Landscape context modifies the rate and distribution of predation around habitat restoration sites

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ABSTRACT

The rate and distribution of ecological functions is modified by how species respond to the composition of landscapes. Extensive loss of habitats has led to habitat restoration becoming an important management tool, however, it is not clear where restoration sites should be located in heterogeneous landscapes to maximise outcomes for ecological functions. We used restored oyster reefs, and the guild of predators associated with them, as a model system to test whether, and how ecological functioning is modified by the spatial context of restoration sites in marine landscapes (i.e. seascapes). We measured predation rates and surveyed predators using videoed deployments of 'squidpops' (dried squid tethered using fishing line) at multiple restored oyster reefs and nearby control sites in Queensland, Australia. Sites were located in different spatial contexts in a seascape composed of a mosaic of habitat types. Predation rates at restored oyster reefs were double those at control sites. Seascape context was important in modifying these predation rates; consumption near reefs was significantly lower when reefs were close to seagrass and mangroves. By contrast, higher rates were observed on reefs surrounded by non-vegetated seafloor, far from seagrass and mangroves. In addition, the distance over which predation extended into the surrounding unvegetated areas was greater on reefs father from vegetation. Strategically placing restoration sites in heterogeneous landscapes can maximise the effects of habitat restoration for ecosystem functioning and modify the distance over which these effects extent into surrounding seascape.

1. Introduction

The maintenance of ecosystem condition is contingent upon the preservation of ecological functions that enable ecosystems to resist or recover from disturbance (Risser, 1995; Decker et al., 2017). The distribution of many ecological functions in landscapes correlates with the presence or abundance of functionally important species (Brose and Hillebrand, 2016). These functionally important species are under threat from human activities in many settings (Vitousek et al., 1997). For example, habitat loss and degradation has resulted in the loss of functionally important species (e.g. herbivores and predators) in marine (Waycott et al., 2009), freshwater (Quesnelle et al., 2013) and terrestrial ecosystems (Kormann et al., 2016). This can have knock-on effects for the rates and distributions of key ecological functions in both disturbed habitat patches (Valiente-Banuet et al., 2015), and in surrounding landscapes (Tylianakis et al., 2010). Rehabilitating or restoring degraded ecosystems is an increasingly important management

intervention in all modified landscapes (Aerts and Honnay, 2011; Cosentino et al., 2014; Bouley et al., 2018). Whilst habitat restoration has in many settings been shown to increase the rates of key ecological functions (Frainer et al., 2018), it remains uncommon for restoration projects to explicitly target the restoration of mobile animals that perform important ecological functions (Gilby et al., 2018a).

The position of restoration sites in landscapes plays a pivotal role in shaping the assemblages of animals which colonise restored habitats, and the rates of ecological functions that animals provide (Bell et al., 1997; Jones and Davidson, 2016; Gilby et al., 2018a; Laszlo et al., 2018). Restoring habitats at sites with high connectivity to nearby ecosystems, which provide alternative habitats or source populations for animals, can enhance recruitment into restored habitats (Pullinger and Johnson, 2010; zu Ermgassen et al., 2016; Volk et al., 2018). For example, restoring corridors between forest patches increases faunal abundance by facilitating species movement and settlement (Tewksbury et al., 2002; Lees and Peres, 2008). Similarly, restoring

Fig. 1. Distribution of restored oyster reefs, control sites, and other marine habitats in the Noosa estuary, eastern Australia. (Spatial data sources: QLD Department of Environment and Heritage Protection and Gilby et al. (2018b).)

habitat patches in locations with connections to many habitat patches of different types, might serve to enhance the abundance and diversity of animals that use multiple habitats during their lives (Micheli and Peterson, 1999; Nagelkerken et al., 2015). Whilst the principles of landscape ecology are regularly suggested as important considerations in restoration plans, they are rarely implemented when selecting possible sites for restoration activities, with only 12% of restoration sites globally having been placed strategically in landscapes to enhance possible effects on animals (Gilby et al., 2018a). Consequently, empirical data that can be used to test the functional effectiveness of restoration in different landscape contexts is limited. Most studies that have examined possible landscape effects on habitat restoration have focused on changes in animal abundance, however, the abundance of animals does not always correlate with the functions they perform (Bullock et al., 2011; Gamfeldt and Roger, 2017). Quantifying the effects of restoration in different landscape contexts and determining whether these changes in species abundance proliferate to differences in key ecological functions is, therefore, pivotal for optimising the design and placement of restoration efforts (Gilby et al., 2018a).

