RESEARCH ARTICLE

Fish use of restored mangroves matches that in natural mangroves regardless of forest age

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The loss and degradation of mangrove forests have triggered global restoration efforts to support biodiversity and ecosystem services, including fish stock enhancement. As mangrove restoration accelerates, it is important to evaluate outcomes for species that play functional roles in ecosystems and support services, yet this remains a clear knowledge gap. There is remarkably little information, for example, about how fish use of mangroves varies as restored vegetation matures, hampering efforts to include fisheries benefits in natural capital assessments of restoration. We used unbaited underwater cameras within two distinct zones of mangrove forests—fringe and interior—at five pairs of restored-natural mangrove sites of increasing age from restoration in southeast Queensland, Australia. We used deep learning to automatically extract data for the four most common species: yellowfin bream (*Acanthopagrus australis*), sea mullet (*Mugil cephalus*), common toadfish (*Tetractenos hamiltoni*), and common silverbiddy (*Gerres subfasciatus*). The abundance of these species varied among sites and zones, but was equal or greater in restored sites compared to paired natural sites. Despite younger restored sites having dramatically lower structural vegetation complexity, abundances did not increase with restoration site maturity. Furthermore, while yellowfin bream and sea mullet were more abundant in the fringe zone, we observed similarities in how fish used fringe and interior zones across all sites. Our paired, space-for-time design provides a powerful test of restoration outcomes for fish, highlighting that even newly restored sites with immature vegetation are readily utilized by key fish species.

Key words: coastal wetland, estuary, habitat creation, habitat selection, rehabilitation

Implications for Practice

- Restoring mangrove forests may help support fish populations and potentially enhance fisheries productivity.
- Recently restored mangrove forests harbor comparable fish populations to natural forests, so there is surprisingly little need for building in a time lag when including fisheries benefits in natural capital assessments of mangrove restoration.
- Restoration practitioners should consider focusing on providing expansive mangrove fringes to maximize restoration benefits for fish.

Introduction

Mangrove forests are productive ecosystems that have significant cultural, economic and ecological importance (de Souza Queiroz et al. 2017; Friess et al. 2019). These intertidal habitats sequester carbon, improve water quality, and support diverse wildlife, including economically important fisheries species (Duarte et al. 2005; Nagelkerken et al. 2008; Sievers et al. 2019). Despite these goods and services, mangroves have undergone significant historical loss and degradation (Friess et al. 2019). Mangrove restoration has consequently become increasingly important to reverse habitat loss and reinstate key ecosystem services derived from healthy mangrove ecosystems (Worthington & Spalding 2018; Bayraktarov et al. 2020; Su et al. 2021). Such restoration primarily aims to recover the structure and function of

ecosystems (McDonald et al. 2016; Bayraktarov et al. 2020), and involves the direct planting of mangrove trees, eradicating invasive species, or reducing abiotic stressors to encourage natural recolonisation and regrowth (Liu et al. 2016). As global initiatives such as increasing mangrove area by 20% by 2030 (Lee et al. 2019) or the United Nations Decade on Ecosystem Restoration (Waltham et al. 2020) intensifies restoration efforts worldwide, it is pertinent that the resources used result in an effective regaining of ecological structure and function (Young & Schwartz 2019).

Long-term monitoring is useful to evaluate how restoration efforts have contributed to enhancing ecological structure and function (Lindenmayer 2020). Current monitoring of restored coastal habitats focuses overwhelmingly on the recovery and

production of habitat-forming species (e.g., mangrove trees and seedlings) or physical environment (e.g., pH and temperature) and is typically short term (Zhang et al. 2018; Cadier et al. 2020). Despite the fundamental role animals play in maintaining healthy ecosystems, few studies measure faunal responses within restored habitats (Gerona-Daga & Salmo III 2022; Sievers et al. 2022). Shifting focus toward animals will improve our understanding of how restored habitats are functioning, inform future restoration efforts to maximize success, and provide a means to quantify gains in several key ecosystem services and thus inform natural capital assessments of restoration (e.g., fisheries enhancement; Kollmann et al. 2016; Hale et al. 2019; Renzi et al. 2019).

The provision of habitat for fish is a key service of mangroves and a motivator for restoration, but evaluations of how fish utilize restored mangroves are scarce (Carrasquilla-Henao & Juanes 2017; Zu Ermgassen et al. 2021). Quality of restored habitat for fish is often thought to vary depending on the age and structural complexity of the forest (Hutchison et al. 2014; Lee et al. 2019). Whether and how fish utilize restored mangrove habitats may therefore change as vegetation matures. One study found that even once restored mangrove vegetation becomes comparable to natural sites, fish abundances are still more akin to those in degraded mangroves (Ram et al. 2021). Conversely, others found that young planted mangroves harbored greater abundance and biomass of fish compared to more mature restored sites (Peralta-Milan & Salmo III 2013; Salmo et al. 2017). In addition, the extent to which fish utilize restored mangrove forest zones (e.g., forest and interior) is largely unknown, with implications for how restoration may be applied for fish stock enhancement. Greater understanding of these patterns within restored mangroves, particularly in sites that vary in time since restoration, can inform future restoration efforts.

