Exploring the Role of Novel Coral Nursery Infrastructure as Fish Habitat on the Great Barrier Reef

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PhD by Research

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Certificate of Original Authorship

I, **Gemma M Gillette**, declare that this thesis is submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the Faculty of Science at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise referenced or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

This research was supported by the Australian Government Research Training Program and funding to Coral Nurture Program.

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Table of Contents

Certificate of Original Authorship i

Table of Contents ii

Thesis Acknowledgements iv

Thesis Abstract v

Thesis Structure vii

List of Figures viii

List of Supplementary Figures x

List of Tables xiii

List of Supplementary Tables xiii

Chapter 1: General introduction and thesis outline 1

1.1 The future of reef ecosystems under anthropogenic pressures 1

1.2 Reef protection and management 2

1.3 Coral reef restoration approaches 3

1.4 Thesis aims and hypotheses 9

1.5 References 13

Chapter 2: Variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef 25

2.1 Abstract 27

2.2 Introduction 27

2.3 Methods 29

2.4 Results 32

2.5 Discussion 36

2.6 Conclusion 39

2.7 Acknowledgements 40

2.8 References 40

2.9 Supplementary materials 50

Chapter 3: Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef. 57

3.1 Abstract 59

3.2 Introduction 59

3.3 Methods 61

3.4 Results and Discussion 66

3.5 Conclusion 76
3.6 Acknowledgements..77
3.7 References..77
3.8 Supplementary materials..87
Chapter 4: Early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef 98
4.1 Abstract..100
4.2 Introduction..100
4.3 Methods..103
4.4 Results..107
4.5 Discussion..112
4.6 Conclusion 115
4.7 Acknowledgements..115
4.8 References..116
4.9 Supplementary material 124
Chapter 5: General discussion and future directions 140
5.7 References..154

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Thesis Abstract

Adoption of coral propagation and out-planting for restoration-based management has accelerated over the past two decades to foster the resilience of degraded coral reef sites that are of high socio-economic and ecological value. A prerequisite for many stakeholder-led in-water reef restoration projects is the establishment of coral nurseries that can supply large numbers of corals of a size that can be fragmented or out-planted whole. While researchers and restoration practitioners have demonstrated the feasibility of using nurseries to enhance coral growth and biomass generation ("yields"), associated ecological interactions when operating coral nurseries, including the effect on fish assemblages, have been rarely considered. Fish are critical components of ecological reef resilience, contributing to the maintenance of coral-dominated reefs and providing critical ecosystem service values in alignment with restoration goals. Yet – despite the now 1000s of coral nurseries likely in operation worldwide, how they support reef fish assemblages remains almost entirely unknown. This thesis addresses this fundamental knowledge gap – examining fish assemblage interactions with coral nurseries used for coral propagation to in turn provide feasible monitoring techniques for fish-integrated coral propagation techniques.

The aims of this thesis were examined through the Coral Nurture Program, a collaborative tourism industry-research partnership using nursery-based coral prorogation techniques at high-value tourism sites on Australia's Great Barrier Reef (GBR). During my first investigation, I explored the capacity of mid-water coral nurseries used by the Coral Nurture Program, consisting of various coral assemblages, to provide habitat to local fish assemblages. Coral propagation methods and workflows within the Coral Nurture Program have been adapted for integration into daily tourism trips, to increase stakeholder engagement and reduce operating costs. The ability to monitor broader ecological metrics can exceed the capacity of many restoration programs, especially those uniquely challenged by resourcing and time constraints. As such, a rapid fish monitoring method (< 15 min surveys) was developed to capture 74% of the fish assemblage data (55% of fish functional group data) obtained in 1 hr static video survey on coral nurseries. Collectively, these video surveys illustrated for the first time on the GBR that coral nurseries can host a diverse fish assemblage of over 2,333 fish from 24 different families, suggestive of a broader ecological impact of nursery-based coral prorogation than had previously been accounted for.

In my second investigation, I explored the effect of excluding fish assemblages on coral nursery benthic composition at restoration sites on the northern GBR; specifically, to evaluate the nature and extent to which exclusion promoted non-coral organisms that otherwise impact the effectiveness of nursery-based coral propagation. Settlement substrates and fragments of *Acropora* coral species were placed inside cage-exclusion treatments on mid-water coral nurseries for 112 days and data was supplemented with similar rapid video assessments to capture fish interactions. This investigation revealed an average fourfold increase in the biomass of filamentous turf fouling within areas where fishes were excluded access, thus building upon the first investigation to highlight a bidirectional benefit for fish-integrated coral propagation.

In my final investigation, I evaluated the development of fish assemblages in early-phase Coral Nurture Program-based coral propagation, via fixed-table nurseries deployed across three central GBR restoration sites. Fish assemblage metrics (abundance, richness, diversity and biomass), fish species composition and benthic arrangement (coral stock and recruitment of other benthic taxa) on nurseries were evaluated using video surveys at 3 time points across the first year of deployment. Fish assemblage composition on nurseries was observed to develop over time alongside an evolving benthic composition (via turnover of nursery stock). This outcome suggested that, as for natural reefs, a complex interplay exists between substrate, time, and species composition to influence fish community development.

Collectively, my findings illustrate how nurseries used for coral restoration can act to both grow coral biomass and serve as additional fish habitat, thus accruing multiple service benefits. In doing so, this thesis delivered new insights into how stakeholder-led restoration programs need to consider fish assemblage knowledge in restoration program activity – even where the focus may involve coral propagation metrics. I highlight the importance of fish interactions that can enhance coral restoration techniques and propose recommendations to guide future research, implementation, and stakeholder decision-making for a fish-integrated coral restoration approach to reef restoration. My work has demonstrated that as a greater understanding of the interactions between reef restoration and fishes is gained, and as fish-focused research is integrated into the core of restoration efforts, the full potential of coral nurseries as important restoration tools can be realised.

Thesis Structure

This thesis is comprised of an introductory chapter (**Chapter 1**), three data chapters (**Chapters 2** to **4**) in the form of journal manuscripts for peer-review, and a synthesis chapter (**Chapter 5**). At the time of this thesis submission, one data chapter (**Chapter 2**) was under review, while the other data chapters were in preparation for submission (**Chapter 3** and **4**).

Chapter 1: General introduction of background literature.

Chapter 2: This chapter is currently under peer review.
Gillette, G.M., Camp, E.F., Edmondson, J., Booth, D.J., Roper, C., Howlett, L., Woodcock, S., Suggett, D.J. Variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef. *Marine Ecology Progress Series*. *

Chapter 3: This chapter is presented as a fully drafted article formatted for submission to a peer-reviewed journal following thesis submission.
Gillette, G.M., Camp, E.F., Edmondson, J., Booth, D.J., Scott, R.I, Suggett, D.J. Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef. *

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Gillette, G.M., Camp, E.F., Edmondson, J., Booth, D.J., Woodcock, S., Roper, C., Howlett, L., Strudwick, P., Scott, R.I., Hayward, C., Suggett, D.J. Early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef. *

Chapter 5: General discussion, synthesis of results from all data chapters and recommendations for future research and/or restoration practice.

* Please see title pages for Chapter 2 to 4 for signed authorship declarations.

List of Figures

Chapter 1: General introduction and thesis outline

Figure 1.1. The coral propagation method (A). Firstly, practitioners collect coral material either from donor colonies or as a "coral of opportunity", secondly coral fragments are either directly out-planted (secured to consolidated substrate) or are temporarily attached to nursery structures for growth prior to eventual harvesting of nursery grown fragments for subsequent out-planting. Over time the out-planted coral will attach to the substrate. Also shown are commonly used coral nursery designs including fixed net nurseries used by the Gates Coral Lab (B), floating tree nurseries used by Reef Renewal Bonaire (C), fixed line nurseries used by the Coral Gardeners (D), and mid-water floating nurseries used by the Coral Nurture Program (E). Image credits (from left to right): Shayle Matsuda, Lorenzo Mittiga, Coral Gardeners and John Edmonson. 6

Figure 1. 2. The three aims addressed in this thesis are (***1***) to evaluate the variation in fish community composition across coral nurseries stocked for reef restoration (northern Great Barrier Reef), (***2***) To quantify the natural maintenance of fouling on coral nurseries (northern Great Barrier Reef), (***3***) to track the early phase development of reef fish assemblages on coral propagation nurseries (central Great Barrier Reef). 10

Chapter 2: Variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef

Figure 2.1. Location of survey sites within the (A) country, (B) region and (C-F) reef. Reefs include (C) Mackay (-16.047, 145.645), (D) Opal (-16.216, 145.898), (E) Hastings (-16.520, 146.010) and (F) Upolu (-16.673, 145.935), situated on the northern Great Barrier Reef, Australia. Map images © Google 2023 and © Allen Coral Atlas 2023..30

Figure 2.2. Average percentage cumulation curves for fish assemblages observed on 3 coral nurseries (N1, N2, N3) as well as a total average (All) at "Mojo" mooring, Opal Reef, northern Great Barrier Reef. Data was collected using long-form video surveys at 3 time points (n = 3 surveys per nursery; n = 9 total). Cumulation at 9 min is displayed as a dashed line and a percentage on each graph. Shading represents the standard error for each percentage cumulation curve..34

Figure 2.3. Weighted (%) fish abundance per family (including *Scarinae*, a sub-family of *Labridae*) on coral nurseries (n = 48 total) located at "Angels" and "Clem Gardens" (Mackay Reef; green), "Blue Lagoon" and "Rayban" (Opal Reef; yellow), "Wonderwall" (Upolu Reef; red) and, "1770" (Hastings Reef; blue). Rapid short video assessments were randomly used to record fish assemblages on nurseries (n = 69 surveys total)...35

Chapter 3: Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef

Figure 3.1. A schematic of the cage exclusion experimental design. Three mid-water coral nurseries were randomly chosen at 2 reef stewardship locations ("Mojo" and "Rayban"; n = 6 total). Each nursery was fitted with cage treatments: full, partial and controls (n = 3 per site, n = 6 total). Coral fragments (~ 5 cm) of *Acropora* were locally harvested from donor colonies on the adjacent natural reefs and placed within each treatment (n = 2 per sp, per treatment; n = 18 per sp, total). Settlement substrates (~30 x 9 cm) of nursery aluminium mesh were also placed within each treatment (n = 1 per treatment; n = 18 total). 63

Figure 3.2. a) Average fouling biomass (g) in full, partial and control treatments at “Mojo” (light blue) and “Rayban” (dark blue) reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 3 per treatment, per site; n = 6 per treatment, total). Bars represent the standard error and differences between treatments, as determined by a non-parametric Scheirer-Ray-Hare test (significant at $p < 0.05$) and are represented by the absence of a common letter. b) Percentage survival of coral fragments at Mojo (solid light blue, *Acropora aff. abrolhosensis*; n = 18) and Rayban (solid dark blue, *Acropora donei*; striped dark blue, *Acropora kenti*; n = 18 per species). Error bars represent standard error. c) An example of before and after comparison images of experimental treatments at a Mojo nursery upon installation (top) and completion (bottom) of the experiment after 112 days. Objects are placed within each image for scale. 68

Figure 3.3. Weighted total fish abundance, biomass (g), and bite rate (number of bites) per species and coloured by family group (with the inclusion of *Scarinae*, a sub-family of *Labridae*) at “Mojo” and “Rayban” reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 9 video surveys per site). Outlines around plots correspond with site (Mojo: light blue; Rayban: dark blue). 71

Chapter 4: Early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef

Figure 4.1. Location of nursery reef stewardship sites in the Whitsundays, Great Barrier Reef, Australia. “Black Island” (-20.08, 148.89), “Blue Pearl Bay” (-20.05, 148.88) and “Luncheon Bay” (-20.06, 148.95) are displayed with their position within the country (A) and region (B-C). Map images © Google 2023 and © Allen Coral Atlas 2023. 104

Figure 4.2. Weighted (%) surface area of benthic cover, coral genus and coral morphology on coral propagation nurseries at “Black Island” (A-C), “Blue Pearl Bay” (D-F) and “Luncheon Bay” (G-I) reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 total). Averages for each nursery are comprised of surveys taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). 109

Figure 4.3. Average fish assemblage metrics (A-D) and fish assemblage metrics per reef stewardship site (E-H) as seen on coral propagation nurseries. Reef stewardship sites were located at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” (n = 3 nurseries per site; n = 9 total) in the Whitsundays, Great Barrier Reef. Fish surveys on nurseries were taken at three time points: T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). The absence of a common letter over the boxplots indicates significant differences in fish metrics across time and site (Aligned Ranks Transformation ANOVA and Tukey HSD post-hoc; $p < 0.050$). The bold line within each boxplot indicates the median and the faint dashed line represents the mean. The standard error for each boxplot is displayed with horizontal lines attached to whiskers. Whiskers extend from the data minimum to the lower quartile and then from the upper quartile to the data maximum. 110

Figure 4.4. Weighted (%) fish total abundance (A-I) and biomass (g) (J-R) (per family, including *Scarinae*, a sub-family of *Labridae*) on coral propagation nurseries at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 per site; n = 9 total; N1, N2, N3). Coral propagation nurseries were surveyed at three time points: T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n=9 surveys per time point; 27 surveys total). 112

Chapter 5: General discussion and future directions

Figure 5.1. High-level findings of the three aims addressed in this thesis (adapted from ***Chapter 1***, *Figure 1.2.*). Studies were conducted within the operational contexts of the Coral Nurture Program in Cairns-Port Douglas (Aim 1, ***Chapter 2***; Aim 2, ***Chapter 3***) and Whitsundays (Aim 3, ***Chapter 4***) on the Great Barrier Reef. 143

Figure 5.2. A proposed (non-exhaustive) decision framework for fish-integrated coral propagation, adapted from reef restoration workflows (Edwards et al., 2010; Goergen et al., 2020; Shaver et al., 2020) and with consideration of thesis findings. 148

List of Supplementary Figures

Chapter 2: Variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef

Figure S2.1. An example of a mid-water coral nurseries used by the Coral Nurture Program on the Great Barrier Reef. Nursery structures consisted aluminium mesh platform (2.0×1.2 m) fastened with rope to two to four 9 kg besser blocks and two 20 L floats. Nurseries are deployed under Great Barrier Reef Marine Park Authority permit G20/43740.1. Photo credit: John Edmonson (A, B) and Gemma M Gillette (C). 50

Figure S2.2. Weighted (%) (A) fish family abundance and (B) benthic taxon surface area on natural reefs at each mooring site: “Angels” and “Clem Gardens” (Mackay Reef), “Blue Lagoon” and “Rayban” (Opal Reef), “Wonderwall” (Upolu Reef) and, “1770” (Hastings Reef). Fish abundance per family (including *Scarinae*, a sub-family of *Labridae*) is an average of 3 x 30 m transects taken at each site in February 2021. Pastel colours represent benthic taxon that is not hard coral. 51

Figure S2.3. Fish video survey setup consisting of a GoPro Hero 8® camera attached to a GoPro® “Jaws: Flex Clamp” clipped onto an adjacent nursery and positioned so cameras would capture the entirety of the subject nursery. Photo credit: Gemma M Gillette. 52

Figure S2.4. Downward-facing images of nursery 1 (A), nursery 2 (B) and nursery 3 (C) located at “Mojo” tourism mooring site, Opal Reef, Great Barrier Reef. Photo credit: Gemma M Gillette. 52

Figure S2.5. Coral and fish assemblage composition on coral nurseries used for restoration at “Mojo” mooring, Opal Reef (n = 3 nurseries; N1, N2, N3). Fishes were recorded using long-form (1 hr) video surveys at 3 timepoints (n = 3 per nursery; n = 9 total). Boxplots show (A) fish abundance, (B) fish richness, and (C) fish diversity. Coral composition for each nursery (D) was documented at the time of fish survey (27th February – 2nd March 2023). The absence of common letter over of the boxplots shows significant differences between clusters (ANOVA and Tukey HSD post-hoc; $p < 0.050$). The bold line within each boxplot indicates the median and the faint dashed line the mean. Standard error is displayed with horizontal lines attached to whiskers. Whiskers extend from the data minimum to the lower quartile and then from the upper quartile to the data maximum. 53

Figure S2.6. Weighted (%) surface area of benthic composition including (A-F) coral cover, (G-L) coral morphology and (M-R) benthic taxon (coral identified to genus) on coral nurseries (n = 48 total) at tourism mooring restoration sites. Horizonal bars colour mooring sites per Reef: “Angels” and “Clem Gardens” (Mackay Reef; green), “Blue Lagoon” and “Rayban” (Opal Reef; yellow), “Wonderwall” (Upolu Reef; red) and “1770” (Hastings Reef; blue). Rapid video surveys were used at random on nurseries to record fish assemblages (n = 69 surveys total). 54

Chapter 3: Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef

Figure S3.1. Location of sites on Opal Reef, northern Great Barrier Reef (Australia), reef stewardship sites “Mojo” (16°12'23.6"S 145°53'53.7"E) and “Rayban” (16˚13’27"S 145˚53’22"E) in relation to their location within the country (a) and region (b-c). Map images © Google 2023 and © Allen Coral Atlas 2023. 87

Figure S3.2. Example of a coral propagation nursery managed by a Coral Nurture Program tourism partner at “Mojo” reef stewardship site, Opal Reef, northern Great Barrier Reef. Nursery consisted of a 2.0 × 1.2 m aluminium diamond-mesh attached using rope to 2, 9 kg besser blocks, and 2, 20 L floats. All Coral Nurture Program nurseries were deployed under GBRMPA permits G18/40023.1 and G20/43740.1. Photo credit: Gemma M Gillette. 88

Figure S3.3. *Acropora donei* and *Acropora kenti* colonies growing on a coral nursery deployed at “Blue Lagoon” reef stewardship site Opal Reef, northern Great Barrier Reef. Photo credit: Paige Strudwick. 88

Figure S3.4. a) A GoPro Hero 8® camera attached to a GoPro® “Jaws: Flex Clamp” and mounted onto a nursery buoy in preparation for fish video surveys. b) Fish video survey point of view. Treatment control area outlined in pink. Images taken at reef stewardship sites on Opal Reef, northern Great Barrier Reef. Photo credit: Gemma M Gillette. 89

Figure S3.5. Average fish abundance, biomass (g), and bite rate (number of bites) per species and coloured by family group (with the inclusion of *Scarinae*, a sub-family of *Labridae*) at “Mojo” and “Rayban” reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 9 video surveys per site). Error bars represent the standard error. 90

Figure S3.6. Coral nurseries approximately 18 hrs after the removal of full, partial and control cage treatments (a-c) at “Mojo” reef stewardship site, Opal Reef, northern Great Barrier Reef. Images in the top right corner depict the full cage areas at the time of cage removal, approximately 18 hrs earlier. Images Photo credit: Gemma M Gillette. 91

Chapter 4: Early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef

Figure S4.1. Deployment of coral propagation nurseries across reef stewardship sites in the Whitsundays, Great Barrier Reef. Nurseries consist of 1900 x 950 cm diamond aluminium mesh, fastened to two parallel 85 x 85 cm stainless steel frames using stainless steel wire. Stainless steel frames are 50 cm above the substrate and the legs are supported by steel rebar attached to frames using stainless steel wire and hammered into the sand. Nurseries are deployed under Great Barrier Reef Marine Park Authority permit G22/46543-1 Photo credit: Gemma M Gillette. 125

Figure S4.2. Coral propagation nurseries across reef stewardship sites in the Whitsundays, Great Barrier Reef, stocked with coral colonies at the time of deployment (A), six months (B) and 11-12 months post-deployment (C). Nurseries are deployed under Great Barrier Reef Marine Park Authority permit G22/46543-1 Photo credit: Gemma M Gillette and Cass Hayward. 125

Figure S4.3. Fish video survey setup consisting of a GoPro Hero 8® camera attached to a GoPro® "Jaws: Flex Clamp" and clipped onto 180 cm star pickets hammered into sand substrate 2 m from the edge of coral propagation nurseries, deployed across reef stewardship sites in the Whitsundays, Great Barrier Reef. Photo credit: Cass Hayward. 126

Figure S4.4. Weighted (%) surface area of coral genus (A-I) and coral morphology (J-R) per coral nursery (n = 3 per site; n = 9 total; N1, N2, N3) at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef. Coral propagation nurseries were surveyed at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). 127

Figure S4.5. Weighted (%) surface area benthic composition on coral nurseries (n = 3 per site; n = 9 total; N1, N2, N3) at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef. Benthic composition on nurseries was surveyed at T1 (A-C; 1-day post-deployment), T2 (D-F; 186-191 days post-deployment) and T3 (G-I; 340-370 days post-deployment) (n = 9 surveys per time point; 27 surveys total). 128

Figure S4.6. Weighted (%) fish abundance per fish family group (including *Scarinae*, a sub-family of *Labridae*) on natural reefs at (A) "Black Island", (B) "Blue Pearl Bay" and (C) "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef. Fish abundance is an average of 3 x 30 m transects taken at each site. 129

Figure S4.7. Principal components analysis (PCA) of fish assemblage abundance (A) and biomass (B) observed on coral nurseries at three survey time points (colour): T1 (1-day post-deployment), T2 (186-191 days post-deployment) and T3 (340-370 days post-deployment) (n = 27 surveys total). Nurseries were deployed across reef stewardship sites (shapes) located in the Whitsundays, Great Barrier Reef (n = 3 per site, n = 9 total). Ellipses show 90% confidence intervals. The five fish families that contributed the most to PCA loadings were included as loading vectors. PCA loading vectors were scaled to PCA eigenvalues. Vector direction shows the relative contribution of each fish family to the principal components and vector length indicates the strength of this contribution. Fish assemblage abundance (A) PC1 explained 42.8% of the total variance in the abundance of fish family groups, with *Labridae* (49.90%), *Scarinae* (17.60%), *Chaetodontidae* (8.30%), *Pomacentridae* (6.60%) and *Apogonidae* (5.90%) contributing the most to this vector (*Data S6*; *Figure 5A*). An additional 19.6% of the variance in family group abundance was accounted for by PC2, with *Apogonidae* (83.50%) contributing the most to this vector followed by *Labridae* (3.60%) and *Siganidae* (3.50%). The abundance per family along PC1 differed between T1 and T2 (Tukey $p < 0.000$) as well as T1 and T3 (Tukey $p < 0.000$) but did not differ along PC2. Fish assemblage biomass (B) PC1 explained 72.8% of the total variance in biomass between family groups, with *Scarinae* (69.30%) and *Acanthuridae* (27.90%) contributing to this vector. A further 15.8% of the variance in fish family biomass was accounted for by PC2, with Acanthuridae (64.20%) and Scarinae (26.50%) contributing the most to this vector. At each time point the biomass of fish families differed greatly for PC1 (Tukey $p = 0.009$) but only T2 differed from T3 for PC2 (Tukey $p = 0.001$). 130

Figure S4.8. Weighted (%) average fish (A) abundance and (B) biomass (per family, including *Scarinae*, a sub-family of *Labridae*) on coral propagation nurseries at "Black Island", "Blue Pearl Bay", and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site). Averages for each nursery are comprised of surveys taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). 131

List of Tables

Chapter 3: Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef

Table 3.1. Species list of fish species observed across nurseries at Rayban and Mojo (n = 3 nurseries per site) reef stewardship sites, Opal Reef, northern Great Barrier Reef. Asterisks denotes species that were observed to bite nurseries....74

Chapter 5: General discussion and future directions

Table 5.1. The overarching per-month cost equation involved in the estimated nursery fouling maintenance cost for the Coral Nurture Program. Terms are broken down in the subsequent rows. All values are per trip. All costs listed are in $AU as published in Scott et al. (2024). 145

Table 5.2. Future critical reef restoration research and practice priorities to advance understanding of fish interactions with nursery-based restoration. 152

List of Supplementary Tables

Chapter 2: Variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef

Table S2.1. A Kruskal-Wallis test to evaluate differences in fish abundance, richness and diversity on coral nurseries (n = 48) between tide types (high, low, ebb or flow). Nurseries were deployed at “Angels” and “Clem Gardens” (Mackay Reef), “Blue Lagoon” and “Rayban” (Opal Reef), “Wonderwall” (Upolu Reef) and, “1770” (Hastings Reef) restoration sites on the northern Great Barrier Reef. Rapid video surveys were used at random on nurseries to record fish assemblages (n = 69 surveys total). Results were considered statistically significant at $p < 0.05$....55

Table S2.2. A Kruskal-Wallis test to evaluate differences in fish abundance, richness and diversity on coral nurseries (n = 48) between reef locations: Mackay Reef (“Angels” and “Clem Gardens”), Opal Reef (“Blue Lagoon” and “Rayban”), Upolu Reef (“Wonderwall”) and Hastings Reef (“1770”) on the northern Great Barrier Reef. Rapid video surveys were used at random on nurseries deployed to record fish assemblages (n = 69 surveys total). Results were considered significant at $p < 0.05$. 55

Table S2.3. Generalised Additive Models (GAM) on the relationship between coral composition (coral cover, richness, and morphological richness) and fish assemblage metrics (abundance, richness and diversity) on coral nurseries (n = 48). Nurseries were deployed at “Angels” and “Clem Gardens” (Mackay Reef), “Blue Lagoon” and “Rayban” (Opal Reef), “Wonderwall” (Upolu Reef) and, “1770” (Hastings Reef) restoration sites on the northern Great Barrier Reef. Rapid video surveys were used at random on nurseries to record fish assemblages (n = 69 surveys total). GAM models applied the zero-inflated Poisson distribution to count data (fish abundance and richness) and the Tweedie distribution to continuous data (fish diversity and biomass). Results were considered significant at $p < 0.05$....55

Chapter 3: Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef

Table S3.1. The percentage difference in average light intensity (lx) recorded using calibrated Hobo loggers within fish cage exclusion treatments was analysed on 1 coral nursery per reef stewardship site. Reef stewardship sites were located at “Mojo” and “Rayban”, Opal Reef, northern Great Barrier Reef (n = 1 Hobo logger per treatment per site, n = 6 total)..............92

Table S3.2. A one-way Kruskal-Wallis test on light (lx) measurements between fish cage exclusion treatments (control, partial and full cage) on coral nurseries and a Dunn post-hoc test using the Bonferroni method for significant results ($p < 0.05$). Light was recorded using calibrated HOBO^{TM} loggers (n = 1 per treatment per site, n = 6 total) on 1 coral nursery per reef stewardship site. Reef stewardship sites were located at “Mojo” and “Rayban”, Opal Reef, northern Great Barrier Reef. 92

Table S3.3. Experimental treatment plots (full, partial and control) fitted with coral fragments (“Mojo”: *Acropora aff. abrolhosensis*; “Rayban”: *Acropora donei*, *Acropora kenti*) and settlement substrates (~30 x 9 cm nursery aluminium diamond-mesh) upon completion of the experiment (week 17). Full cage treatments had their cages removed prior to being photographed. Photo credit: Gemma M Gillette..............93

Table S3.4. Coral cover on survey nurseries as of 8th of June 2022 at “Mojo” and “Rayban” reef stewardship sites, Opal Reef, northern Great Barrier Reef. Contributions of *Acropora* spp. and *Pocillopora* spp. to coral cover are displayed as separate columns. 94

Table S3.5. Sampling times of fish video surveys at “Rayban” and “Mojo” reef stewardship sites, Opal Reef, northern Great Barrier Reef. Tide times at Port Douglas (https://www.msq.qld.gov.au/tides/tide-tables)..............94

Table S3.6. Estimated cumulative fish abundance, richness, and diversity at 17.5 mins of filming, data expressed as a percentage of totals observed at 1 hr of filming, originate from ***Chapter 2***. This data was collected over 1 hr fish video surveys taken across 3 coral nurseries at 3 time points at “Mojo”, Opal Reef, northern Great Barrier Reef. For further information, see ***Chapter 2***..............95

Table S3.7. The average and standard error of fouling (filamentous turf) dry weight (g) on settlement substrates within fish cage exclusion treatments (control, partial, and full cage) (n = 1 settlement substrate per treatment). Treatments were deployed on coral nurseries located at reef stewardship sites “Rayban” and “Mojo”, Opal Reef, northern Great Barrier Reef (n= 1 full, partial and control treatment per nursery; n = 3 nurseries per site, n = 6 total)..............95

Table S3.8. A two-way Scheirer-Ray-Hare extension to the Kruskal-Wallis test to evaluate differences in dry weight fouling (filamentous turf) biomass (g) on settlement substrates within fish cage exclusion treatments (control, partial, and full cage; n = 1 settlement substrate per treatment) and sites (n = 9 settlement substrates per site; n = 18 total). Treatments were deployed on coral nurseries located at reef stewardship sites “Rayban” and “Mojo”, Opal Reef, northern Great Barrier Reef (n = 1 full, partial and control treatment per nursery; n = 3 nurseries per site, n = 6 total). A Dunn post-hoc test employing the Bonferroni method was used to evaluate statistically significant results ($p < 0.05$). A one-way Kruskal-Wallis test was conducted to evaluate differences in dry weight fouling biomass (g) on settlement substrates between nurseries at each stewardship site..............95

Table S3.9. A one-way Kruskal-Wallis test to evaluate differences between in fish abundance and bite rate on coral nurseries (n = 3 per site, n = 6 total) between “Rayban” and “Mojo” reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 3 video surveys per nursery). Fish richness, and biomass on nurseries between stewardship sites satisfied normality (Shapiro Wilk’s Test) and equal variance (Bartlett’s Test) tests, thus were subject to a one-way ANOVA. Results considered statistically significant at $p < 0.05$. 96

Table S3.10. Coral fragment survival at “Rayban” and “Mojo” reef stewardship sites, Opal Reef, northern Great Barrier Reef. Each cage treatment at “Rayban” enclosed 2 fragments of *Acropora donei* and 2 fragments of *Acropora kenti*. At “Mojo”, 2 fragments of *Acropora aff. abrolhosensis* were included in each treatment. Species specific survivorship is reported at “Rayban”, whereby *Acropora donei* survival is a percentage of the total *Acropora donei* planted within that treatment type (full, partial or control). Total survivorship at “Rayban” is the percentage survivorship of all corals within a treatment. 97

Table S3.11. A one-way Kruskal-Wallis test to evaluate differences in coral survivorship between fish cage exclusion treatments (control, partial and full; n = 6 coral fragments per sp, per treatment type) on coral nurseries at reef stewardship sites (n = 18 per sp, per site). Reef stewardship sites (“Rayban” and “Mojo”) were located at, Opal Reef, northern Great Barrier Reef. Results considered statistically significant at $p < 0.05$. 97

Chapter 4: Early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef

Table S4.1. Sampling times of fish video surveys at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef. Tide times recorded at Bugati Reef (https://www.msq.qld.gov.au/tides/tide-tables). 132

Table S4.2. Coral species list on coral propagation nurseries at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site). Coral surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). 133

Table S4.3. The average and standard error of coral cover (%), richness and morphological richness on coral nurseries at three time points: T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). Averages are comprised of coral nurseries located at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total). 134

Table S4.4. A two-way, non-parametric Aligned Ranks Transformation ANOVA to evaluate differences in coral composition (coral cover, richness, and morphological richness) on nurseries between sites and surveys. Sites were located at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total). Surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). A Tukey HSD post-hoc test evaluated statistically significant results ($p < 0.05$). 135

Table S4.5. A two-way, non-parametric Aligned Ranks Transformation ANOVA to evaluate differences in fish abundance on natural reefs between sites. Sites were located at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef. Results were considered statistically significant at $p < 0.05$. 135

Table S4.6. Fish assemblage species list on coral propagation nurseries at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site). Fish surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). 136

Table S4.7. A two-way, non-parametric Aligned Ranks Transformation ANOVA to evaluate differences in fish assemblage metrics (abundance, richness, diversity, and biomass) on nurseries between sites and surveys. Sites were located at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total). Surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). A Tukey HSD post-hoc test evaluated statistically significant results ($p < 0.05$). 137

Table S4.8. A one-way, non-parametric Kruskal-Wallis test to evaluate differences in fish assemblage metrics (abundance, richness, diversity, and biomass) on nurseries at sites between survey time points. Surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). Surveys recorded fish assemblages at sites: “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total). A Dunn post-hoc test evaluated statistically significant results ($p < 0.05$). 138

Chapter 1: General introduction and thesis outline

1.1 The future of reef ecosystems under anthropogenic pressures

A defining feature of the emerging Anthropocene is the escalation of numerous pressures on the world's ecosystems (Hughes et al., 2017; Williams et al., 2019). Centuries of overfishing and pollution have degraded coral reef ecosystems, compounded by the more recent, superimposed impacts of anthropogenic climate change (Gattuso et al., 2015; Hoegh-Guldberg et al., 2017; Hughes et al., 2017). These pressures have now intensified beyond the evolutionary thresholds of coral stress tolerance and recovery (Hughes et al., 2019; Johnson & Watson, 2021; van der Zande et al., 2021) with significant flow on effects to fish community composition, recruitment dynamics and the ecosystem processes they facilitate (Munday et al., 2008; Pörtner, 2008; Clark et al., 2017; Messmer et al., 2017). This presents a new reality where the majority of coral reefs will increasingly reflect human-induced actions rather than being a product of their long-term natural biophysical setting (Williams et al., 2019). These actions will affect the well-being of millions of people that are directly or indirectly linked to reef ecosystem functioning (Woodhead et al., 2019).

Importantly, coral reefs hold significant Indigenous heritage values and locally afford protection against damaging wave action (Heron et al., 2017; Bay et al., 2023). Coral reefs are the primary sources of food, shelter, and settlement substrate for more than one-third of identified global marine species (Fisher et al., 2015), relied on for protein by millions worldwide (Eddy et al., 2021) and establishing an important foundation for the growing blue economy (e.g. Schmidt-Roach et al., 2020; Cziesielski et al., 2021; Fairoz, 2022). However, recent estimates reveal 14% of the world's coral reefs were lost between 2009 to 2018, due to anthropogenic climate change-induced successive and severe bleaching events and have caused up to 95% coral mortality in some areas in the eastern Pacific (Brainard et al., 2018; Vargas-Angel et al., 2019; Souter et al., 2021), including > 30% mortality of the Great Barrier Reef (Hughes et al., 2017). Concerningly, even acute disturbances that result in as little as 10% declines in local coral cover have affected local fish populations (Pratchett et al., 2011). Together fish and coral assemblages underscore a reef site's attractiveness and are an important contributor to high tourist satisfaction ratings (Uyarra et al., 2009; Le et al., 2019). Indeed, coral reef's high economic value is largely driven by the tourism industry which provides employment and income to over 100 jurisdictions worldwide, and in many small-island jurisdictions, it singularly contributes over 10% to the national Gross Domestic Product (Spalding et al., 2017). However, the capacity of coral reefs to sustain these ecosystem service values continues to diminish under intense anthropogenic pressures (Hoegh-Guldberg et al., 2019; Eddy et al., 2021; Voolstra et al., 2023). As a result, reefs require protection measures to sustain their value and provide reef-dependent communities with additional strategies for social-ecological adaptation in response to the changing reef systems (Mumby & Steneck, 2008; Rogers et al., 2015; Hein et al., 2021a; Kleypas et al., 2021).

1.2 Reef protection and management

Prior to the onset of global coral bleaching events, reef management centred on passive "proactive" approaches and localised stressors were addressed through targeted improvement of catchment water quality and the establishment of marine protected areas (MPAs) to curb overfishing practices (e.g. Claudet et al., 2006; Rinkevich, 2008; Lynam et al., 2010). Despite these protection and mitigation measures aimed at reducing synergistic stressors on corals (Suggett & Smith, 2020; Andrello et al., 2022), efforts have proved inadequate against climate pressures, even for reefs considered extremely well managed, such as the Great Barrier Reef (Hughes et al., 2021; Johnson & Watson, 2021). While the future survival of functioning coral reefs is contingent upon the rapid decarbonisation of global economies (Kleypas et al., 2021), ongoing declines in reef health and hence the associated ecosystem service values are predicted to continue in the short term even under the most optimistic emissions reduction scenarios (Hansen et al., 2007; Klein et al., 2022; Suggett et al., 2023). Active management approaches, also referred to as "reactive" approaches, encompass coral and/or reef restoration, that actively shapes and expedites the ecological recovery process (Hein et al., 2021b). These interventions will inevitably be a useful approach for supporting reef-reliant communities until temperatures stabilise (Hein et al., 2021a).

Shifting focus from solely ecosystem protection to include active restoration efforts is perhaps best illustrated by the central role restoration is taking in national and international commitments under various multilateral environmental agreements (Hein et al., 2021a; Suggett et al., 2023). Internationally, the United Nations (UN) has nominated 2021 to 2030 as ''The Decade on Ecosystem Restoration,'' encouraging further experimentation and acceleration of coral reef restoration (UN, 2019). A landmark declaration in 2022 agreed on by 200 countries (adopted at COP17, Kunming-Montreal biodiversity deal) has presented a meaningful target towards this endeavour: at least 30% of all degraded ecosystems under effective restoration by 2030 (summarised in Suggett et al., 2023). Domestically, the United States National Oceanic and Atmospheric Administration (NOAA) restoration strategy (NOAA, 2018), the Coral Reef Restoration Protocol in Costa Rica (AIDA-America, 2019), Coral Reef Action Plans in Thailand (Suraswadi & Yeemin, 2013), and Australia's Great Barrier Reef Marine Park Authority (GBRMPA) "blueprint for resilience" (GBRMPA, 2017; GBRMPA, 2021) highlights the increased interest in investing in coral reef restoration. As such, blended finance has been established to help meet international goals (e.g. Global Fund for Coral Reefs, CORDAP) by supporting a wide range of locally tailored, but globally applicable restoration approaches (Suggett et al., 2023).

1.3 Coral reef restoration approaches

During its infancy, approaches to reef restoration focused on installing artificial reef structures to restore topographical complexity to reefs damaged by ship groundings and blast fishing (Precht, 2006; Young et al., 2012). In response to increased interest and investment, reef restoration now spans a continuum of approaches with goals ranging from ecosystem repair and rehabilitation to achieving a full recovery to a pre-stress-defined state (e.g. Gann et al., 2019). This has extended to "aggressive" resilience-based strategies, such as assisted evolution, aimed at withholding future climate stress (Hein et al., 2021b; Suggett & van Oppen, 2022). Artificial reefs continue to be used today for shoreline protection (e.g. reef balls; Buccino et al., 2014) or the prevention of harmful activities (e.g. trawling; Iannibelli & Musmarra, 2008), though overwhelmingly to increase potential habitat for reef fauna (enhancing fisheries production, recreational fishing opportunities and diving opportunities) (NOAA 2007; Brochier et al., 2021). However, the most common method to date has been in-water coral propagation and out-planting, also termed "coral gardening" (Boström-Einarsson et al., 2020).

