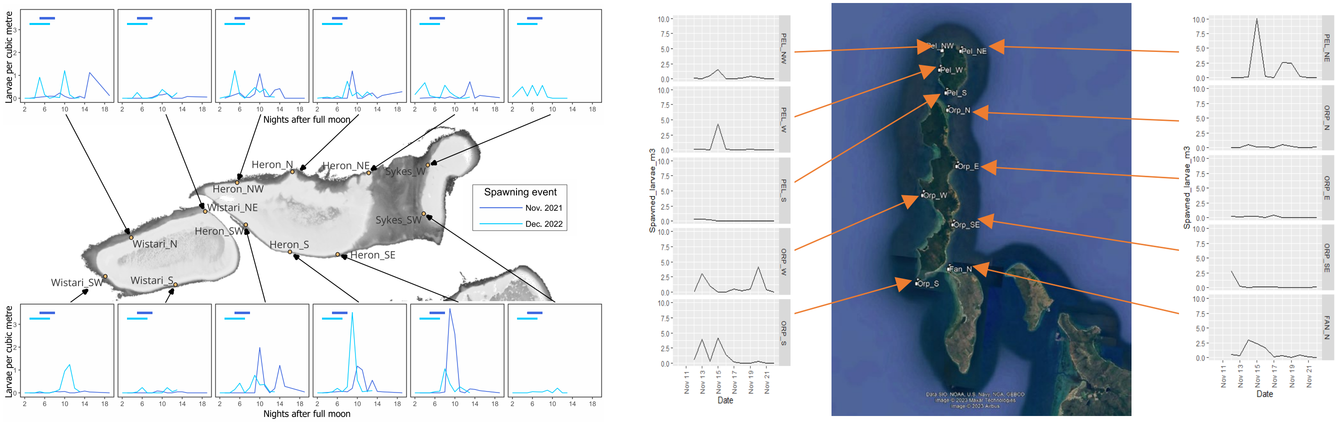
1. The **clustering and density of corals** needed to overcome reproduction bottlenecks to ensure larval supply and promote local resilience. Information will guide the threshold colony density requirements for when restored reefs become self-sustaining and benefit downstream areas. Targeted experiments that manipulate the density of adult corals in contrasting environments will be utilised to define the empirical thresholds.
2. Where **natural larval supply** limits coral recovery. Conservation decision-making utilises predicting larval connectivity so that reefs can be identified that are either major sources of larvae or insufficiently connected such that they will benefit from restoration. We will evaluate the rates of larval supply to reefs, calibrate fine-scale connectivity models, and identify where enhancing larval supply is necessary for intervention applications. Areas of reef along gradients of predicted low to high natural supply of larvae will be targeted to address this question.
3. Limitations to **coral survival from recruits to juveniles to adults.** Studies will assess optimal densities and sizes across different reef environments to define the minimal out-planting efforts necessary that ensure positive colony and population growth for reef recovery. Assessments will occur using a combination of detailed monitoring and targeted experimental manipulations, utilising

environmental settings where RRAP interventions are likely to take place.

3 Research Objectives and Key Findings

A current list of project outputs are listed on the RRAP website: gbrrestoration.org. Key research objectives and findings are detailed below.

Table 1: Key findings of the Project aligned to the overarching and specific research questions for each sub-project.

Objective		**Key Findings and/or Outcomes**
1. Measuring and validating larval connectivity to facilitate long-term coral restoration planning		
1 (a)	Provide empirical rates of larval supply and relationship with settlement	We aimed to understand how coral larvae move and settle across different reef areas to support long-term coral restoration. We measured the number of coral larvae arriving at different reef sites during spawning events in 2021 and 2022. The amount of larvae arriving in the Capricorn-Bunker reef area (Heron and Wistari reefs) varied, ranging from very few to over three larvae per cubic meter of seawater (Figure 2, left). In contrast, the Palm Islands (Pelorus, Orpheus, and Fantome reefs) saw much higher numbers during a major spawning event in 2022, with up to ten larvae per cubic metre (Figure 2, right).  *Figure 2: Time series of larval influx following the full moon at (left) Capricorn-Bunker reefs in the southern offshore GBR (Mason et al. Under Review) and (right) Palm Islands reefs in the central inshore GBR (Mason et al. In Prep).* Importantly, we found a significant connection between the number of larvae arriving and how many successfully settled on the reef. However, the strength of the relationship varied—moderate in the Capricorn-Bunker area (Figure 3, left) and somewhat stronger in the Palm Islands (Figure 3, right). Our findings suggest that while measuring larval arrival is a good indicator of potential coral settlement, there are still unpredictable factors—like natural variability or challenges in sampling—that can affect how many larvae actually settle and survive. For example, we found a positive correlation

between larval settlement and some types of epilithic algae. Overall, this research helps build a clearer picture of how coral populations can rebuild, which is essential for effective reef restoration planning.