Humans have fundamentally transformed many coastal seascapes (i.e. marine landscapes) via the combined effects of urbanisation, poor water quality, dredging and fishing, and these changes have resulted in the loss or degradation of many marine ecosystems (Halpern et al., 2008). Consequently, the restoration of coastal ecosystems has become an important focus in marine spatial planning (Barbier et al., 2011), and enhancing the abundance of animals (especially fishes and large crustaceans) and ecosystem functioning is a primary objective for many restoration projects (Baggett et al., 2015; zu Ermgassen et al., 2016). Oyster reefs are a highly threatened but restorable ecosystem (Beck et al., 2011), consequently oyster restoration projects are now expanding rapidly in number globally (Alleway et al., 2015). Whilst oyster reefs are restored for multiple purposes (e.g. shoreline stabilisation, water quality, return of lost habitats), and provide important habitats for many coastal fish species and are often restored to augment fish abundance and diversity (Baggett et al., 2015), rarely are they restored explicitly to enhance the ecological function performed by mobile fish and crustaceans (Gilby et al., 2018c). Oyster restoration can have positive effects on fish assemblages over what were previously unstructured sediments (Harding and Mann, 1999; Peterson et al., 2003;

Grabowski et al., 2005), however, the possible benefits of oyster restoration for ecological functions have rarely been tested with empirical data (Smyth et al., 2015; Gilby et al., 2018c). The landscape context of oyster reefs can modify the composition of fish assemblages, both over reefs and in surrounding temperate (Micheli and Peterson, 1999; Grabowski et al., 2005), and subtropical (Gilby et al., 2018b) seascapes, but there is no data to describe whether these effects also modify the spatial distribution of ecological functions (Gilby et al., 2018c).

Restoration projects often seek to enhance the condition of ecosystems and the diversity or abundance of animals that use these ecosystems as habitat (Jones and Davidson, 2016; Middendorp et al., 2016). Many restoration efforts also aim to promote ecological functions, but the potential functional effects of restoration are rarely measured or monitored. This study quantified the effects of oyster reef restoration on the rate and distribution of predation in an estuarine seascape. Predation is an important ecological function that helps to maintain community structure in all ecosystems (Ritchie and Johnson, 2009; Estes et al., 2010; Ripple and Beschta, 2012). Quantifying rates of predation around habitat restoration projects is important because predation is significantly, and quickly, modified by the rapid colonisation of predators to restored coastal ecosystems (Harding, 1999; Micheli and Peterson, 1999; Peterson et al., 2003) and predators are sensitive to ecosystem changes as they rely on prey availability to survive and reproduce, and so are good indicator species for this purpose (González-Tokman and Martínez-Garza, 2015; Gilby et al., 2017a). We aimed to determine: 1) the degree to which oyster reef restoration enhances the function of predation at restoration sites; 2) the distance over which predation extends into the seascape surrounding restored oyster reefs, 3) how the seascape context of restored oyster reefs modifies their effects on ecological functions, and 4) the identity of the species performing the function. We surveyed rates of predation at six restored oyster reefs, and in the seascape surrounding each reef, which differed in terms of their proximity to nearby seagrass meadows and mangrove forests. We hypothesised that oyster reef restoration would enhance predation rates both on reefs and in the surrounding seascape (relative to nearby control sites) and expected that these functional effects of restoration would depend on the spatial context of oyster reefs relative to other habitats (e.g. seagrass, mangroves) that provide high-relief and structurally complex habitats for fish.

2. Methods

2.1. Study system

This study was conducted in the Noosa River; a subtropical estuary (~24°S) on the east coast of Australia. The Noosa River seascape is comprised of mangrove forests and seagrass meadows, interspersed among a matrix of unvegetated sandy substrates (Fig. 1). Oyster reefs were historically abundant in the Noosa River, but became functionally extinct in the early 1900s (Thurstan, 2015). Oyster reefs were restored in the Noosa River in November 2017, with a principle aim to restore structurally complex habitats (i.e. relative to 'low complexity' unvegetated muds or sands) and to enhance seascape complexity for fish. Reefs were constructed using coconut-fibre mesh bags (1 m long × 30 cm diameter with a 2 cm aperture) filled with recycled whole Sydney rock oyster (*Saccostrea glomerata*) shell. Each oyster reef site is comprised of nine oyster reef bags stacked in three piles of three at 5 m distances, forming an equilateral triangle and positioned intertidally to abut the level of lowest astronomical tide, and were sited within the historical range of oysters in this seascape (Thurstan, 2015). These reefs provide oyster larvae, which occur naturally in this system (The Nature Conservancy and Ecological Service Professionals, 2015), a place to settle and grow. Over time, oysters will grow and cement oyster shells together to form fully functioning oyster reefs.