1.3.1 Coral propagation and the use of coral nurseries

Coral propagation and out-planting activities aim to reinforce ecological services and re-create self-sustaining reefs by increasing coral cover at a degraded site (Edwards & Gomez, 2007; Edwards et al., 2010). This particular restoration approach is guided by a three-step operation: whereby (i) collected coral fragments that are artificially detached from a donor colony or found as naturally detached "corals of opportunity" are (ii) reared on artificial structures (termed "coral nurseries") for (iii) subsequent out-planting onto the reef substrate (*Figure 1.1.*; Boström-Einarsson et al., 2020). While collected coral fragments can be directly out-planted onto the reef, nurseries are widely used to optimise propagation activities (Rinkevich, 2005; Shafir et al., 2006a; Edwards et al., 2010; Ishida-Castañeda et al., 2020). Specifically, nurseries can enhance out-plant survivorship by allowing fragments to reach a size threshold at which their post out-plant survival may be higher (Shafir et al., 2006b; Boström-Einarsson et al., 2020; Ishida-Castañeda et al., 2020). In addition, once fragments on nurseries have reached a suitable size they can be broken into smaller pieces, and these can be grown on the nursery, multiplying the number of fragments available to out-plant (Rinkevich, 2005; Edwards et al., 2010). Thus, nurseries are particularly useful for avoiding stress inducement on coral donor colonies and supplementing coral material at restoration sites where coral cover is non-existent or too low to collect coral fragments in numbers needed for site restoration using direct out-planting (Epstein et al., 2001; Edwards et al., 2010; Rinkevich, 2014).

The short-term future application of coral propagation methods is likely to diverge towards two different, yet complimentary (ultimately nested) scales; 1) small-scale site stewardship projects and 2) large-scale reef-wide interventions (Suggett et al., 2023). Both scales can deliver recovery of "ecological restoration" but require fundamentally different operational approaches. For example, large-scale interventions require industrialised and engineered operations that move practice away from "coral gardening" and towards mass coral production (e.g. Reef Restoration and Adaptation Program in Australia, RRAP; Bay et al., 2019). In comparison, smaller-scale projects are often pioneered and led by the local stakeholders, including the tourism industry and citizen scientists, that focus efforts on local reef sites, incorporate socio-economic objectives directly and expand locally by mobilising reef stewards (Boström-Einarsson et al., 2020; Suggett et al., 2023). Thus, while large-scale efforts are increasingly introducing more *ex-situ* aquaria-based propagation facilities (e.g. Bay et al., 2023), the majority of projects, and all locally based projects, employ in situ low-cost nurseries that neighbour the reefs targeted for restoration (e.g. Suggett & van Oppen, 2022). As such, a broad array of nurseries have been designed for their specific reef environment. Either designed to float mid-water or fixed to substrate, among the most common are rope or line nurseries with (Shafir et al., 2006a) or without trays (Levy et al., 2010; Frias-Torres & van de Geer, 2015a; Dehnert et al., 2022) frame nurseries (Howlett et al., 2022) or nursery trees (Nedimyer et al., 2011; Sen & Yousif, 2016; Cook et al., 2022) (*Figure 1.1.*). On Australia's Great Barrier Reef (GBR), reef tourism operators initiated, in partnership with coral reef researchers (Coral Nurture Program), coral propagation and out-planting activities using mid-water table nurseries at deeper restoration sites and discrete fixed nurseries at shared tourism-public moorings at shallower sites (Howlett et al., 2021; Scott et al., 2024).

These nurseries in-essence resemble artificial reefs, though differ as their benthic composition is constantly manipulated when reef practitioners actively remove biofouling, fragment corals for out-planting or re-stock nurseries with different coral colonises or even coral species (Boström-Einarsson et al., 2018). Even so, coral nursery structures may attract fish assemblages similar to some artificial reefs (e.g. Frias-Torres et al., 2015b; Knoester et al., 2019). However, the ability of coral nurseries to support fish assemblages, alongside traditional artificial reefs goals to create attractive reef tourism sites and improve fishing industries (Holmlund & Hammer, 1999; Bellwood et al., 2004; Tebbett et al., 2022), has not been widely proven.

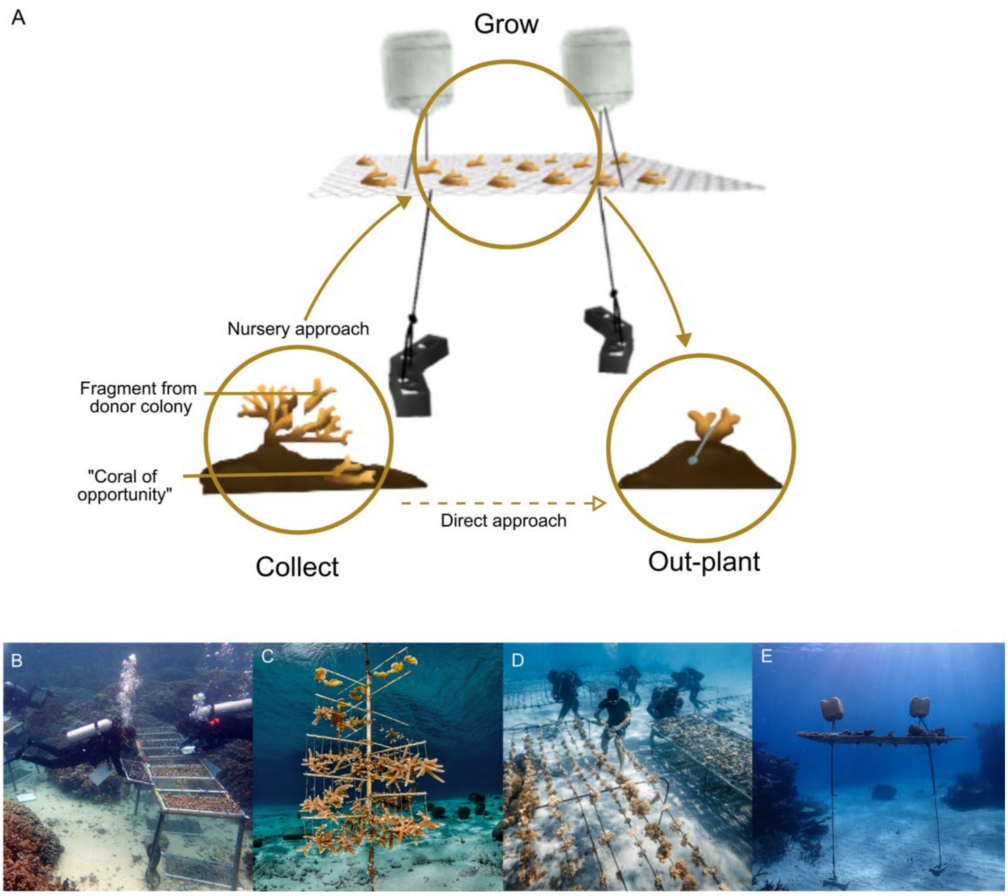

Figure 1.1. The coral propagation method (A). Firstly, practitioners collect coral material either from donor colonies or as a “coral of opportunity”, secondly coral fragments are either directly out-planted (secured to consolidated substrate) or are temporarily attached to nursery structures for growth prior to eventual harvesting of nursery grown fragments for subsequent out-planting. Over time the out-planted coral will attach to the substrate. Also shown are commonly used coral nursery designs including fixed net nurseries used by the Gates Coral Lab (B), floating tree nurseries used by Reef Renewal Bonaire (C), fixed line nurseries used by the Coral Gardeners (D), and mid-water floating nurseries used by the Coral Nurture Program (E). Image credits (from left to right): Shayle Matsuda, Lorenzo Mittiga, Coral Gardeners and John Edmonson.

1.3.2 The importance of fish in restoring coral dominant reefs

Restoration approaches that support high fish species diversity and associated functional diversity are thought to provide additional “ecological protection” against ecosystem degradation and may assist coral restoration efforts (Cheal et al., 2008; Ladd et al., 2018). Several fish groups, especially herbivores, contribute to the maintenance of coral-dominated reefs by removing sediment (Goatley & Bellwood, 2010; Bellwood et al., 2019) cycling nutrients (Francis & Côté, 2018), and controlling the growth of filamentous algae turf and macroalgae (Verges et al., 2012; Bellwood et al., 2019; Tebbett et al., 2022) thus preventing shifts from coral to algae-dominated reefs (i.e. positive feedbacks, see Mumby, 2009; Heenan & Williams, 2013; Ladd & Collado-Vides, 2013). Just as coral communities can be altered after disturbances, so too may the fish assemblages and the functions that are performed (Adam et al., 2011; Pratchett et al., 2011). Anthropogenic pressures that remove even one species may have consequences in key ecosystem functioning where one species is driving functioning (Bellwood et al., 2003; Hoey & Bellwood, 2009). Though the maintenance of ecological functions is generally assumed to be robust if there is a high diversity of fishes performing similar key functional roles (thereby limiting total functional redundancies) (Folke et al., 2004; Pratchett et al., 2014). Consequently, examining how coral restoration can support diverse fish assemblages at a disturbed site should be a critical management priority to reinforcing these important associations and ecological functions (Burkepile & Hay, 2008) that can support coral restoration and contribute to reef resilience (Palmer & Filoso, 2009; Shaver & Silliman, 2017; Ladd et al., 2018; Hein et al., 2020).

1.3.3 Fishes and coral nurseries

The management of coral propagation operations has much to gain by viewing nurseries through the lens of artificial reefs that support fish assemblages. Indeed, maximising service provision requires a broader portfolio of combined restoration approaches and future interventions will likely need to be multidisciplinary to match the scale of the problem (Boström-Einarsson et al., 2020). With operational refinement, coral nurseries may function similarly to artificial structures to increase the habitat of fish assemblages and therefore better meet commonly cited coral restoration aims to accelerate reef recovery (Rinkevich, 2005; Ferse, 2010; Garrison & Ward, 2012) or re-establishing a functioning reef ecosystem (Hunt & Sharp, 2014; Ippolito et al., 2016). Knowledge of fish assemblages has begun to inform coral out-plant strategies and improve coral survivorship (e.g. damselfish territories; Seraphim et al., 2020) and has been used as a functionally important measure of ecosystem-level recovery following restoration activity (e.g. through monitoring “soundscapes”; Lamont et al., 2022). However, in situ coral propagation research at the nursery stage remains largely focused on coral survival, and not fish community form and function (Seraphim et al., 2020) *– though, employing a similar philosophy of ensuring an optimised fish assemblage that facilitates gains in coral biomass is entirely logical for restoration.*

Few observations of fish assemblages on coral nursery propagation structures have been documented to date but remain largely qualitative (e.g. Shafir et al., 2006b; Shafir & Rinkevich, 2010; Huntington et al., 2017) and rarely the main focus of the study. Of the propagation practices operational worldwide only a select few in the Seychelles (Frias-Torres & van de Geer, 2015a; Frias-Torres et al., 2015b), Kenya (Knoester et al., 2019; Knoester et al., 2023) and Singapore (Taira et al., 2017) have investigated fish assemblages on nurseries and their capacity to promote coral propagation efforts. Importantly, this likely reflects that many projects are limited in terms of funding and logistical capacity, and are unable to monitor an exhaustive range of metrics (Boström-Einarsson et al., 2020; Suggett et al., 2023), despite recommendations for coral restoration projects to prioritise the monitoring of ecosystem services that include fish assemblages (Goergen et al., 2020; Seraphim et al., 2020). Assessing coral nurseries with a broader suite of ecological monitoring metrics may enable better assessments of the ecological and demographic processes occurring on coral propagation nurseries – and indeed in coral restoration activity in general – and could therefore identify and map strategies for further optimised nursery techniques.

Operations within current local-scale restoration programs are shaped by their integration into routine stakeholder activity (e.g. Suggett et al., 2023). A notable example of this is how the tourism industry on the Great Barrier Reef has adapted reef restoration methods and workflows as part of daily tourism trips (Coral Nurture Program; Howlett et al., 2022). Such an approach allows a diverse number of benefits that include stakeholder engagement, reduced operating costs and shared learnings (Howlett et al., 2021; Suggett et al., 2023). However, it can result in challenges, for example, time on site can limit the monitoring capacity needed to fully capture ecological responses, in particular via complex ecological restoration experiments (e.g. Howlett et al., 2022; Howlett et al., 2023). Importantly, this raises a fundamental question: How can we optimise nursery operations by enhancing our understanding of reef fish ecology within routine stakeholder activity? This thesis tackles this fundamental question by examining reef fish form and function interactions within the operational constraints imposed by reef restoration practice. All data collection was integrated into the daily activities of the Coral Nurture Program, which has had a large array of nursery structures (> 120) situated across diverse sites (> 27) of the northern Great Barrier Reef since 2018, and recently a further nursery array installed into 3 diverse reef sites in the Whitsundays (central GBR).

1.4 Thesis aims and hypotheses

A combination of management strategies, policies, and active interventions will be required if reefs are to retain ecosystem health in the Anthropocene (Voolstra et al., 2023). For local reef communities, reef stewardship using coral propagation techniques can provide an avenue to sustain important ecosystem services (Hein et al., 2017; Suggett et al., 2023). However, as projects continue to expand in response to increased needs and interest, the integration of fish assemblage interactions within coral nursery management practices needs to be better addressed to achieve ecosystem-wide restoration aims (Goergen et al. 2020, Seraphim et al., 2020). While diverse fish presence on natural reefs has been shown to increase reef resilience to stress (Bellwood et al., 2004; Cheal et al., 2008), and artificial reefs shown to support fish through habitat provision (Brochier et al., 2021; Ramm et al., 2021), coral nurseries have rarely been considered as structures that can in parallel grow coral biomass and provide artificial habitat for fish assemblages that are important to reef restoration. A more extensive understanding of the complex interactions between nursery grown-corals and fish assemblages is particularly important in Australia where the recent acceleration of stakeholder-led restoration activities on the GBR has led to a surge in mid-water floating and fixed table nurseries use for retention of coral biomass and the restoration of broader ecological functioning at high-value tourism sites (*Figure 1.2.*; Howlett et al., 2022; Suggett et al., 2023). **The overall goal of this thesis is therefore to identify and understand the role of coral nursery infrastructure in providing fish habitat, and in turn the role with which attracted fish facilitate nursery practices**. In doing so, I aim to broaden the singular use of coral nurseries to grow coral biomass toward multi-use structures that can offer additional ‘restoration services’ that have previously gone unrecognised. Three data chapters were conducted within the ongoing restoration activities of the Coral Nurture Program to deliver and test the following aims and hypotheses.

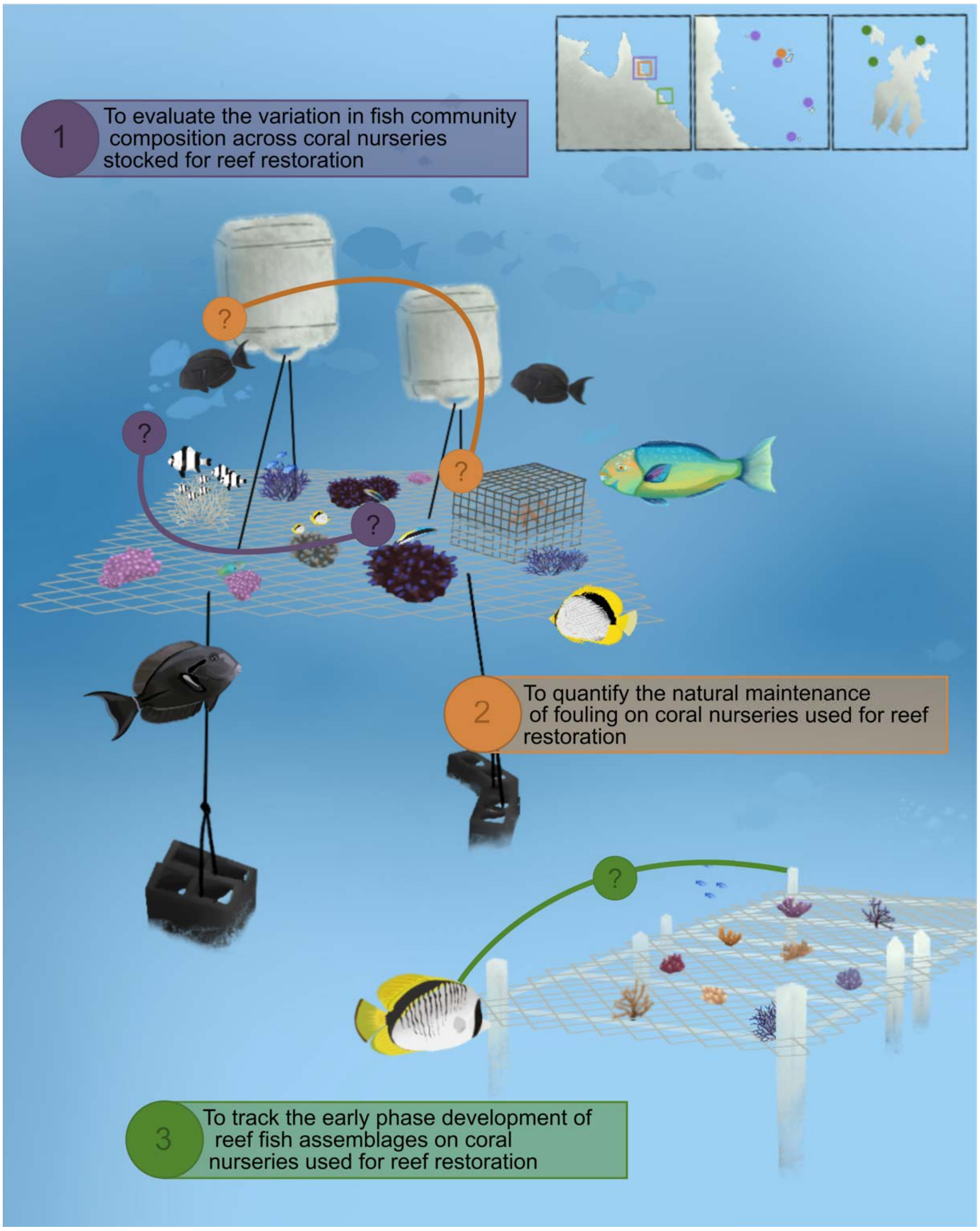

Figure 1. 2. The three aims addressed in this thesis are (*1*) to evaluate the variation in fish community composition across coral nurseries stocked for reef restoration (northern Great Barrier Reef), (*2*) To quantify the natural maintenance of fouling on coral nurseries (northern Great Barrier Reef), (*3*) to track the early phase development of reef fish assemblages on coral propagation nurseries (central Great Barrier Reef).

Aim 1 (*Chapter 2*): To evaluate the variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef.

Fish assemblages contribute an integral role in the functioning of healthy marine ecosystems. Coral nurseries, while primarily viewed as a restoration instrument to produce coral colonies for out-planting, may have the potential to act as reef habitats for local fish assemblages. To investigate the capacity of coral nurseries to provide additional fish habitat, I video-surveyed a total of 48 nurseries of varying coral densities and morphological arrangements across 7 restoration reef sites. Further in this work I assess how short-term videos feasible within a restoration practitioner setting can be used, and consider the data received relative to longer videos.

Within this chapter, the following hypothesis was tested:

i) Coral nursery frames with high coral cover, richness and morphological richness will attract a greater fish richness, diversity, and abundance of fish functional groups.
ii) This relationship will be consistent across multiple reef stewardship sites.

This chapter is currently under peer review: **Gillette, G.M.**, Camp, E.F., Edmondson, J., Booth, D.J., Roper, C., Howlett, L., Woodcock, S., Suggett, D.J. Variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef. *Marine Ecology Progress Series*. In Review.

Aim 2 (*Chapter 3*): To quantify the natural maintenance of fouling on coral nurseries used across the Great Barrier Reef.

Fouling of coral nurseries represents a major issue for restoration projects worldwide, with many projects resorting to removing this fouling by hand with bushes to avoid coral competition that can impair coral growth and survivorship. However, nursery cleaning comes at a significant cost to restoration projects. Here, I investigated the capacity of reef fish assemblages to naturally “maintain” mid-water coral nurseries used on Opal Reef, Great Barrier Reef, in a reduced fouling state. I employed a method designed so that it could be replicated by reef stakeholders to assess the effects of local fish assemblages on nursery operations at relative ease within existing infrastructure and practises. Coral fragments of *Acropora* typically used for propagation on the Great Barrier Reef as well as settlement substrates readily available to stakeholders for the assessment of fouling growth, were placed inside cage-exclusion treatments for 112 days at two reef restoration sites. Findings were supplemented by short-term video surveys to inform the presence of fish species on coral nurseries at sites and to assess interactions, including biting behaviours, with the frames, providing insights as a snapshot of overall activity. Within this chapter, the following hypothesis was tested:

i) Excluding fishes in the nursery area would increase fouling.
ii) An increase in fouling cover will result in lower coral survivorship.

This chapter is presented as a fully drafted article formatted for submission to a peer-reviewed journal following thesis submission: **Gillette, G.M.**, Camp, E.F., Edmondson, J., Booth, D.J., Scott, R.I, Suggett, D.J. Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef.

Aim 3 (*Chapter 4*): To document the early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef.

Coral nursery frames, used to build coral biomass on denude reefs, can become habitats for fish assemblages that in turn feed on filamentous turf fouling and maintain clean nurseries. Despite the importance of fishes to the functioning of coral nurseries, the development of fish assemblages on nurseries over time has never before been reported in literature. To address this, nursery frames were deployed at three locations in the Whitsundays, Great Barrier Reef, and monitored with video surveys and images of coral biomass and fouling development over 11 to 12 months. Within this chapter, the following hypothesis was tested:

i) Fish assemblages (abundance, richness, diversity and biomass) on fixed table nurseries would change rapidly, similar to fish assemblage development of artificial reefs.
ii) Fish species composition on nurseries would vary during the survey period

This chapter is presented as a fully drafted article formatted for submission to a peer-reviewed journal following thesis submission: **Gillette, G.M.**, Camp, E.F., Edmondson, J., Booth, D.J., Woodcock, S., Roper, C., Howlett, L., Strudwick, P., Scott, R.I., Hayward, C., Suggett, D.J. Early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef.

All data chapters are written as complimentary papers for peer review, and hence the General Introduction (this ***Chapter 1***) has been written so as not to introduce repetition that is presented in more detail via the data chapter-specific introductions. The final chapter (***Chapter 5***) is a General Discussion that considers the findings from across all data chapters to consider the reef fish ecology that can be learned within the operational constraints of restoration practice, but in turn, can be used to further advance the cost-effectiveness of coral nursery-based propagation.

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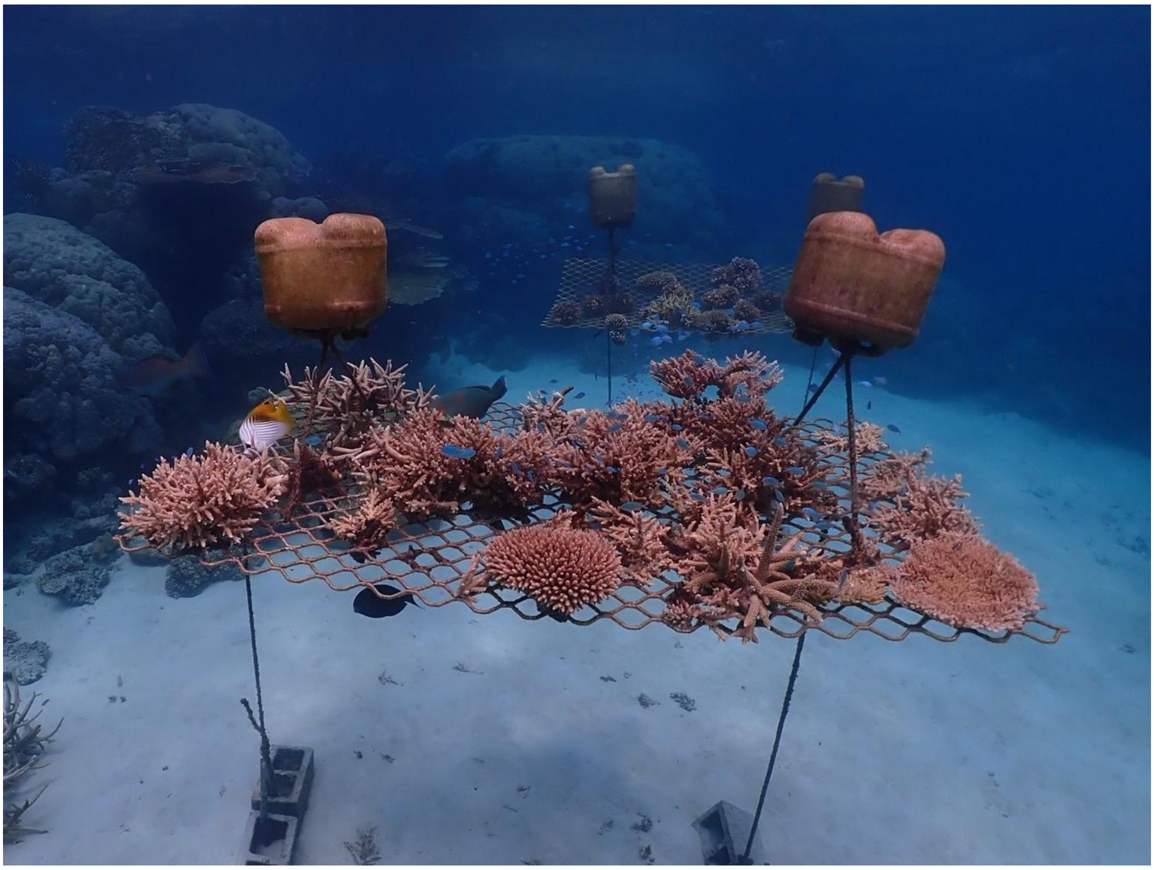
Chapter 2: Variation in fish community composition and function across coral nurseries stocked for reef restoration on the Great Barrier Reef



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2.1 Abstract

Deployment of coral nurseries and stakeholder-led coral propagation practices have been increasingly adopted on Australia's Great Barrier Reef to meet an urgent need for enhanced ecological and social resilience at targeted reef sites. While coral propagation techniques have now been established for decades, limited research has considered how nursery structures affect or integrate with fish assemblages that perform important ecological roles. To address how fishes respond to the presence of nursery structures, 48 nurseries of differing coral compositions were evaluated across 7 moorings at 4 reefs using a combination of long and shorter format video surveys. Across surveys, we explored the extent to which nurseries have developed into novel habitats that support diverse fish assemblages. Underwater video surveys using GoPro® cameras recorded a diverse fish assemblage of over >2, 333 fishes from 24 different families. Nursery coral cover was the main determinant of fish abundance and richness, but not fish diversity. Fish abundance and fish richness also increased with greater coral richness, and fish abundance further increased with coral morphological richness, though fish diversity was unaffected by either coral richness or morphological richness. We consider these findings alongside results from long-standing coral reef ecological research to discuss the potential functional value and, consequently, greater appreciation of fish assemblages in coral nursery propagation practices.

2.2 Introduction

Australia’s Great Barrier Reef (GBR) is a global natural wonder and key to the nation’s identity, culture, and economy, but it has been impacted by repetitive mass coral bleaching events since 2016 (Hughes et al., 2019; Hughes et al., 2021). While meaningful and immediate global-scale action on climate change is the only means to ensure the long-term persistence of coral reef ecosystems, local-scale stewardship techniques are needed to help retain ecological and social resilience at targeted sites (Anthony et al., 2017; Hughes et al., 2018; Bruno et al., 2019; Kleypas et al., 2021; Shaver et al., 2022). Coral propagation, often termed “coral gardening”, is one such stewardship method that can locally boost the natural recovery rate of coral biomass through asexual rearing of coral fragments on *in-situ* nurseries for subsequent out-planting onto adjacent degraded reefs (Boström-Einarsson et al., 2020; Rinkevich, 2020).

A small but growing body of research has shown that akin to artificial reefs, coral propagation nurseries used for restoration can provide a sheltered and stable environment for corals to grow, in turn expanding the habitat for fish assemblages (Burt et al., 2009; Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Amar & Rinkevich, 2017; Knoester et al., 2019). The importance of fishes to coral survival and growth is well documented in reef ecology for reducing competitive interactions with biofouling algae (Bellwood et al., 2004; Mumby et al., 2006a; Hughes et al., 2007) and for their provision of nutrients for coral growth (Allgeier et al., 2014; Shantz et al., 2015; Seraphim et al., 2019; Van Wert et al., 2023). Restoration monitoring guidelines recognise the critical need to evaluate fish assemblages to guide and optimise practice (e.g. Goergen et al., 2020). However, only a limited number of restoration projects have accounted for the presence of fish assemblages during the nursery design and instalment phase (Seraphim et al., 2019). Such projects have emphasised the increased coral survivorship and cost-reduction benefits of placing nurseries near fish assemblages with high herbivore biomass to encourage the removal of biofouling algae, otherwise carried out by humans (Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Knoester et al., 2023). Also, where the benefits provided by herbivore species outweigh the costs of incidentally encouraging corallivore species on nurseries (Knoester et al., 2019). Despite the proven success of integration between reef ecology and restoration elsewhere, no projects have evaluated how fish assemblages resident to the GBR respond to coral nurseries. An initial step towards a comprehensive understanding of how coral propagation practices impact the stewardship sites they aim to restore requires a better understanding of nursery installation and operation from an ecological perspective (Ladd et al., 2018).

Restoration practices have increased in popularity on the GBR following the 2016/17 bleaching events (McLeod et al., 2022). Of these, the widely adopted Coral Nurture Program (CNP), a joint tourism-research partnership, utilises a multi-taxa propagation approach on mid-water frame-based coral nurseries (Howlett et al., 2021; Howlett et al., 2022). Stewardship efforts by the CNP are targeted at local reef sites that are degraded to varying degrees due to severe weather and climatic events but are used by the tourism industry and therefore of high social and economic value (Boström-Einarsson et al., 2020; Suggett & van Oppen, 2022; Suggett et al., 2023). At the time of writing, > 120 nurseries used for coral propagation are operated by CNP tourism partners across Cairns, Port Douglas and the

Whitsunday regions. However, the variation in fish nursery usage with different coral stocking compositions across mid-water coral nurseries remains untested. We therefore examined fish assemblages for coral nurseries across 6 GBR mooring sites across 4 reefs, with video surveys designed to fit within CNP routine tourism site visits (Howlett et al., 2022). We tested the general hypothesis that overall fish assemblage composition (richness, abundance, and diversity) positively correlated with coral nursery stock characteristics (coral cover, richness, and morphological richness). We discuss how such video monitoring of coral nurseries for fish assemblage composition can provide reef restoration practitioners with insights into the broader ecological impacts of coral propagation at their stewardship sites.

2.3 Methods

2.3.1. Site locations and video survey collections

A total of 48 nursery frames of varying coral composition were randomly chosen across 4 reefs (7 mooring sites; *Figure 2.1.*): “1770” on Hastings Reef, “Clam Gardens” and “Angels” on Mackay Reef, “Rayban” and “Blue Lagoon” on Opal Reef, and “Wonderwall” on Upolu Reef. On the reef immediately adjacent to these moorings, fish assemblages were primarily dominated by species from families within the *Pomacentridae* (Damselfish), although *Ambassidae* (Glassfish) were dominant at “1770” (Hastings Reef). *Caesionidae* (Fusiliers) were also in high abundance at “Clam Gardens” (Mackay Reef), as were *Lutjanidae* (Snapper) at “Blue Lagoon” (Opal Reef) and “Wonderwall” (Uplou Reef; *Figure S2.2.*). Hard coral cover at all sites was between 6 - 36%, and comprised mostly *Acropora* or *Pocillopora* (*Figure S2.2.)*

Each nursery consisted of one 2.0×1.2 m aluminium diamond-mesh platform attached with spliced rope to 2 × 20 L floats and 2 × 9 kg besser blocks (*Figure S2.1.*; Howlett et al., 2021). All nursery structures were installed on sand adjacent to natural reefs and suspended approximately 1-2 m above the substrate so that they were at ca. 4-6 m depth at low tide. Nurseries were stocked with either fragments taken manually from nearby wild coral colonies (< 10% of the wild colony), or “corals of opportunity”, unaccreted coral fragments, or small partial coral colonies found on unconsolidated substrate (all approximately < 15 cm in size; Howlett et al., 2022). All activities across sites were conducted under Great Barrier Reef Marine Park Authority (GBRMPA) permits G18/40023.1 and G20/43740.1.

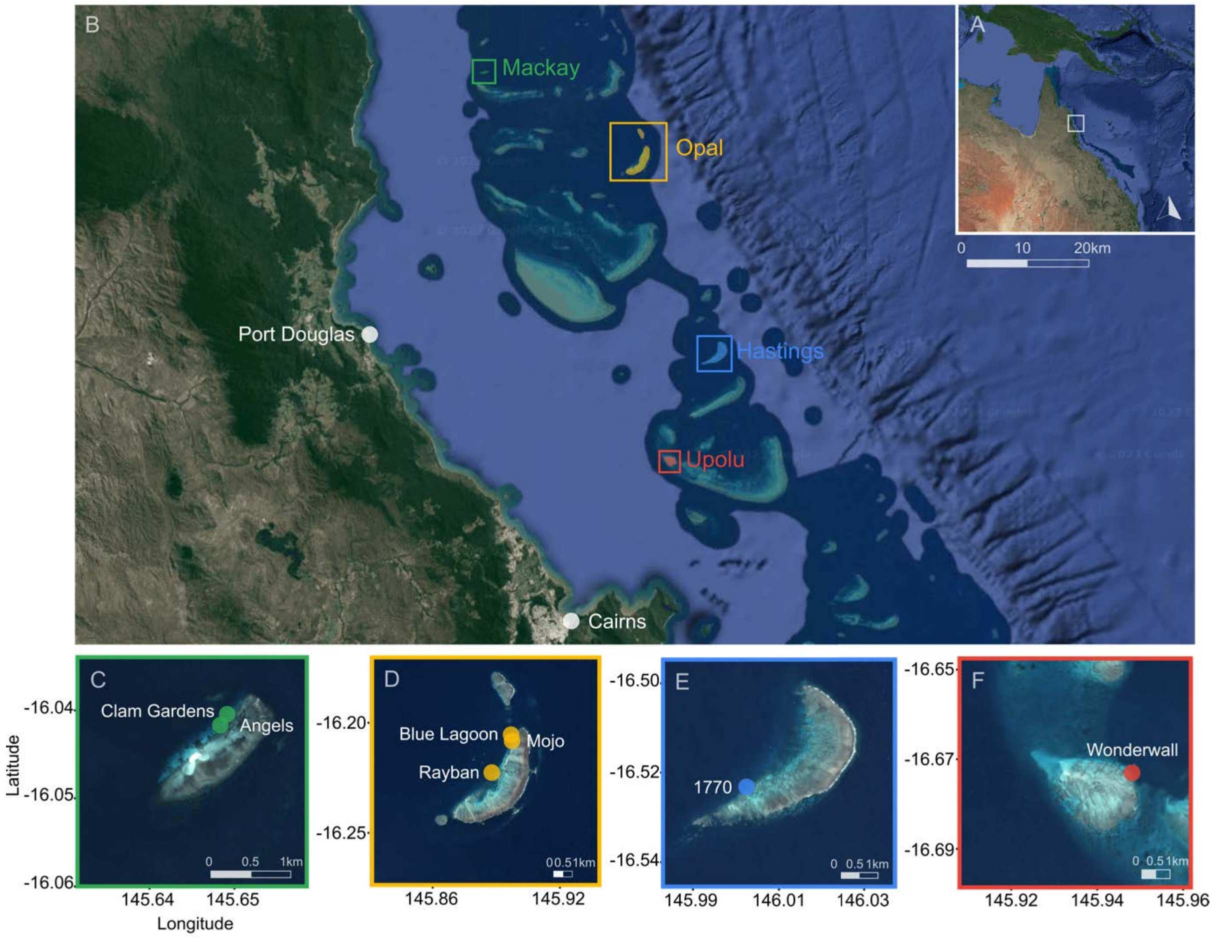

Figure 2.1. Location of survey sites within the (A) country, (B) region and (C-F) reef. Reefs include (C) Mackay (-16.047, 145.645), (D) Opal (-16.216, 145.898), (E) Hastings (-16.520, 146.010) and (F) Upolu (-16.673, 145.935), situated on the northern Great Barrier Reef, Australia. Map images © Google 2023 and © Allen Coral Atlas 2023.

To examine fish assemblages on coral nurseries within the operational constraints imposed by reef restoration practices, surveys involved "rapid" videos taken by the same experienced diver between 9th - 25th February 2021. Each rapid video was 9 min duration; this length represented the duration achieved from trimming 2.5 min from the beginning and end of the shortest survey footage (14 mins) to eliminate diver disturbance. All videos were therefore standardised to this shortest survey time. GoPro Hero 8® cameras were attached to a GoPro® "Jaws: Flex Clamp", mounted onto an adjacent nursery and positioned so cameras would capture the entirety of the subject nursery (*Figure S2.3.*). To reduce variability in fish densities from diurnal influences in behaviour, all videos were restricted to mid-daylight hours (between 2 hours after the sunrise and 2 hours before sunset; time of earliest sunrise 06:11 and sunset 19:53, local time) outside periods of peak crepuscular activity (Thompson & Mapstone, 2002; McClanahan et al., 2007; Powell et al., 2016; Emslie & Cheal, 2018). We examined how the 9 min rapid video effectively captured the nursery fish assemblages in comparison to longer duration videos by conducting 1 hr Remote Underwater Video (RUV)-style surveys on 3 nursery frames at the Mojo CNP tourism mooring site (Opal Reef; Figure S4). RUV surveys involved deploying cameras to capture underwater footage for studying fish assemblages without direct human presence (e.g. Tweedie et al. 2023). Video surveys for each nursery (n= 3) were repeated across 3 days between 27th February - 2nd March 2023 (one video per nursery per day, n = 9). All videos recording durations were based on battery power consumption; however, the shortest video was 1 hr 5 min 32 sec and was used as the maximum duration for all other videos. Again, the first and last 2.5 min of each video were removed to account for immediate diver disturbance, resulting in a total of 1 hr and 32 sec for each fish assemblage analysis. These videos were used solely for species accumulation curves (see data analysis).

2.3.2 Nursery frame fish assemblages

Fish abundance, richness, and diversity metrics were used to describe nursery fish assemblages. During each video, fishes were identified to the highest possible taxonomic resolution. Only clearly visible fishes were included in all surveys, excluding those smaller than 1 cm. MaxN abundance (i.e., the maximum number of individuals per species featured in each video; e.g. Fitzpatrick et al., 2012; Scott et al., 2015; Reeds et al., 2018) were used to avoid overestimations of fish abundance since individuals repeatedly moved in and out of the video field of view. Total fish diversity was calculated using the Shannon-Wiener index in the R statistical environment, version 1.3.1093 (RStudioTeam, 2023).