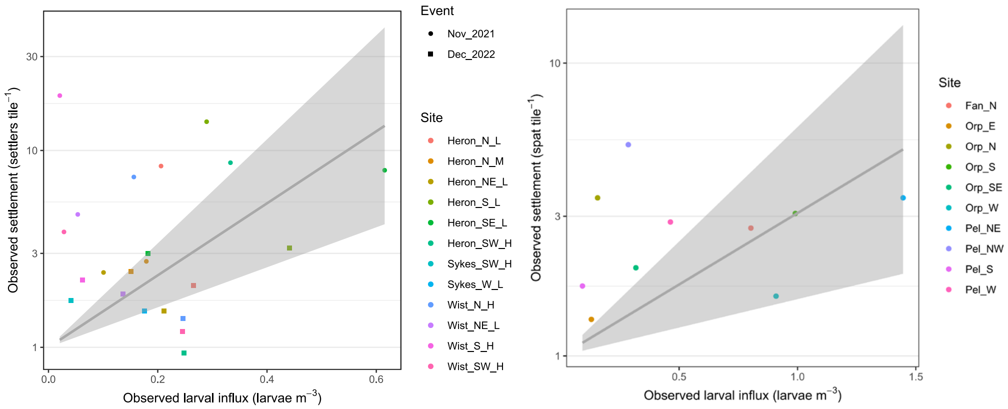


Figure 3: Significant relationships between larval influx and larval settlement at (left) Capricorn-Bunker reefs ($p < 0.001$, $R^2 = 0.26$) in the southern offshore GBR (Mason et al. Under Review) and (right) Palm Islands reefs ($p < 0.001$, $R^2 = 0.39$) in the central inshore GBR (Mason et al. In Prep).

Novel methods were developed to identify and quantify coral larvae from plankton tow samples using molecular techniques. Larval quantification standards were developed using samples with known numbers of larvae from *Acropora spathulata*, *Acropora hyacinthus*, and *Platygyra daedalea* allowing rapid, taxon-specific quantification of coral larvae from controlled rearing conditions. Validation samples with varied larval counts and ages were collected to test the model's accuracy and precision in simple larval samples. Plankton tow samples were spiked with known larval counts to evaluate model performance in complex, environmentally representative conditions (Figure 4). Overall, using quantitative polymerase chain reaction (qPCR) as a tool for both relative and absolute quantification of coral larvae is feasible, with potential applications for monitoring recruitment at fine temporal and spatial scales.

