Fish monitoring of the Pumicestone Shellfish Habitat Restoration Trial

Final Report to Healthy Land and Water

Attraction versus production in restoration: spatial and habitat effects of shellfish reefs for fish in coastal seascapes

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Project Partners

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Summary

Restored shellfish reefs provide valuable habitat for fish, but it is not clear how different approaches affect performance, and either promote new populations (i.e. ‘production’) or simply attract individuals from the broader seascape (i.e. ‘attraction’). We measured the effects of a 1 ha shellfish reef restoration site on fish assemblages in Pumicestone Passage in eastern Australia, which contains replicates of six different restoration units: shell patch reefs, crates of shells, and biodegradable matrix, and each had replicates with and without live oysters. Fish were surveyed before restoration and then every 6 months for 30 months with baited (at restoration and control sites) and unbaited (at 106 sites across the seascape to detect potential fish attraction, and at the different restoration units) underwater cameras. Shellfish reef restoration represents an addition to fish productivity because we found; 1) that restoration significantly enhanced the diversity and abundance of fish assemblages and the density of harvestable fish at the restoration site by 3.8, 10.7 and 16.4 times, respectively, and 2) fish distributions across the broader seascape did not change in response to succession at the restoration site. Fish assemblages did not differ between restoration units. These findings further support the notion that restored shellfish reefs containing a diversity of habitat structures significantly enhance fish abundance and diversity. They also suggest that restored reefs can enhance the overall carrying capacity of seascapes for fish and indicate that this can result from augmentation of fish populations rather than a centralisation of assemblages at restoration sites.

Introduction

Shellfish reefs have become functionally extinct in many coastal systems, often due to excessive harvesting, poor water quality and the spread of invasive diseases and predators (Beck et al., 2011; Gillies et al., 2018). These declines have socio-economic and ecological consequences because shellfish reefs deliver valuable ecosystem services like supporting harvested fish stocks (Peterson et al., 2003; Tolley & Volety, 2005; Gittman et al., 2016; zu Ermgassen et al., 2016). Because the loss of shellfish reefs has been associated with concomitant declines in fish biodiversity and catches (Gilby et al., 2018b), the prevalence and scale of shellfish reef restoration has increased substantially across the world in recent decades (Duarte et al., 2020).

Fish abundance and diversity typically increases rapidly at restoration sites following shellfish reef restoration (Peterson et al., 2003; Grabowski et al., 2005; zu Ermgassen et al., 2016; Gilby et al., 2018b). For example, after only three months, restored shellfish reefs in Australia supported fish assemblages that were 1.4 times more speciose and had 1.8 times more individuals of harvested taxa than before installations (Gilby et al., 2019). It has been estimated that a hectare of restored shellfish reef delivers US$4,123 per year in enhanced commercial fish catches (Grabowski & Peterson, 2007). It is therefore not surprising that enhancing fish populations and assemblages has become an explicit goal in many shellfish restoration projects globally (Baggett et al., 2015; Gilby et al., 2018b).

Notwithstanding reported increases of fish at and near restored reefs, it is generally not known whether observed changes in reef-associated fish represent an aggregative behavioural response to the new structures ('attraction') or whether reefs increase the carrying capacity and productivity of seascapes for fish more broadly ('production') (Pierson & Eggleston, 2014; Gilby et al., 2018b). The abundance of transient fish species found at added structures suggests that the initial response is an attraction of individuals drawn from existing populations near restored reefs (Harding & Mann, 2001; Grabowski et al., 2005; Gregalis et al., 2009; Gilby et al., 2019). By contrast, populations observed at restored reefs may, over time, become self-sustaining as juveniles recruit from more distant areas, local populations reproduce and retain individuals, or both (Tolley & Volety, 2005; Gregalis et al., 2009). New fish may then fill the niches in the broader seascape left by fish that redistribute towards restored shellfish reefs. If behavioural attraction to new structures is the main process, then increases at restored reefs juxtaposed with decreases in the broader seascape surrounding new reefs is the response of reef restoration. This is identified by the abundance of fish declining quickly with increasing distance from the reef restoration site. However, if 'production' is the main process, increased abundance at reef sites will be complemented by stable or more fish in the surrounding seascape. Over time, a net production at the restoration site may cause spill-over effects to the surrounding seascape. At present, however, whether restored shellfish reefs cause a net aggregation effect or net increases in carrying capacity, and how these effects might change over time remain untested.

Identifying whether restored shellfish reefs attract and centralise fish assemblages or enhance fish productivity across coastal seascapes is often difficult because it requires the effects of restoration to be disentangled from variability caused by natural processes. For example, variation in catchment runoff and water quality can markedly influence coastal fish assemblages (Thompson et al., 2014; Henderson et al., 2019b). Similarly, the size and shape of habitats abutting reefs is important in structuring fish assemblages in coastal seascapes (Bostrom et al., 2011; Olds et al., 2016; Pittman, 2018). In practice, separating any long-term effect of restoration on fish assemblages across seascapes from other factors influencing fish requires data that encompass four inter-related facets: 1) changes in fish assemblages due to temporal changes in water quality, 2) seasonal changes associated with fish movement or residency, 3) time scales that are sufficiently long to separate any initial attraction effects from longer-term productivity effects; and 4) spatial sampling coverage that extends beyond the likely influence of restored shellfish reefs on fish assemblages across seascapes. Therefore, analyses attempting to identify ‘production’ versus ‘attraction’ effects must also account for these variables in statistical models.

The condition of restored habitats significantly affects their value for fish (Lehnert & Allen, 2002; Johnson & Smee, 2014; Gilby et al., 2018b), meaning that the choice of restoration dimensions and substrate can affect whether and how fish aggregate at restoration sites, and how this affects fish distributions across seascapes (Peterson et al., 2003; Gilby et al., 2018b; Lemoine et al., 2019). In this context, the physical methods of adding reef structure vary substantially according to the goal of the restoration project and regional practices. For example, ‘living shoreline’ projects have for several decades used granite boulders and mesh bags filled with shells to build restoration units that can be added without heavy machinery to intertidal and shallow subtidal areas (Brumbaugh & Coen, 2009; Gittman et al., 2016; Fitzsimons et al., 2019). Conversely, reefs in deeper water can be constructed from several tonnes of shell, rubble or boulders (Fitzsimons et al., 2019). Technological advancements in steel and polymer habitat matrices, including many that are biodegradable, have advanced significantly in recent years. These modules are designed to provide initial settlement substrate upon which shellfish and other invertebrates settle, thereby assisting the structural restoration of shellfish habitats (e.g. Balestri et al., 2019; BESE Products, 2020; Temmink, 2020). Given the importance of structurally complex habitat with good availability of food for fish, the choice of restoration action or methodology can affect the capacity for restored shellfish reefs to enhance fish diversity and abundance (Peterson et al., 2003; Gilby et al., 2018b; Lemoine et al., 2019). Consequently, identifying efficient and environmentally friendly ways to restore shellfish reefs that maximise effects for fish assemblages is an important research focus (Elliott et al., 2016).

Despite the widespread uptake of reef restoration, there remain fundamental questions as to whether restored reefs attract and centralise fish from throughout coastal seascapes, and how the choice of construction material and methods influence the response of fish to restoration. In this study, we seek to quantify whether shellfish reef restoration enhances the abundance and diversity of fish at the restoration site, determine the degree to which different restoration structures contribute to this overall pattern, and identify whether the restoration results in a net attraction and centralisation of fish across the seascape, or overall production of fish productivity. Here, we contrast localized effects at the restoration site with effects manifested in the broader seascape surrounding the restored reefs, thereby testing whether restoration have net 'attraction' or 'production' effects. We expected fish abundance and diversity to increase rapidly at restored reef structures, but that there would be differences in fish assemblages congregating around the different reef types. We also hypothesised there would be an initial attraction of fish towards the restoration site from the broader seascape, but that this effect would reduce over time.

Figure 1 USC students deploying cameras to survey fish in Pumicestone Passage. Inset is the remote underwater video stations used in two parts of this project.

Methods

Study system and restoration actions

The site of shellfish reef restoration is located in the southern Pumicestone Passage in central eastern Australia (Figure 1,2). Pumicestone Passage is a mesotidal estuary forming a heterogenous seascape of sandy channels, seagrass beds, mangroves forests and urban shorelines (e.g. canal estates, bridges and marinas). The estuary discharges into the northern part of the Moreton Bay Marine Park that borders the state capital city of Brisbane. Historical records indicate the presence of significant shellfish reefs throughout Pumicestone Passage prior to European settlement of the region in the early 1900s (Diggles, 2013). Six different designs of shellfish reef restoration units are deployed in Pumicestone Passage, which covers a single site footprint of approximately 1 ha.

