Bringing fish life back to Noosa: restoring lost oyster reef habitats in the Noosa Biosphere

Final Report

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Summary

Ecological restoration facilitates the recovery of ecosystems and can augment or re-establish animal populations both at restoration sites and across landscapes more broadly. With increasing recognition of the damage that human activities have on ecosystems, ecological restoration activities are increasing in both prevalence and scale across marine, freshwater and terrestrial ecosystems globally, and often have specific goals around enhancing both lost or degraded ecosystems, and the animal populations that those ecosystems support. Despite this, there has been relatively few studies that have quantified the effects of ecological restoration on multiple attributes of restored ecosystems, and then used this information to optimise the design and placement of subsequent efforts.

Oyster reefs, a biogenic coastal ecosystem providing habitat for a diversity of estuarine species, are significantly threatened by human activities. Globally, up to 85% of oyster reefs have been lost, and some regions have experienced up to 96% loss due to the combined effects of disease, declining water quality, and overharvesting. This loss of structurally complex oyster reefs from coastal and estuarine ecosystems has been hypothesised as a significant contributor towards fish diversity and fisheries declines in many coastal systems. Consequently, oyster reef restoration has increased in prevalence globally. Whilst these efforts have increasingly focused on enhancing the abundance and diversity of fish and fisheries at restoration sites, few studies have quantified the effects of oyster restoration on fish in regions outside of North America, on the ecological functions that fish provide around restored reefs, or the degree to which the benefits of oyster restoration expand across entire estuaries. Consequently, this sort of information has rarely been used to optimise oyster reef restoration plans and monitoring programs.

The Noosa River oyster reef restoration trial is the first shellfish restoration project installed in Queensland, Australia. The project sought to restore the structurally complex oyster reefs that were once abundant in the Noosa River, thereby enhancing habitat availability and complexity for fish species of commercial and recreational significance, and subsequently the important ecological functions that these species perform. We installed and surveyed 14 oyster reef restoration sites in the Noosa River estuary, that were placed to encompass differences in seascape connectivity and proximity to nearby mangroves, seagrasses, urban structures and the estuary mouth. These reefs therefore provide the optimal study design to test for the effects of spatial placement and design of oyster restoration actions on fish, fisheries and ecological functions. This report has six key aims. We set the global context for the oyster reef restoration project in Noosa by (1) identifying the degree to

which landscape context is considered in the selection of restoration sites across all environmental realms globally; and (2) identifying gaps in the global understanding of the effectiveness of oyster restoration fin fish, and synthesise current research to optimise future outcomes. We then used the oyster restoration sites in the Noosa River estuary to; (3) identify whether the seascape context of restored oyster reefs (especially seascape connectivity with seagrasses and mangroves) modifies the degree to which they augment fish abundance and diversity; (4) determine the effects of oyster reef restoration on the rate and distribution of the key ecological function of predation at and around the restored oyster reefs; (5) quantify how restored oyster reefs influence the distribution and abundance of fish across the estuary (i.e. beyond the reefs themselves) ; and (6) use spatial modelling techniques to optimise the placement of subsequent oyster reef restoration efforts in the river for oyster growth, fish, fisheries and ecological functioning by incorporating all information gathered in chapters 3, 4 and 5, and our 2018 annual monitoring report.

To identify the degree to which landscape context (i.e. the size, shape, and spatial arrangement of ecosystems) is considered when selecting restoration sites globally (see **Chapter 2**), we reviewed restoration projects from the global primary literature. Fewer than one in eight restoration projects considered landscape context in the selection of restoration sites (11% of 472 projects). This figure was remarkably similar across terrestrial (10% of 243 projects), marine (13% of 89) and freshwater (13% of 164) ecosystems. Of the 54 restoration projects that considered landscape context in site selection, just over half (56%) reported that animal populations were larger or more diverse than in control areas. These results indicate that more tightly integrating concepts from spatial ecology and systematic conservation planning into restoration practice, such as the consideration of the landscape context, could improve the design, optimise placement and enhance the ecological effectiveness of restoration projects in all ecosystems.

To identify gaps in the global understanding of the effectiveness of oyster restoration for finfish and synthesise current research to optimise future outcomes (see **Chapter 3**), we reviewed the global literature of oyster reef restoration for finfish. Global declines in oyster reefs have resulted in reduced habitat heterogeneity, extent, and quality for some coastal finfish, potentially reducing fish populations and catches. Although, it is well established that habitat restoration results in higher finfish biomass and diversity where oyster reefs replace bare sand or mud substrates, the principles of habitat quality, ecological connectivity and broader ecosystem management are poorly integrated within oyster reef restoration ecology. The inclusion of such principles could be instructive in enhancing the benefits of projects on fish populations throughout estuarine seascapes and increase

stakeholder engagement and cost-effectiveness. This review presents a framework for projects seeking to restore both oyster reef habitat and finfish communities.

To identify whether the seascape context of individual reefs modifies the degree to which they augment fish abundance and diversity (see **Chapter 4**), we used baited remote underwater video stations (BRUVS) to survey fish assemblages at the 14-oyster reef and at control sites. The seascape context of coastal ecosystems plays a pivotal role in shaping patterns in fish recruitment, abundance and diversity, however, there is a paucity of information regarding the trajectories in which these relationships follow whilst structuring the recruitment of fish assemblages to restored habitats. Our results found that 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 composition of fish assemblages, species richness or the total abundance of harvestable fishes overall. Our findings highlight the importance of considering species-specific patterns in seascape utilisation when selecting restoration sites and setting restoration goals and suggest that the effects of restoration on fish assemblages might be optimised by focussing efforts in prime positions in coastal seascapes.

To determine the effects of oyster reef restoration on the rate and distribution of predation (see **Chapter 5**), we used squidpop assays (dried squid tethered using fishing line) to measure predation rates and survey predators at six restored oyster reefs and nearby control sites. Ecological functions are important in maintaining, and enhancing, coastal ecosystems. Restoring coastal habitats enhances these functions, but few studies have explicitly quantified the degree and spatial extent of these modifications. It has been well established that the rate and distribution of ecological functions is modified by how species respond to the composition of landscapes, however, it is not clear where restoration sites should be located in heterogeneous landscapes to maximise outcomes for ecosystem functions. 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 farther from vegetation. These 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.

To quantify how the restored oyster reefs modify the distribution and abundance of fish across the estuary (i.e. beyond the reefs themselves) (see **Chapter 6**), we monitored fish at video monitoring sites in a 200m grid across the entire lower Noosa estuary both before and after the installation of oyster reefs. Quantifying the effects that restoration has on the spatial distribution of animals both at restoration sites, and across landscapes is an important focus for restoration ecologists. As the scale of restoration increases across all environmental realms globally, the capacity for the effects of restoration on animal populations, and therefore some of the benefits of restoration, to expand across landscapes increases. We found that fish assemblages varied significantly across temporal scales in the Noosa River, and that there was a significant change in the assemblage composition and distribution of fish in the river following the installation of the oyster reefs. These effects proliferated to effects on species richness and harvested fish abundance, which were both higher at greater distances from the restored reefs following reef installation. These findings run counter to the effects found in other studies in this report that found a significantly higher abundance of fish occurring at reefs and significantly higher rates of key ecological functions. Changes in environmental conditions across the estuary (especially freshwater runoff from catchments) might have hampered the reefs in reaching their ecological potential. These results have several key consequences for the designs of subsequent restoration actions in the Noosa River estuary. Firstly, ensuring that the effects of restoration expand significantly across the entire seascape of the Noosa River (i.e. they increase the overall carrying capacity of the system more broadly) will require larger restoration sites across the entire Noosa seascape to 1) enhance the augmentation effects of the reefs and 2) spread biomass across the estuary. Further, a more thorough consideration of the effects of seascape connectivity with deeper channels, and a long-term commitment to thorough monitoring and evaluation of the effects of the oyster reefs across the entire estuary is required.

To optimise the placement of oyster reef restoration effort for oyster growth, fish, fisheries and ecological functioning (see **Chapter 7**), we used distribution models to identify hotspots in the Noosa River estuary where subsequent restoration efforts would maximise overall benefits. Oyster reefs can be successfully restored throughout the entire Noosa River estuary because oysters successfully settled and grew rapidly at every trial site. Restoration sites also had higher fish species richness, harvestable fish abundance, and rates of key ecological functions (predation and carrion scavenging) than at nearby control sites. However, the growth of oyster reefs (in terms of oyster density and size) was most correlated with the proximity of restoration sites to urbanised shorelines (i.e. sources of oyster larvae) and the estuary mouth (i.e. growth along the salinity gradient), and the area of

mangroves around the site (i.e. source of oyster larvae and juvenile oyster predators). Conversely, the abundance and diversity of fish, and the rates of predation and scavenging at reefs tended to be most related to their isolation from seagrasses and mangroves. This resulted in different metrics driving the scale and distribution of restoration benefits for fishes and functions and meant that the area that maximised outcomes for all of oyster reef growth, fishes, and functions was significantly smaller than the total area that could be restored. Hotspots where oyster restoration would result in the greatest possible outcomes across all of the restoration targets considered occurred near the estuary mouth, on the northern bank of the estuary approximately 2km from the estuary mouth, and in a large lake-like inlet in the far west of the estuary (known locally as Lake Doonella). With the scale of restoration actions increasing across landscapes globally, using information regarding the distribution of likely restoration benefits in a quantitative manner can help to reduce the financial and social costs of restoration, whilst maximising social, economic, and environmental outcomes.

Our findings highlight the importance of two key concepts in optimizing the outcomes of restoration for both ecosystems and the animals that inhabit them;

1. Restoration practitioners should more effectively consider the pivotal role of landscape context and habitat connectivity on the effectiveness of restoration actions for animals, and
2. Restoration practitioners should more thoroughly adopt the principles of systematic conservation planning in the placement and design of restoration actions; especially for the setting of quantitative goals and in the design of subsequent monitoring programs.

Our findings show that ecological restoration of oyster reefs to the Noosa River resulted in;

1. Oyster reef structures that attracted and grew oysters that will eventually develop into self-sustaining oyster reefs,
2. An augmentation of fish species richness (1.4 times), harvestable fish abundance (1.8 times) and the ecological functions of predation (2 times) and scavenging (1.5 times) at the restored reefs relative to nearby controls, and
3. Some effect of the oyster restoration efforts on the distribution of ecological functions and the abundance of fish across the Noosa River estuary more broadly.

In this sense, the Noosa River oyster restoration project has set the standard globally for quantifying, and subsequently optimising restoration actions across landscapes for the purposes of augmenting fish, fisheries, fish biodiversity and ecological functioning.

Chapter 1

Introduction and Background to the Noosa River Oyster Reef Restoration Trial

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Oyster reefs are vital fish habitats

Oyster reefs are biogenic structures where subsequent generations of larval oysters settle on older generations, and grow progressively outwards. Occurring predominantly in the lower intertidal throughout south-east Queensland, oyster reefs provide structurally complex and food-rich habitat for a diversity of fish species, including many species which are of commercial and/or recreational value (Diggles 2013) (Figure 1).

The importance of oyster reefs as a habitat type is recognised by the Convention on Wetlands of International Importance (The Ramsar Convention – habitat type 'Ga') (Kasoar et al. 2015). Oyster reefs provide important habitat for estuarine fishes through two key mechanisms: 1) by offering structurally complex structures within estuaries that fish use as habitat for resting, seeking refuge from predators, and spawning; and 2) by delivering a diversity of food resources for fishes, including planktonic prey, smaller fishes, and the oysters themselves, which occur in higher concentration in and around the reefs (Harding and Mann 2001). As a consequence, just 10m^2 of restored oyster reefs have been shown to yield an *additional* 2.6 kg of fish biomass per year over the lifetime of the reefs relative to sandy substrates (Peterson et al. 2003).

Globally, 85% of oyster reefs have become extinct as a result of overharvesting, disease, and poor water quality (Beck et al. 2011). Lost oyster reefs are commonly replaced with habitats that provide less food or poorer protection from predators for fish, such as bare muds and sands (Grabowski et al. 2012). These profound habitat changes typically propagate to sharp declines in fish diversity and biomass, severely impacting fisheries (Coen et al. 1999). For these reasons, oyster reefs are being restored in many locations worldwide, and often with the explicit goal of enhancing fish and fisheries (Gilby et al. 2018c). It is important to note, therefore, that simply having oysters in a system (e.g. oysters growing on jetties, pylons, artificial rock walls) does not substitute the functional, ecological or habitat roles that natural oyster reefs have for estuarine ecosystems. Urban structures also do not provide the same seascape complexity (Peterson et al. 2003). Therefore, active restoration efforts that restore both the lost oyster reef biogenic structures to estuaries, as well as the structural

complexity and food web benefits derived from oyster reefs that enhance secondary production of fish is vital.

Figure 1 Natural oyster reef structure at Toorbul Point, Queensland in the early 1900's. Reefs constitute a structurally complex, biogenic habitat that provides feeding opportunities, shelter sites and spawning areas for fish in estuaries. Oyster reefs can also slow erosion processes and can improve water quality at a local scale.

Positive effects of reefs on fish are thought to result primarily from enhanced larval settlement and survival, and the movement of adult fish to reefs (Breitburg et al. 1995; Gilby et al. 2018c). Notwithstanding the very large financial investments in reef restoration globally, it is surprising that quantitative data on fish enhancements attributable to reefs, the stated goal of many investments, are limited essentially to very small areas at a few locations in eastern USA (Gilby et al. 2018c; Peterson et al. 2003; zu Ermgassen et al. 2016). It is surprising that quantitative information on the ways restored oyster reefs meet their stated restoration objectives to enhance fish stocks at the scale of whole estuaries is not more prevalent (Gilby *et al.* 2017a).

Fish habitats are typically arranged in a spatial mosaic of different types (i.e. 'seascapes') (Nagelkerken et al. 2015; Olds et al. 2016; Yeager et al. 2011). In these seascapes, the spatial properties of habitats (e.g. their proximity and connectivity to structurally complex habitats

such as mangroves, seagrasses, marshes, and reefs) is important in determining their value as fish habitats (Bostrom et al. 2011; Olds et al. 2012b; Pittman 2018). In the context of restored oyster reefs, it is, therefore, plausible that the spatial properties of a reef may modify any 'reef effects' on fish assemblages and ecological functions performed by fish (Grabowski et al. 2005; Irlandi and Crawford 1997; Micheli and Peterson 1999; Pierson and Eggleston 2014); whilst this is a clear and attractive hypothesis, it has never been tested with empirical data.

History of oyster reefs in the Noosa River

The commercial oyster industry in the Noosa River commenced in the 1870's or 1880s, and ceased, having become economically unviable, by the 1940's (Thurstan 2016). Oystering locations were recorded by local fisheries officials throughout this period (from 1934; see Figure 2), which outline the extent of the oyster lease areas and thereby indicate the most probable historical range of oyster beds within the estuary. These oyster lease areas were dredged intensively for oysters in the early 1900's, resulting in the removal of live oyster beds and the underlying bedrock. This resulted in the loss of large areas of intertidal and subtidal hard substrates that are required for oyster spat to settle, grow, and form reefs. The endpoint of this process was that oyster reefs were no longer present as a substantial habitat in the lower and middle reaches of the estuary (Thurstan 2016).

The species of oysters that occur in south-east Queensland (primarily rock oysters *Saccostrea* spp.) form reefs predominantly in intertidal habitats, and up to a depth of 1 metre below the lowest astronomical tides. This known depth range can be used to predict the likely distribution of oysters (assuming they were not removed by dredging) throughout the system by using bathymetry data for the Noosa River. Historically, the likely spatial extent of oyster reefs in the Noosa River is estimated to be in the range of 41,530 to 207,650 m^2 (ESP 2016). A minimum of 8,241 m^2 of oyster beds was removed per year during the peak oyster harvest. Approximately 16,850m^2 of old oyster beds and oyster rubble is currently buried by sediment in the historical oyster lease areas. Of the original extent of naturally occurring oyster reefs in Noosa River, approximately 20,647 m^2 of degraded living oyster beds (i.e. small and isolated patches, often heavily silt covered and containing many

dead shells) and oyster rubble remain scattered throughout the system. These oyster beds have a low profile and a low surface area – volume ratio, are easily covered by silt (especially from wind suspension or seasonal rain events), and therefore do not provide the same opportunities for oyster recruitment as established oyster reefs do (ESP 2016). Additionally, the current extent of degraded oyster beds and oyster rubble in the Noosa River (20,647 m^2) is only a small fraction of the total area of oyster reef habitats (41,530 to 207,650 m^2) that are likely to have been present before commercial harvesting commenced (ESP 2016). Oyster spat are, however, still present, and abundant, in the Noosa River, and recruit to suitable hard substrate when it is present (TNC and ESP 2015). There is no longer suitable substrate for oyster larvae to settle on natural oyster reef substrate (i.e. biogenic reef substrates) in the river. Therefore, it is clear the methods of dredging oysters from those areas have removed substrate suitable for oyster recruitment. Provision of appropriate substrate to allow oyster reefs to redevelop within the Noosa River, would restore a diversity of habitat to important fisheries species.

As a fish habitat, oyster reefs are now considered functionally extirpated within the system. This drastic habitat change has been accompanied by significant declines in fish stocks over the last century (Thurstan 2016). The extent, composition, and quality of fish habitats in the Noosa River has therefore changed substantially since European settlement, with likely adverse flow-on effects on aquatic biota and resources, including fish and fisheries (Thurstan et al. 2017). The status of fish and fisheries in the Noosa River, and the condition and type of habitats supporting them, is of considerable concern to the local community. This is the catalyst for the current project aimed at restoring oyster reefs as an essential fish habitat that has become extirpated in the system. This project aims to partly redress this habitat loss by restoring oyster reefs at a number of locations in the lower reaches of the estuary, aiming to enhance the quality of habitat for fish species known to be closely associated with estuarine oyster reefs (e.g. yellowfin bream, tailor, moses perch, grouper).

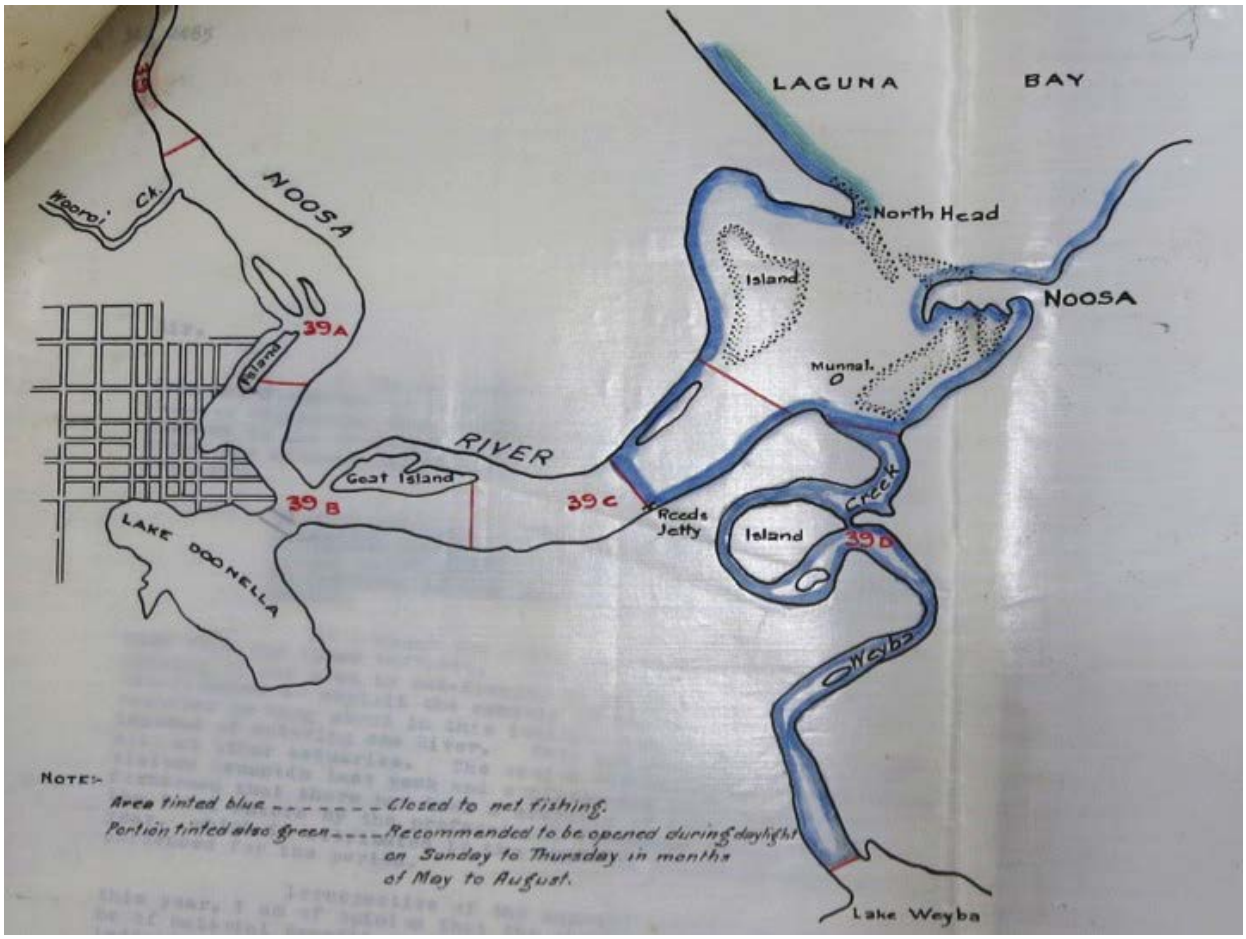

Figure 2 A hand-drawn chart from 1934, made by the Fisheries Inspector to highlight the areas in the Noosa River closed to net fishing. The red numbers indicate the locations of all known Noosa oyster sections. Source: Queensland State Archives.

Oyster reef restoration in the Noosa River

The principal objective of the Noosa River oyster reef restoration project is to restore natural oyster reef habitat in the Noosa Estuary to enhance the abundance and diversity of fish throughout the estuary. This requires the addition of suitable hard substrate for oyster spat to settle, and allowing natural recruitment and reef-formation processes to recover to areas that historically supported oyster reefs.

The oyster settlement substrate comprises *oyster reef restoration units*. These units are made from the most suitable recruitment material - oyster shells held together by a natural coir fibre bag. The units are raised above the muddy and sandy marine substrates, thereby mimicking the vertical relief of the original oyster reefs to facilitate natural recruitment processes (Figure 3, 4). We expected that natural recruitment processes would cement the

dead shell together and form part of the mosaic of habitats within the estuary including both soft and hard structural habitat types, thereby creating a structurally diverse mosaic of habitats that is predicted to be beneficial to a range of fish species, including species of harvested in commercial and recreational fisheries (e.g. yellowfin bream, estuary cod, tailor, mangrove jack, and moses perch).

The restoration sites that were chosen as locations for oyster reef restoration in the Noosa River (Figure 5) because they:

1) are in reaches of the lower Noosa River estuary and in Weyba Creek from which oysters were harvested historically;
2) are within the depth range known to be suitable for oyster reefs to grow;
3) are in locations where viable oyster larvae were recorded during recent recruitment studies; and
4) have an extent where the final restored area will not exceed the historical areal extent of oyster reefs before commercial harvesting took place.

Figure 3 Coir mesh bag filled with recycled oyster shells; the principle restoration unit

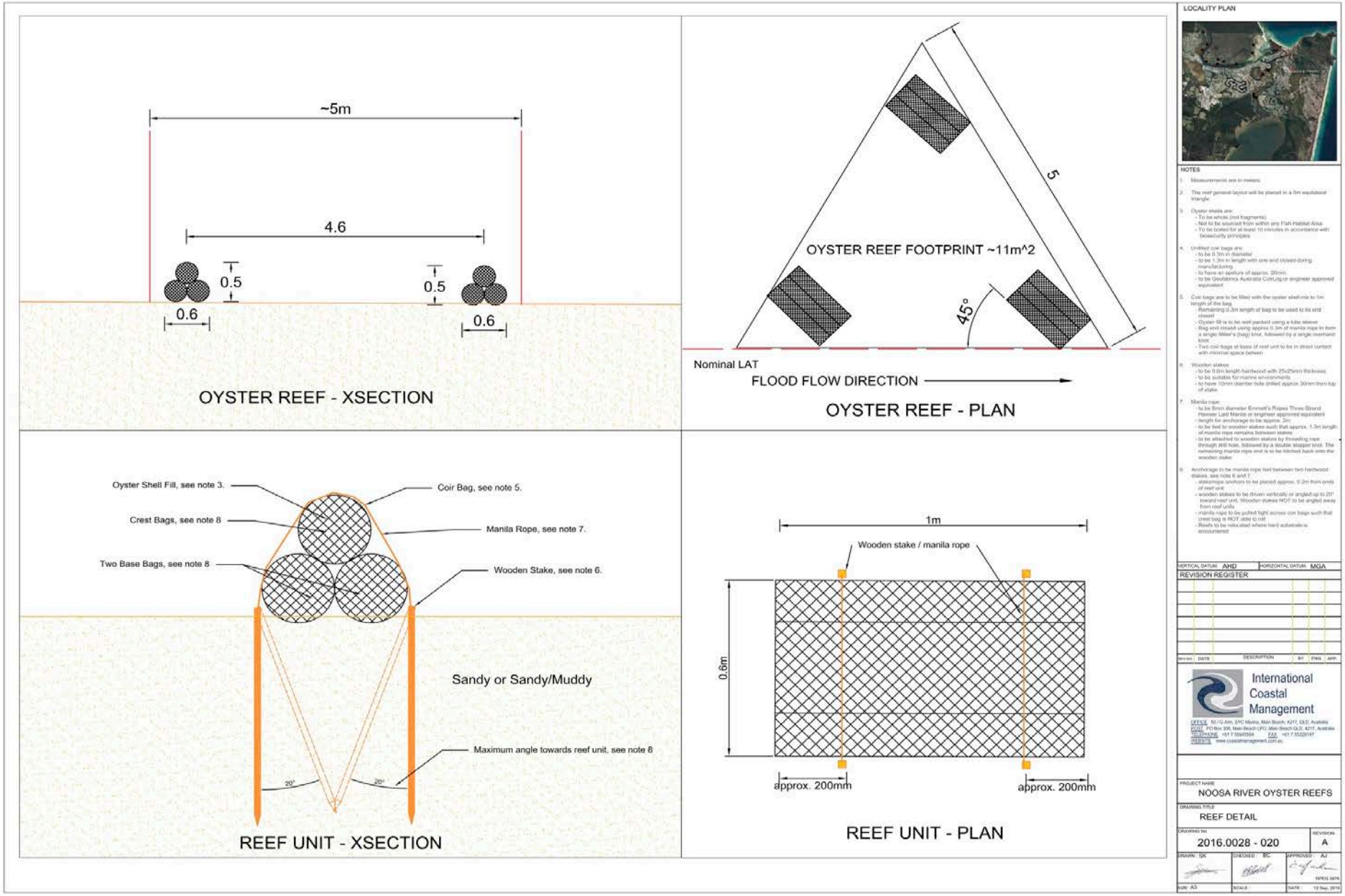

Figure 4 Approved coastal engineering drawing of the oyster reef restoration units installed in the Noosa River

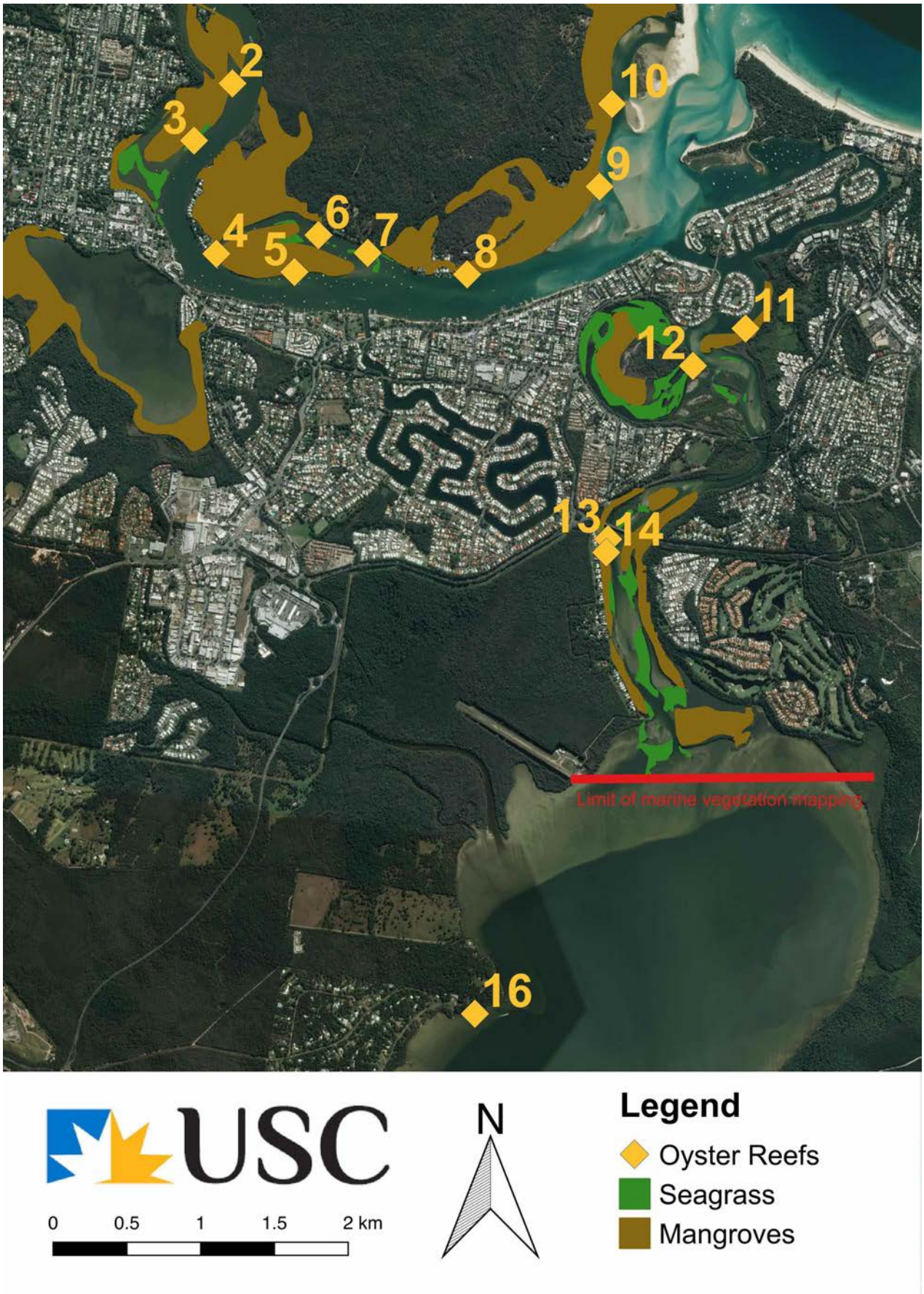

Figure 5 Map of oyster restoration sites and marine habitats in the Noosa River.

The installation of oyster reef units to the Noosa River was done during a period of three days, from 20 to 22 November 2017. All works and surveys were conducted by a team comprising professionals from Noosa Jetty Builders, and marine scientists from the University of the Sunshine Coast. All oyster reef units and signs were installed exactly according to specifications set out in the permit conditions and any instructions provided regarding procedures. All reef units are located to avoid any damage to marine plants or surrounding ecosystem (Table 1). Key observations during the placement of the reef units and associated signage include the following:

- No marine plants were disturbed during the installation of the reef units or signs. Before each reef unit was placed on the seafloor, we carefully examined the site to ascertain that no seagrass, mangrove aerial roots, or any other marine vegetation was present. This ensured that no direct placement impacts occurred at any of the sites (Table 1).
- All operations were localised to the immediate site where reef units were sunk onto the seabed. Thus, no habitat outside the RAA area was impacted in any form by the reef units or the signage.
- Poles holding the signs were installed using a narrow water jet 'spear'. Use of this gear ensured that only a very narrow (< 20 cm diameter in all cases) area of the seabed was disturbed (Figure 6). Sign posts were then driven further into the substrate, to a mean depth of 2.7 m (min 1.8 m, max 3.5 m; Table 1), using a post driver (Figure 6).
- According to engineering specifications, we used marine grade hardwood stakes (sourced from the Australian Hardwood Stake Company) to secure the reef units on the seafloor. The stakes were hammered into the seabed to a mean depth of 0.9 m (min 0.5 m, max 1.2 m) - depending on hardness of the seabed (Table 1), at a mean angle of 82.4º (min 75 º, max 90 º).

Figure 6 The resulting very small footprint of sign posts following installation by the water jet (left) and a completed oyster reef in Weyba Creek (right).

Table 1. Completed oyster-reef installations in the Noosa River, listing their exact position, the date of placement, characteristics of posts and stakes driven into the seabed to secure signage and reef units, and any presence and/or damage to marine vegetation.

Site Number	Position		Installation date	Depth to which sign post is driven into the seabed (m)	Stakes to secure reef units		Presence of, or damage to, marine plants and/or adjacent habitats or ecosystems.
	Latitude	Longitude			Depth of stake into seabed (m)	Angle of stake relative to seabed (degrees)	
1	reef units not installed - seabed not compact enough						
2	-26.38333096	153.045835	20/11/17	2.8	1.2	79	None
3	-26.38673804	153.043291	20/11/17	2.8	1.2	75	None
4	-26.39367197	153.044599	20/11/17	2.9	1.1	84	None
5	-26.394757	153.049933	20/11/17	2.4	0.5	82	None
6	-26.39245399	153.051636	20/11/17	3.2	1.2	85	None
7	-26.39351204	153.054941	20/11/17	3.3	1.2	77	None
8	-26.39491903	153.061679	20/11/17	2.4	1.2	90	None
9	-26.38954598	153.070696	21/11/17	1.8	0.5	86	None
10	-26.38452999	153.071546	21/11/17	2.0	0.6	87	None
11	-26.39817104	153.080595	21/11/17	2.3	0.5	76	None
12	-26.40045603	153.077035	21/11/17	2.9	0.5	79	None
13	-26.41099703	153.071263	22/11/17	3.5	1.2	87	None
14	-26.41184301	153.0712	22/11/17	3.2	0.5	83	None
15	reef units not installed – presence of seagrass						
16	-26.43981904	153.062079	22/11/17	2.9	0.6	84	None

Oyster reef growth and stability monitoring for the Noosa River oyster reef restoration project

As part of the development approval for installing the oyster reefs, the stakeholders are required to report yearly (in December) to Queensland Department of Agriculture and Fisheries on the progress of the oyster restoration project, especially relating to;

1. Oyster restoration unit stability (i.e. oyster reef restoration units remain within the allocated resource allocation areas);
2. Restoration of natural recruitment processes over long term (i.e. spat recruitment rates demonstrate that the biogenic matrix will be sufficient to hold the structure of the oyster reef restoration units in place following complete degradation of the supporting coir material during the establishment phase and to facilitate ongoing natural recruitment processes);
3. Equitable Community Impacts (i.e. ensuring fair community use of the river system is not impacted by placement of the Oyster Reef Restoration Units within the Resource Allocation Areas - to be monitored using a council operated community feedback system); and
4. No negative impact on marine plants or shoreline erosion (i.e. ensuring the oyster restoration units do not impede natural marine plant growth or accelerate coastal erosion processes).

These performance objectives are quantified using established monitoring protocols for oyster reef restoration, and follow international best practice for monitoring restored oyster habitats (Baggett et al. 2014). The monitoring program is designed to be adaptive, with annual reviews against the performance objectives for the project (See Table 2 for detailed monitoring requirements). Note that these monitoring objectives agreed to with the Department of Agriculture and Fisheries refer only to the growth, stability and effects of the oyster reef units themselves, and are <u>not required to monitor any aspect of the fish assemblages recruiting to the reefs</u>. The fish assemblage monitoring undertaken as part of the restoration project is detailed in the other chapters of this report.

Results of the two 2018 compulsory monitoring events are provided as in Appendix 1. In this report, we show that;

1. Oyster restoration units have not moved from the RAA area, nor have they moved greater than 1 m within the RAA area.

2. There has been significant spat settlement and oyster growth at all oyster reef restoration sites. Whilst this has not yet proliferated to coverage of invertebrates on the outside of the coir bags, or to the proper stabilisation of shell within the bags (i.e. cementing of the biogenic reef matrix), these oyster growth results are a positive sign for the likely success of the reefs in achieving these performance criteria in the near future.
3. Whilst we did not identify any wilful damage to the oyster restoration units, we did identify that marker buoys were regularly removed from the oyster restoration sites, and there have been several instances of boat propeller and anchor strikes on the reefs. This was repaired where possible (i.e. corrective actions), and a further education campaign is required to educate river users.
4. There has been no significant change to the distribution, composition or quality of seagrass or mangroves around the oyster reef sites. Similarly, there has been no shoreline erosion at oyster reef sites.

Consequently, two of the four monitoring targets reported on here have been fully met, the third relating to oyster growth is tracking very favourably with the criteria likely to be met in the coming years, and the final relating to community usage may require closer monitoring.

We identified some damage to the oyster reef units from boating activities (principally anchor and prop damage) at many sites during the November 2018 monitoring event. We have some evidence to suggest that the use of oyster reefs by fishers has increased over time, and that some of the ecological benefits of the reefs might therefore be being offset by fishing. Corrective actions were made to these reefs immediately following the monitoring period in November 2018. The three reefs more distant from the main boating activities in Lake Weyba and Weyba Creek (due to the combined effects of limits on access to hire boats, and difficulty of access due to shallow waters) were the most intact oyster reefs, with no damage recorded in either 2018 monitoring events. Whilst these reefs did not necessarily have the highest rates of settlement (the exception being reef number 13, which has the highest average live oyster density), their success might be the most guaranteed as they are less likely to be damaged by the sorts of impacts occurring on reefs in the central stretch of the river.

Removal of oyster restoration units in 2019

Despite the positive outcomes from the 2018 monitoring report, we identified substantial damage to the oyster restoration units following the Christmas and New Year holidays of 2018-2019. The majority of this damage is thought to have been caused by the oyster restoration units being struck by boat propellers or anchors (Figure 7). This resulted in the coir mesh bags being split open, with oyster shells being spilled throughout the restoration area. There appeared to be an increase in the theft of the marker buoys that were placed on the corners of the restoration area to warn boats of the reef locations over the Christmas holidays which may have contributed towards the increased damage.

As a consequence of this damage, a decision was made by the Noosa Biosphere Reserve Foundation to remove ten oyster reef restoration sites from the Noosa River (Figure 8). The removal was conducted by the USC team on the 13th and 14th of February 2019. Oyster restoration units were disposed of immediately at the Cleanaway Doonan Solid Waste Depot, as per the conditions of the Beneficial Reuse Permit for the oyster shells issued by Queensland Department of Environment and Heritage Protection, and the conditions of the approved Development Application.

Figure 7 Two damaged oyster restoration units removed from the Noosa River in February 2019. The unit on the right was positioned as the top bag in the triangular prism restoration units, and sustained substantial damage to the top surface from either a boat propeller or anchor. This sort of damage to the top bags in the oyster restoration units was common following the 2018-19 Christmas holidays.

Table 2 Noosa oyster reef restoration monitoring schedule as agreed to by all stakeholders in RAA 2016CA0575, and including mark-ups from Department of Agriculture and Fisheries dated 6 January 2017. Note that these monitoring objectives agreed to with the Department of Agriculture and Fisheries refer only to the growth, stability and effects of the oyster reef units themselves, and are not required to monitor any aspect of the fish assemblages recruiting to the reefs. The fish assemblage monitoring undertaken as part of the restoration project is detailed below.

Performance objective	Monitoring method	Frequency	Corrective action where performance objective is not met
1. Oyster Restoration Unit location stability			
Oyster restoration units remain within the designated Resource Allocation Areas.	Visually inspect the stability of oyster reef units and record the precise GPS position (± cm scale), and size of each unit (following international best practice: Baggett et al. 2015). Use GIS software to contrast the position, footprint, size and area of oyster reef restoration units between monitoring events and assess any potential movement.	Every 6 months for a minimum of three years Additional monitoring will be conducted within 2 weeks of substantial rainfall events (i.e. events that exceed 50-year Average Rainfall Intervals).	A professional coastal engineer shall be consulted to suggest remedial action for any oyster reef restoration units that collapse, or shift by > 1 m. Any oyster reef restoration units that move outside the designated Resource Allocation Areas within 3 years will be removed. A professional ecologist will confirm the cause of the shift.
2. Natural Recruitment Processes			
Oysters and other sessile benthic invertebrates recruit to reef restoration units to establish a biogenic matrix, which binds oyster shells in place, prior to degradation of coir material. The Key Performance Indicators for this are: **1.) Oyster recruitment**: successful recruitment of oyster spat in at least 1 out of the 3 years (i.e. 33% of the time) post deployment (following international best practice of 40%: Baggett et al. 2015).[1]; 2.**) Cover of oysters and other sessile benthic invertebrates**: an upward trend in the cover of sessile benthic invertebrates	Quantify the recruitment of oysters and other sessile benthic invertebrates to reef restoration units, and measure changes in the cover of oysters and other sessile benthic invertebrates over time (following international best practice: Baggett et al. 2015).[1] The monitoring methods for each Indicators are: **1.) Oyster recruitment**: marked oyster shells will be fastened to the outside of restoration units. These shells will be harvested at regular intervals (15 oyster shells per location on each event – i.e. 5 shells per unit) and the density and size of recruits recorded; 2.**) Cover of oysters and other sessile benthic invertebrates**: photographs of ten quadrats (25 cm x 25cm), distributed in a stratified random design, across each oyster reef restoration unit will be taken at regular intervals to quantify the change in	Every 6 months for a minimum of three years, unless otherwise detailed within corrective actions	We will contrast: 1) the rate of oyster recruitment; 2) the cover of oysters and all other sessile benthic invertebrates; and 3) the stability of the biogenic matrix among oyster reef restoration units and between monitoring events. Any restoration units that fail to meet the Key Performance Indicators within 3 years will be removed. If major damage occurs to the coir mesh of any oyster reef restoration units before a stable biogenic matrix has formed, and loose oyster shells are being lost from the structure, it will be repaired *in-situ* by hand weaving. Any such repairs will be conducted carefully, and by hand, to ensure that there is no damage to established areas of biogenic matrix.

growing on restoration units; and **3.) Establishment of stable biogenic matrix**: structural rigidity of oyster restoration units, denoting a stable biogenic matrix after 3 years post deployment, which is sufficient to hold oyster shells in place.	cover of oysters and other sessile benthic invertebrates (Baggett et al. 2015)[1]. **3.) Establishment of stable biogenic matrix**: assess the structural integrity of each oyster reef restoration unit and monitor the degradation of coir material. Structural integrity will be quantified by measuring the proportion of oyster shells (from 10 shells that are selected at random at each location), which can be removed easily by hand manipulation. The rate of coir degradation will be measured by monitoring changes to the condition of coir mesh over time from the ten photo-quadrats, which are collected twice per year to assess changes in the cover of benthic invertebrates at each oyster reef restoration unit.		
3. Community use and enjoyment of the declared Fish Habitat Area			
Oyster restoration units do not significantly impair community use and enjoyment of the declared Fish Habitat Area, particularly fishing activities.	Maintain records of community feedback, evidence of vandalism, and vessel strikes on the trial oyster reef restoration units. Records will be comprehensive and include, as a minimum set: 1) the number and type of **complaints** received (also, to allow the Department to gauge the success, any positive comments should also be provided); 2) the type, nature, and severity of any acts of **willful vandalism**; and 3) the type and severity of any **vessel strike**.	Annual reporting of all complaints, cases of willful vandalism, and instances of vessel strike received for the three-year trial period.	**Complaints**: within 3 months of receiving each complaint, an investigation (including interview with the complainant if possible) will be conducted to determine whether complaints are directly related to oyster reef restoration units. Potential response actions will be provided to the Department of Agriculture and Fisheries in the annual report. If complaints persist, and grievances exceed the direct benefit of oyster reef restoration, the particular oyster reef restoration unit will be removed as soon as practical, and prior to the 4th anniversary post deployment. **Willful vandalism and vessel Strikes** If there are consistent and / or significant cases of willful vandalism to, or instances of vessels striking, the oyster reef restoration units, the cause of the impact will be identified and used to guide the delivery of a community education campaign aimed at reducing these types of incidents. If the education campaign does not reduce cases of willful vandalism and / or instances of vessel strike, the oyster reef restoration units that are responsible will be removed prior to the 4th anniversary post deployment.