In this study, surveys and experiments were conducted at six oyster reef restoration sites, which were chosen to represent the range of seascape contexts (especially with respect to the areas of nearby mangrove forests and seagrass meadows) available within this system (Fig. 1) (Gilby et al., 2017b). These sites also represent a gradient of salinity and light penetration in the river. These metrics, therefore, were the key environmental metrics tested in this study (Table 1). These metrics have been shown in previous studies in the region to be important drivers of the distribution and diversity of estuarine fish (Gilby et al., 2018b). Six control sites were selected on the basis that they had the same suite of seascape contexts as reef sites, but were at least 200 m from each oyster reef site (Fig. 1).

2.2. Study design

The fundamental premise of our study design was to quantify the function of predation, and the species performing the function of predation at reefs sites and nearby controls, and with increasing distance away from these sites. To do this, we quantified predatory fish assemblages and predation using eight underwater camera units at pre-established distances (i.e. camera positions) from each site (i.e. 0, 1, 2, 5, 10, 15, 20, 25 m) (Fig. S1). These distances were selected to mirror the scale of functional effects from similar-sized artificial reefs in other coastal ecosystems (e.g. Jelbart et al., 2007; Layman et al., 2016; Henderson et al., 2017; Skilleter et al., 2017). The first deployment (i.e.

at 0 m) was located in the centre of each oyster reef and control location. All other deployments were placed at random angles seaward from the oyster reef site, at the appropriate distance from this centre point (Fig. S1), and were always placed on unvegetated sands or muds (i.e. not in seagrass meadows or mangrove forests). Surveys and predation experiments were conducted on four occasions: immediately after reefs were installed, and at 2, 4 and 6 months post installation (i.e. survey periods). As surveys were conducted in the first 6 months post installation, individual reefs units were in a similar developmental stage and were not yet significantly altered by the settlement and growth of oysters, or other invertebrates. The effects that we report, therefore, represent a response of fish to the additional structurally complex habitats that reefs provide, rather than any effect of variable food availability among reefs. In surveying our sites across multiple survey periods, our intent was not to quantify any effects of 'time since restoration' as these oyster reefs will take many years to develop and grow. Rather, we sought to account for different environmental conditions between sampling periods.

2.3. Fish surveys and predation experiments

We used 'squidpops' attached to camera units to quantify rates predation and identify predators around our sites. Squidpops are now a standard method for indexing relative predation rates of marine mesopredators, and have been used extensively for this purpose in coastal seascapes (Duffy et al., 2015; Rodemann and Brandl, 2017). Squidpops consist of a single 1cm² piece of dried squid mantle tethered to a 20 cm long bamboo stake using a 10 cm length of fishing line. Camera units were comprised of a 5 kg weight with a GoPro camera recording in high definition (1080p). The squidpop stake was then fastened to the camera unit using a 15 mm gauge PVC arm at a distance of 45 cm from the camera, so that the squidpop was visible at all times (Fig. S2). A total of 384 squidpop deployments were conducted during this study. All camera deployments were made on unvegetated substrate (i.e. not in seagrass meadows or mangrove forests) and were conducted 2 h either side of high tide to maximise water visibility and accessibility to oyster reef sites (Gilby et al., 2017a). Each camera deployment was 1 h; deployment times were selected based on a pilot study in the Noosa River in 2017. Squidpops were consumed by predators when the squid piece had been entirely removed by a fish. The identity of fish predators was determined by viewing video footage from each deployment.

2.4. Data analyses

Our analytical approach comprised three key steps. First, we used a logistic regression in R (R-Core-Team, 2017) to determine how the effect of treatment (fixed factor, two levels; oyster reefs and control sites) and survey period (fixed factor, four levels; event 1, 2, 3, 4) influenced predation rates across all deployments (a binomial response variable,

Table 1
Environmental metrics included in statistical models, their definitions and sources (where applicable).

Variable	Definition	Source
Distance from reef	Pre-established distances (i.e. camera positions) from each site (i.e. 0, 1, 2, 5, 10, 15, 20, 25 m) in metres from the centre of the restored reef.	–
Seascape context		
Seagrass area	The area covered by seagrass in metres within a 500 m distance buffer. This was selected based on the likely home ranges of fish in these estuarine systems (Olds et al., 2012).	(Olds et al., 2012; Gilby et al., 2018b)
Mangrove area	The area covered by mangroves in metres within a 500 m distance buffer, selected based on the likely home ranges of fish in these estuarine systems (Olds et al., 2012).	(Olds et al., 2012) GIS, habitat layers from Olds et al. (2012) and Queensland Government (2016)
Water quality		
Salinity	The salinity (psu) of the water at each site, quantified using a refractometer at the time of deployment of every camera.	–
Secchi depth (turbidity)	The measure of water column light penetration (m) at each site using a standard 30 cm diameter secchi disk at the time of deployment of every camera.	–