Monitoring fish in mangroves is difficult given the structural complexity and shallow nature of these forests (Piggott et al. 2020). Consequently, many conventional survey methods, such as using nets, traps, and underwater visual census, are labor-intensive and can suffer from biases and low-replicability over short-time scales (Sheaves et al. 2016). The use of underwater video cameras has revolutionized marine monitoring by increasing the duration, cost-effectiveness, and replicability and has allowed monitoring in even the most structurally complex habitats (Murphy & Jenkins 2010; Mallet & Pelletier 2014). Automated processing with artificial intelligence (AI) has also decreased analysis cost and time lag (Weinstein 2018). Deep learning (DL) a type of AI, can accurately classify and detect fish species in a range of marine environments (Villon et al. 2018; Ditria et al. 2020b; Lopez-Marcano et al. 2021). DL implementation in ecology is increasing the speed, accuracy, and volume of information available, and now can be leveraged to evaluate past, and inform future, restoration efforts.

Here, we aim to gain a better understanding of fish use of restored and natural mangroves using DL methodologies. Focusing on common fish species inhabiting mangroves in southeast Queensland, Australia, we evaluate the effect of time since restoration using a paired, space-for-time substitution design. We also identify how fish utilize different forest zones in both natural and restored mangrove ecosystems. Despite mixed findings in the literature, by adopting a more robust study design, we expect to find a positive relationship between time since restoration and relative abundance, whereby fish populations in restored and natural sites converge as restored vegetation matures and becomes more comparable to vegetation at natural sites.

Methods

Study Setting

We surveyed five paired restored and natural mangrove sites in Moreton Bay, Queensland, Australia (Fig. 1; i.e., 10 separate forests). These sites are primarily a mix of *Avicennia marina* and *Rhizophora stylosa*, with smaller amounts of *Aegiceras corniculatum* at some sites (see Table S1 for planted species). While Moreton Bay mangroves are generally stable, mangroves in these sites are threatened by, and have largely been lost to, land conversion (Broadwater Parklands) and hydrological changes (other four sites; Table S1; Sievers et al. 2020). Time since restoration varied from 2 to 42 years, with the youngest sites containing small saplings with limited branching and few pneumatophores (Fig. 1). We selected sites based on the presence of a physically planted mangrove habitat near a comparable natural mangrove habitat (paired control; see Table S1 for site details). Effort was made to match natural sites to restored sites in habitat area, water depth, tidal movement, and coastal geomorphology and elevation. We surveyed the mangrove fringe and interior at all sites between June and August 2021 (site pairs 1 and 5 were visited on consecutive days). The mangrove fringe is the area dominated by continuous mangrove pneumatophores between the edge of the estuary channel and 1–2 m into the forest, while the mangrove interior is the area within the mangrove forest closer to land (Sheaves et al. 2016; Dubuc et al. 2019). Depth at the fringe cameras was ~0.8 m at the top of the tide, and total tidal amplitude varies among sites from 1.6 to 2.1 m.