4. Other potential effects:			
Oyster reef restoration units do not cause a decline in the extent of marine plants within a 50 m radius of the restoration units, and are not attributed to erosion of adjacent shorelines or other ambient environmental impacts.	Map the area of marine plant habitats (seagrass, mangroves) in the immediate vicinity (i.e. with a 50 m buffer) of each oyster restoration area, using high-resolution GPS (cm scale) and field-validated aerial imagery (sourced from Nearmap). Monitor changes in the composition coverage and condition of seagrass within 50 m radius around the oyster reefs. Map the location and condition of estuarine shorelines that occur in the immediate vicinity (i.e. with a 50 m buffer) of each oyster reef, using high-resolution GPS (cm scale) and field-validated aerial imagery (sourced from Nearmap).	Annually for a minimum of three years, or until any failed restoration units have been removed.	Where monitoring shows that there are substantial, and consistent, losses of marine plants, or erosion of estuarine shorelines, in the immediate vicinity of oyster reef restoration units, and these changes can unambiguously be attributed to oyster reef restoration activities, the problem units that are responsible for such impacts shall be removed (as soon as practical and prior to the following annual reporting anniversary).

Figure 8 Map of oyster restoration sites removed during February 2018, and those that remain.

Objectives

The broader Noosa River oyster restoration project therefore had six key components. Each of these components are reported on in separate chapters here:

- **Review of all restoration literature:** Identify the degree to which landscape context was considered to guide the selection of restoration sites (Chapter 2);
- **Review of oyster reef restoration for fish literature:** Identify gaps in the global understanding of the effectiveness of oyster restoration for fin fish, and synthesise current research to optimise future outcomes (Chapter 3);
- **Seascape context:** Identify whether the seascape context of individual reefs modified their augmentation of the abundance and diversity of fish (Chapter 4);
- **Ecological functioning**: Determine the effects of oyster reef restoration on the rate and distribution of predation in an estuarine seascape (Chapter 5);
- **Effects of oyster reefs throughout seascapes:** Quantify how the restored reefs influence the distribution and abundance of fish across the estuary (i.e. beyond the reefs themselves) (Chapter 6); and,
- **Spatial prioritisation mapping:** Optimise the placement of oyster reef restoration effort for oyster growth, fish, fisheries and ecological functioning using statistical and spatial modelling techniques by incorporating all information gathered in chapters 4, 5 and 6, and the 2018 annual monitoring report (Chapter 7).

Chapter 2

Spatial restoration ecology: placing restoration in a landscape context

Gilby BL, Olds AD, Connolly RM, Henderson CJ, Schlacher TA (2018) Spatial Restoration Ecology: Placing Restoration in a Landscape Context. BioScience 68:1007-1019

Introduction

Establishing nature reserves and restoring ecosystems are complementary approaches in conservation (Holl et al. 2003; Palmer et al. 2016; Pressey et al. 2007; Soule 1985) that require significant financial investment (De Groot et al. 2013; Wilson et al. 2006). Maximising the net returns of these investments, in terms of both biodiversity and ecosystem protection, is therefore sensible (Halpern et al. 2013; Possingham et al. 2015). Common strategies for enhancing conservation returns are to place reserves in areas that are threatened, support high biodiversity, or incur lower social and economic costs (Halpern et al. 2013), or to protect or restore sites that might have synergistic benefits for conservation (Moilanen et al. 2011; Thomson et al. 2009).

Conservation and restoration areas, by their very nature, are positioned within heterogeneous landscapes, which comprise multiple ecosystems of different sizes and shapes, and with varying degrees of inter-connectedness (Forman 1995; Olds et al. 2018c). The landscape context can strongly influence several key biotic attributes of a site (Holl et al. 2003). Many of these attributes are of direct conservation and restoration concern (e.g. population dynamics, biodiversity, productivity) (Bunn and Arthington 2002; Ward et al. 1999), across terrestrial (Hanski and Saccheri 2006), marine (Micheli and Peterson 1999) and freshwater (Wiens 2002) realms. Animals respond strongly to landscape configuration because most move throughout landscapes, and some use different habitats throughout their lifecycles. Some sites are, therefore, of higher ecological value for animals than others because they differ in terms of their food resources, refuge value from weather or predators, accessibility to dispersal pathways, and numerous other ecological properties that help to shape the fitness of individuals, demographics of populations, and the composition of assemblages (Pittman et al. 2011).

Globally, across multiple ecosystems and realms, it has been established that placing conservation areas strategically within landscapes can have synergistic benefits for their ecological effects on both ecosystems, and the animals that inhabit them (Olds et al. 2016; Rudnick et al. 2012). For example, many marine fish move among coral reefs, seagrass meadows and mangrove forests throughout their lives, and both fish abundance and diversity is often greatest inside marine reserves that conserve these ecosystems and the pathways that link them across landscapes (Edwards et al. 2009; Mumby 2006; Olds et al. 2016). Because some of these fish perform important ecological functions (e.g. herbivory), protecting connections between coral reefs, seagrasses, and mangroves can also help to improve the spatial resilience of these ecosystems to disturbance (e.g. Magris et al. 2014; Olds et al. 2014). Furthermore, the benefits of placing reserves into networks to maximise the

exchange of individuals, matter and energy among them is widely recognised (e.g. Arturo Sánchez-Azofeifa et al. 2003; Harrison et al. 2012; Hermoso et al. 2016). Reserves that are placed in areas with greater connectivity among populations, among ecosystems, or with other reserves, therefore often perform better than reserves with impoverished landscape connections (Olds et al. 2016; Ribeiro et al. 2009; Stoms et al. 2005).

Landscape context can have similarly positive ecological effects on the performance of restoration projects (Metzger and Brancalion 2016). Restored ecosystems with strong connections to other habitat patches, of either the same or different ecosystem types, are more likely to be settled by animals, and receive larger subsidies of matter and energy from adjacent ecosystems. This landscape context modifies the distribution, abundance and diversity of animals and plants across landscapes (Fahrig 2001; Hodgson et al. 2011; Lees and Peres 2008; Pottier et al. 2009), and potentially improves the ecological functioning of restored habitats (da Silva et al. 2015; Jones and Davidson 2016a).

Modern algorithms for reserve selection explicitly recognize the importance of positioning within the broader landscape (Hilty et al. 2006; Magris et al. 2016; Rudnick et al. 2012; Weeks 2017). These algorithms have developed, now, to the point that system-specific, and species-specific, data are being used in association with commonly used modelling techniques (e.g. MARXAN, Zonation and network models), broadly across regions, and within individual systems (Engelhard et al. 2017; Kool et al. 2013; Weeks 2017). Whereas the selection of locations for reserves is often guided by spatial concepts from landscape ecology, including connectivity and landscape context (Almany et al. 2009; Margules and Pressey 2000; Sarkar et al. 2006), site selection for restoration appears to adopt these principles less frequently (Hodgson et al. 2011). However, spatial prioritisation is not widely used in restoration (e.g. Adame et al. 2015; Ikin et al. 2016), so, there have been recent calls for tighter integration of the spatial principles from landscape ecology and conservation biology (Audino et al. 2017; Wiens and Hobbs 2015) to both inform the design of restoration projects, and guide the selection of restoration sites (Jones and Davidson 2016a; McAlpine et al. 2016). This is surprising because there have long been calls for the more strategic placement of restoration across landscapes, including in some important global restoration guidelines and policies (Keenleyside et al. 2012; SER 2008).

The landscape context of restoration sites is likely to be one of the most important factors influencing the outcomes of restoration investments, particularly for projects that aim to enhance

animal populations (Figure 1) (Miller and Hobbs 2007; Moreno-Mateos et al. 2012). Because restoration sites usually require colonisation by animal populations from other habitat patches, the degree of connectivity between restoration sites and other patches of existing habitat is critical (Hodgson et al. 2011; Hodgson et al. 2009; Scott et al. 2001). Restoration sites might be placed in areas that are considered appropriate for the establishment and growth of habitat-forming species, but which are so isolated or poorly connected that animal populations respond to a lesser degree; thereby reducing the overall values of the habitat restoration for the whole ecosystem or landscape (Howe and Martinez-Garza 2014; Jones and Davidson 2016a). For example, restoring to enhance connectivity between habitat fragments can help with restoring metapopulation dynamics (Fischer and Lindenmayer 2007; Montalvo et al. 1997). Increased consideration of metapopulation structure and connectivity can serve to enhance the available genetic pool of animal populations thereby potentially increasing their fitness (Baguette et al. 2013), reducing population extinction risk (Reed 2004), and increasing resilience to exogenous disturbances (Etienne 2004). Such considerations are now often considered in the placement of marine reserves, especially where fisheries enhancement is a goal (Gerber et al. 2003; Puckett and Eggleston 2016). However, the regularity to which landscape context more broadly is considered in restoration site selection, and how this affects inhabiting animal populations has, however, not been established (Metzger and Brancalion 2016). Consequently, the lines of evidence required for practitioners to properly justify the integration of principles from landscape ecology into the design of individual restoration projects have not been established.

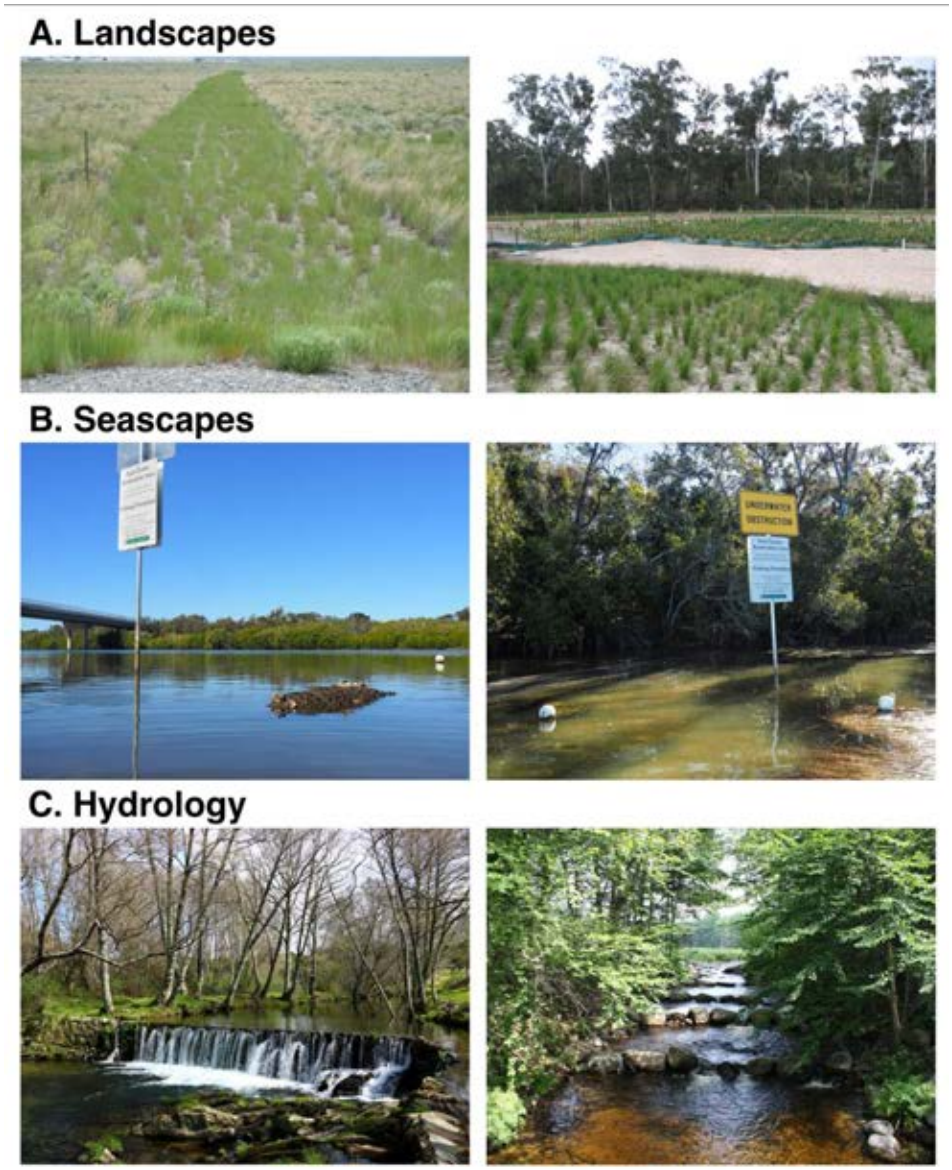

Figure 1 The landscape context of restoration sites has significant consequences for the number and types of animals which inhabit restored ecosystems on land (A), in the sea (B), and where hydrologic connectivity (C) is vital, especially in freshwater ecosystems, and wetlands. For example, isolated patches of restored grassland (A., left), might perform less effectively for animals than restored grasslands close to nearby alternate habitats (right). In the sea (B), connectivity between multiple habitats is often an important consideration because fauna use multiple habitats throughout their lifecycle. Here, restored oyster reefs in the Noosa River, Australia in two seascape contexts; at a distance from nearby mangroves (left), and very close to nearby mangroves and seagrasses (right). Hydrologic connectivity (C) is limited where weirs or dams can restrict flow of propagules and animals (left). These challenges can be overcome by considering connectivity between water bodies and movement of fauna and implementing restoration interventions such as waterway remeandering and fish ways (right). Images courtesy C. Duncan, M. Lavin (CC-BY-SA2.0), N. Carson.

In this study, we identified restoration projects from the global primary literature and assessed the degree to which landscape context was used as a criterion to help guide the selection of sites for restoration when the restoration of associated animal populations is also a principle goal, and under which scenarios this is most likely to occur. We chose habitat restoration for animal populations as the focus because animals move throughout landscape, and so spatial metrics are likely to be investigated first for these over other aims for restoration. We conducted literature searches using a structured literature classification framework. We reviewed the literature using multiple terms used for ecological restoration and a suite of ecosystem- and animal-specific phrases. We then categorised projects into those that considered landscape context in site selection, and those that did not, and further categorised projects into environmental realms, ecosystems, and the animal communities they seek to enhance. We conclude by outlining how greater uptake of fundamental principles gleaned from landscape ecology can improve restoration success.

Methods

Literature searches

Restoration projects were identified using targeted literature searches and a structured literature classification framework (Figure 2). All literature searches were conducted using the ISI Web of Knowledge database in July 2017. The initial search was for the term- (("habitat restoration" or "ecological restoration" or "ecosystem restoration") and (fauna or inhabit* or animal* or biodivers* or wildlife or fish)), resulting in 2183 articles returned and 333 articles downloaded for potential inclusion. Based on the composition of this initial shortlist, follow up searches included components of the initial search, as well as: wetland*, seagrass, oyster*, fish*, mangrove*, forest*, grass*, insect*, invert*, bird*, mammal*, reptil*, stream*, river*, lake*, and coral*. All review articles and meta-analyses identified by literature searches were downloaded and scanned by the first author for additional articles that could be included. This method of literature searching was not designed to be exhaustive (i.e. systematic, comprehensive) in identifying all restoration projects in the literature that also sought to enhance animals. It was, however, designed to give the best possible representation of restoration projects across multiple environmental realms and ecosystems, and within the constraints of our search terms.

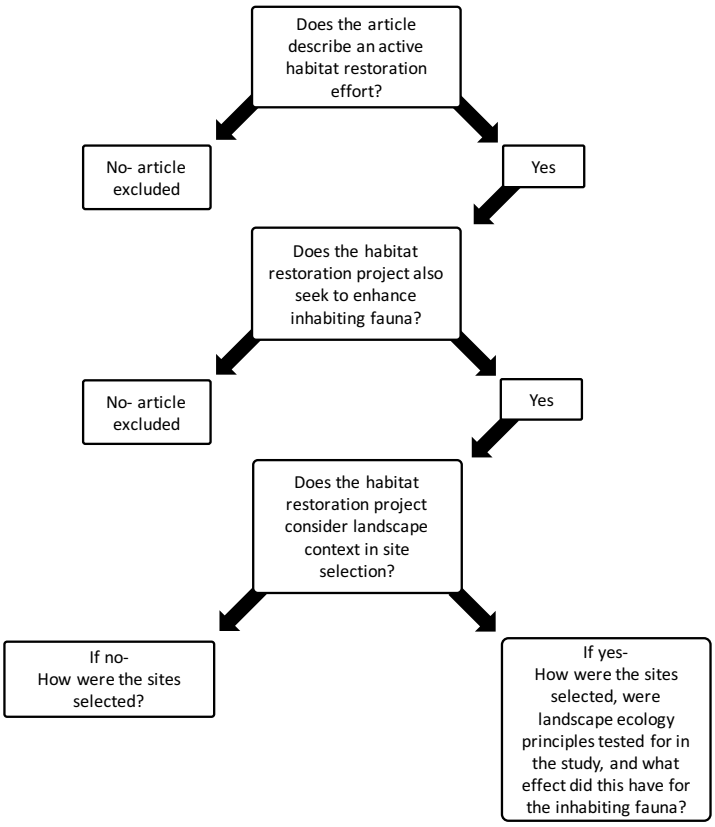

Figure 2 Literature classification framework and decision flow chart used to identify restoration projects from the global primary literature.

Inclusion criteria and data extracted

We followed a set classification framework for all studies identified by literature searches (Figure 2). Restoration projects were classified as also targeting the restoration of animals inhabiting animals within them if: (1) the study tested for effects of the restoration effort for animals, or (2) if the article states explicitly that a goal of the restoration effort was also to increase the abundance and/or diversity of animals.

We concluded that a restoration project considered the landscape context of restoration sites if the project specifically chose sites or systems over other areas because of their position within the landscape, especially if the restoration project: (1) aimed to reconnect habitat fragments; (2) considered the position of sites relative to patches of either similar, or different, habitat types; or (3) incorporated an aspect or understanding of animal movement, dispersal capacity or connectivity into site selection. We did not consider a study to have considered landscape context if sites were simply chosen: (1) on the basis of existing impacts (e.g. restoration of oil spill sites, erosion mitigation); (2) to revegetate mined land; (3) using 'habitat suitability' models for growth of habitat

forming species when the position of sites relative to other habitat patches was not also considered; or (4) if sites were randomly selected using a number generator, GIS, or similar.

Restoration projects were grouped according to country, region and habitat restored, and we pooled studies that reported on the same restoration project to avoid overlap in counting projects. We also identified the types of animals (in broad groups; e.g. birds, mammals, fish, insects, or any combination of these) that each restoration project sought to enhance, based on stated outcomes. For projects that did incorporate landscape context into their site selection, we identified whether the restoration effort resulted in the stated aims being achieved for that species (i.e. 'positive' effects on fauna).

Studies were classified into environmental realms (terrestrial, marine, or freshwater) according to their location and the animal species being restored. For example, wetlands can be either freshwater, marine or terrestrial; a restored wetland in saltwater seeking to restore habitat for fish is classified as marine, whereas a wetland in saltwater enhancing birds or insects is classified as terrestrial.

Results

Distribution and thematic focus of identified restoration projects

The final database included 472 restoration projects described in English language journals that sought to enhance animal populations from restoration efforts (For the full list of included articles contact the USC team). We identified restoration projects in 34 countries; most projects were from the USA (n = 212, 45%), followed by Australia (n = 44, 9%), Finland (n = 20, 4%), Sweden (n = 14, 3%), and the United Kingdom (n = 14, 3%). The most common ecosystems restored were forests (n = 134; 28%), followed by streams (n = 87; 18%), and grasslands (n = 67; 14%). Overall, 37% of studies stated explicitly that the landscape context of restoration sites was important in determining the effectiveness of restoration for animals, irrespective of whether or not they actually implemented landscape concepts into site selection.

Terrestrial projects comprised just over half of our dataset (n = 243, 52%) (Figure 3). Forests (n = 36, 15% of terrestrial projects) and grasslands (n = 34, 14%) in the USA, and forests in Australia (n = 30, 12%) were the ecosystems most often targeted for restoration (Figure 4). Terrestrial restoration projects most often sought to enhance populations of birds (n = 107, 44%), insects (n = 53, 22%) and mammals (n = 23; 9%). Freshwater projects comprised roughly one third of our dataset (n = 151,

32%) (Figure 3). Streams and rivers in the USA (n = 47, 31% of freshwater projects) and Finland (n = 11, 7%) were the ecosystems most often targeted for restoration (Figure 5). Freshwater restoration projects most often sought to enhance populations of fish (n = 89, 59%) and macroinvertebrates (n = 60, 40%). Marine projects comprised roughly one sixth of our dataset (n = 78, 17%) (Figure 3). Oyster reefs (n = 30, 44% of marine projects) and saltmarshes (n = 10, 13%) in the USA were the ecosystems most often targeted for restoration (Figure 6). Marine restoration projects most often sought to enhance populations of fish (n = 63, 81%), nektonic crustaceans (n = 21, 27%) or macroinvertebrate infauna (n = 20, 26%).

Effects of landscape context in restoration

Across all realms, 11% of projects (54 of 472) included landscape context as a criterion in the selection of restoration sites (Table 1, Figure 3). The integration of landscape context in restoration projects was remarkably similar across realms: terrestrial (10% of 243 projects), marine (13% of 89) and freshwater (13% of 164). In terrestrial ecosystems, projects that used landscape context most often were those in peatlands (100% of peatland projects, but only one was identified), wetlands (14% of wetland projects) and forests (10%) (Figure 4B), and those that targeted amphibians (29%) and mammals (13%). Freshwater projects that considered landscape context most often were those in rivers (40%) and streams (7%) (Figure 5B), and those targeting amphibians (40%) and macroinvertebrate infauna (13%). In marine systems, the consideration of landscape context was most prevalent in marine wetlands (30%) and in seagrass (29%) (Figure 6B), and when restoration targeted birds (33%) or macroinvertebrate infauna (15%).

Table 1. Summary of restoration projects in terrestrial, freshwater and marine realms for (A) all restoration studies; (B) restoration studies that considered landscape context in the design phase; and (C) restoration studies that did not consider landscape context in the design phase.

	Terrestrial		Freshwater		Marine		All realms	
	% of projects	# of projects	% of projects	# of projects	% of projects	# of projects	% of projects	# of projects
A. All restoration studies	51	243	32	151	17	78	100	472
B. Landscape context considered in design	10	25	13	19	13	10	11	54
Positive effects	7	18	4	6	8	6	6	30
No effects reported	4	9	7	11	5	4	5	24
Landscape ecology concept used								
Connectivity with patches of similar habitat	8	20	8	12	6	5	8	37
Connectivity with other habitats	1	1	1	1	1	1	1	3
Hydrology	1	2	2	3	4	3	2	8
Other	1	2	2	3	1	1	1	6
C. Landscape context NOT considered in design	46	218	28	132	14	68	88	417
Reason for exclusion								
Located on a mine site	7	15	0	0	0	0	4	15
Minimise erosion effects	0	0	3	4	0	0	1	4
Random placement	5	10	2	2	0	0	3	12
Indiscernible	81	177	86	113	85	58	83	348
Other	7	16	10	13	15	10	9	39

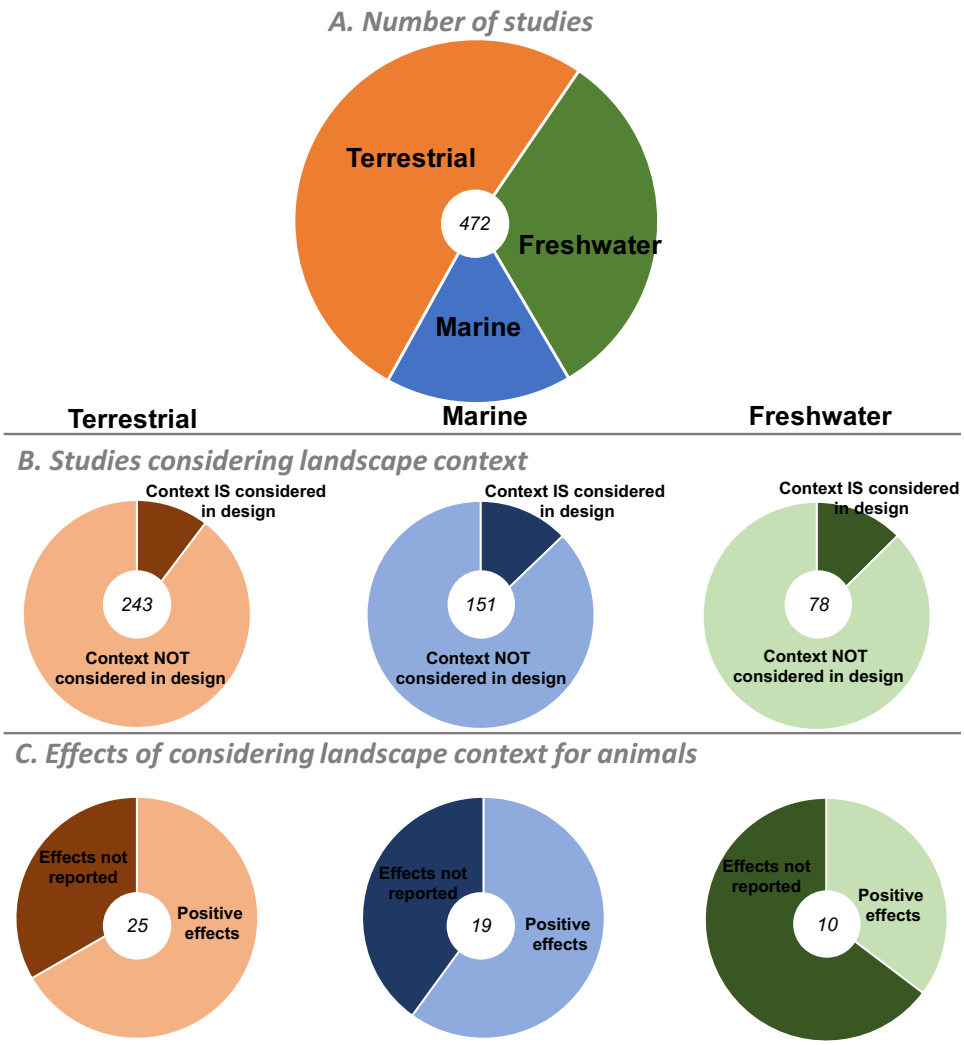

Figure 3 Summary of included studies. Numbers in white circles in the centre of each chart denote the number of studies in each category. A) the total number of studies included in the database, divided by environmental realm. B) The proportion of studies which did, and did not, consider the spatial context of restoration sites during ecosystem restoration projects. C) The proportion of studies that did consider landscape context during the restoration design process that either did, or did not, report the direction of outcomes for animals.

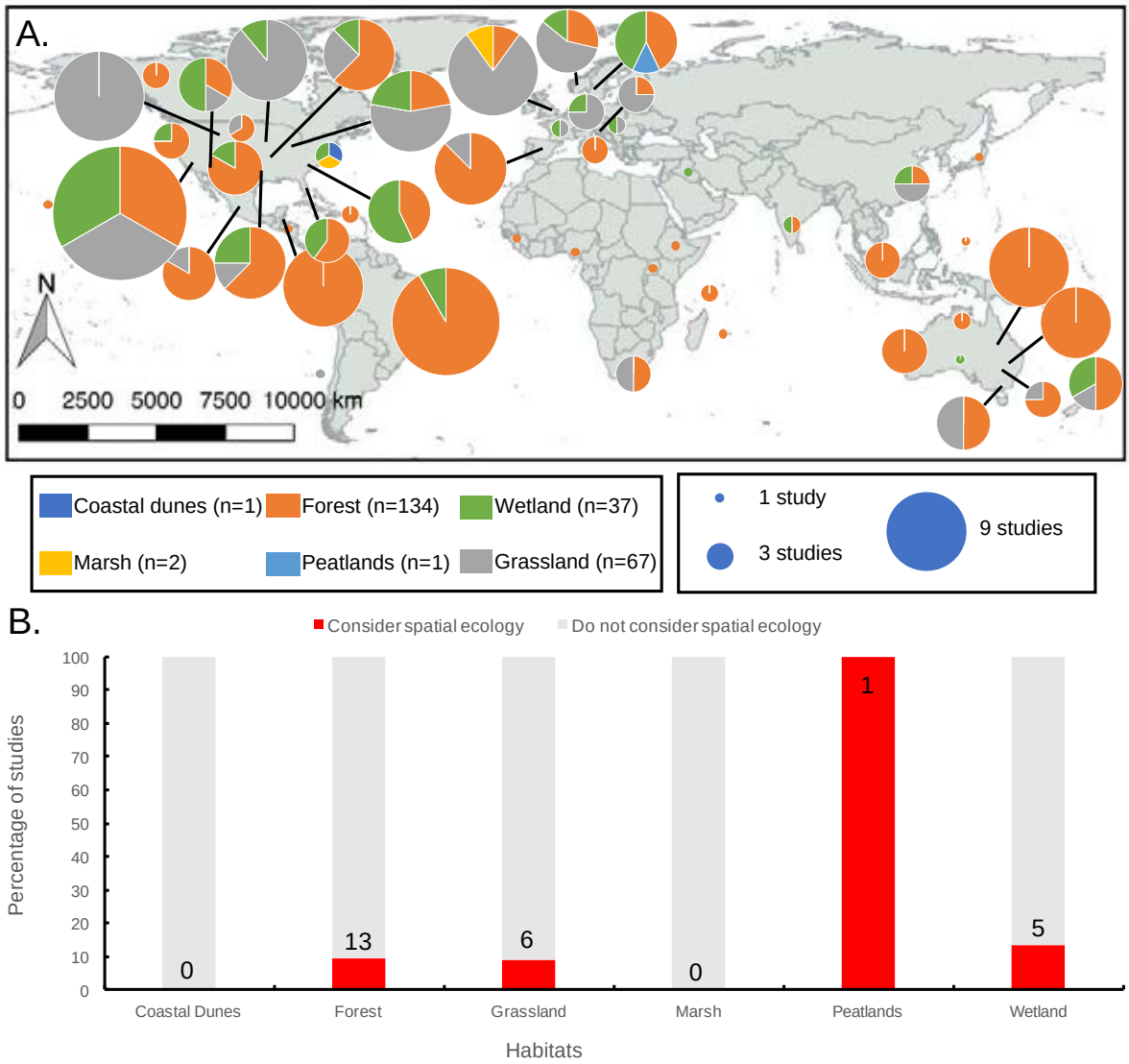

Figure 4 (A) Global distribution of terrestrial restoration projects that aimed to restore animal populations, assemblages, or diversity. (B) Of the 243 terrestrial restoration projects, only 25 (10%) considered landscape context in their design phase (Table 1). The integration of landscape attributes did, however, differ among terrestrial ecosystems. Numbers above bars indicate the number of projects that considered landscape context in site selection.

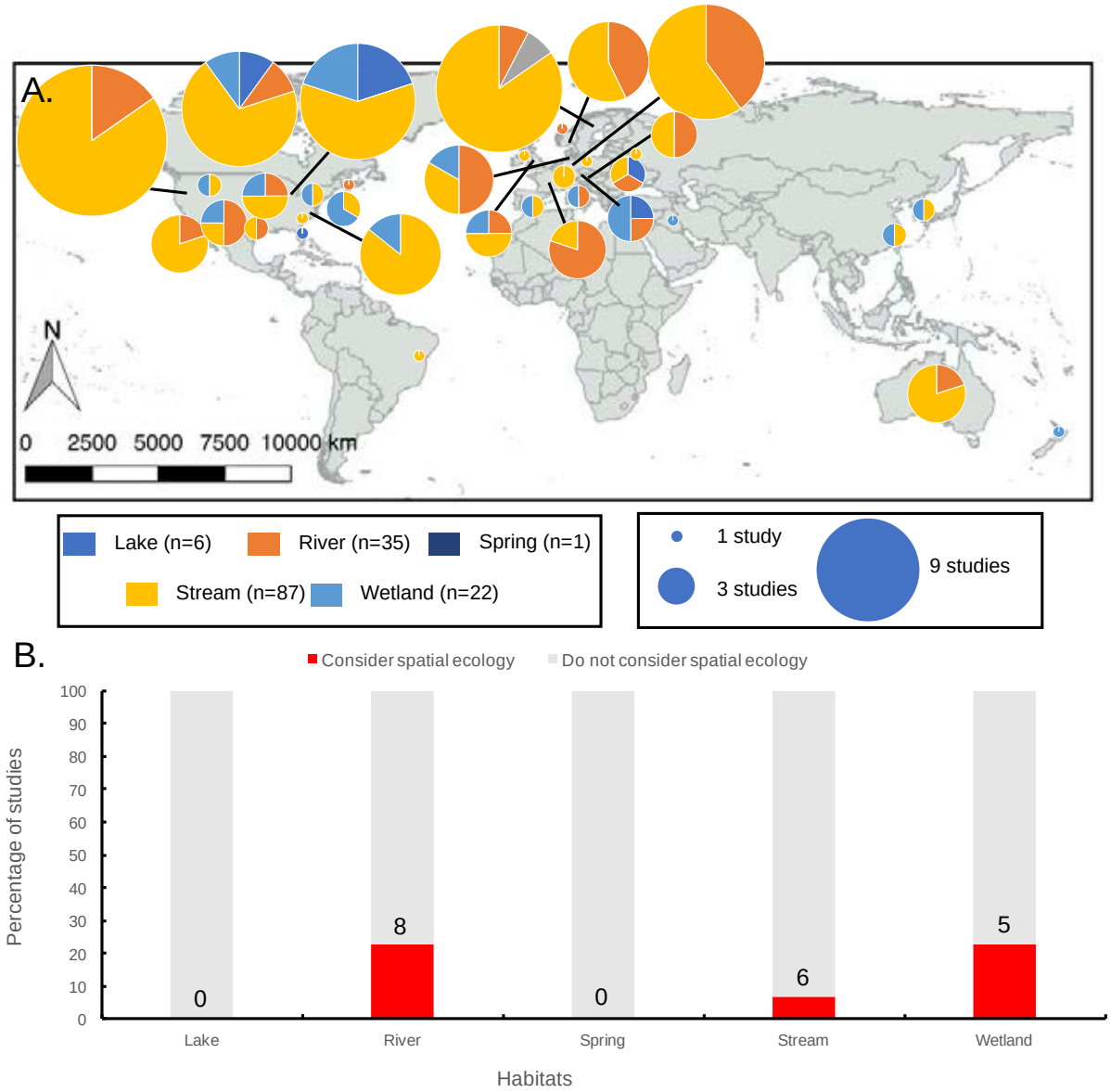

Figure 5 (A) Global distribution of freshwater restoration projects that aimed to restore animal populations, assemblages, or diversity. (B) Of the 151 freshwater restoration projects, only 19 (13%) considered landscape context in their design phase (Table 1). The integration of landscape attributes did, however, differ among freshwater ecosystems. Numbers above bars indicate the number of projects that considered landscape context in site selection.

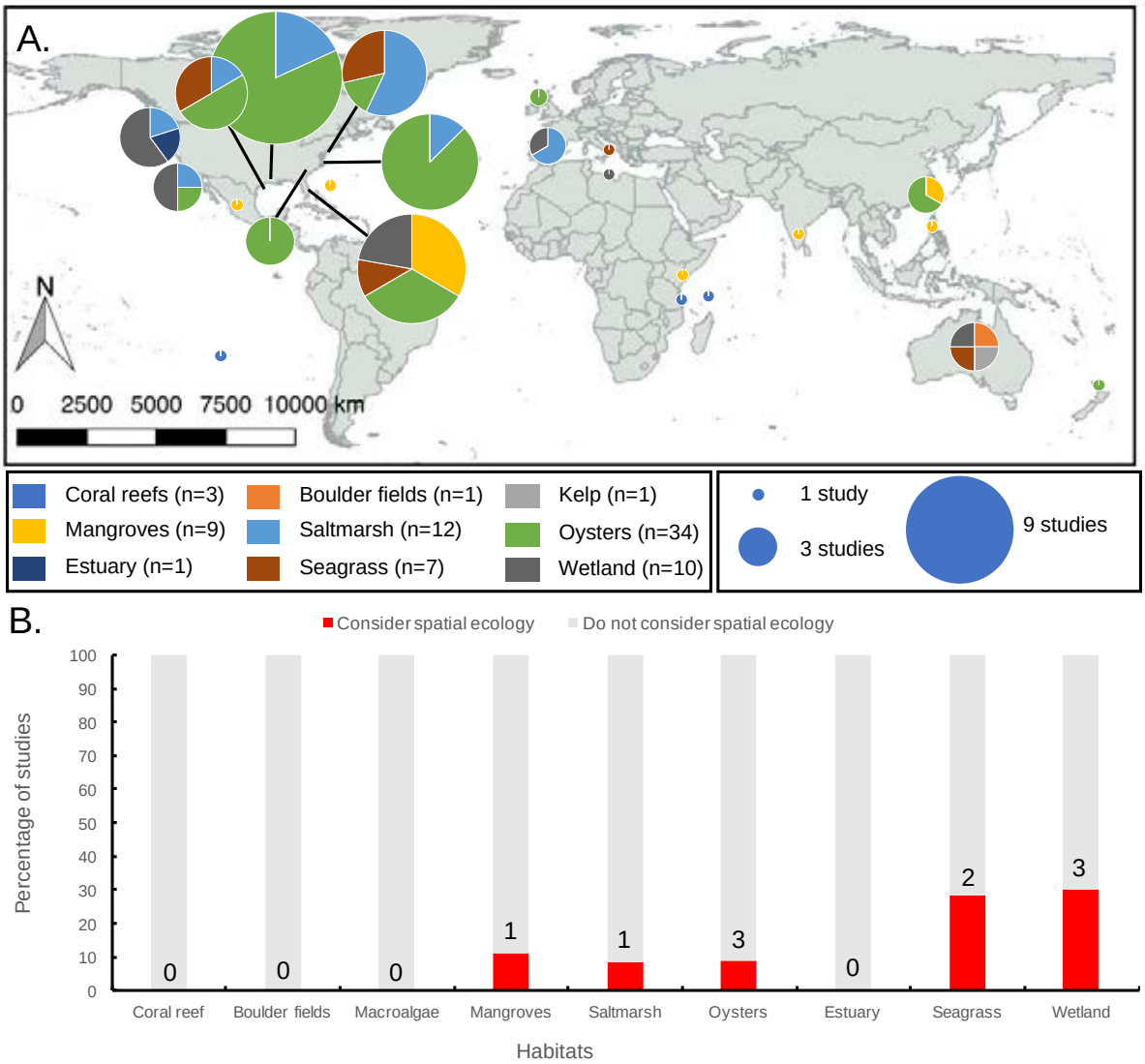

Figure 6 (A) Global distribution of marine restoration projects that aimed to restore animal populations, assemblages, or diversity. (B) Of the 78 marine restoration projects, only 10 (13%) considered landscape context in their design phase (Table 1). The integration of landscape attributes did, however, differ among marine ecosystems. Numbers above bars indicate the number of projects that considered landscape context in site selection.

There was good evidence to suggest that incorporating landscape context into the selection of restoration sites resulted in positive outcomes for animals, with 56% of projects (30 of 54 projects) that did consider landscape context reporting positive outcomes for animals (Table 1, Figure 3). The remaining 44% (24 of 54) of projects did not explicitly test whether landscape context affected animals directly. Projects that reported positive effects of landscape context on animals were more common on land (72% of 25 projects) and in the sea (60% of 10), than in freshwater (32% of 19).

Most included studies focussed on the ecological effects of connectivity (74% of 54 projects), either between patches of the same habitat, or with other habitats. Projects that reported positive effects of connectivity on animals were common across terrestrial (84% of 25 projects), marine (60% of 10), and freshwater (68% of 19) landscapes. The majority of these (69% of 54 projects) considered connectivity between patches of similar habitats, and fewer considered the effects of connectivity with adjacent alternate habitats (3% of 54 projects, and one in each environmental realm; Table 1). The potential ecological effects of other landscape concepts have, however, rarely been tested with empirical data (26% of 54 projects), with most research limited to the effects of hydrology in aquatic ecosystems (Table 1).