1 = squidpop consumed, 0 = squidpop not consumed). Secondly, we used generalised additive models (GAMs) in the *mgcv* package (Wood, 2018) to examine correlations between predation rates and our environmental metrics of interest (Table 1). We calculated models with all possible combinations of factors using *MuMIn* package (Barton, 2018), and selected the best fit model using Akaike's Information Criterion (AIC). Relative factor importance was calculated for each variable by taking the sum of weighted AIC values for all models in which that factor was included (Burnham, 2002). Finally, we used generalised linear models (GLMs) to quantify how the variables from the best fit model interacted with each other. Here, we analysed interactions between pairs of variables from the best fit model separately (as opposed to calculating all comparisons, including three or four way interactions in the same model) to avoid over interpreting these interaction effects given the number of reef sites (n = 6) sampled.

3. Results

3.1. Habitat restoration enhances ecological function

We measured predation to be 212% higher at oyster reefs (n = 106 events) than at control sites (n = 50 events). Six species consumed squidpops (Fig. 2A): yellowfin bream (Sparidae; *Acanthopagrus australis*), narrow-lined puffer (Tetraodontidae; *Arothron manilensis*), butter bream (Monodactylidae; *Monodactylus argenteus*), common ponyfish (Leiognathidae; *Leiognathus equulus*), mud crab (Portunidae; *Scylla serrata*) and yellowfin tripodfish (Triacanthidae; *Tripodichthys angustifrons*). Predation was dominated by yellowfin bream, which consumed 88% of all deployments, followed by narrow-lined puffer (7%) and butter bream (2%) (Fig. 2B). The likelihood of predation was significantly higher at oyster reefs than at control sites ($x^2 = 34.5$, P < 0.001) (Fig. 2C). The likelihood of predation also increased significantly with survey period ($x^2 = 34$, P < 0.001) (Fig. 2D). However, these factors did not interact significantly. The high rates of predation at restored oyster reefs mirrored the distribution and feeding actions of yellowfin bream, which were more abundant at oyster reefs than at control locations (Fig. 2B). By contrast, the diversity of predators was greater at control sites (n = 5 species), than at restored oyster reefs (n = 3 species). Given the strong, and consistent effects of oyster reefs on predation rates, all subsequent analyses considered reef sites and control sites separately.

3.2. Seascape context shapes the effects of habitat restoration on ecological function

The likelihood of predation at oyster reefs was best explained by a combination of the distance of survey sites to the oyster reefs, and the area of mangroves and seagrass in the seascape surrounding the oyster reefs (Table 2, Fig. 3). No other variables were included in the best fit model (Table 3). The probability of predation decreased with increasing distance from restored oyster reefs (Fig. 3A), and was also lower adjacent to reefs that were bordered by a larger area of mangroves or seagrasses (Table 2, Fig. 3B, C). At control sites, the likelihood of predation was best explained by a combination of salinity and area of seagrass and mangroves (Table S1). The best fit model for control sites did not include distance from reefs, thereby confirming that the effects found at reefs were due to the restoration of reefs, and not any effects of 'bait attraction'. The presence of mangroves or seagrasses in the seascape surrounding restored oyster reefs did not modify the rate at which the probability of predation declined with distance from individual reefs (i.e. there was no interaction between distance from reef and area of adjoining habitat) (Table 3, Fig. 4). Predation rates were higher at reefs without nearby mangroves or seagrasses and this remained consistent with increasing distance from the oyster reef (Fig. 4).

4. Discussion

An important goal of many habitat restoration projects is to re-establish animal populations and the ecological functions they perform (Coen and Luckenbach, 2000; Miller, 2002; Kaiser-Bunbury et al., 2017). The potential effects of habitat restoration on ecological functions are, however, rarely quantified. Our results show that oyster reef restoration enhances the ecological function of predation on previously unstructured substrates and indicate that the spatial context of restored ecosystems can shape their functional effects in coastal seascapes. In this sense, high seascape complexity, characterised in this study by extensive areas of nearby seagrasses or mangroves, reduces the rate of predation relative to sites with lower extents of mangroves or seagrasses nearby. Similarly, we found that these effects remained consistent with increasing distance into the nearby low complexity unvegetated areas and that there was no effect of nearby seascape elements on the rate of decline of predation rates with increasing distance. We suggest that these effects are likely because the value of the restored oyster reefs for fish is contingent on the quality contrast between the reef and the surrounding habitat patches. Here, we hypothesise that the fish are using the reefs as a central point of their home range and performing feeding excursions radially from the reef at relatively fixed distances. Where there are existing high-quality habitats near to restored oyster reefs, fish are less likely to move to a new structured habitat, thereby reducing the augmentation effect of restoration efforts (Gilby et al., 2019). These findings suggest that placing restoration sites in strategically selected locations within heterogeneous landscapes can maximise the rates of ecological function at restoration sites, and the distance over which they extend away from the restoration site.