Sampling Method

We sampled fish using standard, noninvasive remote underwater videos consisting of SJCAM Action Cameras (1080p) mounted on concrete pavers. Cameras were unbaited to avoid attracting fish from adjacent habitats or biasing sampling toward predatory species (Bradley et al. 2017). We surveyed site pairs simultaneously to perfectly align abundance comparisons with tides and weather. We also surveyed the mangrove fringe and interior simultaneously based on methodology of Sheaves et al. (2016). We deployed a set of five cameras (each separated by 5 m) at each site along the forest fringe facing the estuary channel, and a second set of five cameras within the mangrove interior, 5–10 m from the cameras in the fringe (this distance varied due to topography, size of the forest, and land
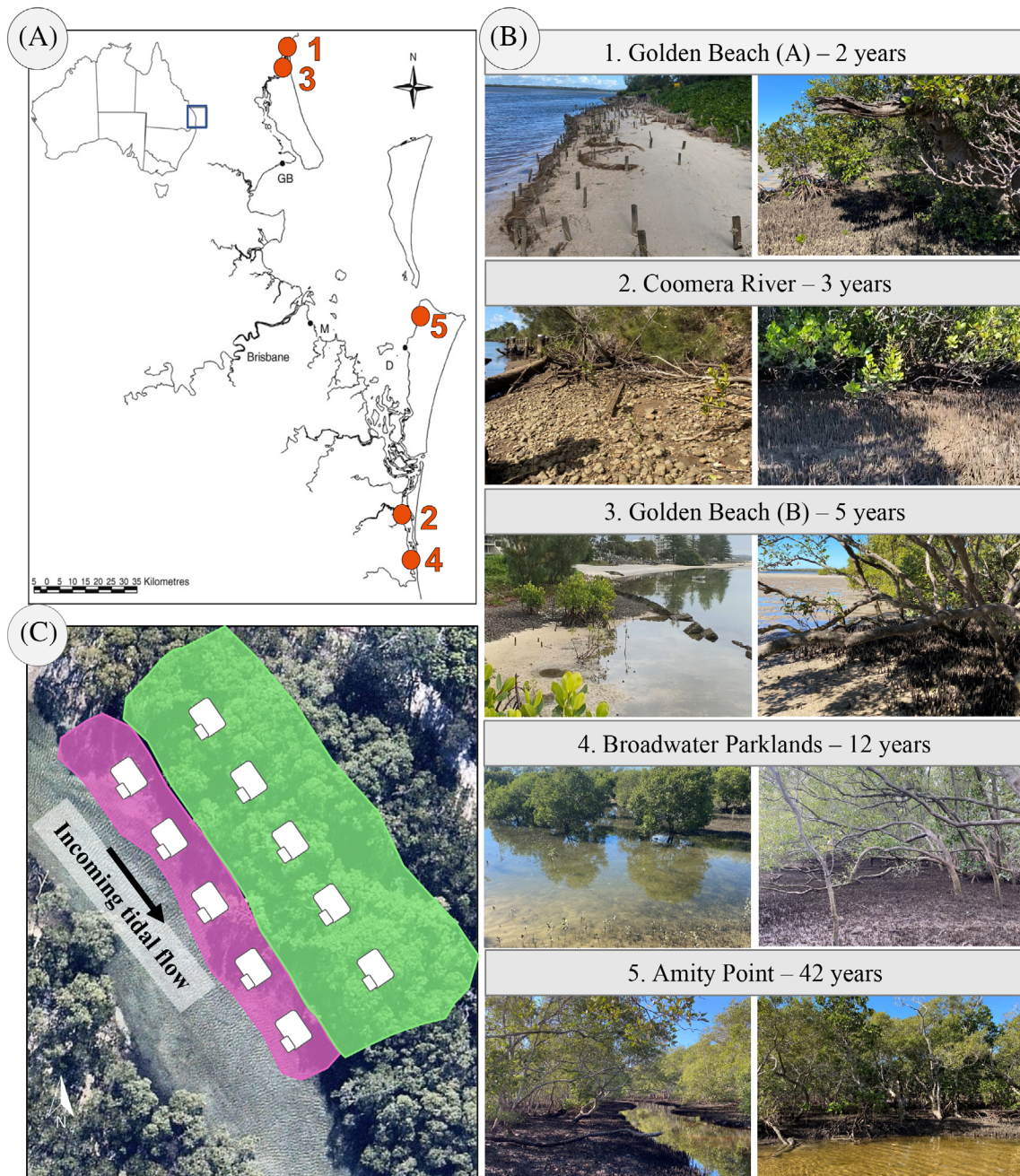
Figure 1. (A) Location of the five restored mangrove sites sampled within Moreton Bay, Queensland, Australia. At each location a nearby, paired natural mangrove (control) was also sampled. (B) Photographs of the paired restored (left) and natural (right) mangrove sites surveyed during the study. (C) Example of camera placement and mangrove zonation at Amity Point, North Stradbroke Island. The purple polygon shows the mangrove fringe zone and the green polygon shows the mangrove interior zone. Source: NearMap 2021.

development; Fig. 3). We positioned cameras 13 cm above the sediment, facing seaward, at the start of the incoming tide and collected them at high tide, with batteries replaced every 1.5 hours. Duration of camera deployment varied across locations and zones due to differences in estuary bank slope, resulting in an uneven number of periods for each site-zone combination (see "Video Processing" section).

Vegetation Survey

We surveyed mangrove vegetation at each site to quantify the key physical attributes that might influence habitat use by fish. We ran 10-m transects along both mangrove zones, parallel with the estuary channel. Pneumatophore height and density, structural density, and canopy cover were measured at three random points along each transect. We estimated pneumatophore density and

height by counting and measuring, respectively, individual pneumatophores within 1-m^2 quadrats. To measure canopy cover, we photographed the canopy from 20 cm above the sediment. To measure structural density, we took a photograph horizontally into the vegetation with a white sheet background at 3 m distance (Bryan-Brown 2019). We converted photographs to black and white, and used the ratio of black-to-white pixels as proxies for canopy cover and structural density, using ImageJ (Schneider et al. 2012).