Shellfish reef restoration started in December 2017, with the initial restoration effort being 16 reef units encompassing six different designs spread randomly across the restoration site (Figure 1,2, Table 1). Patch reefs installed in 2017 are 0.5 m high and 4 m in diameter and consisted of 5 m^3 of recycled, dead oyster shells surrounded by breeze block fences. Two patch reefs were installed with a veneer of live oysters from a local oyster producer, and two were installed without the live oyster veneer, for four patch reefs total (Table 1). Crates installed in 2017 are 1 m^2 by 0.5 m high steel mesh crate filled with recycled oyster shell. Again, two were installed in 2017 with a veneer of live oysters, and two were installed without the live oyster veneer, for four crates total (Table 1). Finally, eight biodegradable matrix reefs built from approximately 1 m wide x 0.5 m high and 3 m long Biodegradable Ecosystem Engineering Elements (BESE-elements, hereafter referred to as BESE; see BESE Products, 2020) were installed at the site in 2017. BESE are interlocking sheets of biodegradable mesh sheets that provide settlement locations for invertebrates. For the purpose of our study, 25 sheets were combined to form a 50-cm high 3D honeycomb-shaped matrix. Four of the eight BESE installations were deployed with live oysters integrated into the mesh (Table 1). Two additional patch reefs were added to the site in December 2018, including one approximately 10 m long x 4 m wide x 1 m high made from 33 m^3 of recycled oyster shell with a veneer of live oysters, and the other approximately 8 m long x 3 m wide x 1 m high made from 22 m^3 of recycled oyster shell (Table 1).

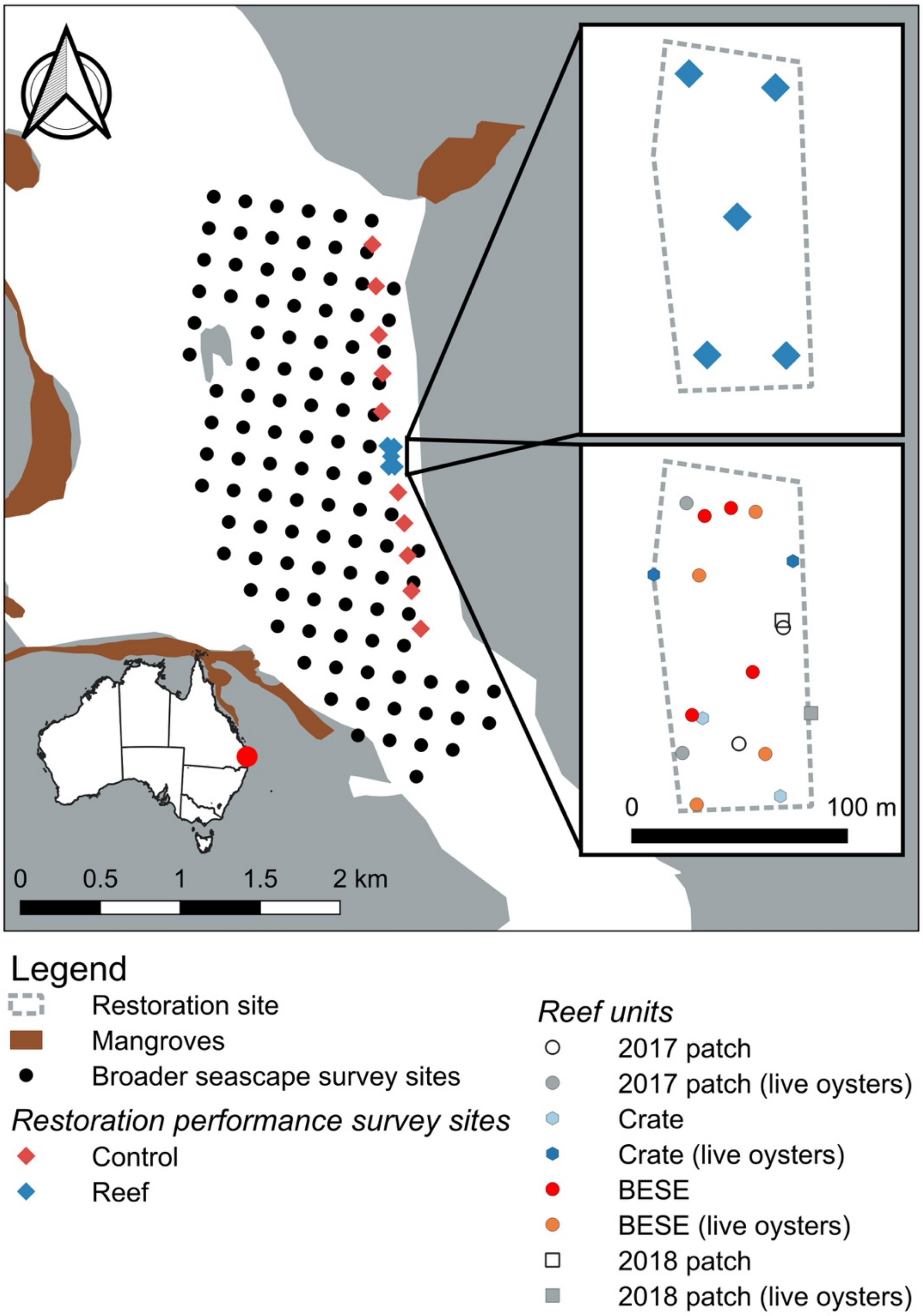

Figure 2 Location and map of the study area (Pumicestone Passage, Australia), the placement and type of reef restoration units used (insert demarcated with stippled lines), and a grid of fish survey sites to quantify broader seascape effects on the distribution, abundance and diversity of fish. Details of reef units are provided in Table S1.

Table 1 List of shellfish reef restoration units installed at Pumicestone Passage.

Installation date	Reef unit type	Number installed	Reef unit composition
December 2017	Patch	2	4m diameter and 0.5 m high in the centre, containing approximately 5 m^3 of recycled oyster shell, and contained by a fence built of 32 Besser blocks
	Patch (live shell)	2	4m diameter and 0.5 m high in the centre, containing approximately 5 m^3 of recycled oyster shell with a one shell thick veneer or live oysters, and contained by a fence built of 32 Besser blocks
	Crate	2	Lines of three 1 m long x 1 m wide x 0.5 m high steel cages, for 1 x 3 x.5 m total size. Cages filled with recycled oyster shell.
	Crate (live shell)	2	Lines of three 1 m long x 1 m wide x 0.5 m high steel cages, for 1 x 3 x.5 m total size. Cages filled with recycled oyster shell with a one shell thick veneer or live oysters.
	BESE	4	3 m long x 0.5 m wide x 0.5 m high modules made of biodegradable ecosystem engineering elements (BESE-elements) (BESE Products, 2020)
	BESE (live shell)	4	3 m long x 0.5 m wide x 0.5 m high modules made of biodegradable ecosystem engineering elements (BESE-elements) (BESE Products, 2020), with approximately 30 live oysters incorporated int the top of the BESE-elements mesh.
December 2018	Patch	1	10 m long x 4 m wide x 1 m high in the centre containing approximately 33 m^3 of recycled oyster shell, and contained by a fence built of 75 Besser blocks
	Patch (live shell)	1	8 m long x 3 m wide x 1 m high in the centre containing approximately 22 m^3 of recycled oyster shell, and contained by a fence built of 65 Besser blocks

Sampling approach

Fish assemblage surveys began in November and early December 2017, prior to the commencement of restoration. These 'before installation' surveys provided baselines for the abundance and distribution of fish across the Pumicestone Passage. The first post-installation sampling was done in June 2018; six months after the first set of reef installations. We repeated fish sampling at six-monthly intervals until June 2020. The December 2018 surveys were done prior to the installation of the two additional patch reefs. All fish surveys were conducted two hours either side of a daytime high tide to ensure that all surrounding habitats (principally mangroves) were also submerged and to maximise water visibility. The full complement of sampling per event required field deployments over three consecutive days, and sites were sampled randomly in this three-day window.

During this study, we used two fish survey methods to reach three distinct but complimentary datasets. Firstly, we used baited remote underwater video stations (BRUVS) to test hypotheses relating to the performance of the entire restoration site for fish by comparing the restoration site to nearby controls. BRUVS are preferred for quantifying these effects as they give a broader idea of general fish patterns within an area due to the aggregating of fish towards baits, as opposed to any habitat-specific effects. Data from this survey will henceforth be referred to as *restoration performance data*. Secondly, we used remote underwater video stations (RUVS; i.e. unbaited BRUVS) to test hypotheses related to differences in fish assemblages between the six different restoration units. These were deployed only at the restoration site. RUVS do not attract fish using baits, thereby avoiding the confounding effects of baited cameras drawing fishes from other habitats, and so are used to quantify fish-habitat associations (see Sheaves et al., 2016; Bradley et al., 2017; Gilby et al., 2018a). Data from this survey will henceforth be referred to as *restoration units data*. Finally, we used RUVS to test hypotheses about the effects of restoration on the distribution of fish more broadly throughout the seascape, and whether there was any 'attraction' effects of the reef. These were deployed throughout the broader Pumicestone Passage, and not at the restoration site. Data from this survey will henceforth be referred to as *broader seascape data*.

Quantifying restoration performance

We quantified fish assemblages congregating at the shellfish restoration site and at nearby control sites using one-hour deployments of BRUVS in each sampling period; this resulted in our restoration performance. BRUVS consist of 3 kg weight that serves as a base and attachment point for cameras (GoPro recording at 1080p) and a PVC pole that holds the bait bag at 50 cm in front of the camera. The bait was 500 g of pilchards *Sardinops sagax* placed in a 20 x 30 cm mesh bag with 0.5 cm openings. We deployed five BRUVS units at the shellfish restoration site (i.e. restoration performance reef sites in Figure 2) and ten units at control sites along the eastern edge of the estuary that had similar water depth to the reef restoration site (i.e. restoration performance control sites in Figure 2). Here, we positioned five cameras in a line north of the restoration sites, and five south of the restoration site, with 200 m distance between each BRUVS deployment.