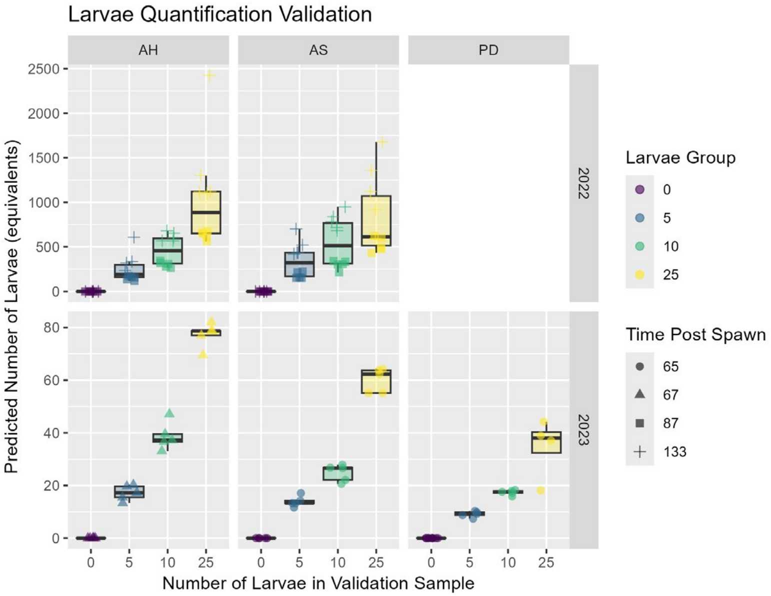
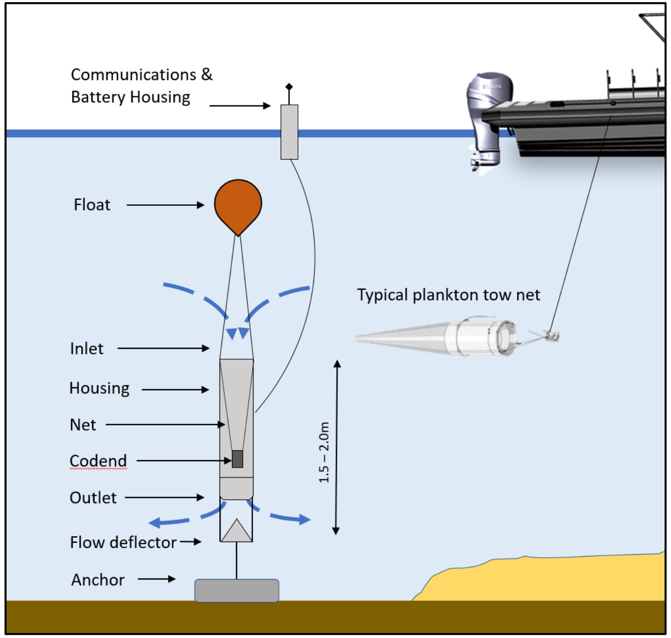
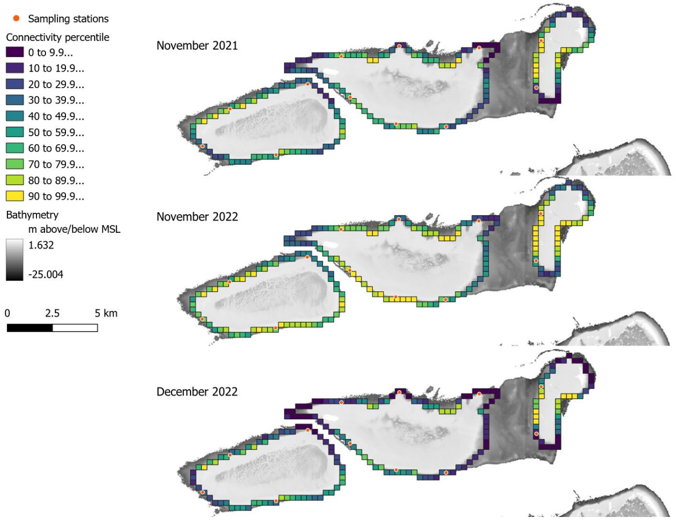


Figure 4: Predicted larvae equivalents from validation samples containing a known number of larvae (Craw et al. In Prep).

Collecting data on coral larvae supply is limited in time and space by sampling. We developed the SaLP (Sampler of Larvae and Plankton) autosampler (Figure 5), a prototype system that automates larval collection using a reef-anchored mooring to filter and concentrate samples for lab analysis. By enabling frequent, high-resolution sampling, the SaLP—combined with molecular identification techniques—offers a promising tool for advancing coral reef research, monitoring, and restoration efforts. Field testing showed that the SaLP system successfully met key performance goals, proving it can efficiently collect multiple water samples within power and time limits. Stratified sampling of larvae conducted over tidal cycles, using traditional plankton tows, showed that differences in larval influx between sites were generally still detectable even when sites were sampled at different times. However, occasionally time of day did affect larval abundance. The SaLP may provide a means to address this issue.

		 *Figure 5: A schematic diagram of the SaLP sampler (left) and a typical plankton net tow (right) (Moscatt et al. 2024).*
1 (b)	Identify where and when enhancement of larval supply is warranted	Enhancement of larval supply is warranted in areas and times where natural larval input is consistently low or highly variable, particularly when such limitations may constrain reef recovery or resilience. Model results indicate that certain reef sectors, such as the northern edge of Heron Reef and the south-west quadrant of Wistari Reef, consistently receive lower larval supply, suggesting these may benefit from targeted larval enhancement (Figure 6). Temporal variation also plays a role: observed and modelled data indicate that larval settlement was lowest following the December 2022 spawning event, likely due to reduced inter-reef connectivity and the effects of split spawning. Thus, enhancement efforts may be most beneficial in these lower-supply areas and during spawning periods characterised by reduced connectivity or larval output.