In most projects (89% of 472 projects), landscape context was not listed as a criterion in the selection of restoration sites (Table 1, Figure 3). Where restoration studies did not consider the spatial attributes of landscapes, projects were most often at mine sites (15 projects, 6% of terrestrial projects), located to minimise the effects of erosion on freshwater ecosystems (4 projects, 3% of freshwater projects), or placed randomly in landscapes (12 projects, 4% of terrestrial projects and 1% of freshwater projects). For most studies, however, we were not able to identify how restoration sites were selected from the descriptions provided (74% of 472 projects). This was a common trend across terrestrial (177, 73% of all terrestrial projects), marine (58, 75% of all marine projects) and freshwater (113, 75% of all freshwater projects) realms.

The first restoration studies that explicitly considered landscape context when selecting restoration sites were published in 1996 for freshwater ecosystems, 2001 for terrestrial ecosystems, and 2004 for marine ecosystems (Figure 7A). The proportion of studies that considered landscape context has remained highly variable with no clear trend between

years over the past three decades (Figure 7A). By contrast, there has been a sharp increase in the integration of spatial concepts from landscape ecology into the wider fields of biology and ecology during this period (Figure 7B).

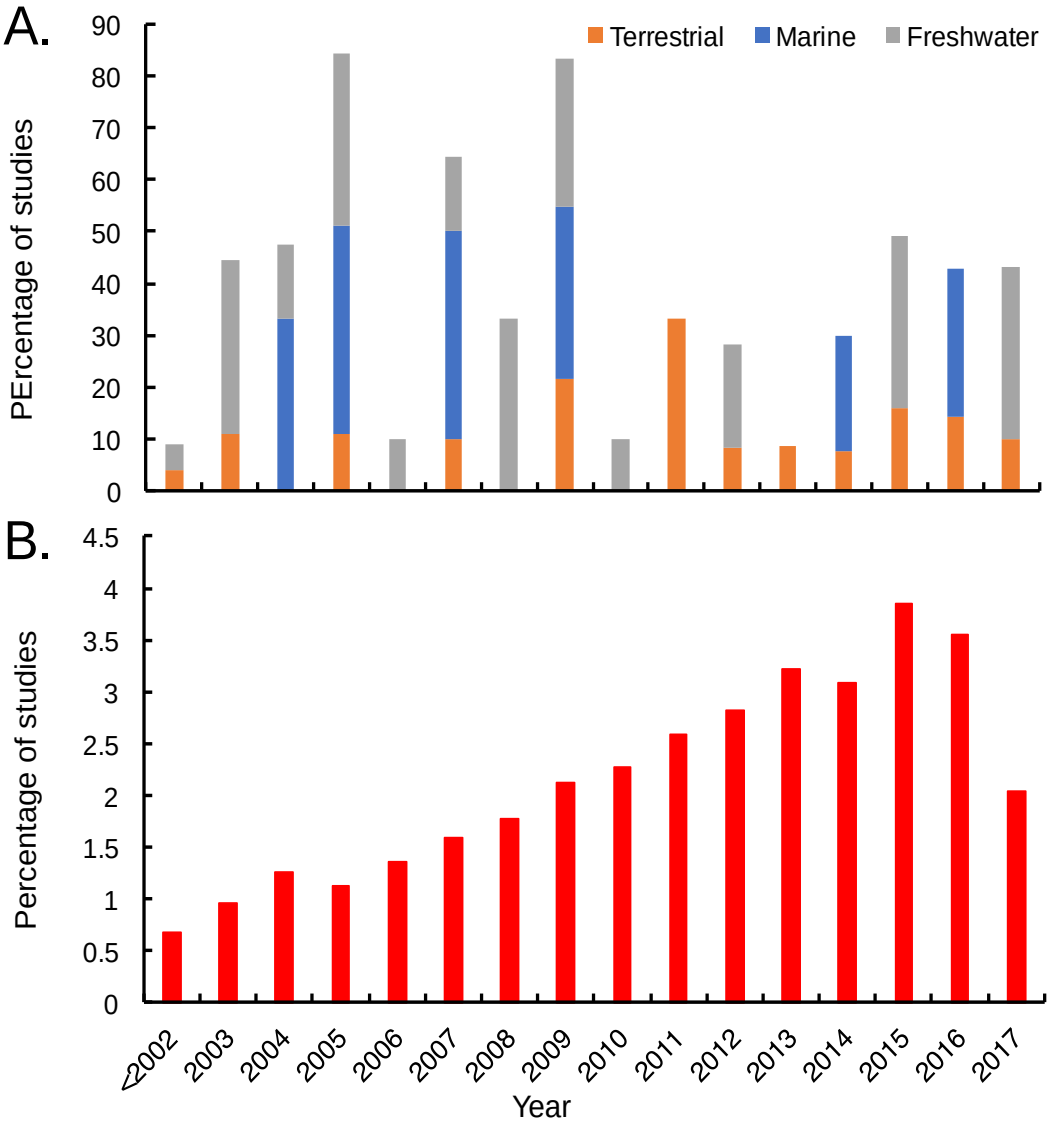

Figure 7 Summary of published studies that have considered landscape context in: (A) restoration (separated for terrestrial, marine and freshwater realms); and (B) across the fields of biology and ecology. Data extracted from ISI Web of Knowledge the key words restoration ("habitat restoration" or "ecological restoration" or "ecosystem restoration"), “biology” or “ecology”, and “landscape ecology” or “spatial ecology”. 2017 is part year only.

Discussion

The ecological outcomes of restoration projects can, in many cases, be improved by placing sites at locations in landscapes to maximise the recruitment of individuals to newly created habitats (Jones and Davidson 2016a). Whereas it is widely appreciated that the landscape context of restored habitats can shape the success of restoration projects, the principles of landscape ecology remain rarely considered in restoration decisions. In this study, we show that a marked discrepancy exists between the stated importance of landscape context for restoration (37% of studies reviewed), and the extent to which the spatial properties of landscapes are considered in restoration projects (12% of studies reviewed). Furthermore, we found no evidence that the consideration of landscape context in restoration has increased over the past three decades. This is surprising as spatial concepts have been more widely adopted in conservation during the same period, and there are important global restoration policy documents which advocate for its inclusion (Keenleyside et al. 2012; SER 2008). This result could eventuate because of underreporting in the description of restoration sites, restricting our use of only the primary. However, peer-reviewed literature offers some safeguard against substantial under-reporting of the design process.

We found no clear evidence as to why the uptake of spatial ecological principles varied across different habitats; likely because the uptake was consistently low across all habitats. The exceptions were habitats where few restoration projects were identified, but had very high uptake of landscape context principles (e.g. peatlands); however, little can be gleaned from these few examples from habitats with fewer restoration projects. There were also no clear trends in habitats which have been studied extensively in terms of landscape context. For example, the study of landscape context on coral reefs is highly advanced (Pittman and Olds 2015), but no coral restoration projects have yet considered it in restoration site selection.

We identified several key types of spatial metrics that are considered in the selection of restoration sites. Predominantly, studies assessed connectivity with similar patches of habitats (e.g. Angelieri et al. 2016; Derhe et al. 2016); unsurprising given that the role of restoration is often to enhance or reconnect threatened habitats, so considering nearby patches of this habitat is usually important. Concepts such as hydrologic connectivity and connectivity with alternative habitats (i.e. those other than the habitat being restored) were, however considered an order of magnitude less than connectivity with similar habitat

patches. This relatively low number of studies focusing on hydrologic connectivity is surprising because reconnecting water bodies hydrologically is an important focus in wetlands, and aquatic ecosystems globally (Jackson and Pringle 2010; Kondolf et al. 2006). Similarly, concepts regarding the spread of propagules by wind or other mechanisms received little attention in the studies we identified. This means that there are several key concepts and metrics within spatial ecology that have yet to be properly studied in restoration, but that are likely to be helpful in placing restoration efforts. Broadening the scope of the types of considerations and metrics used to place restoration should be a key focus of restoration researchers and practitioners alike.

Most projects that incorporated concepts from landscape ecology into their design and site selection reported positive outcomes for animals, albeit with some variation between terrestrial (72% positive outcomes), marine (60%) and freshwater (31%) realms. For example, in freshwater ecosystems, wetland restorations for amphibians reported marked increases in adult breeding populations within three years of restoration of ponds that were highly connected to each other (Petranka et al. 2003); an effect that is inconsistent for other similar freshwater restoration projects where context was not considered (Shulse et al. 2012). These sorts of considerations of adult, breeding metapopulations were rare, but are likely instructive for the enhancement of animal populations across landscapes (McAlpine et al. 2016; Montalvo et al. 1997). Some counterintuitive results were uncovered for oyster reefs. Higher connectivity (in this case, simply proximity) with adjacent habitats is usually viewed as beneficial for coastal marine organisms (Olds et al. 2018c). However, restored reefs in North America contained higher fish abundance when further from existing marshes because they provided new complex habitats on previously low complexity muddy areas (Grabowski et al. 2005). Conversely, higher connectivity between extant reefs and restored reefs was viewed as a positive influence on inhabiting fauna in other studies (Gregalis et al. 2009). Although no studies have assessed how projects or sites that did incorporate spatial context into their design, versus those that didn't (e.g. randomly, or for some other ecological reasoning) performed relative to each other, these findings suggest that the spatial properties of landscapes might have broad, and largely unrecognised, effects on the success of ecological restoration projects.

Ecological restoration is conducted for many purposes, and not all types of restoration are designed to benefit animals. For example, many restoration projects seek to restore whole

ecosystems (e.g. whole of lake restoration), to reverse a particular type of impact (e.g. mine site rehabilitation, oil spill remediation) (e.g. Brady and Noske 2010), or to limit the ecological effects of ongoing disturbances, such as erosion, sedimentation, nutrient enrichment or pollution (e.g. restoring oyster reefs to reduce shoreline retreat, or forests to reduce gully erosion) (e.g. Piazza et al. 2005). Under these circumstances, restoration sites might be placed in areas that are considered appropriate for the establishment of habitat-forming species, but which might be isolated from other remnant patches of the same habitat that serve as sources for the recruitment of animals. Because the locations of these types of projects are often fixed, it might not always be possible for restoration decisions to be placed in a landscape context. Alternatively, restoration sites might be placed in areas to limit the potential for conflict with other human uses (e.g. fishing, farming, recreational use, transport), or legislation (e.g. mooring areas, other forms of conservation) (Pressey and Bottrill 2008), and these might not be optimal for the restoration of ecosystems, or their inhabiting animals (Fahrig 2001; Pottier et al. 2009). Both approaches might result in restoration sites being unintentionally restricted to locations that provide poor habitat values for animals (cf. 'residual' conservation areas) (Pressey and Bottrill 2008; Pressey et al. 2000), and which therefore have the potential to yield suboptimal restoration returns for animals.

There are several key research areas that should be promoted to assist in better prioritising restoration across landscapes. We raise in this review a paucity of restoration projects incorporating systematic conservation planning regimens in the selection of restoration sites. Studies should be conducted to determine the validity of using systematic conservation practices (Margules and Pressey 2000) for restoration across environmental realms (research question 1; Table 2). Despite this review uncovering a diversity of ecosystems and animals that have been the focus of restoration, there are several ecosystems (research question 2; Table 2) and animal groups (research question 3; Table 2) that remain underrepresented within the literature. For example, very few studies have assessed the capacity for coastal dunes to be restored for animals, especially birds, despite beach ecosystems being regularly restored for these purposes (Maslo et al. 2012; Maslo et al. 2011). To date, most work on the effects of landscape context on the outcomes of restoration have focused specifically on how the metric of connectivity (especially proximity and isolation) between patches of similar habitat affects the abundance of animals. Restoration sites are always positioned within heterogeneous landscapes of multiple habitat

types, so further research should be conducted on how connectivity with nearby patches of different habitat types affects the success of restoration more broadly (research question 4; Table 2), as well as the condition of animal populations themselves, where this is a key restoration goal (research question 5; Table 2). Similarly, there are several landscape metrics, beyond simple distance-based connectivity metrics (especially Euclidean distance), that might assist in developing more robust and representative models for incorporating landscapes ecology into restoration. Landscape ecologists have developed several multivariate or multimetric variables that can be used to describe the complexity of landscapes for animals (e.g. McGarigal et al. 2012). The efficacy of these metrics in restoration should be further investigated for different ecosystems and target animals (research question 6; Table 2). Several authors have discussed the validity of landscape metrics, and concepts across environmental realms (Pittman et al. 2018). For example, there is some evidence to suggest that the best metrics to describe spatial patterns in animal abundance might differ between the land and the sea due to the movement of water bodies in aquatic ecosystems (Pittman et al. 2018). Establishing the validity of these metrics across environmental realms will assist in generalising restoration planning regimens across realms (research question 7; Table 2). Collectively, answering these priority research questions will assist in establishing more effective regimens for systematic landscape restoration across all environmental realms, and provide the evidence that managers need to support their decision making-processes.

Table 2. List of priority research questions for integrating landscape principles into restoration ecology.

	Priority Research Questions
1.	Are the principles of systematic conservation planning (Margules and Pressey 2000) directly translatable to all restoration projects, and if not, which principles need to be tailored specifically for restoration?
2.	For which habitats does landscape context matter most, and which metrics, and which connections, should be prioritised for individual habitat types?
3.	For which animal groups does landscape context matter most, and which metrics, and which connections, should be prioritised for individual animal groups?
4.	To what degree does considering connectivity with other habitats (i.e. inter-habitat connectivity) affect the outcomes of restoration projects (e.g. Unsworth et al. 2008)? To date, most research and focus in the literature has been on connectivity between patches of the same habitat (i.e. intra-habitat connectivity).
5.	To what degree can incorporating metapopulation dynamics and connectivity into restoration planning enhance animal population fitness, persistence, and resilience?
6.	Are there more thorough, or better, metrics that can be used to optimise the spatial placement of restoration (e.g. McGarigal et al. 2012)? To date, most work on the spatial metrics that influence restoration has focused on connectivity, especially proximity (Euclidean) between similar habitat patches.
7.	Is there consistency in the efficacy of spatial metrics across environmental realms? (e.g. Pittman et al. 2018)

Systematic conservation planning has made great progress in using a diversity of landscape characteristics and sophisticated algorithms to guide the design of protected areas and reserve networks (Margules and Pressey 2000; Moilanen et al. 2009). The principles of landscape ecology, and the techniques of conservation planning, might be useful in the design of restoration areas, but have not been widely applied to introduce a critical spatial element to restoration planning (Hodgson et al. 2011). When selecting sites for a network of reserves, the conservation planning process starts with a broad, landscape-scale perspective. Ecosystems, habitats and locations are selected for protection to maximise conservation benefits across the entire landscape, and some potential sites are then eliminated because of other consideration (e.g. extractive industries, tourism) (Watts et al. 2009). By contrast, restoration projects often start with a narrower perspective focusing on the specific ecosystem or habitat to be restored. Sites are then selected based on their suitability to support the particular ecosystem of interest, with little consideration given to the attributes of landscapes beyond the restoration site. Incorporating the lessons learned from systematic conservation planning (i.e. goal setting, data-based feedbacks, and improvements) and the principles of landscape ecology (i.e. the placement of sites in heterogeneous land- and seascapes) into restoration should, therefore, lead to significant improvements in the design, placement and ecological effectiveness of restoration projects. We advocate for a landscape-scale approach to restoration, and suggest that spatial restoration ecology should start with the identification of ecosystems and habitats that are in the greatest need of restoration (based on the best historical information available). Sites for restoration should then be selected from all suitable locations within the landscape of interest to maximise their potential ecological benefits for the ecosystems themselves, the animals and foodwebs these support, and the ecological functions and ecosystem services they provide. This spatial approach to restoration ecology should, therefore, help to broaden both the scope and perceived ecological benefits of many restoration projects, and might also improve returns on investment across restored landscapes.

Chapter 3

Maximising the benefits of oyster reef restoration for finfish and their fisheries

Gilby BL, Olds AD, Peterson CH, Connolly RM, Voss CM, Bishop MJ, Elliott M, Grabowski JH, Ortodossi NL, Schlacher TA (2018) Maximizing the benefits of oyster reef restoration for finfish and their fisheries. Fish and Fisheries 19:931-947

Introduction

Globally, 85% of oyster reefs have been lost, mainly due to overharvesting, disease, and poor water quality (Beck et al. 2011). Lost oyster reefs are often replaced with ecosystems that provide lower habitat values for fish (i.e. less food, or poorer protection from predators), such as bare sediments (Grabowski et al. 2012). These changes can be associated with reductions in fish diversity, biomass and abundance, and with declines in the landings of recreational and commercial fishes (Coen et al. 1999; Peterson et al. 2003). As a consequence, the restoration of oyster reefs as fish habitats, and therefore to enhance fish and/or fisheries is often, but not always, a key aim of oyster restoration projects (Coen and Luckenbach 2000; zu Ermgassen et al. 2016).

Ecological restoration of oyster reefs for finfish and their fisheries is an important component of many coastal management and enhancement schemes (Baggett et al. 2015; Creighton et al. 2015; Humphries and La Peyre 2015). Oyster reef restoration encompasses both categories of ecoengineering; Type A, the restoration of habitats thus allowing the desired species to colonise or expand, and Type B, which involves the direct increase of a species, such as through restocking or replanting (Elliott et al. 2016). Globally, 46 studies detail oyster restoration projects which seek to enhance finfish and/or their fisheries around reefs (as identified from the ISI Web of Knowledge; Figure 1, Table S1). Restoring oyster reefs can augment fish biomass by up to 260 g/m^2 of restored reef per year (Peterson et al. 2003). These effects of restoration on fish populations result from enhanced larval settlement and survival (Breitburg et al. 1995), and the immigration of adult fish to reefs, where they feed and take shelter (Gittman et al. 2016; Harwell et al. 2011). By enhancing fish biomass, restored oyster reefs can convey economic benefits of up to US$4123 $ha^{-1}yr^{-1}$ for local commercial fisheries (Grabowski et al. 2012). While restored oyster reefs are relatively common in North America (87% of studies have been conducted on the Atlantic or Gulf coasts of the USA; Figure 1), oyster reef restoration projects focusing on fish enhancement are only just gaining interest and momentum in Australia (Gillies et al. 2015b), Europe (Farinas-Franco and Roberts 2014) and Asia (Quan et al. 2009). Whilst enhancement of fish populations is just one of the multiple ecosystem services provided by restored oyster reefs, and is not always the key driver of restoration (e.g. intertidal oyster reef restoration may be to stabilise shorelines and protect them against erosion) (Grabowski et al. 2012), win-win scenarios (for the ecology and the economy) may be created if, irrespective of the key goal, reefs are also designed to enhance fish. By expanding the goals of oyster reef

restoration to include fish and fisheries, we might, therefore, also enhance the economic, social and cultural values associated with restoration efforts, and maximise stakeholder engagement, both locally and globally (La Peyre et al. 2012).

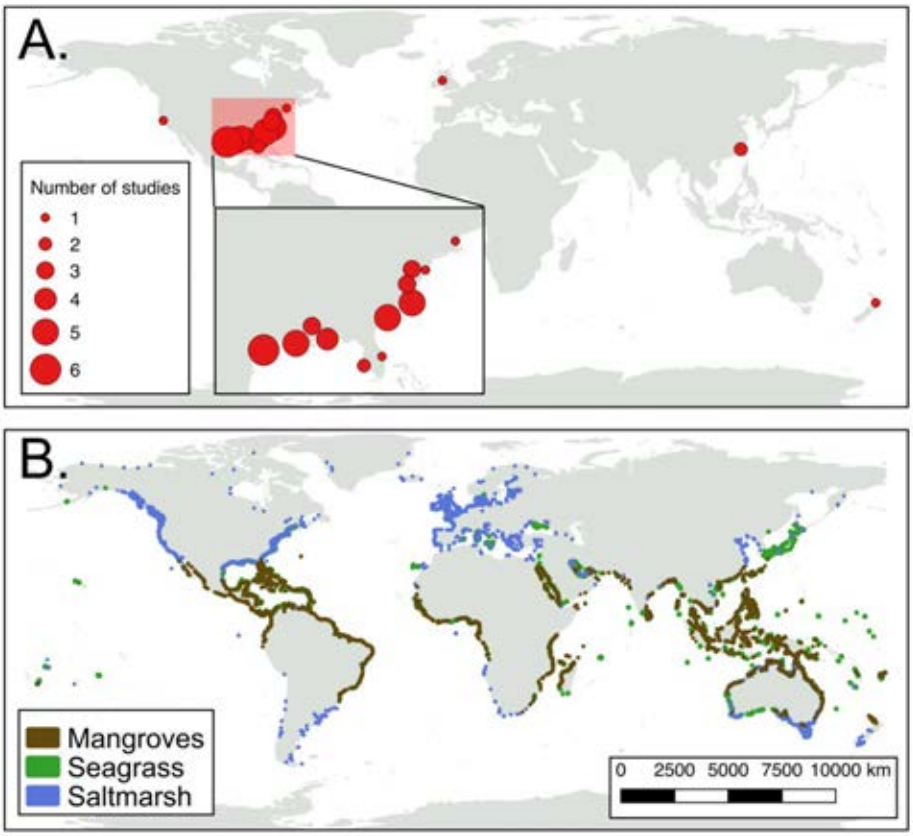

Figure 1 Global distributions of (A) studies assessing the effects of oyster reef restoration for fish (as identified from ISI Web of Knowledge search for *(oyster* and fish and restor*)*), and (B) the global distribution of key habitats with which oyster reefs have a functional linkage. Information on the extent and geographic distribution of ecosystem types sourced from the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC).

While it is well established that restoring oyster reefs can augment fish biomass and enhance finfish fisheries, the published literature on oyster reef restoration poorly integrates several important ecological concepts that shape fish populations in coastal waters. For example, it is widely accepted that the extent of key coastal nursery habitats, such as seagrass, marshes, and mangroves (Nagelkerken et al. 2015), and the degree to which these habitats are connected (Olds et al. 2016; Pittman et al. 2011), are significant determinants of fish assemblages in coastal seascapes. Therefore, future oyster reef restoration projects can build on the first generation of oyster reef projects, which have demonstrated that reefs augment the productivity of a number of finfish species, by adopting a landscape-scale approach that accounts for how reefs interact with other structured habitats (Bostrom et al. 2011). Advances in our understanding of how managing catchment water supply, sediment and nutrient runoff affects coastal ecosystems (Gorman et al. 2009; Klein et al. 2012), and more effective fisheries restrictions (Gilby et al. 2017b) can also improve the ecological condition of coastal habitats and modify the composition of fish assemblages. An increasing literature on ecohydrology with ecoengineering principles are providing case-studies of success and failure (Elliott et al. 2016). However, the extent to which these interventions affect the outcomes of oyster reef restoration projects for fish is unclear. The capacity of oyster restoration projects to promote fish biomass and enhance fisheries can, therefore, be improved by better incorporating modern concepts in fish ecology and fisheries management into the design of reef projects.

In this paper, we review the relevant literature to better integrate the fields of fish habitat research, seascape ecology, and coastal management into oyster reef restoration projects. First, we outline three important prerequisites that must be established for oyster reef restoration projects that seek to enhance fish populations and fisheries (Figure 2). We then introduce four key concepts (Figure 3) that will improve restoration outcomes for fish and fisheries: (1) view oyster reefs as fish habitats; (2) recognise that oyster reefs are part of a wider seascape that includes other fish habitats; (3) consider the impact of other management interventions (e.g. fishing restrictions, catchment runoff reductions), and (4) monitor the effects of restoration for both oysters and fish across the entire seascape, and implement changes to restoration plans where necessary. The overarching intent is to fine-tune the design, placement, and management of restored oyster reefs to minimise their economic costs and maximise their ecological benefits for *both* oyster reefs and finfish fisheries.

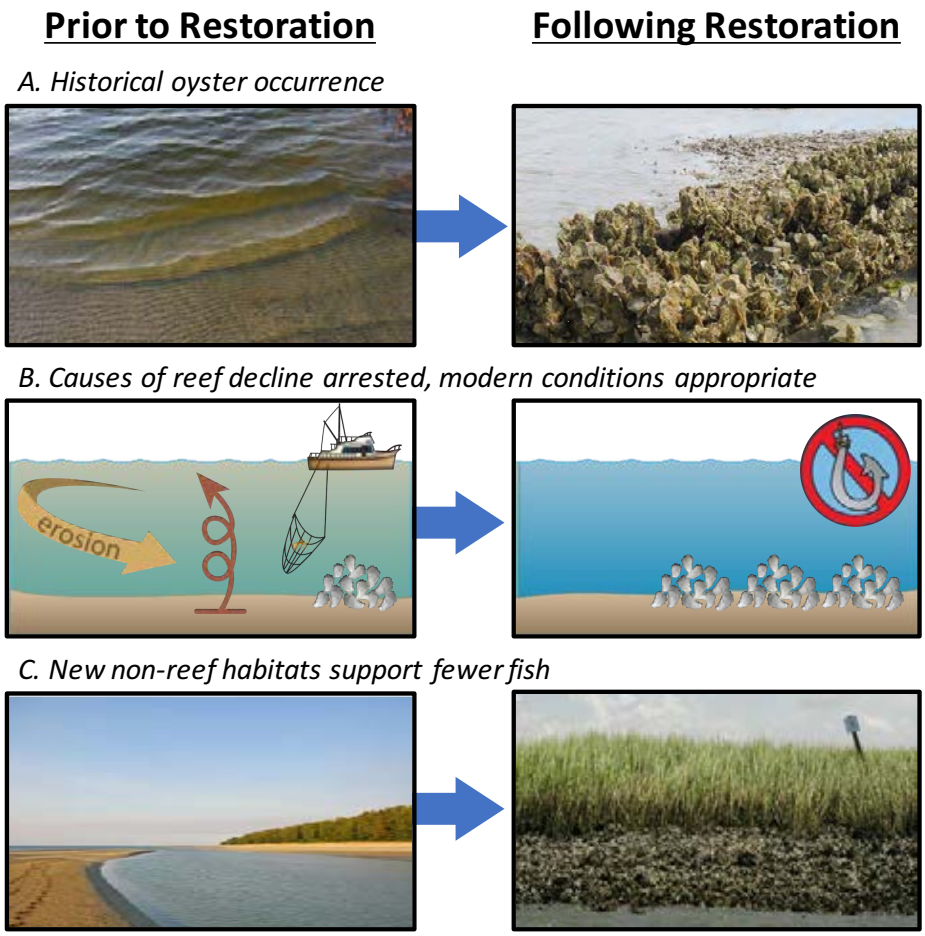

Figure 2 There are three important prerequisites for oyster reef restoration projects that seek to enhance finfish and their fisheries: (A) evidence for the historical occurrence of oyster reefs in the target region; (B) whether the detrimental effects of human activities that caused the loss of oyster reefs have been controlled and modern conditions are suitable for reef restoration; and (C) if lost reefs were replaced by habitats (e.g. bare sediments) that support significantly fewer fish than oyster reefs. Images courtesy US Fish and Wildlife Service, Kaensu (Flickr) (CC BY 2.0), and D. Schwen (CC BY 3.0).

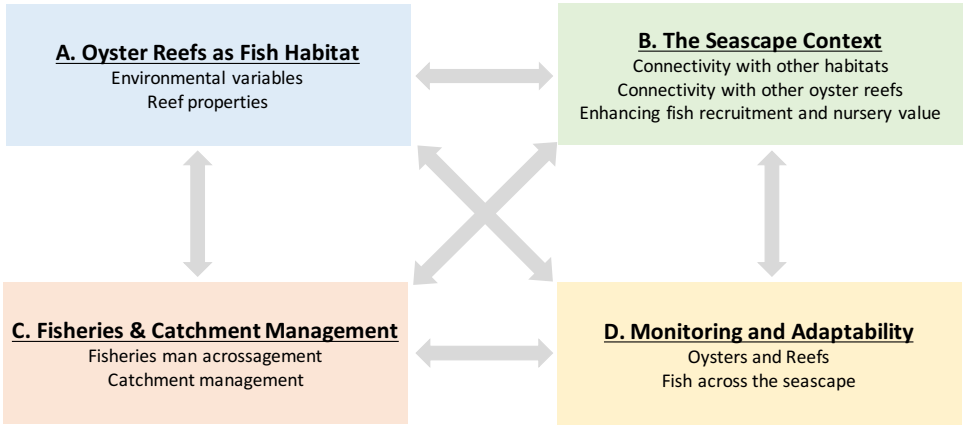

Figure 3 Key concepts to improve restoration outcomes for fish and fisheries. (A) Oyster reefs must be healthy and complex biogenic habitats that are positioned within the physicochemical niche of both oysters and fish. (B) Oyster reef restoration projects should be positioned to improve connectivity (between reefs and among reefs and other habitats), promote fish recruitment and enhance the nursery function of coastal seascapes for fish. (C) Other impacting processes (e.g. fishing, sedimentation, eutrophication) must be managed to limit their effects on the performance of restored oyster reefs. (D) Management decisions must be adaptable, responding to key criteria from thorough monitoring programs that are specifically designed to ascertain the health and development of the reefs, and detect the effects of oyster reefs for fish both on reefs, and in the surrounding seascape.

Prerequisites for restoring oyster reefs for finfish and their fisheries

Adding oyster reefs to systems where they did not occur historically (i.e. at an ecosystem or embayment-wide scale) can be viewed as the artificial modification of coastal seascapes. The absence of oyster reefs from where areas where they are to be restored might be because the area is has either unsuitable substratum or water quality (including turbidity and salinity) or there not being any spat supply. In the case of a degraded system, e.g. where historical populations are now absent, failing to remedy the human activities that led to the degradation, or loss, of oyster reefs or prevent their recovery (e.g. over-harvesting, poor water quality) will severely limit the success of any restoration project. In some instances, oyster reefs may have been replaced by other structurally complex ecosystems (e.g. seagrass, kelps, or mangroves) that also provide important habitat for fish; restoring oyster reefs in these locations might not result in overall net improvements in fish or fisheries (Grabowski et al. 2005). Consequently, there are three important considerations (Figure 2) for oyster reef restoration projects that seek to enhance fish and fisheries:

A) evidence for the historical occurrence of oyster reefs in the target region;

B) causes of oyster reef decline must be reversed, and modern day conditions are suitable for oyster growth; and,

C) new non-reef habitats support fewer fish than oyster reefs.

Key concepts to improve restoration outcomes for fish and fisheries

1. View oyster reefs as fish habitats

The environmental conditions under which oyster reef restoration is most successful are well documented (e.g. Baggett et al. 2015). Many of the conditions that affect the outcomes of oyster production also influence fish abundance and diversity, thereby functionally linking oyster reef habitats with fish via water quality and other attributes of the environment. We will, therefore, examine how the factors that control establishment of restored oyster reefs might also affect the fish assemblages that colonise these reefs.

Environmental variables

Both oysters and individual fish species each have optimal, and often different, physicochemical envelopes in which they prefer to live (e.g. Solan and Whiteley 2016). For example, oyster restoration sites must be located within the physiological tolerances of the main reef-building oyster and/or mussel species, with respect to temperature, salinity, dissolved oxygen, and turbidity (Baggett et al. 2015). Catchment run-off, tides, waves, and currents modify these environmental variables over a variety of temporal scales (Rodriguez et al. 2014), thereby emphasising the need for a good understanding of ecohydrology principles (Wolanski and Elliott 2015). Therefore, consideration of the range and threshold (tolerances) values of these abiotic factors is more important than their mean values in determining the placement of oyster reefs. In addition, for a self-sustaining bed, the site has to be within a suitable hydrographic regime to get the spat delivered to the area, i.e. hydrographic concentration. Selecting sites that match the optimal environmental tolerance envelopes for both oysters and fish should therefore be considered a key goal when seeking to restore fish assemblages around restored oyster reefs.

Most estuarine fish species have evolved to cope with variation in the physicochemical properties of coastal waters (Elliott and Quintino 2007), but are nevertheless also susceptible to extreme water temperatures (Marshall and Elliott 1998), salinity levels (Bachman and Rand 2008; Marshall and Elliott 1998), and low dissolved oxygen concentrations (Stevens et al. 2006) that are beyond their physiological limits. To minimise

effects of variable and especially poor water quality on both oysters and fish, oyster reef restoration projects can target locations that provide highly oxygenated waters with good water flow (Lenihan et al. 1999; Lenihan et al. 2001). The appropriate water quality has to be at the reef site, as well as the site of the source oyster or fish populations.

High sedimentation, especially from fine silts and clays, detrimentally affects oyster spat settlement, and lowers the body condition, reproductive output, and growth of oysters (Kimbro et al. 2014; Lenihan 1999; Tamburri et al. 2008). High turbidity levels can also be harmful to some estuarine fish species (Benfield and Minello 1996), particularly visually-orienting predators (Lunt and Smee 2015). Whilst oyster reefs can help to reduce turbidity at local scales, this effect may take several years to develop and relies on the persistence of adult oysters (La Peyre et al. 2014b; Newell and Koch 2004). Positioning oyster reefs at sites within estuaries that regularly experience very high turbidity may, therefore, limit both the growth of oyster reefs and the rate at which they are colonised by fish. Many estuaries, especially macrotidal ones, have strong erosion-deposition cycles which need incorporating into the assessment of risk to the beds.

Reef properties

A prime function of restored oyster reefs is often to create or enhance fish habitat. The biological and structural properties of restored oyster reefs are often important factors in determining the quality of reef habitat to fish, including providing food and shelter from predation (i.e. reef size, vertical relief, water cover, and structural complexity). The reef could produce the appropriate habitat even if the oysters were no longer alive.

Oyster reefs are actively restored either by replacing hard substrata that have been lost, thereby allowing new oyster spat to settle and grow (e.g. Type A ecoengineering), and/or by reintroducing living oysters (Baggett et al. 2015; La Peyre et al. 2014a), (e.g. Type B ecoengineering) (Elliott et al. 2016). Both methods require successful larval settlement, which can result from mature oysters on restored reefs or as oyster spat brought from other locations (Lipcius et al. 2008). Reef-associated fishes often feed directly on oyster spat, adult oysters and other invertebrates (e.g. polychaetes, amphipods, sponges, mussels) that grow on oyster reefs, or use reefs as habitats (Johnson and Smee 2014; Lehnert and Allen 2002). Therefore, productive reefs composed of healthy oysters, and other invertebrates, are likely to be more beneficial for fish (Peterson et al. 2003).

Subtidal reefs that extend high above the seabed and out of potential low oxygen concentration boundary layers, result in improved oyster settlement, growth, and survival on the reef crests (Lenihan et al. 1999). Taller reefs might also be more resilient to the potential impacts of sedimentation, sea-level rise, parasites and diseases (Lenihan et al. 1999; Rodriguez et al. 2014). However, as with marine mussels the increase in bivalve individual size to make the organisms protrude above the bed boundary layer could make them susceptible to begin pulled off the bed by the stronger currents. Oyster reefs with greater vertical relief provide more calm water in their lee (i.e. current shadow), which is favoured by some fish species (Breitburg et al. 1995; Lenihan 1999), and can be positively related to fish biomass (Gratwicke and Speight 2005b).

Placing reefs in intertidal locations results in their drying at low tide, thus restricting the time for fish to use the area. Because fish need water, the habitat value of intertidal reefs for fish may be lower than that of subtidal reefs (e.g. Lehnert and Allen 2002). While these intertidal reefs, like many other intertidal habitats (e.g. mangroves, intertidal flats), might provide rich feeding opportunities during high tide, the structure of the fish assemblage that utilises them often depends on the composition of the surrounding seascape that fish use during low tide (Olds et al. 2012a; Pittman et al. 2004). This indicates the importance of the knowledge of the biological and hydrographic connectivity between areas and hence feeding, breeding or refugia migrations. The dispersal rates of larvae (of oysters) and post-larvae (of fishes) combined with tidal discursion distances will dictate the delivery of spat and recruits to the restored areas. This concept is similar to the effects of tides on the habitat functions of mangroves; mangrove forests that fall dry at low tide are often poorer fish habitats that those that are submerged permanently (e.g. Baker et al. 2015). Where projects necessitate intertidal reefs (e.g. due to oyster species biology, disease considerations, or to ensure safe navigation by boats), it may be important that they are positioned closer to subtidal habitats nearby where fishes can seek refuge during low tides, such as on seagrass or other reefs (Olds et al. 2012b; Peterson et al. 2003).

In terms of reef and project extent, a restoration project seeking to enhance seascape heterogeneity for fish can aim to restore the greatest extent of oyster reefs possible within financial and time limitations, up to any established historic extents of oysters in the target estuary. The size of a restoration site has two complementary facets: 1) the area of seabed

covered by living and non-living oyster shells, and 2) the total aerial dimensions of the project footprint, including any non-reef areas between oyster reefs (Baggett et al. 2015). Habitat complexity and extent will dictate the ability of the restored area to gain or regain it functioning; for example, Wootton (1992) emphasised that fish diversity increased with habitat heterogeneity, then size and then productivity. Habitats that are structurally complex (e.g. reefs, mangroves, seagrass) typically harbour higher fish biomass and diversity than habitats that are simpler (e.g. sand and mud flats) (Grabowski et al. 2005; Gratwicke and Speight 2005a; Sherman et al. 2002). The architectural complexity of oyster reefs can be measured in the form of rugosity (roughness) (scale: cm to tens of m), and in the form of new spatial heterogeneity that the reefs add to coastal seascapes (scale: m to km). At the scale of individual oyster reefs, the provision of holes and crevices of variable sizes that can be inhabited by a range of fishes, and used as refuges, feeding grounds, and spawning sites, which will help to promote fish diversity and biomass (Gratwicke and Speight 2005a). At the scale of oyster restoration projects, reefs that are designed to provide a diversity of habitat structures (i.e., with high rugosity and vertical relief) across the site are likely to contain more and a higher diversity of fish (Bozec et al. 2015) because they provide more feeding opportunities and better sanctuaries from predators, especially for juvenile fish (Peterson et al. 2003). These concepts are widely accepted for artificial reefs (Sherman et al. 2002; Wilson and Elliott 2009), but require further investigation for oyster reefs (Table 1).

Table 1 List of research questions for fish and fisheries associated with restored oyster reefs.

Research Field	Priority Research Questions
A. Oyster reefs as fish habitats	***1. Food for fish:*** Under what scenarios are oysters, and the larvae of other sessile invertebrate (e.g. ascidian, polychaete, sponge), most likely to settle, grow, and provide high-quality food for fish? (e.g. Grabowski et al. 2005) ***2. Protection from predators:*** What attributes of oyster reefs (i.e. area, height, architecture) provide fish with the best protection from predators? (e.g. Sherman et al. 2002)
B. Oyster reefs as part of wider seascapes	***3. Connectivity:*** How does the seascape context of oyster reefs affect ecological processes (predation, nutrient turn- over), fish larval settlement, and habitat value for adult and juvenile fishes (e.g. Bostrom et al. 2011; Grabowski et al. 2005), are these patterns consistent across different types of seascapes, and which oyster reef designs maximise these metrics? ***4. Fish movement:*** To which alternate habitats should oyster reefs be connected to maximise reef value to fishes, and over what scales do these connectivity effects occur? (e.g. Nagelkerken et al. 2015)
C. Fisheries and catchment management	***5. People and oyster reefs:*** What are the effects of fishers and fishing on the restoration of fish biomass? (e.g. Powers et al. 2009) What are the social and cultural values of restored oyster reefs, and how can these be maximised? (e.g. Kingsley-Smith et al. 2015; Venturelli et al. 2017)
D. Monitoring and adaptability	***6. Indicator species and processes:*** What are the best ecological indicators of restoration success for finfish, and which suite of indicators are most appropriate for monitoring effects on ecosystem condition and function? (e.g. Valesini et al. 2017)

2. Recognise that oyster reefs are part of a wider seascape that includes other fish habitats

The successful restoration requires a good knowledge of ecological principles. Firstly that the physico-chemical environment will set up the fundamental substratum or water column niches which then get occupied by organisms to give community structure (the so-called environment-biology relationships) (Gray and Elliott 2009). Following this, biology-biology relationships create the ecological functioning from the structure, and then the biota start modifying the environment (biology-environment relationships) especially in the case of ecosystem engineers such as reef-forming species.

Seascape ecology transfers ecological principles and concepts from landscape ecology to marine systems (Pittman et al. 2011). At the core of seascape ecology is the recognition that the ecological functions of ecosystems are contingent on the type, condition and spatial arrangement of other ecosystem structures across entire seascapes (Bostrom et al. 2011; Gustafson 1998). The movement of matter and organisms across seascapes functionally links ecosystems, and this ecological connectivity shapes species distributions, food web structure, and ecosystem function (Olds et al. 2016; Pittman et al. 2011). The recovery of fish assemblages on restored oyster reefs relies on colonisation from elsewhere in the seascape; therefore, seascape positioning is a vital consideration when restoring oyster reefs for fish.

Connectivity with other habitats

In coastal seascapes, many fish move daily, or tidally, between marshes, mangroves, seagrasses and natural reefs at scales of metres to hundreds of metres (Bostrom et al. 2011; Grober-Dunsmore et al. 2009; Olds et al. 2018c; Potter et al. 2015). Ecosystems that are better connected (i.e., closer together, or linked by currents), therefore, usually harbour more fish than those that are isolated (Nagelkerken et al. 2015; Olds et al. 2018c) (Figure 4). The level of connectivity between oyster reefs and other ecosystems is, therefore, an important consideration in the design of oyster restoration projects; particularly for intertidal reefs that dry on ebb tides and force fish to move into subtidal habitats (Grabowski et al. 2005; Peterson et al. 2003). Despite this, connectivity is particularly difficult to quantify. The UK Marine Conservation Zone concept aimed for a coherent and connected set of sites and defined sites to be connected as dictated by larval time in the water column (Roberts et al. 2010). However, such a connectivity rule-of-thumb then depends on the tidal excursion, tidal oscillations and the presence of oceanic fronts which can be a barrier to movement (Green et al. 2014; Olds et al. 2018c).

As restoration projects are increasingly being conducted in highly modified seascapes, the degree to which built infrastructure may serve as a barrier to fish movements (Bishop et al. 2017), thereby reducing the benefits of restoration projects for finfish, may also be a significant consideration. Connections with marshes, seagrasses, and mangroves are likely to be the most important for oyster reefs (Figure 1), depending on the seascape in which they are imbedded (Bostrom et al. 2011; Gain et al. 2017) and on the local fish community requirements for feeding, spawning and refugia migrations. Globally, studies on habitat connectivity with oyster reefs are entirely restricted to marsh-dominated seascapes (Figure 1), with no studies conducted in subtropical seascapes, especially around mangroves, despite the current or historical presence of oyster reefs in many of these areas. While seagrasses occur in both marsh and mangrove-dominated seascapes, few studies have explicitly assessed the effects of seagrass connectivity for fish on oyster reefs (Table S1). Determining the importance of these connections with alternate habitats, and the distances over they function in different seascape compositions (e.g. mangrove- versus marsh-dominated seascapes), should therefore be a priority for research (research priorities 3 and 4, Table 1).