Quantifying differences between restoration units

We quantified fish assemblages congregating individual reef restoration units using 30-minute deployments of RUVS in each sampling period; this resulted in our restoration unit data. RUVS consist of 3 kg weight that serves as a base and attachment point for cameras (GoPro recording at 1080p) (Figure 1). Pre-installation controls for reef restoration units constituted 16 RUVS (i.e. the same number as the initial number of reef restoration units) deployed randomly within the restoration site footprint. Given our aim of quantifying the contribution of different reef restoration unit types towards overall assemblages at the broader reef restoration site and across the seascape, RUVS were deployed in random orientation within 2 m of each reef restoration unit and without having the reef unit in the field of view. This is crucial, as the size of the field of view is important in standardising underwater camera surveys between survey events (Cappo et al., 2003; Watson et al., 2005; Langlois et al., 2010; Logan et al., 2017). Having reef restoration units within the field of view can restrict the number of fish counted and maintaining consistency of field of view on reef restoration units between sampling events is exceedingly difficult. Therefore, placing the cameras nearby, but without the reef restoration unit in the field of view is the optimal design for our research question.

Quantifying effects across the broader seascape

We quantified fish assemblages across the broader Pumicestone Passage seascape using 30-minute deployments of RUVS at 106 sites spread across the seascape in each sampling period (Figure 2); this resulted in our broader seascape data. Survey sites were arranged in a 200 m grid at all subtidal positions within 2 km of the restoration site. This site spacing and number of sites maximises the seascape heterogeneity surveyed, and encompasses the likely maximum distance of the influence of the restoration site on fish assemblages (Brook et al., 2018).

Video Analyses

Fish assemblage composition was quantified from all videos using the standard *MaxN* statistic; the maximum number of individuals of each species identified any single frame of each video. *MaxN* is a conservative measure of relative abundance that avoids the recounting of individuals that repeatedly visit. We calculated three key indicators of fish assemblages from each video; species richness being the number of unique species identified from each camera deployment, harvestable fish abundance being the sum of *MaxN* values for all species harvested commercially or recreationally in southeast Queensland, and total fish abundance being the sum of *MaxN* values for all species identified from each camera deployment.

Statistical analyses

We identified differences in fish assemblages between sampling periods and the reef site and nearby control sites (from BRUVS data), and between sampling periods and reef unit types (from RUVS on reef restoration units data) using ManyGLMs in the *mvabund* package (Wang et al., 2012) of R (R Core Team, 2020). ManyGLM is a multivariate analysis that also identifies species driving the overall assemblage pattern. Differences in species richness, harvestable fish abundance, and total fish abundance between sampling events, reef restoration unit types (from reef restoration units RUVS data), and between the broader restoration and nearby control sites (from BRUVS data) were quantified using generalised linear models (GLMs) in R.

We quantified relationships between fish assemblages across the broader seascape (from the gridded RUVS surveys) and eleven environmental variables (Table 2). These variables could be broadly grouped into three categories. Firstly, we included variables relating to the restoration effort, including categorising surveys conducted before and after restoration began, the time (in months) since restoration began, and the proximity of survey sites to the restoration site. Secondly, we included variables relating to the water depth and seascape context of monitoring sites, including the proximity of sites to the estuary mouth and mangroves, and the extent of mangroves within 1000 m of each site. These spatial variables have been shown in previous studies in the estuaries of this region to be significant predictors of fish assemblage composition and distribution (Gilby et al., 2018a), including at other shellfish reef restoration projects within the region (Duncan et al., 2019; Gilby et al., 2019). Finally, we included variables relating to the water quality of each site during each sampling event, including water column turbidity, salinity and temperature. Variation in water quality has been shown in previous studies to modify fish assemblage structure on reefs in the region (Gilby et al., 2016).

We quantified the effect of the eleven environmental variables on the assemblage composition and distribution of fish across the broader seascape using a ManyGLM. The ManyGLM model included interactions between before/after restoration commenced and proximity to reef, and time since first installations and proximity to reef, along with main effects of all other variables. The intent with this model structure was to establish whether fish assemblages centralised around the restoration site, determine whether this effect persisted over time, and correct for the effects of potentially confounding variables that modify fish assemblages spatially and temporally and might mask restoration effects. Here, a significant interaction between proximity to reef, and either of the restoration variables indicates a change in the distribution of fish across the broader estuary relative to the restoration site (i.e. potentially an attraction or centralisation effect of the restoration site). Conversely, no significant interactions indicate no significant change in the effect of proximity to reef on fish assemblages over time, and therefore a lack of attraction or centralisation effect for the area surveyed. The best fit ManyGLM was identified using backwards stepwise simplification on Akaike's information criterion (AIC). These patterns were further interrogated by quantifying correlations between environmental variables and species richness, harvestable fish abundance and total fish abundance using GLMs.

Table 2 List of included environmental variables, their definitions and data sources. All GIS calculations made in QGIS (QGIS Development Team, 2020).

Variable	Definition	Data source
Before/after restoration commenced	Categorical variable of sampling events before (December 20170 and after (all other sampling events) reef installations began.	-
Time since first installations (months)	Scale variable of months since reef installations began.	-
Distance to shellfish reef (m)	Distance of the survey site to the nearest shellfish restoration unit at the restoration site	-
Water depth (m)	Water depths in meters at the time of sampling.	Garmin sounder onboard research vessel
Distance to mangroves (m)	Distance of the survey site to the nearest mangroves.	Queensland Government (2015)
Area of mangroves within 500 m (m^2)	Area of mangroves within 500 m of each sampling site clipped from local habitat mapping layers.	Queensland Government (2015)
Area of mangroves within 1000 m (m^2)	Area of mangroves within 1000 m of each sampling site clipped from local habitat mapping layers.	Queensland Government (2015)
Distance to the estuary mouth (m)	Distance of the survey site to the centre of the estuary mouth.	-
Salinity (ppt)#	Salinity of the water at the benthos during the month of sampling.	EHMP (2020)
Water column turbidity (NTUs) #	Turbidity of the water at the benthos during the month of sampling.	EHMP (2020)
Water temperature (°C) #	Temperature of the water at the benthos during the month of sampling.	EHMP (2020)

Because water quality monitoring sites did not align precisely with fish survey sites, we estimated water quality values by interpolating all water quality monitoring sites to each site (using IDW interpolations) per sampling event.

Results

Restoration performance

Restoration performance data (derived from BRUVS surveys) identified 42 species of fish within the footprint of the reef site, 14 of which are harvested in commercial and/or recreational fisheries, and 55 species of fish outside the reef site, 20 of which are harvested in commercial and/or recreational fisheries during BRUVS surveys. These differences were, however, likely due to the higher replication conducted at control sites (n=10) than at the reef site (n=5) as species accumulation curves indicate little difference between the reef site and controls (Figure 3). Before the placement of reef structures, there was no significant difference in fish assemblages between control sites and the sites where reefs were installed (Figure 4A). By contrast, after installation of the shellfish reef restoration units, fish assemblages shifted significantly between reef and control sites; this spatial separation attributable to reef restoration increased as the reefs matured (Figure 4A). Patterns in fish assemblages at the reef site were best explained by variability in the abundance of yellowfin tripodfish *Tripodichthys angustifrons*, paradise whiptail *Pentapodus paradiseus* and black rabbitfish *Siganus fuscescens*. Black rabbitfish increased in abundance with time and was always in higher abundance at the reef site than at controls. Both paradise whiptail and yellowfin tripodfish were variable in abundance through time, but mostly higher in abundance at the reef site than at control sites (Figure 4, 5).

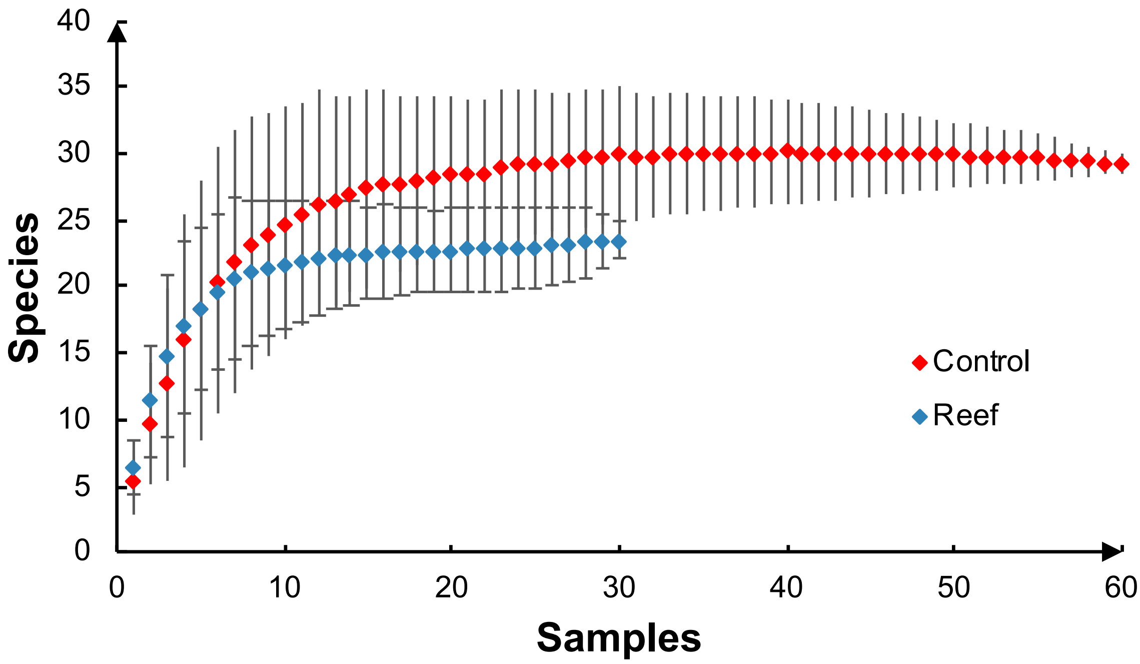

Figure 3 Species accumulation curve (+/- SD) to account for differences in sampling between reefs and controls in reef performance data. Reef points have error bar caps, while control points do not.

