




Original Article

Seascape context modifies how fish respond to restored oyster reef structures

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The seascape context of coastal ecosystems plays a pivotal role in shaping patterns in fish recruitment, abundance, and diversity. It might also be a principal determinant in structuring the recruitment of fish assemblages to restored habitats, but the trajectories of these relationships require further testing. In this study, we surveyed fish assemblages from 14 restored oyster reefs and 14 control sites in the Noosa River, Queensland, Australia, that differed in the presence or absence of seagrass within 500 m, over four periods using baited cameras. Fish assemblages at oyster reefs differed from those at control sites, with higher species richness (1.4 times) and more individuals of taxa that are harvested by fishers (1.8 times). The presence or absence of seagrass nearby affected the abundance of a key harvestable fish species (yellowfin bream *Acanthopagrus australis*) on oyster reefs, but not the overall composition of fish assemblages, species richness, or the total abundance of harvestable fish overall. These findings highlight the importance of considering species-specific patterns in seascape utilization when selecting restoration sites and setting restoration goals, and suggest that the effects of restoration on fish assemblages might be optimized by focusing efforts in prime positions in coastal seascapes.

Keywords: mangroves, Noosa River, seagrass, seascape

Introduction

Habitats that provide high structural complexity and vertical relief in coastal seascapes are often hotspots for fish biodiversity (Whitfield, 2017). Fish congregate around structurally complex habitats for protection from predation, access to alternate food sources, or to shelter from currents (Lenihan, 1999; Micheli and Peterson, 1999; Brook *et al.*, 2018). However, these habitats, that include rocky outcrops, log snags, mangroves, and seagrasses, are among the first to be removed when humans modify aquatic ecosystems for shipping, shoreline stabilization, urban development, or fishing activities (Halpern *et al.*, 2008). Consequently, the restoration of structurally complex habitats is a technique that has been used widely in aquatic ecosystems to augment or aggregate fish biomass,

richness, or fisheries values following disturbance from human activities (Miller, 2002; Roni *et al.*, 2002; zu Ermgassen *et al.*, 2016; Sun *et al.*, 2017; Becker *et al.*, 2018). However, some restoration efforts do not fully consider how the placement of sites could maximize the abundance or diversity of fish around them, meaning that the full benefits of restoration might not be achieved (Jones and Davidson, 2016; Gilby *et al.*, 2018a).

The seascape context of habitats relative to other ecosystems, together with variation in the size and quality of habitat patches, structure the composition of fish assemblages across coastal seascapes (Grober-Dunsmore *et al.*, 2009; Pittman, 2018). For example, the proximity of mangrove, log snags, and rocky outcrops to nearby seagrass meadows shapes the composition of fish

assemblages across subtropical estuarine seascapes (Gilby *et al.*, 2018b). Similarly, the proximity of coral reefs and mangrove forests modifies the abundance and diversity of fish in tropical reef seascapes across the Pacific Ocean (Olds *et al.*, 2013) and Caribbean Sea (Mumby *et al.*, 2004). Consequently, connectivity between ecosystems is now an important consideration in marine conservation planning (Hidalgo *et al.*, 2016; Weeks, 2017). In temperate seascapes, marsh fragmentation influences both the abundance and diversity of fish in nearby subtidal channels, and the effects of this habitat transformation on fish and fisheries are further compounded by the impacts of urbanization and sea level rise (Torio and Chmura, 2015; Rudershausen *et al.*, 2018). In addition to these effects on fish assemblages, the seascape context of ecosystems can shape the distribution of ecological functions in coastal seascapes (Martin *et al.*, 2018; Olds *et al.*, 2018a), and modify the benefits of restoration and conservation for both biodiversity and ecosystem functioning (Grabowski *et al.*, 2005; Olds *et al.*, 2016; Henderson *et al.*, 2017). With restoration projects now established for many ecosystems globally, information regarding the growth and health of these restored ecosystems is often readily available, meaning that we are now better poised to determine how the placement of restoration sites in heterogeneous seascapes might optimize their performance (Rudnick *et al.*, 2012; Gilby *et al.*, 2018a). As a result, we might enhance the recruitment of fish to new habitats (either restored or artificial) by optimizing habitat detectability, accessibility, and location in coastal seascapes (Huntington and Lirman, 2012).

Oyster reefs are structurally complex coastal ecosystems, which provide high value habitat for fish assemblages because they provide abundant food and protection from predation, especially for juvenile and smaller fish (Peterson *et al.*, 2003; zu Ermgassen *et al.*, 2016). Oyster reefs are, however, also threatened, with an estimated 85% lost globally (Beck *et al.*, 2011), and up to 96% lost in some regions (Diggles, 2013). Consequently, oyster reef restoration has become a widespread management response globally (Gillies *et al.*, 2015b). Whilst there are several potential benefits to restoring oyster reefs, including improved water quality, reduced sedimentation, and increased nutrient sequestration (Coen *et al.*, 2007; Gillies *et al.*, 2015a), many projects explicitly seek to restore reefs to enhance the value of coastal seascapes for fish and fisheries (Coen and Luckenbach, 2000; zu Ermgassen *et al.*, 2016). Previous research has established that the seascape context of restored oyster reefs can affect both the abundance and diversity of fish in surrounding seascapes (Grabowski *et al.*, 2005). For example, connections with nearby marshes structure the abundance and diversity of macroinvertebrate assemblages on oyster reefs, and the rates at which key ecological functions, such as predation, are performed (Micheli and Peterson, 1999). The long-term effects of the placement of restored reefs in different contexts can often be species specific (Ziegler *et al.*, 2018). On occasion, however, fish abundance and diversity are greater on restored oyster reefs that are isolated from other ecosystems, possibly because these isolated reefs provide new, and structurally complex, habitat in locations that were previously low complexity, unvegetated soft sediments, and that reefs placed near other biogenic habitats (e.g. marshes) might not be as effective as isolated reefs for enhancing fish and crustacean abundance (Grabowski *et al.*, 2005; Geraldi *et al.*, 2009; Ziegler *et al.*, 2018). The understandings beginning to emerge from these studies on seascape effects for fish on oyster reef effects have been

predominantly built from a narrow geographic range. For example, most studies of the effects of seascape context on the fish assemblages of natural or restored oyster reefs have been conducted in temperate, marsh-dominated seascapes, and it is not clear whether similar effects occur in subtropical or tropical seascapes where mangroves dominate (Gilby *et al.*, 2018c). Effects of restored oyster reefs in mangrove-dominated systems, especially in meso- or macrotidal areas, might differ to effects in marsh-dominated seascapes due to differences in mangrove accessibility, food availability, or protection from predators (e.g. Sheaves *et al.*, 2016).