Whilst it can be generalised broadly across coastal ecosystems, that higher connectivity with alternate habitats is positive for fish assemblages (Olds et al. 2018c), there are some contrasting results within the oyster reef literature. For example, studies on oyster reefs in North Carolina, USA, concluded that restored reefs directly adjacent (<10 m) to existing vegetated habitats did not augment fish abundance to the same degree as more isolated reefs (e.g. on mud flats) (Geraldi et al. 2009; Grabowski et al. 2005). Conversely, a recent study in Texas, USA, indicated that reefs near to seagrass had higher abundance of macrofauna than more poorly connected reefs (Gain et al. 2017). The consistency of these effects within mangrove- or seagrass-dominated seascapes therefore remains unclear. Consequently, further studies which seek to determine the optimal distance for the isolation are an important requirement for optimising future restoration projects (research priorities 3 and 4, Table 1).

The scale of patch connectivity effects between habitats is usually between 100 and 1000 m in most coastal seascapes (Bostrom et al. 2011), and is dictated by: 1) fish mobility; 2) the type of migration being undertaken (e.g. feeding, reproductive); 3) the composition of

seascapes; and 4) hydrology (Edwards et al. 2009; Nagelkerken 2009; Olds et al. 2012b). For example, fish move smaller distances among habitats to feed than they do during ontogenetic migrations. Feeding migrations into seagrass meadows are often shorter than similar forays into habitats with more vertical relief (e.g. mangroves, reefs), and tidal migrations among habitats are shorter in microtidal systems than in areas that experience larger tidal ranges whose tidal excursion can be used as a transport mechanism (Grober-Dunsmore et al. 2009; Olds et al. 2018c). System-specific information on the location and condition of other fish habitats, and the scale over which fish movements link ecosystems in focal seascapes is therefore vital (Gilby et al. 2018b; Nagelkerken et al. 2015) (Table 1).

Connectivity with other oyster reefs

Habitats that are close to other patches of the same type of habitat often support higher fish diversity, abundance, and biomass than isolated patches (Gustafson and Gardner 1996; Soons et al. 2005). Effects of this type of habitat connectivity have been reported widely in seagrass, marsh, and coral reef ecosystems, but are rarely tested for oyster reefs (Bostrom et al. 2011). Where they have been tested, connectivity has shown highly variable effects (Grabowski et al. 2005; Gregalis et al. 2009). Whilst the 'optimal' distance that maximises fish movement between oyster reefs is unknown (Table 1), distances are likely to be system-specific, and scale on the dispersal capacity of species within individual systems. From published literature on both oysters and fish, we can surmise that restored oyster reefs should be sufficiently to existing reefs to ensure that they receive a good supply of both oyster larvae and fish (Gregalis et al. 2008; Steppe et al. 2016), but also sufficiently far apart to provide additional reef nodes in the network of oyster reefs that are linked by fish movement (Gustafson and Gardner 1996; Soons et al. 2005) (Figure 4).

The spatial separation of restored oyster reefs should be informed by the migration patterns of fish species that are targets for restoration. Fish should be able to move easily among oyster reefs to access multiple restored reefs in the focal seascape. Previous studies have suggested that multiple smaller reefs might provide similar habitat values for fish as single larger reefs (Harwell et al. 2011). Consequently, several smaller restored reefs that are well connected to each other (within the 100 to 1000 m range) across a seascape, therefore are more likely to effective at enhancing fish populations across entire estuaries (Table 1; Figure 4). The hydrology of estuaries and coastal waters also shapes the composition of fish assemblages by regulating the likelihood of juvenile settlement (Hannan and Williams 1998)

and the probability of visitation by adults (Connolly and Hindell 2006; Henderson et al. 2017a). Fish employ tidal excursion currents to traverse large distances between inshore habitats (e.g. feeding areas, juvenile nursery habitats) and offshore habitats (e.g. spawning areas, adult habitats), and use other structurally complex ecosystems as stepping stones (i.e., feeding and resting areas) during these migrations (Engelhard et al. 2017; Nagelkerken et al. 2015) (Figure 4). By selectively restoring oyster reefs in locations to add both spatial and structural heterogeneity to coastal seascapes, restoration projects might also provide additional habitats for fish to use as stepping stones during these ontogenetic migrations (Mullaney 1991; zu Ermgassen et al. 2016) (Figure 4). Hence this also ensures connectivity which is the central mechanism for creating coherence amongst restored and protected environments (D'Agostini et al. 2015; Planes et al. 2009).

Enhancing fish recruitment and nursery value

Oyster reefs are important sites for fish spawning (Tolley and Volety 2005), attract fish larvae (Breitburg et al. 1995), and function as nursery areas for many fish species (Coen et al. 1998; Peterson et al. 2003; zu Ermgassen et al. 2016) (Figure 4). The extent to which oyster reefs function as nursery habitats for juvenile fishes is determined by three inter-related factors: (1) the likelihood that fish larvae settle on reefs; (2) the abundance, growth and survival, of juveniles; and (3) the level of success that juvenile fish have in migrating from oyster reefs to their adult habitats habitats (sensu Beck et al. 2001).

Fish larvae often enter estuaries through passages to the open sea (e.g. estuary mouths, coastal bays, surf bars) (Blaber 2008), and some estuarine fishes spawn over surf bars in these passages in many regions of the world (Olds et al. 2017; Sheaves et al. 1999). Placing oyster reefs near the mouths of estuaries might, therefore, enhance the likelihood of reefs being used as spawning sites, and also promote the likelihood of larval settlement (Pichler et al. 2017). Larval recruitment might also be enhanced by creating more complex, and taller oyster reefs, which create eddies in which larvae accumulate (Breitburg et al. 1995). However, the placement of reefs nearer to estuary mouths might increase their vulnerability to being covered by moving sediments, and oyster disease in some parts of the world (associated with higher salinity; Lenihan et al. 1999). Despite this, reef beds at the mouths of estuaries may not be self-sustaining if the larvae get transported away and there are no seeding populations within the interconnected hydrographic systems (Wolanski and Elliott 2015).

The growth and survival of juvenile fish depends on the availability of quality food, and protection from predation (Blaber 2008). This is turn relies on the presence, and creation or loss of habitats, which again are influenced by habitat change through restoration or anthropogenic pressures (Amorim et al. 2017). As many coastal fish require multiple habitats throughout their lives, especially during early ontogenetic movements, it is the quality of both individual habitats and the surrounding seascape that enhances nursery value for larval and post-settlement fishes (Nagelkerken et al. 2015). Once fish have recruited to oyster reefs, or into the surrounding seascape, the area's value as a nursery is determined by food availability, predation pressure, competitive interactions for food and space with cohabitants, and the availability of alternative foraging and refuge habitats in the seascape (Gittman et al. 2016; Pittman et al. 2007). Oyster reefs that are restored in appropriate locations can modify each of these features by providing feeding and sheltering opportunities, which serve to reduce competition and predator-induced mortality for fish on reefs and in adjacent habitats, and might therefore enhance the nursery function of coastal seascapes (Figure 4).

3. Consider the impact of fisheries and catchment management

Anthropogenic stressors such as runoff from altered catchments (Gilby et al. 2015; Lerberg et al. 2000) and overharvesting both in the catchment and at sea (Pauly et al. 2003; Pauly et al. 2005) have substantial consequences for marine ecosystem condition and resilience. In the context of managing fish stocks associated with restored oyster reefs, managers need to consider:

(1) how to manage fish stocks using catch restrictions, including the designation or expansion of no-take reserves; and
(2) how to manage other potential impacts from the catchment, and wider seascapes, in which reefs are located.

This level of management therefore has to respond to a whole suite of pressures, both exogenic unmanaged and endogenic ones (Elliott 2011). The exogenic pressures, which emanate from outside the management area and in which management sometimes only be able to respond to the consequences and not the causes, include climate change effects, runoff, and the loss of breeding fish populations away from the site. These can be both out at sea and also elsewhere in the catchment (Elliott et al. 2017). The endogenic managed pressures include those impacts in an area such as habitat loss and polluting discharges.

Fisheries management

The effective management of fisheries in coastal ecosystems relies on maintaining a high biomass of large, mature breeding fish. The most common management intervention is catch restrictions in the form of either reserves (Edgar et al. 2014) or by implementing size and bag limits (Bartholomew and Bohnsack 2005). Notwithstanding some uncertainty regarding the survival rates of released individuals, and the critical effects of the degree of enforcement (Guidetti et al. 2008), and fishing effort displaced by reserve declaration (Halpern et al. 2004; Lédée et al. 2012), the consensus is that catch restrictions (i.e. limits on the numbers by size class of fish caught by anglers) have positive effects on the abundance of harvested species in the great majority of cases (Edgar et al. 2014; Tetzlaff et al. 2013).

Strategically placed reserves, which are wholly no-take, well-designed, and well-policed, increase the abundance and biomass of harvested species (Edgar et al. 2014), restore trophic relationships and food webs, resulting in habitat improvements (Gilby and Stevens 2014), and in some cases, enhance surrounding fisheries (Halpern et al. 2009). Where they are designed to form a coherent network, as is required by an increasing amount of legislation globally (e.g. the UK Marine and Coastal Access Act), then all the sites have to be considered as a functional unit. Reserve effectiveness is enhanced by protecting multiple fish habitats and the spatial connections, and corridors, between these habitats (Olds et al. 2016). Consequently, we suggest that it would be prudent to establish restored oyster reefs in no-take marine reserves, and any important connection corridors with adjacent habitats (Olds et al. 2012a). We suggest that oyster reefs that are restored in optimal positions in heterogeneous seascapes (Bostrom et al. 2011; Micheli and Peterson 1999) and also protected in no-take marine reserves, would likely function better for both oysters and fish, than restored reefs that are open to fishing (Olds et al. 2016). Conversely, reefs open to non-sustainable oyster harvesting will likely be quickly degraded (Kirby 2004; Rothschild et al. 1994), thereby likely also reducing any value for associated fish communities. However, the degree to which fish biomass on restored oyster reefs is augmented by placement within marine reserves has not been tested (Nevins et al. 2014) (Table 1).

Catchment management

Human pressures on estuarine and coastal ecosystems are diverse (e.g. pollution, fishing, habitat destruction) and occur throughout the adjacent catchment and marine areas (Elliott

et al. 2014; Lotze et al. 2006). This suite of exogenic and endogenic anthropogenic stressors and their large spatial footprint necessitates a broad 'land-to-sea' framework for managing potential changes in water quality, fish populations, and habitats (Cicchetti and Greening 2011; Gilby et al. 2016). Oyster reef restoration can be compromised by excessive nutrient and sediment inputs (Walles et al. 2016), associated eutrophic symptoms including hypoxia (Beck et al. 2011), and loss of connectivity with functionally linked habitats (e.g. seagrasses, mangroves, coastal seas; Nagelkerken et al. 2015; Olds et al. 2017; Whitfield 2017) through either habitat degradation. Fish access to reefs and/or estuaries might be limited by blocking of fish passage through coastal defences, sandbank development due to low river flow from increased abstraction upstream, and urban barriers and infrastructures (Bishop et al. 2017). The outcomes of oyster reef restoration will, therefore, be maximised only when management minimises the deleterious effects of other impacting processes that affect the focal estuary and its catchment. The expansion of oyster reef habitat can, however, augment other estuarine habitats through the introduction of production ecosystem services leading to societal goods and benefits (Elliott et al. 2017; Turner and Schaafsma 2015). These include: (1) improving water quality by reducing excess nitrogen (Piehler and Smyth 2011; Smyth et al. 2015) and filtering particulates, which increases the level of sunlight reaching the seabed (Wall et al. 2008); (2) the fertilization of benthic habitats from pseudofaeces (Peterson and Heck 1999). These services facilitate marsh and seagrass habitats, which in turn increase fish production (Whitfield 2017) and again in turn lead to increased societal goods and benefits such as commercial fish yields, recreation benefits or coastal defences (Turner and Schaafsma 2015).

4. Monitor reefs and fish across the seascape for management, and implement changes where required

Restoration projects should have explicit goals, executed by best practices that can be adapted based on results from ongoing monitoring and new research (Margules and Pressey 2000; Wiens and Hobbs 2015). Indeed, failed or ineffective restoration is often due to poor or ill-defined objectives (Elliott et al. 2016). Hence, management of oyster reef restoration projects requires the review of existing management interventions, and the refinement of any practices that are ineffective (see the lessons learned in Elliott et al. 2016). Thus, oyster reef restoration projects should continually measure how effective actions are in meeting restoration goals (Wiens and Hobbs 2015). While monitoring protocols and metrics for restored oyster reefs are established for the reefs themselves (see Baggett et al. 2015 for

specific details), and basic monitoring protocols have been detailed for finfish (Baggett et al. 2014), general metrics for assessing how reefs affect the quality of surrounding fish and fisheries, beyond the restoration site (i.e. at a seascape scale) have not been established.

In general, there are two alternatives to determining whether the restored site is performing as desired: one is that a comparison with the restored site and another control site (or another control time) could be used, or alternatively the environmental managers need to clearly indicate what is desired for a restored site and then all of the monitoring is to check deviation from that objective; both of these are wholly dependent on clear objectives being set for the restored site and its dependent populations and species.

The choice of monitoring metrics will largely be determined by the goals and objectives of specific projects (McDonald et al. 2016). There are, however, several minimum requirements that should be met to enable proper estimations of the effects of oyster reefs on fish. At a minimum, all monitoring should encompass counts of entire fish assemblages at multiple time points and control sites both before and after restoration. Such a BACI-PS (Before-After-Control-Impact Paired Series) design is needed to disentangle the effects of tidal, seasonal or annual variation on fish assemblages (Underwood 1994), and to measure secondary production (i.e. the accumulation of fish biomass over time). It is also desirable to monitor not only restoration and control sites, but also references sites or remnant habitats of the type which the restoration effort is aspiring to recreate (Grayson et al. 1999; McDonald et al. 2016). The physico-chemical environment needs to be monitored as well as the ecological structure and functioning otherwise changes in the latter cannot be explained. Ideally, multiple control estuaries, with no oyster reef restoration (again following BACI-PS), should also be monitored during the period of reef establishment and fish recruitment, so that the ecological benefits of oyster restoration can be properly separated from any other regional changes that might also be affecting oyster reefs and fish assemblages (Underwood 1994). Projects running for a number of years will benefit greatly from measuring the recruitment and size distributions of focal species (Shin et al. 2005).

As fish move among ecosystems in coastal seascapes (e.g. from oyster reefs to other habitats) (Nagelkerken et al. 2015), the potential fisheries benefits of restored oyster reefs will not be restricted to the near-field footprint of individual restoration projects but also require consideration of far-field effects. To establish the extent of any such fisheries

benefits it will, therefore, be beneficial to measure potential changes to fish assemblages and fish catches at a wider seascape scale (i.e. up to km from restored oyster reefs). In essence, the monitoring has to cover all component pairs: environment-oysters, environment-fishes, oysters-fishes, oysters-predators, and fishes-predators. This gives both the structural and functional measurements.

In addition to monitoring fish, there are several metrics that might be monitored, and that are usually correlated or associated with the abundance of fish, that managers can use to demonstrate the effectiveness of oyster reefs for fish, and for the ecosystem more broadly. Several ecological processes, such as scavenging (Webley 2008), predation, and nutrient sequestration or turnover (Kellogg et al. 2013), are intimately linked with the abundance of fishes in coastal ecosystems, and so are increasingly used as measures of ecosystem health (Havstad and Herrick 2003). The use of indicators of ecosystem condition and functioning (e.g. indicator species, umbrella species) is increasing for estuaries globally (e,g. Gilby et al. 2017a; Montagna et al. 2008; Valesini et al. 2017). However, further studies are required to identify potential indicator species that might be useful for oyster reefs; especially those that might be used to compare patterns across biogeographic regions (Table 1). As restored oyster reefs accumulate fish biomass, they might also alter the spatial distribution of fishing effort in coastal seascapes (i.e., fishing could easily become concentrated over successful oyster reefs). Alternatively, depending on the gear used, the reef may discourage bottom trawling thereby acting as a de-facto no-take zone. Hence, monitoring potential changes in the distribution of fishing effort (e.g. mapping anglers and commercial fishing in relations to reefs) is, therefore, necessary to investigate how the combined effects of restoration and fishing alter fish assemblages on oyster reefs.

It has been recommended that the settlement and growth of oysters on restored reefs should be monitored for up to 6 years post installation (Baggett et al. 2015). Fish assemblages will continue to change through this period (i.e., as oyster reefs become established), and could take upwards of 10 years to develop (zu Ermgassen et al. 2016). Monitoring recovery towards the generic standards provided by McDonald et al. (2016) would therefore reduce ambiguity around goals and success.

These criteria should of course be considered as ideal or optimal sampling regimes. Gathering of even basic abundance and diversity data at individual sites should be

considered an important goal for all oyster reef restoration projects. Similarly, cost-effective methods of measuring habitat size and/or quality using, for example, LIDAR or drone techniques, will deliver rapid information on the supporting ecosystem services.

Discussion

Oyster reef restoration is costly, so restoration efforts should seek win-win scenarios (e.g. for ecology and economy), where oyster reef restoration achieves multiple benefits (e.g. shoreline stabilisation, and enhancement of fisheries productivity). Restoring oyster reefs augments fish biomass relative to bare substrata, and integrating several key concepts from estuarine fish ecology into the design and monitoring of restoration projects will help maximise their return on investment. Placing complex reef structures in strategic locations within heterogeneous estuarine seascapes might enhance estuarine habitat diversity and promote the performance of restored oyster reefs for fish and fisheries. The physical installation of oyster reefs should not be viewed as the final outcome of restoration programs. Restored reefs must be managed, together with other impacting processes that might threaten restoration success (e.g. fishing, sedimentation, eutrophication), and monitored over time to maximise the accumulation of fish biomass, and the benefits of restoration for fisheries (Margules and Pressey 2000; Wiens and Hobbs 2015). Oyster reef restoration projects that account for the reef designs or placements that might serve to maximise the utility of seascapes for fish will lead to greater fish diversity, abundance, and harvestable fish biomass throughout coastal ecosystems. As shown in this review, there are several important research questions that need addressing (Table 1), however, there are also several important questions for managers to ask based on existing literature when aiming create successful and sustainable reefs for finfish and their fisheries (Table 2). By understanding the need for appropriate management measures and targets (such as those in Table 2) which have to respond to the large uncertainties in the ecological functioning, then the likelihood of successful and sustainable reefs can be enhanced.

In many instances, there are logistic and legislative challenges to optimising the design, positioning, management and monitoring of reefs according to these criteria. For example, the locations in which oyster reefs can be restored might be limited by regulations concerning shipping, recreational activities, or habitat conservation (e.g. legislative protection of marine plants). They may be limited by a poor knowledge of historical evidence of oysters or the unknown reasons for the decline of the previous stocks. Funding

agencies might also prefer simple oyster reef designs for ease of installation, to limit costs, or to maximise their accessibility (Kingsley-Smith et al. 2015). In many instances, the actual design of oyster restoration projects will be a compromise across these multiple constraints, and depend on specific project goals. For example, the enhancement of fisheries may be secondary to shoreline stabilisation under some scenarios. Notwithstanding these challenges, if the goal of oyster reef restoration is to enhance fish populations and benefit fisheries it is imperative to optimise the habitat values, seascape context, and ongoing monitoring and management of restored reefs.

Table 2 Questions for management where restoration seeks to restore both oyster reefs and surrounding finfish and their fisheries

Broad fields	Specific questions for management
Prerequisites	
Did oyster reefs historically occur in the area?	- what was their extent / distribution? - which species occurred?
What is the timeline and reasons of decline / extirpation?	- diseases / pathogens / parasites? - fishing / harvesting? - water quality (e.g. suspended solids)? - has this reason been arrested?
Are there now fewer fish?	- evidence of declined biodiversity and/or catches? - can this be tied to the loss of oyster reefs?
A- Oyster reefs as fish habitats	
Do the right habitats and physico-chemical conditions exist for oysters?	- is there the appropriate elevation/depth? - is the hydrographic connectivity maintained both upstream and at sea? - is the salinity, turbidity, primary (plankton) productivity, suitable for settlement, survival and long-term growth?
Can the environmental variables that affect fish and oysters be matched?	- what environmental envelopes does the target oyster species prefer? - what environmental envelopes do the target fish species prefer? - where are the areas in the estuary in which these values overlap?
Reef structures suitable for fish?	- how can the growth of invertebrates and small fish be encouraged to enhance feeding opportunities for fish? - how does the reef function to improve protection from predation?
B- The seascape context	
Is the area available and suitable for reef placements?	- restrictions due to shipping, boating or recreational usages? - restrictions on oyster translocation (e.g. Biosecurity exclusions)?
Linkages to other habitat types?	- which alternate habitats (e.g. seagrass, marsh, mangroves) are most important in terms of linkages within each system? - over which scales do these linkages occur? - can the placement of reefs be optimized under this context to improve carrying capacity?
Linkages to other oyster reefs?	- are there sources available for oyster larvae from other reefs? - can fish use the restored reefs as a network? - over which scales do these linkages occur? - can the placement of reefs be optimized under this context to improve carrying capacity?
C- Fisheries and catchment management	
Are existing fisheries management sufficient?	- do existing bag limits or marine reserves serve to enhance the breeding biomass of fish around reefs? - if no, can, and how might this be changed to do so?
Are existing catchment management plans sufficient?	- are there exogenous threats to the survival or growth of oysters and/or fish? - what are they, where do they exist (at the site, upstream, or in the catchment?), and to what degree do they influence outcomes for fish and oysters (i.e. in which order should you tackle them?) - what approaches should be taken to minimise or negate their effects?
D- Monitoring and adaptability	
Are there appropriate restoration goals?	- what are the specific, quantifiable goals of restoration? - are these achievable within the lifetime of the project? - how will monitoring address whether these goals are met? - how will lessons from monitoring be fed back into the management of the reefs or broader estuary?
How will the reefs and fish be monitored?	- which metrics, what methods? - how does this relate to the value of the reef habitat for fish (e.g. food and/or protection from predators?)? - fish beyond the reef site? (i.e. at a seascape scale) - how does this relate to the broader project goals?

The restoration of habitats and biodiversity is valued by society, and can convey significant psychological benefits to users (Fuller et al. 2007; Rey Benayas et al. 2009). Successful restoration projects that improve the condition of habitats, or enhance fish populations, also provide valuable ecosystem services and societal goods and benefits (e.g. food provision, bank reinforcement, biodiversity enhancement) and are, therefore, an asset to local people. Restoring lost habitats should be viewed as a significant achievement, irrespective of the goals of the project or whether fisheries are enhanced by the restoration efforts. By better integrating the goal of supplementing fish and fisheries, with the objectives of oyster reef restoration, we might therefore increase stakeholder engagement (La Peyre et al. 2012), and help to ensure that restored oyster reefs function optimally within socio-ecological systems. In essence, the aim will be to improve the ecological structure and functioning and not merely achieve an exercise of more value 'to the ecologists than the ecology' (Elliott et al., 2016).

Further development of these concepts requires ongoing investigation of the effects of oyster reef restoration on fish assemblages. Designing oyster reef structures that are attractive as both sources of food and refuges from predation must be a priority for oyster reef restoration projects where restoring fish and fisheries is also a goal (research priorities 1 and 2, Table 1). While many studies have demonstrated that reefs serve as nursery and adult finfish habitats, and augment fish production locally (10s to 100s m), the next critical step is to determine whether these benefits convey to fish populations (e.g. Peterson et al. 2003), ecological functions (e.g. Rodney and Paynter 2006), or nursery values (Nagelkerken et al. 2015) at larger spatial scales (km to 10s of km) beyond the reef sites. Furthermore, while studies have demonstrated that better-connected reefs harbour more animals (e.g. Gain et al. 2017), the degree to which these metrics of fish and fish-associated ecological functions are enhanced across different types of seascapes, whether these effects are consistent, and which oyster reef designs optimize the effects is unclear (research priorities 3 and 4, Table 1). Properly managing fish biomass on, and around, restored oyster reefs requires a clearer understanding of how people interact with reefs, and how these interactions might modify the responses of recovering fish communities (research priority 5, Table 1). To help optimise future restoration projects for finfish, we must identify suitable indicators that can be used to measure restoration success for finfish specifically (research priority 6, Table 1). There is now an accepted list of attributes required by suitable indicators (e.g. Elliott 2011) to ensure

that not only are they operational but that managers will know when they have been reached. Hence the central function of management being that measures (such as restoration) will be seen to achieved the desired aims.

Restoring oyster reefs can have significant, often positive, effects for fish and fisheries. The management and research recommendations presented here are a basic set that can be expanded, refined, and adapted by individual projects to best match goals and objectives, and can be easily integrated into most projects. We emphasise that the effectiveness of oyster reef restoration projects for fish and fisheries can be improved by optimising the habitat values and seascape context of individual reefs, by managing other impacting processes, and through adaptive monitoring with appropriate indicators of restoration performance.

Supplementary Materials

Table S1 List of studies that investigate the effects of restored oyster reefs for fish globally. These studies were sourced using an ISI Web of Knowledge search of the term (oyster* and fish and restor*).

Authors	Year	Title	Journal	Volume	Pages	Region
Abbott, R. R. and R. Obernolte	2012	Acoustically tagged fish utilization of an artificial reef constructed for native *Olympia* oyster restoration	Journal of Shellfish Research	31	257-258	California
Arve, J.	1960	Preliminary report on attracting fish by oyster-shell plantings in Chincoteague Bay, Maryland	Chesapeake Science	1	58-65	Maryland
Boswell, K. M., M. P. Wilson, P. S. D. MacRae, C. A. Wilson and J. H. Cowan	2010	Seasonal estimates of fish biomass and length distributions using acoustics and traditional nets to identify estuarine habitat preferences in Barataria Bay, Louisiana	Marine and Coastal Fisheries	2	83-97	Louisiana
Broekhuizen, N., C. J. Lundquist, M. G. Hadfield and S. N. Brown	2011	Dispersal of oyster (*Ostrea chilensis*) larvae in Tasman Bay inferred by using a verified particle tracking model that incorporates larval behaviour	Journal of Shellfish Research	30	643-658	New Zealand
Brown, L. A., J. N. Furlong, K. M. Brown and M. K. La Peyre	2014	Oyster reef restoration in the northern Gulf of Mexico: effect of artificial substrate and age on nekton and benthic macroinvertebrate assemblage Use	Restoration Ecology	22	214-222	Mississippi and others
Dillon, K. S., M. S. Peterson and C. A. May	2015	Functional equivalence of constructed and natural intertidal eastern oyster reef habitats in a northern Gulf of Mexico estuary	Marine Ecology Progress Series	528	187-203	Mississippi
Farinas-Franco, J. M. and D. Roberts	2014	Early faunal successional patterns in artificial reefs used for restoration of impacted biogenic habitats	Hydrobiologia	727	75-94	Ireland
George, L. M., K. De Santiago, T. A. Palmer and J. B. Pollack	2015	Oyster reef restoration: effect of alternative substrates on oyster recruitment and nekton habitat use	Journal of Coastal Conservation	19	13-22	Texas
Geraldi, N. R., S. P. Powers, K. L. Heck and J. Cebrian	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	Alabama
Gittman, R. K., C. H. Peterson, C. A. Currin, F. J. Fodrie, M. F. Piehler and J. F. Bruno	2016	Living shorelines can enhance the nursery role of threatened estuarine habitats	Ecological Applications	26	249-263	North Carolina
Grabowski, J. H., A. R. Hughes, D. L. Kimbro and M. A. Dolan	2005	How habitat setting influences restored oyster reef communities	Ecology	86	1926-1935	North Carolina
Gregalis, K. C., M. W. Johnson and S. P. Powers	2009	Restored oyster reef location and design affect responses of resident and transient fish, crab, and shellfish species in Mobile Bay, Alabama	Transactions of the American Fisheries Society	138	314-327	Alabama
Harding, J. M. and R. Mann	1999	Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia	Bulletin of Marine Science	65	289-299	Virginia
Harding, J. M. and R. Mann	2000	Estimates of naked Goby (*Gobiosoma bosc*), striped blenny (*Chasmodes bosquianus*) and Eastern oyster (*Crassostrea virginica*) larval production around a restored Chesapeake Bay oyster reef	Bulletin of Marine Science	66	29-45	Virginia
Harding, J. M. and R. Mann	2001	Oyster reefs as fish habitat: Opportunistic use of restored reefs by transient fishes	Journal of Shellfish Research	20	951-959	Virginia
Harwell, H. D., M. H. Posey and T. D. Alphin	2011	Landscape aspects of oyster reefs: Effects of fragmentation on habitat utilization	Journal of Experimental Marine Biology and Ecology	409	30-41	North Carolina
Humphries, A. T. and M. K. La Peyre	2015	Oyster reef restoration supports increased nekton biomass and potential commercial fishery value	Peerj	3	e1111	Louisiana

Humphries, A. T., M. K. La Peyre, M. E. Kimball and L. P. Rozas	2011	Testing the effect of habitat structure and complexity on nekton assemblages using experimental oyster reefs	Journal of Experimental Marine Biology and Ecology	409	172-179	Louisiana
Kellogg, M. L., J. C. Cornwell, M. S. Owens and K. T. Paynter	2013	Nitrogen removal and nutrient sequestration of a restored oyster reef	Marine Ecology Progress Series	480	1-19	Maryland
Kingsley-Smith, P. R., R. E. Joyce, S. A. Arnott, W. A. Roumillat, C. J. McDonough and M. J. M. Reichert	2012	Habitat use of intertidal eastern oyster (*Crassostrea virginica*) reefs by nekton in South Carolina Estuaries	Journal of Shellfish Research	31	1009-1021	South Carolina
La Peyre, M. K., A. T. Humphries, S. M. Casas and J. F. La Peyre	2014	Temporal variation in development of ecosystem services from oyster reef restoration	Ecological Engineering	63	34-44	Louisiana
Lehnert, R. L. and D. M. Allen	2002	Nekton use of subtidal oyster shell habitat in a southeastern US estuary	Estuaries	25	1015-1024	South Carolina
Lenihan, H. S.	1999	Physical-biological coupling on oyster reefs: How habitat structure influences individual performance	Ecological Monographs	69	251-275	North Carolina
Lenihan, H. S., C. H. Peterson, J. E. Byers, J. H. Grabowski, G. W. Thayer and D. R. Colby	2001	Cascading of habitat degradation: Oyster reefs invaded by refugee fishes escaping stress	Ecological Applications	11	764-782	North Carolina
Lunt, J., J. Reustle and D. L. Smee	2017	Wave energy and flow reduce the abundance and size of benthic species on oyster reefs	Marine Ecology Progress Series	569	25-36	Texas
MacRae, P. S. D. and J. H. Cowan Jr.	2010	Habitat preferences of spotted seatrout, *Cynoscion nebulosus*, in coastal Louisiana: A step towards informing spatial management in estuarine ecosystems	The Open Fish Science Journal	3	154-163	Louisiana
Marenghi, F., G. Ozbay, P. Erbland and K. Rossi-Snook	2010	A comparison of the habitat value of sub-tidal and floating oyster (*Crassostrea virginica*) aquaculture gear with a created reef in Delaware's Inland Bays, USA	Aquaculture International	18	69-81	Delaware
Nevins, J. A., J. B. Pollack and G. W. Stunz	2014	Characterizing the nekton use of the largest unfished oyster reef in the United States compared with adjacent estuarine habitats	Journal of Shellfish Research	33	227-238	Texas
Peters, J. R., L. A. Yeager and C. A. Layman	2015	Comparison of fish assemblages in restored and natural mangrove habitats along an urban shoreline	Bulletin of Marine Science	91	125-139	East Florida
Quan, W. M., L. Zheng, B. J. Li and C. G. An	2013	Habitat values for artificial oyster (*Crassostrea ariakensis*) reefs compared with natural shallow-water habitats in Changjiang River estuary	Chinese Journal of Oceanology and Limnology	31	957-969	China
Quan, W.-m., J.-x. Zhu, Y. Ni, L.-y. Shi and Y.-q. Chen	2009	Faunal utilization of constructed intertidal oyster (*Crassostrea rivularis*) reef in the Yangtze River estuary, China	Ecological Engineering	35	1466-1475	China
Rezek, R. J., B. Lebreton, E. B. Roark, T. A. Palmer and J. B. Pollack	2017	How does a restored oyster reef develop? An assessment based on stable isotopes and community metrics	Marine Biology	164	54	Texas
Robillard, M. M. R., G. W. Stunz and J. Simons	2010	Relative value of deep subtidal oyster reefs to other estuarine habitat types using a novel sampling method	Journal of Shellfish Research	29	291-302	Texas
Rodney, W. S. and K. T. Paynter	2006	Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland	Journal of Experimental Marine Biology and Ecology	335	39-51	Maryland
Scyphers, S. B., S. P. Powers and K. L. Heck, Jr.	2015	Ecological value of submerged breakwaters for habitat enhancement on a residential scale	Environmental Management	55	383-391	Alabama
Scyphers, S. B., S. P. Powers, K. L. Heck, Jr. and D. Byron	2011	Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries	Plos One	6	e22396	Alabama
Stunz, G. W., T. J. Minello and L. P. Rozas	2010	Relative value of oyster reef as habitat for estuarine nekton in Galveston Bay, Texas	Marine Ecology Progress Series	406	147-159	Texas

Taylor, J. and D. Bushek	2008	Intertidal oyster reefs can persist and function in a temperate North American Atlantic estuary	Marine Ecology Progress Series	361	301-306	North Atlantic
Tolley, S. G. and A. K. Volety	2005	The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans	Journal of Shellfish Research	24	1007-1012	West Florida
Tolley, S. G., A. K. Volety and M. Savarese	2005	Influence of salinity on the habitat use of oyster reefs in three southwest Florida estuaries	Journal of Shellfish Research	24	127-137	West Florida
Ulanowicz, R. E. and J. H. Tuttle	1992	The trophic consequences of oyster stock rehabilitation in Chesapeake Bay	Estuaries	15	298-306	Maryland and others
Walters, K. and L. D. Coen	2006	A comparison of statistical approaches to analyzing community convergence between natural and constructed oyster reefs	Journal of Experimental Marine Biology and Ecology	330	81-95	South Carolina
Wenner, E., H. R. Beatty and L. Coen	1996	A method for quantitatively sampling nekton on intertidal oyster reefs	Journal of Shellfish Research	15	769-775	South Carolina
Wilber, D. H., N. H. Hadley and D. G. Clarke	2012	Resident crab associations with sedimentation on restored intertidal oyster reefs in South Carolina and the implications for secondary consumers	North American Journal of Fisheries Management	32	838-847	South Carolina
Workman, I., A. Shah, D. Foster and B. Hataway	2002	Habitat preferences and site fidelity of juvenile red snapper (*Lutjanus campechanus*)	ICES Journal of Marine Science	59	S43-S50	Mississippi

Chapter 4

Seascape context modifies how fish respond to restored oyster reef structures

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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 (Brook et al. 2018; Lenihan 1999; Micheli and Peterson 1999). 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 stabilisation, 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 (Becker et al. 2018; Miller 2002; Roni et al. 2002; Sun et al. 2017; zu Ermgassen et al. 2016). However, some restoration efforts do not fully consider how the placement of sites could maximise the abundance or diversity of fish around them, meaning that the full benefits of restoration might not be achieved (Gilby et al. 2018a; Jones and Davidson 2016a).

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 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 urbanisation and sea level rise (Rudershausen et al. 2018; Torio and Chmura 2015). 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; Henderson et al. 2017b; Olds et al. 2016). 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 optimise their performance (Gilby et al. 2018a; Rudnick et

al. 2012). As a result, we might enhance the recruitment of fish to new habitats (either restored or artificial) by optimising 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 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 is 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 (Grabowski et al. 2005; Ziegler et al. 2018), 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 (Geraldi et al. 2009). 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 had been functionally extirpated over a century ago, and used these as a model system to test whether the seascape context of individual reefs modified their augmentation of 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 hypothesised 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 utilisation.

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 in this 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 principle 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 ~1-2m). Naturally occurring oyster larvae, which remain present

in 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.

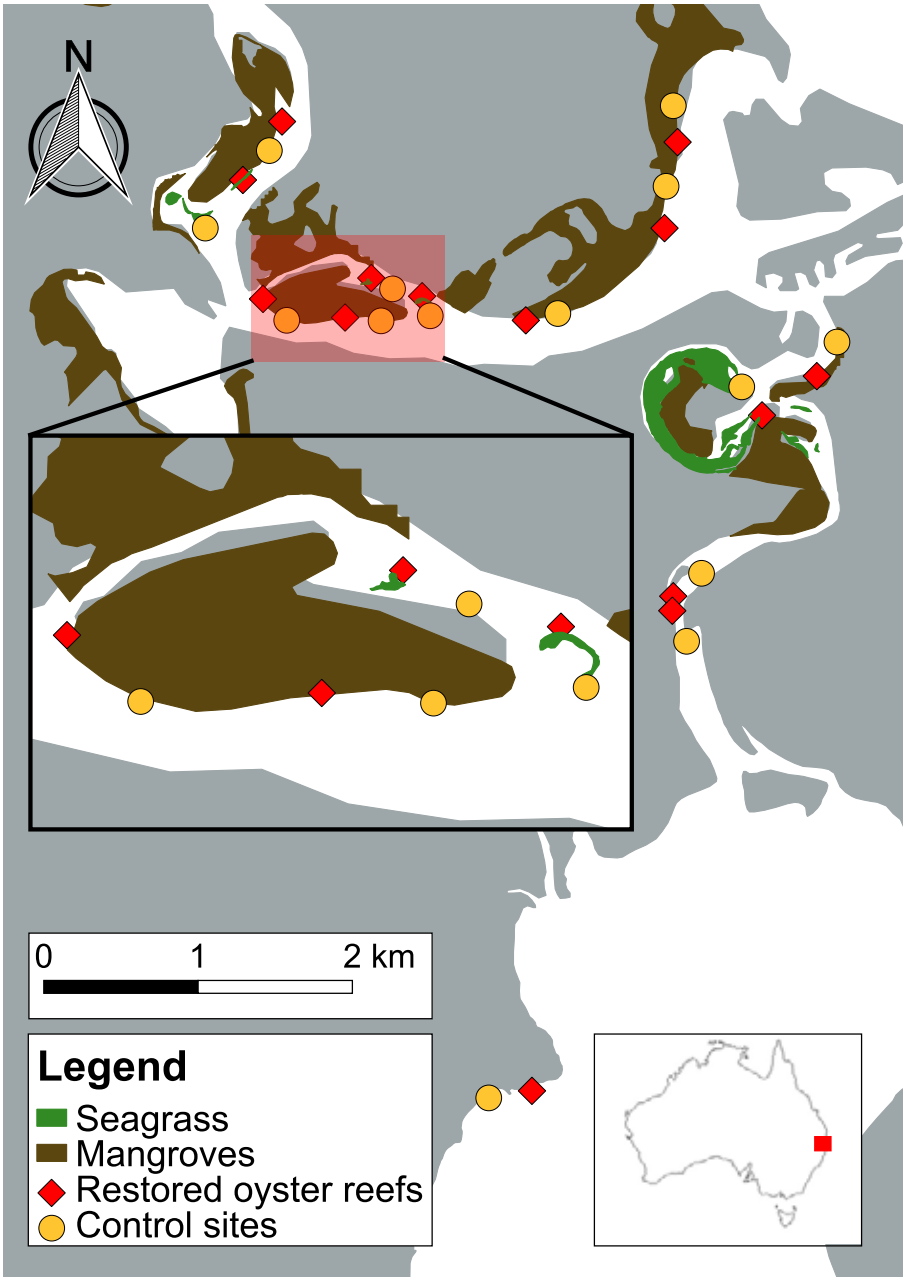


Figure 1 Location of restored oyster reefs, control sites and habitats in the Noosa River, eastern Australia.

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 (Gilby et al. 2018b; Olds et al. 2012b). By contrast, reef structures differed in terms of their connectivity with persistent seagrass beds (i.e. present over the last two 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 (Gilby et al. 2018b; Olds et al. 2012b). 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 x 30 cm mesh bag with 5 mm openings. BRUVS were deployed for a period of 1 hour at each site during each survey event. Because salinity is a principle 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 hrs) and within two hours of high tide to minimise 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. 2017a). 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, 2 levels), with variation in the presence or absence of seagrass nearby (fixed factor, 2 levels; seagrass present or seagrass absent nearby), and the interaction between these factors, whilst accounting for sampling period (covariable, 4 levels; 0, 6, 12, and 18 weeks). PERMANOVA results were visualised using canonical analysis of principle components (CAP). 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 generalised linear models (GLMs) in R to test for correlations between 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 (Figure S1). Of the species occurring on reefs, 12 species occurred exclusively at reefs (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 se) than control sites (2.6 +/-0.2 se) across all sampling periods (Figure 2A). Similarly, oyster reefs supported 1.8 times more harvestable fish (6.5 +/- 0.7 se) than control sites (3.6 +/- 0.5 se) 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. By 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, 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, moses 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, 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, B, Table 3, 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 that 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).