2.3.3 Nursery frame coral composition

Coral species, cover, richness, and morphological richness (number of morphologies) were used as descriptors of coral composition on nurseries. Downward-facing photographs were taken with an Olympus Camera (Tough TG-6) at ca. 2 m height above each nursery. Coral colonies along with fouling and non-target species (such as *Millepora alcicornis*) were identified and individually traced using image J and coral cover calculated per nursery (Schneider et al., 2012). Corals were assigned to morphology categories as described by Madin et al. (2016). Morphologies were assigned based on how the corals presented at the time they were photographed (i.e. 2 corals of the same species may either be a small colony with a closed branching morphology, or a larger colony with an open branching morphology).

2.3.4 Data analysis

The use of rapid videos enabled many surveys to be collected across a variety of sites and coral nurseries. With the large number of nurseries surveyed, a Generalized Additive Model (GAM) was employed to analyse how nursery coral composition (cover, richness and morphological richness) related to fish assemblages (abundance, richness and diversity). GAM methods were selected for their common use in ecological studies (Knudby et al., 2010) and flexibility in analysing non-linear data (Hastie, 2017). GAM models were constructed in the R statistical environment, version 1.3.1093 (RStudioTeam, 2023), utilizing the "gam" function from the "mgcv" package. The "ziP" method was applied to select smoothing parameters suitable for zero-inflated Poisson distribution count data (fish richness and abundance metrics), and the "tw" method, suitable for Tweedie distribution continuous data (fish diversity metrics), to the relevant models. Both zero-inflated Poisson and Tweedie distributions address the challenge of handling a high number of low counts, which is common in ecological data. These distributions were assigned to fish variables based on the initial visualisation of the data (El-Shaarawi et al., 2011; Bonat et al., 2018). A one-way non-parametric Kruskal-Wallis test, applied due to non-normality as indicated by the Shapiro-Wilk's Test, revealed no significant differences ($\alpha = 0.05$) in all fish richness, abundance, and diversity metrics among tide types (high, low, ebb, flow; *Table S2.1.*), as well as between reefs (*Table S2.2)*. As such, these were removed from the GAM model, and coral composition and fish assemblage data was included exclusively.

To ensure the shorter videos were adequately gathering fish metrics, the longer format videos were subject to a cumulative stepwise assessment of fish assemblage data every 5 min. Fish Shannon-Wiener diversity metrics were calculated at every timepoint for each sample, and all fish metrics were averaged per nursery (n = 3; Mojo) to create fish assemblage cumulative plots. All plots were created using "ggplot" in the *R* statistical environment, version 1.3.1093 (RStudio Team 2023).

2.4 Results

2.4.1 Nursery frame benthic composition

Rapid short video assessments enabled many nurseries to be surveyed (n = 48) encompassing a wide variety of coral compositions (*Figure S2.6.*). Most nurseries were of < 30% coral cover with only 7 nurseries between 30-50% and only 4 nurseries > 50% (*Figure S2.6A-F.*). Nurseries with the highest (75%) and lowest (0%) coral cover were both located at Blue Lagoon mooring (*Figure S2.6C.*). Coral morphological richness on nurseries ranged from 0-6 across sites, with most nurseries consisting of 1-5 morphologies (46 nurseries; *Figure S2.6G-L.*). Of the 2 remaining nurseries, 1 was stocked with no coral and the other with 6 morphologies (*Figure S2.6C.*). Among morphologies, corymbose taxa were most prominent across sites (39% of all corals stocked; *Figure S2.6G-L.*). Table (27%), open branching (19%) and, to a lesser extent, closed branching (9%) taxa were collectively the most abundant morphologies (*Figure S2.6G-L.*). Hispidose morphologies were present, but not in high abundance (1.62% of all corals on nurseries; *Figure S2.6G-L.*). Coral richness ranged from 0-16 species on nurseries (*Figure S2.6M-R.*). Most nurseries were stocked with 2-5 different coral species (18 nurseries), but with several (n = 11) stocked with 8 species (*Figure S2.6M-R.*). Beyond this, coral richness was relatively variable across nurseries; however, only 3 nurseries included > 13 different species (*Figure S2.6M-R.*). Species of *Acropora* were dominant on the majority of nurseries (44 nurseries) surveyed. Of the nurseries where *Acropora* was not dominant, the surface area largely comprised of species of *Pocillopora* (2 nurseries) or was not yet populated with corals (1 nursery; *Figure S2.6M-R.*).

2.4.2 Nursery frame fish assemblages

Species accumulation curves from longer 1 hr survey videos revealed that on average 64% of fish abundance, 74% of fish richness and 84% of fish diversity was captured within the first 9 min of footage (*Figure 2.2.*). As such, for the purpose of this study, these values therefore operate as the confidence levels within which fish assemblages we describe from the rapid (9 min videos) represent those from longer term video deployments.

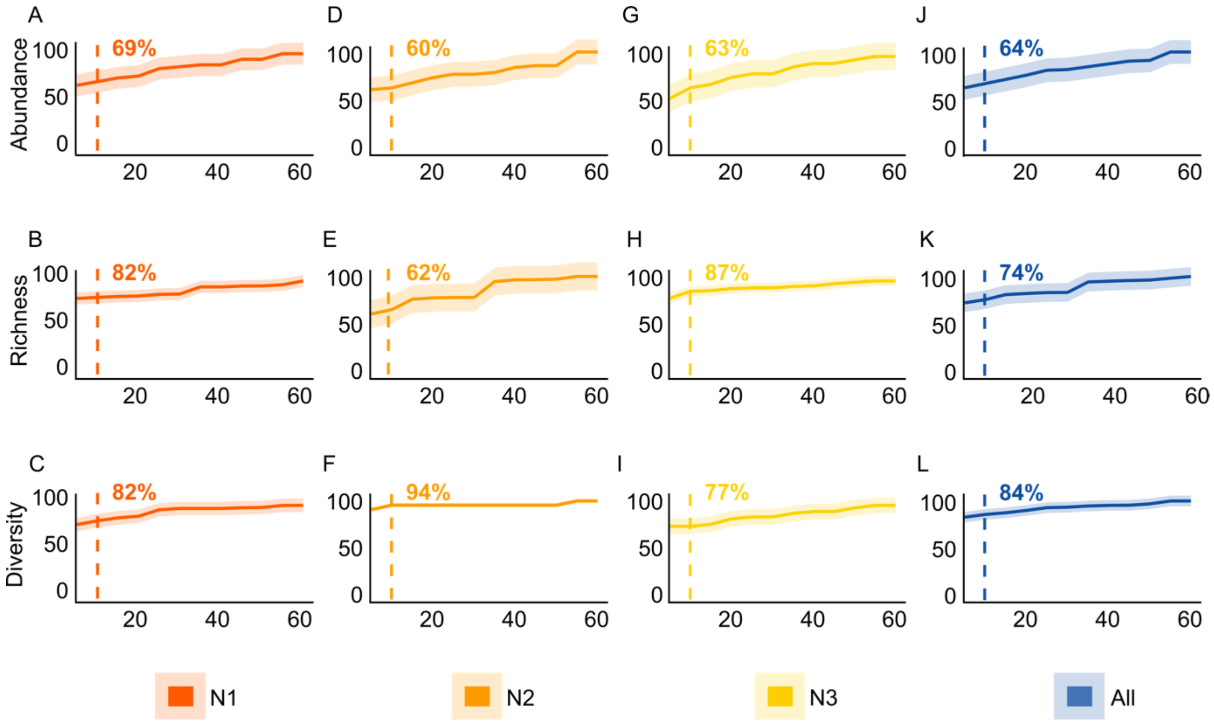

Figure 2.2. Average percentage cumulation curves for fish assemblages observed on 3 coral nurseries (N1, N2, N3) as well as a total average (All) at "Mojo" mooring, Opal Reef, northern Great Barrier Reef. Data was collected using long-form video surveys at 3 time points (n = 3 surveys per nursery; n = 9 total). Cumulation at 9 min is displayed as a dashed line and a percentage on each graph. Shading represents the standard error for each percentage cumulation curve.

Across surveys, >2, 330 fishes from 107 species and 24 different families were documented on nursery structures. Rapid video surveys across all sites revealed diverse fish assemblages on the GBR coral restoration frames. In total, fishes from 24 families were identified, with *Acanthuridae* (Surgeonfish; 72% of all surveys), and *Scarinae* (Parrotfish; 69% of all surveys), and *Pomacentridae* (Damselfish; 53% of all surveys) as most common, whereas *Monacanthidae* (Filefish; >2% of surveys) and *Fistulariidae* (Flutemouths; >2% of surveys) were the rarest observed (*Figure 2.3.*). The maximum number of fish families on a single coral nursery was 14, with 2 frames containing no fish (*Figure 2.3.*). Mean MaxN on a given nursery was 16.36 individuals. On average, each frame hosted 5.72 fish families, with an average diversity index of 0.86.

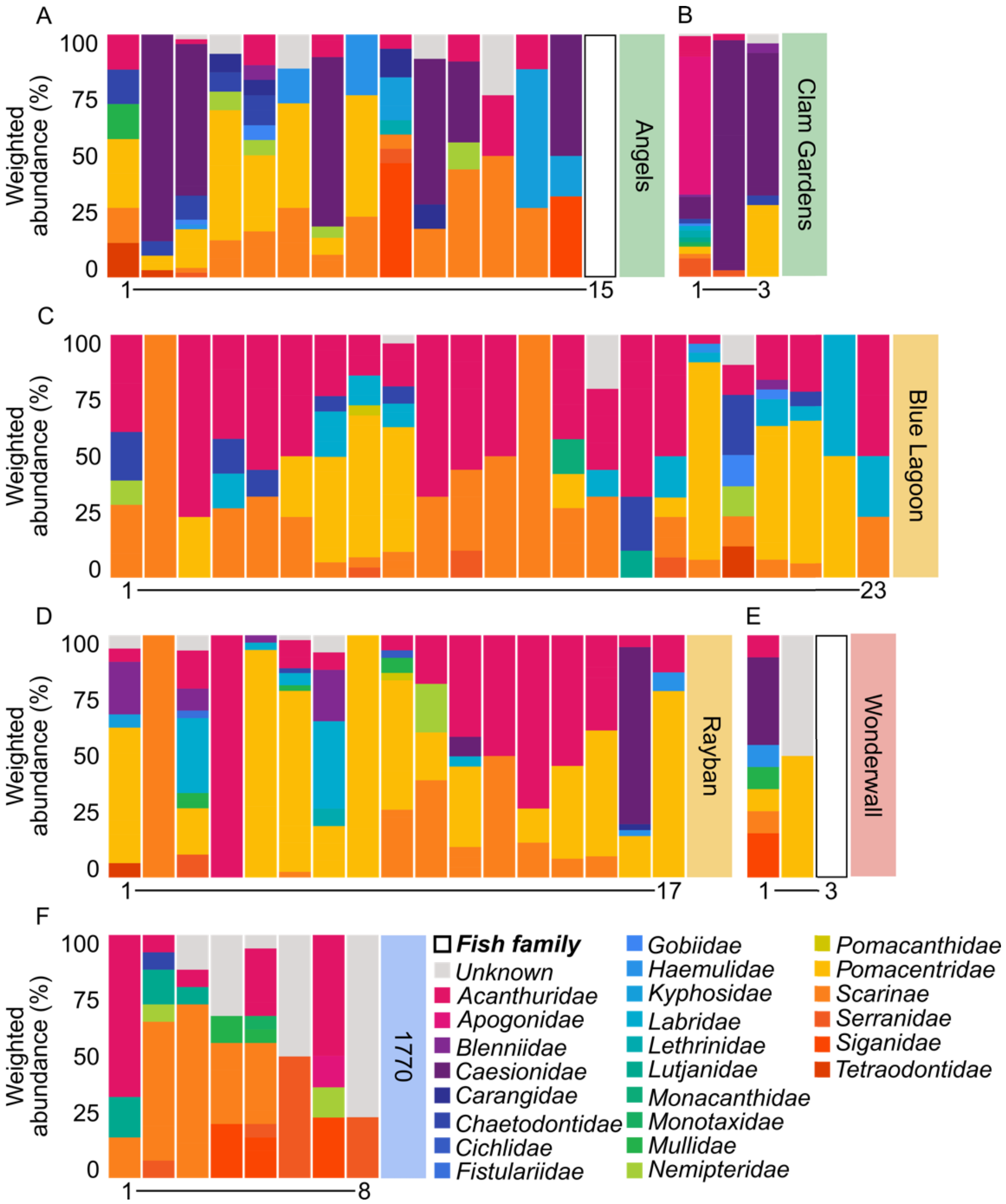

Figure 2.3. Weighted (%) fish abundance per family (including *Scarinae*, a sub-family of *Labridae*) on coral nurseries (n = 48 total) located at "Angels" and "Clem Gardens" (Mackay Reef; green), "Blue Lagoon" and "Rayban" (Opal Reef; yellow), "Wonderwall" (Upolu Reef; red) and, "1770" (Hastings Reef; blue). Rapid short video assessments were randomly used to record fish assemblages on nurseries (n = 69 surveys total).

2.4.3 Nursery frame fish assemblage relative to coral composition of nursery frames

Overall, coral cover (GAM, $df = 8.61$, $\chi2 = 169.90$, $p < 0.000$; *Table S2.3.*), coral richness (GAM, $Est = -0.05$, $z = -2.01$, $p = 0.044$; *Table S2.3.*) and coral morphological richness (GAM, $Est = -0.33$, $z = -6.05$, $p < 0.000$; *Table S2.3.*) each exhibited a significant positive relationship with fish abundance. In contrast, only coral cover (GAM, $df = 1.00$, $\chi2 = 6.81$, $p = 0.009$; *Table S2.3.*) and coral richness (GAM, $Est = 0.08$, $z = 2.83$,

$p = 0.005$; *Table S2.3.*) exhibited a significant positive relationship with fish richness. In contrast, fish diversity was not largely impacted by either coral cover, richness or morphological richness (*Table S2.3.*). Therefore, across the nursery structures examined, coral cover and coral richness – as descriptors of coral composition – emerged as crucial overarching factors corresponding with fish richness and abundance, but did not correspond with fish diversity.

2.5 Discussion

The adoption of coral nurseries for coral reef stewardship is accelerating worldwide as reefs continue to deteriorate (Boström-Einarsson et al., 2020). However, how fish assemblages use these nurseries – as artificial structures introduced into reef environments – remains largely unexplored. Here we show that mid-water floating coral nursery structures widely employed on GBR tourism sites adjacent to the neighbouring reef (Howlett et al., 2022) can host abundant fish assemblages; specifically, where higher abundance and richness of fishes corresponded with greater coral cover on nurseries. High coral cover is generally known to increase the abundance and richness of fishes on natural reefs (Wilson et al., 2006; Williamson et al., 2014; Russ et al., 2020; Tsai et al., 2022) as well as on artificial reefs (Higgins et al., 2019; Mwaura et al., 2022). Similarly, Frias-Torres et al. (2015a) observed that the presence of corals on nurseries was important for hosting higher abundance of fishes from nearby reefs. Established mid-water nurseries, such as those observed during this study, have the advantage of being able to directly control how much coral cover is maintained on nurseries over time, as a result of routine restocking and pruning of colonies to create coral fragments that can be out-planted (Suggett et al. 2019, Howlett et al. 2022, Scott et al. 2024). Our findings of greater fish abundance on nurseries with higher coral cover would suggest that nursery managers may benefit from "pruning" back coral stock – as opposed to complete removal (and replacement with new small material) – to maintain a base-level of coral cover for fish assemblages. However, this would need to be carefully balanced with total time any given colony is retained in nurseries where aging and susceptibility to stressors may increase (refs). Established mid-water nurseries, such as those observed during this study, will generally increase in coral cover within a relatively short period due to being stocked with fast-growing coral species (Howlett et al., 2021; Ortiz et al., 2021; Suggett et al., 2023) that have access to increased flow rates compared to corals on benthic substrates (Nedimyer et al., 2011). As such, nurseries may still provide a continuous coral supply for out-planting while enhancing their appeal to local fish assemblages.

Including a rich variety of coral species with different morphologies could further enhance appeal of coral nurseries to fish assemblages compared to nurseries that stock only one coral species or morphology. In our study, fish assemblage abundance and richness increased with a greater variety of coral species and further increased with a wider range of coral morphologies. Among the nurseries examined in our study, tabular, branching and corymbose forms - those typically more "complex" in architecture - were abundant. Such complex physical structures can attract a greater number of fishes by offering a variety of food resources, as well as providing diverse of shelter types, particularly for small-bodied resident fishes (Holbrook et al. 2002, Cole et al. 2008, Kerry & Bellwood 2011, Kerry & Bellwood 2015, Pereira & Munday 2016, Darling et al. 2017). Greater variety of coral morphologies also contributes more broadly to habitat complexity used by transient reef fishes as temporary predation avoidance (Khan et al., 2016), protection from solar irradiance (Kerry & Bellwood, 2015), or for energetic benefits in avoiding hydrodynamic action (Johansen et al., 2008; Kawabata et al., 2011). Fish assemblages attracted to more morphologically rich coral habitats may enhance potential to contribute functions that assist in coral propagation effectiveness. For instance, among the fish species observed on nurseries, small-bodied resident fishes belonging to the *Pomacentridae* (Damselfish) family were abundant across surveys. Experimental studies have shown *Pomacentridae* (Damselfish) species enhance the growth of their coral hosts by increasing water circulation and oxygenation within colonies (Goldshmid et al. 2004), greatly enhancing the capacity of host corals to withstand sediment stress (Chase et al. 2020), ameliorate coral bleaching (Chase et al. 2018) and may slow coral disease progression (e.g. *Pomacentrus moluccensis*, Chong-Seng et al. 2011). Consequently, incorporating higher coral cover and greater coral richness on nurseries may be advantageous for corals on nurseries. That said, whilst such benefits have been proven on natural reefs, studies have yet to demonstrate whether they similarly apply for corals grown in nurseries and therefore warrants further investigation.

Following *Pomacentridae* (Damselfishes), families *Acanthuridae* (Surgeonfish) and *Scarinae* (Parrotfish) were the most abundant across our video surveys. Both *Acanthuridae* (Surgeonfish) and *Scarinae* (Parrotfish) have been shown to be key actors in removing biofouling algal from nurseries in the Seychelles (Frias-Torres et al. 2015a) and Kenya (Knoester et al. 2019, Knoester et al. 2023). Strong negative relationships exist between structural complexity and algal cover on natural reefs (McManus & Polsenberg 2004, Vergés et al. 2011, Graham & Nash 2013), emphasising the importance of considering complexity for ensuring enhanced biofouling removal by fish. Such a trend is perhaps of added importance on GBR tourism sites where nurseries are in view of tourists and hence need to retain aesthetic appeal. Manual algae removal by divers would otherwise introduce high costs to restoration practices (Knoester et al. 2023, Scott et al. 2024); for example, ~3 times fewer person-hours were spent on cleaning mid water nurseries when herbivorous fish were present in the Seychelles (Frias-Torres et al. 2015a). Further investigation is clearly needed to understand what ultimately attracts particular fish taxa to nurseries with a diverse array of coral species of varying morphologies and therefore ensure a variety of fish with different ecological roles. Diverse coral compositions that enhance the abundance and richness of reef fishes appear to be one of the principal ecological characteristics dive tourists like to see (Williams & Polunin 2000, Uyarra et al. 2009, Le et al. 2019). Therefore, nurseries with diverse corals can retain maximum ecological and aesthetic benefits, which is especially important for nurseries that are a part of GBR tourism dive sites (Howlett et al. 2022). Resolving whether fishes with important roles are attracted (i.e. the net abundance of fishes at reefs and surrounding areas are not changed) or produced (i.e. a net increase in overall abundance) (Brickhill et al. 2005) on nurseries with added coral cover requires more targeted investigation in future.

Rapid video surveys were used in this study because this timeframe could be accommodated during routine tourism site visits. Specifically, a large number of video surveys could be collected by eliminating the need for dedicated research days otherwise required for long-form fish surveys. Rapid surveys using short videos (ca. 5-10 minutes) of a large number of replicates (15 - 50) have previously been used to assess fish assemblages on natural reefs (Longo et al. 2014, Canterle et al. 2020, Fontoura et al. 2020, Garcia et al. 2021). As time and the number of replications is a common trade-off, studies have shown that videos as short as 5 minutes, with 5 replicates, recorded 80% of the total biomass and the entire species composition (e.g., Garcia et al. 2021). Cumulative analysis of fish during this study revealed rapid video assessments captured > 60% of fish richness, abundance, and diversity (and > 70% of fish functional group richness and diversity) when compared to longer format videos. Whilst longer videos captured greater fish abundance and richness within a single survey, they did not record as many fish species as compared to the shorter video set (i.e. when there were more replicates). Shorter videos are likely to inherently be biased towards capturing resident fish species that have obligate relationships with corals and stay on nurseries for long periods of time. As such, greater video replication should always be factored into the design of using shorter video surveys to ensure that both resident and transient fish species are recorded. If possible, it is always preferred that longer videos be taken at large replication; however, as reef stewardship projects such as CNP are often restricted in terms of time dedicated to research (e.g. Scott et al. 2024), shorter videos, as seen in our current research, can still provide valuable data. As with many video survey methods, cryptic species may still be as readily detected, highlighting the ongoing need for methodological refinements in biodiversity assessments.

2.6 Conclusion

Nurseries examined within this study as part of GBR tourism-led site restoration and maintenance activities were associated with a fish assemblage of >2,330 fish from 24 families. Similar to studies examining natural reefs, our work here demonstrates that diverse coral species and morphologies on nurseries can enhance nursery fish abundance and richness. Reef stewards and restoration practitioners aiming to attract fish to nurseries may prioritise high coral cover encompassing a diverse array of species and morphologies, although monitoring of nurseries is essential to evaluate how fishes respond. Our rapid 9 minute video surveys have proven effective for efficiently assessing fish assemblages within time restricted monitoring efforts. These surveys, capturing substantial proportions of fish richness, abundance, and diversity compared to longer methods, offer practical insights for ongoing nursery management. However, longer-term and targeted observations will be needed to identify whether fish habitat provided by coral nurseries ultimately can support new fish recruitment and assess the greater presence of cryptobenthic species. As coral propagation efforts continue to expand globally, optimising nursery design with a rich variety of coral species and morphologies and further advancing fish monitoring methods hold promise for enhancing both ecological and aesthetic benefits, particularly in tourism-driven reef restoration initiatives.

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2.9 Supplementary materials

2.9.1 Supplementary figures

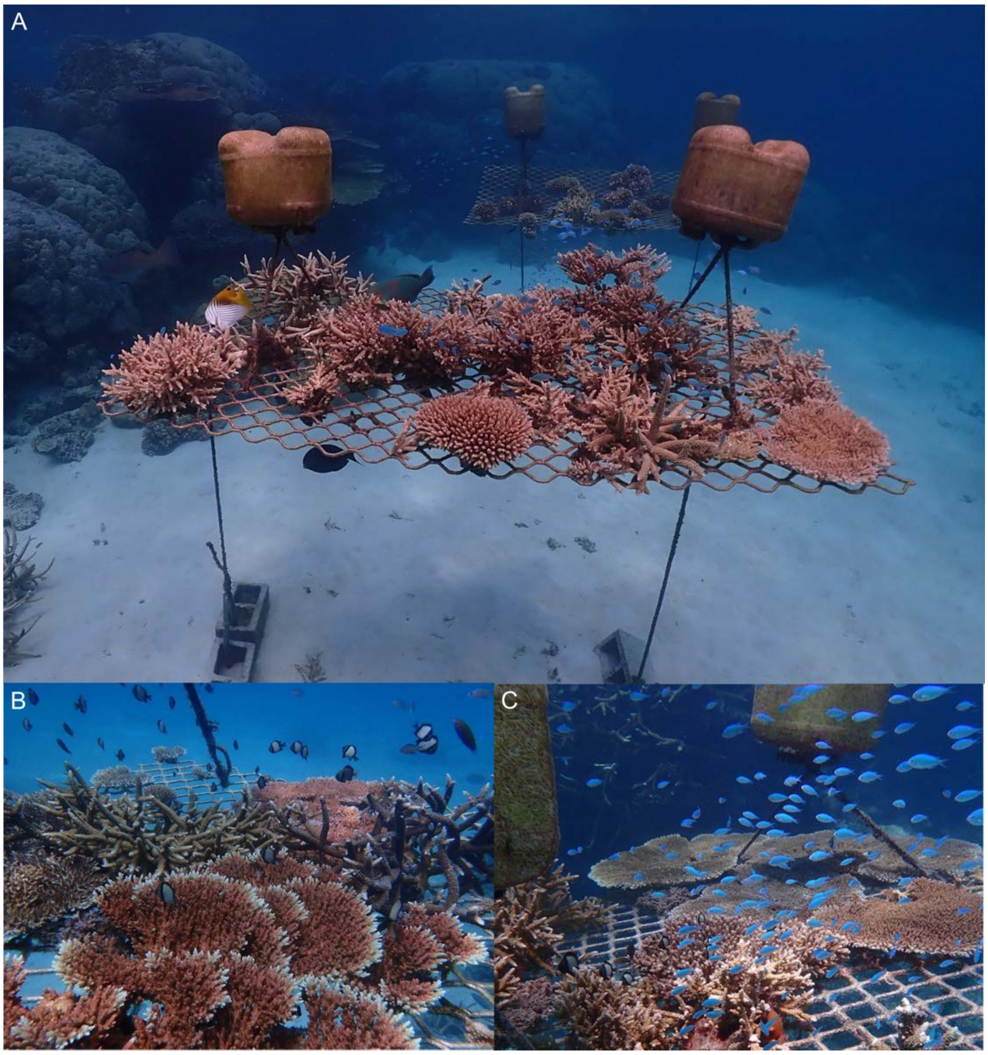


Figure S2.1. An example of a mid-water coral nurseries used by the Coral Nurture Program on the Great Barrier Reef. Nursery structures consisted aluminium mesh platform (2.0×1.2 m) fastened with rope to two to four 9 kg besser blocks and two 20 L floats. Nurseries are deployed under Great Barrier Reef Marine Park Authority permit G20/43740.1. Photo credit: John Edmonson (A, B) and Gemma M Gillette (C).

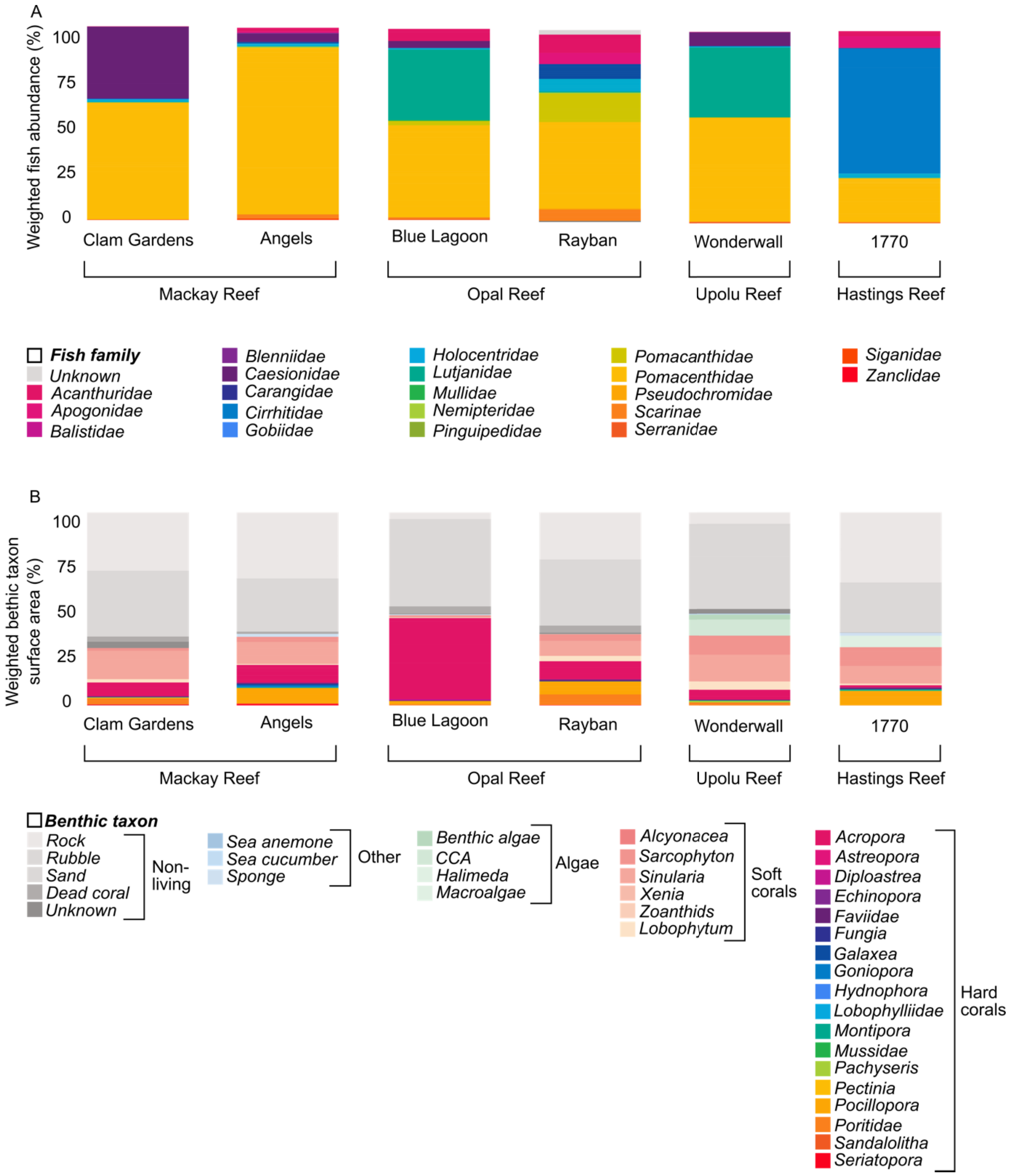


Figure S2.2. Weighted (%) (A) fish family abundance and (B) benthic taxon surface area on natural reefs at each mooring site: "Angels" and "Clem Gardens" (Mackay Reef), "Blue Lagoon" and "Rayban" (Opal Reef), "Wonderwall" (Upolu Reef) and, "1770" (Hastings Reef). Fish abundance per family (including *Scarinae*, a sub-family of *Labridae*) is an average of 3 x 30 m transects taken at each site in February 2021. Pastel colours represent benthic taxon that is not hard coral.

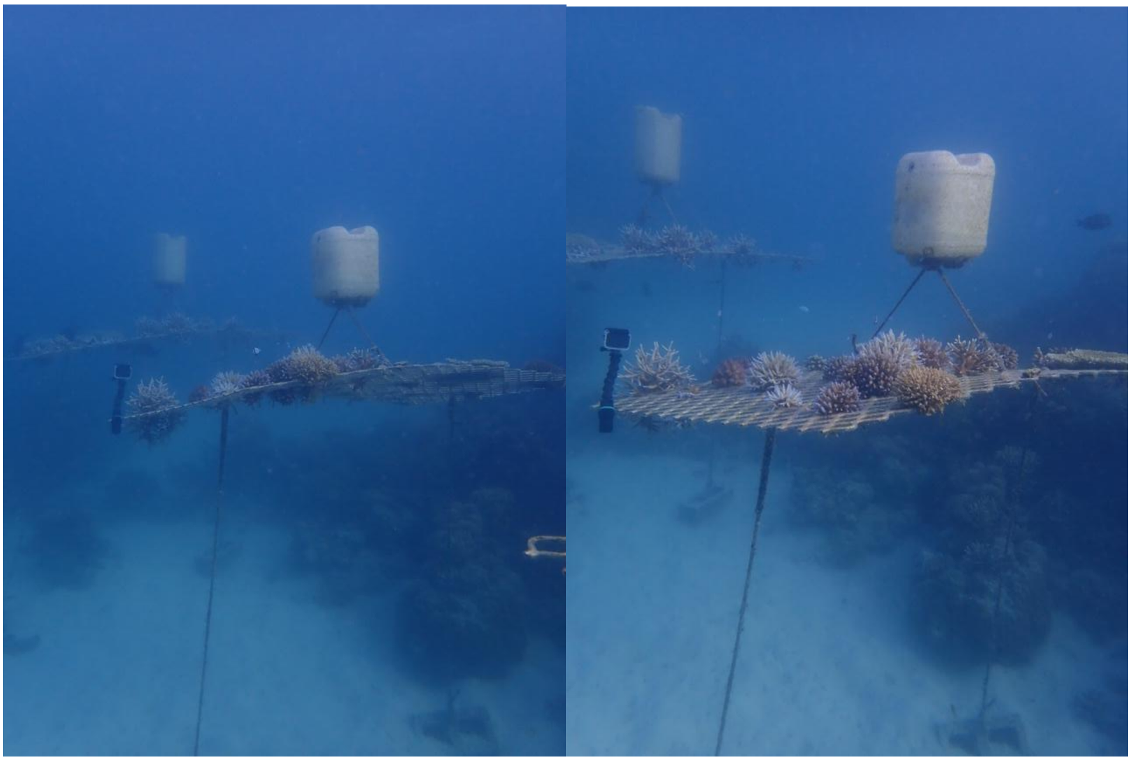


Figure S2.3. Fish video survey setup consisting of a GoPro Hero 8$^{®}$ camera attached to a GoPro$^{®}$ "Jaws: Flex Clamp" clipped onto an adjacent nursery and positioned so cameras would capture the entirety of the subject nursery. Photo credit: Gemma M Gillette.

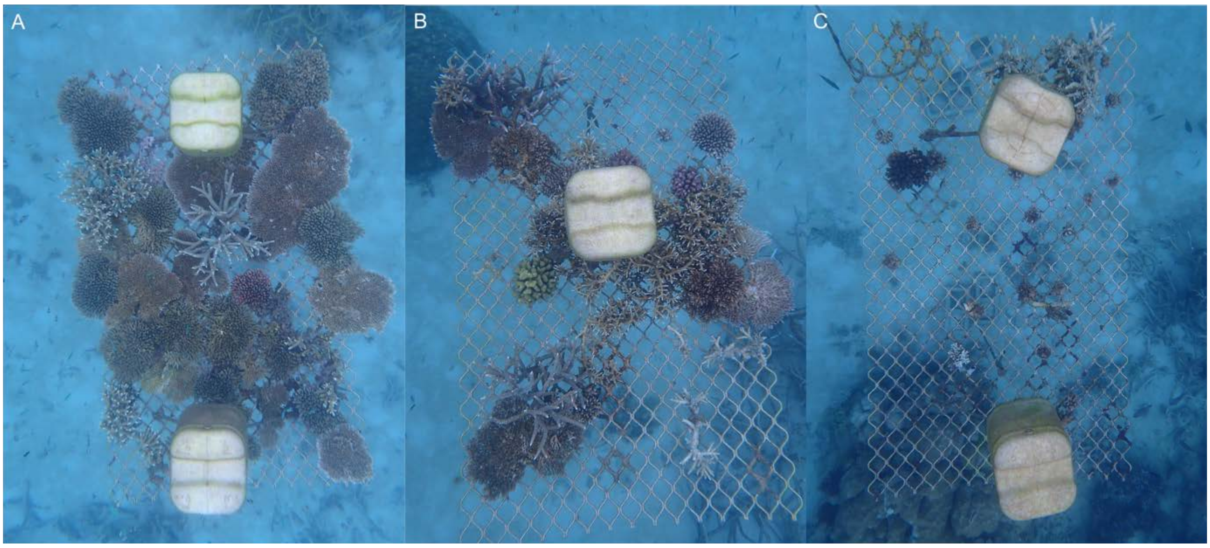
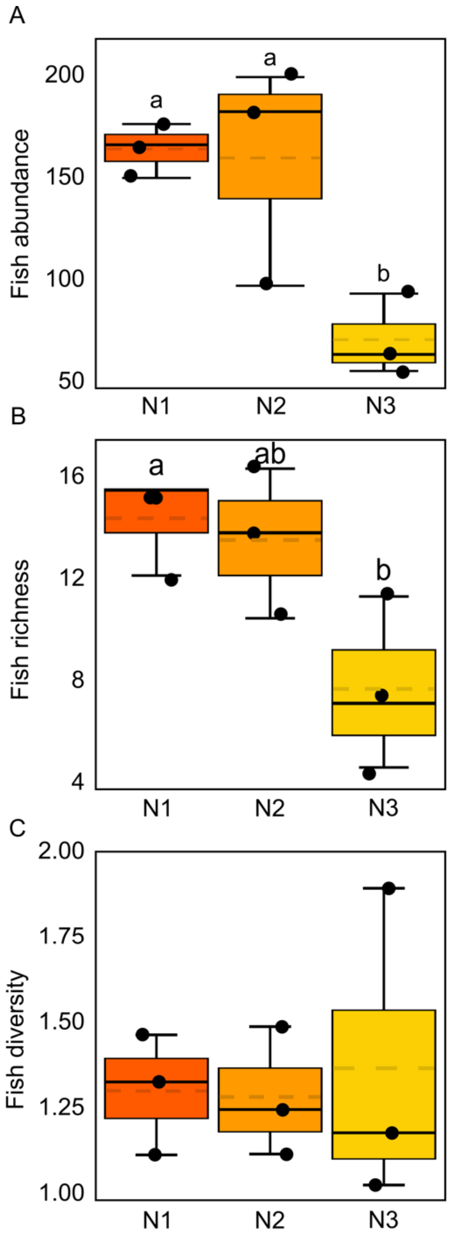


Figure S2.4. Downward-facing images of nursery 1 (A), nursery 2 (B) and nursery 3 (C) located at "Mojo" tourism mooring site, Opal Reef, Great Barrier Reef. Photo credit: Gemma M Gillette.



D

	N1	N2	N3
Coral composition	🟥	🟧	🟨
Coral morphological richness	5	5	4
Coral richness	12	12	3
Coral cover (%)	60	38	9

Figure S2.5. Coral and fish assemblage composition on coral nurseries used for restoration at "Mojo" mooring, Opal Reef (n = 3 nurseries; N1, N2, N3). Fishes were recorded using long-form (1 hr) video surveys at 3 timepoints (n = 3 per nursery; n = 9 total). Boxplots show (A) fish abundance, (B) fish richness, and (C) fish diversity. Coral composition for each nursery (D) was documented at the time of fish survey (27th February – 2nd March 2023). The absence of common letter over of the boxplots shows significant differences between clusters (ANOVA and Tukey HSD post-hoc; $p < 0.050$). The bold line within each boxplot indicates the median and the faint dashed line the mean. Standard error is displayed with horizontal lines attached to whiskers. Whiskers extend from the data minimum to the lower quartile and then from the upper quartile to the data maximum.