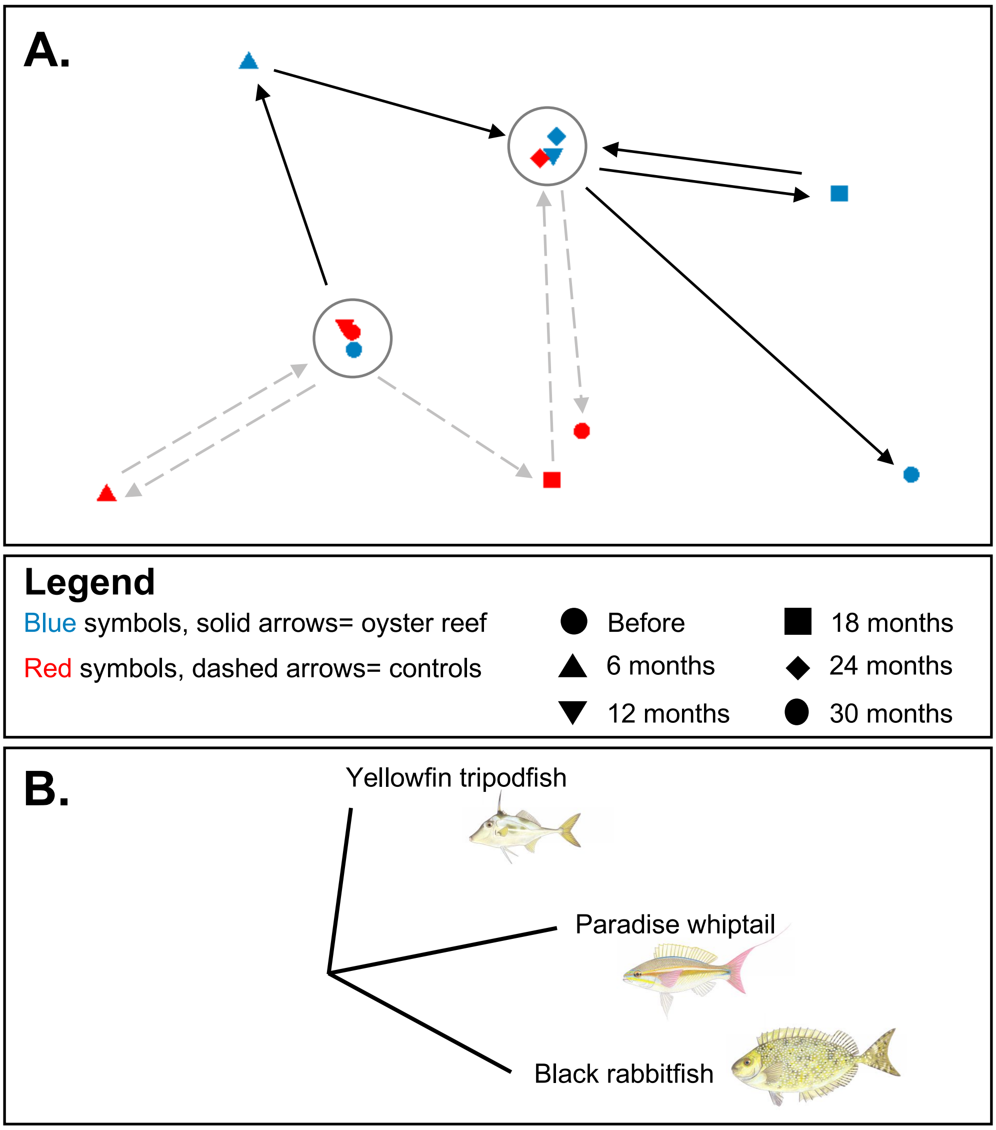

Figure 4 A) Non-metric multidimensional scaling (nMDS) ordination of centroids of BRUVS surveys at the shellfish reef restoration site and control sites between sampling events before and after the installation of the first shellfish reef restoration units. B) Vectors illustrate indicator species from the best fit ManyGLM. Points within ellipses are not statistically different to each other.

We found no significant difference between the reef restoration site and control sites during pre-installation surveys for species richness, total fish abundance and harvestable fish abundance (Figure 6). However, there was a strong initial effect of reefs on fish diversity and abundance; restoring shellfish reefs resulted in significant increases in species richness, and the number of total individuals and harvestable individuals within six months (Figure 6). As the reefs matured, we recorded some variation in the effect size attributable to reefs, notably 24 months post installation, but generally more species and individuals were found associated with reefs with time (Figure 6). Thirty months post-installation, fish assemblages at the reef site were 3.8 times more speciose and had 16.4 and 10.7 times more harvestable fish and total fish abundance, respectively, than during pre-installation surveys. Similarly, fish assemblages at the reef site during the June 2020 surveys were 1.7 times more speciose and had 2.1 and 3.4 more harvestable fish and fish in total, respectively, than control sites.

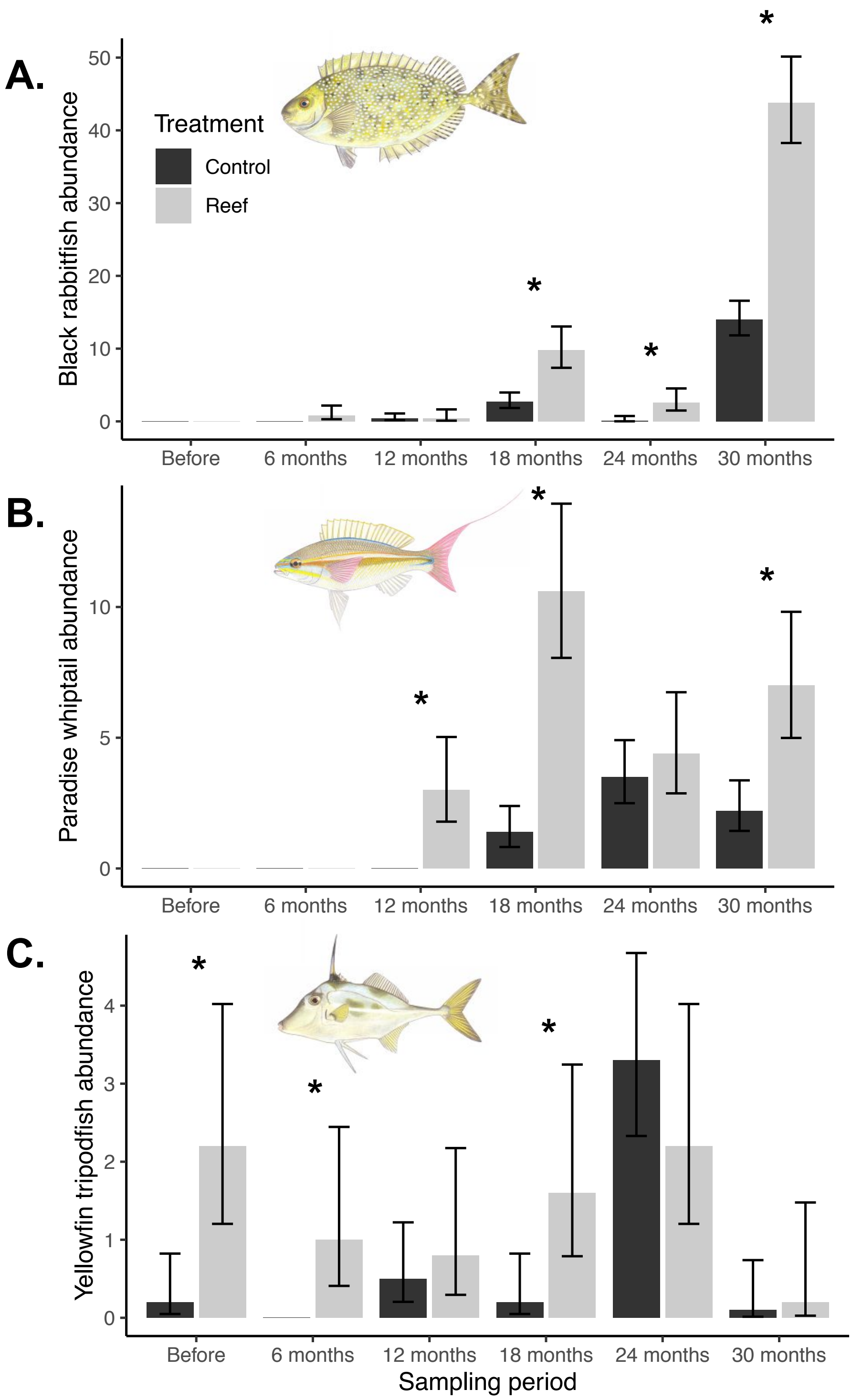

Figure 5 Average abundance (+/- SE) of A) black rabbitfish, B) paradise whiptail, and C) yellowfin tripodfish between reefs and control sites over 30 months of post-installation sampling. * indicates significant difference between control and reef sites for that sampling period.