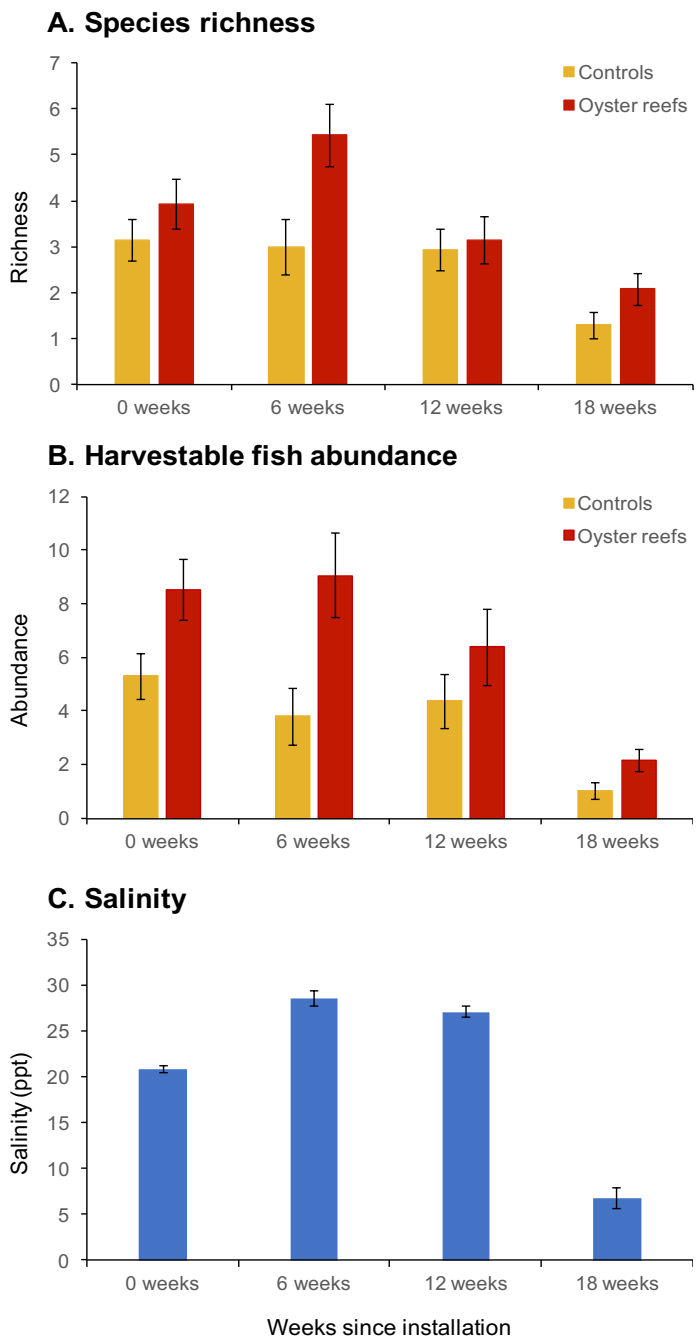


Figure 2 Average (+/- SE) (A) species richness, (B) harvestable fish abundance and (C) salinity values for all sites between controls and oyster reefs across the four sampling periods.

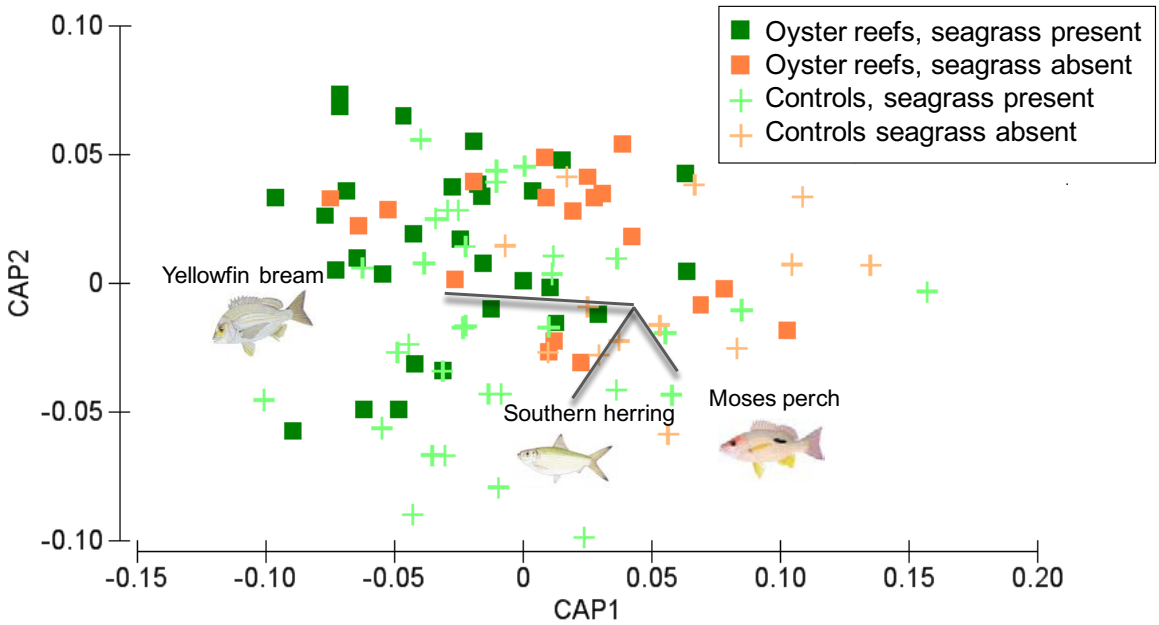


Figure 3 Canonical analysis of principle components visualising fish assemblages around restored oyster reefs in the Noosa River, Australia for differences across treatment, and with seagrass present or absent nearby. Vector overlays are Pearson correlations of potential indicator species from Dufrene-Legendre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

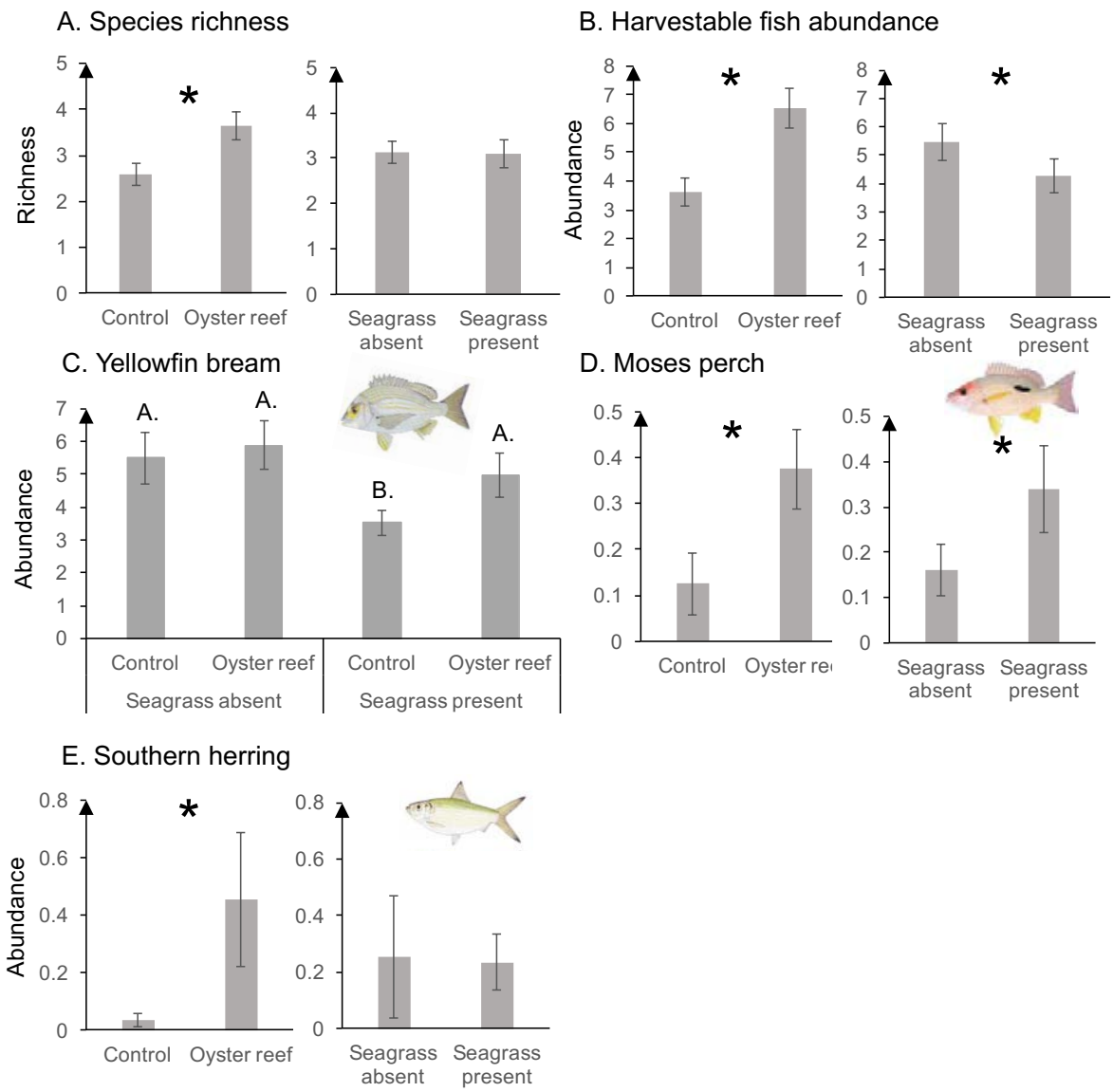


Figure 4 Average (+/- SE) of (A) species richness and (B) harvestable fish abundance, and the abundance of significant indicator species (C-E) at restored oyster reefs and control sites, and with seagrass present or absent nearby (i.e. within 500 m). Plots reflect the results of GLM analyses (Table 3). 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.

Table 1 Permutational multivariate analysis of variance output testing assemblage level differences between treatment (fixed factor, 2 levels; oyster reefs or control sites) and seagrass presence nearby (fixed factor, 2 levels; seagrass absent and seagrass present nearby), corrected for sampling period (covariate). P values in **bold** significant at α=0.05.

Source	df	MS	Pseudo-F	P
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 x Se	1	2527.6	0.8	0.627
Res	107	3164.4		
Total	111			

Table 2 Indicator species analysis testing for the species that contribute most towards differences in assemblages between oyster reefs and control sites. 'Group' indicates the level of factor 'Treatment' for which that species is a significant indicator.

Species	**Group**	**Indicator Value**	**P**
Yellowfin bream	Oyster reefs	0.56	0.001
Moses perch	Oyster reefs	0.21	0.013
Southern herring	Oyster reefs	0.17	0.015

Table 3 Generalised linear model results testing for correlations between key attributes of fish assemblages and significant indicator species (see Table 1) with treatment (fixed factor, 2 levels; oyster reefs or control sites) and seagrass presence nearby (fixed factor, 2 levels; seagrass absent and seagrass present nearby), corrected for sampling period (covariate). P values in **bold** significant at α=0.05.

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

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; Grabowski and Peterson 2007; Heck et al. 2003). Restoration sites that are strategically placed within heterogeneous estuarine seascapes might be 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 (Gilby et al. 2018c; Grabowski and Peterson 2007; Peterson et al. 2003). 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. Grabowski et al. 2005; Harding and Mann 1999; La Peyre et al. 2014b) 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 another harvested species (i.e. moses perch) more broadly across the entire seascape (Olds et al. 2018b; Webley et al. 2015). This finding suggests that ecological benefits of oyster reef restoration can depend on both 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; Gilby et al. 2018a; Guerrero et al. 2017; Hallett et al. 2013).

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. 2012b; 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. 2012b, Martin et al. 2018). They recruit into estuaries as juveniles and move to offshore reefs as

adults were 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 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 moses 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 (Gilby et al. 2018b; Pittman et al. 2004; Skilleter et al. 2017). The effects of seagrass on the fish assemblages of adjacent structural complex habitats often occur over a scale of 500 m (Gilby et al. 2018b; Olds et al. 2012b). 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 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 hypothesise 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 centralise, we might more efficiently reach our conservation, restoration, or fisheries-related goals.

Supplementary Materials

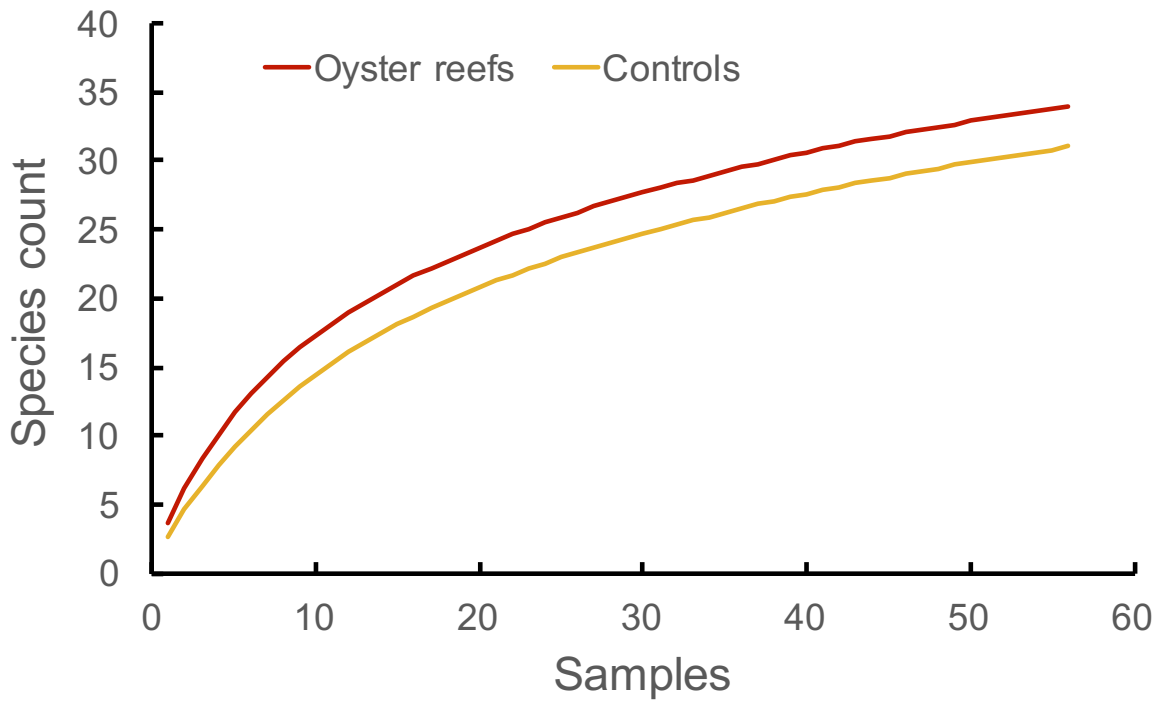


Figure S1 Species accumulation curves for restored oyster reef structures and nearby control sites in the Noosa River, Australia.

Table S1 List of species identified at restored oyster reef structures and nearby control sites in the Noosa River, Australia, and their frequency of occurrence (FOC) at these two types of sites (out of a total of 56 possible survey events). Species in bold identified exclusively on oyster reefs. 'Harvested?' indicates species classified as targeted by local recreational and commercial fisheries.

Species	Harvested?	FOC at oyster reefs	FOC at controls
Acanthopagrus australis (Yellowfin bream)	Yes	49	35
Ambassis marianus (Estuary perchlet)		7	10
***Anguilla reinhardtii* (Longfin eel)**		5	0
Aptychotrema rostrata (Eastern shovelnose ray)		0	2
Arothron manilensis (Narrow lined puffer)		7	8
Atule mate (Yellow tail scad)	Yes	0	1
***Carangoides chrysophrys* (Longnose Trevally)**	Yes	1	0
Caranx ignobilis (Giant Trevally)	Yes	0	1
***Conger verreauxi* (Conger eel)**		1	0
***Epinephelus coiides* (Estuary cod)**	Yes	2	0
Favonigobius exquisitus (Eastern sand goby)		6	5
Gerres filamentosus (Filamentous biddy)		0	1
Gerres subfasciatus (Silver biddy)		12	6
***Glaucostegus typus* (Giant shovelnose ray)**		1	0
Gymnothora pseudothyrsoideus (Highfin Moray)		0	1
Hemitrygon fluviorum (Estuary ray)		1	5
Herklotsichthys castelnaui (Southern herring)		10	2
Himantura uarnak (Reticulate whipray)		7	8
Hyporhamphus quoyi (Longtail garfish)	Yes	0	1
***Leiognathus equulus* (Ponyfish)**		2	0
***Lutjanus argentimaculatus* (Mangrove jack)**	Yes	1	0
***Lutjanus fulviflamma* (Blackspot snapper)**	Yes	2	0
Lutjanus russellii (Moses perch)	Yes	16	4
Marilyna pleurosticta (Common Toadfish)		2	1
Monodactylus argenteus (Butter bream)		12	4
Mugil sp. (Mullet)	Yes	3	1
Pastinachus ater (Cowtail Stingray)		1	2
Pelates quadrilineatus (Fourlined trumpeter)		6	7
Platycephalus fuscus (Dusky flathead)	Yes	1	2
Pomadsys kaakan (Barred javelin)		2	1
Pomatomus saltatrix (Tailor)	Yes	0	1
***Pseudolabrus guentheri* (Gunther's wrasse)**		1	0
***Pseudorhombus jenynsii* (Small tooth flounder)**		1	0
Rhabdosargus sarba (Tarwhine)	Yes	14	6
Scatophagus argus (Spotted Scat)		3	2
***Selenotoca multifasciata* (Striped scat)**		1	0
Siganus fuscescens (Rabbitfish)	Yes	2	2
Sillago sp. (Whiting)	Yes	15	11
***Sphyraena obtusata* (Striped barracuda)**		1	0
Strongylura krefftii (Longtom)		0	2
Terapon jarbua (Crescent grunter)		3	1
Torquigener pleurogramma (Weeping toadfish)		3	8

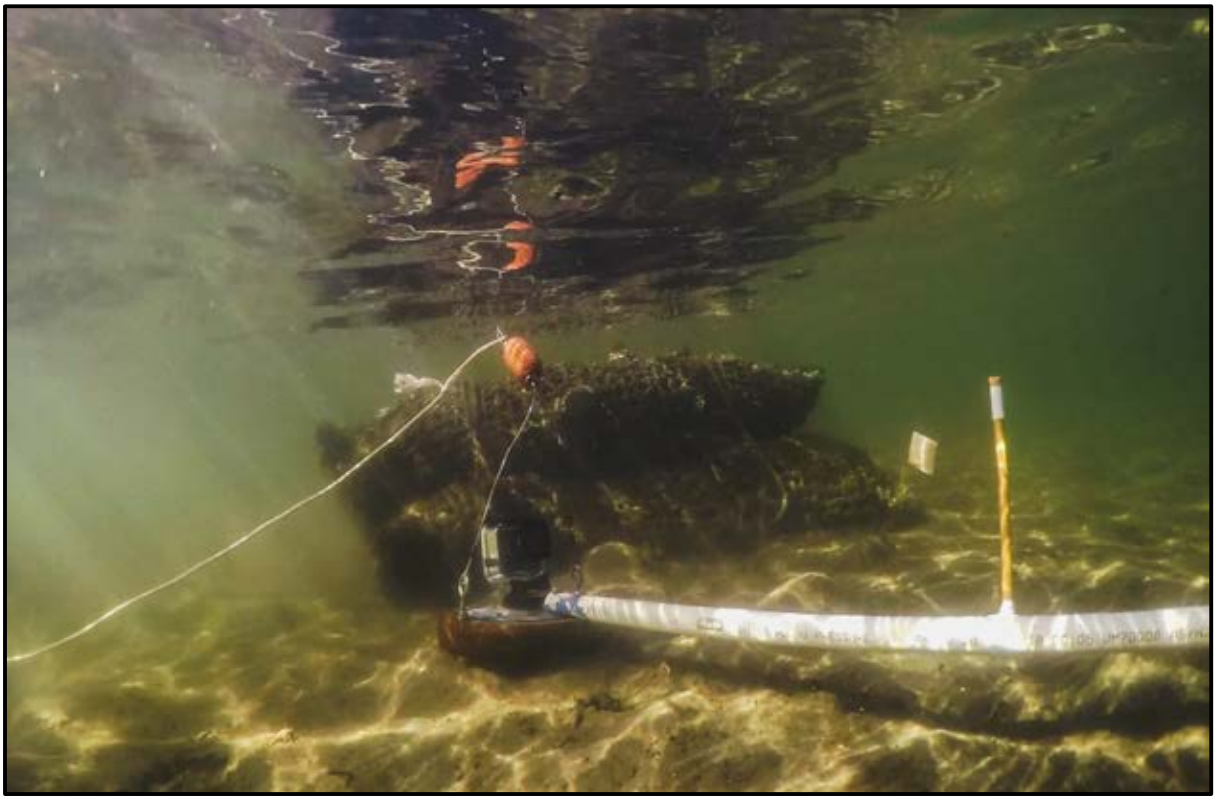
Table S2 List of study sites, and the average values (with standard error (SE)) and frequency of occurrence (where possible; FOC) for species richness, harvested fish abundance and significant indicator species for the factor treatment.

Site	Seagrass presence/absence	Species richness		Harvestable fish abundance		Yellowfin bream			Moses perch			Southern herring	
		Average	SE	Average	SE	FOC	Average	SE	FOC	Average	SE	FOC	Average
Oyster Reef 2	Present	2.8	0.9	3.0	1.1	3	2.9	0.5	1	1.0	0	1	1.1
Oyster Reef 3	Present	4.5	1.7	8.5	3.5	3	9.0	2.3	3	1.7	0.3	2	3.0
Oyster Reef 4	Absent	5.3	1.4	10.3	2.3	3	6.0	1.3	2	1.0	0	1	12.0
Oyster Reef 5	Absent	4.3	1.4	6.1	0.9	4	4.3	1.1	2	1.5	0.4	0	0.0
Oyster Reef 6	Present	3.0	0.8	2.8	0.6	4	1.0	0	3	1.3	0.3	1	1.0
Oyster Reef 7	Present	4.3	1.7	7.8	2.7	4	6.5	2.2	0	0.0	0	1	1.0
Oyster Reef 8	Absent	4.0	0.4	6.5	1.6	4	4.7	0.8	0	0.0	0	1	1.1
Oyster Reef 9	Absent	3.0	1.1	8.7	3.2	3	7.3	1.8	0	0.0	0	1	1.1
Oyster Reef 10	Absent	5.3	1.4	8.5	5	4	5.8	3	1	1.0	0	0	0.0
Oyster Reef 11	Absent	4.0	1.6	6.5	3	3	6.7	1.6	1	1.0	0	0	0.0
Oyster Reef 12	Present	4.0	0.7	6.8	3.8	4	5.0	3.7	1	2.0	0	0	0.0
Oyster Reef 13	Present	2.3	0.3	5.5	2.1	4	4.3	1.7	0	0.0	0	1	1.0
Oyster Reef 14	Present	3.5	0.9	7.0	2.8	4	6.0	2.2	1	1.0	0	1	1.1
Oyster Reef 16	Absent	1.0	0.4	3.7	1.9	2	6.2	0.7	1	1.0	0	0	0.0
Control 2	Present	1.8	0.9	1.5	1	1	1	0	0	0	0	1	1
Control 3	Present	4	1.4	6.3	2.2	3	4.3	1.5	2	2	0.7	0	0
Control 4	Absent	2.5	1	3	2.3	1	4	0	1	1	0	0	0
Control 5	Absent	2.5	0.6	4.3	1	4	3	0.7	0	0	0	0	0
Control 6	Present	1.5	0.6	0.8	0.3	2	1	0	0	0	0	0	0
Control 7	Present	2.3	0.9	3	2	2	4	1.4	0	0	0	0	0
Control 8	Absent	2.8	1.2	3.5	1.3	3	3.7	0.8	0	0	0	0	0
Control 9	Absent	3.3	0.8	6.8	1.8	4	6	1.5	0	0	0	0	0
Control 10	Absent	3.8	1	3.5	1	2	4	0.7	0	0	0	0	0
Control 11	Absent	1.8	0.3	0.8	0.5	2	1.5	0.4	0	0	0	0	0
Control 12	Present	2.3	0.5	2.5	1.6	2	4.5	1.8	0	0	0	0	0
Control 13	Present	2.5	0.6	4.5	1.3	4	3.5	1	0	0	0	0	0
Control 14	Present	5	0.7	7.3	1.8	4	5.5	1.6	1	2	0	1	1
Control 16	Absent	0.5	0.3	3	3	1	12	0	0	0	0	0	0

Chapter 5

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

Duncan C, Gilby B, Olds A, Connolly R, Ortodossi N, Henderson C, Schlacher T (2019) Landscape context modifies the rate and distribution of predation around habitat restoration sites. Biological Conservation. In press.



Introduction

The maintenance of ecosystem condition is contingent upon the preservation of ecological functions that enable ecosystems to resist or recover from disturbance (Decker et al. 2017; Risser 1995). 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; Bouley et al. 2018; Cosentino et al. 2014). 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; Gilby et al. 2018c; Jones and Davidson 2016a; 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; Volk et al. 2018; zu Ermgassen et al. 2016). For example, restoring corridors between forest patches increases faunal abundance by facilitating species movement and settlement (Lees and Peres 2008; Tewksbury et al. 2002). Similarly, restoring 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 of 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), oyster reefs provide important habitats for many coastal fish species and are often restored to augment fish abundance and diversity (Baggett et al. 2015). Oyster restoration can have positive effects on fish assemblages over what were previously unstructured sediments (Grabowski et al. 2005; Harding and Mann 1999; Peterson et al. 2003), however, the possible benefits of oyster restoration for ecological functions have rarely been tested with empirical data (Gilby et al. 2018c; Smyth et al. 2015). The landscape context of oyster reefs can modify the composition of fish assemblages, both over reefs and in surrounding temperate (Grabowski et al. 2005; Micheli and Peterson 1999), 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 2016a; 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 (Estes et al. 2010; Ripple and Beschta 2012; Ritchie and Johnson 2009). 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 (Gilby 2017; González-Tokman and Martínez-Garza 2015). 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.

Methods

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 amongst a matrix of unvegetated sandy substrates (Figure 1). Oyster reefs were historically abundant in the Noosa River, but became functionally extinct in the early 1900's (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 x 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 & 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 (Figure 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 (Figure 1).

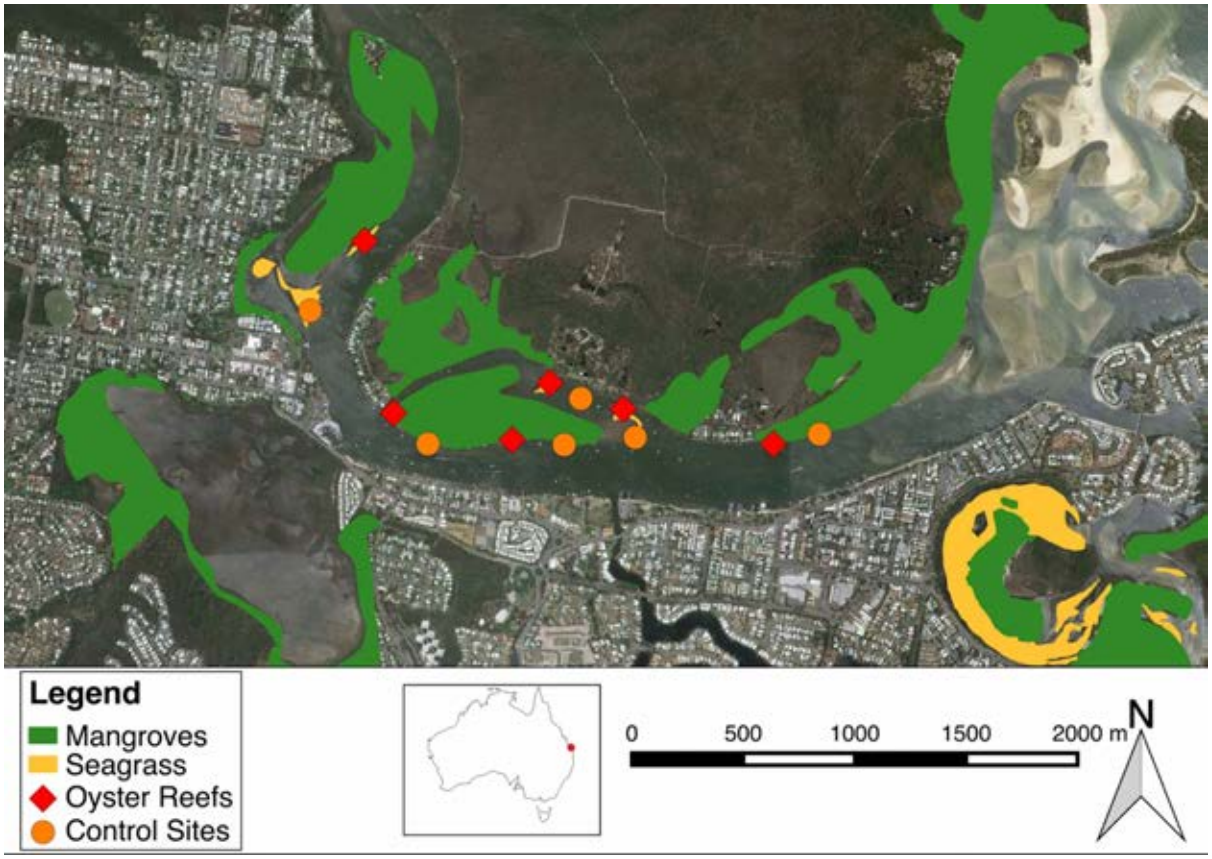


Figure 1 Distribution of restored oyster reefs, control sites, and other marine habitats in the Noosa estuary, eastern Australia (spatial data sources: QLD Department of Environment and Heritage Protection and Gilby et al. (2018b)).

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 500m distance buffer. This was selected based on the likely home ranges of fish in these estuarine systems (Olds et al. 2012b).	(Gilby et al. 2018b; Olds et al. 2012b)
Mangrove area	The area covered by mangroves in metres within a 500m distance buffer, selected based on the likely home ranges of fish in these estuarine systems (Olds et al. 2012b).	(Olds et al. 2012b) GIS, habitat layers from (Olds et al. 2012b; 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.	-

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)(Figure S1). These distances were selected to mirror the scale of functional effects from similar-sized artificial reefs in other coastal ecosystems (e.g. Henderson et al. 2017; Jelbart et al. 2007; Layman et al. 2016; 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 (Figure S1), nd 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.

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 meso-predators, and have been used extensively for this purpose in coastal seascapes (Duffy et al. 2015; Rodemann and Brandl 2017). Squidpops consist of a single 1cm^2 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 5kg 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 (Figure 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 hours 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 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.

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, 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 Aikaike'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.

Results

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 (Figure 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*) *a*nd 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%) (Figure 2b). The likelihood of predation was significantly higher at oyster reefs than at control sites (x^2=34.5, P<0.001) (Figure 2c). The likelihood of predation also increased significantly with survey period (x^2=34, P<0.001) (Figure 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 (Figure 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.

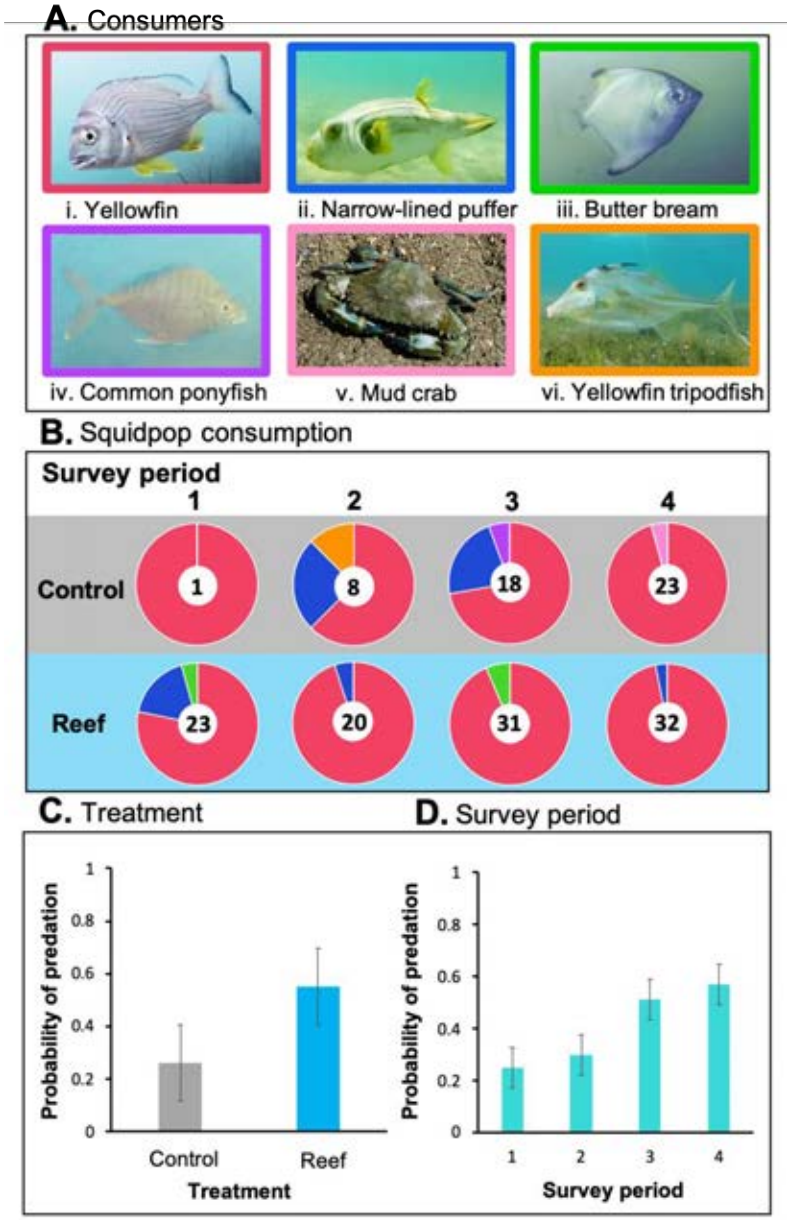


Figure 2 (a) Six predators consumed squidpops in the Noosa River, Australia. (b) Pie charts represent the proportion of squidpops consumed by each predator at restored oyster reefs and control sites during each survey period (colours correspond to those used in panel a). Numbers inside pie charts represent 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 one hour from deployment. (d) Probability of predation across survey periods (1, 2, 3, 4) within one hour 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**

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 x 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 x M	1	0.67	0.41

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, Figure 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 (Figure 3A), and was also lower adjacent to reefs that were bordered by a larger area of mangroves or seagrasses (Table 2, Figure 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, Figure 4). Predation rates were higher at reefs without nearby mangroves or seagrasses and this remained consistent with increasing distance from the oyster reef (Figure 4).

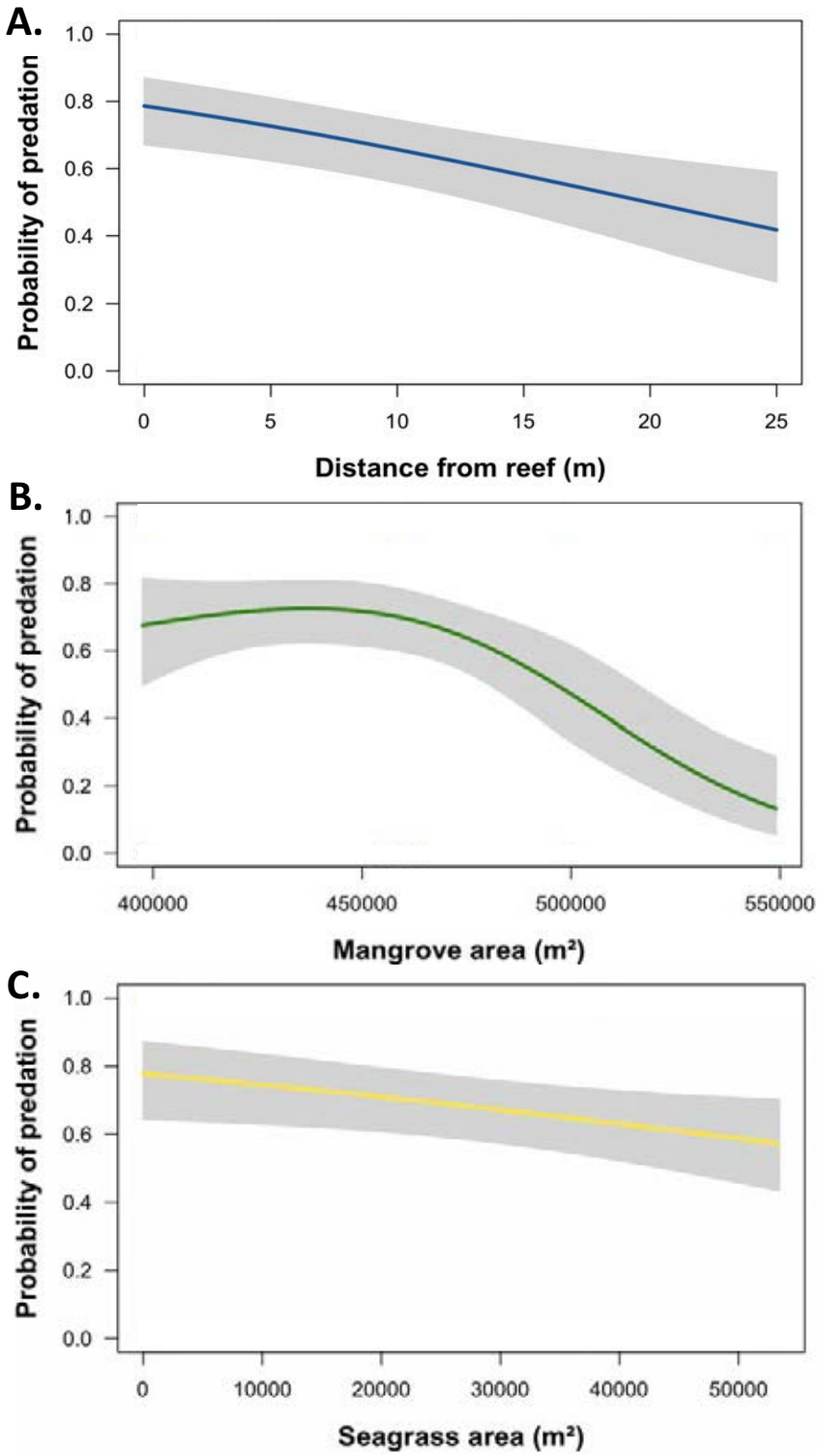


Figure 3 Generalised additive model (GAM) outputs illustrating relationships between the probability of predation and (a) distance from reef, (b) mangrove area, and (c) seagrass area. Grey shaded polygons represent 95% confidence intervals.

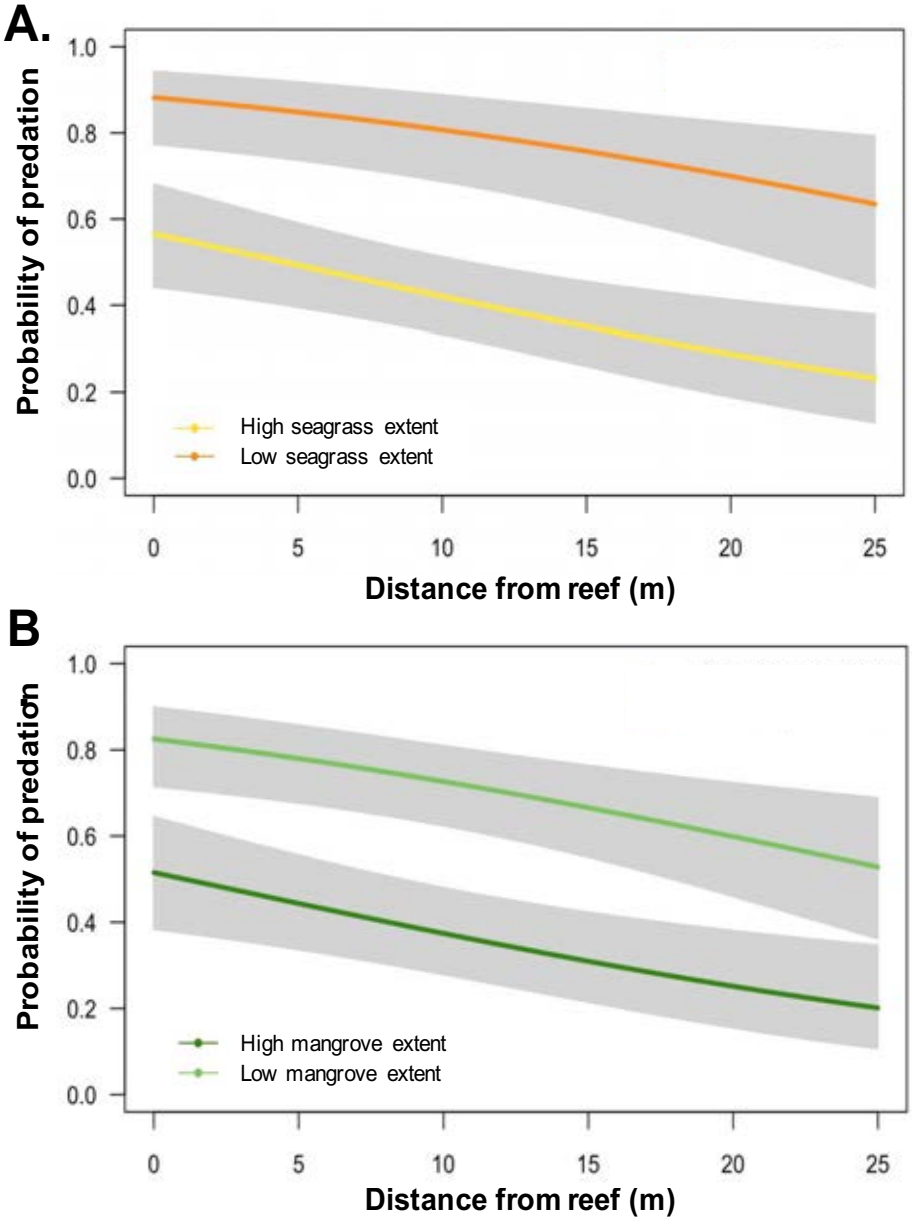


Figure 4 Generalised linear model (GLM) outputs illustrating relationships between the probability of predation and (a) seagrass area, (b) mangrove area, categorised in to low and high by natural splits in the data as distance from reef increases. Grey shaded polygons represent 95% confidence intervals. Note that the analyses underlying these graphs were run on two continuous variables (distance from reef, and area of habitat within 500m 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= 397489.12m^2 - 459372.51m^2, high = 463206.33m^2 - 549056.19m^2; for seagrass, low=seagrass absent within 500m, high=seagrass present within 500m).

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; Kaiser-Bunbury et al. 2017; Miller 2002). 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 2016a; 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. 2018a), 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. 2018) 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 (Olds et al. 2018a; Pollock 1982), 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 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 (Gilby et al. 2018b; Olds et al. 2012b). 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 (Geraldi et al. 2009; Grabowski et al. 2005). Our findings show that 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 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. 2018). By contrast, fish will also move some distance over low complexity habitat to congregate around restored structures (Gregalis et al. 2009; Irlandi and Crawford 1997). 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 also 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 the 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 m^2) 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. 2018c). 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 scales, and there might be a given seascape scale (likely many hundreds of meters) over which thresholds occur on the effects of seascape connectivity (Martin et al. 2015; Olds et al. 2012b). 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 (Bauer et al. 2010; Foam et al. 2005). This is unlikely, since predation rates were lower 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 these 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. These effects, however, require 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.