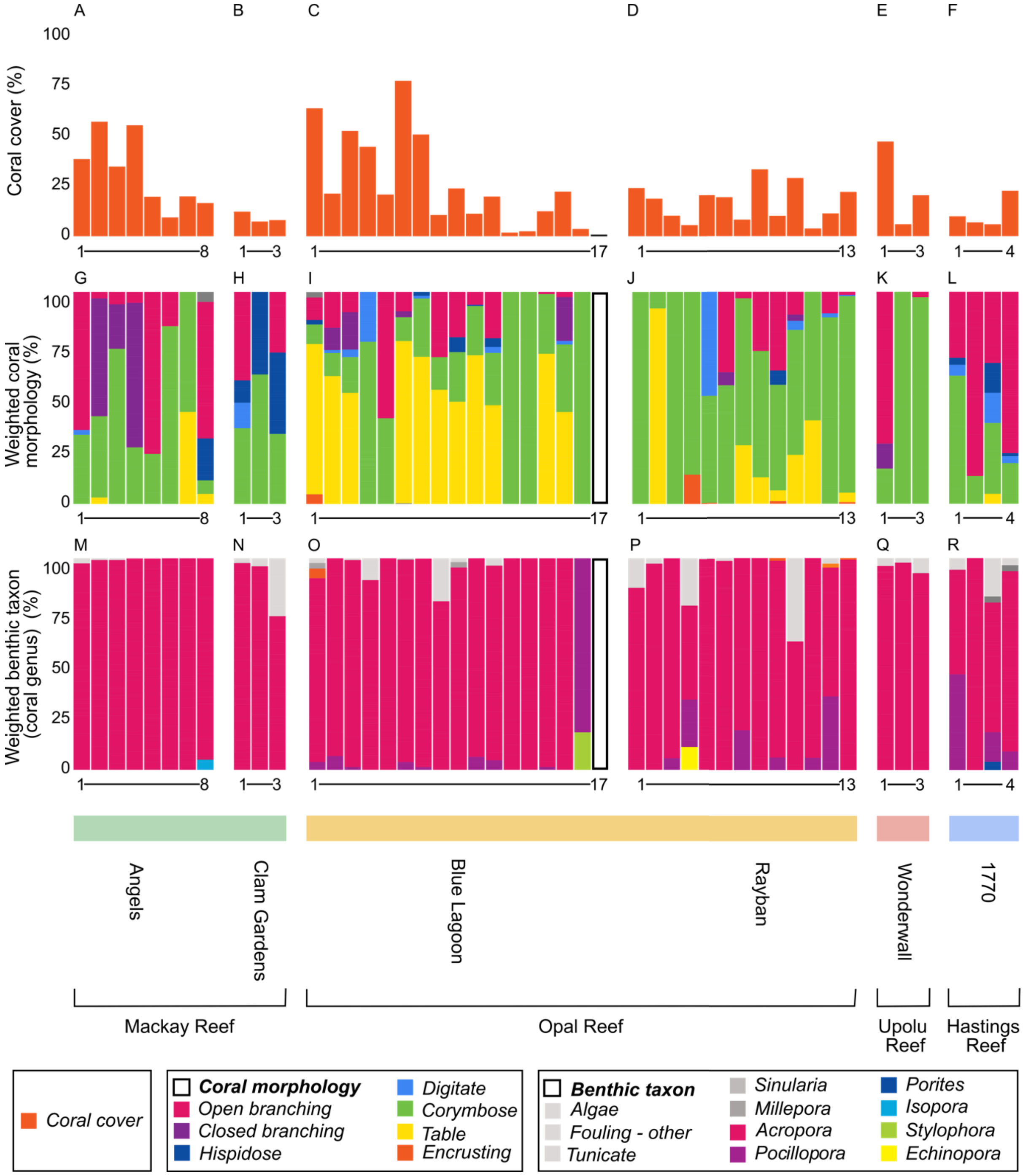


Figure S2.6. Weighted (%) surface area of benthic composition including (A-F) coral cover, (G-L) coral morphology and (M-R) benthic taxon (coral identified to genus) on coral nurseries (n = 48 total) at tourism mooring restoration sites. Horizonal bars colour mooring sites per Reef: “Angels” and “Clem Gardens” (Mackay Reef; green), “Blue Lagoon” and “Rayban” (Opal Reef; yellow), “Wonderwall” (Upolu Reef; red) and “1770” (Hastings Reef; blue). Rapid video surveys were used at random on nurseries to record fish assemblages (n = 69 surveys total).

2.9.2 Supplementary tables

Table S2.1. A Kruskal-Wallis test to evaluate differences in fish abundance, richness and diversity on coral nurseries (n = 48) between tide types (high, low, ebb or flow). Nurseries were deployed at "Angels" and "Clem Gardens" (Mackay Reef), "Blue Lagoon" and "Rayban" (Opal Reef), "Wonderwall" (Upolu Reef) and, "1770" (Hastings Reef) restoration sites on the northern Great Barrier Reef. Rapid video surveys were used at random on nurseries to record fish assemblages (n = 69 surveys total). Results were considered statistically significant at $p < 0.05$.

	Chi-squared	**df**	**p value**
Abundance	2.41	2.00	0.299
Richness	3.17	2.00	0.205
Diversity	2.25	2.00	0.324

Table S2.2. A Kruskal-Wallis test to evaluate differences in fish abundance, richness and diversity on coral nurseries (n = 48) between reef locations: Mackay Reef ("Angels" and "Clem Gardens"), Opal Reef ("Blue Lagoon" and "Rayban"), Upolu Reef ("Wonderwall") and Hastings Reef ("1770") on the northern Great Barrier Reef. Rapid video surveys were used at random on nurseries deployed to record fish assemblages (n = 69 surveys total). Results were considered significant at $p < 0.05$.

	Chi-squared	**df**	**p value**
Abundance	7.26	3.00	0.064
Richness	2.76	3.00	0.430
Diversity	3.79	3.00	0.286

Table S2.3. Generalised Additive Models (GAM) on the relationship between coral composition (coral cover, richness, and morphological richness) and fish assemblage metrics (abundance, richness and diversity) on coral nurseries (n = 48). Nurseries were deployed at "Angels" and "Clem Gardens" (Mackay Reef), "Blue Lagoon" and "Rayban" (Opal Reef), "Wonderwall" (Upolu Reef) and, "1770" (Hastings Reef) restoration sites on the northern Great Barrier Reef. Rapid video surveys were used at random on nurseries to record fish assemblages (n = 69 surveys total). GAM models applied the zero-inflated Poisson distribution to count data (fish abundance and richness) and the Tweedie distribution to continuous data (fish diversity and biomass). Results were considered significant at $p < 0.05$.

Fish abundance						
Fish abundance: Coral cover and coral richness						
		Estimate	SE	z value	p value	Deviance explained (%)
Coral richness		-0.05	0.02	-2.01	0.044	
Coral richness	Coral cover	0.00	0.00	2.74	0.006	49.80
		edf	Ref.df	Chi.sq	p value	
Coral cover		8.61	8.96	169.90	0.000	
Fish abundance: Coral cover and coral morphological richness						
		Estimate	SE	z value	p value	Deviance explained (%)
Coral morphological richness		-0.33	0.05	-6.05	0.000	
Coral morphological richness	Coral cover	0.01	0.00	5.06	0.000	47.50

		edf	Ref.df	Chi.sq	p value	
Coral cover		8.61	8.95	161.8	0.000	
Fish richness						
Fish richness: Coral cover and coral richness						
		Estimate	SE	z value	p value	Deviance explained (%)
Coral richness		0.08	0.03	2.83	0.005	
Coral richness	Coral cover	0.00	0.00	-1.56	0.119	20.80
		edf	Ref.df	Chi.sq	p value	
Coral cover		1.00	1.00	6.81	0.009	
Fish richness: Coral cover and coral morphological richness						
		Estimate	SE	z value	p value	Deviance explained (%)
Coral morphological richness		-0.05	0.05	-0.92	0.356	
Coral morphological richness	Coral cover	0.00	0.00	0.58	0.562	20.30
		edf	Ref.df	Chi.sq	p value	
Coral cover		1.00	1.00	1.98	0.160	
Fish diversity						
Fish diversity: Coral cover and coral richness						
		Estimate	SE	z value	p value	Deviance explained (%)
Coral richness		0.06	0.03	1.86	0.068	
Coral richness	Coral cover	0.00	0.00	-1.06	0.291	7.73
		edf	Ref.df	F value	p value	
Coral cover		1.00	1.00	1.40	0.241	
Fish diversity: Coral cover and coral morphological richness						
		Estimate	SE	z value	p value	Deviance explained (%)
Coral morphological richness		0.04	0.07	0.62	0.539	
Coral morphological richness	Coral cover	0.00	0.00	-0.19	0.853	3.61
		edf	Ref.df	F value	p value	
Coral cover		1.00	1.00	0.321	0.573	

Chapter 3: Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef.

This chapter has been prepared as a fully drafted manuscript for submission.

Gillette, G.M., Camp, E.F., Edmondson, J., Booth, D.J., Scott, R.I, Suggett, D.J. Natural maintenance of fouling on coral nurseries used across the Great Barrier Reef.

Author contributions:
GMG, DJS, EFC, DJB conceived the research. GMG, DJS, EFC, JE, RIS contributed to the planning and execution of data collection. GMG conducted data analysis and drafted the manuscript with editorials from EFC and DJS. All authors provided subsequent editorial input.

All authors declare that the author contributions outlined above are a true reflection of the authorship of this thesis chapter:

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3.1 Abstract

In-situ coral nurseries have become widespread across the Great Barrier Reef (GBR) as part of tourism-led stewardship efforts to grow and replant coral at sites of high socio-economic value. Such nursery practices are aimed at reducing costs and increasing propagation efficiency to remain effective at scale. Nurseries are therefore routinely placed in proximity (1-3 m) to natural reefs with diverse fish assemblages, where the presence of fishes is assumed to reduce turf fouling on nursery structures that compete with coral for space. However, the extent to which this fouling occurs has not yet been examined. We therefore assessed the influence of excluding fishes > 2.5 cm on the coral nursery benthic composition at two GBR sites. Settlement substrates to assess fouling, as well as coral fragments of *Acropora* typically used for propagation on the GBR, were placed inside cage-exclusion treatments on nurseries at 2 reef sites for 112 days. Short-term video surveys were used to inform fish species present on nurseries that would be excluded by the cages. Across sites, an average fourfold increase in the biomass of filamentous turf was observed within cages compared to uncaged treatments. Coral survivorship within cages with enhanced biofouling was species-specific and varied between sites. Fish assemblages on nurseries at both sites were dominated by *Pomacentridae* abundance; however, biomass largely comprised species belonging to *Scarinae* and *Acanthuridae*. Bite rate analysis showed that *Scarinae* and *Acanthuridae* families interacted the most with nursery frames and that these interactions were likely removed within caged areas. Results presented here demonstrate the importance of fish assemblages in supporting nursery operations.

3.2 Introduction

The preservation of reef ecosystems and the wealth of ecological, economic, social, and cultural values they provide is contingent on the immediate mitigation of anthropogenically induced stress (Hein et al., 2017; Sully et al., 2022; Bay et al., 2023). This will require a hybrid approach whereby global emissions and local water quality and fisheries management occur alongside strategic, active management approaches that enhance the resilience of coral reef ecosystems against future climate conditions (Anthony et al., 2020; Shaver et al., 2022; Suggett et al., 2023). Coral propagation practices, regarded as active management strategies, are widespread among reef stakeholders and stewardship-led projects that aim to protect socio-ecological values at degraded reef sites (Boström-Einarsson et al., 2020). Coral cover at these sites is improved whereby naturally detached, or deliberately produced, coral fragments are reared on man-made structures known as "nurseries", then subsequently attached (out-planted) onto natural reef substrate (McLeod et al., 2020).

The success of these propagation and out-planting practices hinges on the ability to optimise and scale up approaches (Suggett et al., 2019; Boström-Einarsson et al., 2020). As such, nurseries that facilitate the growth of coral fragments to a size where out-plant survival is enhanced have been widely employed across reef stewardship projects (Rinkevich, 2005; Boström-Einarsson et al., 2020). The design of nurseries is often tailored to the specific reef environments within which they are deployed (Rinkevich, 2019), to meet outcome-specific requirements such as to grow particular morphologies (Nedimyer et al., 2011) or to increase the diversity of coral taxa for out-planting (Howlett et al., 2021). However, all coral nurseries inevitably attract additional species from the local environment and form complex systems of diverse interacting organisms (Shafir & Rinkevich, 2010). These commonly include local fish assemblages, though also fouling organisms that settle on nursery structures and may impede the ability of nurseries to support coral growth (Shafir et al., 2009).

Fouling by primary producers (filamentous turf, crustose coralline algae and macroalgae) or sessile invertebrates (tunicates, sponges, hydroids, bivalves, and barnacles) may adversely impact coral growth and survivorship on nurseries as species compete for shared resources (Shafir & Rinkevich, 2010; Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Knoester et al., 2019; Knoester et al., 2023). Consequently, fouling maintenance on nurseries is an essential but costly investment for coral propagation activities (Shafir et al. 2010; Johnson et al. 2011; Hyde et al. 2013). However, in areas with reduced coral biomass but stable fish assemblages, coral propagation often occurs against a backdrop of "natural maintenance" on adjacent reefs, facilitated by local fish assemblages (Green & Bellwood, 2009; Frias-Torres et al., 2015a; Tebbett et al., 2022). While the presence of fish assemblages in structuring benthic communities on natural reefs is well established (e.g. Burkepile & Hay, 2008; Green & Bellwood, 2009; Bellwood et al., 2014a; Tebbett et al., 2022) their influence on nurseries remain scarce, particularly on the Great Barrier Reef (GBR) where the rate of fouling or fouling reduction in the presence of fish assemblages has not been explored, yet forms a key aspect of nursery operations.

On the GBR, > 120 mid-water coral nurseries have been deployed at > 30 stewardship sites through the science-tourism site stewardship initiative, the Coral Nurture Program (CNP). These nurseries not only support coral stewardship-based management activities by generating coral biomass for subsequent out-planting (Howlett et al., 2022) but also serve as additional habitats for various fish species (***Chapter 2***). Importantly, CNP reef stakeholders deploy nurseries in close proximity (1-3 m) to natural reefs to encourage fish usage of structures, since their presence has been assumed to reduce filamentous turf fouling. Though, the extent to which this fouling occurs is unknown. We therefore employed a low-cost and small-scale method to empirically examine the impact of excluding fishes (> 2.5 cm) on nursery benthic communities. This method was designed so it could be replicated by reef stakeholders to assess the effects of local fish assemblages on nursery productivity at relative ease within existing infrastructure and practices. Coral fragments of *Acropora* typically used for propagation on the GBR as well as settlement substrates readily available to stewards for the assessment of fouling growth were placed inside cage-exclusion treatments for 112 days at 2 reef stewardship sites. Findings were supplemented by short-term video surveys to inform the presence of fish species on coral nurseries at sites and to assess interactions, including biting behaviours, with the frames, providing insights as a snapshot of overall activity. We discuss these findings and the species interactions that are key to CNP cost-effective nursery operations. In doing so, we demonstrate how early evaluations of prospective nursery sites may be crucial for tailoring site-specific best practices for nursery management.

3.3 Methods

The experiment and observations were conducted from February to June 2022, covering the transition from Austral summer to winter, at 2 CNP nursery sites on Opal Reef (16°13’37.5”S 145°53’42.0”E), an offshore reef on the northern GBR (detailed in Suggett et al., 2019; Howlett et al., 2021; *Figure S3.1.*). Opal Reef spans 2 zones created by the Great Barrier Reef Marine Park Authority (GBRMPA) (GBRMPA 2017). As such, sites are subject to contrasting zoning as well as specific environmental conditions: (i) site “Mojo”, located in a Conservation Park Zone, permits limited hook-and-line fishing and experiences strong tidal currents owed to its position near a deep-water channel leading to the Coral Sea; and (ii) site “Rayban”, centrally situated on Opal Reef in a sheltered sandy lagoon area that lacks strong currents and is within a Marine National Park Zone that prohibits fishing activities (see Suggett et al., 2019; Howlett et al., 2021; Strudwick et al., 2023; *Figure S3.1.*).

Propagation activities using coral nurseries, established at both sites since 2018, are aimed at preserving tourism service values in response to the 2016-2017 mass bleaching events (Suggett et al., 2019; Howlett et al., 2021; Howlett et al., 2022; Roper et al., 2022). Routine benthic and fish surveys on natural reefs were undertaken prior to this study (February 2021). Surveys were conducted at the Rayban nursery site and ~150 m from the Mojo nursery site, at a neighbouring mooring ("Blue Lagoon"; detailed in ***Chapter 2***). Fish assemblage abundance on natural reefs at both sites was dominated by *Pomacentridae*, *Lutjanidae* and *Pomacanthidae* families (***Chapter 2***). Mean coral cover was 25% and 46% at Rayban and Blue Lagoon, respectively. *Acropora* was the most abundant genus across sites. Percentage coral cover at Blue Lagoon was consistent with later surveys conducted at the Mojo nursery site (Roper et al., 2022).

Each nursery consisted of aluminium mesh (2.0 × 1.2 m), fastened with rope to 2-4, 9 kg besser blocks, and 2, 20 L floats. This arrangement suspended the aluminium mesh mid-water column, approximately 1-2 m above the substrate, reaching a depth of 4-6 m at low tide (Howlett et al., 2021; *Figure S3.2.*). All nursery structures were positioned on sand about 1-5 m from the natural reef and all activities within the study were carried out under GBRMPA permits G18/40023.1 and G20/43740.1.

3.3.1 Cage exclusion experiment

A small-scale cage exclusion experiment was deployed for 112 days to quantify the turf fouling accumulation on nurseries when fishes > 2.5 cm were excluded. Six nurseries were included in this study 3 nurseries that were randomly chosen from arrays of 10 nurseries at each of the 2 sites. Nurseries were spaced between 5 and 100 m apart at each site. Each of the 6 nurseries was equipped with a set of cage exclusion treatments, including (i) a full cage; (ii) a partial cage with sides only and no top covering, to allow feeding access and to act as a test control for caging effects, such as altered light availability or flow (Thacker et al., 2001; Bonaldo and Bellwood, 2011); and (iii) a cattle tag marked area with no caging to act as a full control (*Figure 3.1.*). Within each treatment was a settlement substrate and multiple fragments of *Acropora* that were fastened to the nursery using cable ties. Settlement substrates consisted of a small piece (~30 x 9 cm) of pre-weighed nursery aluminium mesh. Treatments at Mojo enclosed *Acropora aff. abrolhosensis* (2 fragments per treatment, n = 18 total). At Rayban 2 fragments of *Acropora donei* and 2 fragments of *Acropora kenti* were included per treatment (2 fragments per species, per treatment, n = 18 per species total). While coral species varied between sites within treatments, the selected species were representative of their site. They were harvested from donor colonies located on the adjacent natural reef and commonly grown on nurseries, at times near each other (e.g. *Acropora donei* and *Acropora kenti*; see *Figure S3.3.*). Coral fragments were ca. 5 cm maximum length and hence were of sizes typically used for propagation on nurseries (Suggett et al., 2019; Howlett et al., 2022).

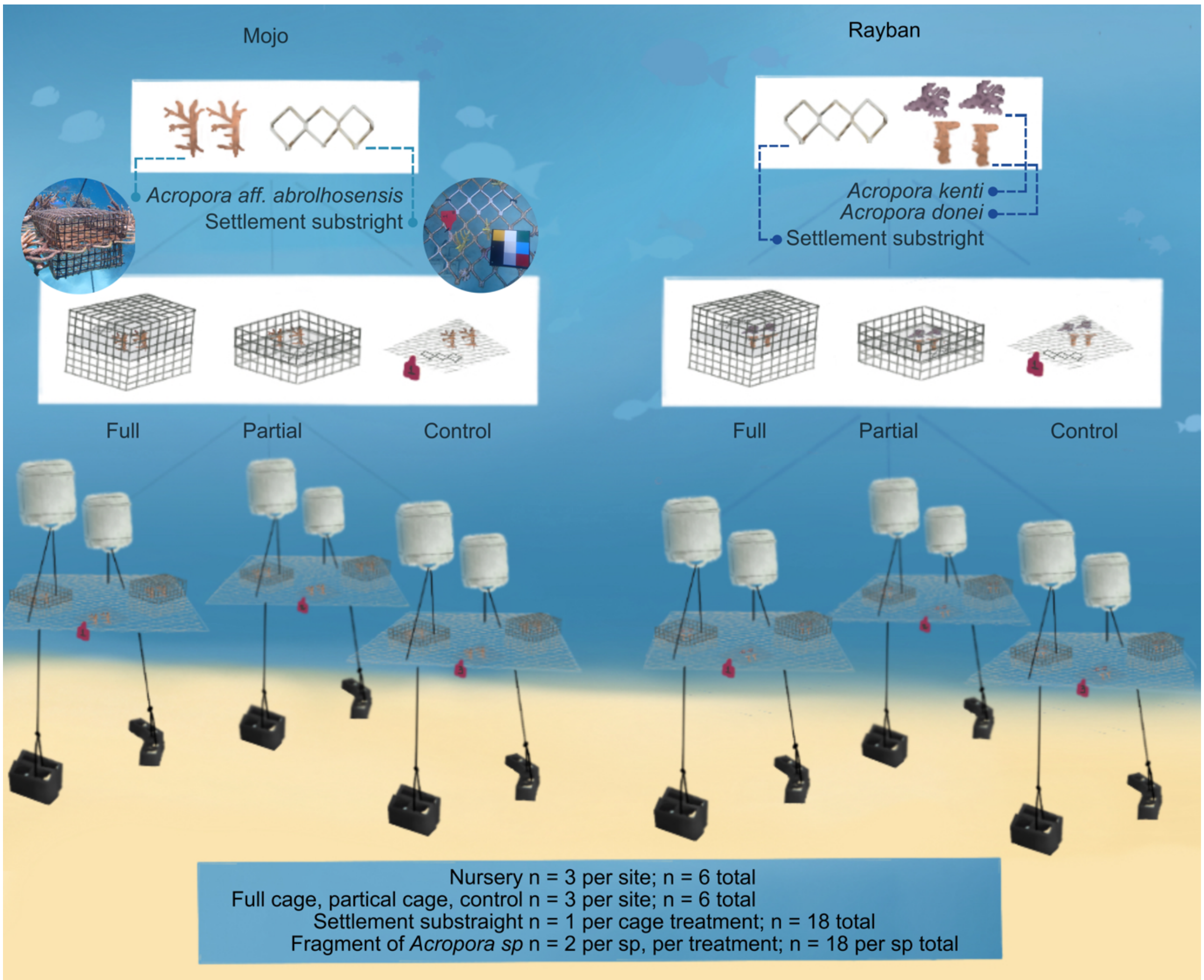

Figure 3.1. A schematic of the cage exclusion experimental design. Three mid-water coral nurseries were randomly chosen at 2 reef stewardship locations (“Mojo” and “Rayban”; n = 6 total). Each nursery was fitted with cage treatments: full, partial and controls (n = 3 per site, n = 6 total). Coral fragments (~ 5 cm) of *Acropora* were locally harvested from donor colonies on the adjacent natural reefs and placed within each treatment (n = 2 per sp, per treatment; n = 18 per sp, total). Settlement

substrates (~30 x 9 cm) of nursery aluminium mesh were also placed within each treatment (n = 1 per treatment; n = 18 total).

Full and partial cages were installed on the top and underside of nurseries. Cages were assembled using 32 x 32 x 32 cm plastic mesh held together using cable ties and were mesh comprising square openings that excluded fishes > 2.5 cm^2. Cages were inspected four weeks after deployment, and any fouling accumulation on the mesh cages was removed using fine bristle brushes. To further indicate any potential cage-induced shading effects, temperature (°C) and light (lx) levels were measured using intercalibrated $HOBO^{TM}$ data loggers on a calm, cloud-free day (February 2022). One nursery at each site was randomly selected and loggers were deployed within treatments (full, partial and control). Loggers were positioned flush to the aluminium mesh and recorded at 1-min intervals between 1130-1750 hr or 1400-1750 hr (local time) at Mojo or Rayban, respectively. Replication of HOBO readings within treatments at the site was not carried out; instead, this information served as an indication of any shading effects. Average temperature between treatments was consistently 29°C. Light intensity (lx) within control treatments was on average 24-54 % greater than the full cage and 5-49 % greater than the partial cage. Light intensity within partial cages was 3-23 % greater than full cage treatment (*Table S3.1.; Table S3.2.*).

All treatments were photographed using an Olympus TG6 Tough Camera at the start and end of the experiment (e.g. *Figure 3.2c.*; *Table S3.3.*). Upon termination of the experiment, but before removing cages and settlement substrates, the total coral cover on nurseries, including fragments within control and partial cage treatments, was assessed using downward-facing photographs (*Table S3.3.*). Coral survivorship within treatments (the number of coral fragments with any living tissue, e.g. Ware et al., 2020; Howlett et al., 2021) was recorded. At this time, 1 Rayban nursery, with a full set of treatments (full, partial, and control), was found to have lost flotation, though was still partially raised off the substrate (19 cm), resting on 4 besser blocks. Nurseries underwent regular inspections every 1-2 weeks, suggesting that this likely occurred just prior to the conclusion of the experimental period. We retained the use of this replicate and discuss its impact on the experimental trends. All settlement substrates within treatments were placed in labelled zip lock bags, returned to land within 4 hrs and blotted dry inside aluminium containers. Substrates were then oven-dried (100°C) for 12 hrs and weighed (e.g. EnricSalaa & Boudouresque, 1997; McAndrews et al., 2019).

3.3.2 Fish video surveys

Fish families on nurseries were surveyed using short-form video surveys in the 3 days prior to termination of the experiment (June 2022). While fish assemblages on artificial structures are known to change over time (Godoy et al., 2002; Neves dos Santos & Zalmon, 2015; Jaxion-Harm et al., 2018), we focused on the presence of fishes at the end of the experiment only, aiming to understand their potential interaction with nurseries as a snapshot of activity. Video survey length was determined by time onsite as per normal tourism operator site visitation. One video survey per nursery per day (n = 18 total) lasted 20-25 mins each. GoPro Hero 8® cameras were attached to a GoPro® "Jaws: Flex Clamp" and affixed to nursery floats (*Figure S3.4.*). As such, cameras were high enough to capture the entire nurseries, with all 3 treatments in view (full, partial and control; *Figure S3.4.*). Videos were taken between 0900-1700 hr and were evenly distributed between low and high tides (*Table S3.5.*). Water clarity during this time was between 10-13 m horizontal visibility.

Use of our shorter-form video approach was previously verified at Opal Reef sites (***Chapter 2***) and predicted to capture an average of > 80% of fish abundance compared to longer > 1 hr videos (***Chapter 2***; *Table S3.6.*). A period of 2.5 mins was removed from the start and end of recorded footage to account for diver disturbance, resulting in video footage lasting 17.5 mins. Fishes throughout these videos were counted and identified to species level. Individual fishes that could not be confidently identified to species were grouped into their respective families or documented as "unknown". MaxN abundance (i.e., the maximum number of individuals per species featured in each video, e.g. Fitzpatrick et al., 2012; Scott et al., 2015; Reeds et al., 2018) were recorded per species and length class (2.5-5, 5.1–7.5, 7.6–10, 10.1–15, 15.1–20, 20.1–25, 25.1–30, >30 cm). MaxN counts were used to avoid overestimations of fish abundance since individuals repeatedly moved in and out of the video field of view. Fish length class was estimated using the nurseries of known size as a reference guide as well as the Image J (Schneider et al., 2012) measuring feature to calibrate the viewer's length estimates at the start of each video processing session. Fish biomass estimates were calculated using the power model equation: $W = aL^b$, using species-specific length-weight relationships (Wolfe et al., 2020) documented on Fishbase (Froese & Pauly, 2018) and the mean length of each length class. Bite rates observed per species were recorded irrespective of MaxN abundance and are not synonymous with consumption. Rather bite rates are used to highlight which fish families interacted the most with nurseries. Singular bites were defined as those involving a rapid movement of the head toward and away from the nursery (Bellwood & Fulton, 2008). Only visible bites were counted, therefore fish feeding behind the floating buoys not captured by the video were omitted.

3.3.3 Statistical analysis

Analysis was performed using *R* version 1.3.1093 (RStudio Team 2023). Dry weight fouling biomass (g) was compared between treatments and sites. A non-parametric two-way Scheirer-Ray-Hare extension to the Kruskal-Wallis test was used due to data non-normality as indicated by the Shapiro Wilks Test (McKight & Najab, 2010; Hanusz & Tarasińska, 2015). In the case of a significant *p*-value (alpha = 0.05), Dunn's post-hoc test with the Bonferroni–Holm method was used to assess differences.

Analysis of coral survivorship between treatments was conducted on a species basis. The Shapiro Wilks Test (McKight & Najab, 2010; Hanusz & Tarasińska, 2015) confirmed data non-normality, thus a one-way, non-parametric Kruskal-Wallis test was used to independently evaluate *Acropora donei* and *Acropora kenti* survivorship between treatments at the Rayban stewardship site. At the Mojo stewardship site, *Acropora aff. abrolhosensis* exhibited 100% survival and a Kruskal-Wallis was not used as there were no differences between treatments.

Fish video richness and biomass data on nurseries passed tests for normality (Shapiro Wilk’s Test; Hanusz & Tarasińska, 2015) and equal variance (Bartlett’s Test; Arsham & Lovric, 2011), thus a one-way Analysis of Variance test (ANOVA; St & Wold, 1989) was used to assess differences between sites. Fish abundance and bite rate data did not pass the Shapiro-Wilks Test for normality, thus a one-way non-parametric Kruskal-Wallis test examined differences between sites (McKight & Najab, 2010).

3.4 Results and Discussion

Coral nursery structures naturally biofoul, a process that is widely documented to reduce coral growth and survivorship (McCook et al., 2001; Chadwick & Morrow, 2011; Bica & Solomonovich, 2020; Olinger et al., 2021). Fouling on nurseries is typically removed by hand with brushes (Johnson et al., 2011; Henry et al., 2021; Dehnert et al., 2022; Maurer et al., 2022), a time- and cost-intensive practice yet to be commonly applied by CNP nursery operators on the GBR (Howlett et al., 2021). A small-scale assessment conducted within CNP routine stewardship activities therefore tested the extent to which the exclusion of fishes changed nursery benthic composition.

3.4.1 Filamentous turf accumulation

Fouling was quantified as total dry weight without further qualifying the fouling species. However, we observed the community broadly, noting that it almost entirely consisted of filamentous turf. Exclusion of fishes > 2.5 cm increased the biomass of this filamentous turf on coral nurseries at both Mojo and Rayban reef stewardship sites (n = 3 nurseries per site; Scheirer-Ray-Hare, $H = 5.95$, $p = 0.015$; *Figure 3.2.*; *Table S3.7.; Table S3.8.*). Despite distinct flow regimes (Mojo of higher flow compared to Rayban) previously documented at these sites (Strudwick et al., 2023), filamentous turf fouling between treatments was greater than in controls at the two sites (Scheirer-Ray-Hare, $H = 0.10$, $p = 0.747$; *Figure 3.2.*; *Table S3.8.*). Specifically, filamentous turf biomass in the full cage treatments was on average > 3-fold greater than the control treatments at Mojo and > 4-fold greater at Rayban (Dunn's post hoc test, Z = -2.84, $p_{.adj} = 0.013$; *Figure 3.2.*; *Table S3.7.; Table S3.8.*). Over the course of the experiment 1 Rayban nursery lost flotation and rested on besser blocks 19 cm off the substrate, but fouling extent for this nursery was still consistent with that for the 2 other nurseries intact at this site (Kruskal–Wallis test, $X^2 = 0.64$, $p = 0.725$; *Table S3.8.*).

Mean filamentous turf accumulation in full cage treatments at Rayban was twice that in partial cage treatments, and within the partial cage treatments fouling was more than doubled compared to the controls ($p < 0.05$, see *Table S3.8.; Table S3.7.*). Similarly, filamentous turf biomass within full cage treatments at Mojo exceeded that of partially-cage treatments, exhibiting an increase of > 3-fold in fouling growth compared to partial caged plots ($p < 0.05$, see *Table S3.8.; Table S3.7.*). Intriguingly, partial-cage treatments at Mojo had marginally less filamentous turf (2.7%) than the controls, though this difference was not statistically significant ($p > 0.05$, *Table S3.8.; Table S3.7.*).

Given the shading effects induced by the cages (*Table S3.2.*), the extent of fouling accumulation observed in cage treatments may be an underestimate, and thus filamentous turf growth may have been even higher with greater access to increased light (see Dajka et al. 2021).

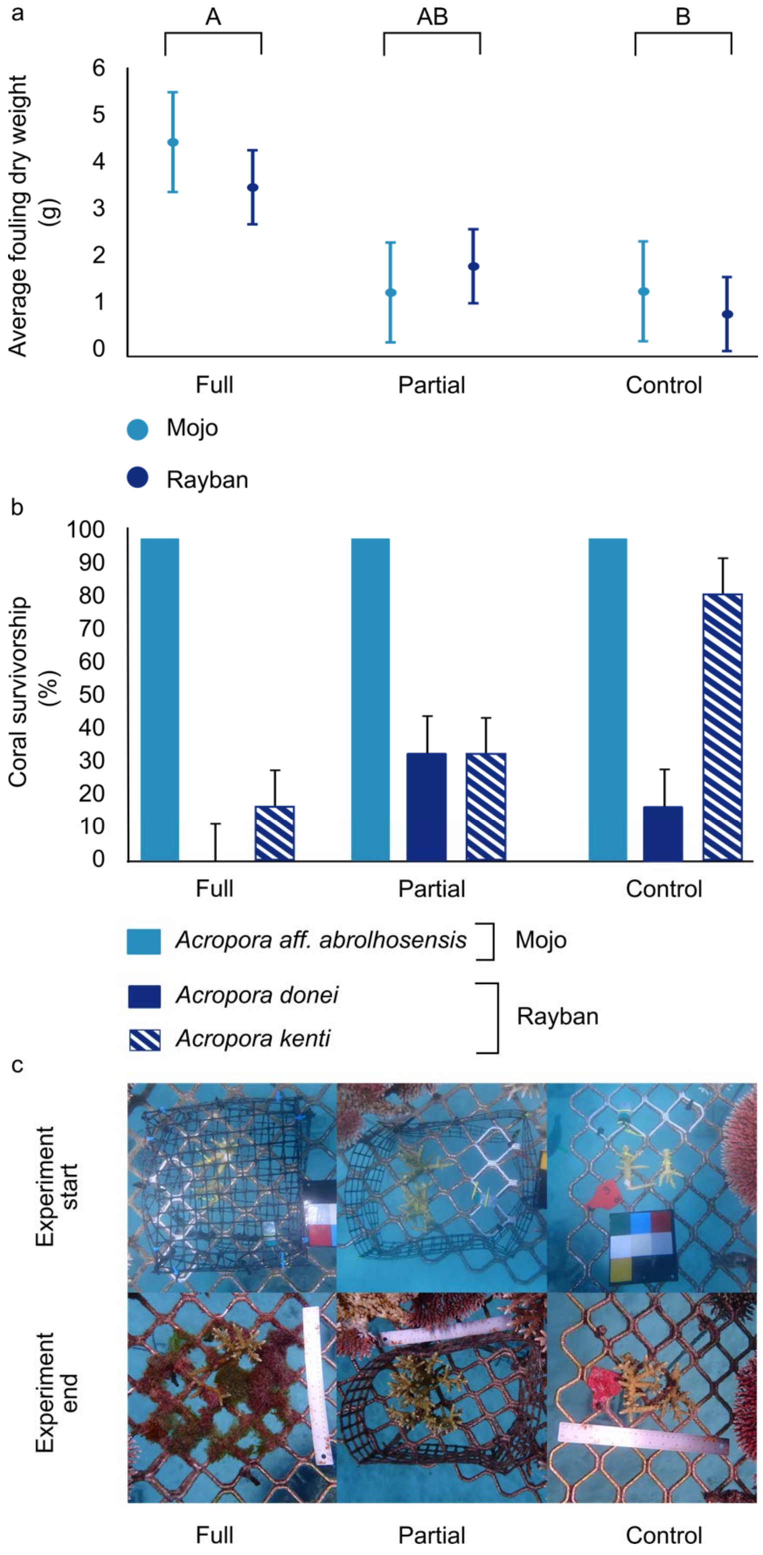

Figure 3.2. a) Average fouling biomass (g) in full, partial and control treatments at "Mojo" (light blue) and "Rayban" (dark blue) reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 3 per treatment, per site; n = 6 per treatment, total). Bars represent the standard error and differences

between treatments, as determined by a non-parametric Scheirer-Ray-Hare test (significant at $p < 0.05$) and are represented by the absence of a common letter. b) Percentage survival of coral fragments at Mojo (solid light blue, *Acropora aff. abrolhosensis*; n = 18) and Rayban (solid dark blue, *Acropora donei*; striped dark blue, *Acropora kenti*; n = 18 per species). Error bars represent standard error. c) An example of before and after comparison images of experimental treatments at a Mojo nursery upon installation (top) and completion (bottom) of the experiment after 112 days. Objects are placed within each image for scale.

The rapid accumulation of fouling we observed aligns with those of the only previous cage exclusion experiment to evaluate the effect of fish presence on nursery fouling. After 100 days, Kenyan Coral Tree^{TM} nurseries exhibited an 8-fold increase in a combination of macroalgae, crustose coralline algae (CCA), epilithic algae matrix (EAM) and molluscs where fishes were not allowed access (Knoester et al., 2019). Findings are consistent with evidence of increases in algae on natural reefs when fishes have been excluded; for example, on the GBR (90 – 200% increase in macroalgae after 30 months; Hughes et al., 2007) and in other regions globally (e.g. in Japan > 40% increase in epilithic algae after 25−50 days; Akita et al., 2022). Fouling on nursery structure can be diverse, not limited to algae, and include organisms such as tunicates, sponges and barnacles (Edwards et al., 2010; Johnson et al., 2011; Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b). Filamentous turf algae observed within this study appears to be a ubiquitous concern across many restoration projects that aim to support coral growth (Edwards et al., 2010; Cetz-Navarro et al., 2013; Frias-Torres et al., 2015a), which has led to investments in anti-fouling approaches, particularly through the application of coatings (e.g. Shafir et al., 2009; Tebben et al., 2014; Roepke et al., 2022). Despite these efforts, most coral nursery projects continue to rely on manual de-fouling performed by humans (Johnson et al., 2011; Hyde et al., 2013; Maurer et al., 2022). Though, nearly all efforts to minimise fouling beyond the natural maintenance performed by fishes inevitably results in additional costs.