		 *Figure 6: Relative connectivity around the perimeters of Heron, Wistari and Sykes Reefs (Mason et al. Under Review).*
1 (c)	Validate connectivity modelling so that restoration strategies are well informed	Coral dispersal was measured and modelled using high intensity spatial and temporal sampling of coral larvae and high resolution hydrodynamical models in the inshore Palm Island reefs (2022) (Mason et al. In prep) and offshore Capricorn Group reefs (2021-2023) (Mason et al. Under Review). In general, the modelled larval fluxes and settlement could not be reconciled with the observational datasets at the scale important for restoration, i.e. 10’s m to 100’s m. The modelled predictions of larval supply were not correlated with observational datasets. While observations of larval settlement were correlated with predictions for the Capricorn Bunkers ($p = 0.03$, $R^2 = 0.11$), they were highly variable (Figure 7). Predicted versus observed patterns of larval settlement were not correlated for the Palm Islands. In the case of larval abundance, natural stochasticity may have introduced an additional confounding effect, however, coral settlement provided a signal for model validation that was independent of this issue. This suggests that additional ecological and biophysical parameters are affecting the predictive ability of the particle modelling at the fine scale of spatial resolution being tested (<1 km^2). The underlying hydrodynamic models correlated well with *in situ* instrumentation of sea level and currents, when instruments were deployed in areas of relatively simple reef morphology and measured general wind-driven and tidal-driven circulation around the reefs. However, closer to reef areas of high morphological complexity such as near channels and small passages, the correlation degraded, sometimes drastically. While using ~100m resolution hydrodynamical models, the effective modelled resolution was found to be closer to ~1km. For example, at Heron, Wistari and Sykes Reefs, the hydrodynamical model can discriminate between regions of high and low larval supply, but these regions cover around 10 model grid cells (Figure 6). This suggests that the effective modelled resolution needs to get closer to ~100 m to be able to directly compare with high intensity spatial and temporal sampling.

<table>
<tr><td></td><td></td><td>Importantly, while many studies have applied connectivity modelling to inform marine spatial conservation planning, these remain untested and should be validated alongside operationalisation to improve on the efficacy of zoning. Similarly, while it has been proposed that connectivity be incorporated for restoration activities, the scale of restoration activities are typically 10-100s of metres and therefore caution needs to be applied to the use of such high-resolution models for decision making until they are adequately validated.

Model validation may benefit from developing a quantitative framework to guide the design of future connectivity validation attempts. This framework should unite the spatial scale, temporal scale and location-specific aspects of hydrodynamic model error, propagule variability, and the error tolerance of the connectivity end use.