We restored oyster reefs in the Noosa River in Queensland, eastern Australia, a system where oyster reefs became functionally extirpated over a century ago, and used these as a model system to test whether the seascape context of individual reefs modified the degree to which they augment the abundance and diversity of fish. We anticipated that fish assemblages would differ between oyster reefs and nearby unvegetated locations, which were surveyed as control sites, with greater species richness and abundance of harvestable fish expected on oyster reefs. However, the oyster reefs also differed in terms of their positions relative to seagrass meadows, and variation in the degree of seagrass connectivity can structure the composition of fish assemblages across estuarine seascapes (Gilby *et al.*, 2018b). Consequently, we hypothesized that the effectiveness of restoring oyster reefs for fish would depend on their proximity to adjacent seagrass meadows, but that the direction that this relationship affects fish assemblages would be dependent on species-specific patterns of seagrass utilization.

Material and methods

Study system

The Noosa River is a subtropical estuary in eastern Australia (~24°S) (Figure 1). It supports a heterogeneous mix of unvegetated sandy substrate, mangroves (mostly *Avicennia marina*), and seagrass meadows (mostly *Zostera muelleri* with leaf lengths 30–40 cm), which contributes to the diversity and abundance of fishes across the seascape (Gilby *et al.*, 2018b). Mangroves are, however, the dominant component of the seascape in terms of area, with over 200 times more aerial extent of mangroves than seagrass throughout the Noosa River. Oyster reefs were once abundant in the estuary, but disappeared from the system in the early to mid-1900s, likely due to the combined effects of overharvesting, disease, and declining water quality (Thurstan, 2016).

Oyster reef restoration commenced at 14 sites in the Noosa River estuary in November 2017, and so form part of an active restoration effort in the Noosa region. The principal goal of the oyster reef restoration effort is to restore structurally complex habitats and to enhance seascape complexity for fish, including for species of commercial and recreational significance. The structures that were installed to restore oyster reefs were comprised of three 1 m long by 30 cm diameter bags of 2.5 cm gauge coconut mesh filled with oyster shells stacked in a triangular prism. Each reef site included three of these structures, which were arranged in a triangle (with 5 m sides) and positioned at the depth of lowest astronomical tide, so that reef emerged at low tide approximately twice annually in this mesotidal estuary (tidal range ~1–2 m). Naturally occurring oyster larvae, which remain present in

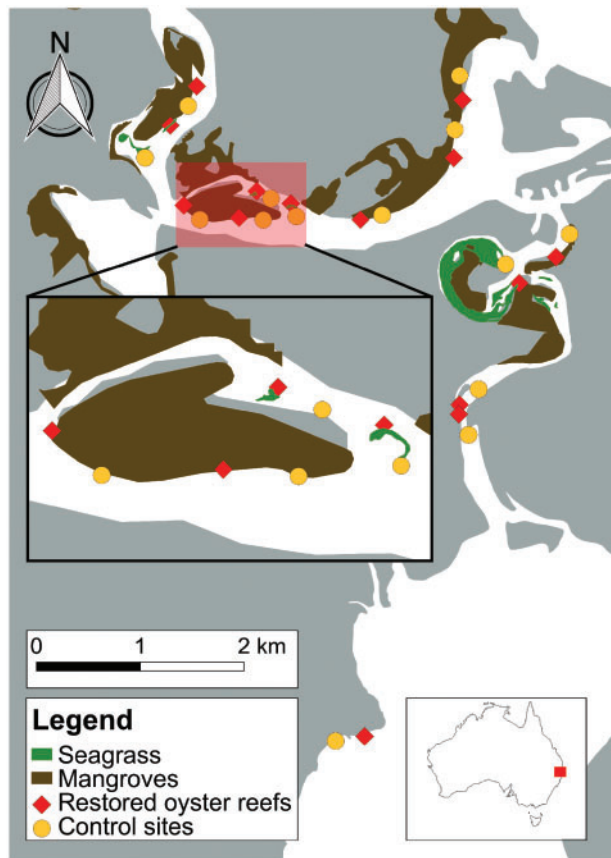


Figure 1. Location of restored oyster reefs, control sites, and habitats in the Noosa River, eastern Australia.

sufficient numbers in the river to allow restoration, settle on the reef structures, and are expected to cement them together to form functioning oyster reefs after approximately three years.

Oyster reef sites were positioned evenly along the lower estuary within the historic range of oyster reefs in the river (Thurstan, 2016) (Figure 1). All reef structures were placed within 100 m of adjacent mangroves. Therefore, effects from mangroves on fish congregating around oyster reefs were consistent across all sites (Olds *et al.*, 2012; Gilby *et al.*, 2018b). In contrast, reef structures differed in terms of their connectivity with persistent seagrass beds (i.e. present over the last 2 years) (Gilby *et al.*, 2018b). Seagrass meadows influence the composition of fish assemblages on rocky reefs in estuaries across the region for up to 500 m; the distance that best reflects the daily home ranges of many fish species that inhabit oyster reefs in the area (Olds *et al.*, 2012; Gilby *et al.*, 2018b). Consequently, oyster reefs were grouped based on the presence or absence of seagrass nearby (i.e. within 500 m). We selected 14 control sites spread throughout the Noosa River in the same range as oyster reefs, always on unvegetated sediments at least 200 m from oyster reefs and other control sites to ensure spatial independence, and with the same number of seagrass sites present or absent nearby as for oyster reef sites (Figure 1).