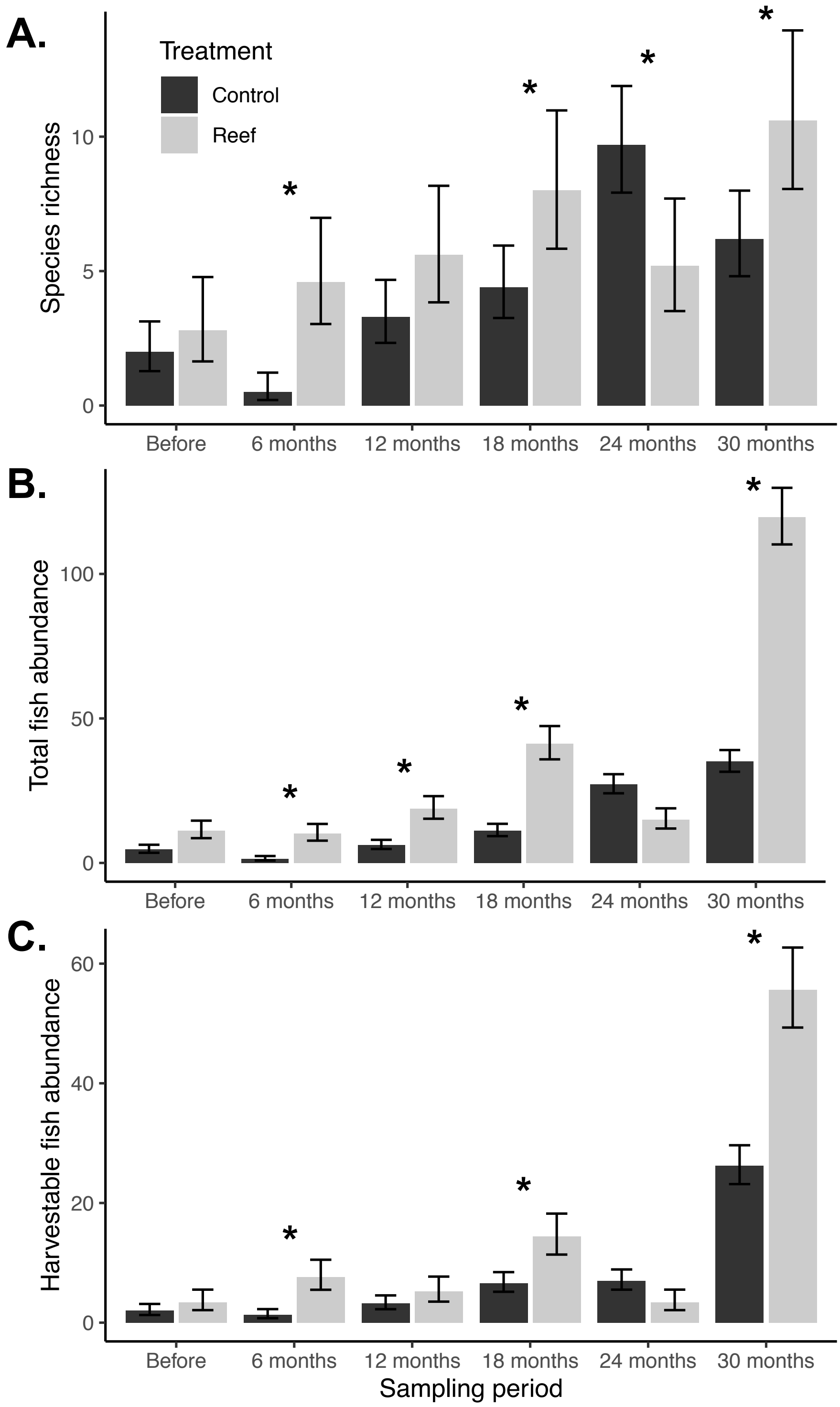

Figure 6 Average (+/- SE) of A) species richness, B) total fish abundance, and C) harvestable fish abundance between reefs and control sites over 30 months of post-installation sampling (as quantified from BRUVS data). * indicates significant difference between control and reef sites for that sampling period.

Differences between restoration units

Reef units data (derived from RUVS surveys around individual reef units) indicated that the type of reef structure and substrate did not significantly influence the structure of fish assemblages associated with these added structures (X^2=11.45, P=0.13). In contrast to the lack of a distinct effect attributable to reef type, assemblage structure varied significantly over time (X^2=16.59, P=0.001) (Figure 7A). These temporal contrasts are best explained by variation in the abundance of four species; southern herring *Herklotsichthys castelnaui*, black rabbitfish, rainbow monocle bream *Scolopsis monogramma* and blacksaddle goatfish *Parupeneus spilurus*. Southern herring and black rabbitfish were in greatest abundance during the 30-month surveys, while rainbow monacle bream and blacksaddle goatfish were in greatest abundance during 18- and 24-month surveys (Figure 7B).

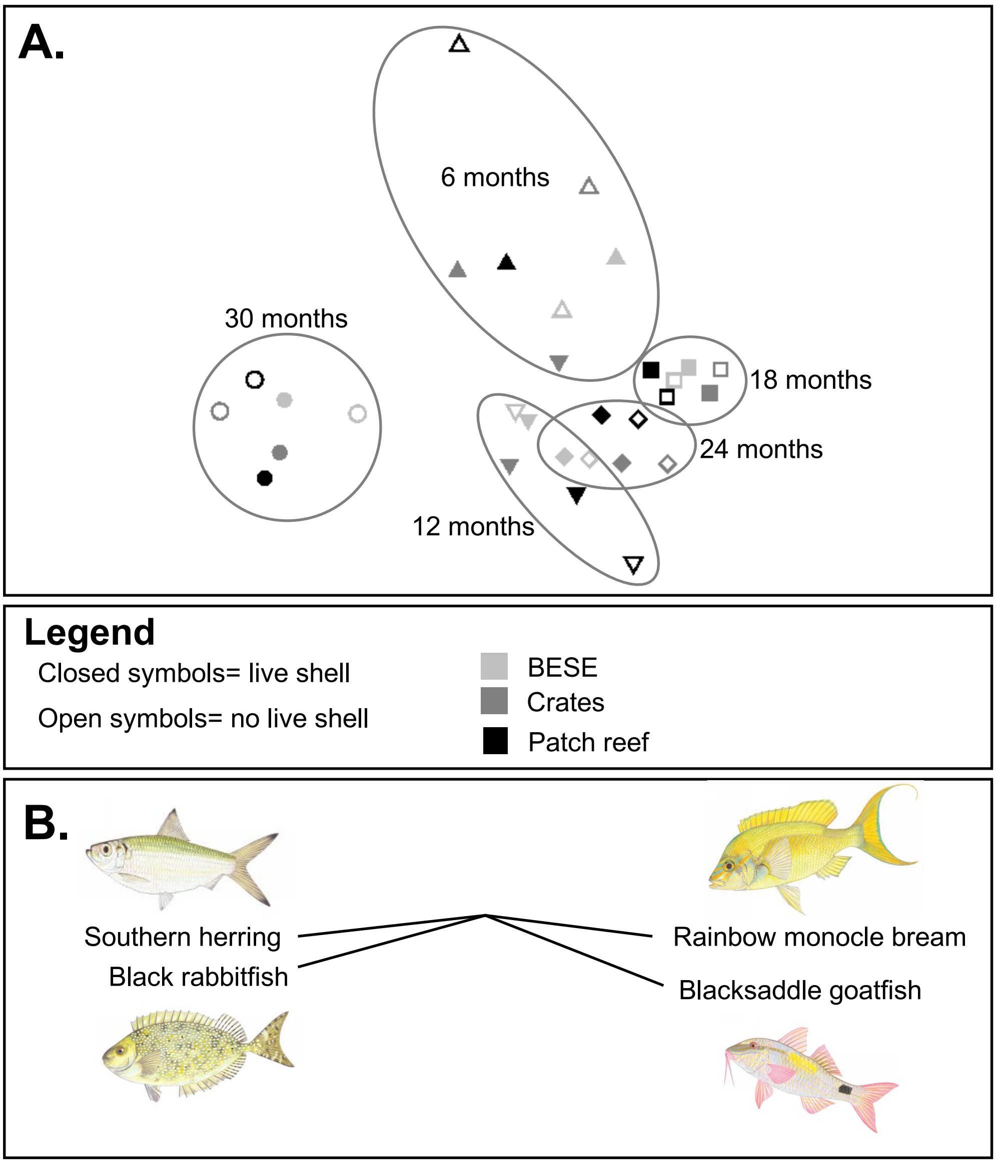

Figure 7 A) Non-metric multidimensional scaling (nMDS) ordination of centroids of RUVS surveys at the shellfish reef restoration units between sampling events before and after the installation of the first shellfish reef restoration units. B) Vectors illustrate indicator species from the ManyGLM