DL Model Description and Performance

We developed a DL model that detected and counted the four most common species with a widespread distribution in mangroves in Moreton Bay: yellowfin bream (*Acanthopagrus australis*), sea mullet (*Mugil cephalus*), common toadfish (*Tetractenos hamiltoni*), and common silverbiddy (*Gerres subfasciatus*). The training of the DL model required short video snippets of the target species. We used 255 snippets of varying lengths (between 10 and 90 s) that contained the target species from various angles at different turbidity levels. All target fish on the training dataset were manually annotated with bounding boxes resulting in 13,928 fish annotations (Fig. 2). We supplemented the training dataset (i.e., transfer learning) with a previously trained model of the target species from southeast Queensland (Ditria et al. 2021). In addition to the target species, we annotated five less common and patchily distributed species to increase the accuracy of predictions for target species (Connolly et al. 2021). These five species were: sand whiting (*Sillago ciliata*), crescent grunter

(*Terapon jarbua*), moses snapper (*Lutjanus russellii*), banded toadfish (*Marilyna pleurosticta*), and weeping toadfish (*Torquigener pleurogramma*).

We used an 80:20 validation ratio to train the DL model, where 80% of data was used to train the model, and 20% to validate model accuracy. We tested the DL model with a test dataset that contained 4,112 fish annotations from 76 videos of 1 of the 5 cameras (per site-zone combination) that was excluded from the training, providing a robust test of the expected performance of the final model (Ditria et al. 2020*a*).

We determined the performance of the DL model using the F1 score on abundance estimates. F1 is a summary statistic (out of 100) that accounts for overestimate and underestimate of a metric, which in our case was MaxN (Everingham et al. 2010). MaxN, defined as the maximum number of individuals within a frame, is commonly used when analyzing RUV footage as it minimizes the risk of overestimating abundance by counting the same individual multiple times (Whitmarsh et al. 2017). Overall model F1 was 79% (see Table S3 for per species F1 scores).

Abundance Predictions and Analysis

The multispecies DL model estimated MaxN abundance for the four target species on 280 hours of video footage. The DL model analyzed the videos at a rate of five frames per second and raw DL detections were postprocessed using species-specific confidence threshold of 95, 90, 70, and 60% for yellowfin bream, common toadfish, sea mullet, and common silverbiddy,
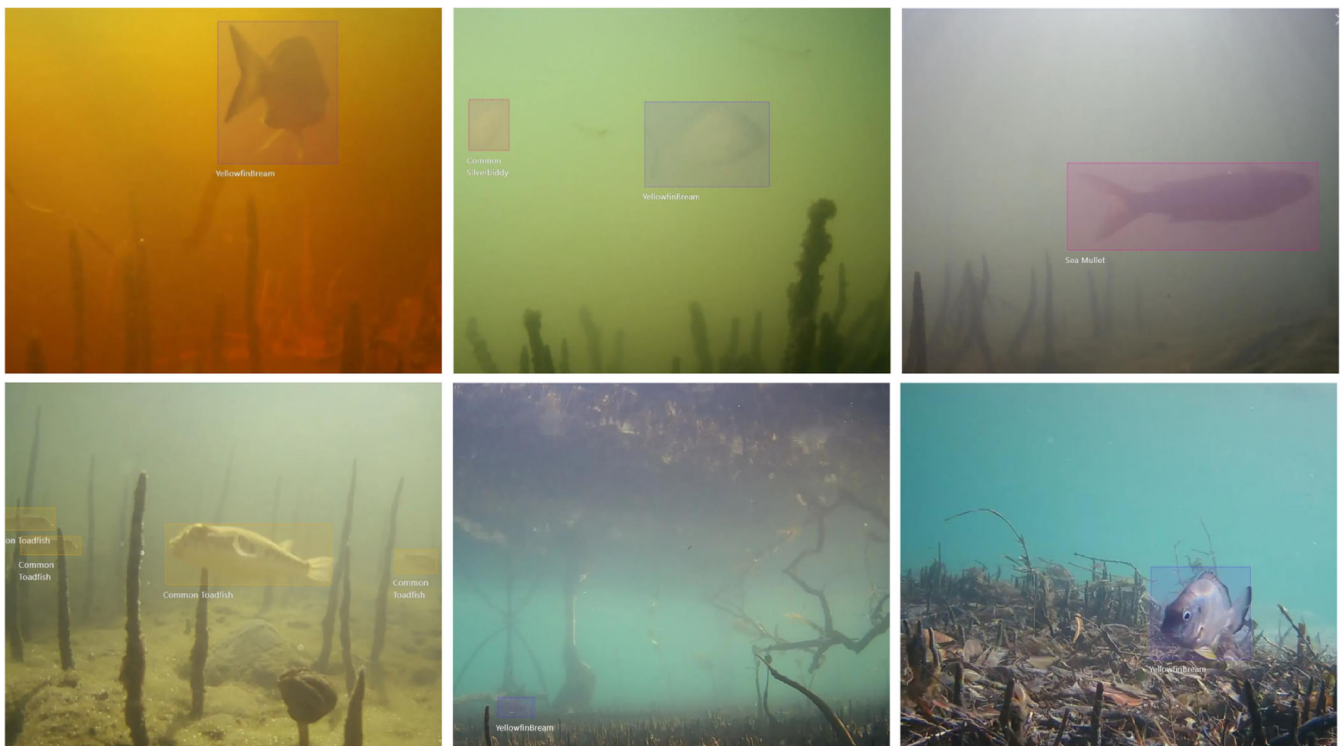