The colonisation of functionally important species to restoration sites is contingent on the benefits supplied by restored habitats relative to alternative habitats (Jones and Davidson, 2016; zu Ermgassen et al., 2016). Furthermore, restoring ecosystems to enhance the diversity of animals performing the functions (i.e. functional redundancy) can increase the capacity of ecosystem to withstand the loss of individual species (Micheli and Halpern, 2005). In this study, predation was significantly higher at oyster restoration sites than at nearby unvegetated control sites, irrespective of their landscape context. This positive effect of habitat restoration on ecological functions is likely due to fish congregating around structurally complex habitats for foraging, refuge, spawning and dispersal across different life stages (Blaber and Blaber, 1980; Whitfield, 2017). Previous studies have shown that this can extend to the functions that congregating species provide (Layman et al., 2013; Layman et al., 2014; Olds et al., 2018), though this is rarely quantified for restoration actions (Gilby et al., 2018a). Despite these positive effects of restoration, we found relatively low functional redundancy in the composition of predator assemblages on reefs. Previous studies on both the effects of restoration on rates of predation and/or the availability of prey resources (Micheli and Peterson, 1999; Ziegler et al., 2017) have illustrated similar patterns in regards to the value of restored oyster reefs for the survival of various macro invertebrate species (i.e. crustaceans, bivalves and gastropods) across different life stages. Predation on reefs was dominated by yellowfin bream, a voracious generalist consumer in this estuary (Pollock, 1982; Olds et al., 2018), which aggregates around a variety of structurally complex habitats, including oyster reefs and artificial structures (Gilby et al., 2018b). Yellowfin bream might competitively exclude other potential predators from restored oyster reefs because they are abundant and aggressive predators in this system, an effect that would be exacerbated on reefs that are at early successional stages, and which might provide only a limited pool of resources to be partitioned by mobile consumers. Given that the diversity of predators was highest at unstructured control sites, and is also likely to increase at oyster reefs over time, it will be important to determine how these spatial and temporal changes combine to shape functional redundancy in the composition of predator
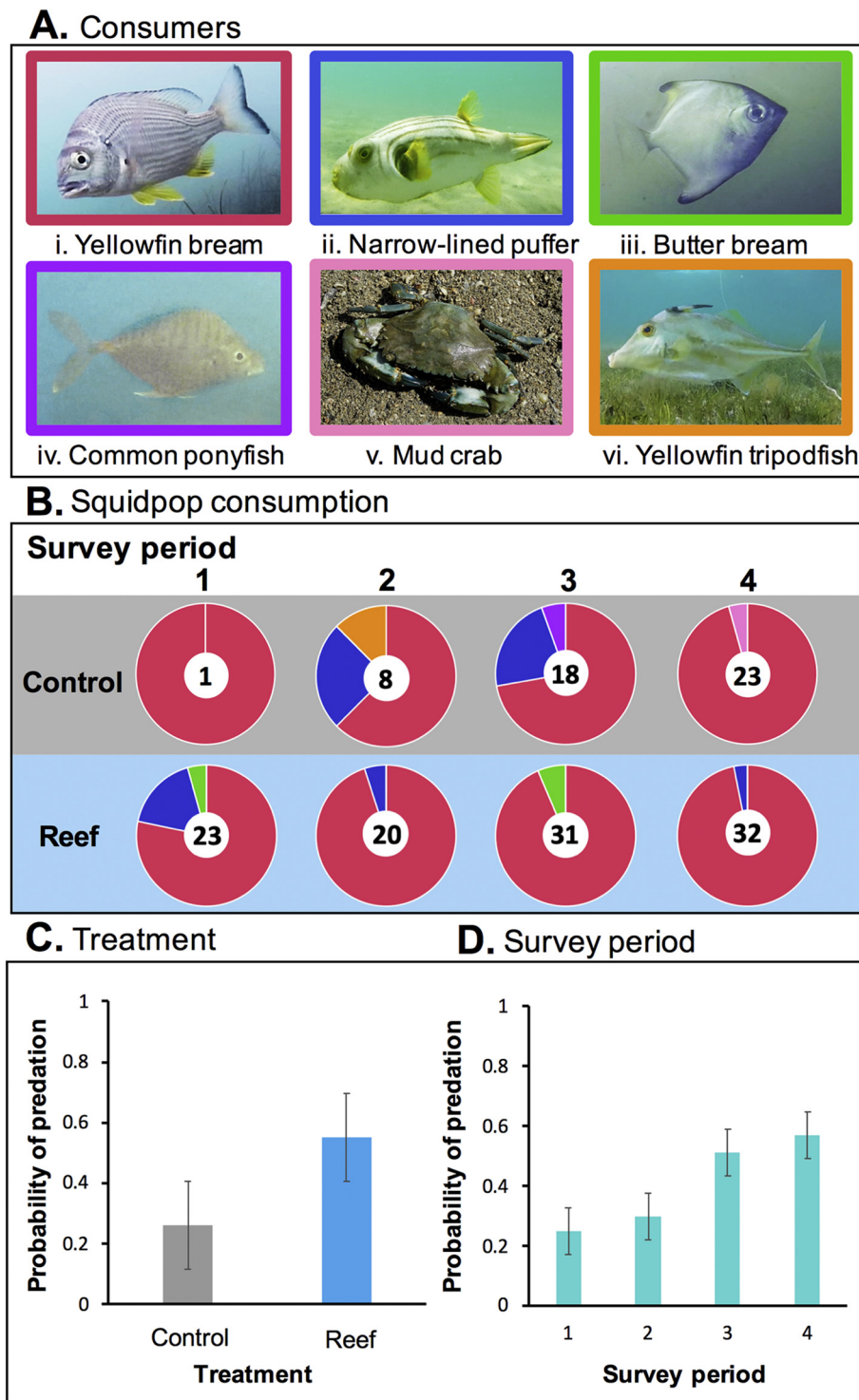
Fig. 2. (A) Six predators consumed squidpops in the Noosa River, Australia. (B) Pie charts represent the proportion of squidpops consumed by each predator at restored oyster reefs and control sites during each survey period (colours correspond to those used in panel A). Numbers inside pie charts represent the total number of predation events for that treatment by sampling period combination (out of 48 total deployments). (C) Probability of predation at restored oyster reefs and control sites within 1 h from deployment. (D) Probability of predation across survey periods (1, 2, 3, 4) within 1 h from deployment.