We found a significant interaction between sampling period and reef unit type on the species richness (X^2=52.73, P<0.001l; Figure 8A), total fish abundance (X^2=424.87, P<0.001; Figure 8B) and abundance of harvestable fish (X^2=156.23, P<0.001; Figure 8C) recorded at reefs. After six months on the seabed, diversity and abundance of fish was significantly higher on BESE, BESE with live oysters, and patch reefs with live oysters than all other reef unit types. These patterns mostly maintained after twelve months, except for a reduction in harvestable fish abundance at BESE units and an increase in both total and harvestable fish abundance on crates with live oysters (Figure 8). From 18-month surveys and on, however, we identified significant differences between most reef unit types and pre-installation controls. By the 30-month surveys, all reef unit types and metrics were significantly higher than pre-installation controls, and there were very few differences in metrics between reef unit types (Figure 8). Here, we found no significant difference in species richness between any of the reef unit types after 30 months (Figure 8A). Total fish abundance was higher on crates than any other reef unit type after 30 months (P<0.03), and all other reef unit types were not significantly different to each other (Figure 8B). Finally, harvestable fish abundance was highest on crates with live oysters, followed by patch reefs with live oysters, crates, and then all other reef unit types (Figure 8C).

Effects across the broader seascape

Broader seascape data (derived from RUVS surveys deployed broadly throughout the seascape and not at the restoration site) indicated no interaction between distance to shellfish reef and before/after restoration commenced or time since first installations began and the time of restoration intervention; this denotes that there was no change in the distribution of fish as a consequence of placing reef structures. There were effects of water column characteristics (including turbidity, salinity and depth), as well as the distance to mangroves and the estuary mouth, the area of mangroves within 1 km of a site, and the time since first installations began (Figure 9A). These patterns were best explained by variation in the abundance of ten indicator species; yellowfin tripodfish, eastern striped grunter *Helotes sexlineatus*, black rabbitfish, yellowfin bream *Acanthopagrus australis*, paradise whiptail, silver biddy *Gerres subfasciatus*, sand whiting *Sillago cilliata*, fanbellied leatherjacket *Monacanthus chinensis*, weeping toadfish *Torquigener pleurogramma,* and blacksaddle goatfish (Figure 9B).

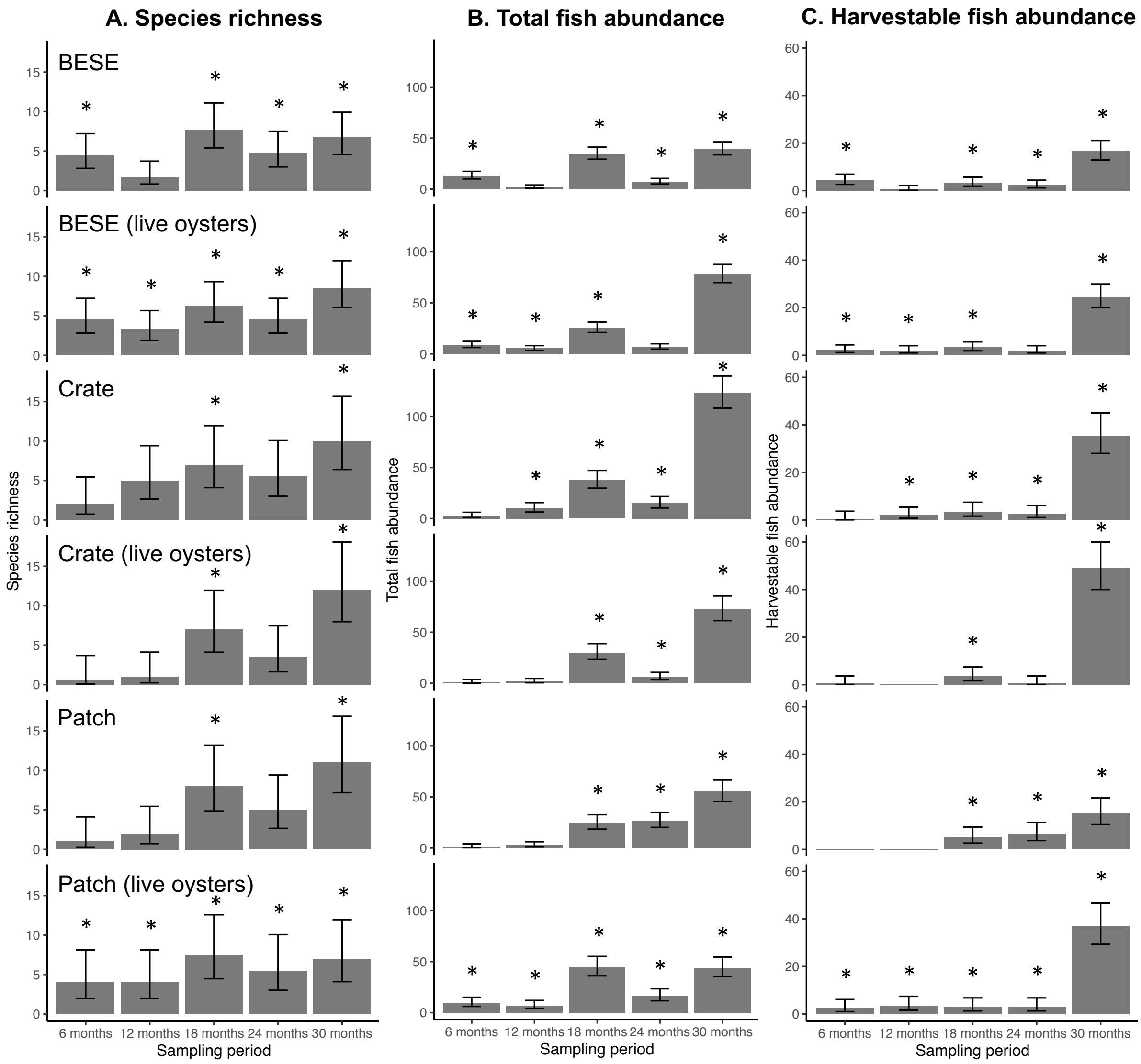

Figure 8 Average (+/- SE) of A) species richness, B) total fish abundance, and C) harvestable fish abundance between reef unit types 30 months of post-installation sampling (from RUVS data). * indicates significant difference between that column and pre-installation controls. Pre-installation control averages; species richness=1.68 species, total fish abundance=2.81 fish and harvestable fish abundance =0.68 fish.

We found no significant interaction between distance to shellfish reef and before/after restoration commenced, or the time since first installations for species richness, total fish abundance, and harvestable fish abundance, or for any key indicator species (Table 3). This means that the distribution of key attributes of fish assemblages did not change significantly with respect to adding structure to the shellfish reef restoration site. Similarly, the spatial patterns we recorded for fish diversity and abundance did not follow different trajectory at sites very close to reef and those distant. We also found no negative relationships between fish species richness, total fish abundance and harvestable fish abundance with time since first installations (Table 3, Figure 10). Fish species richness was highest at sites with more mangroves nearby, shallower water and higher salinity (Table 3A, Figure 10A). Similarly, total fish abundance was also greater near extensive mangroves and in shallower water, as well as during sampling events undertaken later after reef construction (Table 3A, Figure 10B). Harvestable fish abundance was highest at sites with a greater extent of mangroves nearby, lower salinity and later after reef construction (Table 3A, Figure 10C). Finally, we found variable effects of our environmental variables on the abundance of indicator species across the seascape. Crucially, however, none of these species showed significant interactions between distance to shellfish reef and before/after restoration commenced or time since first installations, none changed in abundance with proximity to the shellfish reef restoration sites, and nine out of ten species were more abundant across the seascape with time (Table 3B).