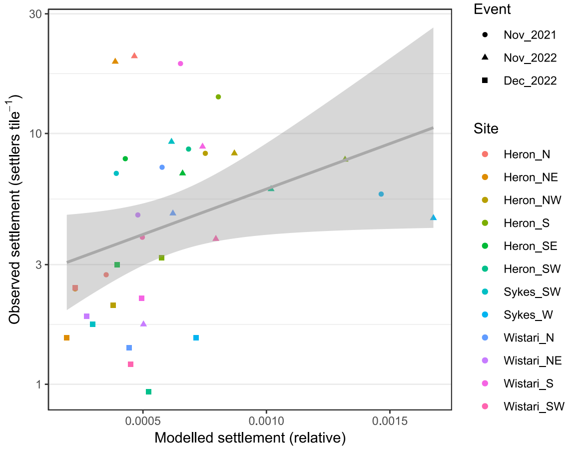


Figure 7: Observed versus modelled coral settlement over all three spawning events in the Capricorn-Bunker reefs. The line is the linear regression, for which $R^2 = 0.11$*, and the grey area is the 95% CI (Mason et al. Under Review).*</td></tr>
<tr><td colspan="3">**2. Quantifying the drivers of coral mortality following recruitment or transplantation to the reef**</td></tr>
<tr><td>2 (a)</td><td>Provide guidance on the size, density and species of coral juveniles that are likely to survive in different reef environments</td><td>Larger juvenile corals have a better chance of survival across most reef environments, with survival increasing steadily as size increases (Figure 8). Any coral greater than 10 mm in diameter has a 50% change of yearly survival. However, survival rates also depend on the coral species and location, with some reefs showing different patterns—like the Palm and Keppel Islands, where increasing size had no or even negative influence. Water temperature also plays a key role, with different species responding in different ways: some, like *Acropora*, survive better in cooler southern reefs, while others, like massive *Porites* and submassive Merulindae, do better in warmer northern reefs. These findings suggest that successful coral restoration depends on choosing the right coral species, size, and location to match local conditions.</td></tr>
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		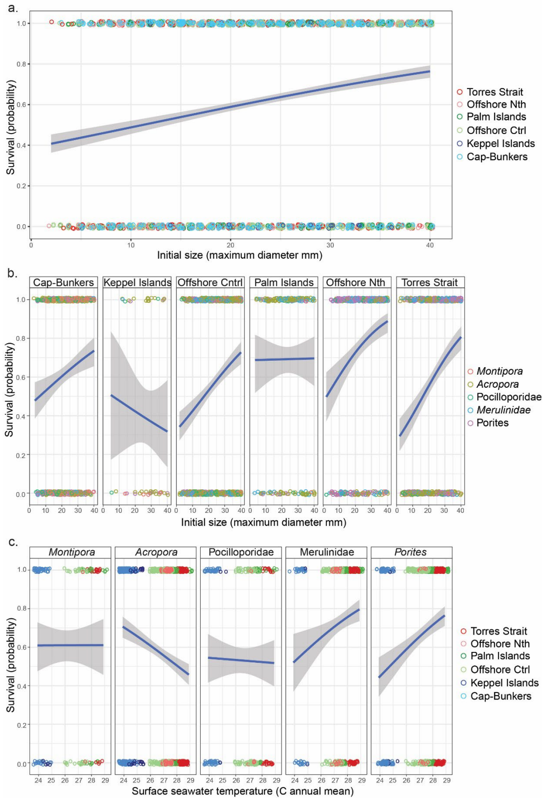 *Figure 8: Annual survival probabilities of juvenile corals as a function of (a) initial coral colony size, (b) initial size across reef clusters, and (c) seawater temperature for each major taxon across the reef clusters (Doropoulos et al. In Prep).*
2 (b)	Determine the criteria of site selection for macro- and micro-habitat restoration	While juvenile coral survival and growth vary with species, size, and environmental factors like sediment and water flow, some patterns—such as the positive influence of water flow and coral size—are consistent across the Great Barrier Reef and Torres Strait. Cooler offshore sites favour *Acropora* recruitment, while *Porites* thrive in warmer offshore areas. Survival isn't strongly affected by temperature overall, but responses varied by species. Predation on out planted juvenile size coral fragments is lower in areas with higher existing coral cover (Figure 9), and bleaching of juvenile sized coral fragments is higher as size increases. These insights can guide restoration efforts by helping practitioners select suitable sites based on factors like species preferences, water conditions, and existing coral density.

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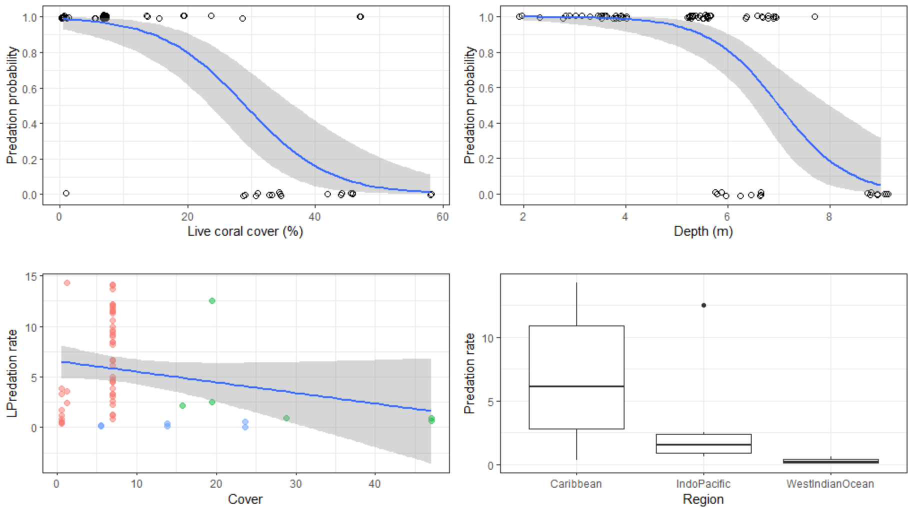

Figure 9: Relationship between predation probability with live coral cover and depth, and predation rate with live coral cover in different regions (Rowell 2025).
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<td>2 (c)</td>
<td>Identify sites that match criteria for restoration and recovery and where reefs would remain dependent on restored corals</td>
<td>
Coral recruitment and survival patterns varied widely across different reef areas and coral types (Figure 10). Some reef sites, like the Capricorn-Bunker and Offshore Central reefs, had strong natural recovery potential—especially for *Acropora* corals, which are often targeted for restoration—because they showed both high recruitment (lots of new corals settling in) and relatively high turnover (net coral gains).

However, these same areas also had high coral mortality, particularly for *Acropora*, meaning that even though new corals arrive, many don’t survive long term. This suggests that while these reefs are good candidates for restoration, they are also likely to remain dependent on continued support (e.g. coral planting or habitat management) to maintain healthy populations.