Fish surveys

We used baited remote underwater video stations (BRUVS) to survey fish on oyster reef structures and at control sites. BRUVS consisted of a 5-kg weight with a 1-m length of PVC pipe to

attach baits at a fixed distance of 50 cm from a GoPro camera recording in high definition (1080p). Baits were 500 g of crushed pilchards *Sardinops sagax* placed in a 20 × 30 cm mesh bag with 5 mm openings. BRUVS were deployed for a period of 1 h at each site during each survey event. Because salinity is a principal determinant for the distribution of fish in estuaries, salinity was measured at each site BRUVS deployment. All BRUVS were deployed in the centre of oyster reef sites. Surveys were conducted during the day (0900–1600 hr) and within 2 h of high tide to minimize potential confounding effects from tidal and diel variation. We surveyed fish assemblages immediately following installation of oyster reefs (time 0), and then at 6-week intervals for three additional events (i.e. $n = 4$ events in total). We survey these reefs in the first 6 months of installation when the value of individual reefs units for fish are similar, and have not yet been significantly modified by differential growth in potential food items on the reefs themselves (Gilby *et al.*, 2018c). Further, as this restoration effort is considered an active and developing restoration effort, and there has been little settlement of invertebrates amongst the oyster reef units to this point, we can assume that any responses found in this study are due mostly to the addition of structurally complex habitat to the estuary, as opposed to any significant prey- or food-availability effects. Reefs were purposefully positioned in areas in the estuary with intermediate tidal flow rates to (1) reduce scouring around the reefs by high tidal flows, but (2) still provide ample oyster larval recruitment to reefs. Consequently, there is unlikely to be any significant differences in odour plumes from BRUVS that would bias results.

Fish assemblages were quantified from video footage using the standard *MaxN* metric (see Gilby *et al.*, 2017). To account for variable visibility, fish were only counted if they swam through the field of view within 1 m of the camera (as determined by the above-described length of PVC pipe). Visibility was sufficient to use this 1 m field of view for all surveys, hence there was no effect of water column turbidity or visibility on the effectiveness of our surveys. We calculated species richness (i.e. total number of species) and number of harvestable fish (fished status according to FishBase, and equals the sum of *MaxN* values of all species considered “harvested” within the region) (Froese and Pauly, 2018) for each BRUVS deployment.

Statistical analyses

We used permutational multivariate analysis of variance (PERMANOVA) calculated on square root transformed Bray Curtis dissimilarity to test for differences in the composition of fish assemblages between oyster reefs and control sites (fixed factor, two levels), with variation in the presence or absence of seagrass nearby (fixed factor, two levels; seagrass present or seagrass absent nearby), and the interaction between these factors, whilst accounting for sampling period (covariable, four levels; 0, 6, 12, and 18 weeks). PERMANOVA results were visualized using canonical analysis of principal (CAP) components. In using “sampling period”, our focus was not to ascertain whether “time since restoration” resulted in any threshold effects for fish assemblages on oyster reef structures (i.e. reef assemblages reaching “maturity”), as this is likely to take many years to develop (zu Ermgassen *et al.*, 2016), but rather to account for potential differences in environmental conditions between sampling periods. PERMANOVA was followed by Dufrene–Legendre indicator species analyses (Dufrene and Legendre, 1997) in the labdsv package

of the R statistical framework (R Core Team, 2018) to determine the fish species contributing most to differences between oyster reefs and control sites.

We then used generalized linear models (GLMs) in R to test for patterns in the abundance of species identified from indicator species analyses, along with species richness and the abundance of harvestable species (i.e. the sum of MaxN of species identified as harvested by Froese and Pauly, 2018). The factors and model structure of GLMs were identical to those used in PERMANOVA analyses.

Results

Fish assemblages

We recorded 42 fish species across all surveys, with 34 species occurring on oyster reefs, and 31 species at control sites (Supplementary Figure S1). Of the species occurring on reefs, 12 species occurred exclusively at reefs (Supplementary Table S1); eight of these are targeted by local fisheries. Conversely, eight species occurred only at control sites, of which three species are targeted by local fisheries. Oyster reefs supported, on average, 1.4 times more fish species (3.6 ± 0.3 s.e.) than control sites (2.6 ± 0.2 s.e.) across all sampling periods (Figure 2a). Similarly, oyster reefs supported 1.8 times more harvestable fish (6.5 ± 0.7 s.e.) than control sites (3.6 ± 0.5 s.e.) across all sampling periods (Figure 2b). Fish assemblages on reefs were dominated numerically by estuary perchlet (*Ambassis marianus*; Ambassidae), yellowfin bream (*Acanthopagrus australis*; Sparidae), tarwhine (*Rhabdosargus sarba*; Sparidae), and southern herring (*Herklotsichthys castelnaui*; Clupeidae), which comprised 43%, 27%, 4%, and 3% of total fish abundance respectively. In contrast, fish assemblages at control sites were dominated numerically by estuary perchlet, yellowfin bream, weeping toadfish (*Torquigener pleurogramma*; Tetraodontidae), and striped trumpeter (*Pelates quadrilineatus*; Terapontidae), which comprised 69%, 27%, 4%, and 3% of total fish abundance respectively.

Effects of seascape position on reef fish

Fish assemblages differed between oyster reefs and control sites, and between sites where seagrass was present and absent nearby (Figure 3), but these two factors did not interact (Table 1). The composition of fish assemblages also differed among sampling periods, with both fewer fish species and fewer harvestable fishes being recorded on the final sampling event (Figure 2a and b). Sampling period was significantly correlated with salinity; salinity was very low across the entire estuary on final sampling event, following heavy rainfall in the catchment (Figure 2c). Therefore, salinity values were not included in subsequent analyses. Whilst the species richness of assemblages and the abundance of harvestable fish was lower during this final sampling, values were still significantly higher on oyster reefs than at control sites for three of the four sampling periods (Figure 2). Differences in assemblage composition, species richness, and fish abundance between oyster reefs and control sites were primarily driven by variation in the abundance of yellowfin bream, moose perch (*Lutjanus russelli*; Lutjanidae), and southern herring, which were all more abundant and occurred more often on reefs than at control sites (Figure 3, Table 2, Supplementary Table S2).

The presence or absence of seagrass near oyster reefs did not affect species richness or modify the abundance of harvestable fishes on oyster reefs (Figure 4a and b, Table 3, Supplementary