Supplementary Materials

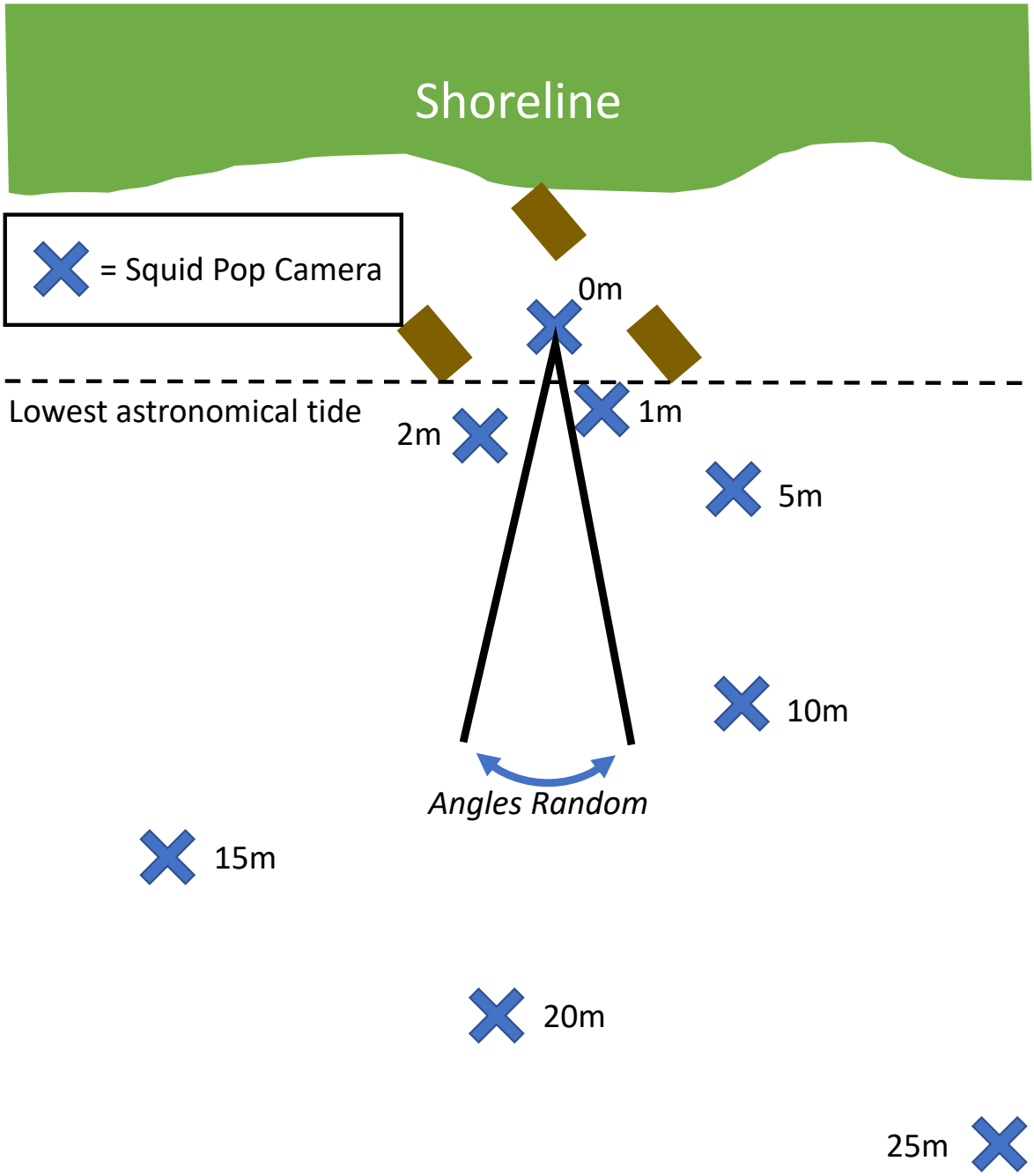


Figure S1 Conceptual diagram illustrating camera positions at 0, 1, 2, 5, 10, 15, 20, 25m distances from a reef site. The first camera unit is located within the centre of the reef (i.e. 0m), the remaining (i.e. 1, 2, 5, 10, 15, 20, 25m) are positioned at random angles seaward from the first camera.

Figure S2 Squidpop assay design. Squidpops consist of a single 1cm^2 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 5kg 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 and for ease when deploying from a boat.

Table S1 Best fit model on probabilities of predation at control 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**
Salinity	0.99	24.11	**<0.001**
Mangrove area	0.95	23.93	**<0.001**
Seagrass area	0.57	25.95	**<0.001**
Secchi depth	0.67	5.3	**0.09**

Chapter 6

Effects of oyster reef restoration extend across coastal seascapes

Ortodossi NL, Gilby BL, Schlacher TA, Henderson CJ, Olds AD (2019) Effects of oyster reef restoration extend across coastal seascapes.

Introduction

Landscape fragmentation and habitat degradation from anthropogenic disturbances results in a simplification of the structural complexity of habitats, and these changes have led to unprecedented losses in biodiversity and ecosystem services, globally (Butchart et al. 2010; Montoya et al. 2012; Sannigrahi et al. 2018). These negative consequences from habitat loss and modification have motivated significant interest in the restoration of degraded ecosystems on land, and in the sea (Loke et al. 2015; Montoya et al. 2012). Restored ecosystems increase landscape diversity, and habitat complexity, and can enhance biodiversity, re-establish ecosystem functioning and safeguard ecosystem services (Loke et al. 2015; Micheli and Peterson 1999). These positive effects of restoration, particularly enhancement of animal abundance and diversity, have been reported widely, and from most restored ecosystems (Bullock et al. 2011; Rey Benayas et al. 2009). There is, however, some uncertainty as to whether the high abundance and diversity of fauna results from the movement of animals into restored habitats from nearby locations (i.e. attraction) or from the increased carrying capacity that restored habitats confer to landscapes, and provide new opportunities for the colonisation of additional individuals (i.e. supplementation). These attraction versus supplementation hypotheses have been debated for some time, particularly in relation to the habitat values of artificial reefs (Brickhill et al. 2005; Pickering and Whitmarsh 1997), but the concept has not been sufficiently examined when considering the potential values of restoration projects on land, or in the sea.

The extent and condition of many coastal and estuarine ecosystems have been reduced due to the cumulative impacts of multiple anthropogenic stressors, with detrimental effects to biodiversity, food-webs, ecological functioning and ecological resilience (Elliott et al. 2007; Hughes et al. 2005; Worm and Duffy 2003). Many restoration efforts have, therefore, been employed in coastal and estuarine seascapes to combat declining biodiversity and promote ecosystems services (Coen et al. 2007; Elliott et al. 2007; Hughes et al. 2005). Positive effects of habitat restoration have been reported widely for many marine organisms, but especially for fishes, from a range of coastal ecosystems, including seagrass meadows (Blandon and zu Ermgassen 2014), mangrove forests (Bosire et al. 2008), salt marshes (Raposa 2002) and oyster reefs (Gilby et al. 2019). It is, however, not clear whether these effects of restoration result from the movement of mobile marine organisms into restored habitats from nearby locations (i.e. attraction), or from the recruitment and colonisation of new individuals (i.e. supplementation) (Brickhill et al. 2005; Pickering and Whitmarsh 1997). It is important to distinguish between these two processes because increasing the biomass/carrying capacity of coastal and estuarine systems, particularly for fish and crustaceans, is

important for sustaining the substantial recreational and commercial fisheries that are derived from these ecosystems around the world (Barbier et al. 2011; Taylor et al. 2017).

Oyster reefs are structurally complex coastal ecosystems, and are widely regarded as one of the most valuable and productive coastal fish habitats (Coen et al. 2007; Grabowski and Peterson 2007). Oyster reefs have, however, experienced significant declines in the last century, with >85% of all oyster reefs being reported as functionally extinct due to the combined effects of overharvesting, disease, and declining water quality, globally (Beck et al. 2011; Coen et al. 2007; Grabowski et al. 2012). Lost oyster reefs are commonly replaced with habitats that provide less food or poorer protection from predators for fish, such as bare muds and sands (Gilby et al. 2018c; Grabowski et al. 2012; Grabowski et al. 2005). These profound habitat changes are often irreversible without intervention, and are typically associated with declines in fish diversity, abundance and biomass, and severe impacts to local recreational and commercial fisheries (Coen et al. 1999; Gilby et al. 2018c). For these reasons, an important goal of many oyster reef restoration projects is the enhancement of fish, and fisheries in the areas surrounding restored reefs (Baggett et al. 2015; Humphries and La Peyre 2015). Previous research has established that oyster reefs enhance fish abundance and diversity in areas where reefs are restored on previously bare sediments (Geraldi et al. 2009; Peterson et al. 2003; Pierson and Eggleston 2014; zu Ermgassen et al. 2016). These findings were, however, limited to the immediate vicinity of restored oyster reefs (i.e. m to 10s of m) in temperate marsh-dominated seascapes (Grabowski et al. 2005; Micheli and Peterson 1999). Consequently, it is not clear whether similar effects occur in subtropical or tropical seascapes where mangroves/seagrass dominate, and if these effects can be extended to larger scales (i.e. km to 10's km) to affect the biomass/carrying capacity of entire estuarine seascapes.

In this study, we use restored inter-tidal oyster reefs in a subtropical estuary in south-east Queensland, Australia to test whether the restoration of oyster reefs supplement the fish community by providing additional structurally complex habitats and enhance the biomass/carrying capacity of the estuary, or simply redistribute fish throughout the system. The restored oyster reefs in this system replace low complexity sandy and muddy substrates, and are placed across the estuary in fundamentally different seascape positions in terms of their proximity to other fish habitats (i.e. mangroves, seagrass) and in their level of connectivity with the open sea. This restoration project is, therefore, an ideal test system for quantifying whether, and how, restored oyster reefs augment both the abundance and diversity of fish, and whether the installation of oyster reefs redistribute their abundance throughout the estuary. Given the potential for oyster

reefs to enhance fish biomass (Geraldi et al. 2009; Peterson et al. 2003; zu Ermgassen et al. 2016), we hypothesise that the restored oyster reefs will augment fish abundance and diversity throughout the system (i.e. large spatial scales ~ km to 10's kms) and re-distribute fish closer to restored oyster reefs.

Methods

Study seascape

We sampled fish with remote underwater video stations (*RUVS*) within the Noosa River estuary, in Queensland, Australia (26°22'S 153°04'E) (Figure 1). The Noosa River estuary is comprised of a heterogeneous mix of natural estuarine habitats including mangroves, seagrass, sand flats, rock bars, and woody debris, and includes a moderately urbanised shoreline (≤ 50 % of the river has urban shorelines). Variation in the composition and arrangement of habitats in this seascape has been linked to changes in the abundance, diversity and distribution of fish in the estuary (Gilby et al. 2018b). Natural oyster reefs were once abundant throughout the Noosa River estuary, but declined precipitously throughout the early 1900's due to anthropogenic activities (especially overharvesting, declining water quality, and associated rick of disease), and are now functionally extinct (Thurstan 2016). The transition of these complex oyster reefs to un-vegetated sandy substrates has contributed significantly to reductions in fish diversity and fish catches throughout the estuary (Thurstan 2016). Oyster reefs were restored to the Noosa River estuary in November 2017, with the primary objective of enhancing fish abundance and diversity by replacing the lost habitat values, and heterogeneity, in the seascape.

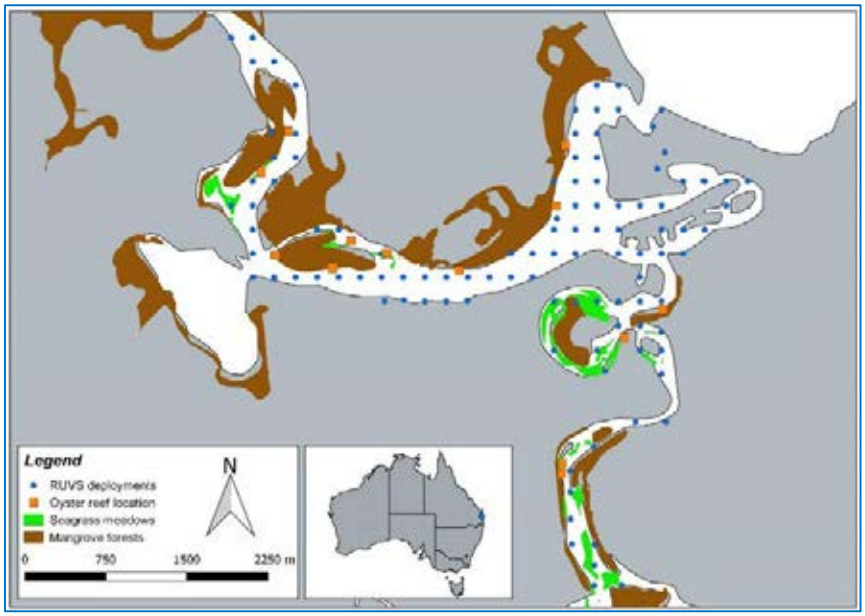


Figure 1. Location of restoration sites (orange) and remote underwater video stations (RUVS) deployments (blue) in the Noosa River estuary, Australia.

Oyster reef design

Oyster reefs were constructed of biodegradable coconut mesh bags (1 m long x 30 cm diameter) filled with recycled oyster shells obtained from local suppliers. Naturally occurring oyster larvae settle and grow on this restored structure, and over time solidify the recycled oyster shells together, forming functioning oyster reefs once the coconut mesh casing degrades away. Each oyster reef is comprised of 9 oyster-shell filled bags stacked in three piles of three in triangular prisms, with one side positioned at lowest astronomical tide (LAT), and with each pile separated by 5 m. A total of 14 sites throughout the estuary were restored with these oyster reefs. Restoration sites were chosen based on three key criteria: 1) positioned within the historical range of natural oyster reefs in the estuary; 2) positioned to represent the full spectrum of seascape contexts available throughout the estuary; and 3) positioned to provide stepping stones for fish migrations throughout the estuary. The restored oyster reefs in this system, therefore, differ in terms of their proximity to other fish habitats (i.e. mangroves, seagrass) and in their level of connectivity with the open sea (a source of fish and oyster larvae); making them an ideal natural laboratory to test how oyster reef restoration initiatives can modify fish abundance and diversity, and potentially enhance fisheries over large spatial scales.

Fish surveys

Fish assemblages were sampled using remote underwater video stations (RUVS). RUVS consisted of a GoPro camera (Hero 5 recording in 1080p high definition) mounted to a 3kg custom-built deployment device. RUVS are increasingly used for this type of study as they do not bias the structure of fish assemblages via the use of bait attractants (Gilby et al. 2018b). Surveys were conducted at three month intervals between February 2017 and August 2018, and included three sampling events before the installation of the oyster reefs, and three sampling events after installation. All surveys were conducted during daylight (07:00-16:00 h), and within 2 hrs either side of high tide, to maximise visibility and accessibility to sites in the shallow reaches of the estuary. We deployed RUVS at 100 sites, which were selected by using Quantum GIS to overlay a grid with 200 m intervals over the entire marine reach of the Noosa River estuary (i.e. from the mouth to the most upstream reaches covering all areas where oyster reef restoration occurred). Each RUVS deployment sampled fish for 30 minutes, giving a total video sampling time of 50 hrs per sampling event and 300 hrs over all for the study. Fish abundance and diversity were quantified from videos using the standard *MaxN* statistic; the maximum number of individuals of a species observed in any single video frame (Ortodossi et al. 2018). We also quantified the number of species which were harvested

by both recreational and commercial fishers using information from FishBase (Froese and Pauly 2018).

Data analysis

We used permutational multivariate analysis of variance (PERMANOVA) in PRIMER E (Anderson et al. 2008) to determine differences in the assemblages of fish in the Noosa River between pre- and post-installation events (fixed factor, two levels), and survey months (fixed factor, three levels; February, May and July/August). PERMANOVA results were visualised using non-metric multi-dimensional scaling (nMDS) ordinations. Fish species that drove these differences were identified using indicator species analysis (INDVAL) (Dufrene and Legendre 1997) in the labdsv package (Roberts 2013) of the R statistical framework (R Core Team 2019). Significant indicator species were plotted over the nMDS ordination using Pearson vector overlays.

We further interrogated these patterns by testing for the interactive effects of the distance of each survey site to the nearest oyster reef restoration site (distance to reef), pre- and post-installation events, and survey months on species richness and harvestable fish abundance across the estuary. These differences were visualised using 'Heat Maps' created in QGIS (QGIS Development Team 2019).

Results

Fish assemblages

Fish assemblages in the Noosa River varied significantly between pre- and post-installation events, and with survey month (Table 1). Pairwise tests indicated that all pairwise comparisons of the pre/post installation and survey month interaction term differed significantly (Figure 2). Six species were identified in INDVAL analysis as being the principle drivers of these patterns; yellowfin bream *Acanthopagrus australis*, sand whiting *Sillago cilliata*, sea mullet *Mugil cephalus*, spotted scat *Scatophagus argus*, southern herring *Herklotsichthys castelnaui*, and narrow-lined puffer *Arothron manilensis*. Yellowfin bream and sand whiting were significant indictors of the Pre (July/August) event, whereas each of the other species were significant indicators Pre (February) event. We identified a significant reduction in average species richness and harvestable fish abundance between the three pre installation surveys and the three post installation surveys (Figure 3).

Table 1. Permutational multivariate analysis of variance results (PERMANOVA) testing for the effects of pre/post installation and survey month on the assemblage of fish at all sites surveyed in the Noosa River. Pairwise tests indicate that all combinations in the interaction term differed significant to each other.

Source	df	SS	MS	Pseudo-F	P
Pre/Post Installation	1	14734	14734	4.1099	**0.003**
Survey month	2	79795	39897	11.129	**0.001**
Pre/Post Installation x Survey Month	2	51417	25708	7.1709	**0.001**
Residual	602	2.16E+06	3585.1		
Total	607	2.30E+06			

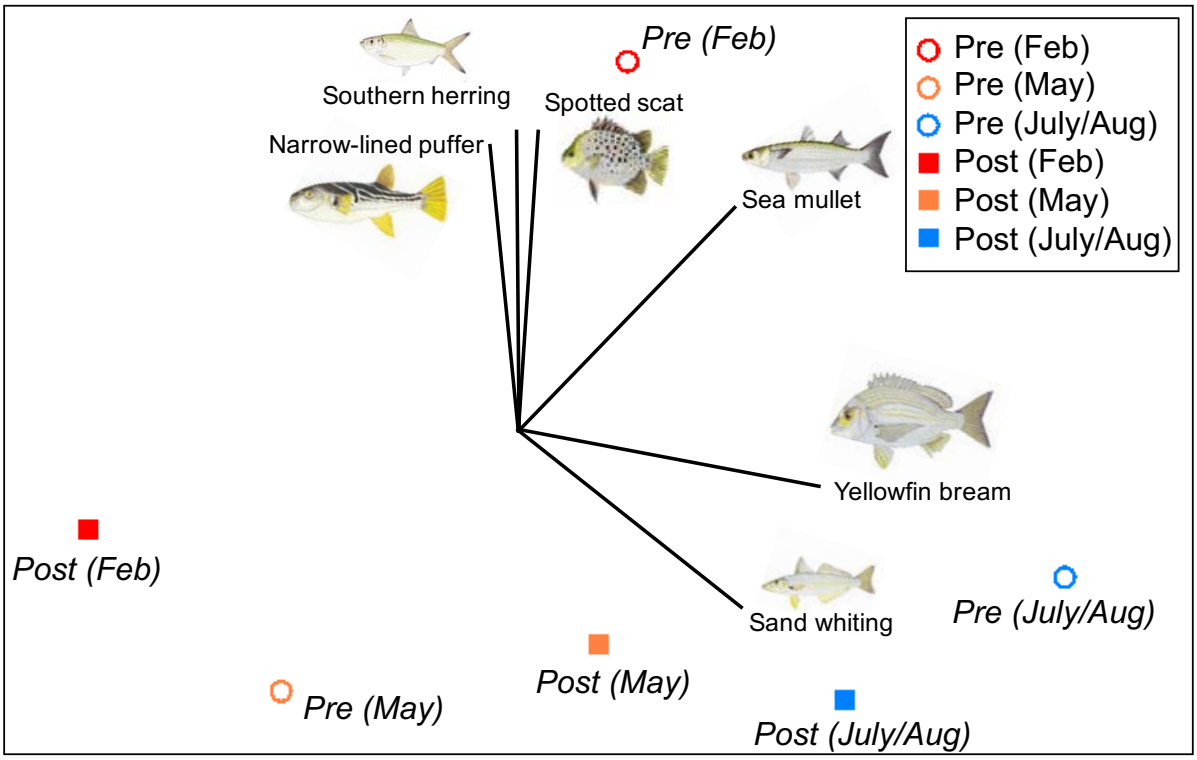


Figure 2. Non-metric multidimensional scaling ordination (nMDS) of centroids for pairs of pre/post installation and survey month with Pearson vector overlays of significant species from INDVAL analyses.

Effects of proximity to restored oyster reefs

Fish diversity and abundance were concentrated in the same place both before, and after, installation (Figure 4); in the lower estuary, that usually has high salinity, an abundance of structure habitats (in particular log snags, mangroves and urban structures, and is positioned at the meeting point of two different estuaries (Weyba Creek, and the main Noosa River). Species richness in the Noosa River estuary was modified by the distance of monitoring sites to reefs, and the interaction between pre/post installation and survey month (Table 2, Figures 4, 5). Here, species richness was highest at monitoring sites farthest from oyster reefs (Figure 4, 5A), and was variable, with no consistent patterning, between survey months and survey events pre and post installation (Figure 4B). The abundance of harvestable fish in the Noosa River estuary was modified by the interactions between pre/post installation and distance to reef, pre/post installation and survey month, and survey month and distance to reef (Table 2, Figure 4, 6). Here, the abundance of harvestable fish increased consistently with distance from restored reefs, but increased to a greater degree post installation (Figure 6A). Similarly, to the patterns through time with species richness, harvestable fish abundance varied considerably through time in the estuary, with no consistent patterns (Figure 6B).

Table 2. Results of generalised linear model analyses testing for the effects of distance to oyster reef, pre/post installation and survey month on A) species richness and B) harvestable fish abundance.

Source	**Df**	**X^2**	**P**
Species Richness			
Pre/post installation	1	24.8	**<0.001**
Distance to reef	1	8.1	**<0.001**
Survey month	2	33.9	**<0.001**
Pre/post installation x Distance to reef	1	1.7	0.189
Pre/post installation x Survey month	2	85.4	**<0.001**
Survey month x Distance to reef	2	1.0	0.612
Pre/post installation x Distance to reef X Survey month	2	0.9	0.625
Harvestable fish abundance			
Pre/post installation	1	116.1	**<0.001**
Distance to reef	1	19.8	**<0.001**
Survey month	2	149.5	**<0.001**
Pre/post installation x Distance to reef	1	13.4	**<0.001**
Pre/post installation x Survey month	2	258.1	**<0.001**
Survey month x Distance to reef	2	45.1	**<0.001**
Pre/post installation x Distance to reef X Survey month	2	4.0	0.137

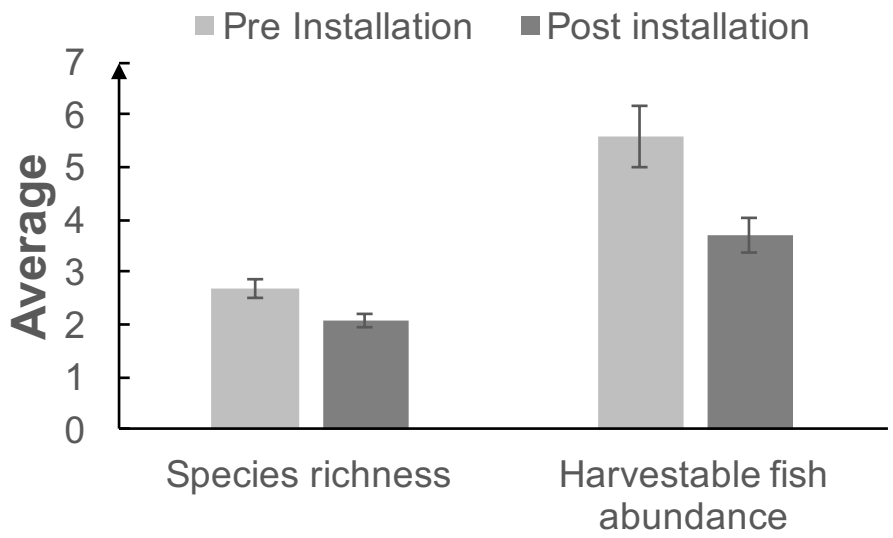


Figure 3 Average (+/- SE) species richness and harvestable fish abundance across all sites for the three monitoring events prior to reef installation, and the three events after reef installation.

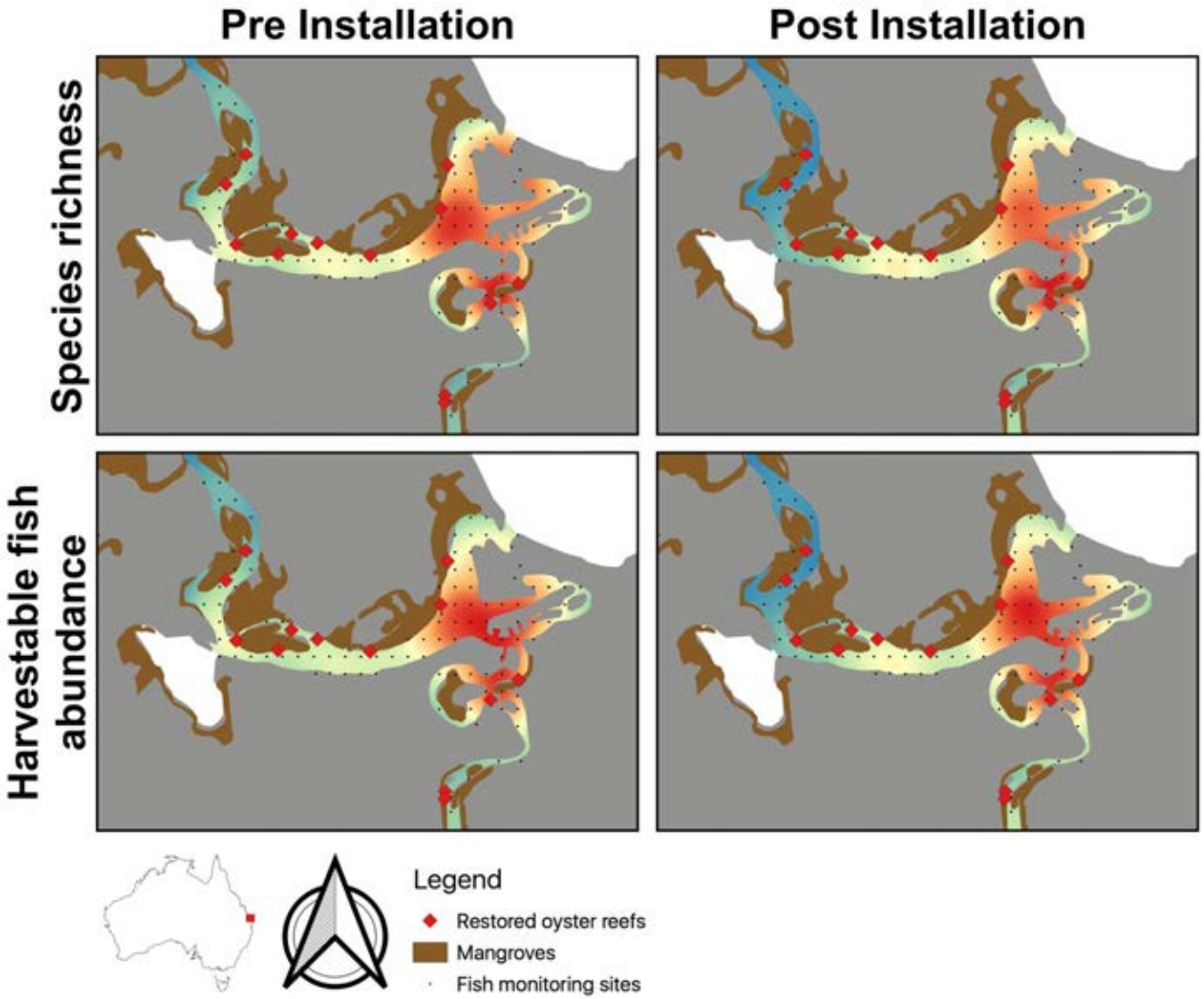


Figure 4 Heat maps of before and after reef installation for species richness and harvestable fish abundance.

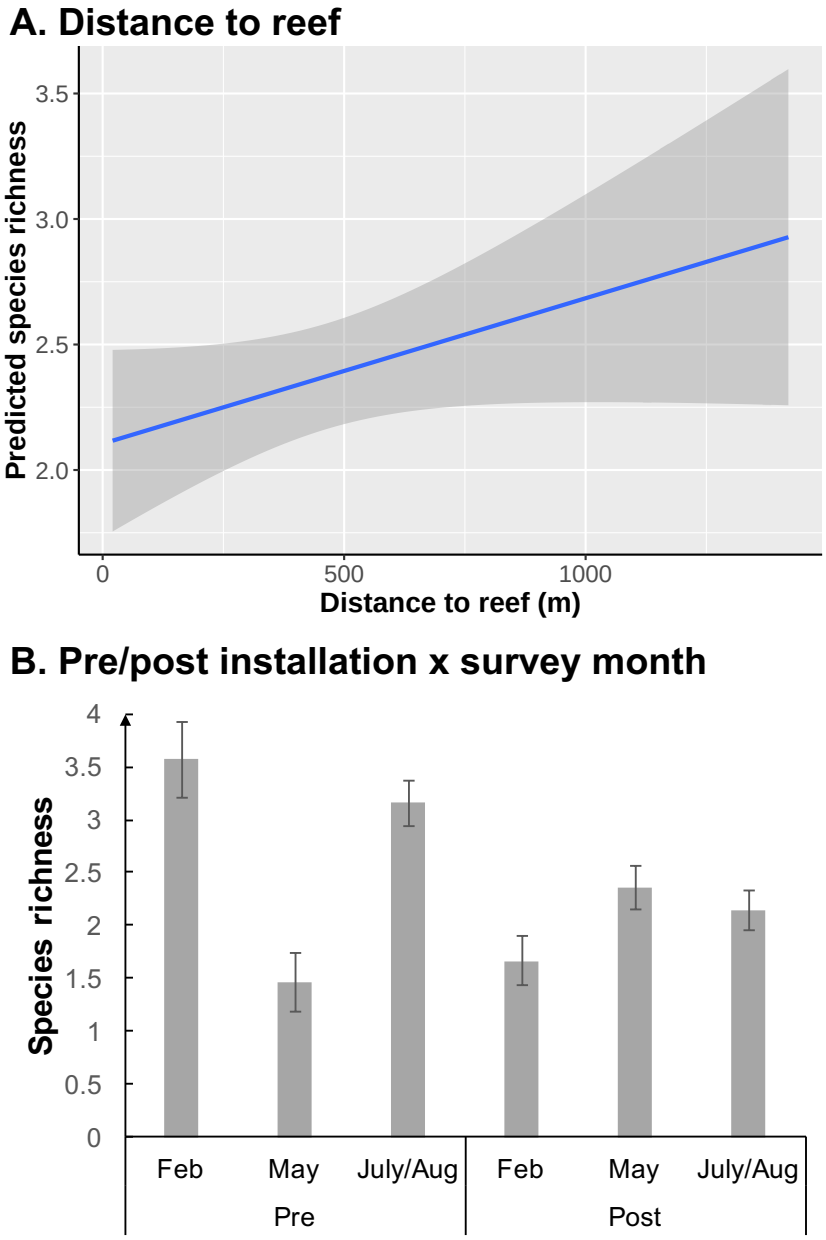


Figure 5 Effects of A) distance to reef and B) the interaction between pre/post installation by survey month on species richness.

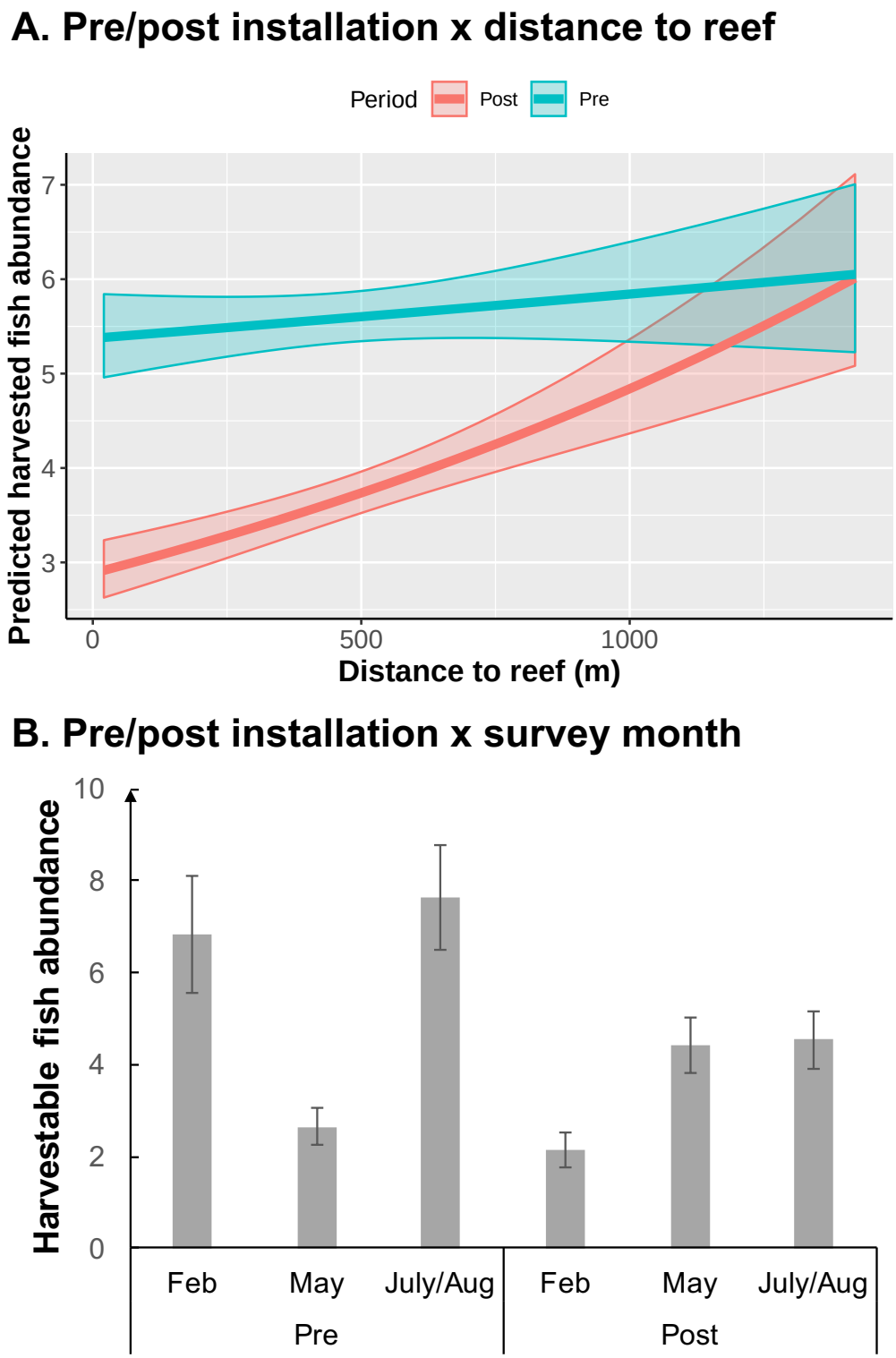


Figure 6 Effects of A) the interaction between pre/post installation and distance to reef and B) the interaction between pre/post installation by survey month on harvestable fish abundance.

Discussion

Quantifying the effects that restoration has on the spatial distribution of animals both at restoration sites, and across landscapes is an important focus for restoration ecologists (Gilby et al. 2018a; Jones and Davidson 2016). As the scale of restoration increases across all environmental realms globally, the capacity for the effects of restoration on animal populations to expand across landscapes also increases. Quantifying the degree to which current restoration actions modify these effects, and the attributes of restoration projects that might maximize the proliferation of restoration effects more broadly, is therefore vital in optimizing future restoration plans (Guerrero et al. 2017; Hagger et al. 2017). In this study, we found that fish assemblages varied significantly across temporal scales in the Noosa River, and that there was a significant change in the assemblage composition and distribution of fish in the river following the installation of the oyster reefs. Here, all significant indicator species were in higher abundance and more prevalent prior to the installation of the restored oyster reefs. These effects proliferated to effects on species richness and harvested fish abundance, which were both higher at greater distances from the restored reefs. Similarly, we identified higher species richness and harvestable fish abundance during the monitoring events prior to the installation of the oyster reefs than after. These findings are counter to the effects found in other studies, including other studies of these reefs that found a significantly higher abundance of fish occurring at reefs and significantly higher rates of key ecological functions. These studies identified a significant effect of freshwater runoff from catchments on the diversity and abundance of fish in the Noosa River estuary (Gilby et al. 2019), and the second year of our monitoring program here had significantly higher rainfall in the broader Noosa catchment than the first year of sampling (Bureau of Meteorology 2019). This suggests that additional environmental variables will need to be accounted for in subsequent analyses to properly quantify the effects of the reefs on fish assemblages throughout the estuary. Consequently, given the findings of other studies on these reefs (Duncan 2018; Gilby et al. 2019), and the fact that the effects of oyster reefs on fish can take several years to develop (this study was completed during the year following oyster reef installation) (zu Ermgassen et al. 2016), we cannot conclude that the effects of the installation of the reefs has been an overall decline in fish abundance and diversity in the river, as analyses that account for variable runoff will be required. Similarly, we cannot conclusively determine whether there has been an overall additive or take-back effect of the reefs on the broader fish assemblage throughout the Noosa River. More complex spatial analyses, and potentially more survey events will be required to better disentangle these effects. Irrespective of these patterns, the results found here will provide invaluable baseline information regarding the effects of oyster reefs on fish and fisheries throughout the Noosa River, especially with plans to expand the restoration efforts in Noosa more broadly now underway.

It has been well established globally that restoring oyster reefs to previously unvegetated, sandy or muddy substrates augments the abundance and diversity of fish (Peterson et al. 2003; zu Ermgassen et al. 2016). In the Noosa River estuary, restored oyster reefs contained 1.4 times the number of species and 1.8 times the abundance of harvestable fish than at nearby control sites (Gilby et al. 2019). Similarly, studies quantifying the distribution of key ecological functions around the restored reefs found opposing effects to the results found here (Duncan 2018). The function of predation, an important function that maintains food web structure and ensures the exchange of nutrients and energy through food webs, declined with increasing distance from these restored oyster reefs (Duncan 2018). Our findings in this study were therefore counter to our predictions of the effects of restoration on the distribution of fish. No studies, however, have attempted to quantify the effects of oyster restoration across seascapes (i.e. away from restoration sites) to the scale attempted here.

There are several potential explanations for the patterns we found in this study. Firstly, it is likely that changes in environmental conditions within the estuary between the 2017 and 2018 sampling events had a substantial effect on the composition of fish within the estuary (Gilby et al. 2017a; Gilby et al. 2019). Secondly, the oyster reefs installed in Noosa are relatively small; we restored 14 oyster reefs of (approximately 25m^2) for a total restoration footprint of approximately 350m^2 across the entire estuary. This means that these reefs remain a relatively small component of the broader seascape, so their effects were relatively low across the seascape despite our finding of significant benefits at the reef sites themselves (Duncan 2018; Gilby et al. 2019). Areas in the Noosa River study area that are farthest from oyster reefs, are also those near the mouth, and where Weyba Creek joins the main system. This is where fish abundance and diversity was aggregated both before and after the reefs were installed. The stronger effects of distance from reefs on fish assemblages post-installation likely reflects to the aggregation of more fish from more species in these areas after the reefs went in. This is not likely related to the reefs themselves, but rather possibly reflects movement downstream to spawn, or following successive rainfall events. Increasing the size of restoration sites in subsequent iterations of the restoration efforts in Noosa is therefore a key recommendation, and will likely result in a greater, and more immediately detectable, effect on fish and fisheries across the entire estuary. Global analyses of the effects of restored oyster reefs on fish indicate that it can take up to 15 years for the effects of restoration on fish assemblages to fully develop (zu Ermgassen et al. 2016). These time frames reflect the time frames identified for the development of effects for marine reserves (Edgar et al. 2014). The short, one year period surveyed here may not have provided sufficient time for the effects of the reefs to even be detected properly

across the Noosa River estuary, let alone fully mature, especially in the background of the increased rainfall experienced in the second year of surveys (Bureau of Meteorology 2019). Consequently, long-term monitoring of restoration efforts is encouraged so that the full benefits can be properly quantified in the context of annual and seasonal variations in temperature, rainfall and fishing pressure (Underwood 1991). Maintaining such long-term, consistent monitoring has been a significant challenge for restoration in many systems, but serves to better inform stakeholders of the benefits that restoration brings, increases the capacity to optimize subsequent restoration actions, and provides long-term evidence of restoration benefits (Baggett et al. 2015; Elliott et al. 2016; Gilby et al. 2018c).

The positioning of oyster reefs on intertidal banks may have contributed towards the higher assemblage species richness and abundance of harvestable fish further away from restored oyster reefs. All of the oyster reefs restored in the Noosa River estuary were placed intertidally, and the vast majority were placed on the northern bank of the estuary. This means that the deeper channels which fish use to migrate in and out of the estuary, and seek shelter during low tides were located some distance from the restoration sites. Broadly, connectivity with these deeper channels has shown to be a significant factor that changes the distribution of fish across the estuarine seascapes of Noosa and the Sunshine Coast (Brook et al. 2018; Gilby et al. 2017b). Consequently, we have two key recommendations from this finding. Firstly, subsequent analyses should account for the distance of these deeper channels from the monitoring sites, and for the actual depth of each monitoring sites. Similarly, subsequent restoration efforts in the Noosa River should better account for connectivity with these deeper water channels, as these are important movement pathways for many of the harvestable fish species for which the Noosa restoration actions seek to enhance (Davis et al. 2014; Davis et al. 2017).