On the other hand, reefs like the Offshore Northern cluster had lower coral death rates and some strong natural gains, especially for *Porites* corals. These areas may be better suited to recovery without as much long-term intervention.

Environmental stressors like high temperatures, sediment, and turf algae (small, weedy plants on the reef) had clear impacts. *Acropora* corals were particularly sensitive to these conditions, while other coral types were more resilient.

In short, some reefs show promise for recovery but would likely still rely on ongoing restoration efforts, especially where sensitive corals like *Acropora* are dominant and stress levels are high.
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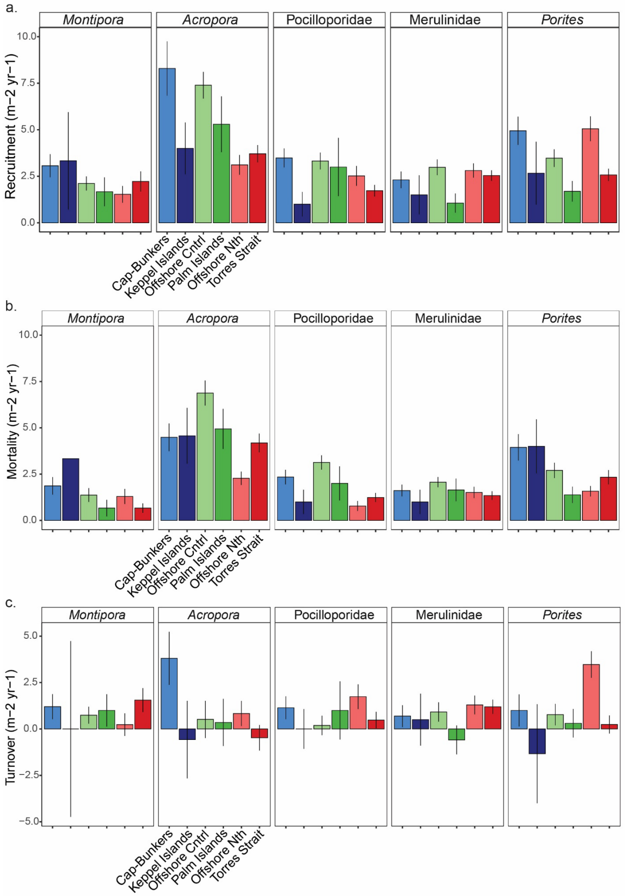
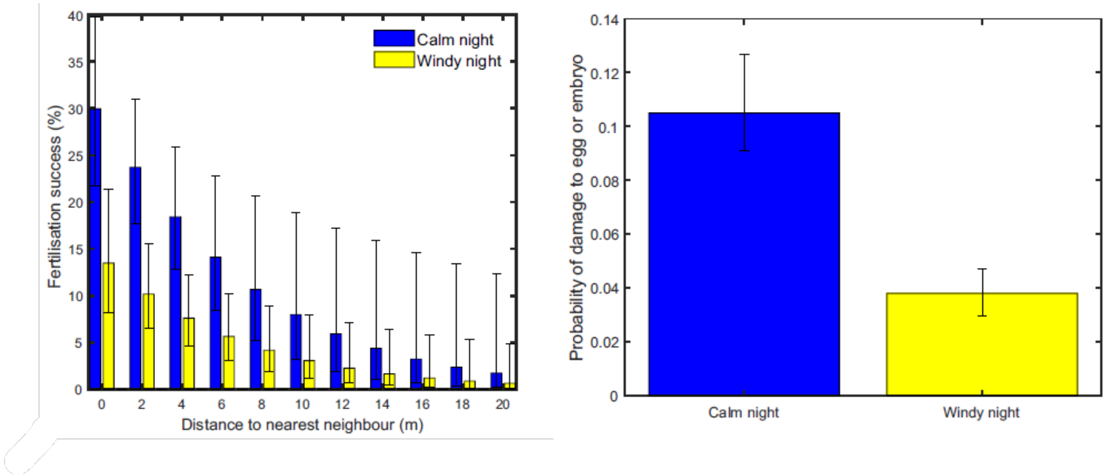
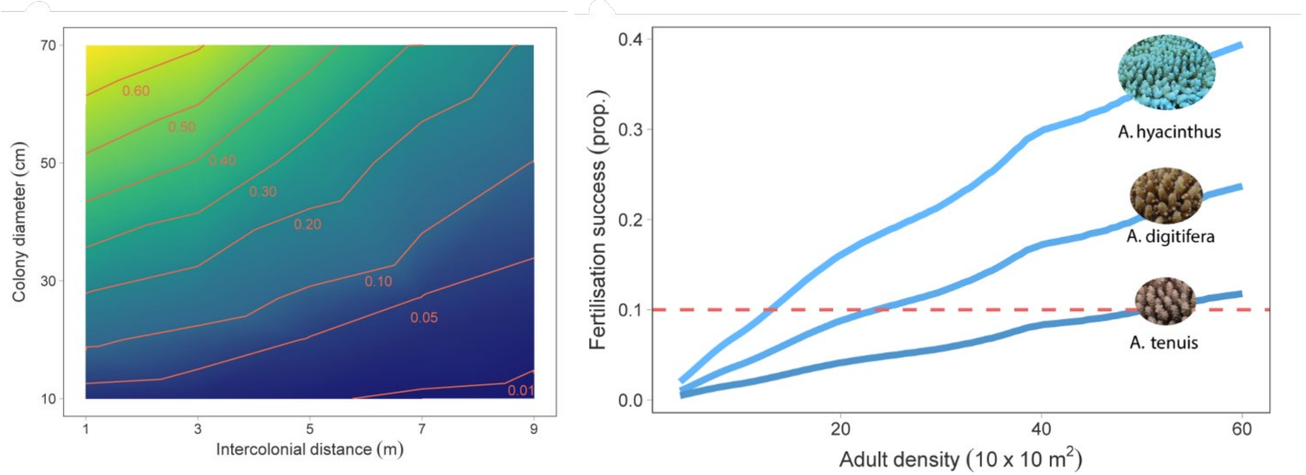
		 *Figure 10: Annual mean (a) recruitment, (b) mortality, and (c) turnover rates of juvenile corals for each major taxa across the GBR and Torres Strait (Doropoulos et al. In Prep).*
3. Quantifying the adult coral size-density thresholds needed to overcome reproduction bottlenecks and promote recovery		
3 (a)	Characterise the critical densities of corals needed for effective local reproduction	Our goal was to characterise how close coral colonies need to be to one another to successfully reproduce. This matters because climate change is reducing coral populations and spreading them out, making it harder for their eggs and sperm to meet during spawning events. This can cause what is known as an "Allee effect," where reproduction fails because individuals are too far apart. In our research, we studied a common table coral species (*Acropora hyacinthus*) in Palau, and we also ran field experiments in both Palau and on the Great Barrier Reef using *A. hyacinthus, A. digitifera,* and *A. tenuis*. We found that fertilisation