3.4.2 Fish abundance, biomass, and interaction with nursery structures

Fish assemblages on nurseries surveyed before the end of the experiment were characterised by abundant *Pomacentrinae* (predominantly *Chromis viridis*) fishes, alongside several *Scarinae* and *Acanthuridae* species that comprised the majority of fish biomass at both reef stewardship sites (*Figure 3.3.*). At Mojo, *Plectropomus oligacanthus* fish also contributed considerably to total biomass counts, as fish sheltering under nurseries for extended periods (*Figure 3.3.*). In spite of Mojo being situated within a Conservation Park Zone (allowing limited hook-and-line fishing), and Rayban within a Marine National Park Zone (where fishing is prohibited), fish assemblages between the 2 reef stewardship sites did not statistically differ in abundance (Kruskal–Wallis test, $X^2 = 1.71$, $p = 0.191$; *Table S3.9.*), biomass (ANOVA, $F = 0.32$, $p = 0.571$; *Table S3.9.*) or species richness (ANOVA, $F = 3.10$, $p = 0.097$; *Table S3.9.*) though bite rates differed between sites and were greater at Rayban (Kruskal–Wallis test, $X^2 = 3.90$, $p = 0.048$; *Table S3.9.*).

During video assessments, bite rates were also counted, and were highest for *Scarinae* (particularly *Scarus oviceps*) at Rayban and *Acanthuridae* (particularly, *Ctenochaetus binotatus*) at Mojo. A number of other fishes including *Labridae* species were also observed to bite on Mojo nurseries though to a lesser extent (*Figure 3.3.; Table 3.1.; Figure S3.5.*). These results indicate that these fishes frequently interact with the nursery frame. However, this study did not aim to assess consumption, and further work would be required to ascertain how much, if any, of the filamentous turf was directly ingested by fishes. Intriguingly, upon revisiting the experimental nurseries approximately 18 hrs after removing the exclusion cages, all filamentous turf fouling that had previously accumulated within the caged treatments had been cleared (per observation G. Gillette, see *Figure S3.6.*). Unfortunately, our surveys did not capture the organisms responsible for this rapid removal of filamentous turf after the experiment's end.

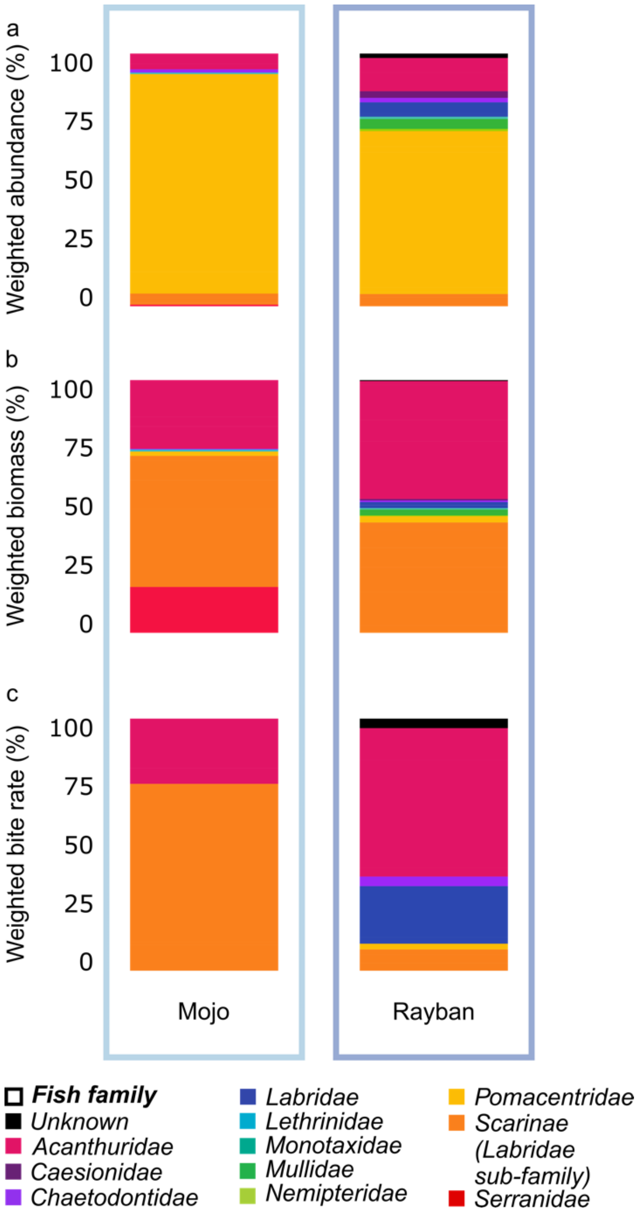

Figure 3.3. Weighted total fish abundance, biomass (g), and bite rate (number of bites) per species and coloured by family group (with the inclusion of *Scarinae*, a sub-family of *Labridae*) at "Mojo" and "Rayban" reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 9 video surveys per site). Outlines around plots correspond with site (Mojo: light blue; Rayban: dark blue).

Motivations for fish attraction to nurseries, which appear to correspond with fouling reduction, are secondary to the importance of fouling quantity removed, as the latter has important direct implications for time and funding resource allocation for nursery maintenance (e.g. Knoester et al., 2024; Scott et al., 2024). There are inherent challenges involved in recording all fish species within any constrained survey method (Colvocoresses & Acosta, 2007; Dickens et al., 2011; Misa et al., 2016). Our study aimed to document fish presence as a snapshot of activity, within the confines of normal stewardship operation, thereby diverging from conventional fish studies. However, insights gained from decades of fish trait-based, feeding function and ecological research may be useful for reef stakeholders looking to anticipate the function of background fish assemblages on nurseries. Though, predicted benefits of fish assemblages to nurseries should always be experimentally confirmed prior to significant restoration investment. Methods presented here offer a low-cost, small-scale means for reef stakeholders to empirically test how fish presence may influence nursery benthic communities. Given the extensive recognition of the importance of fishes in maintaining coral-dominant reefs (Nyström & Folke, 2001; Bellwood et al., 2004; Nyström et al., 2008; Diaz-Pulido et al., 2009; Tebbett et al., 2022), presence of fish assemblages on nurseries may be an important, but still poorly documented, component of nursery management. Our present study did not aim to directly assess consumption of filamentous turf (or other fouling material) on nurseries and thus direct fish function will only be putatively discussed.

Across survey sites, *Scarinae* fish, a sub-family of *Labridae*, constituted the greatest biomass and exhibited the highest interaction with nurseries, particularly prominent at the Mojo stewardship site. *Labridae* species observed to interact with Rayban nurseries, although to a lesser extent, target prey that ranges from benthic algae to benthic invertebrates and free-swimming fishes (Randall, 1967; Hobson, 1974; Westneat, 1995; Rice et al., 2008). Though, a series of detailed morphological, dietary, and behavioural studies have highlighted specifically the sub-family *Scarinae* as predominantly “microphages” (Clements et al., 2017; Nicholson & Clements, 2021; Nicholson & Clements, 2022; Manning & McCoy, 2023; Nicholson & Clements, 2023). Such studies demonstrate that *Scarinae* primarily target microscopic photoautotrophs, notably cyanobacteria, found on filamentous turfs, crustose coralline algae, or mat-forming benthic cyanobacteria (Clements et al., 2017; Nicholson & Clements, 2021; Nicholson & Clements, 2022; Manning & McCoy, 2023; Nicholson & Clements, 2023). Fishes such as these, may inadvertently remove other materials while feeding, though these actions are likely consequences of their feeding behaviour rather than underlying causes (Clements et al., 2017; Nicholson & Clements, 2021; Nicholson & Clements, 2022; Manning & McCoy, 2023; Nicholson & Clements, 2023). In addition, *Acanthuridae* species, extensively engaged with nurseries and followed *Scarinae* as the dominant components of biomass on CNP nurseries. These species could be further classified into functional groups with distinct modes of feeding (Tebbett et al., 2022). Predominate interacting species ranged from “brushers” to “sediment suckers” (Tebbett et al., 2022). Sediment suckers including *Acanthurus nigricauda*, the most abundant *Acanthuridae* species on nurseries, and brushers, such as *Ctenochaetus binotatus*, the most frequently observed interacting within nurseries, contributed to the particularly high incidence of bites at Rayban, selectively extracted particulate material (organic detritus and inorganic sediments) from turfs and microalgal films (Choat et al., 2002; Crossman et al., 2005; Bellwood et al., 2014b; Tebbett et al., 2018). These feeding modes can also remove diatoms, cyanobacteria and other microalgae and microbes from hard substrata (Marshell & Mumby, 2012; Tebbett et al., 2018) which are likely to be a nutritional resource to brushers and sediment suckers (Choat & Clements, 1998; Choat et al., 2004; Cissell et al., 2019), as they are for *Scarinae* species (Clements et al., 2017; Clements & Choat, 2018). Though, brushers can efficiently remove particulate material and minimise the removal of algae (Kelly et al., 2016; Tebbett et al., 2017), sediment suckers cannot selectively remove detritus and are likely to remove algae as well as particulates (Purcell & Bellwood, 1993; Tebbett et al., 2022). *Labridae* fish also observed to interact with Rayban nurseries, though to a lesser extent, target prey that ranges from benthic algae to benthic invertebrates and free-swimming fishes (Randall, 1967, 1980; Hobson, 1974; Westneat, 1995a, b). Grazing by *Scarinae*, *Acanthuridae* species alike may act as a disturbance that maintains reef substrates (particularly if dominated by particulate material and cyanobacteria) in cropped early successional states (Carpenter, 1986; Clements et al., 2017; Tebbett et al., 2022). Though, grazing intensities within and among species are likely to differ (Tebbett et al., 2022; Manning & McCoy, 2023). Additionally, further research could explore strategies to attract coral-associated fishes with these feeding patterns to nurseries in various locations, to better understand their ecological interactions and the potential benefits they provide for nursery operations.

Fish species believed to contribute to fouling reduction within other propagation initiatives are diverse across the few studies that directly assess fish fouling maintenance on nurseries. A variety of 32 species was documented contributing to fouling removal on rope nurseries in the Seychelles (Frias-Torres & van de Geer, 2015b). In particular, *Balistoides viridescens* was of key importance for the removal of barnacles, a main source of fouling for this project (Frias-Torres & van de Geer, 2015b). Also in the Seychelles, a high abundance of large fishes (*Ephippidae*, *Scarinae* and *Siganidae*) led to 2.75 times fewer person-hours spent on net nursery fouling maintenance (Frias-Torres et al., 2015a). Moreover, on Kenyan Coral Tree^{TM} nurseries, *Ctenochaetus spp* reportedly removed the majority of fouling (microalgae, filamentous algal turfs, juvenile stages of macroalgae and detrital material) and contributed to increased coral survivorship in 2 successive studies (Knoester et al., 2019; Knoester et al., 2023). Despite differences in fish species observed and nursery designs used, the presence of fish assemblages has reportedly led to reduced fouling and a positive indirect effect on nursery grown corals across all studies. However, research thus far has taken place exclusively in the Indian Ocean, despite significant variations in fish species composition and functional feeding capabilities known to occur between ocean regions, notably differing from the East Pacific (Bellwood et al., 2019). That said, granting access to fish assemblages in any region will inevitably entail providing access to species also capable of corallivory. While the high survivorship of corals within studies emphasises a net benefit of fish assemblages in reducing filamentous turf fouling on nurseries, stewards may not always have access to sites with fish assemblages capable of net positive effects. This may be the case for candidate nursery sites on reefs impacted by severe stress events, as these events can alter the feeding composition or reduce the abundance of fish assemblages (Booth & Beretta, 2002; Robinson et al., 2019; Magel et al., 2020). Thus, initial monitoring on new or prospective sites is encouraged to assess (i) if there is an abundant natural fish population and (ii) the potential impact of local fish feeding groups on nursery-reared corals. Trade-offs may occur in selecting stewardship sites in fish-rich areas, where nature-based cleaning can be relied upon, versus manual nursery cleaning at an added cost in fish-depauperate sites which may have an equal or greater need for coral restoration.

Table 3.1. Species list of fish species observed across nurseries at Rayban and Mojo (n = 3 nurseries per site) reef stewardship sites, Opal Reef, northern Great Barrier Reef. Asterisks denotes species that were observed to bite nurseries.

Family	**Species**	
	Mojo	**Rayban**
Acanthuridae	*Acanthurus nigricauda**	*Acanthurus nigricauda**
Acanthuridae	*Ctenochaetus binotatus**	*Ctenochaetus binotatus**
Acanthuridae	*Surgeonfish spp**	*Surgeonfish spp**
Acanthuridae		*Zebrasoma velifer*
Caesionidae		*Caesio caerulaurea*
Chaetodontidae	*Chaetodon trifascialis*	*Chaetodon trifascialis**
Labridae		*Cheilinus fasciatus**
Labridae		*Hologymnosus annulatus**
Labridae		*Thalassoma hardwicke*
Labridae		*Wrasse spp**
Lethrinidae	*Gymnocranius microdon*	
Mullidae		*Mulloidichthys flavolineatus*
Mullidae		*Parupeneus barberinus*

Nemipteridae	*Monotaxis grandoculis*	*Monotaxis grandoculis*
Nemipteridae		*Scolopsis bilineata*
Nemipteridae		*Scolopsis taenioptera*
Pomacentridae		*Amblyglyphidodon curacao*
Pomacentridae	*Chromis amboinensis*	
Pomacentridae	*Chromis margaritifer*	*Chromis margaritifer**
Pomacentridae	*Chromis viridis*	*Chromis viridis*
Pomacentridae		*Dascyllus aruanus*
Pomacentridae	*Dascyllus reticulatus*	*Dascyllus reticulatus**
Pomacentridae		*Pomacentrus moluccensis*
Scarinae		*Chlorurus sordidus*
Scarinae	*Parrotfish spp**	*Parrotfish spp*
Scarinae	*Scarus flavipectoralis**	*Scarus flavipectoralis**
Scarinae	*Scarus globiceps**	*Scarus globiceps**
Scarinae	*Scarus niger**	*Scarus niger**
Scarinae	*Scarus oviceps**	
Scarinae		*Scarus schlegeli*
Serranidae	*Plectropomus oligacanthus*	
Unknown		Unknown*

3.4.3 Coral survivorship

Overall, coral survivorship was highest in areas where fish had unobstructed access. Though, when fish were excluded, trends in coral survivorship differed between sites. At Mojo, all *Acropora aff. abrolhosensis* fragments, the only species within caged plots, survived irrespective of treatment (*Figure 3.2b.*). In contrast, *Acropora kenti* at Rayban experienced reduced survival across full-cage (17% survival) and partial-cage treatments (33% survival) compared to the controls (83% survival; *Figure 3.2b.*; *Table S3.10.*). Survival of *Acropora donei* (Rayban) was also lowest in full-caged treatments (0% survival), but differences between the same treatments were highly variable at the site. The Rayban nursery that was found resting 19 cm above the substrate on besser blocks after losing flotation did not vary in coral survivorship of *Acropora donei* (Kruskal–Wallis test, $X^2 = 1.17$, $p = 0.558$; *Table S3.11.*) or *Acropora kenti* (Kruskal–Wallis test, $X^2 = 4.60$, $p = 0.100$; *Table S3.11.*) compared to the other two intact nurseries at the site.

Differences in survivorship are perhaps expected, given the unique coral species and location of restoration sites. In a previous investigation, light and temperature were monitored in addition to flow over a period of 14 days at Rayban and Mojo restoration sites (Strudwick et al., 2023). Rayban and Mojo displayed discernible abiotic differences, where Mojo was characterised as a high-flow environment with high light attenuation (resulting in low water clarity) and comparatively lower temperatures compared to Rayban (February 2021, Strudwick et al., 2023). These factors have previously been identified to benefit corals (e.g. high light attenuation/lower temperatures, Cacciapaglia & van Woesik, 2016; greater flow, Schutter et al., 2010) and corals out-planted onto natural reefs at Mojo have previously performed better compared to those out-planted at Rayban (Strudwick et al., 2023). However, the variation in species used between the 2 nursery sites precluded us disentangling whether location-specific environmental differences, or species-specific tolerance to competition with filamentous turf led to higher survivorship at Mojo. Inevitably, coral species-specific responses to environmental differences will likely be an area for continued research, particularly as positioning nurseries in favourable biotic and abiotic environments is an accessible management strategy for reef stakeholders who seek to safeguard investments in nursery-grown coral fragments.

3.5 Conclusion

Coral nurseries that propagate multiple coral species inevitably host complex and diverse assemblages of interacting organisms. Our study found in areas on multi-taxa coral nurseries where fishes > 2.5 cm were excluded, there was an average 4-fold increase in fouling biomass of filamentous turf. *Acanthuridae* and *Scarinae* fishes were the most conspicuous species on nurseries, notable for their high biomass and frequent interactions. Methods implemented in this study provide an affordable, small-scale approach for reef stakeholders to empirically examine the impact of fish presence on nursery benthic communities. While propagation practitioners may prioritise nursery sites with abundant local fish assemblages that improve nursery operations, as conditions on the reef worsen, there are likely to be fish-depauperate sites that may have an equal or greater need for coral restoration. In these scenarios, environmental influences acting upon coral-fouling competition may dictate prevailing species. However, ongoing research is required to untangle how environmental characteristics modulate competition between benthic organisms. Ultimately, an understanding of site capacity for cost-effective natural versus more expensive manual cleaning will be a critical first step in ensuring an optimised design and implementation for any given nursery practice.

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3.8 Supplementary materials

3.8.1 Supplementary figures

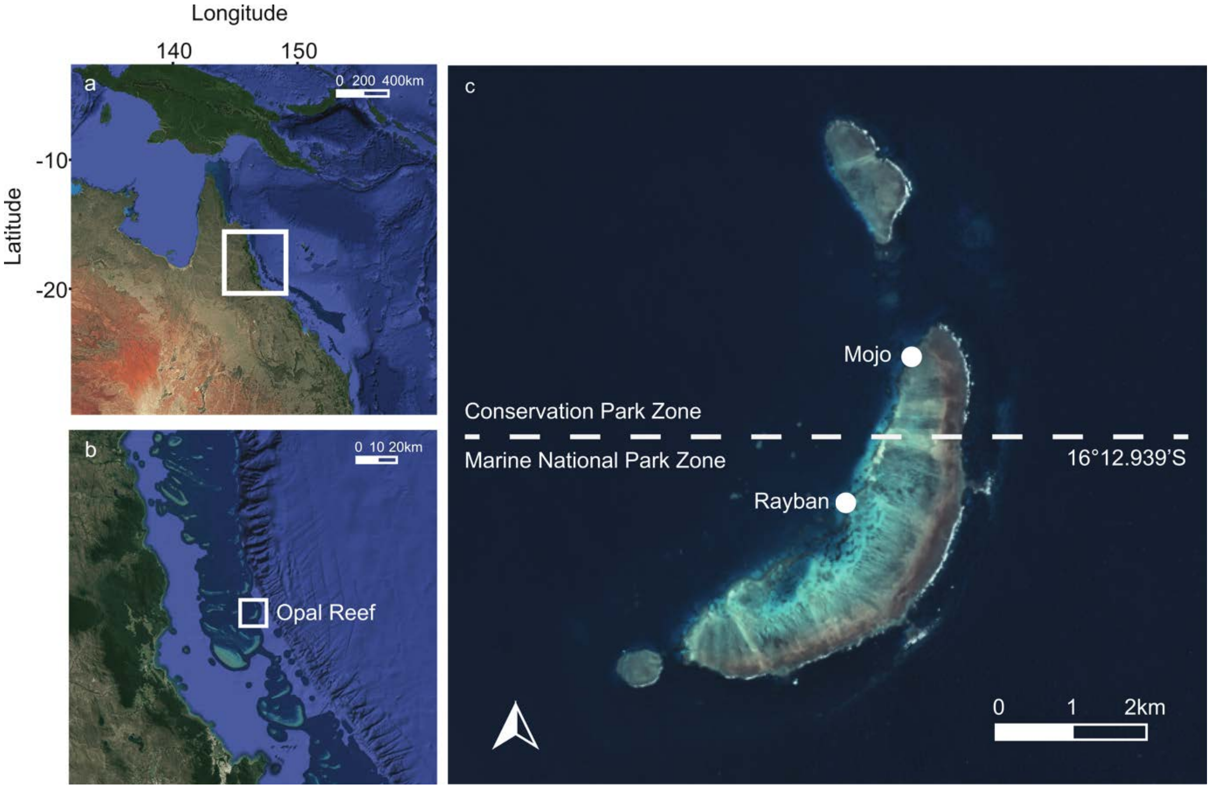


Figure S3.1. Location of sites on Opal Reef, northern Great Barrier Reef (Australia), reef stewardship sites “Mojo” (16°12'23.6"S 145°53'53.7"E) and “Rayban” (16°13’27"S 145°53’22"E) in relation to their location within the country (a) and region (b-c). Map images © Google 2023 and © Allen Coral Atlas 2023.

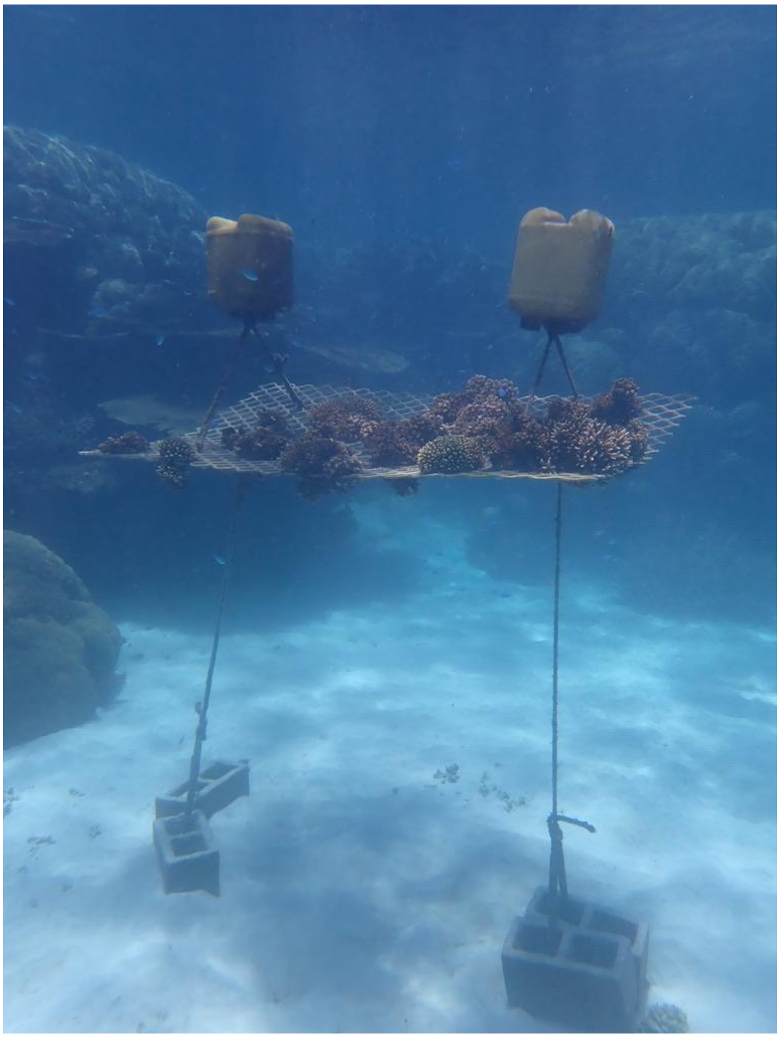


Figure S3.2. Example of a coral propagation nursery managed by a Coral Nurture Program tourism partner at "Mojo" reef stewardship site, Opal Reef, northern Great Barrier Reef. Nursery consisted of a 2.0 × 1.2 m aluminium diamond-mesh attached using rope to 2, 9 kg besser blocks, and 2, 20 L floats. All Coral Nurture Program nurseries were deployed under GBRMPA permits G18/40023.1 and G20/43740.1. Photo credit: Gemma M Gillette.

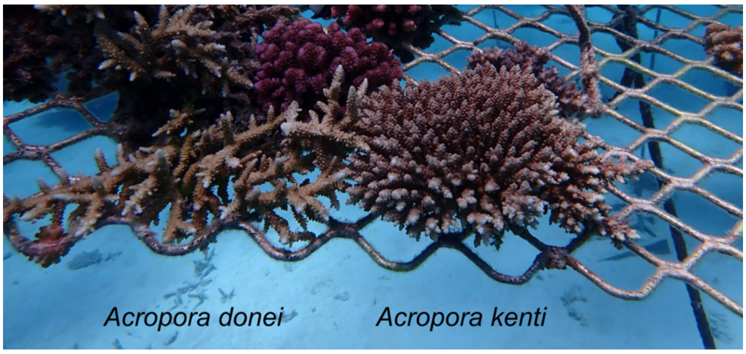


Figure S3.3. *Acropora donei* and *Acropora kenti* colonies growing on a coral nursery deployed at "Blue Lagoon" reef stewardship site Opal Reef, northern Great Barrier Reef. Photo credit: Paige Strudwick.

Figure S3.4. a) A GoPro Hero 8® camera attached to a GoPro® "Jaws: Flex Clamp" and mounted onto a nursery buoy in preparation for fish video surveys. b) Fish video survey point of view. Treatment control area outlined in pink. Images taken at reef stewardship sites on Opal Reef, northern Great Barrier Reef. Photo credit: Gemma M Gillette.

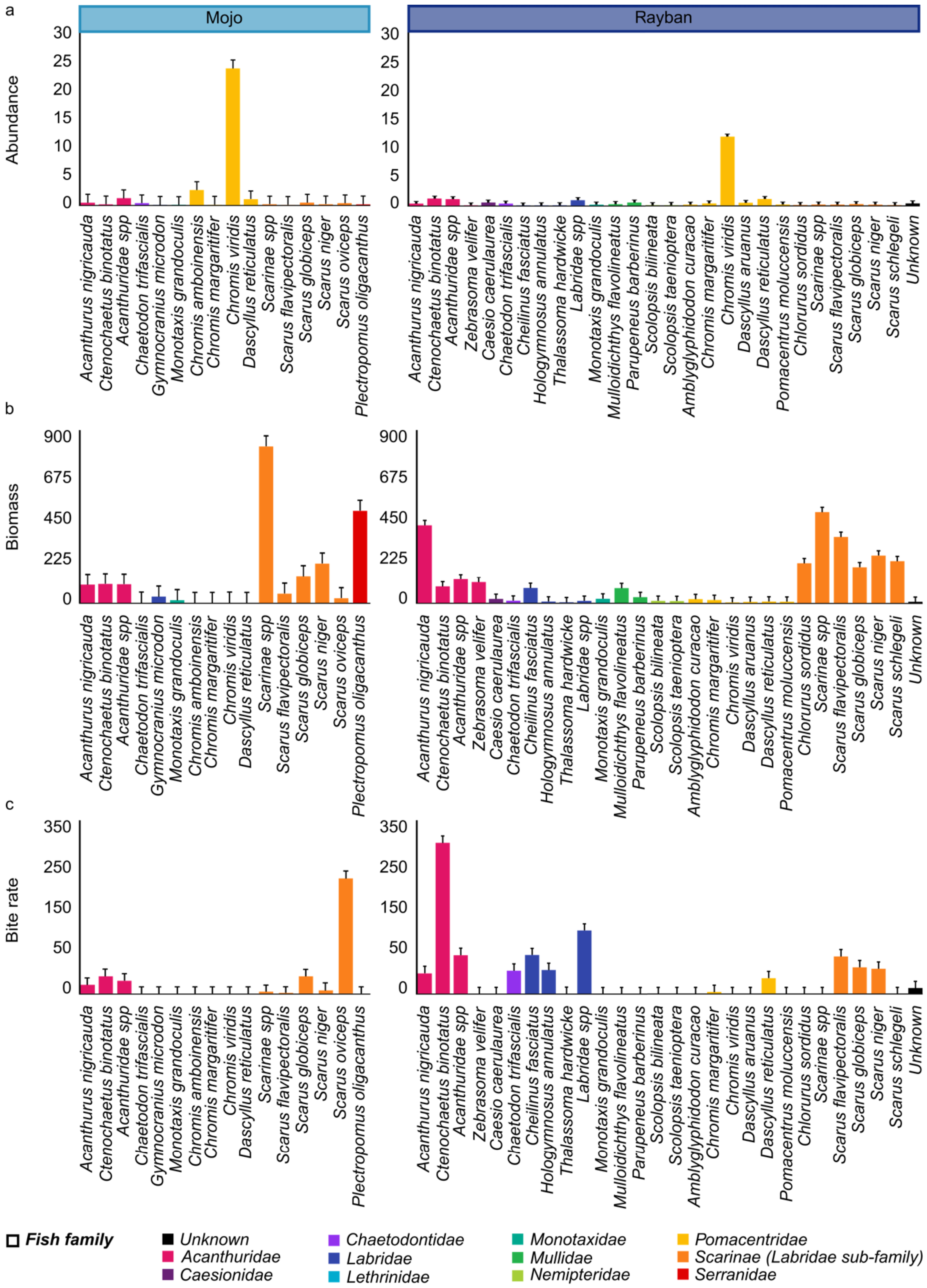


Figure S3.5. Average fish abundance, biomass (g), and bite rate (number of bites) per species and coloured by family group (with the inclusion of *Scarinae*, a sub-family of *Labridae*) at “Mojo” and “Rayban” reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 9 video surveys per site). Error bars represent the standard error.

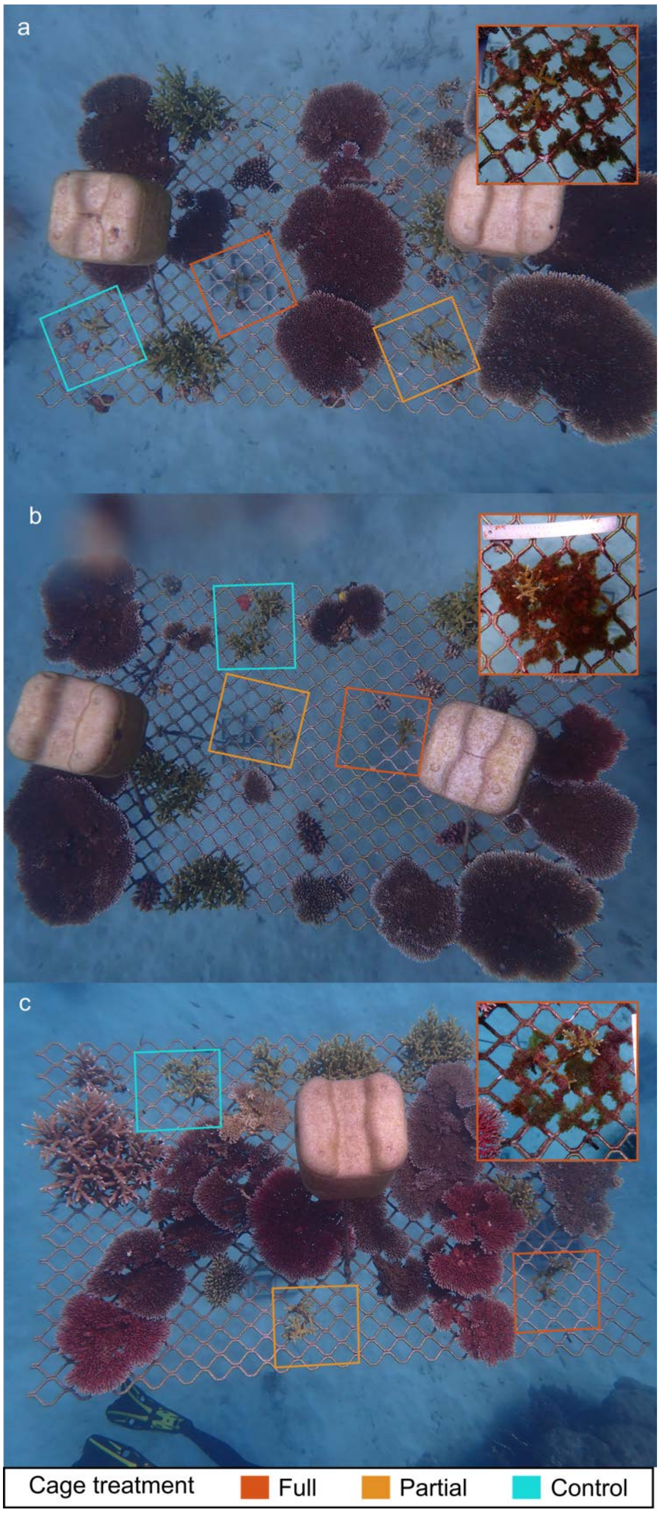


Figure S3.6. Coral nurseries approximately 18 hrs after the removal of full, partial and control cage treatments (a-c) at “Mojo” reef stewardship site, Opal Reef, northern Great Barrier Reef. Images in the top right corner depict the full cage areas at the time of cage removal, approximately 18 hrs earlier. Images Photo credit: Gemma M Gillette.

3.8.2 Supplementary tables

Table S3.1. The percentage difference in average light intensity (lx) recorded using calibrated Hobo loggers within fish cage exclusion treatments was analysed on 1 coral nursery per reef stewardship site. Reef stewardship sites were located at "Mojo" and "Rayban", Opal Reef, northern Great Barrier Reef (n = 1 Hobo logger per treatment per site, n = 6 total).

Site	**Treatment**		**Light (lx) difference (%)**
Mojo	Control	Full	53.68
	Control	Partial	47.85
	Partial	Full	3.94
Rayban	Control	Full	29.50
	Control	Partial	5.55
	Partial	Full	22.70

Table S3.2. A one-way Kruskal-Wallis test on light (lx) measurements between fish cage exclusion treatments (control, partial and full cage) on coral nurseries and a Dunn post-hoc test using the Bonferroni method for significant results ($p < 0.05$). Light was recorded using calibrated HOBO^{TM} loggers (n = 1 per treatment per site, n = 6 total) on 1 coral nursery per reef stewardship site. Reef stewardship sites were located at "Mojo" and "Rayban", Opal Reef, northern Great Barrier Reef.

One-way Kruskal-Wallis test on light (lx)

Site	Chi-squared	df	p value
Mojo	38.13	2	0.000
Rayban	16.04	2	0.000

Dunn post-hoc test on light (lx)

Site	Treatment		Chi-squared	Z value	p.unadj	p.adj
Mojo	Control	Full	38.13	6.06	0.00	0.000
	Control	Partial	38.13	4.06	0.00	0.000
	Full	Partial	38.13	-2.00	0.00	0.000
Rayban	Control	Full	16.04	3.94	0.00	0.001
	Control	Partial	16.04	1.36	0.09	0.263
	Full	Partial	16.04	-2.59	0.00	0.015

Table S3.3. Experimental treatment plots (full, partial and control) fitted with coral fragments (“Mojo”: *Acropora aff. abrolhosensis*; “Rayban”: *Acropora donei*, *Acropora kenti*) and settlement substrates (~30 x 9 cm nursery aluminium diamond-mesh) upon completion of the experiment (week 17). Full cage treatments had their cages removed prior to being photographed. Photo credit: Gemma M Gillette.

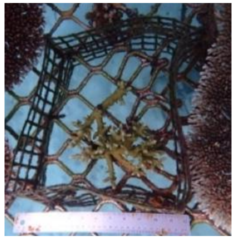
	Mojo			**Rayban**		
	Nursery 1	Nursery 2	Nursery 3	Nursery 1	Nursery 2	Nursery 3
Full						
Partial						
Control						

Table S3.4. Coral cover on survey nurseries as of 8th of June 2022 at "Mojo" and "Rayban" reef stewardship sites, Opal Reef, northern Great Barrier Reef. Contributions of *Acropora* spp. and *Pocillopora* spp. to coral cover are displayed as separate columns.

Location	**Nursery number**	**Coral cover (%)**	***Acropora* spp. (%)**	***Pocillopora* spp. (%)**
Mojo	1	66.74	99.98	0.02
	2	51.77	99.97	0.03
	3	57.84	100.00	0.00
Rayban	1	10.42	99.42	0.58
	2	20.60	99.45	0.55
	3	21.85	99.95	0.05

Table S3.5. Sampling times of fish video surveys at "Rayban" and "Mojo" reef stewardship sites, Opal Reef, northern Great Barrier Reef. Tide times at Port Douglas (https://www.msq.qld.gov.au/tides/tide-tables).

Sampling time		
Date	Site	Time
5/6/2022	Rayban	10:23
	Mojo	11:38
6/6/2022	Rayban	10:25
	Mojo	12:01
7/6/2022	Rayban	10:22
	Mojo	11:46

Tide			
Date	Tide	Time	Meters
5/6/2022	High	01:18	2.23
	Low	18:06	1.27
6/6/2022	High	02:53	2.25
	Low	10:42	1.35
	High	15:43	1.51
	Low	20:09	1.36
7/6/2022	High	03:47	2.30
	Low	10:57	1.22
	High	16:38	1.68
	Low	21:44	1.34

Table S3.6. Estimated cumulative fish abundance, richness, and diversity at 17.5 mins of filming, data expressed as a percentage of totals observed at 1 hr of filming, originate from ***Chapter 2***. This data was collected over 1 hr fish video surveys taken across 3 coral nurseries at 3 time points at "Mojo", Opal Reef, northern Great Barrier Reef. For further information, see ***Chapter 2***.

Time	Abundance (%)	Richness (%)	Diversity (%)
5	70.89	60.47	82.01
10	74.42	65.12	85.09
15	80.02	69.77	86.97
17.5	80.59	72.09	88.25
20	81.17	74.42	89.52
25	82.24	79.84	92.63
30	82.40	80.62	93.12
35	93.91	83.72	94.46
40	94.82	86.82	95.07
45	95.56	89.92	95.31
50	96.05	90.70	96.78
55	98.11	100.00	100.00
60	100.00	100.00	100.00

Table S3.7. The average and standard error of fouling (filamentous turf) dry weight (g) on settlement substrates within fish cage exclusion treatments (control, partial, and full cage) (n = 1 settlement substrate per treatment). Treatments were deployed on coral nurseries located at reef stewardship sites "Rayban" and "Mojo", Opal Reef, northern Great Barrier Reef (n= 1 full, partial and control treatment per nursery; n = 3 nurseries per site, n = 6 total).