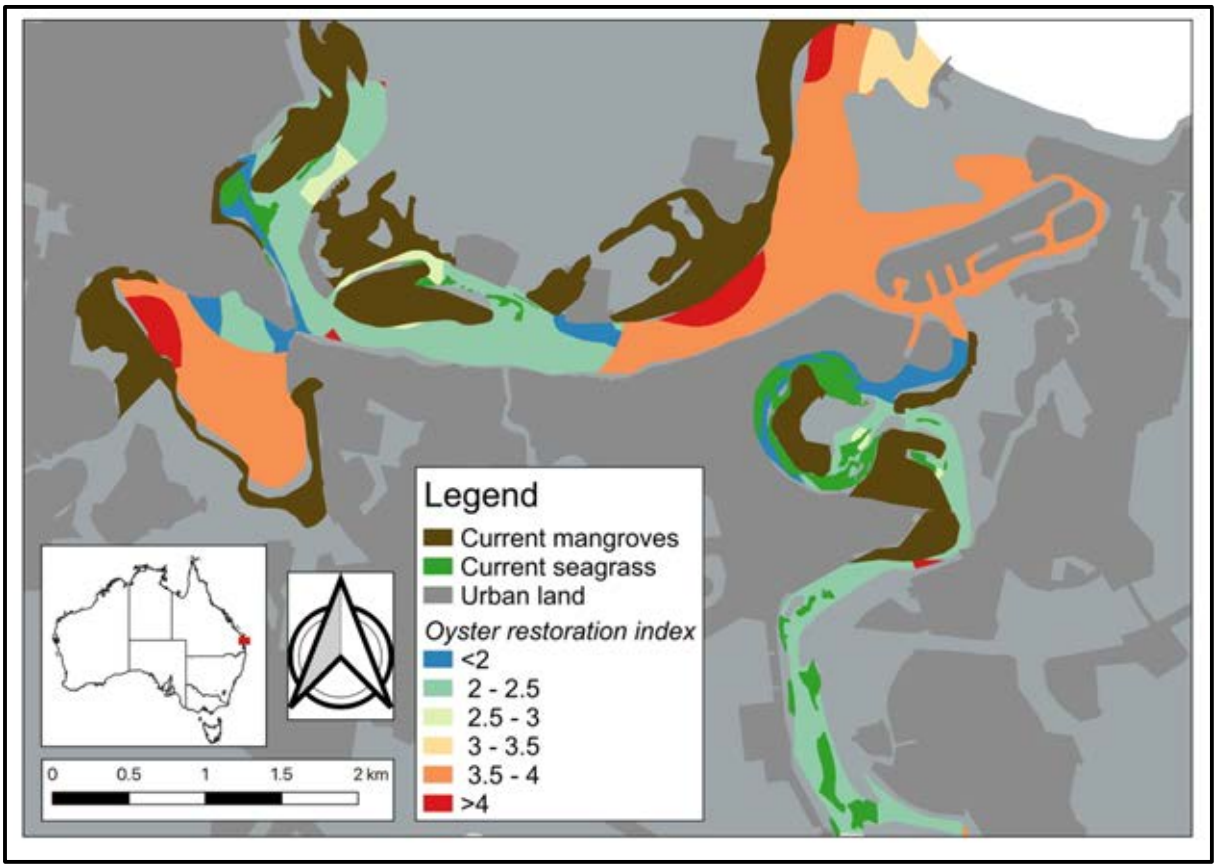
The effects of conservation interventions on the broader distribution of animals throughout landscapes has been a significant focus over many years. Here, studies have principally focused on the effects of nature reserves on the distribution of animals around reserves. These types of studies have focused on this 'spillover' effect in two ways; positively through the spillover of harvestable biomass and larvae to fished areas from marine reserves as fish assemblages within marine reserves mature (McClanahan and Mangi 2000; Stobart et al. 2009), and the negative effects of animal interactions and pathogens spilling over to areas of human habituation from national parks as the carry capacity of the park is reached (Kilpatrick et al. 2009; Ripple and Beschta 2007). Expanding research into the effects of restoration on these 'spillover' effects to surrounding, unrestored sites

will enhance our capacity to optimize restoration in several key ways analogous to those conducted for reserves; we can optimize our restoration designs in situations where the spillover of biomass is favourable (like the case study here), and limit conflicts when such spillover is less favourable. Despite the equivocal results found here regarding the effects of oyster reef installation on the assemblages of fish, and distance to restoration sites following restoration, several key conclusions can still be drawn for future restoration efforts in Noosa. Principally, ensuring that the effects of restoration expand significantly across the entire seascape of the Noosa River (i.e. they increase the overall carrying capacity of the system more broadly) will require larger restoration sites across the entire Noosa seascape to; 1) enhance the augmentation effects of the reefs, and 2) spread biomass across the estuary. Further, better consideration of connectivity effects with deeper channels, and a long-term commitment to thorough monitoring and evaluation of the effects of the oyster reefs across the entire estuary is required.

Chapter 7

Identifying restoration hotspots to maximise outcomes for multiple restoration benefits

Gilby B, Olds A, Duncan C, Ortodossi N, Henderson C, Schlacher T (2019) Identifying restoration hotspots to maximise outcomes for multiple restoration benefits. (under review)



Introduction

The prevalence and size of ecological restoration projects is increasing across marine, freshwater and terrestrial ecosystems globally (Middendorp et al. 2016; Paice et al. 2016). Ecological restoration principally seeks to re-establish or restore lost or degraded ecosystems and their functioning (Balaguer et al. 2014; Hagger et al. 2017; Stanturf et al. 2014). Restoration projects can also have important goals around enhancing or re-establishing populations of animals (Gilby et al. 2018a; Jones and Davidson 2016b), and the provision of ecosystem services (Dame and Libes 1993; Smyth et al. 2015). Using quantitative information to optimise restoration plans may result in greater ecological, economic and social benefits derived from restoration for the same financial costs, and can potentially minimise social costs and disruptions (Bullock et al. 2011). Identifying restoration actions that create hotspots for multiple restoration benefits (i.e. animal populations, ecological functions and/or ecosystems services, in addition to the growth of lost or degraded ecosystems) is therefore an important goal for ecologists and restoration practitioners (Schulz and Schroder 2017).

The principle of managing or improving ecosystems for multiple benefits has been long-recognised (Hector and Bagchi 2007; Peng et al. 2019), but only rarely applied to the design of restoration projects in a formal manner (Crossman and Bryan 2009; Gilby et al. 2018c). For example, there is increasing recognition that managing ecosystems to enhance biodiversity, and therefore rates and redundancy of multiple ecological functions (e.g. recruitment, predation, herbivory and scavenging), can increase the resilience of ecosystems to a range of potential disturbances (Cardinale et al. 2006; Gamfeldt and Roger 2017). Restoration literature has increasingly recognised the importance of designing and placing restoration efforts to maximise biodiversity outcomes, increase rates of key ecological functions, and provide ecosystem services (like carbon sequestration and harvestable species) (Stanturf et al. 2014; Wortley et al. 2013) both at restoration sites, and throughout landscapes more broadly (Brudvig 2011; Holl et al. 2003). Such important 'secondary' benefits of ecological restoration (i.e. beyond simply the recovery of lost or degraded ecosystems) have gradually steered restoration targets away from the restoration of ecosystems to historical baselines or reference sites, and towards more complex goals focused on the provision of ecological services and the restoration of self-sustaining ecosystems, in addition to reversing biodiversity losses (Bullock et al. 2011; Rey Benayas et al. 2009). However, quantifying the features of restoration sites that maximise multiple benefits in a structured manner, and then setting quantitative restoration goals to optimise restoration plans, remains rare (Guerrero et al. 2017; Tobon et al. 2017; Wiens and Hobbs 2015).

The landscape context of ecosystems (their size, shape and spatial arrangement) modifies the condition and composition of habitat-forming species, their value as habitats for animals, and the rates and distribution of the ecological functions those animals provide (Massol et al. 2011; Pittman et al. 2011). The landscape context of restoration sites can therefore affect plant and animal recruitment, species persistence, rates of key ecological functions, and the provision of ecosystem services (Grabowski et al. 2005; Schultz and Crone 2005; Simenstad et al. 2006). These effects can have knock-on consequences for the condition of restored ecosystems, the time in which restored ecosystems take to become self-sustaining, and the likelihood of achieving restoration targets (Brudvig et al. 2009; Rudnick et al. 2012; Tambosi et al. 2014). Despite the recognised importance of landscape context in outcomes for restoration actions, only approximately 11% of restoration sites have been selected with proper consideration of landscape effects (Gilby et al. 2018a). Identifying restoration sites within heterogeneous landscapes that fulfil both the biological requirements of habitat forming species, and that also maximise restoration outcomes for multiple secondary restoration targets (i.e. animals and multifunctionality) is challenging, and reliant upon understanding the spatial drivers of all restoration benefits (Schulz and Schroder 2017). After decades of research focusing on the ways to maximise the growth of habitat forming species in restoration projects, and with landscape scale restoration plans being implemented in many settings, researchers can now focus more strongly on optimising the spatial placement of restoration actions in landscapes to ensure outcomes for multiple benefits (Gilby et al. 2018c; Jones and Davidson 2016a; Rudnick et al. 2012; Wortley et al. 2013).

Coastal ecosystems are ideal study systems to quantify the effects of restoration actions for multiple benefits. Coastal ecosystems are highly threatened by human activities (Halpern et al. 2008), but are also vital habitats and nurseries for many coastal animal species (Whitfield 2017), meaning that there is a strong demand for active coastal restoration (Bayraktarov et al. 2016). For example, an estimated 85% of native oyster reefs have been lost globally due to overharvesting, declining water quality and disease (Beck et al. 2011). The replacement of structurally complex oyster reefs with low complexity sandy and muddy substrates are likely contributors towards both fisheries declines (Peterson et al. 2003; zu Ermgassen et al. 2016) and reductions in ecological functioning in many coastal ecosystems (Grabowski et al. 2005; Micheli and Peterson 1999). Therefore, oyster reef restoration is often used to re-establish lost habitats, as well as to enhance populations of animals and the ecological functions they provide (Gilby et al. 2019; Grabowski et al. 2005; Turner et al. 1999). There is a mounting body of evidence to suggest that the effects of restored oyster reefs on fish assemblages is modified significantly by their landscape context (Duncan 2018; Gilby et al. 2019;

Grabowski et al. 2005). However, oysters also often have narrow environmental envelopes in which they can recruit, grow and thrive (e.g. tide, salinity, turbidity and temperature ranges) (Baggett et al. 2015; Lenihan et al. 1996; Tamburri et al. 2008). This means that restoration plans may need to incorporate system-specific information on the spatial distribution of oyster reef growth, assemblages of fish at restoration sites, and rates of key ecological functions to maximise the scale of overall benefits (Gilby et al. 2018c).

With increasing investments being made globally on ecological restoration, and the scale of restoration projects increasing concomitantly, identifying restoration sites in landscapes that result in hotspots for multiple restoration benefits is an increasing research focus (Zhang et al. 2018). This requires the selection of sites where the physical restoration effort will be successful, as well as providing heightened secondary benefits that people covet. In this study, we survey the growth of oysters and the development of secondary benefits at 13 restored oyster reefs in the Noosa River Estuary in Queensland, Australia. Oyster reefs were historically abundant in the estuary, but were extirpated from the system in the early 1900's due to the combined effects of overharvesting, sedimentation, declining water quality, and disease (Thurstan 2016). This loss of complex, biogenic habitats from the system has been suggested as contributing to reduced fish catches and ecosystem condition in the estuary over the past century. Enhancing fish abundance and diversity (especially of harvestable species) is therefore a principle goal of the current restoration project. Previous studies at the restored reefs in Noosa showed 1.4 times greater species richness, 1.8 times more fish that are targeted by commercial and recreational fishers, and doubling of predation rates than at nearby control sites (Duncan 2018; Gilby et al. 2019). The basic premise of this study was to identify locations where placing additional restored oyster reefs would result in the greatest net benefits. We surveyed six potential restoration benefits (i.e. restoration benefits) at each of the restored reefs in the Noosa River estuary that could be broadly grouped into three categories. Firstly, we quantified the density and size of oysters growing on the restoration units, thereby providing information regarding the growth of the primary habitat forming species. Secondly, we quantified the diversity of fish assemblages and the abundance of harvested fish species at reefs, thereby providing information on the fish assemblages congregating around the restored reefs. Finally, we quantified rates of predation and carrion scavenging, thereby providing information on the key ecological functions that support oyster reefs within this estuary. We then used regression analyses and distribution models to identify restoration hotspots that are most likely to maximise restoration outcomes for all six variables. This study represents one of the first attempts to use thorough spatial

analyses of multiple aspects of restoration efforts to identify restoration hotspots in coastal ecosystems for multiple restoration benefits.

Material and Methods

Study system

Oyster reefs were restored to 13 sites in the Noosa River estuary in southern Queensland, Australia, in November 2017 (Figure 1). Oyster reef restoration units comprised three 1 m long by 30 cm diameter coir mesh bags (2.5 cm aperture) filled with recycled oyster shells stacked in a triangular prism. Three of these oyster reef units were placed in a triangle with 5 m sides and one side at the position of lowest astronomical tide at each restoration site. These oyster reef structures are designed to allow oyster larvae, which still occur in numbers great enough to allow natural recruitment and growth, to settle amongst the oyster shells and cement them together over time.

The Noosa River estuary supports a heterogeneous mix of unvegetated sandy substrates, mangrove forests (mostly *Avicennia marina*), seagrass beds (mostly *Zostera muelleri*) and hardened (urbanised) shorelines (Figure 1). The 13 oyster reef sites represent the diversity of landscape contexts (especially with respect to proximity to nearby seagrasses and mangroves) that exist currently within the estuary.

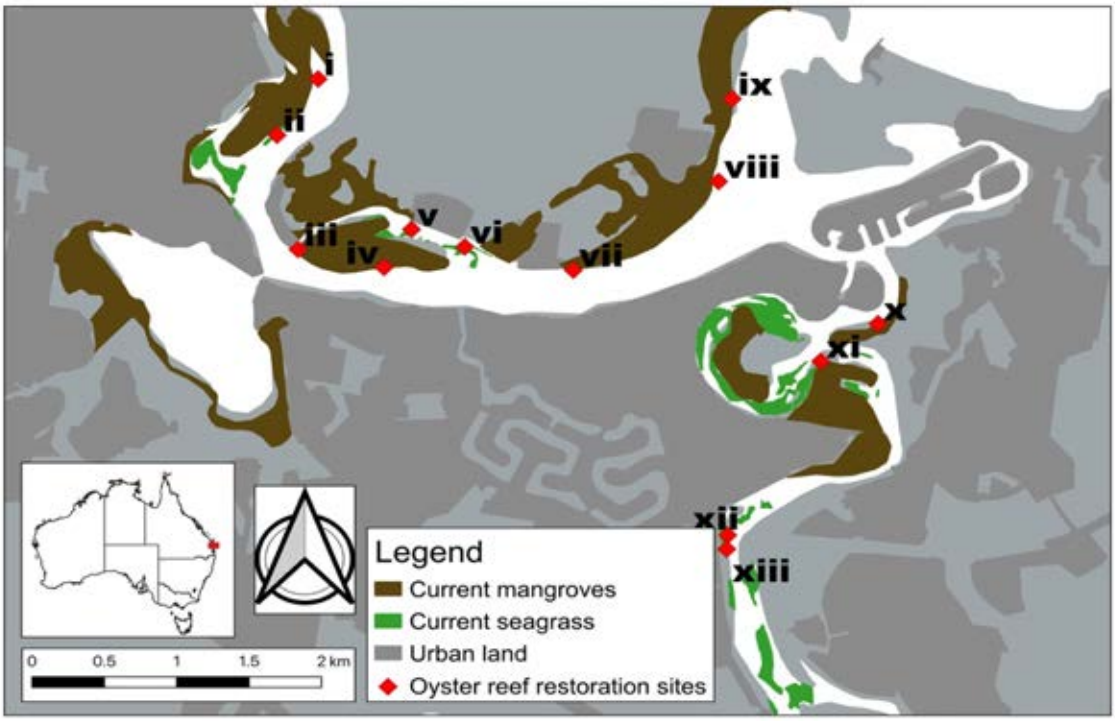


Figure 1 Map of the Noosa River estuary, oyster restoration sites and current-day distributions of seagrass beds and mangrove forests. Site numbers provided for oyster restoration sites.

Field surveys

We surveyed six attributes of oyster restoration sites, henceforth 'restoration benefits', that could be broadly grouped into three categories; oyster spat settlement and growth, fish assemblage richness and harvestable fish abundance, and ecological functioning.

Oyster spat settlement and growth surveys

We quantified the number and size of Sydney rock oysters *Saccostrea glomerata* (i.e. the key reef-forming oyster species in this system) settling on the oyster restoration units using two techniques. Firstly, six shells were affixed to the outside of the coir bags using fishing line and were used to quantify the number and size of juvenile oysters settling on the outside of the oyster units (i.e. the 'necklace' method). Secondly, six shells were randomly removed from each oyster reef restoration unit to quantify the number and size of juvenile oysters settling within the matrix of the oyster restoration unit itself. Shells were collected from the oyster restoration units at periods of six months (i.e. May 2018) and one year (i.e. November 2018) after the oyster reefs were installed, and were placed immediately on ice and then frozen prior to quantification in the laboratory. Oyster density was estimated by counting the number of Sydney rock oysters identified on all surfaces of collected shells, and using a transparent, flexible plastic sheet with a 1cm grid overlay to estimate the total surface area (to the nearest cm^2) of each shell removed from the field. Quantification of oyster size followed previous oyster growth quantification methods, and involved measuring the height of each oyster (i.e. the distance from the umbo to the distal margin of the shell) using Vernier callipers to the nearest 1/10 mm (Baggett et al. 2015).

Fish assemblage richness and harvestable fish abundance surveys

We surveyed fish assemblages at oyster reef restoration sites using baited remote underwater video stations (BRUVS) at six-week intervals for four events following the installation of the reefs. BRUVS were comprised of a GoPro camera recording in high-definition (1080) mounted to a 5kg weight, with a bait bag secured 50cm from the camera using a 1m long bait arm made of 15mm gauge PVC pipe. BRUVS were baited with ~500g of pilchards (*Sardinops sagax*) in a 20 x 30cm mesh bait bag with $0.5cm^2$ aperture; the standard bait and quantity for coastal fish surveys using BRUVS (e.g. Henderson et al. 2017a). BRUVS were deployed at the centre of oyster reef restoration site for one hour. Surveys were conducted two hours either side of high tide to maximise fish accessibility to the reefs and water visibility (Gilby et al. 2017a). Video footage was analysed by quantifying *MaxN*; the maximum number of each species identified in any one frame within each video. To account for variable water clarity, only fish seen swimming between the camera and the end of the bait arm (i.e.

1 m from the camera) were counted. No surveys were conducted where the end of the bait arm could not be seen by observers, so water column turbidity did not influence our results. Species richness (i.e. the total number of species) and the abundance of harvested fish species (the sum of *MaxN* values for all harvested species identified in FishBase) (Froese and Pauly 2018) were then calculated from the resulting matrix of *MaxN* values.

Scavenging rate surveys

Carrion consumption (i.e. scavenging) is an important ecological function in coastal ecosystems. Many fish and invertebrate species scavenge animal carcasses, and their actions recycle nutrients and energy, and prevent the buildup of potentially harmful carrion (Olds et al. 2018; Wilson and Wolkovich 2011)

Scavenging rates were quantified at restored oyster reefs during BRUVS surveys by deploying three pilchard carcasses of known weight to the surface of each BRUVS bait bag (Olds et al. 2018). After the 1hr deployment, pilchard carcasses were re-weighed to establish the change in weight during the deployment, with scavenging rate as the proportion of bait consumed during the one hour deployment. Control deployments (where scavenging did not occur during deployments) show no significant change in weight over the one hour deployment period (Olds et al. 2018).

Predation surveys

Predation is an important ecological function that helps to maintain food web structure and the exchange of energy in all ecosystems (Estes et al. 2010; Ripple and Beschta 2012; Ritchie and Johnson 2009). 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, and predation around reefs is a good indicator that food webs are developing in association with the restored structures (Harding 1999; Micheli and Peterson 1999; Peterson et al. 2003).

We used squidpops to quantify relative predation around our sites at 8-week intervals across four events following the installation of reefs, with the first survey occurring in the week following oyster reef installation. Squidpops are a standard method used in coastal seascapes to index the relative predation rates of meso-predators (Duffy et al. 2015). Squidpops are designed to mimic a small invertebrate or fish swimming in the water column and are made of a 1cm^2 piece of squid mantle connected to a bamboo stake with a 10cm piece of fishing line. Eight squidpops were deployed

around each oyster reef (at least 1 m from each other), during each survey period. Squidpops were deployed on the same video arrays described above for the BRUVS (in place of the pilchards and bait bag, and never on the same day as BRUVS), on the PVC pipe arm at a distance of 45cm from the camera GoPro camera, to ensure the squidpops remained visible. We deployed squidpops arrays for one hour (based on the results of a pilot study prior to the commencement of surveys), during a period two hours either side of high tide (to align with periods that we also sampled fish assemblages), to maximise accessibility to the oyster reefs, and to maximise visibility on the videos. Squidpops are classified as consumed when an animal removes the entire piece of squid from the array. Cameras were used to confirm that predation events were due to consumption by animals, and not the result of any other random event (e.g. loss of squid mantle due to current/tides etc). A subset of 6 sites (reefs iii through viii) was chosen for predation surveys that represented the full suite of contexts in which reefs were restored.

Statistical Analysis

Environmental variables

Environmental variables could be broadly grouped into two categories (Table 1). Firstly, we accounted for differences in experimental design (for oyster growth metrics only; i.e. oyster growth method) and the timing of surveys (i.e. event). Secondly, we included four variables relating to the landscape context of the oyster reef restoration sites relative to nearby seagrass meadows, mangrove forests, hardened shorelines (i.e. urbanised shorelines), and the estuary mouth. These variables were chosen because we had specific hypotheses for the ways in which they would modify the benefits of restoration that were based on the results of previous studies in the region (Table 1).

Identifying spatial patterns in benefits of oyster reef restoration

We tested for correlations between the six restoration benefits (i.e. the dependent variables in these models) and environmental variables using generalised additive models in the mgcv package (Wood 2017) of R (R Core Team 2018). Model overfitting was minimised by fitting GAMs with four polynomial lines or fewer (i.e. $k<4$), and by running all possible combinations of four variables or fewer (Burnham and Anderson 2002). Best fit models were those with the lowest Aikaike Information Criterion (AIC) value.

Identifying oyster hotspots

We used the best fit models for restoration benefits to create distribution models (using the *predict* function in mgcv) for the whole Noosa River estuary at 5m pixel resolution (chosen to reflect the size

of current restoration sites). All distribution models were mapped in QGIS (QGIS Development Team 2019). Where either sampling event or oyster growth method was present in the best fit model, we quantified the distribution model using mean values for all levels within that factor.

Values were extracted from each pixel for each of the six distribution models. Values for each restoration benefit were standardised from 0 (the minimum value for each target) and 1 (the maximum value for each target). Oyster reef restoration hotspots were identified using two separate oyster reef restoration indices; the first by taking a sum of these standardised values (resulting in an index ranging from 0 to 6), and the second, taking an average of these standardised values (resulting in an index ranging from 0 to 1). The distribution of these restoration indices was then also mapped in QGIS.

Table 1 List of environmental metrics included in analyses, their definitions, hypotheses underlying their inclusion in models, and sources.

Metric	Definition and justification	Hypothesis- oyster growth	Hypothesis- fish assemblages and ecological functions	Data source
Experimental design				
Oyster growth method	Included in oyster growth analyses only. Two methods- 1) shells removed directly from the oyster restoration units, and 2) marked shells affixed to the outside of the oyster restoration units.	-	Not included	-
Event	Survey period in time since the installation of the oyster reefs. Patterns may change over time or between seasons.	-	-	-
Landscape context				
Seagrass	The presence or absence of seagrass within 500 m of each oyster reef site. Reefs were deliberately placed in the estuary to be either within 500m of seagrasses, or beyond 500m of seagrasses; a factor shown in previous studies to be important in structuring fish assemblages in this region (Gilby et al. 2018b; Gilby et al. 2019).	The presence of nearby seagrass will modify the number and size of oysters will be lower at sites near to seagrass by providing subsidies and modifying oyster predation risk.	The presence of nearby seagrass will modify habitat connectivity, and therefore the number and type of fish congregating at oyster reefs.	Gilby et al. (2018b)
Mangroves	The area (in m^2) of mangroves within 500 m of each oyster reef site. All oyster reefs were placed within 100m of mangroves, meaning that the effects of proximity to mangroves were consistent across sites in this seascape (Gilby et al. 2018b; Gilby et al. 2017a). There were, however, variations in the area of mangroves within 500m of the sites.	The extent of nearby mangroves will modify the number and size of oysters by providing subsidies and modifying oyster predation risk.	The extent of nearby mangroves will modify habitat connectivity, and therefore the number and type of fish congregating at oyster reefs.	Queensland Government (2015b)
Distance to hardened shorelines	The distance (in m) from each oyster reef to the nearest hardened shoreline. Hardened shorelines are important sources of oyster spat and homes for fish, and their effects proliferate in predictable distances into surrounding seascapes (Brook et al. 2018; Gilby et al. 2018b).	Hardened shorelines are sources for oyster larvae, so oyster density will be higher nearer to hardened shorelines, but size might be lower due to higher predation risk.	The proximity of sites to hardened shorelines modifies habitat connectivity, and therefore the number and type of fish congregating at oyster reefs.	Queensland Government (2015a)
Distance to estuary mouth	The distance (in m) from each oyster reef to the centre of the estuary mouth. Proximity to the estuary mouth modifies likelihood of recruitment and migration to different sites (Gilby et al. 2018b; Henderson et al. 2017a).	Oyster growth and abundance will be greater nearer to the estuary mouth due to higher salinity levels.	Fish diversity and the abundance of targeted fish species tends to be lower with increasing distance from the estuary mouth	QGIS Development Team (2019)

Results

Patterns in the benefits of oyster reef restoration

We identified extensive oyster growth on the oyster restoration units, with between 145.7 and 946 oysters growing on average per square metre of shell, and to an average size of between 12.4 and 17.4mm (Table 2). The density of oysters growing on the oyster restoration units was highest on the 'necklace' method on the outside of the restoration units, and at restoration sites with an intermediate area of mangroves nearby, at distances approximately 3000 m and 6000 m from the estuary mouth, and at sites nearer to hardened shorelines (Table 3, Figure S1, Figure 2A). Oysters grew larger with increasing time since restoration, at restoration sites with a lower area of mangroves nearby, and at sites nearer to the estuary mouth and further from hardened shorelines (Table 3, Figure S1, Figure 2B).

Diverse and abundant fish assemblages recruited to the restored oyster reef restoration units, with between 2.3 and 5.3 species, and 2.5 and 10.3 harvestable fish identified on average at each oyster restoration site per survey (Table 2). Previous studies have shown that this equates to 1.4 times greater species richness and 1.8 times more harvestable fish at restoration sites than at nearby control sites (Gilby et al. 2019). The species richness of fish assembles and the abundance of harvestable fish congregating at oyster restoration sites was variable over time, but always higher at sites without seagrass nearby (Table 3, Figure S2, Figure 2C, D). The abundance of harvestable fish was also higher at oyster restoration sites with a lower extent of mangroves nearby (Table 3, Figure S2, Figure 2D).

Predation rates ranged between 13 and 81% likelihood of predation, and scavenging rates between 19 and 100% consumption on average (Table 2). Previous studies have shown that this equates to a doubling of predation rates at restoration sites than at nearby control sites (Duncan 2018). Scavenging rates were 32% higher at oyster restoration sites than at nearby control sites (Figure S3). Rates of predation were variable through time but were highest at oyster restoration sites without seagrass nearby and with less than 50ha of mangroves within 500m (Table 3, Figure S4, Figure 2E). Rates of scavenging was higher at oyster restoration sites progressively further from the estuary mouth and at sites with less than 45 ha of mangroves within 500m, and lowest at oyster restoration sites greater than 400m from hardened shorelines (Table 3, Figure S4, Figure 2F).

Table 2 Average values (with standard deviation) for each restoration target at each of the 13 oyster reef restoration sites (per Figure 1).

Site	Oyster density (oysters/m^2)		Oyster size (mm)		Fish species richness		Harvestable fish abundance		Predation (probability)		Scavenging (proportion consumed)	
	Av.	**StDev**	**Av.**	**StDev**	**Av.**	**StDev**	**Av.**	**StDev**	**Av.**	**StDev**	**Av.**	**StDev**
i	149.4	249.6	17.4	8.1	2.8	1.9	3.0	2.1	-	-	0.19	0.30
ii	161.8	225.8	13.0	4.8	4.5	3.4	8.5	7	0.13	0.34	0.50	0.37
iii	145.7	216.3	13.0	5.3	5.3	2.8	10.3	4.6	0.81	0.40	0.98	0.04
iv	722.6	665.9	14.0	6.4	4.3	2.9	6.1	1.9	0.56	0.50	0.97	0.03
v	271.7	345.1	15.5	5.6	3	1.6	2.5	1	0.38	0.49	0.24	0.21
vi	252.6	342.5	15.6	4.6	4.3	3.3	7.8	5.4	0.66	0.48	0.99	0.03
vii	946.0	888.1	14.0	5.2	4	0.8	6.5	3.1	0.78	0.42	1	0
viii	312.8	536.7	12.6	6.9	3	2.2	8.7	6.4	-	-	0.62	0.45
ix	282.0	472.0	15.9	6.1	5.3	2.8	8.5	9.9	-	-	0.88	0.23
x	317.9	403.1	12.7	6.3	4	3.3	6.5	5.9	-	-	0.98	0.04
xi	424.9	467.2	14.9	5.4	4	1.4	6.8	7.7	-	-	0.70	0.48
xii	627.9	493.3	13.4	5.7	2.3	0.5	5.5	4.1	-	-	0.82	0.35
xiii	351.8	482.4	12.4	5.8	3.5	1.7	7.0	5.6	-	-	0.40	0.45

Table 3 Results of generalised additive model and multi-model inference analyses. Values provided for environmental variables are variable importance values, with values nearer to one indicating greater contribution towards top-ranked models. Bold values indicate variables included in best fit model for each restoration target. R^2 and weight values provided for the overall best fit model. 'Weight' is the weighted AIC value for the best fit model. 'Secondary models' indicates the number of models which explained a similar amount of variance to the best-fit model (i.e. those within 2 AICc of the best fit model), with variables in parentheses being those included in additional secondary models. Where no variables are provided, secondary models contained only combinations of those included in the best fit model.

	Environmental variables						**Model attributes**		
Restoration target	**Method**	**Event**	**Seagrass**	**Mangroves**	**Hardened shorelines**	**Distance to estuary mouth**	**R^2**	**Weight**	**Secondary models**
Oyster density	**1**	0.33	0.07	**1**	**0.42**	**1**	0.23	0.42	2 (Event)
Oyster size	0.18	**1**	0.22	**0.38**	**0.99**	**0.56**	0.14	0.21	3
Fish species richness	-	**0.96**	**0.36**	0.28	0.31	0.27	0.17	0.13	5 (Mouth, hardened shorelines, mangroves)
Harvestable fish abundance	-	**0.99**	**0.6**	**0.48**	0.28	0.31	0.2	0.21	5 (Mouth, hardened shorelines)
Predation	-	**0.95**	**0.49**	**0.84**	0.45	0.37	0.25	0.19	7 (Mouth, hardened shorelines)
Scavenging	-	0.2	0.41	**0.85**	**0.53**	**0.71**	0.4	0.17	4 (Mouth, seagrass)

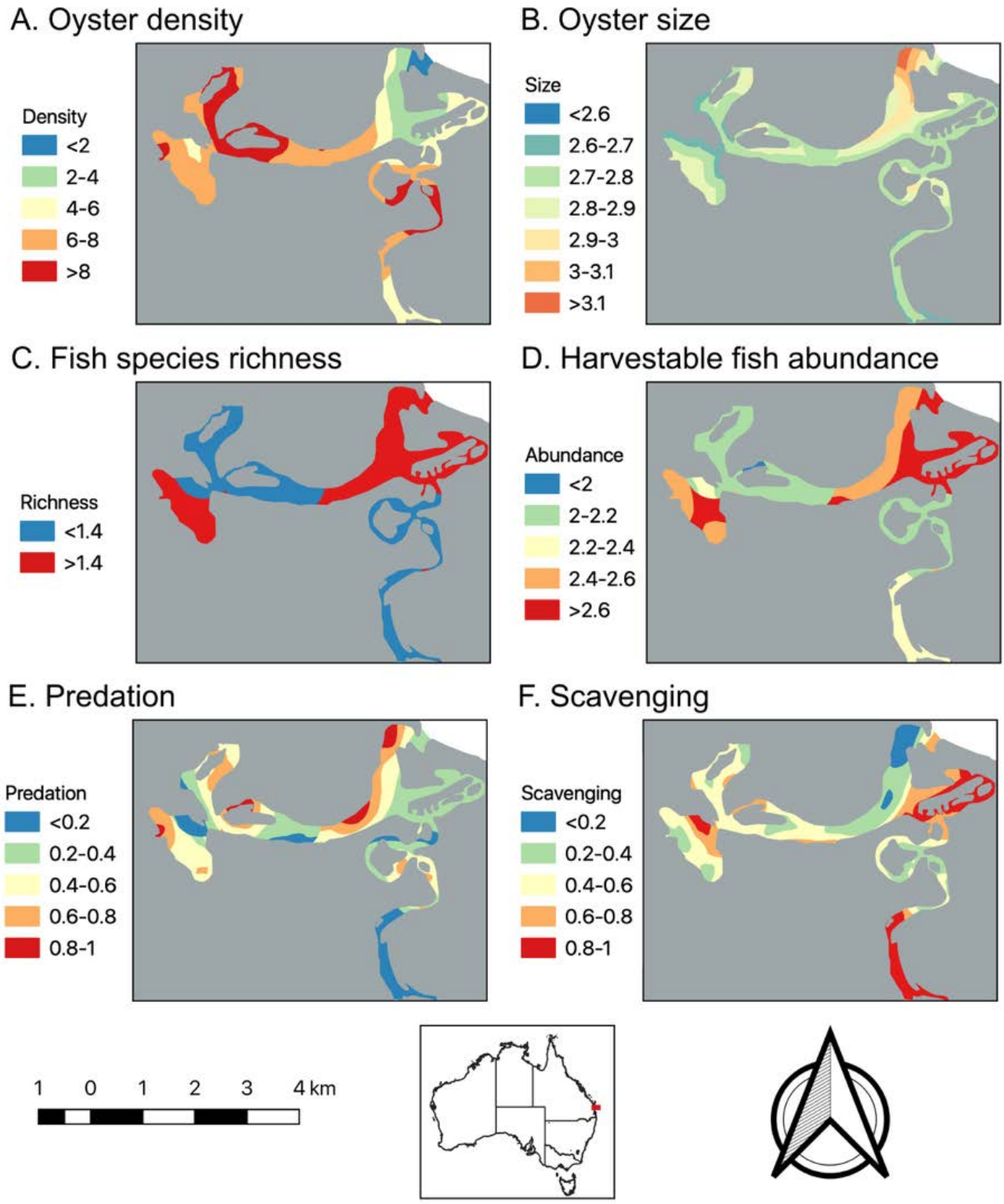


Figure 2 Distribution models for A) oyster density, B) oyster size, C) fish species richness, D) harvestable fish abundance, E) predation and F) scavenging calculated using the best fit generalised additive models for each restoration benefit (described in Table 2).

Hotspots for restoration effectiveness

Because settlement and growth of oysters was great enough to allow successful restoration at all sites, we did not need to first consider where restoration could be successful in the Noosa Estuary. Therefore, we simply pooled the standardised values for oyster growth metrics with the other restoration benefits to identify restoration hotspots.

Whilst the sum and average approaches to calculating the restoration index differ slightly conceptually (i.e. total restoration benefits at sites versus average restoration benefits), we found few differences in the outcomes when using the sum versus average approach to create the oyster restoration indices (Figure 3). Hotspots where oyster restoration would result in the greatest possible outcomes across all of the restoration targets considered (i.e. restoration index category 6 in figures 3A and B) occurred near the estuary mouth, on the northern bank of the estuary approximately 2km from the estuary mouth, and in a large lake-like inlet in the far west of the estuary (known locally as Lake Doonella). These hotspots were in similar positions for both sum (Figure 3A) and average approaches (Figure 3B). However, the total area of category 6 restoration index values (i.e. high restoration benefits) would be reduced somewhat if restoration occurs only in intertidal areas (i.e. those similar to the locations used for restoration sites in this study) (Figure 3C).

We found no locations that were classified as the highest restoration index category for all restoration benefits. Patterns in the relative values of each of the restoration benefits across the different levels of restoration indices were inconsistent (Table 3). Here, there was no clear sequence in increasing values for each restoration benefit across increasing restoration index categories, irrespective of which approach was used to quantify the index (Table 4). Only predation was highest at category 6 than all other categories, whilst fish species richness was equal highest with at least one other restoration category (Table 4). In fact, often, the values for several of the restoration benefits are much lower at the higher categories, and for scavenging, the value is actually at its lowest. The approaches used to calculate the restoration index simply means that locations with high scores have the greatest overall positive effects across the whole suite of metrics quantified and does not necessarily mean that all restoration benefits are maximised.

Table 4 List of oyster restoration index categories (from Figure 3), the average values for each restoration target for category 1 (i.e. the lowest restoration index category), and the percentage difference in average values from the category one average for each of the subsequent four categories for A) the approach of taking the sum of standardised restoration target values, and B) taking the average of standardised restoration target values.

Oyster restoration index category	Oyster density	Oyster size	Fish species richness	Harvestable fish abundance	Predation	Scavenging
A. Sum approach						
Category 1 (minimum)	6.8 oysters/m^2	2.7 mm	1.4 species	2.2 fish	0.2 probability	0.49 prop. consumed
2	11.6	1.4	0.0	-1.0	33.1	15.1
3	34.1	3.1	0.0	-6.2	214.6	16.3
4	-81.8	6.0	13.5	21.0	68.9	0.0
5	-18.6	2.5	14.0	20.9	104.4	6.1
6	2.8	6.4	14.0	16.6	253.5	-40.2
B. Average Approach						
Category 1 (minimum)	7.1 oysters/m^2	2.7 mm	1.4 species	2.2 fish	0.2 probability	0.6 prop. consumed
2	23.7	2.3	0.0	-4.6	176.3	-23.2
3	33.5	3.7	0.0	-7.8	298.3	8.9
4	-86.1	5.5	14.0	21.8	79.3	-18.0
5	-47.3	4.8	14.0	20.7	117.8	-24.4
6	-8.9	1.4	14.0	19.9	150.5	-10.3

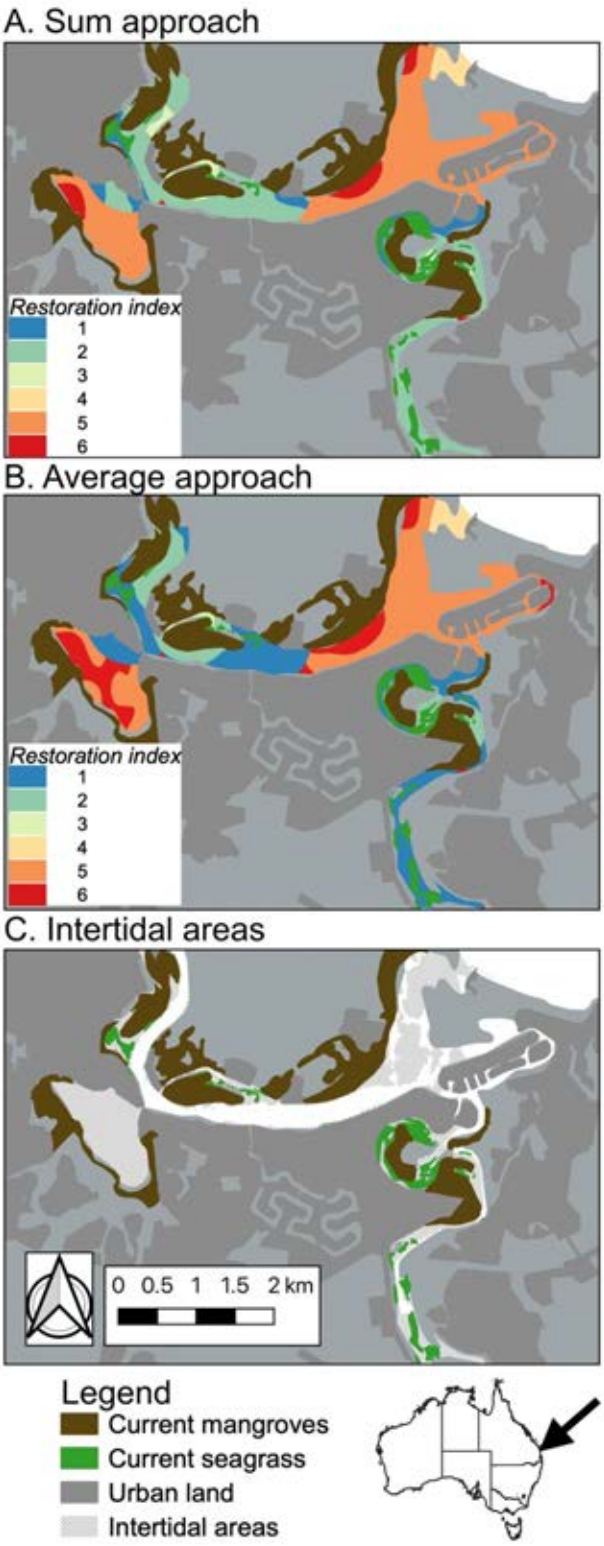


Figure 3 Map of the final outputs of the restoration prioritisation process illustrating hotspots for oyster restoration benefits in the Noosa River, Australia using summed (A) and averaging (B) approaches, and (C) the intertidal areas within the Noosa River.