		worked best when colonies were very close together—within half a meter, fertilisation averaged around 30%. But as the distance increased, fertilisation rates dropped quickly—falling below 10% at 10 meters and nearly zero between 15 and 20 metres (Figure 11). We also discovered that the distance to the nearest reproductive neighbour was a better predictor of fertilisation success than just counting how many corals were nearby. Corals that were closer together also tended to spawn more in sync, which likely boosted their chances of success. On one windy night, even though more corals were spawning, fertilisation dropped significantly—showing how weather conditions can also play a big role (Figure 11).  *Figure 11: Effect of distance (left) and wind (right) on fertilisation of A. hyacinthus in a natural population (Mumby et al. 2024).* These findings highlight how important it is to not only preserve coral numbers but also to keep colonies close enough together. For restoration projects, this means planning carefully to ensure that coral colonies are spaced within 10 meters of each other to support natural reproduction and long-term reef recovery.
3 (b)	Identify the minimum target coral density that stimulates faster natural recovery	We set out to determine the minimum coral density needed for reefs to recover naturally. Through field experiments and modelling, we found that coral populations need to exceed 13 to 50 colonies per 100 square meters to maintain basic reproductive function (Figure 12). The different threshold densities of corals are related to different species of *Acropora* – with the plating larger *A. hyacinthus* needing less corals for fertilisation, compared to the smaller-sized digitate *A. digitifera,* and then the corymbose *A. tenuis* (Figure 12). Below these thresholds, fertilisation rates drop sharply, especially when colonies are spaced more than 10 to 15 meters apart.