Figure 2. Fish annotations on still frames that highlight the environmental variation of the training dataset.

respectively. Species-specific confidence thresholds were chosen to maximize accuracy by minimizing the number of false-positive and false-negative identifications (Lindenmayer 2020). In addition, we used a spatiotemporal filter called sequential nonmaximum suppression to minimize false detections and increase the accuracy of true detections (Han et al. 2016; Lopez-Marcano et al. 2021). To calculate MaxN, we followed Davis et al. (2017) and measured MaxN in 20-minute periods, which provide accurate estimates of fish abundance when using RUVs (Piggott et al. 2020). We averaged the MaxN for each target species across the five replicate cameras and zone combination to calculate the mean MaxN per 20-minute period.

Statistical Analysis

We calculated species-specific mean differences in abundance between paired restored and natural sites for each location. To evaluate whether fish use of restored sites is dependent on the age of restored sites, we tested for a correlation between time since restoration and mean difference using Spearman rank correlation tests. We then constructed a linear model with location (five restored–natural pairs), treatment (restored or natural), and zone (interior or fringe) fitted as fixed factors. We included all two-way interactions but excluded the three-way interaction to achieve model parsimony given the complexity of the dataset. We transformed (log $[x + 1]$) the response variable (MaxN per 20-minute period) prior to analysis to meet the assumption of normality and heteroscedasticity and conducted species-specific analysis of variance to test for significance at $\alpha = 0.05$. To remove bias from occasional video segments substantially shorter than 20 minutes (which are more likely to have lower abundance), we excluded video segments less than 10 minutes. Vegetation characteristics were compared among locations, sites, and zones using a principal component analysis (PCA). All analyses were run using R statistical software Version 4.1.2 (R Development Core Team 2017).

Results

Fish Abundance Within Restored Mangroves

Abundance was higher in restored than in paired natural sites for sea mullet ($F = 14.9$, $p < 0.001$), and not different for the other three species (Table S4; Fig. 3). For three of the four species, the difference between restored and natural varied significantly among locations and zones (Table S4, Location × Zone interaction). The pattern of differences among locations did not, however, correlate with time since restoration, except for common silverbiddy (Fig. 3). This is despite clear differences in vegetation structure with age of restoration (see "Mangrove vegetation" section). Common silverbiddy was the only species for which the differential abundance in restored and natural showed a relationship with restoration age, and this was a negative relationship, with a higher relative abundance in younger restored sites (Fig. 4; $\rho = -0.47$, $p < 0.001$). Of the four species included, common silverbiddy was the most widespread and abundant species
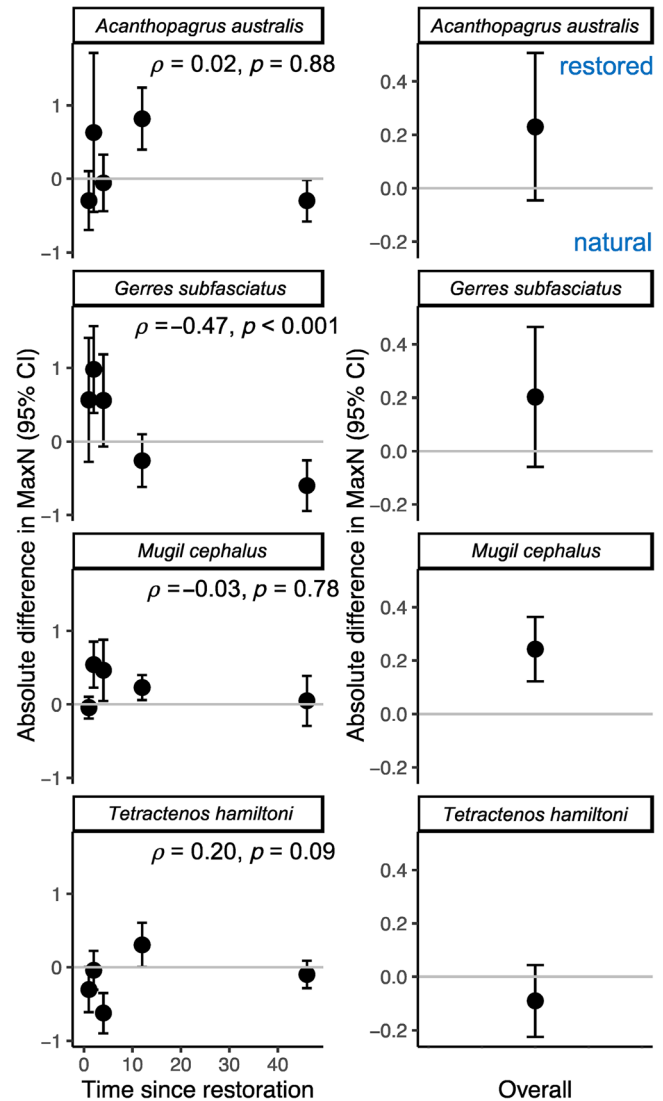