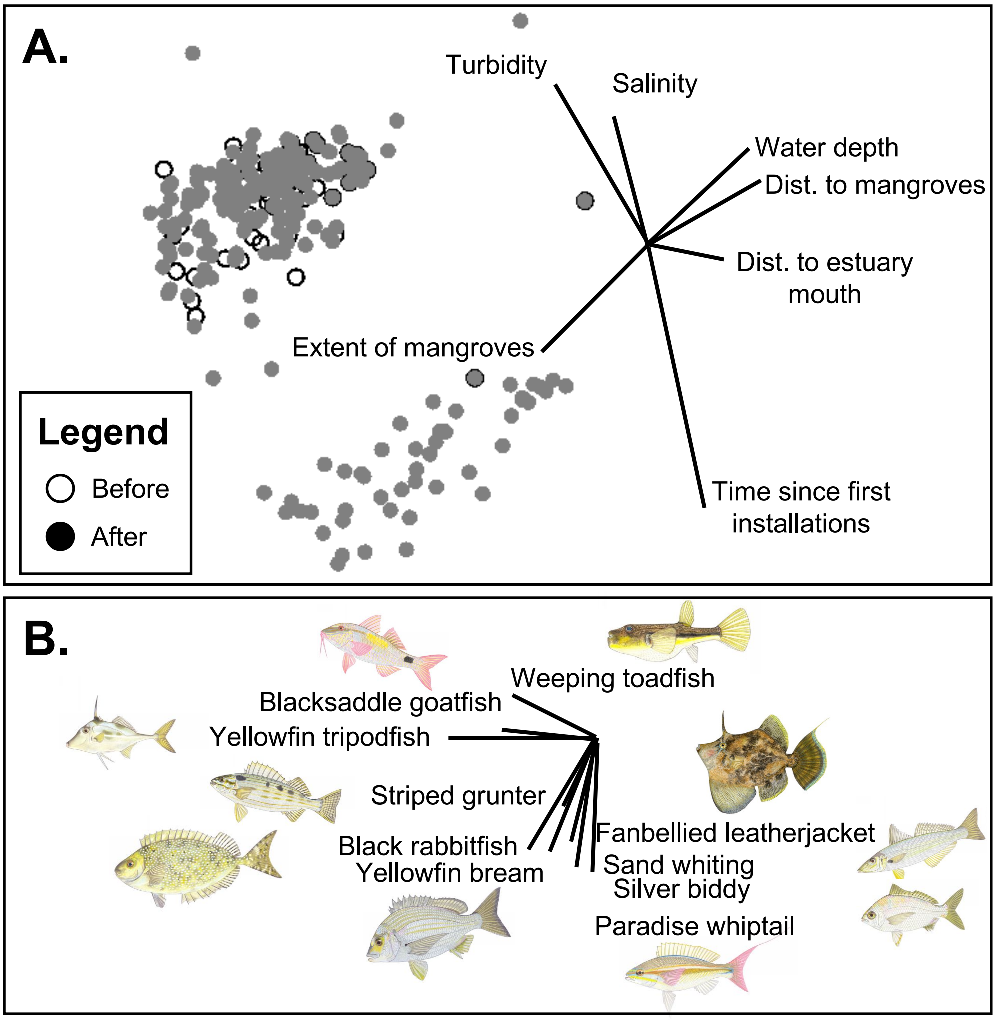

Figure 9 Non-metric multidimensional scaling (nMDS) ordination of RUVS survey sites. Vectors indicate A) variables and B) indicator species from the best fit ManyGLM.

Table 3 List of A) compound metrics and B) indicator species from the RUVS ManyGLM, variables that best explain the distribution of these species across the seascape and the trajectory of these relationships (as shown by arrows; = positive correlation, =negative correlation). Blank cells indicate variables that did not appear in the best fit model for that particular metric or species. All other variables did not explain a significant proportion of variance in the distribution of these species. We found no significant interaction between distance to the oyster reef, before/after restoration began or time since restoration commenced for the abundance of these indicator species.

Metric/species	Time since first installations	Water depth	Distance to mangroves	Area of mangroves within 1000 m	Salinity	Turbidity
A. Compound metrics						
Species richness		X^2=27.58, P<0.001 ↓		X^2=58.8, P<0.001 ↑	X^2=33.69, P<0.001 ↑	
Total fish abundance	X^2=261.93, P<0.001 ↑	X^2=254.64, P<0.001 ↓		X^2=831.94, P<0.001 ↑		
Harvestable fish abundance	X^2=937, P<0.001 ↑			X^2=268.16, P<0.001 ↑	X^2=248.51, P<0.001 ↓	
B. Indicator species						
Yellowfin bream	X^2=60.7, P<0.001 ↑			X^2=64.5, P<0.001 ↑	X^2=62.7, P<0.001 ↓	
Silver biddy	X^2=322, P<0.001 ↑			X^2=11.2, P<0.001 ↑	X^2=65.3, P=0.02 ↑	
Fanbellied leatherjacket	X^2=43.7, P<0.001 ↑			X^2=6.1, P=0.01 ↑		
Blacksaddle goatfish			X^2=85.1, P<0.001 ↓		X^2=35.2, P<0.001 ↑	X^2=38.9, P<0.001 ↓
Striped grunter	X^2=195.1, P<0.001 ↑	X^2=30.5, P<0.001 ↓		X^2=83.8, P<0.001 ↑		
Paradise whiptail	X^2=36.2, P<0.001 ↑			X^2=10.1, P=0.001 ↑		
Sand whiting	X^2=42.8, P<0.001 ↑				X^2=6.4, P=0.01 ↓	X^2=35.5, P<0.001 ↑
Black rabbitfish	X^2=809, P<0.001 ↑			X^2=185.1, P<0.001 ↓	X^2=250.9, P<0.001 ↓	
Weeping toadfish	X^2=18.3, P<0.001 ↓				X^2=19.8, P<0.001 ↑	X^2=14.4, P<0.001 ↓
Yellowfin tripodfish	X^2=13.9, P<0.001 ↓				X^2=165.2, P<0.001 ↑	X^2=366.9, P<0.001 ↓

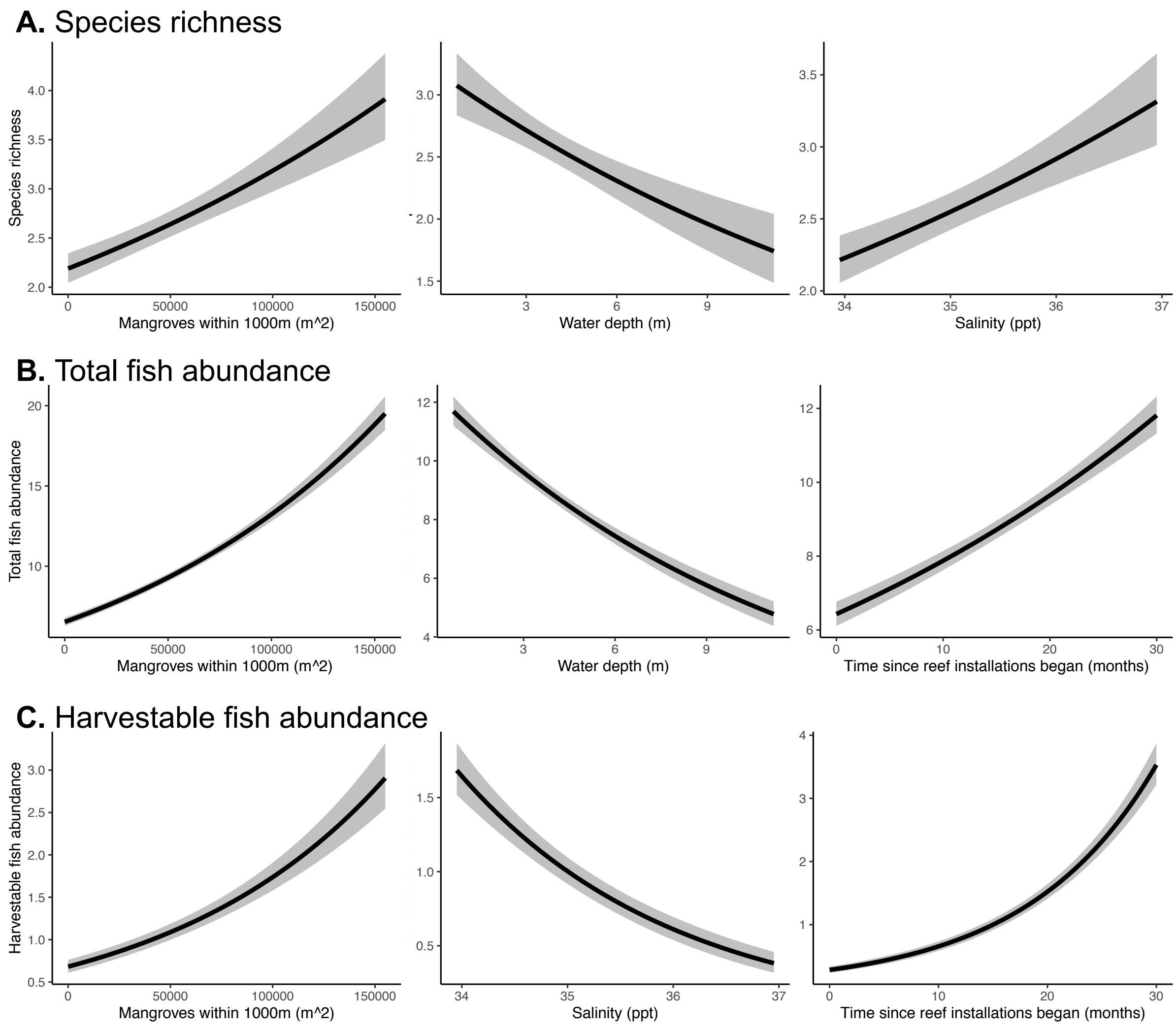

Figure 10 Generalised linear model outputs illustrating relationships between A) species richness, B) total fish abundance, and C) harvestable fish abundance and variables from the best-fit models for each dependent variable. We found no significant interaction between distance to reef and time since first installations or before/after restoration commenced for any variable. Time zero in time since installations began plots are pre-installation surveys.