Treatment	Rayban		Mojo	
	Average	SE	Average	SE
Full	3.42	2.28	4.39	0.95
Partial	1.72	0.22	1.15	0.18
Control	0.69	0.11	1.18	0.22

Table S3.8. A two-way Scheirer-Ray-Hare extension to the Kruskal-Wallis test to evaluate differences in dry weight fouling (filamentous turf) biomass (g) on settlement substrates within fish cage exclusion treatments (control, partial, and full cage; n = 1 settlement substrate per treatment) and sites (n = 9 settlement substrates per site; n = 18 total). Treatments were deployed on coral nurseries located at reef stewardship sites "Rayban" and "Mojo", Opal Reef, northern Great Barrier Reef (n = 1 full, partial and control treatment per nursery; n = 3 nurseries per site, n = 6 total). A Dunn post-hoc test employing the Bonferroni method was used to evaluate statistically significant results ($p < 0.05$). A one-way Kruskal-Wallis test was conducted to evaluate differences in dry weight fouling biomass (g) on settlement substrates between nurseries at each stewardship site.

Scheirer-Ray-Hare extension to the Kruskal-Wallis test on fouling between treatments and sites		
	H statistic	p value
Treatment	5.95	0.015

Site	0.10	0.747

Dunn's post-hoc test on fouling between treatments

Treatment		Z value	p.unadj	p.adj
Control	Full	-2.85	0.00	0.013
Control	Partial	-1.71	0.09	0.260
Full	Partial	1.14	0.25	0.760

Kruskal-Wallis test on fouling between coral nurseries

Site	Chi-squared	df	p value
Rayabn	0.64	2.00	0.725
Mojo	1.07	2.00	0.587

Table S3.9. A one-way Kruskal-Wallis test to evaluate differences between in fish abundance and bite rate on coral nurseries (n = 3 per site, n = 6 total) between “Rayban” and “Mojo” reef stewardship sites, Opal Reef, northern Great Barrier Reef (n = 3 video surveys per nursery). Fish richness, and biomass on nurseries between stewardship sites satisfied normality (Shapiro Wilk’s Test) and equal variance (Bartlett’s Test) tests, thus were subject to a one-way ANOVA. Results considered statistically significant at $p < 0.05$.

Kruskal-Wallis test on fish abundance

	Chi-squared	df	p value
Site	1.71	1.00	0.191

Kruskal-Wallis test on fish bite rate

	Chi-squared	df	p value
Site	3.90	1.00	0.048

ANOVA on fish richness

	df	Sum Sq	Mean Sq	F value	p value
Site	1.00	16.06	16.06	3.10	0.097

ANOVA on fish biomass

	df	Sum sq	Mean sq	F value	p value
Site	1.00	8410.00	8410.00	0.32	0.571

Table S3.10. Coral fragment survival at "Rayban" and "Mojo" reef stewardship sites, Opal Reef, northern Great Barrier Reef. Each cage treatment at "Rayban" enclosed 2 fragments of *Acropora donei* and 2 fragments of *Acropora kenti*. At "Mojo", 2 fragments of *Acropora aff. abrolhosensis* were included in each treatment. Species specific survivorship is reported at "Rayban", whereby *Acropora donei* survival is a percentage of the total *Acropora donei* planted within that treatment type (full, partial or control). Total survivorship at "Rayban" is the percentage survivorship of all corals within a treatment.

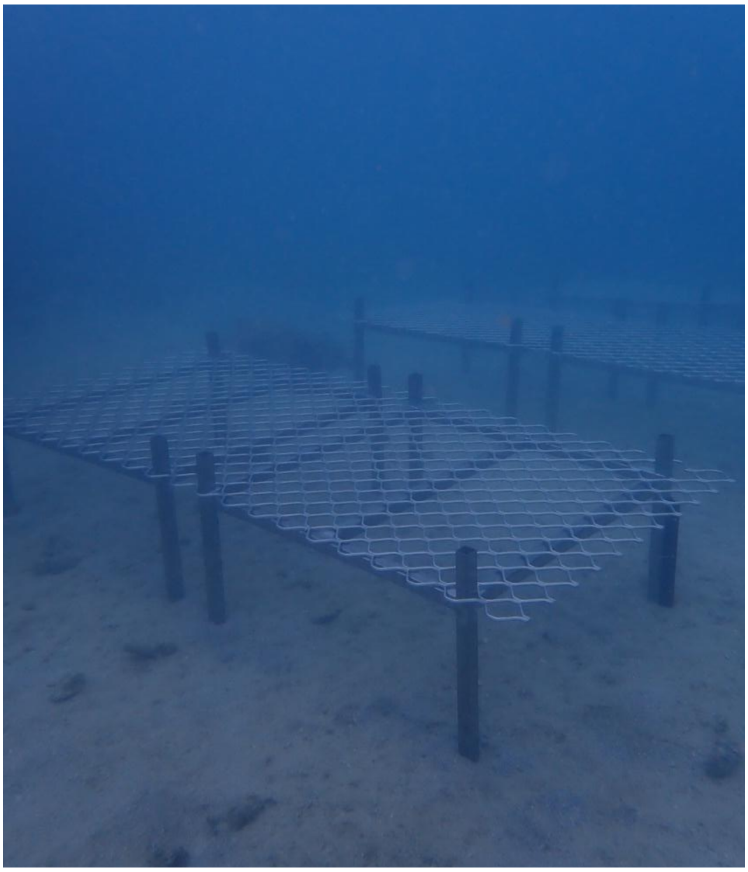
Treatment	**Species**	**Rayban survivorship (%)**	**Species**	**Mojo survivorship (%)**
Full	*Acropora donei*	0.00	*Acropora aff. abrolhosensis*	100
	Acropora kenti	16.67		
	Total	8.33		
Partial	*Acropora donei*	33.33	*Acropora aff. abrolhosensis*	100
	Acropora kenti	33.33		
	Total	33.33		
Control	*Acropora donei*	16.67	*Acropora aff. abrolhosensis*	100
	Acropora kenti	83.33		
	Total	50.00		

Table S3.11. A one-way Kruskal-Wallis test to evaluate differences in coral survivorship between fish cage exclusion treatments (control, partial and full; n = 6 coral fragments per sp, per treatment type) on coral nurseries at reef stewardship sites (n = 18 per sp, per site). Reef stewardship sites ("Rayban" and "Mojo") were located at, Opal Reef, northern Great Barrier Reef. Results considered statistically significant at $p < 0.05$.

Kruskal-Wallis test on coral survivorship between treatments				
Site	Species	Chi-squared	df	p value
Rayban	*Acropora donei*	2.00	2.00	0.368
	Acropora kenti	2.00	2.00	0.368
Mojo	*Acropora aff. abrolhosensis*	NA	NA	NA

Kruskal-Wallis test on coral survivorship between nurseries				
Site	Species	Chi-squared	df	p value
Rayban	*Acropora donei*	1.17	2.00	0.558
	Acropora kenti	4.60	2.00	0.100
Mojo	*Acropora aff. abrolhosensis*	NA	NA	NA

Chapter 4: Early phase development of reef fish assemblages on coral propagation nurseries installed in the Whitsundays, Great Barrier Reef



This chapter has been prepared as a fully drafted manuscript for submission.

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Author contributions:

GMG, DJS, EFC, DJB conceived the research. GMG, DJS, EFC, CH, EM, MV contributed to the planning and execution of data collection. GMG conducted data analysis with statistical advice from SW and drafted the manuscript with editorials from EFC, DJS and CH. All authors provided subsequent editorial input.

All authors declare that the author contributions outlined above are a true reflection of the authorship of this thesis chapter:

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4.1 Abstract

The rearing of asexual coral fragments within *in-situ* nurseries is a widespread reef stewardship strategy to produce coral biomass for out-planting onto "high-value", yet degraded, reef sites. Recently, coral nurseries have been found to serve as multiuse structures that provide additional habitat for local fish assemblages, which in turn reduce nursery biofouling and maintenance costs. Despite the importance of fish assemblages to the functioning of coral nurseries, their establishment onto newly deployed nurseries has rarely been reported in the literature and never before on the Great Barrier Reef (GBR). Within this study, we examine the development of fish assemblages onto early-phase fixed table nurseries deployed across three locally important reef sites in the Whitsundays, GBR. Fish assemblage metrics (abundance, richness, diversity, and biomass), fish species composition and benthic arrangement (coral stock and recruitment of other benthic taxa) were evaluated using video surveys at three time points: T1 (1-day post nursery installation), T2 (186-191 days post-installation), and T3 (340-370 days post-installation). Total mean fish assemblage metrics in nurseries increased from T1 to T2 and were similar or greater at T3, however, site-specific differences were observed. The development of fish assemblages coincided with a changing nursery benthic community as coral material grew and fouling developed. *Nemipteridae* and *Caesionidae* species were the primary early settlers on nurseries, with *Scarinae* (at T2 and T3) and *Acanthuridae* species (at T3) later becoming the dominant components of fish biomass. There was also a notable rise at T2 and T3 in the abundance of small-bodied and juvenile *Labridae*, *Chaetodontidae*, *Apogonidae*, and *Pomacentridae* species. Collectively these results demonstrate that nursery structures from their early deployment can develop diverse fish assemblages that differ by site on the GBR.

4.2 Introduction

There is a long history of using *in-situ* coral nursery structures for scientific research (e.g. coral disease Ruiz-Diaz et al., 2016; deoxygenation, Howard et al., 2023), and to cultivate propagated corals for the aquarium or ornamental trades (Kimani et al., 2015; Barton et al., 2017). However, in recent years the most common use for nursery structures has been to propagate larval propagules and/or coral fragments in coral "nurseries" as a continuous source of material for planting on reefs (Epstein et al., 2001; Arnold & Steneck, 2011;

Rinkevich, 2019). Coral propagation initiatives that plant corals have the potential to retain or boost coral biomass at local-scale reef sites, in particular "high-value" sites affected by anthropogenic activity or natural disasters that are targeted for restoration (e.g. Hesley et al., 2017; Howlett et al., 2022; Nuñez Lendo et al., 2024). Coral nurseries support restoration operations by reducing the need to harvest wild colonies and the time costs associated with travelling to donor sites to gather coral material (Edwards & Fisk, 2010). Numerous examples of nurseries have been employed, from free-floating mid-water platforms (Levy et al., 2010; Mbije et al., 2010; Rachmilovitz & Rinkevich, 2017), or frames directly fixed to reef-neighbouring substrates (Shaish et al., 2008; Bongiorni et al., 2011; Hernández-Delgado et al., 2014; Schopmeyer et al., 2017). These different designs, or approaches, are tailored to meet site-specific or operational contexts, involving the use of local coral species for propagation and typically employing low-cost materials (Rinkevich, 2019; McLeod et al., 2022). While the primary function of all nurseries is to support growing coral material, observations of fish assemblages utilising nursery structures for food and shelter indicate that they can also provide important functions beyond that of coral propagation (Shafir & Rinkevich, 2010). For example, evidence from mid-water nurseries in the Seychelles (Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b), Kenya (Knoester et al., 2019; Knoester et al., 2023) and more recently in the Cairns/Port Douglas region on the Great Barrier Reef (GBR; ***Chapter 2***; ***Chapter 3***) has shown that nursery structures can provide resources for local fish assemblages (Ladd & Shantz, 2020) and hence enhance outcomes for propagation activities.

Fishes assist reef ecosystem functioning and drive many of the key ecological services reefs provide (Burkepile & Hay, 2006; Brandl et al., 2019). Such a core attribute is recognised by several restoration projects that directly aim to support fish assemblages with artificial reef structures to encourage processes that drive a coral-dominated reef (Seraphim et al., 2020; Williams et al., 2019; Nuñez Lendo et al., 2024), where fish generally have a net-positive impact on coral recovery following an impact event (Mcleod et al., 2019). Coral nurseries share the features of an artificial reef including as a submerged structure and differ only in their purpose: to imitate characteristics of a natural reef or create an attraction for divers or attract animals for fishing purposes (Ammar, 2009; Great Barrier Reef Marine Park Authority (GBRMPA), 2022) as opposed to grow coral biomass for restoration or restoration practices (McLeod et al., 2022). As such, coral nurseries are rarely evaluated in terms of artificial reef structures and the associated ecological roles and benefits that are indirectly achieved. A deeper understanding of the ecological services that coral nurseries provide to fish assemblages is critical since fostering natural processes that assist coral growth on natural reefs provides an obvious means for improving propagation effectiveness (Ladd et al., 2018). On mid-water coral nurseries with significant fish assemblages, coral survival increased where fishes maintained biofouling (the growth of not target species) to a steady state (Knoester et al., 2019; Knoester et al., 2023; ***Chapter 3***), therefore decreasing person-hours spent in nursery cleaning (Frias-Torres et al., 2015a). Despite such positive processes, site ecology, and even less so background fish assemblages, are rarely accounted for when establishing and operating reef stewardship programs. For example, of 116 scientific papers on coral restoration published between 1987 and 2017 most studies focused on factors such as the growth and survivorship of corals either in nurseries or out-planted to reefs, whereas only 19% incorporated ecological processes (e.g. recruitment, predation, herbivory) (Ladd et al., 2018). Such a trend is indicative of a broader pattern of measuring single metrics of success for restoration projects despite goals that are often centred on recovering broad ecosystem service values.

In 2018, a reef restoration program, the Coral Nurture Program (CNP), was established as a partnership between reef researchers and tourism operators in the Cairns and Port Douglas region on the northern GBR (Howlett et al., 2022; Suggett et al., 2023). In this GBR region, the project employed mid-water floating coral nurseries for coral propagation activities at high-value tourism sites. Fish assemblages are of particular importance to this project, as they are often a highly desired, if not the most sought-after, natural attraction by tourists (Williams & Polunin, 2000; Uyarra et al., 2009; Le et al., 2019). Nurseries have been progressively deployed over time (Howlett et al., 2022) and in 2021 the first studies of fish assemblages on CNP nurseries identified their ability to provide habitat for local fish assemblages (***Chapter 2***) that in-turn reduced nursery fouling (***Chapter 3***). In August 2022, CNP expanded their operations to the Whitsundays, central GBR, in tourism-led efforts to improve coral biomass that had deteriorated in response to poor water quality compounded by the 2017 Cyclone Debbie (Williamson et al., 2019; Ceccarelli et al., 2020). CNP partnered with three local tourism operators to propagate and re-plant coral at three inshore reef sites each with shared tourism and public moorings and hence of high usage (GBRMPA, 2023a). However, because of high and unpredictable boat traffic, in contrast to previous CNP efforts, a fixed table nursery design was used. The different restoration context within the Whitsundays, thus presented an opportunity to assess whether and how fixed table nursery designs, i.e. that did not sit mid-water, could still mirror artificial reefs to host fish assemblages. In doing so, this study aimed to fill knowledge gaps concerning the development of fish assemblages on nurseries over time (first 11-12 months of deployment). Specifically, we addressed two main points: i) the extent to which fish assemblages (abundance, richness, diversity, and biomass) change on fixed table nurseries during the early stages of deployment; and ii) whether fish species composition on nurseries varies during this period. It is hypothesised that fish assemblages on newly deployed coral nurseries would increase in abundance and biomass over time as nursery benthic composition evolved, either through natural growth or propagation activities. We discuss these findings within the context of fish assemblages associated with nurseries around the world and emphasise the influence of these nurseries on their surrounding biotic environment beyond the production of coral for out-planting activities.

4.3 Methods

4.3.1 Site description

Three sites, each with three table nurseries, were established in the Whitsundays, located within the inner-shelf of the central GBR in August 2022: "Blue Pearl Bay" (29th - 31st August) on Hayman Island, "Black Island" (29th - 31st August), and "Luncheon Bay" (1st – 3rd September) on Hook Island (*Figure 4.1.*), under GBRMPA permit G22/46543-1 (issued to EFC, DJS). Such inshore reef sites are situated in relatively turbid waters, as sediment-suspended solids, nutrients, pesticide residues and other contaminants are delivered by catchment runoff during seasonal flooding of adjacent rivers (Devlin & Brodie, 2005; Devlin & Schaffelke, 2009; Brodie et al., 2012). The shallow continental shelf retains much of this material, where it continues to undergo cycles of deposition and resuspension leaving corals susceptible to sediment smothering (Orpin & Ridd, 2012). Escalations in nutrient runoff are intricately linked to outbreaks of Crown-of-Thorns Starfish (COTS) and continues to exert additional negative impacts on corals within the region (Brodie et al., 2008; Caballes & Pratchett, 2014; GBRMPA, 2023b). In 2017, stressors were compounded in the Whitsunday region by Cyclone Debbie (Category 4) which exposed the sites (and other N−SE facing reef sites) for 24 hrs to 200 km/hr winds and seas up to 12 m. The cyclone caused extensive physical damage, which reduced coral cover and further increased sediment loading (Williamson et al., 2019; Ceccarelli et al., 2020; Moynihan et al., 2022). All sites within our study are still used extensively by the public and local tourism operators with multiple shared moorings present at each site (GBRMPA, 2023a). The significance of these sites to local tourism, despite their significant degradation, contributed to their selection by CNP for reef stewardship activities involving coral propagation and out-planting techniques (Scott et al., 2024).

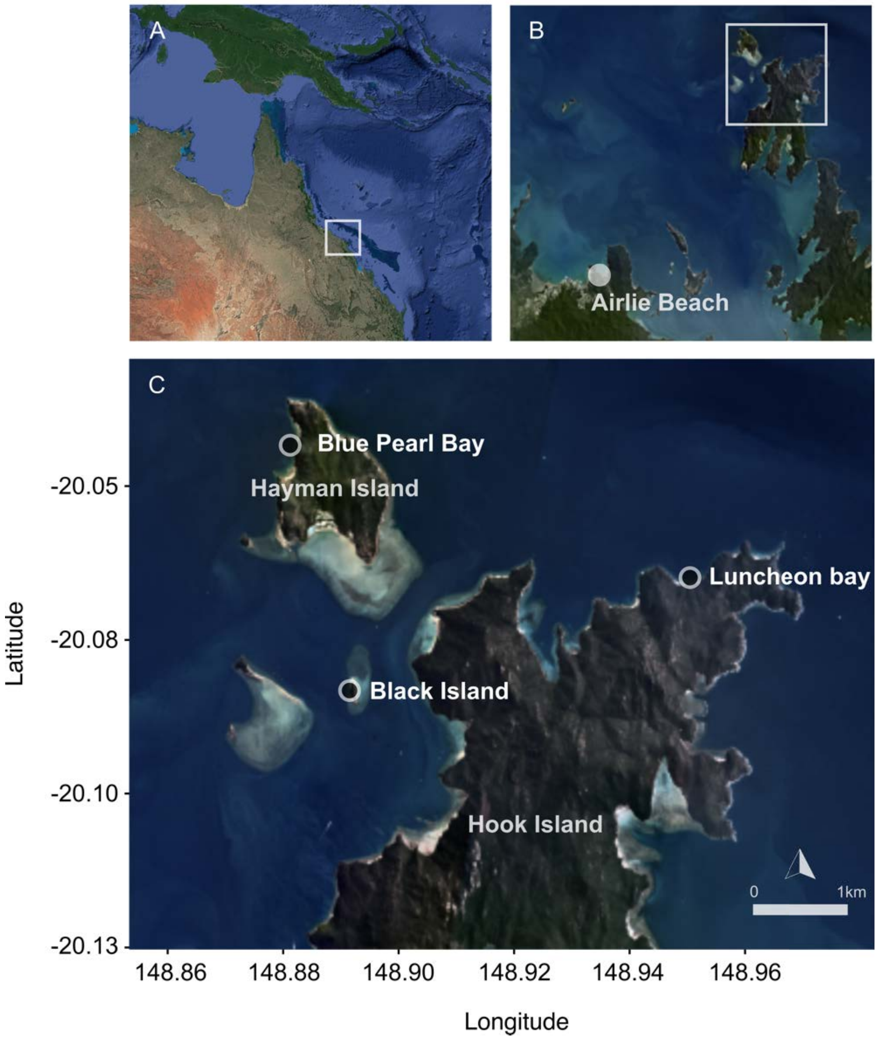

Figure 4.1. Location of nursery reef stewardship sites in the Whitsundays, Great Barrier Reef, Australia. "Black Island" (-20.08, 148.89), "Blue Pearl Bay" (-20.05, 148.88) and "Luncheon Bay" (-20.06, 148.95) are displayed with their position within the country (A) and region (B-C). Map images © Google 2023 and © Allen Coral Atlas 2023.

4.3.2 Nursery site establishment and maintenance

At each site, three table nurseries were installed side by side (minimum spacing of 1-2 m) at a depth of 3-4 m (on low tide), on a rocky-sand substate approximately 1-3 m from the neighbouring reef (*Figure 4.1.; Figure S4.1.*). Each nursery consisted of a 1900 x 950 cm diamond aluminium mesh, fastened to two parallel 85 x 85 x 50 cm stainless steel frames using stainless steel wire. The legs of the frames were supported by steel rebar hammered into the substrate and attached using stainless steel wire.

Nurseries were initially stocked with coral material in August 2022 from nearby donor reef sites located within 10 km of the respective site where hard coral cover ranged from 17-38% (Scott et al., 2024). The collected material was largely "corals of opportunity", un-accreted coral fragments or small partial colonies found on unconsolidated substrate. Occasionally coral material was supplemented with *in-situ* fragmentation of donor colonies to enhance the diversity of propagated species. A hammer and chisel or wire cutters were used to fragment donor colonies within permit conditions (< 10% of parent colony, fragments > 15 cm in size). Coral material was either transported underwater or within shaded buckets filled with seawater back to the nursery site. Corals were initially "wedged" into the spaces of the diamond mesh to keep fragments upright (*Figure S4.2A.*) and later fastened in place (Luncheon Bay, February 2023; Blue Pearl Bay and Black Island, March 2023) with plastic cable ties. From March to August 2023 corals were periodically harvested for out-planting actives (e.g. Scott et al., 2024), lost due to *Bolbometopon muricatum* (Bumphead parrotfish) grazing or died after one instance of COTS grazing. The nurseries were regularly restocked after any occurrence of coral loss to sustain coral biomass.

To understand the background fish assemblages on natural reefs at the nursery sites continuous roving line-intercept video transects (n = 3 x 30 m per reef site) were conducted using GoPro Hero 8® and Hero 9® cameras at the time of nursery site establishment (August 2022; T1). Transect tapes were laid (5 – 15 m apart), and followed the site habitat contours, perpendicular to the shoreline at 3-5 m depth (Howlett et al., 2021; Howlett et al., 2022; Roper et al., 2022). Divers swam out of sight for ca. 5 min to allow fishes to return before filming. The total abundance of fish per species, counting all individuals within visible range, was tallied along transects. Background coral assemblages were also considered at each site and are detailed in Scott et al. (2024).

4.3.3 Fish videos

The fish assemblages on the nursery tables were recorded using GoPro Hero 8® cameras immediately after coral placement onto the nurseries (1-day post-installation, T1), with subsequent recordings at T2 (186-191 days post-installation) and T3 (340-370 days post-installation; *Table S4.1.*). Sampling variations arose from operational constraints related to accessing the sites. Star pickets of 180 cm were hammered into a sand substrate 2 m from the edge of the nurseries (*Figure S4.3.*). GoPro® cameras were clipped ¾ of the way up the star pickets and positioned towards the nursery using the GoPro® "Jaws: Flex Clamp" to capture the nursery in full.

Video recordings of the nurseries were conducted largely as per ***Chapter 2*** and ***Chapter 3*** Specifically, surveys were taken across a variety of times, though, to minimise fluctuations in fish population densities caused by daily changes in behaviour, all video recordings were limited to mid-daylight hours, within 2 hrs after sunrise to 2 hrs before sunset, to exclude peak crepuscular activity periods (*Table S4.1.*; Thompson & Mapstone, 2002; McClanahan et al., 2007; Powell et al., 2016; Emslie & Cheal, 2018). Sampling occurred primarily at high tide; however, Black Island and Blue Pearl Bay were sampled on an Ebb tide at T2 and Luncheon Bay was sampled on a flood tide at T3 (*Table S4.1.*). Filming lasted 40 min per replicate and all divers stayed out of visible sight of nurseries during filming to minimise diver disturbance. The first and last 2.5 min of each video were cut to allow for diver disturbance. During each video, fish species were identified to the highest possible taxonomic resolution, and the MaxN (i.e., the maximum number of individuals per species featured in each video; e.g. Fitzpatrick et al., 2012; Scott et al., 2015; Reeds et al., 2018) recorded. MaxN counts were used to avoid overestimations of fish abundance since individuals repeatedly moved in and out of the video field of view. Short 1-minute roaming videos, 5-10 cm away from each nursery, were taken to help later validate the species identification of smaller fishes > 3 cm.

All fishes were identified to species level, counted and categorised using visual estimation of total length (TL) in size classes 0–2.5, 2.5–5, 5–7.5, 7.5–10, 10–15, 15–20, 20–25, 25–30, 30–40, 40–50 and 50+ cm. Fish length class was estimated using the nursery frames of known size as a reference guide via the image J measuring feature (Schneider et al., 2012) to calibrate the length estimates at the start of each video processing session (Faradonbe et al., 2015). Individual fish that could not be confidently identified to species level, due to either poor water visibility or swimming outside of clear visible range, were grouped into their respective families or documented as "unknown". The weight of all species and all size classes was calculated using the length-weight relationship $W = a \times TL^b$, where W is the weight in grams, TL is the average total length of the size class in cm (Wolfe et al., 2020), while *a* and *b* are species-specific constants obtained from the literature (Froese & Pauly, 2018). If *a* and *b* values were not available, parameters of closely related species with a similar shape and average length were used. Fish biomass allowed for data to be compared with other artificial reef studies using similar metrics, usually corresponding with aims to increase fish biomass for fisheries use (Santos et al., 2011).

4.3.4 Nursery benthic composition

Downward-facing images of nurseries were taken from ca. 2 m height at T1 after coral stocking using an Olympus TG-6 Tough Camera (e.g. *Figure S4.2B.*). Coral species, cover, richness and morphological richness (number of different morphologies) were used as descriptors of coral composition. Coral colonies, fouling and any non-target species (such as *Millepora alcicornis*) were identified and individually traced using Image J (Schneider et al., 2012) and the coral cover was calculated per nursery. Corals were assigned to morphological categories as described by Madin et al. (2016).

4.3.5 Data analysis

All statistical analyses were run in RStudio Team version 1.3.1093 (RStuido Team 2023). To visualise fish assemblage and coral characteristics, stacked bar charts were created using the "ggplot" package. Total fish diversity was calculated using the Shannon-Wiener index. Variation in fish family abundance and biomass between time points was visualised using Principal Component Analysis (PCA). The five fish families that contributed the most to PCA loadings were included as loading vectors. A 2-way non-parametric Aligned Ranks Transformation (ART) Analysis of Variance (ANOVA) was used to compare the extracted ordination axes for principal component 1 (PC1) and principal component 2 (PC2) between sites and time and their combined interaction. Non-parametric ANOVA tests were used due to data non-normality as per the Shapiro-Wilk's Test (Hanusz & Tarasińska, 2015). For statistical tests, differences were considered significant when p-values < 0.05.

4.4 Results

4.4.1 Nursery benthic composition

Site-specific coral collections for initial nursery stocking included taxa that have rarely been grown in previous restoration initiatives (e.g. species of *Leptastrea*, *Pectinia;* Scott et al., 2024). Over time coral species composition on nurseries changed as corals were out-planted onto the reef and replaced with new fragments. Over the survey period, 51 coral species from 12 coral genera, spanning 10 different morphologies were grown on coral nurseries (*Figure 4.2.; Table S4.2*). Nevertheless, the predominant corals across all time points belonged to the *Acropora* genus, primarily of corymbose morphology, followed by open branching forms (*Figure 4.2.*; *Figure S4.4.*). Mean coral cover on nurseries across sites was lowest at T1 (% ± SE; 16.48% ± 2.31) compared to T2 (29.04% ± 1.65) and T3 (33.61% ± 3.83; *Table S4.3.*). In contrast, mean coral richness and morphological richness across sites were relatively consistent over the three time points, though coral morphological richness differed between sites (*Table S4.4.*) most likely due to site-specific differences in the coral source material (Scott et al., 2024). Turf fouling on nurseries was present at T2 and T3 time points (*Figure 4.2.*; *Figure S4.5.*). Any dead coral or macrofouling were removed from nurseries during site stewardship activities as per permitting requirements, and as such, they were in low abundance throughout (*Figure 4.2.*; *Figure S4.5.*).

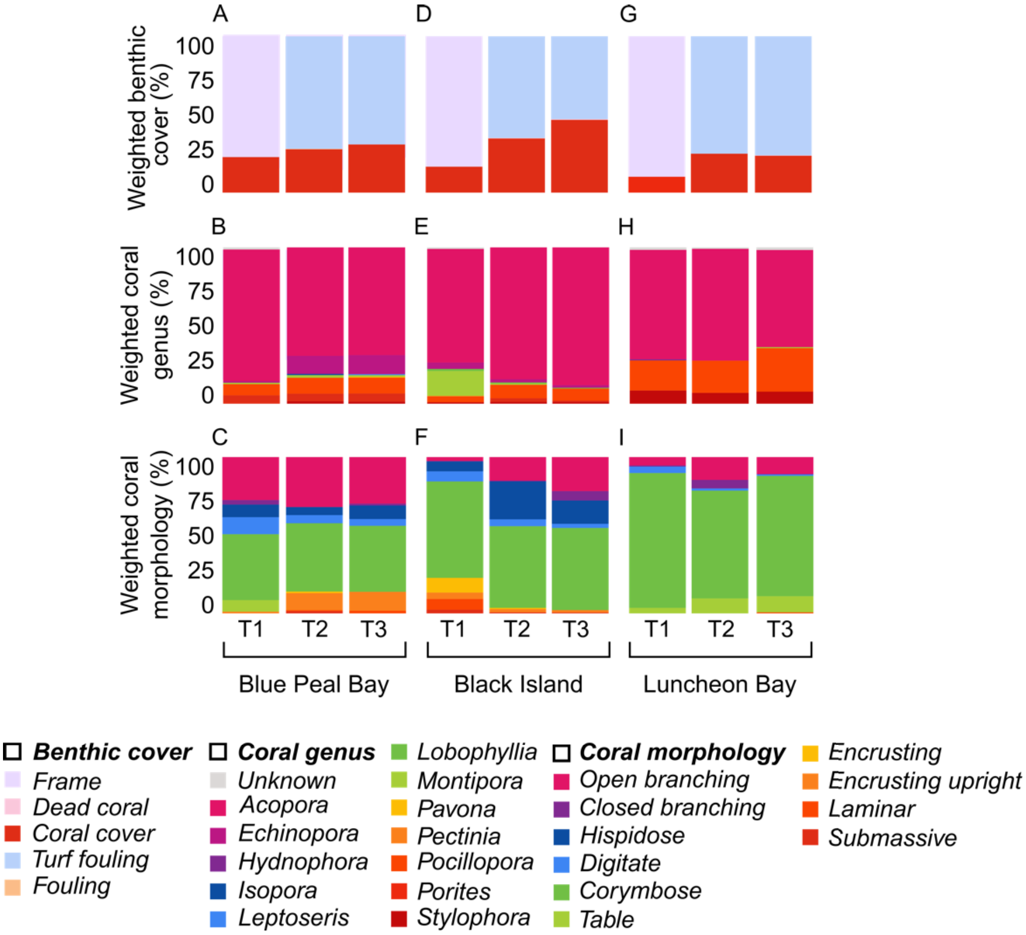

Figure 4.2. Weighted (%) surface area of benthic cover, coral genus and coral morphology on coral propagation nurseries at "Black Island" (A-C), "Blue Pearl Bay" (D-F) and "Luncheon Bay" (G-I) reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 total). Averages for each nursery are comprised of surveys taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total).

4.4.2 Nursery and neighbouring reef fish assemblages

Transect surveys on neighbouring reefs at T1 recorded 44 species from 15 families (*Figure S4.6.*) and were dominated by species within the *Pomacentridae* family across all sites. *Caesionidae* species were also present in high abundance at Black Island but not at other sites (*Figure S4.6.*). Even so, these background fish assemblage abundance did not differ between sites (Kruskal-Wallis, $X^2 = 1.64$, $df = 2.00$, $p = 0.440$; *Table S4.5.*).

Fixed table nurseries deployed by CNP supported a diverse and abundant fish assemblage (*Figure 4.4.; Table S4.6.*). Across the survey period, 50 fish species from 16 families were recorded (*Figure 4.4.; Table S4.6.*). The aggregate mean abundance, richness, diversity, and biomass of fish assemblages increased significantly from T1 (1-day post-installation) to T2 (186-191 days post-installation) and were similar or greater at T3 (340-370 days post-installation) (*Table S4.7.*). Notably, there was a large spread in the data at T2, driven by fish assemblage differences at Luncheon Bay in comparison to other sites (*Figure 4.3H.; Table S4.8.*). Further site-specific differences were evident at T1. Blue Pearl Bay fish abundance, richness, and diversity were greater than at the other sites (Kruskal-Wallis, $p < 0.023$; *Table S4.8.*), with fish biomass also exceeding that of Luncheon Bay at this time point (Dunn, $X^2 = 6.21$, $Z = 2.44$, $p_{adj} = 0.022$; *Table S4.8.*). Despite the site-specific differences in fish assemblage metrics at T1, and the large spread in the data at T2, all fish metrics between sites were similar at T3 (*Figure 4.3E-H.; Table S4.8.*).

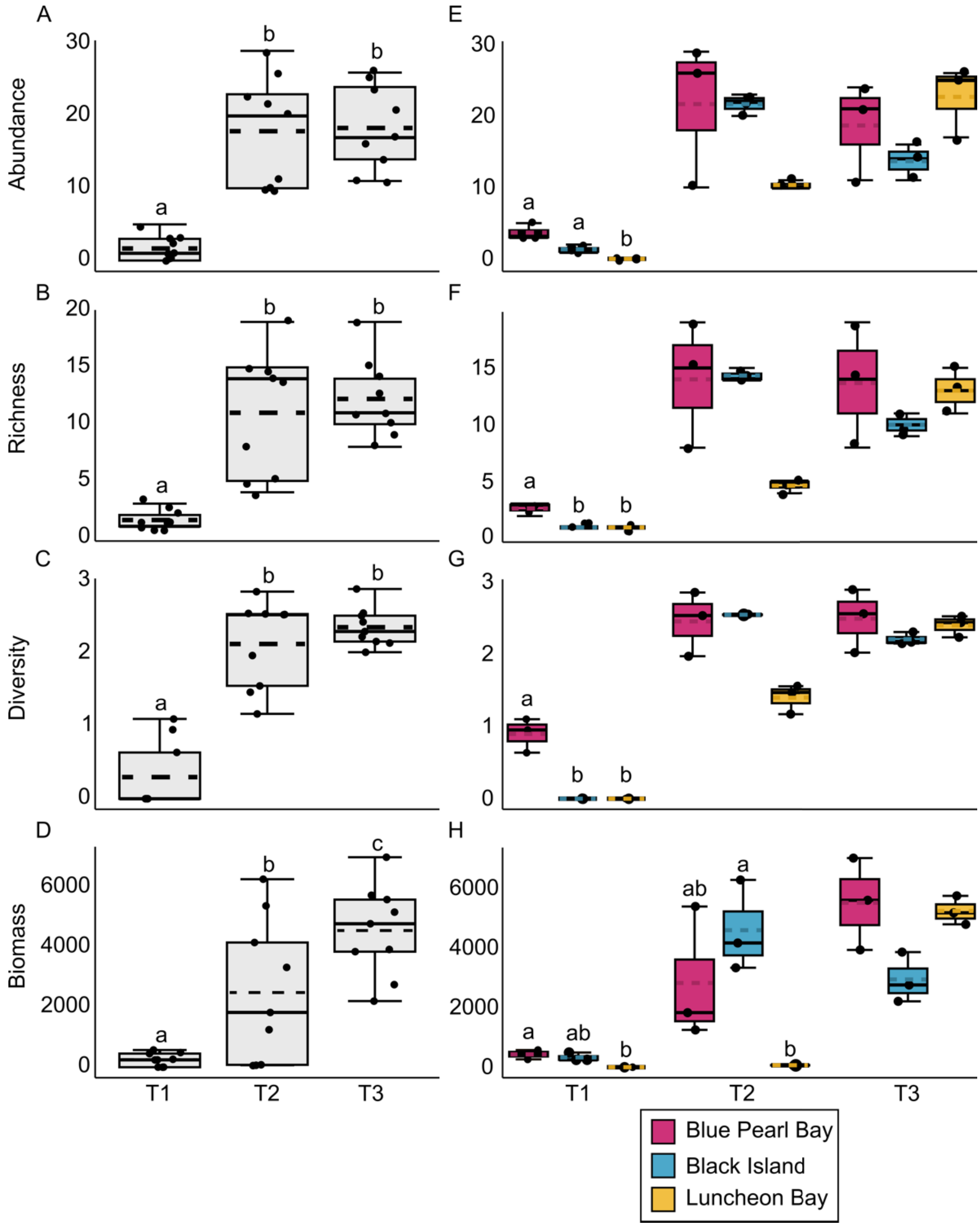

Figure 4.3. Average fish assemblage metrics (A-D) and fish assemblage metrics per reef stewardship site (E-H) as seen on coral propagation nurseries. Reef stewardship sites were located at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" (n = 3 nurseries per site; n = 9 total) in the Whitsundays, Great Barrier Reef. Fish surveys on nurseries were taken at three time points: T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). The absence of a common letter over the boxplots indicates significant differences in fish metrics across time and site (Aligned Ranks Transformation ANOVA and Tukey HSD post-hoc; $p < 0.050$). The bold line within each boxplot indicates the median and the faint dashed line represents the mean. The standard error for each boxplot is displayed with horizontal lines attached to whiskers. Whiskers extend from the data minimum to the lower quartile and then from the upper quartile to the data maximum.

When nurseries were first deployed (T1) fish biomass consisted of three family groups - *Caesionidae* (*Caesio cuning* and *Scolopsis margaritifer*), *Labridae* (one individual *Labridae sp.*) and *Nemipteridae* (*Scolopsis monogramma* and *Scolopsis margaritifer*) - at Blue Pearl Bay, solely of *Nemipteridae* (*Scolopsis margaritifer*) at Black Island, and no fish species were recorded at Luncheon Bay (*Figure 4.3C/G.; Figure 4.4.*). After 6 months (T2) at Blue Pearl Bay and Black Island, the *Scarinae* (predominantly *Scarus ghobban* and *Scarus quoyi*), a sub-family of *Labridae*, contributed the most to overall biomass. However, at Luncheon Bay, *Pomacentridae* (predominantly *Chromis margaritifer*) constituted the majority of the biomass (*Figure 4.4.; Figure S4.7.*). At T3, *Scarinae* (primarily *Hipposcarus longiceps* and *Scarus rivulatus*) followed by *Acanthuridae* (mainly *Acanthurus nigricauda*) families contributed the most to fish biomass on nurseries across all sites at this final time point (*Figure 4.4.; Figure S4.7.*). Prior to T3, neither *Scarinae* nor *Acanthuridae* species had been recorded at Luncheon Bay (*Figure 4.4.*).