Images by the authors and B. Sarangi (CC 1.0).

Table 2

Best fit model on probabilities of predation around oyster reef sites from generalised additive model output with importance values. The best fit model had an r^2 value of 0.26. Values in bold are significant at P = 0.05.

Source	Variable importance	ChiSq	P
Distance from reef	0.99	10.99	**< 0.001**
Mangrove area	0.95	23.82	**< 0.001**
Seagrass area	0.57	4.46	**0.035**

assemblages across this coastal seascape.

Conventionally, high seascape heterogeneity is thought to enhance ecological functioning in coastal habitat patches due to increased connectivity between adjacent habitats (Micheli and Peterson, 1999; Pottier et al., 2009), including in systems within our study region (Olds et al., 2012; Gilby et al., 2018b). We show, however, that this is not always the case for restoration. Previous studies have identified greater fish abundance and diversity at oyster reef restoration sites more isolated from nearby marshes because they provide new, structurally complex habitat to previously low-complexity muddy substrata (Grabowski et al., 2005; Geraldi et al., 2009). Our findings show that
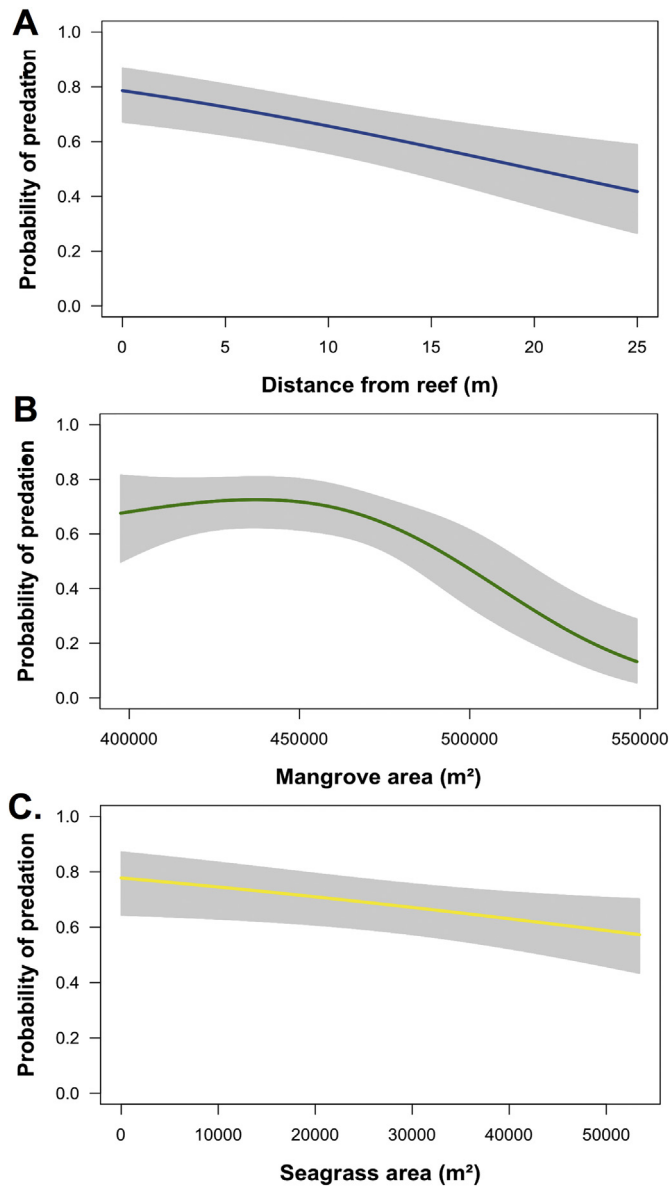
Fig. 3. Generalised additive model (GAM) outputs illustrating relationships between the probability of predation and (A) distance from reef, (B) mangrove area, and (C) seagrass area. Grey shaded polygons represent 95% confidence intervals.