Figure 3. Differences in fish abundance at restored sites relative to natural (control) sites as a function of time since restoration (left), and when pooled across the five site pairs (right). Points represent the absolute difference in mean MaxN per 20-minute period ($\pm$ SE), thus positive values reflect more fish in restored sites. Dashed horizontal line at $y = 0$ indicates where abundance is identical between restored and natural sites. Rho and p-values are from Spearman's rank correlation tests, and no overlap of confidence intervals with $y = 0$ indicates significance at $p < 0.05$. Yellowfin bream (*Acanthopagrus australis*), sea mullet (*Mugil cephalus*), common toadfish (*Tetractenos hamiltoni*), and common silverbiddy (*Gerres subfasciatus*).

and was present in 84% of all the 20-minute time periods, followed by yellowfin bream (69%), common toadfish (56%), and sea mullet (55%).

Fish Abundance Between Mangrove Forest Zones

Fish used fringe and forest zones similarly across restored and natural sites (Fig. 4). Yellowfin bream, sea mullet, and silverbiddy were significantly more abundant within the fringe zone compared to the interior zone (Fig. 4).
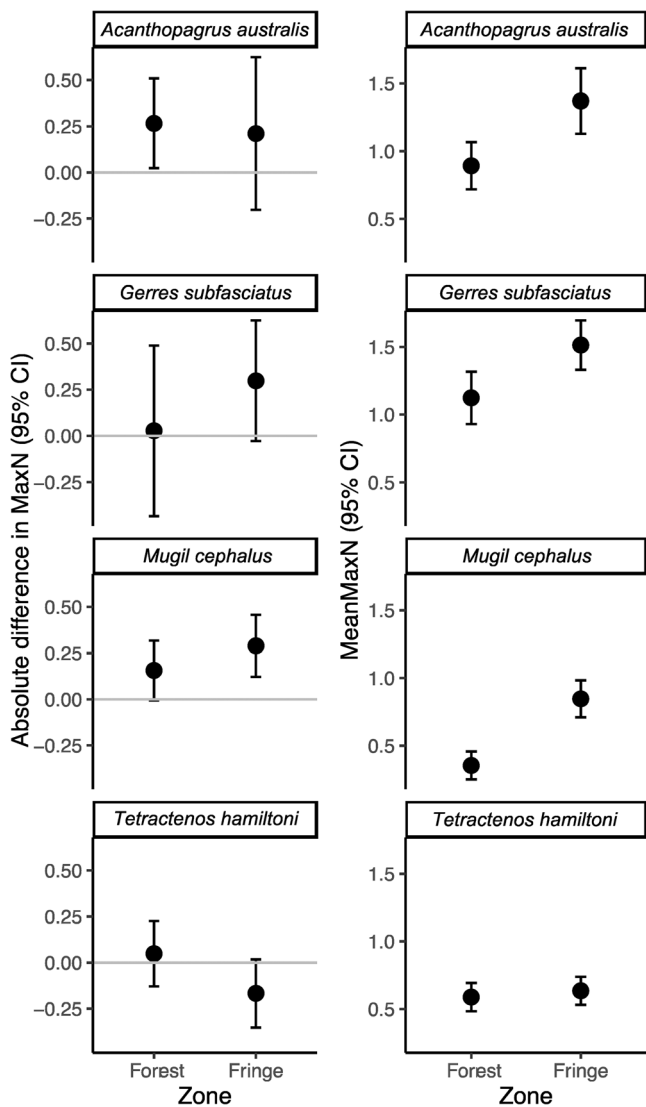
Figure 4. Differences in fish abundance at restored sites relative to natural (control) sites, as a function of mangrove forest zone (left), and mean MaxN as a function of mangrove forest zone (pooling restored and natural sites; right). Points (for left) represent the absolute difference in mean MaxN per 20-minute period ($\pm$ SE), thus positive values reflect more fish in restored sites. Dashed horizontal line at $y = 0$ indicates where abundance is identical between restored and natural sites, with no overlap of confidence intervals with this line indicating significance at $p < 0.05$. Yellowfin bream (*Acanthopagrus australis*), sea mullet (*Mugil cephalus*), common toadfish (*Tetractenos hamiltoni*), and common silverbiddy (*Gerres subfasciatus*).
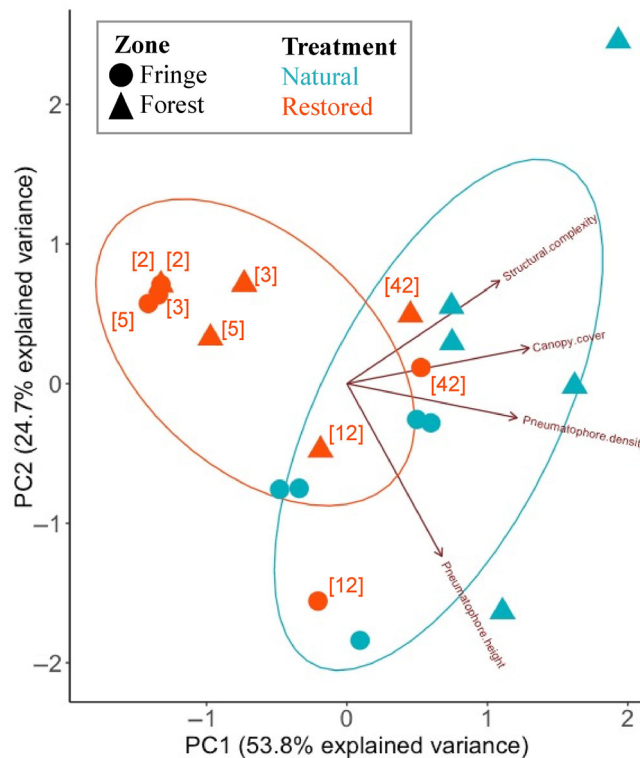