		 *Figure 12: Relationships between (left) colony distance and colony size with fertilisation success and (right) patch (10 × 10 m) density characteristics and fertilisation success of A. hyacinthus, A. digitifera, and A. tenuis (Ricardo et al. 2024).* These results show that both coral density and spacing are critical. At low densities, colonies become reproductively isolated, and recovery slows or stalls. To support natural recovery, restoration efforts should aim to re-establish coral populations within this minimum density range, with colonies placed close enough to ensure successful fertilisation.
3 (c)	Provide criteria of when coral density is too low or sufficiently high for site selection.	Based on our findings, we recommend the following criteria for assessing whether a site has a coral density that supports natural recovery: • **Too Low** Sites with fewer than 13 adult colonies per 100 square meters are considered too sparse. At this density, **fertilisation** success is extremely limited due to reduced chances of gamete encounters, especially if colonies are spaced more than 10–15 meters apart. • **Sufficiently High** Sites with at least 50 colonies per 100 square meters offer a much better chance for natural recovery, particularly if most colonies are within 4–10 meters of each other. At these densities and distances, fertilisation success is significantly improved. • Cluster corals in **groups of ≥25 colonies** rather than evenly spaced individuals A maximum recommended spacing should be five metres between colonies, though higher densities can deliver greater fertilisation success. For site selection, we recommend prioritising areas that either already meet these density thresholds or have the potential to be restored to these levels through strategic coral planting or translocation.

Adjustments to key research objectives

Table 2: Variation in the Project over time.

Initial Research Question	Explain when, how and why the research question changed
No adjustments to report	

4 Future Research Recommendations

To optimise coral reef restoration and ensure the long-term persistence of coral populations, future research must address significant gaps in our understanding of the coral life cycle, particularly regarding early life-history processes, connectivity, and reproductive thresholds. A primary focus should be on refining our empirical understanding of the **relationships between fecundity, larval production,** and the **link between larval supply, settlement, and juvenile survival**. These relationships vary across biological and environmental gradients. Quantifying them in different reef states will improve our predictive capacity for restoration success and intervention strategies.

One of the most pressing areas for future research is determining the **realised self-retention** of coral larvae, as this factor directly influences the **efficacy of restoration efforts** and the recovery of degraded reefs. Repeated sampling at key reef sites will be essential for validating models of larval dispersal and connectivity. By integrating molecular identification methods with *in situ* oceanographic instrumentation, researchers can track the movement and survival of larvae, providing critical data for enhancing restoration techniques. These studies will help refine spatially explicit strategies for larval enhancement, ensuring that interventions target the most effective locations and conditions for coral recruitment. Current models of larval dispersal and settlement across the GBR have demonstrated mismatches between predicted and observed settlement patterns, underscoring the need for a robust, quantitative framework to validate and calibrate these models. This includes accounting for spatial and temporal scales, biological variability, and model error tolerance.

Research should prioritise identifying the proportion of a reef that is **functionally reproductive**, particularly across species with varying reproductive strategies. Factors such as aggregation, sperm competition, and nearest-neighbour distances influence fertilisation success, especially for rare or non-Acropora corals. These dynamics must be studied within the context of reef patch structure and spatial heterogeneity. Tools like EcoRRAP orthomosaics can map coral colonies on the GBR, helping optimise restoration by balancing fertilisation success and genetic diversity. Empirical studies also need to assess how colony fecundity, larval output, and reef conditions—affected by health, age, and stressors like bleaching—impact reproductive success. This information will guide the selection of colonies for transplantation and improve predictions of recruitment under changing conditions. Recent findings from March–April 2025 underscore the role of local oceanography in larval retention and reproductive thresholds. In Palau, two spawning failures occurred where gametes were lost to deep water due to tidal flows, preventing fertilisation. In contrast, high fertilisation was observed where gametes remained over shallow areas. **Identifying sites that are located in areas with a high probability of achieving successful fertilisation** is now an emerging priority.

In addition to refining the understanding of fecundity, future research should continue to build on existing demographic data to establish more precise **survival thresholds for juvenile corals following stress**. These thresholds, based on factors such as size, density, species, and local habitat features, are crucial for developing outplanting guidelines that maximise juvenile survival and growth. Understanding how juvenile corals respond to environmental stressors and disturbances at different stages of development will be instrumental for planning effective restoration efforts that consider both ecological and socio-economic factors. Linking these demographic insights to **broader tourism and stakeholder planning** will further support adaptive, location-specific management strategies.

Ultimately, future research must focus on defining the critical adult coral densities and spatial configurations required to surpass Allee thresholds—conditions under which coral populations can experience positive growth despite environmental challenges. Identifying species-specific fertilisation curves and recovery thresholds, while accounting for key abiotic factors such as temperature and ocean currents, will **empower restoration practitioners to maximise natural recovery and enhance reproductive success in restored populations**. By addressing these foundational knowledge gaps, we can better ensure the success of coral reef restoration efforts, improving the resilience and sustainability of these critical ecosystems for future generations.

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