Table 3
Summary of generalised linear models testing for relationships between the probability of predation and three predictors: Distance from reef (D), seagrass area (S) and mangrove area (M). Values in bold are significant at P = 0.05.

Source	df	x^2	P
Seagrass			
Distance from reef (D)	1	9.12	**0.003**
Seagrass area (S)	1	23.23	**< 0.001**
D × S	1	2.55	0.11
Mangroves			
Distance from reef (D)	1	9.12	**0.003**
Mangrove area (M)	1	24.59	**< 0.001**
D × M	1	0.67	0.41

these effects of restoration on fish assemblages can also extend to key ecological functions. Where existing complex habitats are available, fish may be less likely to migrate to newly restored ecosystems nearby
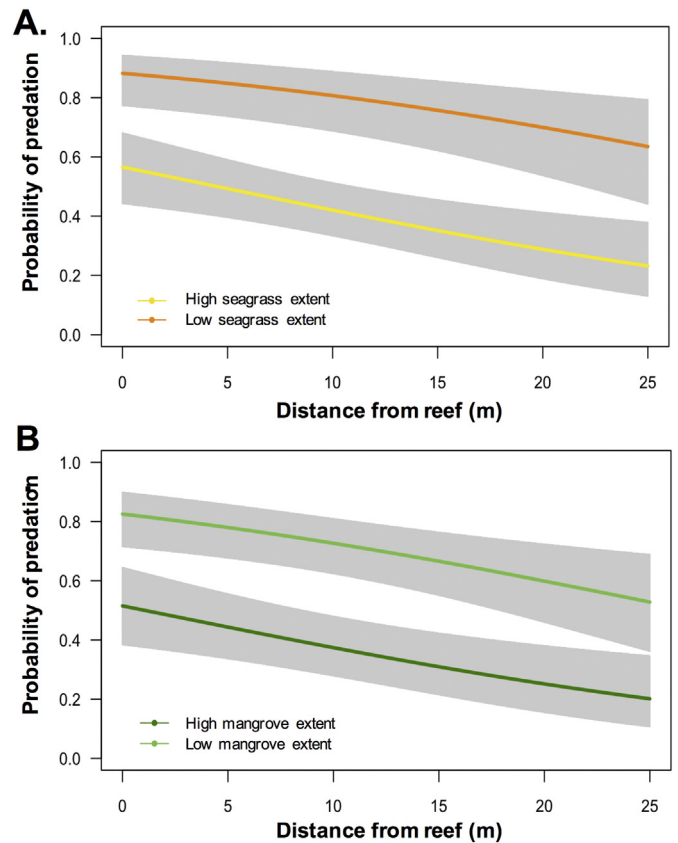