Figure 5. Principal component analysis (PCA) plot showing relative differences among sites based on four vegetation characteristics. Restored (orange) and natural (teal) sites are shown as points, with ellipses encircling treatments. The shape denotes the zone (fringe and forest), and the integer indicates the time since restoration in years. Vectors show the relationship between the vegetation characteristics and each site, with the length of the arrow signifying the importance, and the angle between variables denoting the strength of correlation between variables.

Mangrove Vegetation

As restored sites matured (i.e., increasing time since restoration), the vegetation characteristics more closely resemble the natural sites (Table S2; Fig. 5). The first two principal components (PC1 and PC2) explained 78.5% of the observed variance. In general, the natural sites were associated with higher values for: pneumatophore height (9.5, 69.8; variable contribution to PC1, PC2), pneumatophore density (30.6, 2.7), canopy cover (35.2, 3.0), and structural density (24.7, 24.7), indicating more structurally complex and mature vegetation. Recently restored sites were all similar, and as sites mature (including natural sites), there is more variability both among sites and between zones within those sites (Fig. 5).

Discussion

Pooling across sites, sea mullet abundance was higher in restored relative to natural sites, while common silverbiddy, common toadfish, and yellowfin bream did not differ. Relative differences between restored and natural sites did, however, vary considerably among locations for all species, and in ways mostly unrelated to the maturity of the restored site. Restoration age and thus vegetation structure were therefore not a strong driver of fish abundance for these species, with even newly restored sites with very immature vegetation readily utilized by all the common fish species.

The effectiveness of mangrove restoration in improving and creating fish habitat has been questioned, with mixed accounts of success (Lewis & Gilmore 2007; Ram et al. 2021; Su et al. 2021). Despite variability among species and locations, our findings show that restored mangrove habitats throughout

Moreton Bay are generally inhabited by as, or more, abundant fish populations as their natural counterparts. Given this variability, our hypothesis that relative fish abundance would increase as restored mangrove vegetation became more mature (sensu Barimo & Serafy 2003; Ram et al. 2021) was not supported. Despite this prevailing view, some studies in the Philippines have also failed to find a correlation between fish abundances and mangrove restoration age (Peralta-Milan & Salmo III 2013; Salmo et al. 2017), suggesting that other factors not considered here might be more important in influencing fish use of restored mangroves (e.g., local environmental context and connectivity with other ecosystem types; Bradley et al. 2020, 2022; Enchelmaier et al. 2020).