A notable observation was the higher abundance of small-bodied fish species across sites at T2 and T3. *Labridae* species, predominantly *Labroides dimidiatus* and juvenile *Thalassoma lunare* were the most abundant fishes across the sites. Other small-bodies fishes were also in abundance, including *Apogonidae* (*Apogonidae spp*), particularly at Luncheon Bay, as well as Pomacentridae (predominantly *Chromis margaritifer* and *Pomacentrus alexanderae*), and *Chaetodontidae* (including *Coradion altivelis* and *Chaetodon pelewensis* but also of juvenile *Chaetodon ocellicaudus*), across all sites (*Figure 4.4.*). Collectively these results highlight variations in fish species composition as a driving force behind the biomass and abundance development on the Whitsundays nursery structures.

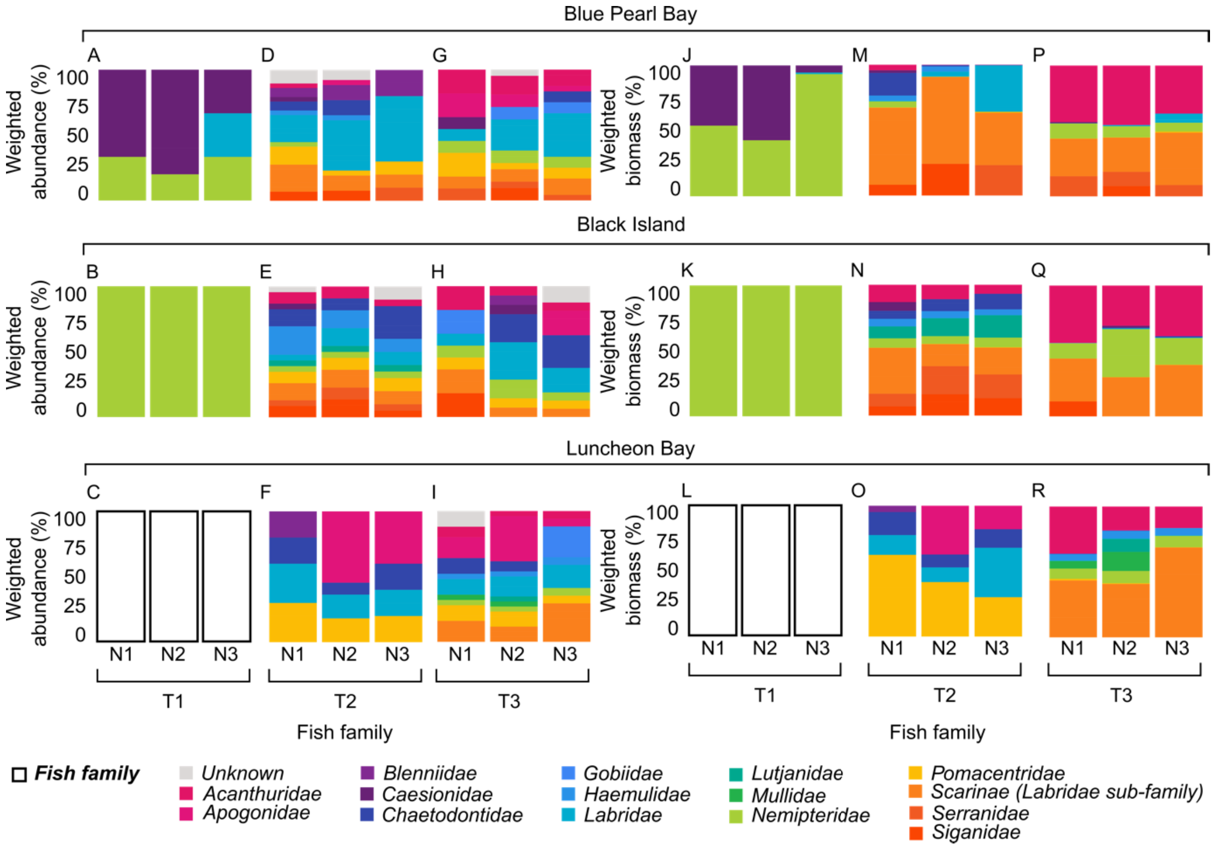

Figure 4.4. Weighted (%) fish total abundance (A-I) and biomass (g) (J-R) (per family, including *Scarinae*, a sub-family of *Labridae*) on coral propagation nurseries at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 per site; n = 9 total; N1, N2, N3). Coral propagation nurseries were surveyed at three time points: T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n=9 surveys per time point; 27 surveys total).

4.5 Discussion

Coral nurseries newly deployed in the Whitsundays to assist reef stewardship activities showed a rapid increase in the presence of fishes, parallel to the development of benthic composition over the first 11-12 months of deployment. These results confirmed that within the initial phase (e.g. first year) of deployment, the fixed table nursery structures can host a diverse fish assemblage from the adjacent natural reefs, building on previous studies that have documented this at different geographic locations (Shafir & Rinkevich, 2010; Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Knoester et al., 2019; Knoester et al., 2023) and also on other artificial structures (Alevizon & Gorham, 1989; Cummings, 1994; Golani & Diamant, 1999; Paxton et al., 2018).

A collective assessment of the sites revealed that, as time progressed, mean fish abundance, richness, diversity and biomass metrics increased from T1 to T2 and were similar or greater at T3. Despite early site-specific differences, namely a greater fish abundance, richness, diversity, and biomass at Blue Pearl Bay at T1 and a large spread in data at T2, fish assemblage abundance, richness, diversity, and biomass were similar across all sites at the final time point (T3). While previous studies that explicitly regard fish on nurseries also report diverse fish assemblages (9-98 species), no studies to date have evaluated how fish assemblages alter with time after nursery deployment (Shafir & Rinkevich, 2010; Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Knoester et al., 2019; Knoester et al., 2023). More commonly, studies have examined whether the presence of fishes drives a reduction in nursery fouling (Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Knoester et al., 2019; Knoester et al., 2023). These studies have lasted between 15 days and 8 months and in many cases used newly deployed nurseries to test hypotheses (Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Taira et al., 2017; Knoester et al., 2019; Knoester et al., 2023). However, as shown here, fish assemblages on newly deployed nurseries can rapidly change over the first 6 months (T1-T2) of deployment and may take 11-12 months (T3) to become similar between sites. These observations appear to be consistent with studies on artificial reef structures. While fish colonisation of artificial structures occurs rapidly, even within hours of deployment (Cummings, 1994; Clark & Edwards, 1999; Golani & Diamant, 1999), fish assemblages often do not reach stabilisation (i.e. limited fluctuation around the mean e.g. Walsh, 1985) until months after structures are deployed (Turner et al., 1969; Stone et al., 1979; Bohnsack & Talbot, 1980). Artificial reef studies that use natural reefs or other artificial reef structures as a proxy report that fish assemblage stabilisation can range from 2-5 months (Alevizon & Gorham, 1989; Cummings, 1994; Golani & Diamant, 1999; Paxton et al., 2018) to more substantial time frames of > 1 year (Fadli et al., 2012; Fariñas-Franco & Roberts, 2014). While this study examined fish assemblages on fixed table nurseries in the in-shore Whitsunday region of the GBR over an 11-12 month period, previous observations taken at a single time point (February 2022) on off-shore mid-water nurseries aged 1-4 years across the northern GBR appeared remarkably similar (***Chapter 2***). In both studies, nurseries hosted fish assemblages with similar predominant families (*Scarinae*, *Acanthuridae*, *Labridae* and *Pomacentridae*) despite the differences in location, nursery design and the seasonal timing of sampling. However, ongoing assessment of the Whitsunday's nurseries is necessary to ascertain if the patterns observed at T3 indicate a stabilised community and whether patterns remain consistent throughout seasonal fluctuations.

The predominate change in nursery fish assemblages between T1 and T2, relative to T2 and T3, coincided with an evolving nursery benthic community as coral material grew and fouling developed. The progression of benthic composition with time precluded us from disentangling whether time, or both time and benthic composition, led to the subsequent shifts in fish assemblages. However, it is well established that changes in benthic composition can shape fish assemblages (Adam et al., 2011; Chong-Seng et al., 2012; Seraphim et al., 2020; Hall & Kingsford, 2021). For instance, an increase in fishes with feeding tactics that target filamentous turfs, which proliferated structures at T2 and T3, may support this theory. Specifically, *Scarinae* species, predominantly scraper feeders from the genera *Scarus* and *Hipposcarus* (as per Bellwood & Choat, 1990; Green & Bellwood, 2009), and *Acanthuridae* species, predominantly sediment suckers from the genus *Acanthurus* (as per Tebbett et al., 2022), which represented the greatest biomass on nurseries at T2 and T3, typically graze on open substratum in pursuit of diatoms, cyanobacteria and other microalgae and microbes within filamentous turfs (Choat & Clements, 1998; Choat et al., 2004; Clements et al., 2017; Clements & Choat, 2018). Furthermore, as coral cover increased on nurseries, so did the abundance of obligate coral dwellers, supporting the hypothesis that benthic conditions influence assemblage composition. This may in part be reflective of smaller-bodied or juvenile fishes that are known to have a strong association with reef structures including those from *Labridae, Chaetodontidae* as well as *Apogonidae* and *Pomacentridae* families (Jones et al., 2004; Munday et al., 2007; Cole et al., 2008; Coker et al., 2014) that, while abundant at T2 and T3, were not captured within biomass measurements. Observations of these fishes are not unusual for coral nurseries that naturally generate high-density coral environments (Frias-Torres et al., 2015a; Frias-Torres & van de Geer, 2015b; Taira et al., 2017; Knoester et al., 2019; Knoester et al., 2023). Shafir and Rinkevich (2010) similarly reported (albeit anecdotally) that small-bodied members of the *Pomacentridae* family and *Pseudanthias squamipinnis* joined an increasing variety of fishes on nurseries as coral colonies grew. Notably, the presence of small fish, particularly *Pomacentridae* species, on coral nurseries mirrors reports on mid-water floating nurseries also deployed on the GBR (***Chapter 2***; ***Chapter 3***). Thus, the results presented here may be indicative of a broader trend of fish species development on nurseries used for coral restoration.

4.6 Conclusion

Coral nurseries employed for propagation-based restoration can host an array of fish species over a relatively short time period. Video surveys from newly established table nurseries revealed mean fish abundance, richness, diversity and biomass metrics across sites increased from T1 (1-day post-installation) to T2 (186-191 days post-installation) and were similar or greater at T3 (340-370 days post-installation). *Nemipteridae* and *Caesionidae* species were the most abundant early colonisers on nurseries followed by *Scarinae* (at T2 and T3) and *Acanthuridae* species (at T3) which became the predominant components of fish biomass across sites. At T2 and T3 the abundance of small-bodied and juvenile *Labridae*, *Chaetodontidae*, *Apogonidae* and *Pomacentridae* species increased considerably. This time-based development of fish assemblages occurred against a backdrop of an evolving nursery benthic community, as coral material grew, and turf fouling developed. These results demonstrate that coral nurseries are structures that do more than grow corals, hosting complex assemblages. As the use of coral nurseries increases on the GBR and worldwide, their interactions with the surrounding environment, and the way in which this affects reef stewardship activities, should be a focus for ongoing research.

4.7 Acknowledgements

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4.9 Supplementary material

4.9.1 Supplementary figures

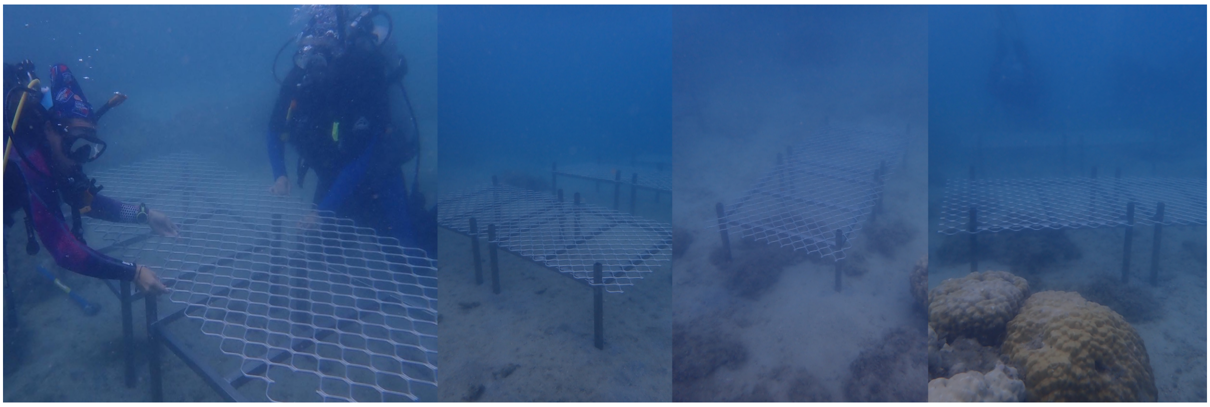

Figure S4.1. Deployment of coral propagation nurseries across reef stewardship sites in the Whitsundays, Great Barrier Reef. Nurseries consist of 1900 x 950 cm diamond aluminium mesh, fastened to two parallel 85 x 85 cm stainless steel frames using stainless steel wire. Stainless steel frames are 50 cm above the substrate and the legs are supported by steel rebar attached to frames using stainless steel wire and hammered into the sand. Nurseries are deployed under Great Barrier Reef Marine Park Authority permit G22/46543-1 Photo credit: Gemma M Gillette.

Figure S4.2. Coral propagation nurseries across reef stewardship sites in the Whitsundays, Great Barrier Reef, stocked with coral colonies at the time of deployment (A), six months (B) and 11-12 months post-deployment (C). Nurseries are deployed under Great Barrier Reef Marine Park Authority permit G22/46543-1 Photo credit: Gemma M Gillette and Cass Hayward.

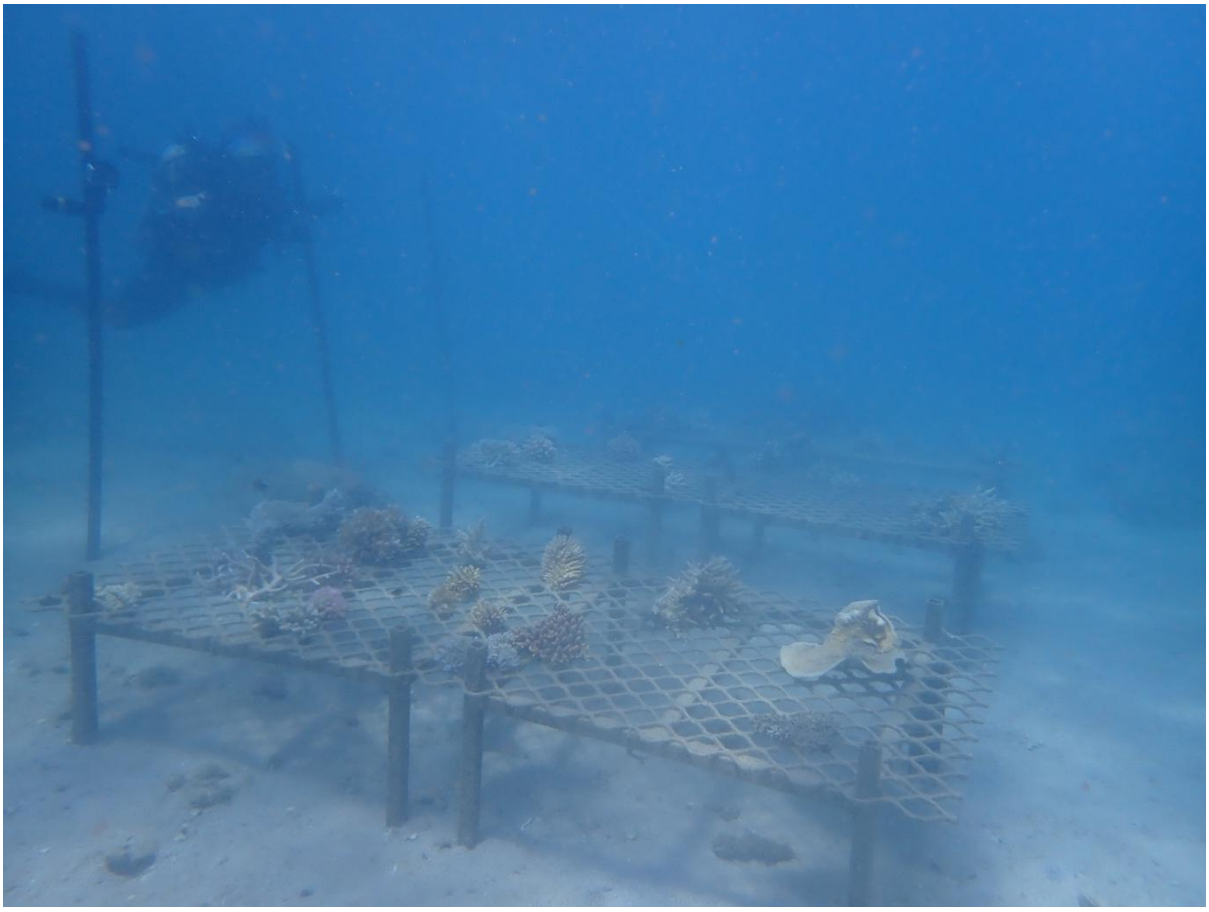

Figure S4.3. Fish video survey setup consisting of a GoPro Hero 8® camera attached to a GoPro® "Jaws: Flex Clamp" and clipped onto 180 cm star pickets hammered into sand substrate 2 m from the edge of coral propagation nurseries, deployed across reef stewardship sites in the Whitsundays, Great Barrier Reef. Photo credit: Cass Hayward.

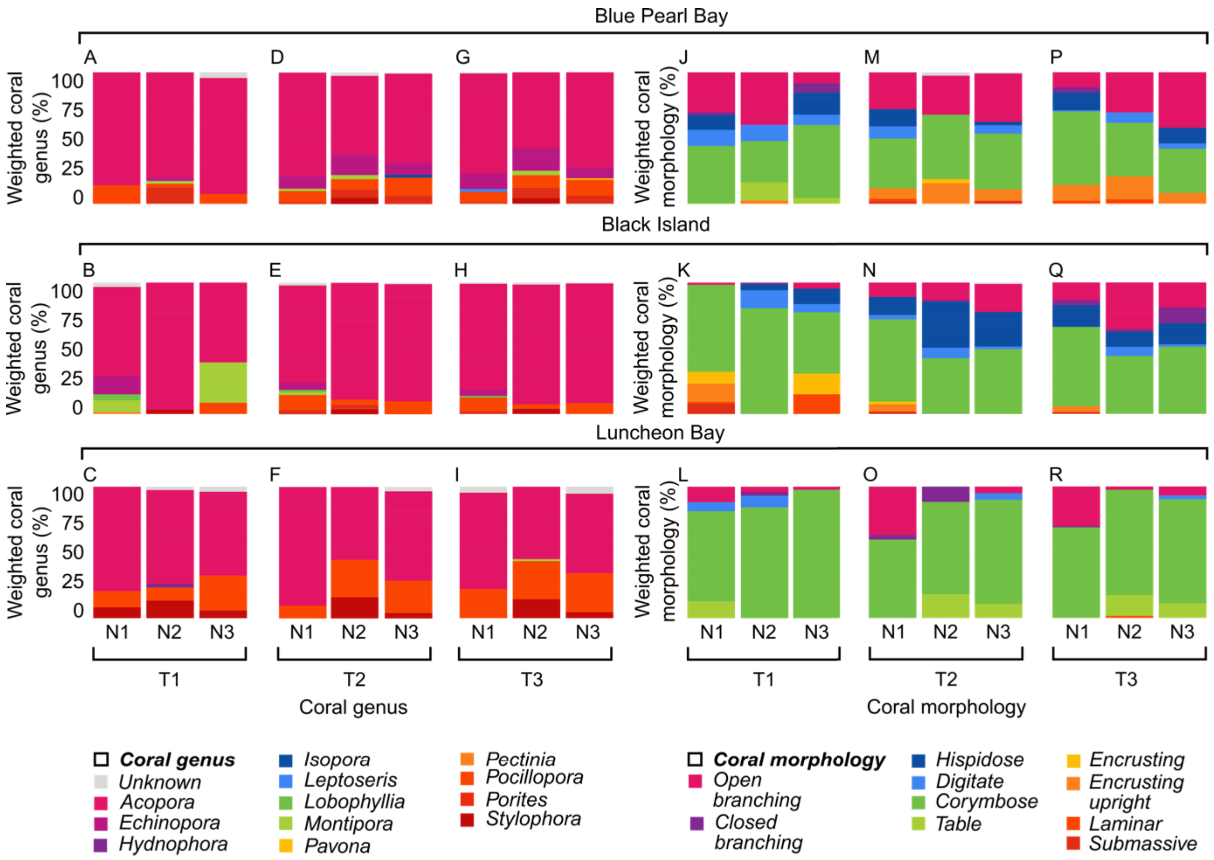

Figure S4.4. Weighted (%) surface area of coral genus (A-I) and coral morphology (J-R) per coral nursery (n = 3 per site; n = 9 total; N1, N2, N3) at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef. Coral propagation nurseries were surveyed at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total).

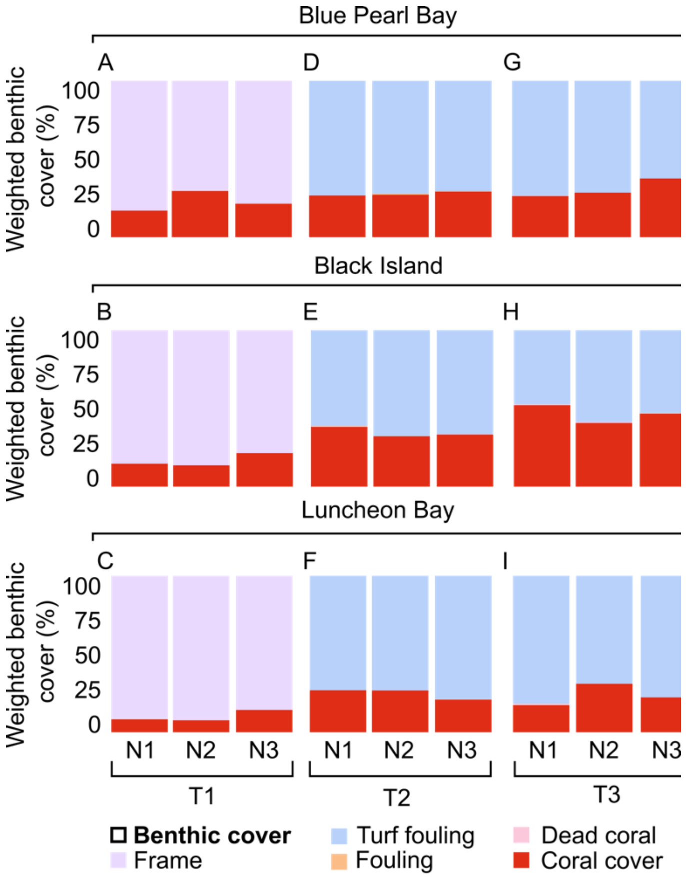

Figure S4.5. Weighted (%) surface area benthic composition on coral nurseries (n = 3 per site; n = 9 total; N1, N2, N3) at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef. Benthic composition on nurseries was surveyed at T1 (A-C; 1-day post-deployment), T2 (D-F; 186-191 days post-deployment) and T3 (G-I; 340-370 days post-deployment) (n = 9 surveys per time point; 27 surveys total).

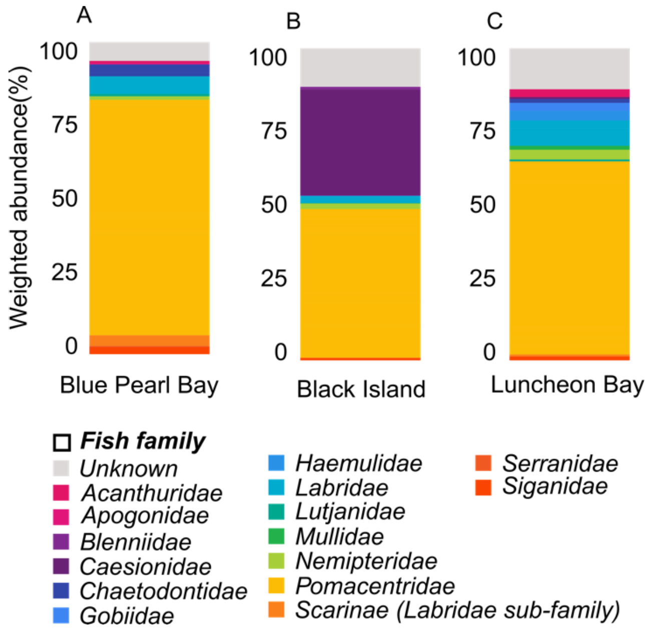

Figure S4.6. Weighted (%) fish abundance per fish family group (including *Scarinae*, a sub-family of *Labridae*) on natural reefs at (A) "Black Island", (B) "Blue Pearl Bay" and (C) "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef. Fish abundance is an average of 3 x 30 m transects taken at each site.

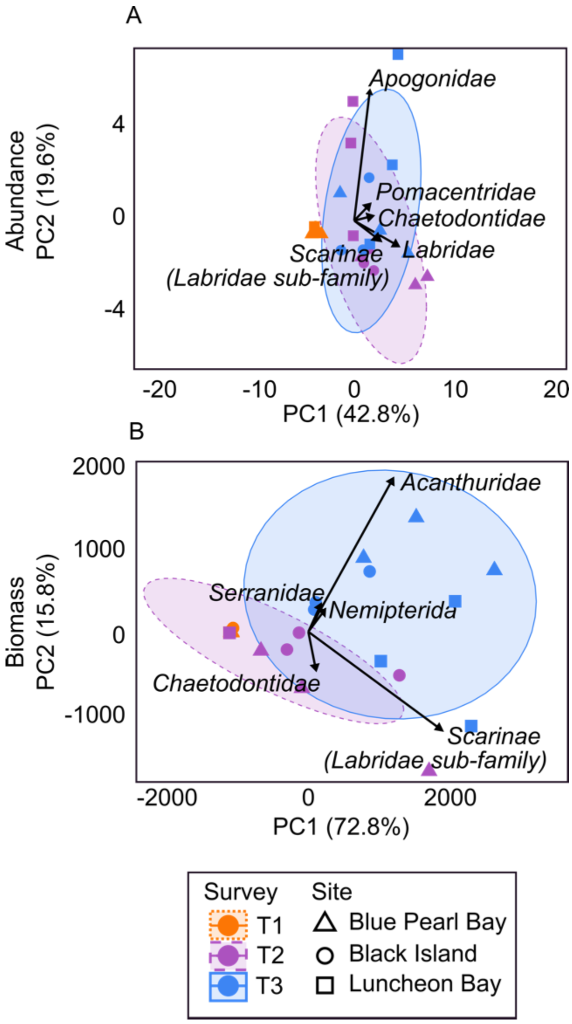

Figure S4.7. Principal components analysis (PCA) of fish assemblage abundance (A) and biomass (B) observed on coral nurseries at three survey time points (colour): T1 (1-day post-deployment), T2 (186-191 days post-deployment) and T3 (340-370 days post-deployment) (n = 27 surveys total). Nurseries were deployed across reef stewardship sites (shapes) located in the Whitsundays, Great Barrier Reef (n = 3 per site, n = 9 total). Ellipses show 90% confidence intervals. The five fish families that contributed the most to PCA loadings were included as loading vectors. PCA loading vectors were scaled to PCA eigenvalues. Vector direction shows the relative contribution of each fish family to the principal components and vector length indicates the strength of this contribution. Fish assemblage abundance (A) PC1 explained 42.8% of the total variance in the abundance of fish family groups, with *Labridae* (49.90%), *Scarinae* (17.60%), *Chaetodontidae* (8.30%), *Pomacentridae* (6.60%) and *Apogonidae* (5.90%) contributing the most to this vector (*Data S6*; *Figure 5A*). An additional 19.6% of the variance in family group abundance was accounted for by PC2, with *Apogonidae* (83.50%) contributing the most to this vector followed by *Labridae* (3.60%) and *Siganidae* (3.50%). The abundance per family along PC1 differed between T1 and T2 (Tukey $p < 0.000$) as well as T1 and T3 (Tukey $p < 0.000$) but did not differ along PC2. Fish assemblage biomass (B) PC1 explained 72.8% of the total variance in biomass between family groups, with *Scarinae* (69.30%) and *Acanthuridae* (27.90%) contributing to this vector. A further 15.8% of the variance in fish family biomass was accounted for by PC2, with Acanthuridae (64.20%) and Scarinae (26.50%) contributing the most to this vector. At each time point the biomass of fish families differed greatly for PC1 (Tukey $p = 0.009$) but only T2 differed from T3 for PC2 (Tukey $p = 0.001$).

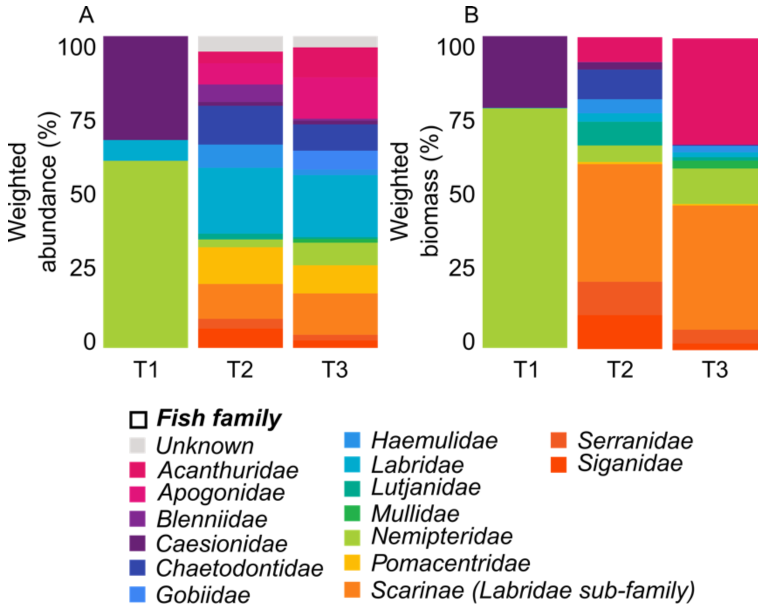

Figure S4.8. Weighted (%) average fish (A) abundance and (B) biomass (per family, including *Scarinae*, a sub-family of *Labridae*) on coral propagation nurseries at "Black Island", "Blue Pearl Bay", and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site). Averages for each nursery are comprised of surveys taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total).

4.9.2 Supplementary tables

Table S4.1. Sampling times of fish video surveys at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef. Tide times recorded at Bugati Reef (https://www.msq.qld.gov.au/tides/tide-tables).

Sample time				
Site	Date	Time	Survey	Days post nursery deployment
Black Island	31.08.22	11:00	1	1
Blue Pearl Bay	28.08.22	9:35	1	1
Luncheon Bay	03.09.22	12:57	1	1
Black Island	06.03.23	11:06	2	187
Blue Pearl Bay	07.03.23	13:11	2	191
Luncheon Bay	08.03.23	9:19	2	186
Black Island	03.09.23	11:38	3	367
Blue Pearl Bay	03.09.23	10:05	3	370
Luncheon Bay	09.08.23	12:59	3	340

Tide				
Site	Date	Tide	Time	Meters
Black Island	31.08.22	Low	05:54	0.64
		High	12:16	2.2
		Low	17:57	0.84
Blue Pearl Bay	28.08.22	Low	04:30	0.7
		High	10:27	2.14
		Low	16:07	0.51
		High	22:46	2.8
Luncheon Bay	03.09.22	High	02:08	1.88
		Low	08:29	0.75
		High	15:52	2.26
		Low	22:13	1.21
Black Island	06.03.23	Low	03:11	0.68
		High	09:49	3.02
		Low	15:58	0.83
		High	21:55	2.36
Blue Pearl Bay	07.03.23	Low	03:36	0.70
		High	10:10	2.99
		Low	16:17	0.84
		High	22:18	2.41
Luncheon Bay	08.03.23	Low	04:00	0.73

		High	10:32	2.93
		Low	16:36	0.83
		High	22:44	2.45
Black Island Blue Pearl Bay	03.09.23	Low	05:56	0.48
		High	12:22	2.52
		Low	18:07	0.75
Luncheon Bay	09.08.23	High	04:28	1.96
		Low	10:48	0.74
		High	18:02	2.48

Table S4.2. Coral species list on coral propagation nurseries at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site). Coral surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total).

Genus	Species
Acopora	*Acropora spathulata*
Acopora	*Acropora selago*
Acopora	*Acropora latistella*
Acopora	*Acropora elseyi*
Acopora	*Acropora cerealis*
Acopora	*Acropora rosaria*
Acopora	*Acropora spp*
Acopora	*Acropora millepora*
Acopora	*Acropora yongei*
Acopora	*Acropora humilis*
Acopora	*Acropora loripes*
Acopora	*Acopora cerealis*
Acopora	*Acropora muricata*
Acopora	*Acropora bushyensis*
Acopora	*Acropora nasuta*
Acopora	*Acropora intermedia*
Acopora	*Acropora abrolhosensis*
Acopora	*Acropora microphthalma*
Acopora	*Acropora gemmifera*
Acopora	*Acropora florida*
Acopora	*Acropora aculeus*
Acopora	*Acropora pectinata*
Acopora	*Acropora kenti*
Acopora	*Acropora hyacinthus*

Acopora	*Acropora verweyi*
Acopora	*Acropora robusta*
Acopora	*Acropora cytherea*
Acopora	*Acropora micropthalma*
Acopora	*Acropora subulata*
Acopora	*Acropora carduus*
Acopora	*Acropora valenciennesi*
Acopora	*Acrpora nasutua*
Acopora	*Acropora hyacinthis*
Acopora	*Acropora sarmentosa*
Acopora	*Acopora bushyensis*
Echinopora	*Echinopora horrida*
Echinopora	*Echinopora lamellosa*
Hydnophora	*Hydnophora rigida*
Isopora	*Isopora spp*
Leptoseris	*Leptoseris explanata*
Lobophyllia	*Lobophyllia spp*
Montipora	*Montipora spp*
Montipora	*Montipora aequituberculata*
Montipora	*Montipora hispida*
Pavona	*Pavona cactus*
Pectinia	*Pectinia paeonia*
Pocillopora	*Pocillopora damicornis*
Pocillopora	*Pocillopora verrucosa*
Pocillopora	*Pocilopora damicornis*
Pocillopora	*Pocillopora acuta*
Pocillopora	*Pocilopora acuta*
Pocillopora	*Pocilopora verucosa*
Porites	*Porites rus*
Porites	*Porites cylindrica*
Stylophora	*Stylophora pistillata*

Table S4.3. The average and standard error of coral cover (%), richness and morphological richness on coral nurseries at three time points: T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). Averages are comprised of coral nurseries located at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total).

	Coral cover (%)		Coral richness		Coral morphological richness	
	Average	SE	Average	SE	Average	SE
T1	16.48	2.31	12.11	0.68	4.67	0.44
T2	29.04	1.65	13.78	1.29	5.11	0.54

T3	33.61	3.83	12.33	1.03	4.89	0.39

Table S4.4. A two-way, non-parametric Aligned Ranks Transformation ANOVA to evaluate differences in coral composition (coral cover, richness, and morphological richness) on nurseries between sites and surveys. Sites were located at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total). Surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). A Tukey HSD post-hoc test evaluated statistically significant results (*p* < 0.05).

Aligned ranks transformation ANOVA				
Coral cover				
	df	df.res	F value	p value
Site	2.00	18.00	0.91	0.418
Survey	2.00	18.00	23.81	0.000
Site:Survey	4.00	18.00	13.42	0.000
Coral richness				
	df	df.res	F value	p value
Site	2.00	18.00	0.24	0.791
Survey	2.00	18.00	0.74	0.489
Site:Survey	4.00	18.00	2.85	0.054
Coral morphological richness				
	df	df.res	F value	p value
Site	2.00	18.00	9.82	0.001
Survey	2.00	18.00	0.49	0.623
Site:Survey	4.00	18.00	4.49	0.011

Tukey HSD post-hoc test						
Coral cover						
Survey		Estimate	SE	df	t ratio	p value
T11	T6	4.56	2.35	18.00	1.94	0.158
T11	T0	15.78	2.35	18.00	6.70	0.000
T6	T0	11.22	2.35	18.00	4.77	0.000
Coral morphological richness						
Survey		Estimate	SE	df	t ratio	p value
Black Island	Blue Pearl Bay	3.22	3.08	18.00	1.05	0.310
Black Island	Luncheon Bay	13.11	3.08	18.00	4.25	0.001
Blue Pearl Bay	Luncheon Bay	9.89	3.08	18.00	3.21	0.005

Table S4.5. A two-way, non-parametric Aligned Ranks Transformation ANOVA to evaluate differences in fish abundance on natural reefs between sites. Sites were located at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef. Results were considered statistically significant at *p* < 0.05.

Kruskal-Wallis test			
	Chi.sq	df	p value
Sites	1.64	2.00	0.440

Table S4.6. Fish assemblage species list on coral propagation nurseries at “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site). Fish surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total).