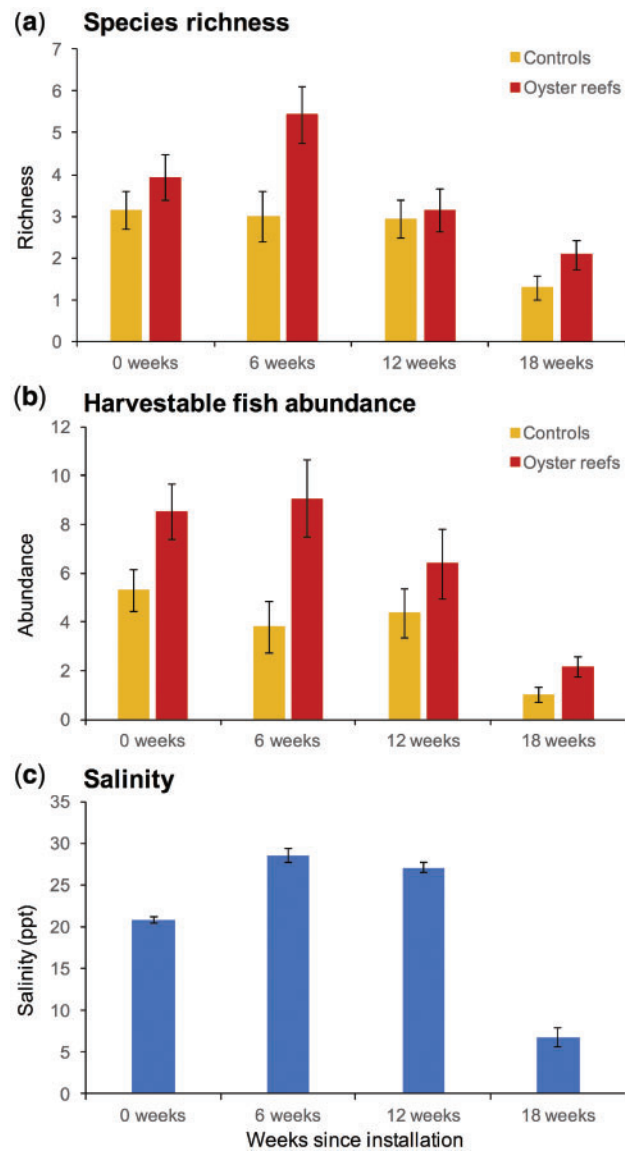


Figure 2. Average (\pm s.e.) (a) species richness, (b) harvestable fish abundance, and (c) salinity values for all sites between controls and oyster reefs across the four sampling periods.

Table S2). Despite there being no interaction between treatment and seagrass presence at the assemblage level, yellowfin bream were more abundant at oyster reefs than control sites, but only when oyster reefs were near seagrass (Figure 4c, Table 3). Moses perch were more abundant on oyster reefs than at control sites, but were also common at both oyster reefs and control sites near seagrass (Figure 4d, Table 3). Southern herring were more abundant on oyster reefs than at control sites, and were not affected by the presence or absence of seagrass nearby (Figure 4e, Table 3).

Discussion

Habitats are often restored in coastal seascapes to enhance fish abundance and diversity, or to improve the fisheries values of estuaries (Coen and Luckenbach, 2000; Heck et al., 2003; Grabowski and Peterson, 2007). Restoration sites that are strategically placed within heterogeneous estuarine seascapes might be

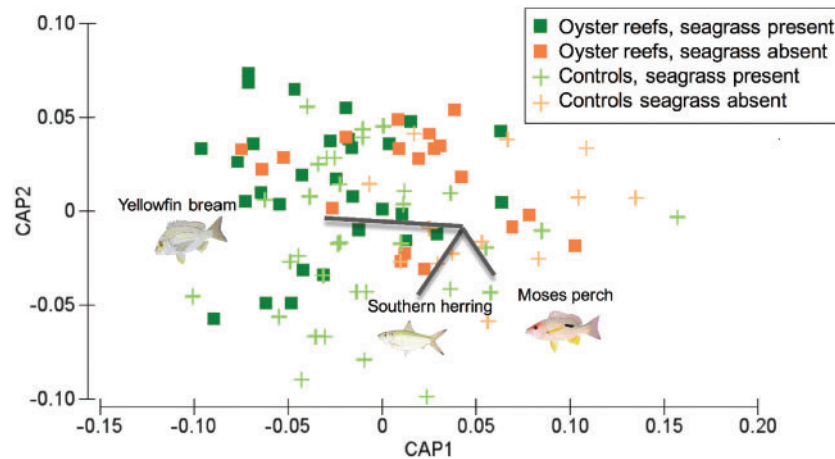


Figure 3. Canonical analysis of principal components visualizing fish assemblages around restored oyster reefs in the Noosa River, Australia for differences across treatment, and with seagrass present or absent nearby. Vector overlays are Pearson correlations of potential indicator species from Dufrene–Legendre indicator species analysis.

Table 1. Permutational multivariate analysis of variance output testing assemblage level differences between treatment (fixed factor, two levels; oyster reefs or control sites) and seagrass presence nearby (fixed factor, two levels; seagrass absent and seagrass present nearby), corrected for sampling period (covariate).

Source	df	MS	Pseudo-F	<i>p</i>
Sampling period	1	10900	3.4	0.001
Treatment (Tr)	1	7771.4	2.5	0.009
Seagrass presence (Se)	1	6963.7	2.2	0.018
Tr × Se	1	2527.6	0.8	0.627
Res	107	3164.4		
Total	111			

p values in bold significant at $\alpha = 0.05$.

Table 2. Indicator species analysis testing for the species that contribute most toward differences in assemblages between oyster reefs and control sites.

Species	Group	Indicator value	<i>p</i>
Yellowfin bream	Oyster reefs	0.56	0.001
Moses perch	Oyster reefs	0.21	0.013
Southern herring	Oyster reefs	0.17	0.015

“Group” indicates the level of factor “Treatment” for which that species is a significant indicator.

more effective for these purposes, but the trajectories of these relationships, and consistencies in patterns across different types of seascapes requires further investigation (Gilby *et al.*, 2018c). In this study, we found that the fish assemblages of restored oyster reefs were more diverse and contained a higher abundance of harvestable fish than control sites. Our results also show that the effects of restoration for some species, including taxa that were a target for oyster reef restoration, can be modified by the seascape context in which habitats are restored. The presence or absence of seagrass nearby affected the abundance of a key harvestable fish species (i.e. yellowfin bream) on oyster reefs, but not the composition of fish assemblages, fish species richness, or the total abundance of harvestable fishes. Whilst these findings are at this stage

likely only responses of fish to the oyster reef structures themselves, as opposed to any benefits of significant oyster growth, these findings suggest that the ecological benefits of restoration for both fish assemblages, and species that are harvested by fishers, might be improved by optimizing the seascape context in which restoration takes place.