Fig. 4. Generalised linear model (GLM) outputs illustrating relationships between the probability of predation and (A) seagrass area, (B) mangrove area, categorised in to low and high by natural splits in the data as distance from reef increases. Grey shaded polygons represent 95% confidence intervals. Note that the analyses underlying these graphs were run on two continuous variables (distance from reef, and area of habitat within 500 m of the reefs), but area values are shown here as categories for ease of illustration, with categories based on natural splits in the values of habitat extent (for mangroves low = 397,489.12 m² – 459,372.51 m², high = 463,206.33 m² – 549,056.19 m²; for seagrass, low = seagrass absent within 500 m, high = seagrass present within 500 m).

because they may provide less food, have a higher risk of predation, or are energetically more expensive to reach or inhabit (Grabowski and Powers, 2004; Ziegler et al., 2017). By contrast, fish will also move some distance over low complexity habitat to congregate around restored structures (Irlandi and Crawford, 1997; Gregalis et al., 2009). In this sense, the value of a restored habitat patch in a coastal seascape is contingent upon the contrast between the value of the restored habitat and the value of the habitats immediately surrounding the restoration site. In addition, it is likely that the overall value of the restored oyster reefs for fish is shaped by the combined effects of 1) the level of connectedness that the restored habitats have with alternate habitats, 2) the movement capacity of the fish within the system and the scales over which they move, and 3) the relative predation risk felt by fish making movements to the new reefs. However, the restored oyster reefs in this study were relatively small structural components in the overall seascape, particularly in comparison to the extensive nearby remnant seagrass and mangrove habitats. The effects of landscape context on very large restoration sites (i.e. 10s of m²) might be different to those found here because the effect of reefs drawing fish away from nearby naturally occurring structurally complex habitats might be greater with a larger restoration footprint. Seeking consistencies in these effects on restoration for different restored reef designs, in multiple settings, and across multiple functions is therefore an important research gap.

Habitat restoration can affect the distribution of animals and the

functions they provide beyond the footprint of the ecosystems that have been restored (Gilby et al., 2018a). Our results indicated significant declines in predation with increasing distance from restored reefs and show that the trajectory of this effect was consistent irrespective of the complexity of the seascape around each reef. However, we did not identify a distance at which the effects of the reef on the function plateaued. This is surprising because the effects of artificial cinderblock reefs, which are of a similar size to our oyster reefs, have been shown to extend for only 15 m into the surrounding seagrass-dominated seascape (Layman et al., 2016). Previous studies on reefs in this region have shown that the scale of seascapes can modify the effects of connectivity on fish assemblages. In this sense, the effects we find here might not confer to seascapes of a larger scale, and there might be a given seascape scale (likely many hundreds of metres) over which thresholds occur on the effects of seascape connectivity (Olds et al., 2012; Martin et al., 2015). The main predatory fish in our system might have larger home ranges than those in other studies (Pollock, 1982), and the lack of extensive structurally complex seagrasses around our reefs might result in fish being less tightly associated with these reefs than they were in other studies. Alternatively, these effects might be due to high levels of natural predation across all ecosystems in the seascape we studied (Foam et al., 2005; Bauer et al., 2010). This is unlikely, since predation rates were higher on reefs surrounded by low complexity seascapes than on reefs that were bordered by complex habitats, and these trajectories did not intercept at the furthest distance surveyed. It is therefore more likely, that the distances from reefs that we surveyed were simply not far enough to detect these effects, and so further study is needed to understand the distance over which the functional effects of restored oyster reefs extend into surrounding seascapes. Whilst we found significantly higher rates of predation with increasing time (i.e. survey period), it is difficult to conclude that these effects were due to the restoration efforts because 1) we did not have a significant interaction between survey period and treatment, and 2) there are several seasonal and environmental considerations that are likely to overwhelm these 'time' effects.

In this study, we show that the augmentation of ecological functions at restoration sites is contingent upon their position in heterogeneous landscapes, and how functionally important species respond to landscape patterns. In addition, we show that the restoration of a lost habitat to a low complexity, unvegetated area in coastal ecosystems can result in key ecological functions having a footprint that extends significantly beyond the restoration site itself. If the species we identified as predators in this study were simply responding to the positive effects of the restored structure only (i.e. reefs units only and not necessarily to any food-item benefits that might be gained from a fully grown, mature reefs), then it might be hypothesised that these effects would only strengthen with time. This, however, requires further testing. Our findings have important implications for planning restoration actions both in sea and on land because they necessitate that practitioners understand the basic spatial patterns that are likely to drive the abundance and distribution of functionally important species across ecosystems. These results also signal the importance of quantifying system-specific responses to restoration, because the patterns that we found went against the conventional wisdom regarding landscape patterns for our study system. Given the paucity of information about the effects of habitat restoration on ecological functions, determining whether these effects found in this study are consistent across functions, ecosystems and environmental realms, is important to optimise future restoration efforts.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.06.028.

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