Common silverbiddy was the only species to display a correlation with restoration age, showing higher relative abundance at younger restored sites, and equal or lower relative abundance at more mature restored sites. Common silverbiddy is typically more pelagic than the other target species included in this study (Froese & Pauly 2021). Research within the same area by Davis et al. (2017) found that common silverbiddy displayed greater preference for unvegetated habitats over vegetated habitats (e.g., seagrass). Younger restored mangroves had significantly less complex vegetation and thus more bare substrate which could explain the higher abundance of common silverbiddy found within these sites.

An understanding of the extent to which fish utilize distinct mangrove zones (e.g., fringe and interior) is necessary to optimize restored forest landscapes for fisheries benefits, yet we are unaware of such evaluations of restored mangrove zones. Research in natural mangroves shows that differences in mangrove inundation means the distribution and abundance of fish is highly variable between forest zones, with higher fish diversity and abundance at the forest fringe than the forest interior (Sheaves 2005; Sheaves et al. 2016; Dubuc et al. 2019). While fish use of the fringe and interior zones were similar between restored and natural mangroves, even at the youngest restored site which lacked mature vegetation, general patterns were species-specific (supporting research in natural mangrove forests; Rönnbäck et al. 1999; Vance et al. 2002; Sheaves et al. 2016; Dubuc et al. 2019). For instance, across both natural and restored sites, the common toadfish generally utilized both the fringe and interior zones equally. Conversely, the often larger and more transient species (i.e., silverbiddy, sea mullet, and yellowfin bream) were less abundant within mangrove interior zones. In line with previous findings in natural mangrove habitats, we also suggest that some species may only enter mangrove interior zones when presented with substantial feeding opportunities or threats (e.g., arrival of larger predators; Laegdsgaard & Johnson 2001; Reis-Filho et al. 2016; Sheaves et al. 2016; Dubuc et al. 2019). The higher relative abundance of economically valuable species found within mangrove fringe zones in this study could help tailor future restoration projects aimed at enhancing fisheries species.

There are several caveats to consider when interpreting our results. First, although our results evaluate restored sites relative to natural, we do not have prerestoration data and are thus limited in our capacity to make broad conclusions on restoration "success." For instance, it is possible that fish abundance at restored sites may be similar with degraded mangroves or bare substrates. Second, environmental context (e.g., proximity to other connected intertidal habitats; Pittman et al. 2007; Martin et al. 2015) can influence fish abundance (Nagelkerken et al. 2008). While we did not explicitly examine this, our paired design with natural controls near restored sites reduces the influence of broader environmental context, providing a robust test. Third, the general lack of observed relationships between restoration age and fish abundance may partially be explained by the spatial scale (i.e., all sites located within Moreton Bay) or the uneven distribution of ages, with 60% of sites restored less than 5 years ago. Further exploring this relationship would benefit from sampling more site pairs and sites that span a greater spatial range. Fourth, while our survey design may have resulted in some level of pseudoreplication (i.e., repeat detections of the same fish), we reduced the influence of pseudoreplication by estimating a single MaxN value within each 20-minute period and averaging the MaxN across replicate cameras. Fifth, we focus our analysis on common species that may be relatively hardy and less influenced by habitat maturity. Rarer or less hardy species may exhibit strong trends with respect to greater utilization of more mature restored sites or only utilizing natural sites; future work on whole fish communities could reveal additional insights. Finally, although our DL model did not achieve >90% accuracy, cameras provided the opportunity to monitor fish in complex habitats where alternative methods are likely to be biased and less accurate.

In summary, understanding how fish utilize restored mangroves can guide future restoration efforts aimed at enhancing fish populations and assist efforts to include fisheries benefits in natural capital assessments of restoration. We used a paired design, cameras, and automated DL models to reveal key insights into how fish utilize restored mangroves. Generally, fish abundances of four common species were equal between restored and natural sites, and largely unrelated to time since restoration despite younger sites having substantially different vegetation characteristics. We found strong species-specific differences in how mangrove forests are utilized, with restoration that targets producing sufficient fringing zones most beneficial for economically valuable species such as yellowfin bream and sea mullet. Our study adds to the small but growing body of literature evaluating fish use of restored mangroves that can inform future restoration projects and guide monitoring practices to enhance outcomes for fish.

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Supporting Information

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

Table S1. Site information for the restored mangrove sites within Moreton Bay, Queensland, Australia.

Table S2. Vegetation characteristics used in the principal components analysis.

Table S3. MaxN detection results for the target species of the final multispecies model.

Table S4. Output from analysis of variance (ANOVA) on the abundance of target fish species (as mean MaxN per 20-minute period).