Oyster reefs are a globally threatened ecosystem (Beck *et al.*, 2011) providing significant value to surrounding fish assemblages and associated fisheries (Grabowski *et al.*, 2012; Humphries and La Peyre, 2015). Consequently, the restoration of fish biomass and/or biodiversity is often a key goal of oyster reef restoration projects (Peterson *et al.*, 2003; Grabowski and Peterson, 2007; Gilby *et al.*, 2018c). In this study, we report positive effects of oyster reef restoration on both fish abundance and diversity, even early in the growth of these restored reefs. These results concur with the findings of several studies (e.g. Harding and Mann, 1999; Grabowski *et al.*, 2005; La Peyre *et al.*, 2014) and two seminal review papers (Peterson *et al.*, 2003; zu Ermgassen *et al.*, 2016), which conclude that oyster reef restoration can augment fish diversity and abundance in coastal seascapes. Most studies have, however, been conducted in marsh and seagrass dominated seascapes in the northern hemisphere (Gilby *et al.*, 2018c). Our results show, for the first time, that oyster reef restoration can also benefit fish assemblages in mangrove-dominated seascapes. This is an important finding because the scale of oyster reef restoration is increasing globally, as is the willingness of countries to invest in oyster restoration (Gillies *et al.*, 2015b), and we show that the restoration of oyster reefs can have positive effects on fish abundance and diversity in multiple coastal seascapes, even at early stages of reef development. The restored oyster reefs that we studied were relatively small and young, but our results still demonstrate the potential for this sort of seascape-scale restoration to enhance fish assemblages across estuaries.

The restoration of oyster reefs had strong, consistent, and positive effects on both fish species richness and the total abundance of harvestable fishes. The responses of individual species were, however, more nuanced and depended on the seascape context in which oyster reefs were placed. The presence of seagrass nearby to survey sites modified the abundance of a key species on oyster reefs that are targeted in local fisheries (i.e. yellowfin bream), and

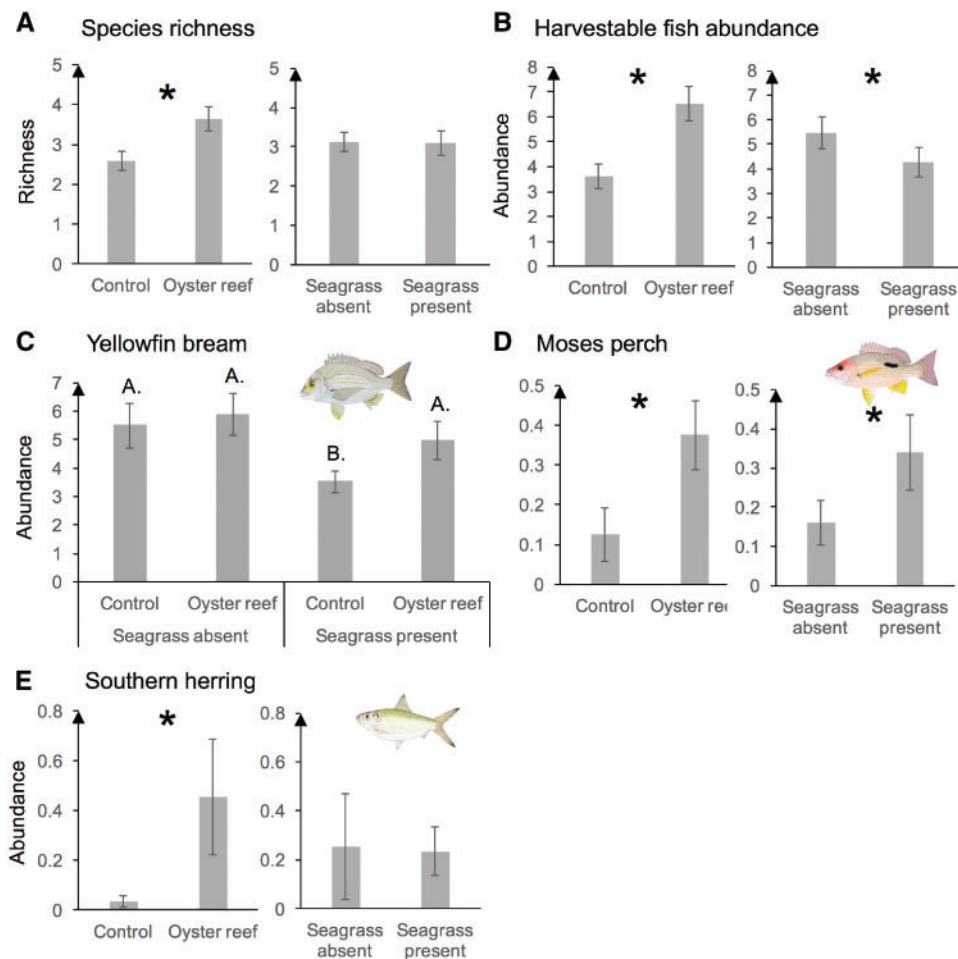


Figure 4. Average (\pm s.e.) of (a) species richness and (b) harvestable fish abundance, and the abundance of significant indicator species (c–e) at restored oyster reefs and control sites, and with seagrass present or absent nearby (i.e. within 500 m). Plots reflect the results of GLM analyses (Table 3). Stars above columns indicate significant differences between levels of that factor using Tukey pairwise comparisons. Lettering on panel C indicates significant differences calculated using Tukey pairwise comparisons on the interaction between treatment and seagrass presence.

another harvested species (i.e. Moses perch) more broadly across the entire seascape (Webley *et al.*, 2015; Olds *et al.*, 2018b). This finding suggests that ecological benefits of oyster reef restoration can depend on the seascape context in which oyster reefs are placed. Placing oyster reefs in locations with different seascape characteristics might, therefore, improve the wider capacity of restoration projects to achieve multiple, or different, fisheries enhancement goals (sensu Gilby *et al.*, 2018c). For example, reefs can be placed in multiple contexts to achieve goals for both erosion control and fisheries benefits, or placed in different contexts to benefit multiple species of fish. This is a strategic approach to habitat restoration, which would require explicit goals, and careful consideration of how restoration performance (including to the level of individual fish species) might be shaped by the spatial features of seascapes (Ehrenfeld, 2000; Hallett *et al.*, 2013; Guerrero *et al.*, 2017; Gilby *et al.*, 2018a).