Discussion

Shellfish reef restoration projects increasingly include the enhancement of fish assemblages and fisheries as an explicit restoration goal (Baggett et al., 2015; Gilby et al., 2018b). Maximising these effects necessitates an understanding of which restoration configuration or methodology maximises these effects, and whether restored shellfish reefs simply serve to centralise fish abundance (i.e. 'attraction'), thereby not enhancing overall fish productivity (i.e. 'production') (Pierson & Eggleston, 2014; Gilby et al., 2018b). In this study, we show that shellfish reef restoration in Pumicestone Passage represents an 'production' to fish productivity because we identify; 1) significant increases in the diversity of fish assemblages and order of magnitude increases in both harvestable fish and total fish abundance at the shellfish reef restoration site, and 2) no interaction between time since restoration began and proximity of broader monitoring sites to the shellfish reef site, and no effect overall of proximity of monitoring sites to the restoration site throughout the broader seascape. With significant increases in fish biodiversity and abundance at the reef site and no change in the distribution of fish more broadly across Pumicestone Passage relative to the restoration site, our results indicate that the shellfish restoration project has increased the carrying capacity of habitats within our study extent for fish. In this sense, there was no effect of the shellfish restoration site on fish distributions outside of the restoration site and the positive influence of restoration on fish assemblages was spatially limited to the restoration site, and at a scale of less than a few hundred metres. Such were the increases in fish abundance and diversity at the restoration site over time, few differences between reef restoration unit types were identifiable after 18 months of surveys.

We found no evidence of the restoration effort centralising fish abundance or diversity at monitoring sites nearer to the restoration site due to the lack of a proximity to reef effect on fish in our broader seascape data. Indeed, the only variables that had persistent effects on fish across the Pumicestone Passage were time, with fish abundance increasing with time since restoration began, and environmental variables already understood to be crucial predictors of fish assemblages composition in the region; water quality and depth (Gilby et al., 2016; Yabsley et al., 2020), and the seascape context of sites relative to mangroves (Gilby et al., 2018a; Henderson et al., 2019a). Placing reefs nearer to mangroves might therefore maximise the diversity and abundance of fish congregating on reefs within this seascape and could have additive effects on reef performance. The consistency of these environmental variables in explaining fish distributions means that incorporating their effects into models disentangling the effects of restoration is crucial (Pittman & Olds, 2015). Not doing so may result in incorrect conclusions regarding the benefits, or otherwise, of shellfish reef restoration for fish assemblages. Fully confirming that the findings found in this study are the result of production and not a net attraction effect, and that these data are not an artifact of the sensitivity of sampling methods requires the tracking of fish across seascapes, and could be a focus of future studies. While we could not in this study identify differences in the size or life history stage of the fish surveyed, it is likely that fish settling onto the reef were a combination of recruits, juveniles and mobile adults. It is possible that movement of adults to the reef was from beyond our survey sites, but given the likely scales of this movement, the effect on populations outside of our study area are likely minimal and have a lower effect than the influence of any of the important environmental variables identified in this study.

Because we show an overall addition of fish to the seascape, and very large increases in fish abundance at the restoration site, fish abundance may eventually spill over from the restoration site and into the surrounding areas; a pattern analogous with the spill over effects of successful marine reserves (Halpern et al., 2009) and the effects of oyster restoration on oyster larvae distribution (Peters et al., 2017). Indeed, we may have identified the early stages of such a pattern in our data due to the increase in fish abundance across the seascape with increasing time since restoration began. This may over time lead to an effect of proximity of monitoring sites to the restoration site. Enhancing structurally complex subtidal habitats like shellfish reefs can also enhance the fitness of fish living nearby and provide greater spawning opportunities. Therefore, it might also be hypothesised that restoration with this level of success for fish might start seeding remnant subtidal structures throughout the broader seascape with recruit and juvenile fish, thereby increasing fish abundance at these sites. This was, however, not found during the duration of our study, likely because fully quantifying these effects will require ongoing monitoring across the seascape for well over a decade (zu Ermgassen et al., 2016).

The science of whether fish simply concentrate or centralise their home ranges around installed structures is synonymous with the attraction-production debate for artificial reefs (Brickhill et al., 2005). However, restored shellfish reefs differ fundamentally from artificial reefs. Restoration seeks to enhance naturally occurring habitats and to restore self-sustaining ecosystems that have persistent and ongoing habitat value for the full spectrum of biodiversity associated with the habitat (Simenstad et al., 2006; Baggett et al., 2015). For shellfish reefs, this includes a substantial focus on the settlement and growth of shellfish and other invertebrates, and small, cryptic fish; all of which provide potential food sources for the sorts of species we quantified across the seascape in this study (Lehnert & Allen, 2002; Peterson et al., 2003; Johnson & Smee, 2014). Conversely, artificial reefs are usually designed with explicit fisheries and fishing opportunity goals, and so it might be argued that these structures have a poorer potential to increase overall carrying capacity within estuaries than for shellfish reefs. Quantifying whether increases in fish abundance and diversity at shellfish reef restoration sites are due to fish assemblages centralising at new structures, or otherwise, must now be quantified at other restoration sites and ecosystems (e.g. coral reefs, mangroves, seagrasses) with different restoration footprints, seascape contexts and configurations to identify the consistency of these effects.

Our finding of increased abundance and diversity of fish assemblages at the shellfish restoration site aligns strongly with most other studies of fish associations with shellfish reef restoration projects (Peterson et al., 2003; zu Ermgassen et al., 2016; Gilby et al., 2018b). The tendency for a gradual increase in fish abundance and diversity at the restoration site over time is an encouraging sign of the ongoing effect of this restoration project for fish. Indeed, it is likely that the full benefits of shellfish reef restoration for fish may take up to a decade to fully establish (zu Ermgassen et al., 2016), meaning that further increases in the abundance and diversity of fish assemblages at the restoration site should be anticipated. Fish assemblages at the restoration site are now strongly reflective of coral and rocky reefs in the broader Moreton Bay region; black rabbitfish, yellowfin tripod fish and paradise whiptail are among the most dominant fish species on rocky and coral reefs in the Moreton Bay region (Gilby et al., 2016). These results come in spite of significant recreational fishing pressure at the shellfish reef restoration site (BG, SC personal observation), which was thought by some local people to be depleting fish stocks at the reef site. This may have been the case for some highly sought-after recreational species like pink snapper *Chrysophrys auratus* and jewfish *Argyrosomus japonicus*; species who would ordinarily associate strongly with these sorts of subtidal structures but were not found to be significant indicators of change in this study. However, the overall pattern for fish assemblages and especially for harvestable fish abundance remains so strong that these effects are apparently minor.

While we identified some early differences in the abundance and diversity of fish around the six different reef restoration unit types, these differences mostly homogenised as the abundance of fish at the restoration site soared, and never translated into assemblage-level differences between reef unit types. Here, effects for monitoring events undertaken 18 months after the initial installations began showed very few differences between the various reef units, especially for fish species richness. Similarly, there were no consistencies in the effects of different reef restoration units on our measures of fish abundance- some had slightly higher total fish abundance after 30 months, whilst others had slightly higher harvestable fish abundance. We also found very few and no consistent differences in fish abundance or diversity at reef units which had incorporated live oyster shell, versus those that did not. There are several potential explanations for this change in pattern from 18 months onwards. There may have been an effect of adding the new reef structures to the restoration area in December 2018 that served to further increase the carrying capacity of the reef restoration site as a whole and proliferated across all reef units. Similarly, there may have been such an influx of fish to the reef site such that fish could no longer make strategic decisions regarding which reef units to settle on; they were forced to congregate on structures irrespective of their true value for fish. Finally, a threshold in the growth and maturity of the reef units deployed in December 2017 may have been reached after 18 months, such that there was an optimal amount of food and protection provided by these units (Coen et al., 1998; Lehnert & Allen, 2002; Peterson et al., 2003). Indeed, the positive results of shellfish and invertebrate monitoring from the project serve to support this conclusion (Diggles et al., 2019). Overall, these results indicate that adding new, structurally complex habitats that have healthy invertebrate communities have a significant, albeit localised effect on fish assemblages in this system. Indeed, it may have been that the diversity of installations at the reef restoration site (i.e. the replicates of the six different reef restoration unit types) provided a diversity of habitat types and increased overall habitat heterogeneity greater than if a single reef unit type was used (Liversage, 2020).

Restoring shellfish reefs is increasingly understood to be effective for enhancing coastal biodiversity and the abundance of fish that people catch and eat (zu Ermgassen et al., 2016; Gilby et al., 2018b). In this study, we show significant positive effects of shellfish reef restoration on fish and demonstrate quantitatively for the first time how this restoration effort has a broader positive impact on the carrying capacity of an entire seascape. Increasing our understanding of how coastal restoration affects fish communities at restoration sites and more broadly across entire seascapes is crucial for three key reasons. Firstly, understanding the entire effect of restoration on fish assemblages is important in properly quantifying the socio-economic benefits of restoration; failing to establish positive effects beyond restoration sites might fail to acknowledge all benefits. Secondly, poorly understanding these effects may lead to poorer ecosystem service estimates and a lack of proper incentivisation for restoration, thereby hampering future efforts. Finally, as the prevalence and scale of coastal restoration projects increases globally (Duarte et al., 2020), understanding how the effects of restoration spill over into adjacent remnant habitats might help enhance the biodiversity, resilience and condition of threatened ecosystems beyond restoration sites. Quantifying the effects of restoration on fish assemblages both at restoration sites, and more broadly throughout entire seascape must therefore be considered a research priority.

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