Family	Scientific name
Acanthuridae	*Acanthurus nigricauda*
Acanthuridae	*Acanthurus blochii*
Acanthuridae	*Acanthurus thompsoni*
Acanthuridae	*Acanthurus dussumieri*
Apogonidae	*Cheilodipterus parazonatus*
Apogonidae	*Apogonidae spp*
Apogonidae	*Cheilodipterus nigrotaeniatus*
Apogonidae	*Ostorhinchus cookii*
Apogonidae	*Apogon angustatus*
Blenniidae	*Aspidontus dussumieri*
Blenniidae	*Blenniidae spp*
Blenniidae	*Meiacanthus lineatus*
Blenniidae	*Meiacanthus atrodorsalis*
Blenniidae	*Meiacanthus ditrema*
Caesionidae	*Caesio cuning*
Chaetodontidae	*Chaetodon pelewensis*
Chaetodontidae	*Coradion altivelis*
Chaetodontidae	*Chaetodon ocellicaudus*
Gobiidae	*Gobiodon okinawae*
Gobiidae	*Amblygobius phalaena*
Haemulidae	*Lethrinus rubrioperulatus*
Haemulidae	*Diagramma pictum*
Labridae	*Labridae spp*
Labridae	*Thalassoma hardwicke*
Labridae	*Labroides dimidiatus*
Labridae	*Thalassoma lutescens*
Labridae	*Halichoeres melanotis*
Labridae	*Choerodon schoenleinii*
Lutjanidae	*Symphorus nematophorus*
Lutjanidae	*Lutjanus johnii*
Mullidae	*Parupeneus barberinus*

Nemipteridae	*Scolopsis monogramma*
Nemipteridae	*Scolopsis margaritifer*
Nemipteridae	*Pentapodus vitta*
Pomacentridae	*Pomacentrus alexanderae*
Pomacentridae	*Neopomacentrus bankieri*
Pomacentridae	*Chromis margaritifer*
Pomacentridae	*Dischistodus perspicillatus*
Pomacentridae	*Chrysiptera glauca*
Pomacentridae	*Pomacentridae spp*
Pomacentridae	*Pomacentrus philippinus*
Pomacentridae	*Dischistodus prosopotaenia*
Scarinae	*Scarus schlegeli*
Scarinae	*Scarus ghobban*
Scarinae	*Scarus quoyi*
Scarinae	*Scarus flavipectoralis*
Scarinae	*Scarus rivulatus*
Scarinae	*Scarinae spp*
Scarinae	*Scarus globiceps*
Scarinae	*Hipposcarus longiceps*
Serranidae	*Plectropomus leopardus*
Siganidae	*Siganus doliatus*
Siganidae	*Siganus punctatus*

Table S4.7. A two-way, non-parametric Aligned Ranks Transformation ANOVA to evaluate differences in fish assemblage metrics (abundance, richness, diversity, and biomass) on nurseries between sites and surveys. Sites were located at "Black Island", "Blue Pearl Bay" and "Luncheon Bay" reef stewardship sites in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total). Surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). A Tukey HSD post-hoc test evaluated statistically significant results (*p* < 0.05).

Aligned Ranks Transformation ANOVA				
Abundance				
	df	df.res	F value	p value
Site	2.00	18.00	2.47	0.112
Survey	2.00	18.00	20.12	0.000
Site:Survey	4.00	18.00	5.09	0.006
Richness				
	df	df.res	F value	p value
Site	2.00	18.00	6.68	0.007
Survey	2.00	18.00	22.41	0.000
Site:Survey	4.00	18.00	6.15	0.003

Diversity				
	df	df.res	F value	p value
Site	2.00	18.00	26.82	0.000
Survey	2.00	18.00	28.32	0.000
Site:Survey	4.00	18.00	11.16	0.000
Biomass				
	df	df.res	F value	p value
Site	2.00	18.00	4.20	0.032
Survey	2.00	18.00	37.01	0.000
Site:Survey	4.00	18.00	10.60	0.000

Tukey HSD post-hoc test						
Abundance						
Survey		Estimate	SE	df	t ratio	p value
T1	T2	-13.00	2.46	18.00	-5.28	0.000
T1	T3	-14.00	2.46	18.00	-5.69	0.000
T2	T3	-1.00	2.46	18.00	-0.41	0.914
Richness						
Survey		Estimate	SE	df	t ratio	p value
T1	T2	-11.89	2.38	18.00	-5.00	0.000
T1	T3	-15.11	2.38	18.00	-6.36	0.000
T2	T3	-3.22	2.38	18.00	-1.36	0.384
Diversity						
Survey		Estimate	SE	df	t ratio	p value
T1	T2	-11.00	2.18	18.00	-5.06	0.000
T1	T3	-16.00	2.18	18.00	-7.36	0.000
T2	T3	-5.00	2.18	18.00	-2.30	0.082
Biomass						
Survey		Estimate	SE	df	t ratio	p value
T1	T2	-10.00	1.99	18.00	-5.04	0.000
T1	T3	-17.00	1.99	18.00	-8.56	0.000
T2	T3	-7.00	1.99	18.00	-3.53	0.007

Table S4.8. A one-way, non-parametric Kruskal-Wallis test to evaluate differences in fish assemblage metrics (abundance, richness, diversity, and biomass) on nurseries at sites between survey time points. Surveys were taken at T1 (1-day post-installation), T2 (186-191 days post-installation) and T3 (340-370 days post-installation) (n = 9 surveys per time point; 27 surveys total). Surveys recorded fish assemblages at sites: “Black Island”, “Blue Pearl Bay” and “Luncheon Bay” in the Whitsundays, Great Barrier Reef (n = 3 nurseries per site; n = 9 nurseries total). A Dunn post-hoc test evaluated statistically significant results ($p < 0.05$).

Kruskal-Wallis test
Abundance

Survey	chi-squared	df	p value
T1	7.58	2.00	0.023
T2	3.40	2.00	0.183
T3	4.10	2.00	0.129

Richness

Survey	chi-squared	df	p value
T1	7.71	2.00	0.021
T2	5.63	2.00	0.060
T3	2.08	2.00	0.353

Diversity

Survey	chi-squared	df	p value
T1	7.62	2.00	0.022
T2	5.60	2.00	0.061
T3	1.69	2.00	0.430

Biomass

Survey	chi-squared	df	p value
T1	6.22	2.00	0.045
T2	5.96	2.00	0.051
T3	5.42	2.00	0.066

Dunn post-hoc test

Abundance at T1

Sites		chi-squared	Z value	p value	p.adj
Black Island	Blue Pearl Bay	7.58	-1.38	0.08	0.253
Black Island	Luncheon Bay	7.58	1.38	0.08	0.253
Blue Pearl Bay	Luncheon Bay	7.58	2.75	0.00	0.009

Richness at T1

Sites		chi-squared	Z value	p value	p.adj
Black Island	Blue Pearl Bay	7.71	-2.41	0.01	0.024
Black Island	Luncheon Bay	7.71	0.00	0.50	1.000
Blue Pearl Bay	Luncheon Bay	7.71	2.41	0.01	0.024

Diversity at T1

Sites		chi-squared	Z value	p value	p.adj
Black Island	Blue Pearl Bay	7.62	-2.39	0.01	0.025
Black Island	Luncheon Bay	7.62	0.00	0.50	1.000
Blue Pearl Bay	Luncheon Bay	7.62	2.39	0.01	0.025

Biomass at T1

Sites		chi-squared	Z value	p value	p.adj
Black Island	Blue Pearl Bay	6.21	-0.76	0.22	0.670
Black Island	Luncheon Bay	6.21	1.68	0.05	0.141
Blue Pearl Bay	Luncheon Bay	6.21	2.44	0.01	0.022

Chapter 5: General discussion and future directions

5.1 Summary

Coral propagation and out-planting restoration techniques using *in-situ* coral nurseries often aim to foster ecological resilience and maintenance of ecosystem services for dependent human communities (Hein et al., 2017; Shaver et al., 2020; Howlett et al., 2022). Interactions of coral and fish assemblages are key contributors to the resilience of coral-dominant reefs and the provision of reef ecological service values (Cheal et al., 2010; Maynard et al., 2017; Hein et al., 2020). However, despite the critical role of fish assemblages in retaining coral reef health (Shaver & Silliman, 2017; Ladd et al., 2018; Bellwood et al., 2019), they are often overlooked in the planning and operation of coral restoration projects (Boström-Einarsson et al., 2018; Hein et al., 2020), and are rarely considered for monitoring during the nursery propagation phase. Research presented in this thesis demonstrates how reef restoration-based management initiatives by stakeholders such as the Great Barrier Reef (GBR) tourism industry can incorporate the monitoring of reef fishes into their restoration practice. This thesis has drawn upon insights from ecological reef studies and in doing so presents observations that have improved the understanding of bidirectional interactions between local fish assemblages and coral nursery structures. Specifically, within this thesis I examined (i) the ability of nurseries to act as novel habitats for fish assemblages (***Chapter 2***, Gillette et al. In Review); (ii) the extent to which filamentous turf fouling accumulates when fish assemblages are excluded from nurseries (***Chapter 3***) and (iii) the development of these fish assemblages on early-phase coral nurseries (***Chapter 4***). In this final chapter, I synthesise the findings presented throughout the thesis, highlight the importance of applying strategies to understand and encourage positive fish interactions with coral nurseries within restoration decision-making and suggest future avenues for research within reef stewardship activities to optimise nursery-based practices.

5.2 Integrating fish assemblage monitoring into coral propagation activities on the Great Barrier Reef

Considering ecological interactions at each stage of the coral propagation process can align projects more closely with the goals of enhancing ecosystem resilience by supporting mutually positive interactions between species (Shaver & Silliman, 2017; Ladd et al., 2018; Hein et al., 2020). On healthy reefs, fish assemblages can have both positive (e.g. herbivory of algae growth, thus preventing overgrowth that can smother corals; Adam et al., 2015) and negative effects (e.g. corallivory or algae farming behaviours; Vermeij et al., 2015; Rice et al., 2019) on corals. Such interactions have also been documented during the nursery and out-planting phase of coral propagation activities for restoration programs (e.g. herbivory/collivory and out-planting/nursery, Ladd et al., 2018; herbivory/collivory and nurseries, Knoester et al., 2019; corallivory and out-planting, Koval et al., 2020). For reef restoration programs, including coral propagation efforts on Australia's Great Barrier Reef (GBR), understanding these interactions is likely to be critical in optimising out-planting practices that aim to assist increases in hard coral cover (Halpern et al., 2007; Johnson et al., 2011; Seraphim et al., 2020). However, the feasibility of translating methods used to investigate ecological interactions on large-scale natural reefs to reef stakeholder-led restoration programs is challenged by operational, time, and resource constraints. In the case of the Coral Nurture Program (CNP) operations on the Great Barrier Reef, data reporting and monitoring are largely governed by tourism schedules, thus restricting time on site (Howlett et al., 2022). Inevitably, research within a restoration program comes with trade-offs (such as those captured in this thesis), whereby efforts to opportunistically capture how fish interact with corals will have a limited resolution compared to efforts conducted on natural reefs within dedicated ecological studies. Despite these constraints, projects have begun to integrate fish monitoring at out-planting sites as a metric of success to inform optimised out-planting strategies (Opel et al., 2017; Koval et al., 2020; Seraphim et al., 2020; Dehnert et al., 2023). However, ecological insights to tailor coral propagation planning, operations, and monitoring at the nursery propagation stage have not been previously integrated for facilitating similar positive feedback interactions.

Research within this thesis has shown for the first time that nurseries used for coral propagation on the GBR can also act as novel habitats for fish assemblages (***Chapter 2***). By examining fish use of coral nurseries, ***Chapter 2*** provides a shift towards a more comprehensive "whole life" (*sensu* Spurgeon, 2001) ecological evaluation of restoration outcomes (Boström-Einarsson et al., 2020; Hein et al., 2020). Within this chapter, a rapid fish monitoring method (< 15 min surveys) was developed to capture 74% of the fish assemblage data (55% of fish functional group data) obtained in 1 hr survey videos on coral nurseries. Such a rapid method was better integrated into time-constrained tourism operations, enabling a greater number of nurseries to be monitored, and thus a better understanding of fish assemblage patterns. With this method, my project has shown that fish assemblages may benefit from coral propagation activities earlier than the out-plant phase, through the provision of novel habitat provided by coral nursery structures (***Chapter 2**; Figure 5.1.*). In ***Chapter 3***, I illustrated that such novel habitat provisioning can in turn, result in positive feedback loops for propagation activities via fish-facilitated removal of fouling organisms that can compete with coral for space (*Figure 5.1.*). Specifically, through a cage exclusion experiment, I found that filamentous turf algae was reduced where fishes had unobstructed access to nursery structures, highlighting intricate interspecies relationships in field-based restoration. These findings verified the proposed, but largely untested, assertions that the integration of ecologically-informed reef restoration practices can improve resource-effectiveness (e.g. reduced need for nursery maintenance) which may have further implications for the success of restoration efforts (Shaver & Silliman, 2017; Ladd et al., 2018). Finally, whilst ***Chapter 2*** and ***3*** evaluated fish assemblage interactions with established coral nurseries, no prior study has documented how fish assemblage abundance, diversity and species composition developed on newly installed *in-situ* nursery structures. Consequently, in ***Chapter 4*** I evaluated fish communities at new nursery sites over their first year of establishment, in turn revealing that fish assemblage composition on nurseries develops over time alongside an evolving benthic composition (*Figure 5.1.*). Such an outcome suggested that, as for natural reefs, a complex interplay exists between substrate, time, and species composition to influence fish community development (Harrison & Booth, 2007; Ceccarelli et al., 2011; Madin et al., 2019). In considering and monitoring fish interactions within restoration practice, the findings of this thesis have advanced understanding of the ways in which fish interactions with coral nursery structures can result in multiple service benefits, thus contributing to several restoration goals. As a greater understanding of the interactions between reef restoration and fishes is gained, and as fish-focused research is integrated into the core of restoration efforts, the full potential of these coral nurseries as important restoration tools can be realised (Hein et al., 2021a, Seraphim et al., 2020).

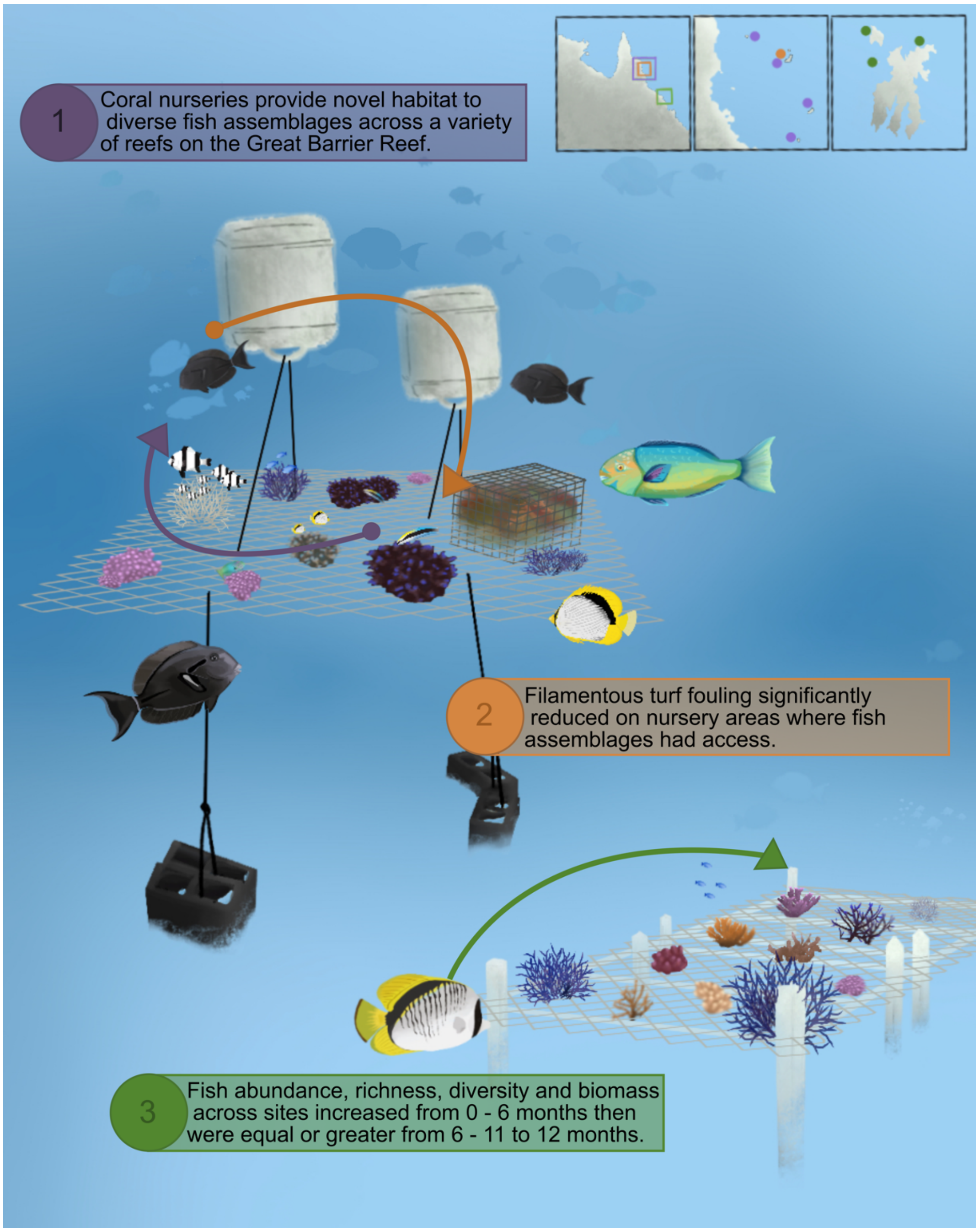

Figure 5.1. High-level findings of the three aims addressed in this thesis (adapted from ***Chapter 1***, *Figure 1.2.*). Studies were conducted within the operational contexts of the Coral Nurture Program in Cairns-Port Douglas (Aim 1, ***Chapter 2***; Aim 2, ***Chapter 3***) and Whitsundays (Aim 3, ***Chapter 4***) on the Great Barrier Reef.

5.3 Fish assemblage-nursery interactions and coral propagation cost-effectiveness

Understanding the feasibility, and ultimately the sustainability, of restoration interventions rests on their financial viability or cost-effectiveness and their ability to showcase "success" against goals to secure funding (Cook et al., 2017; Iacona et al., 2018; Suggett et al., 2023).

Currently, CNP has deployed >100 nurseries across 27 sites in the Cairns and Port Douglas northern GBR region alone (https://www.coralnurtureprogram.org). The scaling of this program has, in part, been attributed to the ability to keep nursery structure costs low, via the in-kind contributions of participating reef tourism operators, as well as low nursery material costs (Scott et al., 2024). In addition, nurseries deployed across Cairns and Port Douglas offshore sites in the northern GBR region rarely require fouling removal when fish assemblages have access (***Chapter 3***) and therefore represent a large cost savings for CNP. In the Whitsundays region, CNP nurseries (n = 3 sites total, n = 9 nurseries total) require fouling removal every 6-8 months. This increased necessity for manual algae removal likely results from poor water quality inherent to the in-shore reefs of the Whitsundays region (Devlin & Brodie, 2005; Devlin & Schaffelke, 2009) that is known to increase algal growth (Smith et al., 2001; Fabricius et al., 2005). Elsewhere, restoration programs have reported more frequent nursery maintenance requirements, necessitating the removal of fouling every month or even 5 times a month (Edwards et al., 2010; Montano et al., 2022).

Based on the CNP costing structure, if nurseries across CNP required monthly fouling removal this would represent a significant financial cost to the project. For example, a buddy pair of two divers takes 45-60 minutes (one dive) to clean 6 nurseries at the Whitsunday sites. Considering this maintenance time, using the costings recently proposed by Scott et al. (2024), and assuming all CNP nurseries (across 9 tourism operations, 6 reefs) required this same level of cleaning per month as recommended by Montano et al. (2022), the cumulative cost of nursery maintenance for the CNP would amount to > AU $39,500.00 per month and over $474,000.00 per year with $82 500 in-person hour costs per year alone (*Table 5.1.*; Scott et al., 2024). Whilst care must be taken when considering this costing given the underlying assumptions, it showcases the magnitude of expenses associated with fouling management in restoration practice. Harnessing ecological interactions that result in natural fouling removal is a well-established method for cost-effectiveness in aquacultural and laboratory-based nurseries by co-culturing corals with grazing invertebrate herbivores (e.g. urchins and snails) to reduce coral recruit competition with algae (Omori, 2005; Craggs et al., 2019; Neil et al., 2021). However, the findings within this thesis underscore the critical need to consider and facilitate reef fish-assisted biofouling of *in-situ* coral nurseries to improve restoration cost-effectiveness, particularly in resource-constrained stakeholder-led programs such as the CNP. Direct cost assessment could not be made, the approximate estimates here illustrate the likely cost savings of facilitating positive species interactions similar to aquaculture co-culture.

Cost-savings to improve cost-effectiveness will be critical if coral propagation activities are to reach the scales needed in the future (Ladd, 2019; Hein et al., 2022; Suggett et al., 2023).

Table 5.1. The overarching per-month cost equation involved in the estimated nursery fouling maintenance cost for the Coral Nurture Program. Terms are broken down in the subsequent rows. All values are per trip. All costs listed are in $AU as published in Scott et al. (2024).

Equation	(($S·BDR) n(D) + ($EqH·BDR + $EqT·D) + $V·BDR) + $EQ·n(D)	
Factor	**Value $AUD**	**Description**
Staff wages ($S)	312.50	Compensated labour costs per tourism staff member (8-hour workday), which includes return travel time to reef sites, and between 60-180 minutes of total dive time.
Boat days required (BDR)	11	Required boat days are calculated based on i) the number of nurseries at a site and the number of sites; ii) the number of nurseries that can be cleaned by two divers in one dive (6 nurseries in the 45 – 60 min allowed per site) and ii) the number of sites that the responsible tourism operator can visit in a day, considering the time needed for travel. Hastings Reef: 18 nurseries, 4 sites, 5 dives total, tourism operator visits 4 sites per day, 3 days needed. Mackay Reef: 12 nurseries, 2 sites, 2 dives total, tourism operator visits 2 sites per day, 2 days needed. Moore Reef: 2 nurseries, 1 site, 1 dive, tourism operator visits 2 sites per day, 1 day needed. Opal Reef: 73 nurseries, 5 sites, 14 dives total, tourism operator visits 3 sites per day, 5 days needed total (noting one whole day may be spent at a single site) Upolu Reef: 7 nurseries, 2 sites, 2 dives, tourism operator visits 2 sites per day, 1 day needed. Whitsundays: 9 nurseries, 3 sites, 3 dives total, contracted operator visits 3 sites per day, 1 day needed.
Number of divers (n(D))	2	Number of CNP staff per maintenance dive.
Dive equipment hirer ($EqH)	1.26	Dive equipment hirer per diver.
Dive SCUBER tank cost ($EqT)	4.00	SCUBA tank refill cost.

Total number of dives (D)	24	Total number of dives is calculated based on i) the number of nurseries at a site and the number of sites; ii) the number of nurseries that can be cleaned by two divers in one dive (6 nurseries in the 45 – 60 min allowed per site) and ii) the number of sites that the responsible tourism operator can visit in a day, considering the time needed for travel (see above).
Vessel costs ($V)	$3,750	Cost of a full-day (~8 hours) return trip to outer reef nursery sites. The true running costs for large tourism vessels on the GBR can be upwards of AU$7,000 per day (including overheads) however dedicated CNP stewardship days were chartered at cost-price.
Equipment cost per diver ($EQ·n(D))	10.47	A once-off equipment cost, including: (i) scrub brush and (ii) weighted carabiner clip

To date, CNP funding has been secured by, and indeed program success has been measured from, simple “activity” metrics such as the number of coral out-planted and how this relates to increased coral cover (Hein et al., 2021b; Suggett et al., 2023). However, major goals for CNP, as for many coral propagation initiatives, centre on building local ecological resilience at a reef level to maintain ecosystem services for dependent human communities (Hein et al., 2017, see also, https://www.coralnurtureprogram.org). Thus, evaluations of success towards this goal to date, particularly at the nursery phase, have largely rested on a few biological metrics of coral (e.g. coral growth and survival; Boström-Einarsson et al., 2020; Howlett et al., 2021) disparate from broader metrics that inform ecosystem resilience or services outcomes (Hein et al., 2021b). Such biological metrics have yet to include the positive role of fish assemblages and their interactions with coral propagation nurseries. Although the monitoring of all positive interactions linking coral propagation activities with reef resilience and community benefits might exceed the capacity of a restoration program, especially in community-based initiatives, the methods presented within this thesis offer reef restoration practitioners a feasible means to incorporate nursery-phase monitoring of fish assemblages, known to support reef resilience. This assessment may highlight when adaptive management should be applied toward this goal, and/or lessons learned from this research may be used to inform future nursery-based restoration planning. Planning for fish usage on the nursery frame may include, for example, when projects aim to propagate several coral species, mixing a variety of coral taxa and morphologies, over homogeneous arrangements (**Chapter 1**). This may be particularly useful when combined with nursery placement near natural reefs, known to enhance fish utilisation (Knoester et al., 2019). As such, an understanding of fish assemblage nursery interaction through monitoring (e.g. this thesis) is a critical first step in informing reef stakeholder decision-making towards a fish-integrated approach to coral propagation. Efforts in coral reef restoration, have not previously been made to systematically incorporate decisions that facilitate fish integrations in nursery operations (Ladd 2019). However, as funding increasingly becomes available for restoration, simple, low-cost methods for incorporating fish assemblages into the planning and monitoring of reef restoration activities may better evaluate the success of these activities towards clearly stated program goals (e.g. *Figure 5.2.*).

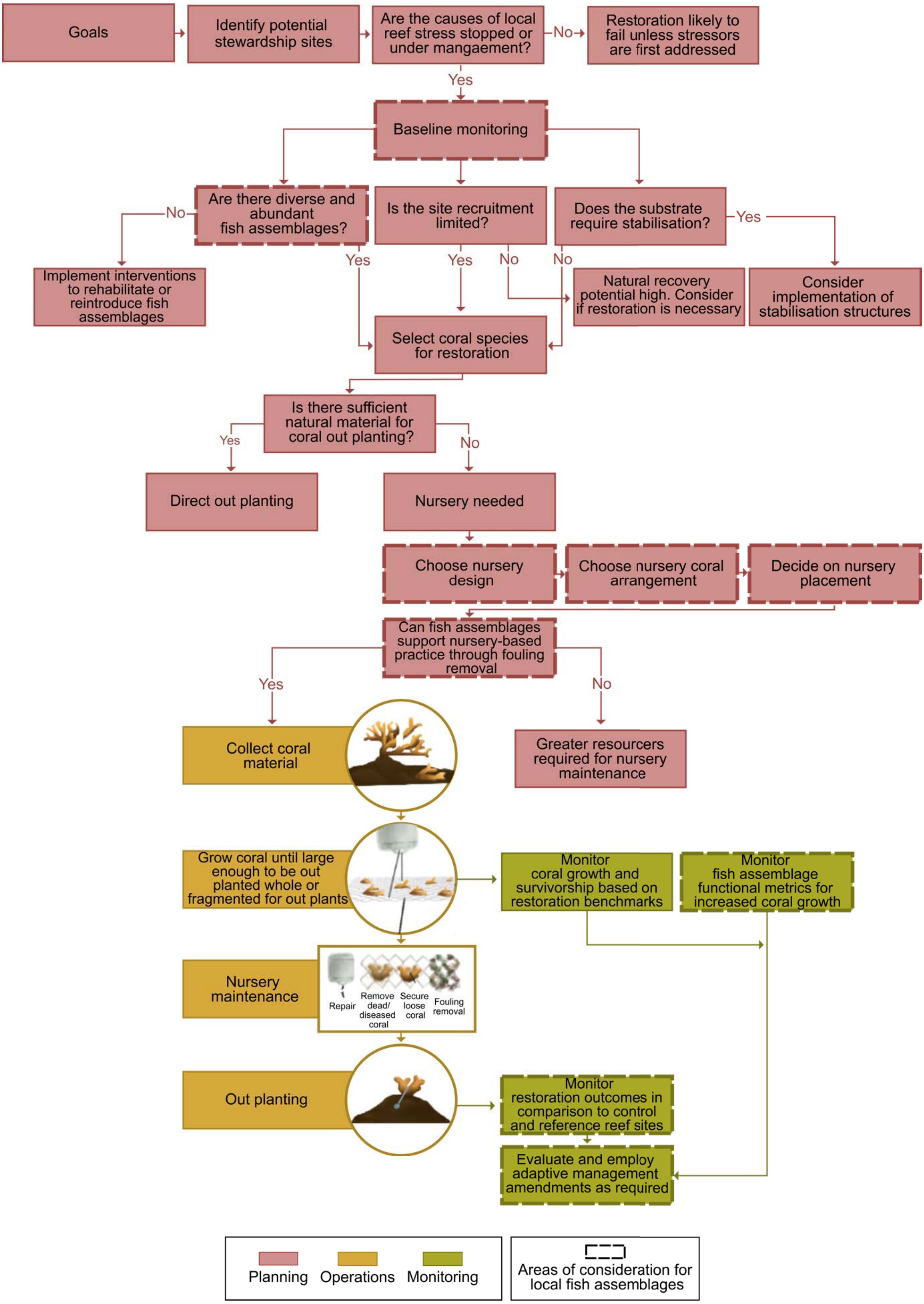

Figure 5.2. A proposed (non-exhaustive) decision framework for fish-integrated coral propagation, adapted from reef restoration workflows (Edwards et al., 2010; Goergen et al., 2020; Shaver et al., 2020) and with consideration of thesis findings.

5.4 Fish function

Reef stakeholders need accessible science in the form of ready-to-use metrics for coral propagation activities to be continuously optimised. Fish functional grouping, characterised by empirically proven links between traits (a combination of morphological and/or behavioural traits) and ecological functioning, can provide valuable knowledge towards adaptive restoration practices (Bellwood et al., 2019). A functional shorthand can be created by combining taxonomically disparate species with a shared ecological function (e.g. Green & Bellwood, 2009; Bellwood et al., 2019; Tebbett et al., 2022). However, the capacity for a fish assemblage to function for the benefit of nursery-grown corals is likely to vary within and between reef sites. For instance, a site harbouring surgeonfish "brushers" (e.g. *Ctenochaetus binotatus*) and "sediment suckers" (e.g. *Acanthurus nigricauda*) can lead to a reduction in filamentous turf fouling on nurseries (***Chapter 2***), thereby resulting in reduced maintenance costs. In contrast, surgeonfish categorised as "water-column feeders", though phylogenetically closely related and visually similar, are less likely to have a comparable impact (Tebbett et al., 2022). A prospective nursery site hosting species with functional roles conducive to optimised management may be preferable among alternatives. Though, discerning the different functional groupings that inevitably differ at a species level, can prove particularly difficult for restoration practitioners.

Currently, coral cards and coral guides have been developed and used to assist restoration practitioners choose species for propagation and monitor the health of corals at a restoration site (e.g. Weil & Hooten, 2008). However, there is currently no widely used resource that informs reef stewardship based on fish function, and information on this topic is sparse in published literature. Furthermore, while benchmarks exist for coral survivorship and growth on nurseries (e.g. Schopmeyer et al., 2017; Goergen et al., 2020), there is currently a lack of established fish functional benchmarks to assist stakeholders in identifying when adaptive management on nurseries is needed. One potential approach could involve developing metrics, such as ratios that describe herbivorous versus corallivorous or species that represent the minimum necessary to support critical nursery functions, to better understand how the abundance of functional groups either promotes or inhibits nursery coral growth. Any such metrics will need to account for the varying rates of individual species' contributions to ecological function (Bonaldo et al., 2014). Inevitably, any tool designed to aid decision-making must also remain adaptive to reflect the continuous evolution of ecological research. For example, the functional groups of herbivores proposed in 2004 (Bellwood et al., 2004) offer a foundational framework but now serve as a coarse representation of the intricate ecological dynamics within each group, thereby limiting their utility for inferring functions. Moreover, while several connections between functional groups and their contributions to ecosystem function have been established, many more have yet to be empirically validated (Bellwood et al., 2019). Ultimately, the specific aims of nursery-based efforts will shape how this evolving knowledge will inform success metrics and operation strategies. Whether the aim is to foster fish-facilitated coral growth by placing nurseries near grazing populations or to conserve fish assemblages by situating nurseries close to abundant and diverse fish populations, in addition to stocking nurseries with branching species preferred by juvenile fish species. A simple assessment tool that consolidates evolving fish functional ecology would be useful to promote the future design of adaptive strategies, improve performance and encourage communication between restoration partners (either locally, regionally, or globally) to increase success.

5.5 Future research

Research presented in this thesis considers fish assemblage interactions with *in-situ* coral propagation nurseries, which in the growing field of reef restoration, has arguably received less attention than the effectiveness of coral out-planting and fish interactions with coral out-plants (Seraphim et al., 2020). Owing to the novelty of this research, several future avenues of research are warranted for further investigation (outlined in *Table 5.2.*). Given the recognised importance of fish assemblages in maintaining coral and algal competition (Adam et al., 2015; Obolski et al., 2016; Bellwood et al., 2019; Tebbett et al., 2023), exploring whether the reintroduction of fishes to sites with severely degraded fish and coral assemblages can enhance the success of nursery and out-planting operations is crucial (*Table 5.2A.*). In instances where fish assemblages are already naturally present at restoration sites, ***Chapter 2*** provides a rapid nursery monitoring method important for adaptive management and gauging coral restoration progress towards fish-integrated restoration goals. To extend this monitoring capability, future research should prioritise the development of user-friendly tools or metrics for assessing fish function, which can further inform coral propagation planning and adaptive management decisions.

In this endeavour, there are three key steps. Firstly, research to inform metrics must take place on a stable, non-evolving fish assemblage to capture a true reflection of fish function on nurseries. Rates at which fish assemblages develop on nurseries can be location-specific (***Chapter 4***). Therefore, to better understand the timing and conditions under which fish assemblage stabilisation occurs, local studies on nursery fish assemblages with regularly repeated surveys (e.g. monthly) over larger timescales should be compared to local coral-dominated reef areas or other locally deployed artificial reef structures (*Table 5.2B.*). Secondly, metrics must account for any inherent biases introduced within a restoration setting. As part of this second line of research, findings from fish functioning studies conducted in diverse natural settings should be directly compared to those carried out on a curated coral nursery environment with a stable fish assemblage to ascertain differences in how fish function (*Table 5.2C.*). Lastly, while not all fish functions will have equal relevance for nursery propagation aims, there must be a comprehensive understanding of the full suite of functions and how these differ between structures (*Table 5.2D.*). For example, the function of fish in the provision of nutrients is important at an ecological scale (Allgeier et al., 2014; Brandl et al., 2019; Schiettekatte et al., 2023), although it is unknown whether this can enhance coral growth on nurseries. In pursuing these areas of research, stakeholders can begin to account for fish assemblages in decision-making, informing the future development of metrics (*Table 5.2E.*) to understand the ways in which fish may facilitate the growth of nursery-grown corals and communicate locally if and when these service benefits occur.

On a broader scale, monitoring data captured on restoration outcomes, including the interaction of coral reef assemblages with *in-situ* nursery structures, can contribute knowledge on how restoration activities can influence, and perhaps even improve, the ecosystem service value of reef sites (Hein et al., 2020; Suggett et al., 2023). Indeed, coral and fish assemblage interactions are recognised in natural reef ecology as key contributors to broader ecosystem service value that is often described in monetary or financial terms (Lachs & Oñate-Casado, 2020; Eddy et al., 2021; Suggett et al., 2023). Increasingly, future work will be required to assign a financial worth to ecosystem attributes, that inevitably include fish assemblages, and change as a result of restoration (e.g. restoration spill-over effects, or flow-on effects for carbonate budgets and biodiversity accounting; *Table 5.2F.*). Longer-term and novel monitoring methods that capture the species present at a site in a timely and more effective manner (e.g. using E-DNA to identify cryptic fish species; Duarte et al., 2023; or detailed recruitment studies, Belmaker et al., 2011; Seraphim et al., 2020) will be crucial to accurately account for these restoration outputs. Such broader evaluations of coral restoration are increasingly used in ecosystem management decision-making to justify investment into restoration programs (Hardisty et al., 2019; Abrina & Bennett, 2021; Suggett et al., 2023). However, an understanding and facilitation of flow-on benefits cannot occur without first empowering reef stakeholders with a means to locally monitor and incorporate fish interactions into commonly used coral nursery propagation and out-planting activities.

Table 5.2. Future critical reef restoration research and practice priorities to advance understanding of fish interactions with nursery-based restoration.

Future research area	Aims	Beneficiary outcomes
A) Assess whether reintroducing fishes to restoration sites with impacted fish and coral assemblages can enhance the success of nursery and out-planting operations.	To investigate the site-specific compatibility of reintroduced fishes with the restoration site and evaluate their potential role in facilitating the growth and survival of coral fragments during the (i) nursery and (ii) out-planting phases.	**Reef stakeholders** Highlight the potential risks and/or benefits involved in reintroducing fishes to enhance nursery and out-planting success and foster reef resilience.
B) Determine if or when fish assemblage stabilisation occurs on coral nurseries.	To compare the long-term change in abundance richness, diversity, biomass, and species composition of fish assemblages on coral nurseries with a commonly used artificial reef design (e.g. Reef Balls) and adjacent natural reefs.	**Researchers** Timing of fish nursery research to ensure assessment of stable, not evolving, fish assemblages.
C) Evaluate the inherent bias introduced within a restoration setting.	To directly compare fish functioning in diverse natural settings to functioning in a curated coral nursery environment.	**Reef stakeholders and researchers** Understand the potential limits to applying fish function predictions for a coral nursery.
D) Discern the full suite of fish functions and effects on nursery-grown corals between different nursery designs.	Identify the impact of key fish species and functions (herbivory, predation, nutrient uptake, bioerosion as per Brandl et al., 2019) for corals grown on commonly used nursery structures (mid-water, fixed table, tree and rope designs).	**Reef stakeholders** Inform nursery design and tailoring of protocols based on how local fish assemblages function.

E) Explore a blueprint for fish functional metrics orientated to facilitate coral growth and survivorship at a low cost.	To consolidate fish functional ecology on natural reefs and on coral nurseries (see E-D and this thesis) to produce user-friendly metrics for nursery-based coral restoration.	**Reef stakeholders** Support the future design of adaptive strategies to improve performance and encourage communication between restoration partners (either locally, regionally, or globally) to assist in wider success.
F) Time-effective and efficient approaches for capturing the natural capital of a reef site.	To develop novel monitoring methods that capture fish assemblage “flow on effects” from coral restoration.	**Reef stakeholders, public and private investors** To meaningfully communicate restoration ecological impacts with accuracy.

5.6 Conclusion

The study and management of the world's coral reefs is at a watershed moment. It is now recognised that maintaining ecosystem functions and services will require a focus on holistic ecosystem- or resilience-based management (e.g. Levin et al., 2009; Graham et al., 2013; Hughes et al., 2017; Vardi et al., 2021). This thesis presents a means to enhance understanding and integrate previously overlooked fish assemblage interactions into coral restoration frameworks, advancing toward these goals. I have shown coral nurseries to be novel habitats for diverse fish assemblages (***Chapter 2***) that in turn reduce fouling on nurseries (***Chapter 3***) in addition to documenting, for the first time, fish assemblage development on newly deployed nurseries (***Chapter 4***). With a deeper understanding of fish interactions within coral restoration activities, this work contributes to ongoing adaptive practices and future integration of holistic restoration frameworks led by stakeholders on the GBR.

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