The responses of yellowfin bream and Moses perch to oyster reef restoration and the presence or absence of seagrass nearby indicate the nuanced responses of individual species to restoration in different contexts. In this sense, the effects from seagrass operated in asymmetrical ways, which corresponded to differences in

the biology and ecology of these species. Oyster reefs that were close to seagrass were more effective for augmenting the abundance of yellowfin bream, which are generalist zoobenthivores that congregate around structurally complex habitats, including oyster reefs and seagrass meadows, to feed on oyster spat, other epibenthic invertebrates and fish (Brook *et al.*, 2018; Olds *et al.*, 2018a). Yellowfin bream recruit to seagrass meadows as juveniles and move to other structurally complex habitats as adults where they are targeted in commercial and recreational fisheries (Olds *et al.*, 2012; Webley *et al.*, 2015), and are therefore an important species for which oyster restoration in the region seeks to enhance. Oyster reefs were effective in enhancing the abundance of Moses perch relative to controls, but these fish were also common at all sites near seagrass. Moses perch are generalist piscivores, which reside in structurally complex mangrove forests, oyster reefs, and seagrass meadows in the subtropical estuaries of eastern Australia (Olds *et al.*, 2012; Martin *et al.*, 2018). They recruit into estuaries as juveniles and move to offshore reefs as adults where they are important targets for fisheries in the region (Webley *et al.*, 2015). Southern herring are seasonal visitors to the estuaries of region, and aggregate around high relief habitats, including

Table 3. Generalized linear model results testing for correlations between key attributes of fish assemblages and significant indicator species (see Table 1) with treatment (fixed factor, two levels; oyster reefs or control sites) and seagrass presence nearby (fixed factor, two levels; seagrass absent and seagrass present nearby), corrected for sampling period (covariate).

Source	d.f.	χ^2	<i>p</i>
General fish assemblage indicators			
<i>Species richness</i>			
Sampling period	1	20.61	<0.001
Treatment (Tr)	1	9.92	<0.001
Seagrass presence (Se)	1	0.1	0.74
Tr × Se	1	0.02	0.87
<i>Harvestable fish abundance</i>			
Sampling period	1	83.03	<0.001
Treatment (Tr)	1	44.22	<0.001
Seagrass presence (Se)	1	9.87	<0.001
Tr × Se	1	0.01	0.91
Indicators of oyster reef assemblages			
<i>Yellowfin bream</i>			
Sampling period	1	75.71	<0.001
Treatment (Tr)	1	31.74	<0.001
Seagrass presence (Se)	1	4.53	0.03
Tr × Se	1	3.67	0.05
<i>Moses perch</i>			
Sampling period	1	0.11	0.74
Treatment (Tr)	1	8.19	<0.01
Seagrass presence (Se)	1	4.73	0.03
Tr × Se	1	1.93	0.16
<i>Southern herring</i>			
Sampling period	1	0.27	0.61
Treatment (Tr)	1	9.93	<0.01
Seagrass presence (Se)	1	0.05	0.81
Tr × Se	1	1.46	0.22

p values in bold significant at $\alpha = 0.05$.

reefs and artificial structures, to shelter from predators and feed on a rich supply of plankton (Waltham and Connolly, 2013). They are also important prey for larger predatory fishes (including both yellowfin bream and moose perch) in the study area (Miller and Skilleter, 2006; Olds *et al.*, 2018b). These findings demonstrate that the restoration of oyster reef structures can improve both the habitat and nursery values of estuarine seascapes, with functional effects on planktivores, zoobenthivores, and piscivores that are suggestive of wider benefits for coastal food-webs. Determining whether these effects continue as the reefs mature, and the availability of different sorts of prey changes (i.e. oysters and other invertebrates will increase in density, and provide other feeding opportunities), is an important next step in quantifying the effects of seascape context on these reefs.

The overall quality of estuarine ecosystems for fish, especially as fish nurseries, is contingent on the presence of a multitude of habitats within a heterogeneous seascape (Nagelkerken *et al.*, 2015; Whitfield, 2017). Whilst the effects of seagrass near oyster reefs were not always positive in this study, the presence of seagrass in estuaries can promote fish abundance and richness, and the fisheries values of estuaries in the region (Pittman *et al.*, 2004; Skilleter *et al.*, 2017; Gilby *et al.*, 2018b). The effects of seagrass on the fish assemblages of adjacent structural complex habitats often occur over a scale of 500 m (Olds *et al.*, 2012; Gilby *et al.*, 2018b). The results of this study, however, suggest seagrass can

exert both positive and neutral effects on the fish species congregating around oyster reefs. The spatial scale over which seagrass influences fish assemblages on oyster reefs will, therefore, be an important consideration for further research. The oyster reefs we studied were, however, only rather small components of the broader seascape in which they were placed. It will, therefore, be important to ascertain whether, and how, the seascape effects we report scale with changes in the relative size of restored oyster reefs. There are multiple other oyster reef restoration projects in Australia, varying in terms of both the size of oyster reefs being restored (from metres to hectares) and the proximity of seagrass beds (Australian Shellfish Reef Restoration Network, 2018), which could be used to test this hypothesis.

In this study, we found that restored oyster reefs in the Noosa River estuary contain fish assemblages that are more diverse, and contain more harvestable fish than at nearby control sites. Our results indicated species-specific effects of seascape positioning on fish assemblages that must be considered when deciding on the location of future restoration efforts. Here, reefs can be placed in specific contexts to target the enhancement individual fish species, or in multiple contexts to benefit two or more species that have different habitat requirements. Whilst the patterns we observed in this study are simply an early indication of the success of the oyster restoration efforts for fish in this estuary, they are likely a response only to the addition of complex structure to previously unvegetated sediments, and so it is important to continue to track these patterns in fish assemblages as the reefs mature and grow. In any case, our results are a positive indication of the potential for restored oyster reefs to augment fish and fisheries values in the Noosa River and beyond. If, given the young age of these reefs, fish surveyed in this study were only responding to the actual structure of the reefs themselves, as opposed to any strong benefits associated with food provision from the reefs as the reefs grow, then we could hypothesize that these patterns in augmentation of richness and harvestable fish will simply increase further over time. This, however, will require further investigation. Our results have consequences for the placement of structurally complex habitats in estuaries more broadly. By strategically placing structures in coastal ecosystems to enhance the specific components of fish assemblages that we seek to augment or centralize, we might more efficiently reach our conservation, restoration, or fisheries-related goals.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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Author contributions

All authors designed and conceived the study. BLG and NLO collected the data. BLG ran the analyses and wrote the first draft. All authors contributed to the interpretation of the results and drafting the manuscript.

References

- Australian Shellfish Reef Restoration Network. 2018. Australian Shellfish Reef Restoration Network. <https://www.shellfishrestoration.org.au/> (last accessed 20 June 2018).
- Beck, M. W., Brumbaugh, R. D., Airoidi, L., Carranza, A., Coen, L. D., Crawford, C., Defeo, O. *et al.* 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience*, 61: 107–116.
- Becker, A., Taylor, M. D., Folpp, H., and Lowry, M. B. 2018. Managing the development of artificial reef systems: the need for quantitative goals. *Fish and Fisheries*, 19: 740–752.
- Brook, T. W., Gilby, B. L., Olds, A., Connolly, R. M., Henderson, C. J., and Schlacher, T. A. 2018. The effects of shoreline armouring on estuarine fish are contingent upon the broader urbanisation context. *Marine Ecology Progress Series*, 605: 195–206.
- Coen, L. D., Brumbaugh, D. R., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P. *et al.* 2007. Ecosystem services related to oyster restoration. *Marine Ecology Progress Series*, 341: 303–307.
- Coen, L. D., and Luckenbach, M. W. 2000. Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? *Ecological Engineering*, 15: 323–343.
- Diggles, B. K. 2013. Historical epidemiology indicates water quality decline drives loss of oyster (*Saccostrea glomerata*) reefs in Moreton Bay, Australia. *New Zealand Journal of Marine and Freshwater Research*, 47: 561–581.
- Dufrene, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.
- Ehrenfeld, J. G. 2000. Defining the limits of restoration: the need for realistic goals. *Restoration Ecology*, 8: 2–9.
- Froese, R., and Pauly, D. 2018. Fishbase. <http://www.fishbase.org/> (last accessed 15 July 2018).
- Geraldi, N. R., Powers, S. P., Heck, K. L., and Cebrian, J. 2009. Can habitat restoration be redundant? Response of mobile fishes and crustaceans to oyster reef restoration in marsh tidal creeks. *Marine Ecology Progress Series*, 389: 171–180.
- Gilby, B. L., Olds, A. D., Connolly, R. M., Henderson, C. J., and Schlacher, T. A. 2018. Spatial restoration ecology: placing restoration in a landscape context. *Bioscience*, 68: 1007–1019.
- Gilby, B. L., Olds, A. D., Connolly, R. M., Maxwell, P. S., Henderson, C. J., and Schlacher, T. A. 2018. Seagrass meadows shape fish assemblages across estuarine seascapes. *Marine Ecology Progress Series*, 588: 179–189.
- Gilby, B. L., Olds, A. D., Connolly, R. M., Yabsley, N. A., Maxwell, P. S., Tibbetts, I. R., Schoeman, D. S. *et al.* 2017. Umbrellas can work under water: using threatened species as indicator and management surrogates can improve coastal conservation. *Estuarine Coastal and Shelf Science*, 199: 132–140.
- Gilby, B. L., Olds, A. D., Peterson, C. H., Connolly, R. M., Voss, C. M., Bishop, M. J., Elliott, M. *et al.* 2018. Maximising the benefits of oyster reef restoration for finfish and their fisheries. *Fish and Fisheries*, 19: 931–947.
- Gillies, C. L., Creighton, C., and McLeod, I. M. 2015a. Shellfish reef habitats: a synopsis to underpin the repair and conservation of Australia's environmentally, socially and economically important bays and estuaries. Report to the National Environmental Science Programme, Marine Biodiversity Hub. 68 pp.
- Gillies, C. L., Fitzsimons, J. A., Branigan, S., Hale, L., Hancock, B., Creighton, C., Alleway, H. *et al.* 2015b. Scaling-up marine restoration efforts in Australia. *Ecological Management & Restoration*, 16: 84–85.
- Grabowski, J. H., Brumbaugh, R. D., Conrad, R. F., Keeler, A. G., Opaluch, J. J., Peterson, C. H., Piehler, M. F. *et al.* 2012. Economic valuation of ecosystem services provided by oyster reefs. *Bioscience*, 62: 900–909.
- Grabowski, J. H., Hughes, A. R., Kimbro, D. L., and Dolan, M. A. 2005. How habitat setting influences restored oyster reef communities. *Ecology*, 86: 1926–1935.
- Grabowski, J. H., and Peterson, C. H. 2007. Restoring oyster reefs to recover ecosystem services. *In Ecosystem Engineers*, pp. 281–298. Ed. by K. Cuddington, J. E. Byers, W. G. Wilson, and A. Hastings. Elsevier Academic Press, Burlington, MA.
- Grober-Dunsmore, R., Pittman, S. J., Caldwell, C., Kendall, M. S., and Frazer, T. K. 2009. A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. *In Ecological Connectivity among Tropical Coastal Ecosystems*, pp. 493–530. Ed. by I. Nagelkerken. Springer, Netherlands.
- Guerrero, A. M., Shoo, L., Iacona, G., Standish, R. J., Catterall, C. P., Rumpff, L., de Bie, K. *et al.* 2017. Using structured decision-making to set restoration objectives when multiple values and preferences exist. *Restoration Ecology*, 25: 858–865.
- Hallett, L. M., Diver, S., Eitzel, M. V., Olson, J. J., Ramage, B. S., Sardinas, H., Statman-Weil, Z. *et al.* 2013. Do we practice what we preach? Goal setting for ecological restoration. *Restoration Ecology*, 21: 312–319.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F. *et al.* 2008. A global map of human impact on marine ecosystems. *Science*, 319: 948–952.
- Harding, J. M., and Mann, R. 1999. Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bulletin of Marine Science*, 65: 289–299.
- Heck, K. L., Hays, G., and Orth, R. J. 2003. Critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series*, 253: 123–136.
- Henderson, C. J., Stevens, T., Gilby, B. L., and Lee, S. Y. 2017. Spatial conservation of large mobile elasmobranchs requires an understanding of spatio-temporal seascape utilisation. *ICES Journal of Marine Science*, 72: 553–561.
- Hidalgo, M., Secor, D. H., and Browman, H. I. 2016. Observing and managing seascapes: linking synoptic oceanography, ecological processes, and geospatial modelling. *ICES Journal of Marine Science*, 73: 1825–1830.
- Humphries, A. T., and La Peyre, M. K. 2015. Oyster reef restoration supports increased nekton biomass and potential commercial fishery value. *PeerJ*, 3: e1111.
- Huntington, B. E., and Lirman, D. 2012. Species-area relationships in coral communities: evaluating mechanisms for a commonly observed pattern. *Coral Reefs*, 31: 929–938.
- Jones, M. E., and Davidson, N. 2016. Applying an animal-centric approach to improve ecological restoration. *Restoration Ecology*, 24: 836–842.
- La Peyre, M. K., Humphries, A. T., Casas, S. M., and La Peyre, J. F. 2014. Temporal variation in development of ecosystem services from oyster reef restoration. *Ecological Engineering*, 63: 34–44.
- Lenihan, H. S. 1999. Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. *Ecological Monographs*, 69: 251–275.
- Martin, T. S. H., Olds, A. D., Olalde, A. B. H., Berkström, C., Gilby, B. L., Schlacher, T. A., Butler, I. R. *et al.* 2018. Habitat proximity exerts opposing effects on key ecological functions. *Landscape Ecology*, 33: 1273–1286.
- Micheli, F., and Peterson, C. H. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology*, 13: 869–881.

- Miller, M. W. 2002. Using ecological processes to advance artificial reef goals. *ICES Journal of Marine Science*, 59: S27–S31.
- Miller, S. J., and Skilleter, G. A. 2006. Temporal variation in habitat use by nekton in a subtropical estuarine system. *Journal of Experimental Marine Biology and Ecology*, 337: 82–95.
- Mumby, P. J., Edwards, A. J., Arias-Gonzalez, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczyńska, M. I. *et al.* 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, 427: 533–536.
- Nagelkerken, I., Sheaves, M., Baker, R., and Connolly, R. M. 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish and Fisheries*, 16: 362–371.
- Olds, A. D., Albert, S., Maxwell, P. S., Pitt, K. A., and Connolly, R. M. 2013. Mangrove-reef connectivity promotes the effectiveness of marine reserves across the western Pacific. *Global Ecology and Biogeography*, 22: 1040–1049.
- Olds, A. D., Connolly, R. M., Pitt, K. A., and Maxwell, P. S. 2012. Primacy of seascape connectivity effects in structuring coral reef fish assemblages. *Marine Ecology Progress Series*, 462: 191–203.
- Olds, A. D., Connolly, R. M., Pitt, K. A., Pittman, S. J., Maxwell, P. S., Huijbers, C. M., Moore, B. R. *et al.* 2016. Quantifying the conservation value of seascape connectivity: a global synthesis. *Global Ecology and Biogeography*, 25: 3–15.
- Olds, A. D., Frohloff, B. A., Gilby, B. L., Connolly, R. M., Yabsley, N. A., Maxwell, P. S., Henderson, C. J. *et al.* 2018a. Urbanisation supplements ecosystem functioning in disturbed estuaries. *Ecography*, 41: 2104–2113.
- Olds, A. D., Gilby, B. L., Connolly, R. M., Tibbetts, I. R., Henderson, C. J., Stevens, T. F., Thackwray, S. K. *et al.* 2018b. Fishes of Moreton Bay: ecology, human impacts and conservation. *In* Moreton Bay Quandamooka and Catchment: Past, present & Future. Ed. by I. R. Tibbetts, P. C. Rothlisberg, D. T. Neil, T. A. Homburg, D. T. Brewer, and A. H. Arthington. University of Queensland Press, Brisbane.
- Peterson, C. H., Grabowski, J. H., and Powers, S. P. 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. *Marine Ecology Progress Series*, 264: 249–264.
- Pittman, S. J. 2018. *Seascape Ecology*. Wiley Blackwell, Oxford.
- Pittman, S. J., McAlpine, C. A., and Pittman, K. M. 2004. Linking fish and prawns to their environment: a hierarchical landscape approach. *Marine Ecology Progress Series*, 283: 233–254.
- R Core Team. 2018. R: A language and environment for statistical computing. <http://www.r-project.org/> (last accessed 5 September 2018).
- Roni, P., Beechie, T. J., Bilby, R. E., Leonetti, F. E., Pollock, M. M., and Pess, G. R. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. *North American Journal of Fisheries Management*, 22: 1–20.
- Rudershausen, P. J., Merrell, J. H., and Buckel, J. A. 2018. Fragmentation of habitat affects communities and movement of nekton in salt marsh tidal creeks. *Marine Ecology Progress Series*, 586: 57–72.
- Rudnick, D., Ryan, S. J., Beier, P., Cushman, S. A., Dieffenbach, F., Epps, C., Gerber, L. R. *et al.* 2012. The role of landscape connectivity in planning and implementing conservation and restoration priorities. *Issues in Ecology*, 16: 1–20.
- Sheaves, M., Johnston, R., and Baker, R. 2016. Use of mangroves by fish: new insights from in-forest videos. *Marine Ecology Progress Series*, 549: 167–182.
- Skilleter, G. A., Loneragan, N. R., Olds, A., Zharikov, Y., and Cameron, B. 2017. Connectivity between seagrass and mangroves influences nekton assemblages using nearshore habitats. *Marine Ecology Progress Series*, 573: 25–43.
- Sun, P., Liu, X. Z., Tang, Y. L., Cheng, W. Z., Sun, R. L., Wang, X. X., Wan, R. *et al.* 2017. The bio-economic effects of artificial reefs: mixed evidence from Shandong, China. *ICES Journal of Marine Science*, 74: 2239–2248.
- Thurstan, R. H. 2016. *Historical Ecology of the Noosa Estuary Fisheries*. University of Queensland, Australia.
- Torio, D. D., and Chmura, G. L. 2015. Impacts of sea level rise on marsh as fish habitat. *Estuaries and Coasts*, 38: 1288–1303.
- Waltham, N. J., and Connolly, R. M. 2013. Artificial tidal lakes: built for humans, home for fish. *Ecological Engineering*, 60: 414–420.
- Webley, J., McInnes, K., Teixeira, D., Lawson, A., and Quinn, R. 2015. *Statewide Recreational Fishing Survey 2013–14*. State of Queensland, Brisbane, Australia.
- Weeks, R. 2017. Incorporating seascape connectivity in conservation prioritisation. *PLoS One*, 12: e0182396.
- Whitfield, A. K. 2017. The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries*, 27: 75–110.
- Ziegler, S. L., Grabowski, J. H., Baillie, C. J., and Fodrie, F. J. 2018. Effects of landscape setting on oyster reef structure and function largely persist more than a decade post-restoration. *Restoration Ecology*, 26: 933–942.
- zu Ermgassen, P. S. E., Grabowski, J. H., Gair, J. R., and Powers, S. P. 2016. Quantifying fish and mobile invertebrate production from a threatened nursery habitat. *Journal of Applied Ecology*, 53: 596–606.

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