Discussion

Ecological restoration projects are increasing in prevalence and size globally (Brudvig 2011; Palmer et al. 2014). Whilst there is a long history of successfully restoring lost or degraded ecosystems, there remains little evidence to suggest that restoration projects are designed to explicitly maximize outcomes for multiple restoration benefits in a systematic way (Gilby et al. 2018a). In this study, oyster reef restoration proved successful for the establishment of growing oyster reefs that will eventually cement together and form self-sustaining oyster reefs (i.e. oyster density and size). These oyster reefs also attracted a diversity and abundance of fish (i.e. fish species richness and harvestable fish abundance) that perform several important ecological functions that are also good indicators of ecosystem and food web condition (i.e. predation and scavenging). Therefore, properly managed oyster restoration units could be restored to any intertidal area of the Noosa River estuary, and this would result in the settlement and growth of oysters, and some additional benefits for ecological functioning and fish assemblages more broadly in comparison to nearby sandy or muddy substrates. However, we also found that the cumulative benefits of future oyster reef restoration efforts can be maximised by more closely considering the spatial placement of restoration sites. In this sense, each of the restoration benefits we tested varied significantly with at least one spatial attribute of the broader landscape. This resulted in the extent of areas where the combined benefits of oyster reef restoration were highest being significantly narrower than the area in which intertidal oyster reefs could theoretically grow. The approach used in this study is deliberately conceptually and computationally simple and serves to demonstrate how decisions can be made across broader areas in defensible, but relatively straight forward ways. Using such approaches to optimise the placement of restoration efforts across landscape will help to maximise the overall benefits of restoration, and potentially serve to reduce social and economic costs.

Given the inconsistent patterns in restoration index scores with the levels of different restoration benefits, there are several potential pathways for selecting optimal restoration sites. If funding is limited, restoration could be placed only in the category 6 restoration index areas because these areas maximise the total outcomes. However, if a broader approach is possible due to greater funding or a desire to spread effort, then restoration plans could select sites across the estuary that fulfil specific criteria relating to the restoration benefits. For example, if we assume that the most important aspect of the restoration effort is the successful growth of the reefs themselves, then restoration plans would start with a combined map of oyster settlement and growth (i.e. figure 2A and B), and then subset from there to place several reefs in different areas that a) fulfil this initial 'oyster growth' criteria' and b) also invite more diverse fish communities or, separately, a higher

abundance of harvestable fish or enhanced rates of ecological functions. This second approach amounts to the CAR (comprehensive, adequate, representative) principle of spatial conservation planning (Commonwealth of Australia 1997). The approach comprehensively restores oyster reefs to areas that provide all of the different benefits for which reefs provide and allows them to be restored in optimal locations for that purpose (as opposed to only in areas that, on average, satisfy all restoration targets to some degree; per Figure 3). It is adequate to the extent that there are several representative samples restored to each of those locations as a contingency in the event that one is destroyed or impacted. Finally, it is representative in the restoration of features of oyster reefs that serve to both maintain the condition of coastal systems and provide for the ecosystem services for which people covet.

Systematically selecting potential restoration locations by using quantitative outcomes from existing restoration efforts has several key advantages. Firstly, sites can be selected with more confidence that the full suite of ecological, social and economic benefits sought from restoration will eventuate following the initial expense (in both financial and time outlays) of the restoration efforts (Gilby et al. 2018a; Wilson et al. 2011). Similarly, using quantitative information to prioritise actions makes decisions highly defensible, is robust to challenges, and can be used to advocate for additional restoration (Margules and Pressey 2000). Using actual values for each of the restoration benefits also allows for quantitative goals to be set more easily; an ongoing challenge for restoration in many settings (Peterson and Lipcius 2003; Rondinini and Chiozza 2010; Thompson 2011). Further, this approach has the potential to reduce social conflicts by reducing the total footprint of restoration sites and allowing for the strategic avoidance of areas where restoration is not possible (e.g. roadways, harbors, areas of human habitation), whilst still ensuring maximum derived restoration benefits. Such approaches will be crucial as the scale and number of restoration projects increases globally. Spatial prioritisation algorithms (e.g. Marxan, Zonation) that better consider social (e.g. avoidance of areas of existing usage), and economic (e.g. cost of restoring in one part of the estuary, versus another) costs would likely enhance the operationalisation of these concepts (Watts et al. 2009). These considerations would, however, likely serve to further reduce the number of candidate sites, meaning that incorporating an existing understanding of designs and restoration siting that likely maximise multiple benefits becomes increasingly important.

We found extensive recruitment and growth of oysters on the oyster restoration units within the Noosa River estuary in all contexts. This finding suggests that oyster reef restoration would be successful in any intertidal area in the system, as long as those reefs are properly managed from

external influences like boat strike, harvesting, or significant sedimentation. Mangroves provide sources of oyster spat that grow on prop roots, but are also homes for potential oyster predators (Sheaves et al. 2015). Therefore, restoration sites with intermediate areas of mangroves nearby likely contained the greatest density of oysters because they had good access to settling spat but were separated spatially from potential predators. Mangroves are, however, also good sources of organic material for the growing oysters (Dittmar et al. 2006), meaning that larger oysters were found at sites with greater extents of mangroves nearby. Similarly, urban structures are both sources of oyster larvae and potential oyster predators such as fish and large crustaceans (Brook et al. 2018). Oyster restoration sites nearer to urban shorelines therefore contain a higher density of oysters, but these oysters are more likely to be consumed by fish that congregate around urban shorelines before they reach a size refuge. Effects of proximity to the estuary mouth are more complex, and likely related to oyster survival with variable salinity further upstream (e.g. Lenihan et al. 1999), the prevalence of potential oyster predators (e.g. Soniat et al. 2004), and perhaps abrasion from mobile sands nearer to the estuary mouth. Previous studies have shown that oysters grow larger and more quickly in more saline waters, potentially due to longer periods of time where oysters can open to feed (oysters close when water is too fresh) (Dove and O'Connor 2007). These findings provide important insights into the areas where oyster restoration would be successful in the estuaries of this region. If restoring the lost oyster habitat was the only goal of future restoration efforts, then practitioners could simply use the distribution models for oyster density and size (i.e. Figure 2A, B) to identify the most successful restoration sites.

Enhancing the abundance and/or diversity of fish assemblages is an important goal of many oyster reef restoration projects globally (Gilby et al. 2018c; zu Ermgassen et al. 2016). We found that the effects of restoration on the richness of fish assemblages, the abundance of harvestable fish congregating around oyster reefs, and the ecological functions these fish perform were variable over time; this was likely due to the effects of variable freshwater runoff in the system (Gilby et al. 2019). There is an increasing body of evidence to suggest that restoring oyster reefs at sites isolated from existing structurally complex ecosystems results in greater augmentation of fish species richness and abundance, and this can often cascade to the ecological functions those fish provide (Duncan 2018; Gilby et al. 2019; Grabowski et al. 2005). This is likely because more isolated restoration actions provide new, and structurally complex, habitat in locations that were previously low complexity, unvegetated soft sediments (Gilby et al. 2019). The findings of this study provide further evidence to support these conclusions regarding the siting of oyster restoration efforts for fish and the ecological function they perform. These findings also provide further evidence to support the use of oyster reef

restoration as a targeted recovery mechanism for restoring multiple aspects of coastal fish assemblages, but also highlight the importance of considering project design and siting in order to maximise these derived benefits.

Landscape-scale restoration efforts necessitate more thorough methods and theories for the planning of restoration actions (Gilby et al. 2018a; Wilson et al. 2011). As financial costs and likelihood of social disruptions increases, ensuring that benefits derived from restoration are maximised per unit cost will be vital. The principles used here to select potential hotspots for restoration outcomes are similar conceptually to the placement of reserves in heterogenous landscapes. Reserve selection processes use maps of the current distribution of habitats, and increasingly consider habitat connectivity (Olds et al. 2016; Weeks 2017), ecological functions and resilience (Olds et al. 2012c), and both natural and human disturbances (Huijbers et al. 2015), and then use quantitative conservation goals to allocate reserve location. These principles have, however, rarely been considered for the placement of restoration sites (Gilby et al. 2018a). Identifying potential restoration sites using quantitative goals based on our best understanding of locations where restoration would be most successful, but also maximise potential additional outcomes, should become the standard approach for planning restoration actions across landscapes.

Supplementary materials

Figure S1 Bar plots and generalised additive model partial plots for the effects of environmental variables on the restoration targets of oyster density (A), and oyster size (B). Variables in red boxes were included in the best-fit model.

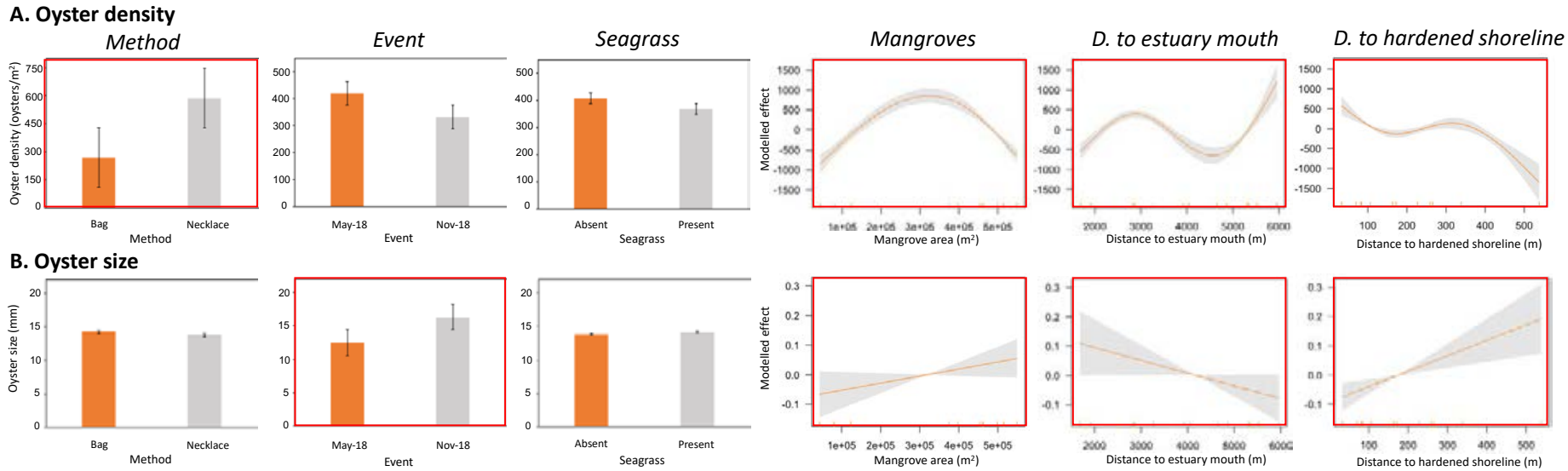


Figure S2 Bar plots and generalised additive model partial plots for the effects of environmental variables on the restoration targets of fish species richness (A), and harvestable fish abundance (B). Variables in red boxes were included in the best-fit model.

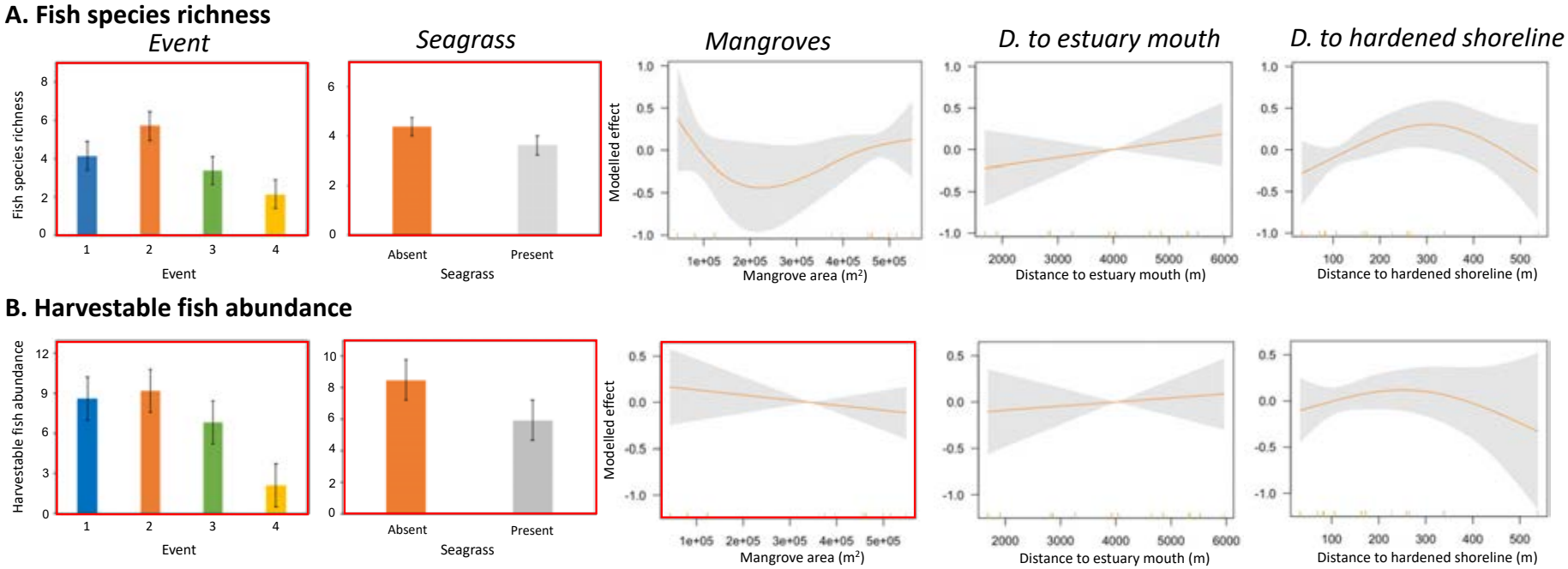


Figure S3 Average (+/- standard error) scavenging rates at oyster restoration sites and nearby control sites. Control sites were selected to be at least 200m from an oyster reef site, and so that the same seascape contexts were covered by both control and restoration sites (i.e. same number near to seagrass, and with similar areas of mangroves nearby). Note that these two values are highly statistically different (t-test, P<0.001).

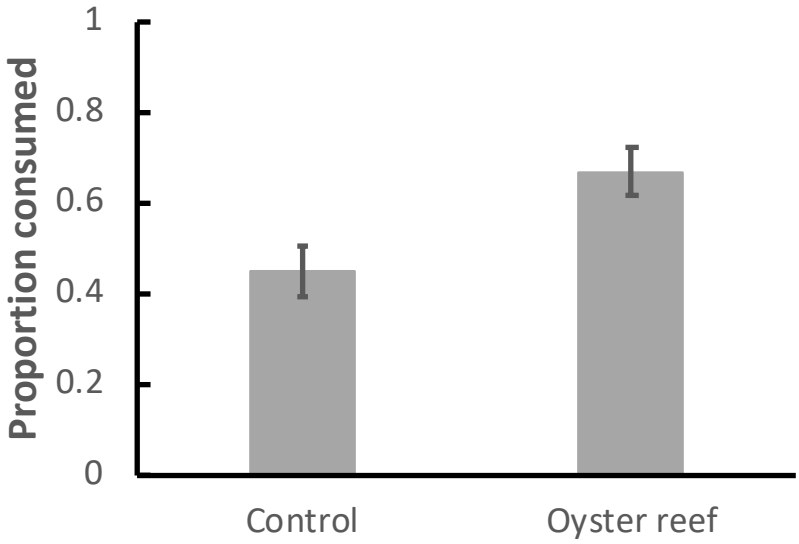
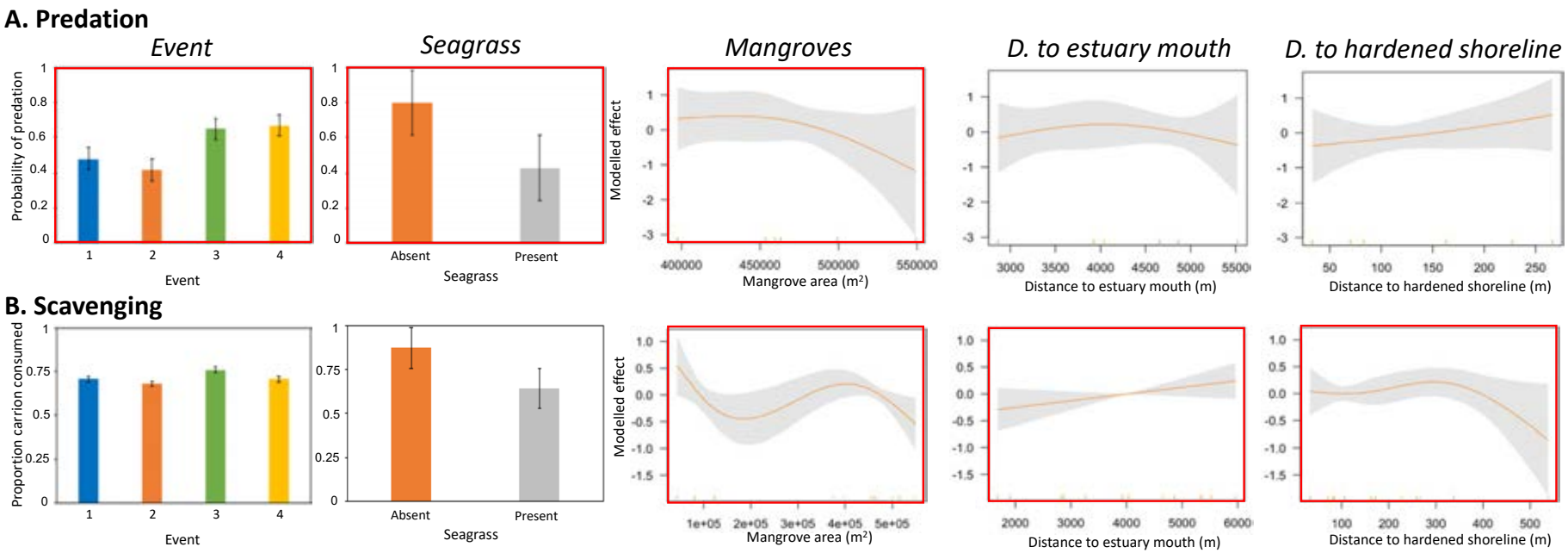


Figure S4 Bar plots and generalised additive model partial plots for the effects of environmental variables on the restoration targets of predation (A), and scavenging (B).

Variables in red boxes were included in the best-fit model.



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Appendix A- Monitoring of the Noosa River Oyster Reefs; November 2017 - November 2018

Report to Noosa Council, and Queensland Department of Agriculture and Fisheries

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Dr Andrew Olds,
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December 2018

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Executive summary

1) **Background & Rationale**
The principle objective of the Noosa Oyster Reef Restoration Project is to restore ecologically-functioning oyster reefs to the Noosa River Estuary. Reef units were installed in November 2017 to begin the restoration. An annual monitoring is part of the approval (OPW17/0016) that needs to report on: a) reef unit stability; b) oyster spat recruitment processes; c) lack of negative community usage; and d) impact on marine plants and shoreline erosion. This report addresses these requirements, reporting on the findings of two mandated monitoring events (May 2018, Nov. 2018) done by USC. The methods used were precisely those prescribed in the approved monitoring schedule, with no modifications.

2) **Stability and Position**
The reef units can be considered stable. The mean recorded change in position over 12 months was 0.16 m (+/- 0.12 m SD). All oyster reef restoration units moved less than 0.65 m over one year. No reef unit moved from the designated resource allocation areas at any site. No reef unit was physically displaced from its anchor points in the sediment or removed otherwise.

3) **Recruitment**
Substantial spat fall and oyster growth was found in both monitoring events. In May 2018, an average spat fall of 387.5 oysters/m^2 (+/- 537.7 oysters/m^2 SD) was recorded, and in November 2018 it was 306.1 oysters/m^2 (+/- 575.1 oysters/m^2 SD). There was a significant increase in the size of newly recruited oysters on the reefs. Here oysters increased in size from 14.3 mm (+/- 6.5 mm SD) in May 2018, to 19.1 mm (+/- 8.9 mm SD) in November 2018. The favourable spat fall and oyster growth are an encouraging bellwether for the reefs to develop into biologically stable systems over the coming years.

4) **Interaction with Public**
There were signs of damage to a few reef units most likely caused by boat propellers and anchors, evident during the November 2018 monitoring event. We repaired these units where possible. Limited data suggest that the use of the oyster reefs by recreational fishers possibly appears to have increased over time. We suggest that closer monitoring of this aspect may be useful in coming years.

5) **Marine Plants & Shoreline Erosion**
Whilst there was some change to the edges of seagrass beds, there were no significant changes to the distribution, cover, or species composition of existing seagrass beds or mangroves forests within 50 m of each reefs. We found no shoreline erosion in the vicinity of the reef units. At two sites in Lake Weyba and Weyba Creek dugong grass *Halophila ovalis was* found near reef sites where it was not recorded at the time of reef placement.

6) **Conclusions**
Overall, the results of the 2018 monitoring of the Noosa oyster reefs are encouraging and positive. Two of the targets have been fully met (reef unit stability, no impact on plants and shorelines). The target of oyster and other invertebrate growth is tracking very favourably. The observation of reef unit damage from anchoring needs consideration of closer monitoring and possibly targeted education / information may be considered for this issue. The next scheduled monitoring event is mandated for May 2019.

Introduction and context

Oyster reef restoration in the Noosa River;

The principal objective of the Noosa River Oyster Reef Restoration project is to restore natural oyster reef habitat in the Noosa Estuary. This requires the addition of suitable hard substrate for oyster spat to settle, and allowing natural recruitment and reef-formation processes to recover to areas that historically supported oyster reefs.

The oyster settlement substrate comprises *oyster reef restoration units*. These units are made from the most suitable recruitment material - oyster shells held together by a natural coir fiber bag. The units are raised above the muddy and sandy marine substrates, thereby mimicking the vertical relief of the original oyster reefs to facilitate natural recruitment processes (Figure 1, 2). We expected that natural recruitment processes would cement the dead shell together and form part of the mosaic of habitats within the estuary including both soft and hard structural habitat types, thereby creating a structurally diverse mosaic of habitats that is predicted to be beneficial to a range of fish species, including species of harvested in commercial and recreational fisheries (e.g. yellowfin bream, estuary cod, tailor, mangrove jack, and moses perch).

The restoration sites that were chosen as locations for oyster reef restoration in the Noosa River (Figure 3) because they:

5) are in reaches of the lower Noosa River estuary and in Weyba Creek from which oysters were harvested historically;
6) are within the depth range known to be suitable for oyster reefs to grow;
7) are in locations where viable oyster larvae were recorded during recent recruitment studies; and
8) have an extent where the final restored area will not exceed the historical areal extent of oyster reefs before commercial harvesting took place.

Figure 1 Coir mesh bag filled with recycled oyster shells; the principle restoration unit

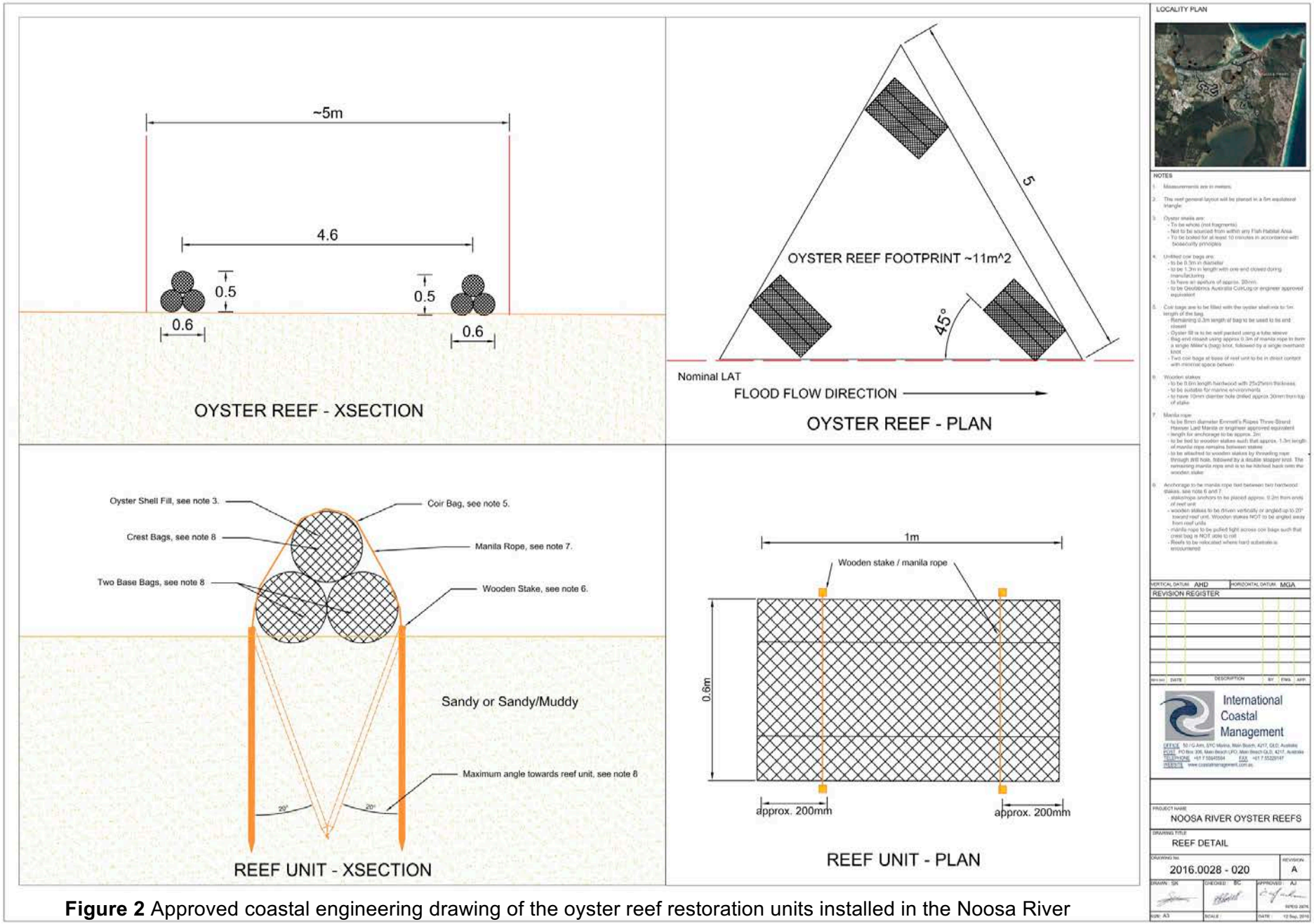

Figure 2 Approved coastal engineering drawing of the oyster reef restoration units installed in the Noosa River

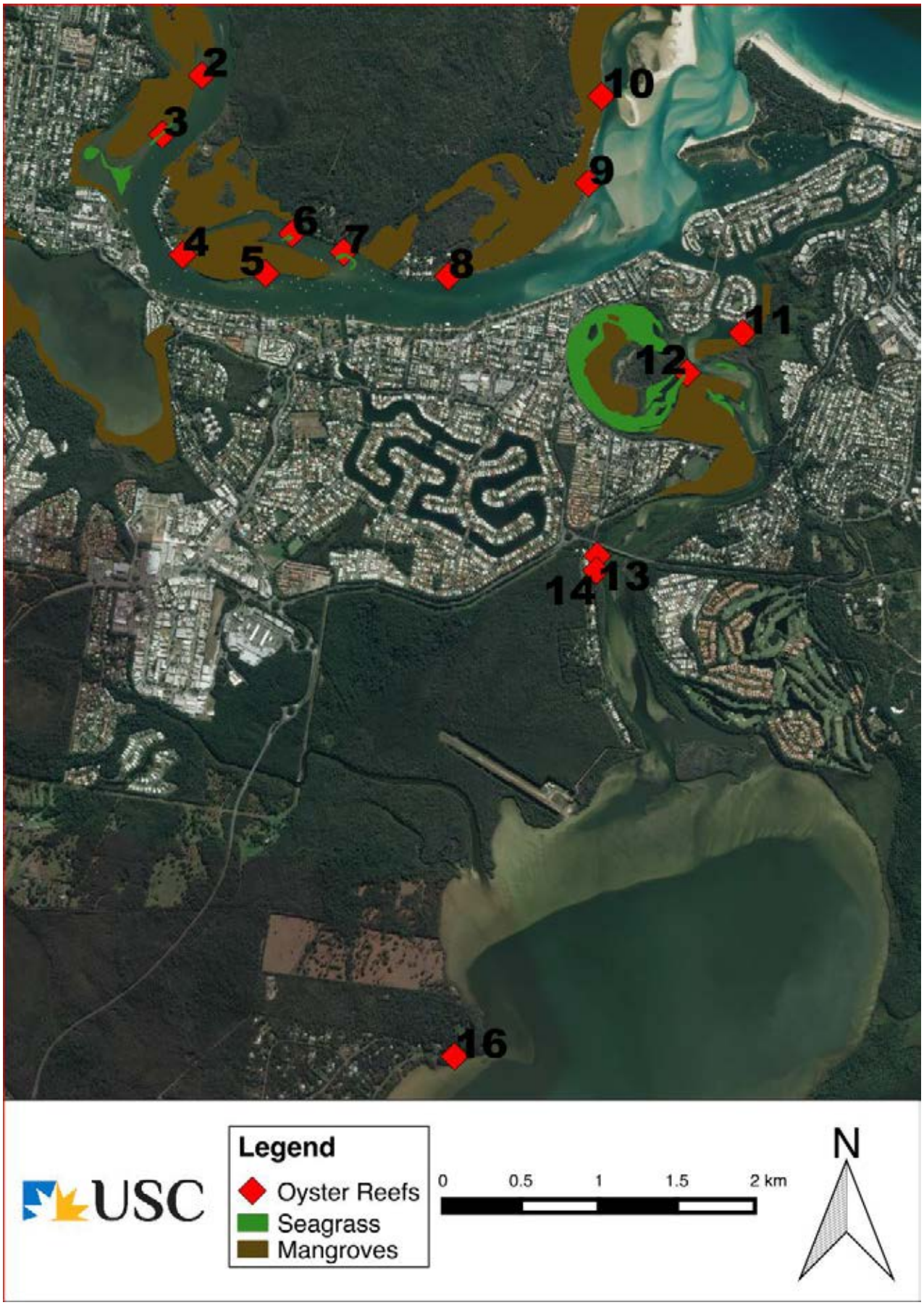

Figure 3 Map of oyster restoration sites and marine habitats in the Noosa River

Oyster reef unit installations

The installation of oyster reef units to the Noosa River was done during a period of three days, from 20 to 22 November 2017 (Figure 4). All works and surveys were conducted by a team comprising professionals of Noosa Jetty Builders, and marine scientists from the University of the Sunshine Coast. All oyster reef units and signs were installed exactly according to specifications set out in the permit conditions and any instructions provided regarding procedures (Table 1). All reef units are located to avoid any damage to marine plants or surrounding ecosystem (Table 1, Figure 4). Key observations during the placement of the reef units and associated signage include the following:

- No marine plants were disturbed during the installation of the reef units or signs. Before each reef unit was placed on the seafloor, we carefully examined the site to ascertain that no seagrass, mangrove aerial roots, or any other marine vegetation was present. This ensured that no direct placement impacts occurred at any of the sites (Table 1).
- All operations were localised to the immediate site where reef units were sunk onto the seabed. Thus, no habitat outside the RAA area was impacted in any form by the reef units or the signage.
- Poles holding the signs were installed using a narrow water jet 'spear'. Use of this gear ensured that only a very narrow (< 20 cm diameter in all cases) area of the seabed was disturbed (Figure 4). Sign posts were then driven further into the substrate, to a mean depth of 2.7 m (min 1.8 m, max 3.5 m; Table 1), using a post driver (Figure 4).
- According to engineering specifications, we used marine grade hardwood stakes (sourced from the Australian Hardwood Stake Company) to secure the reef units on the seafloor. The stakes were hammered into the seabed to a mean depth of 0.9 m (min 0.5 m, max 1.2 m) - depending on hardness of the seabed (Table 1), at a mean angle of 82.4º (min 75 º, max 90 º).
- Pre- and post-installation photographs and videos of all sites are available electronically (OneDrive folder). Full access to the all electronically stored imagery has been provided to Noosa Council. In addition, we are happy to grant access to whoever may require it (please email: bgilby@usc.edu.au).

Figure 4 The resulting very small footprint of sign posts following installation by the water jet (left) and a completed oyster reef in Weyba Creek (right).

Table 1. Completed oyster-reef installations in the Noosa River, listing their exact position, the date of placement, characteristics of posts and stakes driven into the seabed to secure signage and reef units, and any presence and/or damage to marine vegetation.

Site Number	Position		Installation date	Depth to which sign post is driven into the seabed (m)	Stakes to secure reef units		Presence of, or damage to, marine plants and/or adjacent habitats or ecosystems.
	Latitude	Longitude			Depth of stake into seabed (m)	Angle of stake relative to seabed (degrees)	
1	reef units not installed - seabed not compact enough						
2	-26.38333096	153.045835	20/11/17	2.8	1.2	79	None
3	-26.38673804	153.043291	20/11/17	2.8	1.2	75	None
4	-26.39367197	153.044599	20/11/17	2.9	1.1	84	None
5	-26.394757	153.049933	20/11/17	2.4	0.5	82	None
6	-26.39245399	153.051636	20/11/17	3.2	1.2	85	None
7	-26.39351204	153.054941	20/11/17	3.3	1.2	77	None
8	-26.39491903	153.061679	20/11/17	2.4	1.2	90	None
9	-26.38954598	153.070696	21/11/17	1.8	0.5	86	None
10	-26.38452999	153.071546	21/11/17	2.0	0.6	87	None
11	-26.39817104	153.080595	21/11/17	2.3	0.5	76	None
12	-26.40045603	153.077035	21/11/17	2.9	0.5	79	None
13	-26.41099703	153.071263	22/11/17	3.5	1.2	87	None
14	-26.41184301	153.0712	22/11/17	3.2	0.5	83	None
15	reef units not installed – presence of seagrass						
16	-26.43981904	153.062079	22/11/17	2.9	0.6	84	None

Noosa River oyster reef restoration monitoring schedule

As part of the development approval for installing the oyster reefs, the stakeholders report yearly (in December) to Queensland Department of Agriculture and Fisheries on the progress of the oyster restoration project, especially relating to;

5. Oyster restoration unit stability (i.e. oyster reef restoration units remain within the allocated resource allocation areas);
6. Restoration of natural recruitment processes over long term (i.e. spat recruitment rates demonstrate that the biogenic matrix will be sufficient to hold the structure of the oyster reef restoration units in place following complete degradation of the supporting coir material during the establishment phase and to facilitate ongoing natural recruitment processes);
7. Equitable Community Impacts (i.e. ensuring fair community use of the river system is not impacted by placement of the Oyster Reef Restoration Units within the Resource Allocation Areas - to be monitored using a council operated community feedback system); and
8. No negative impact on marine plants or shoreline erosion (i.e. ensuring the oyster restoration units do not impede natural marine plant growth or accelerate coastal erosion processes).

These performance objectives are quantified using established monitoring protocols for oyster reef restoration, and follow international best practice for monitoring restored oyster habitats (Baggett et al. 2014). The monitoring program is designed to be adaptive, with annual reviews against the performance objectives for the project (See Table 2 for detailed monitoring requirements).

Two monitoring events occurred in 2018; one 6 months post installation in May 2018, and the other 12 months post installation in November 2018. The results of these monitoring events are covered in this report. There have also been detailed surveys of the fish and crustacean assemblages associating with the reefs throughout 2018. Although the details of these surveys are not covered in this report, they are available from USC upon request.

Table 2 Noosa oyster reef restoration monitoring schedule as agreed to by all stakeholders in RAA 2016CA0575, and including mark-ups from Department of Agriculture and Fisheries dated 6 January 2017.

Performance objective	Monitoring method	Frequency	Corrective action where performance objective is not met
1. Oyster Restoration Unit location stability			
Oyster restoration units remain within the designated Resource Allocation Areas.	Visually inspect the stability of oyster reef units and record the precise GPS position (± cm scale), and size of each unit (following international best practice: Baggett et al. 2015). Use GIS software to contrast the position, footprint, size and area of oyster reef restoration units between monitoring events and assess any potential movement.	Every 6 months for a minimum of three years Additional monitoring will be conducted within 2 weeks of substantial rainfall events (i.e. events that exceed 50-year Average Rainfall Intervals).	A professional coastal engineer shall be consulted to suggest remedial action for any oyster reef restoration units that collapse, or shift by > 1 m. Any oyster reef restoration units that move outside the designated Resource Allocation Areas within 3 years will be removed. A professional ecologist will confirm the cause of the shift.
2. Natural Recruitment Processes			
Oysters and other sessile benthic invertebrates recruit to reef restoration units to establish a biogenic matrix, which binds oyster shells in place, prior to degradation of coir material. The Key Performance Indicators for this are: **1.) Oyster recruitment**: successful recruitment of oyster spat in at least 1 out of the 3 years (i.e. 33% of the time) post deployment (following international best practice of 40%: Baggett et al. 2015).[1]; 2.**) Cover of oysters and other sessile benthic invertebrates**: an upward trend in the cover of sessile benthic invertebrates growing on restoration units; and **3.) Establishment of stable biogenic matrix**: structural rigidity of oyster restoration units, denoting a stable biogenic matrix after 3 years post deployment, which is sufficient to hold oyster shells in place.	Quantify the recruitment of oysters and other sessile benthic invertebrates to reef restoration units, and measure changes in the cover of oysters and other sessile benthic invertebrates over time (following international best practice: Baggett et al. 2015).[1] The monitoring methods for each Indicators are: **1.) Oyster recruitment**: marked oyster shells will be fastened to the outside of restoration units. These shells will be harvested at regular intervals (15 oyster shells per location on each event – i.e. 5 shells per unit) and the density and size of recruits recorded; 2.**) Cover of oysters and other sessile benthic invertebrates**: photographs of ten quadrats (25 cm x 25cm), distributed in a stratified random design, across each oyster reef restoration unit will be taken at regular intervals to quantify the change in cover of oysters and other sessile benthic invertebrates (Baggett et al. 2015)[1]. **3.) Establishment of stable biogenic matrix**: assess the structural integrity of each oyster reef restoration unit and monitor the degradation of coir material. Structural integrity will be quantified by measuring the proportion of oyster shells (from 10 shells that are selected at random at each location), which can be removed easily by hand	Every 6 months for a minimum of three years, unless otherwise detailed within corrective actions	We will contrast: 1) the rate of oyster recruitment; 2) the cover of oysters and all other sessile benthic invertebrates; and 3) the stability of the biogenic matrix among oyster reef restoration units and between monitoring events. Any restoration units that fail to meet the Key Performance Indicators within 3 years will be removed. If major damage occurs to the coir mesh of any oyster reef restoration units before a stable biogenic matrix has formed, and loose oyster shells are being lost from the structure, it will be repaired *in-situ* by hand weaving. Any such repairs will be conducted carefully, and by hand, to ensure that there is no damage to established areas of biogenic matrix.

	manipulation. The rate of coir degradation will be measured by monitoring changes to the condition of coir mesh over time from the ten photo-quadrats, which are collected twice per year to assess changes in the cover of benthic invertebrates at each oyster reef restoration unit.		
3. Community use and enjoyment of the declared Fish Habitat Area			
Oyster restoration units do not significantly impair community use and enjoyment of the declared Fish Habitat Area, particularly fishing activities.	Maintain records of community feedback, evidence of vandalism, and vessel strikes on the trial oyster reef restoration units. Records will be comprehensive and include, as a minimum set: 1) the number and type of **complaints** received (also, to allow the Department to gauge the success, any positive comments should also be provided); 2) the type, nature, and severity of any acts of **willful vandalism**; and 3) the type and severity of any **vessel strike**.	Annual reporting of all complaints, cases of willful vandalism, and instances of vessel strike received for the three-year trial period.	**Complaints**: within 3 months of receiving each complaint, an investigation (including interview with the complainant if possible) will be conducted to determine whether complaints are directly related to oyster reef restoration units. Potential response actions will be provided to the Department of Agriculture and Fisheries in the annual report. If complaints persist, and grievances exceed the direct benefit of oyster reef restoration, the particular oyster reef restoration unit will be removed as soon as practical, and prior to the 4th anniversary post deployment. **Willful vandalism and vessel Strikes** If there are consistent and / or significant cases of willful vandalism to, or instances of vessels striking, the oyster reef restoration units, the cause of the impact will be identified and used to guide the delivery of a community education campaign aimed at reducing these types of incidents. If the education campaign does not reduce cases of willful vandalism and / or instances of vessel strike, the oyster reef restoration units that are responsible will be removed prior to the 4th anniversary post deployment.
4. Other potential effects:			
Oyster reef restoration units do not cause a decline in the extent of marine plants within a 50 m radius of the restoration units, and are not attributed to erosion of adjacent shorelines or other ambient environmental impacts.	Map the area of marine plant habitats (seagrass, mangroves) in the immediate vicinity (i.e. with a 50 m buffer) of each oyster restoration area, using high-resolution GPS (cm scale) and field-validated aerial imagery (sourced from Nearmap). Monitor changes in the composition coverage and condition of seagrass within 50 m radius around the oyster reefs. Map the location and condition of estuarine shorelines that occur in the immediate vicinity (i.e. with a 50 m buffer) of each oyster reef, using high-resolution GPS (cm scale) and field-validated aerial imagery (sourced from Nearmap).	Annually for a minimum of three years, or until any failed restoration units have been removed.	Where monitoring shows that there are substantial, and consistent, losses of marine plants, or erosion of estuarine shorelines, in the immediate vicinity of oyster reef restoration units, and these changes can unambiguously be attributed to oyster reef restoration activities, the problem units that are responsible for such impacts shall be removed (as soon as practical and prior to the following annual reporting anniversary).

Monitoring criteria 1- Oyster restoration unit location stability

Performance objective

Oyster restoration units remain within the designated Resource Allocation Areas.

Monitoring method and frequency

Visually inspect the stability of oyster reef units and record the precise GPS position (± cm scale), and size of each unit (following international best practice: Baggett et al. 2015). Use GIS software to contrast the position, footprint, size and area of oyster reef restoration units between monitoring events and assess any potential movement.

Frequency: Every 6 months for a minimum of three years. Additional monitoring will be conducted within 2 weeks of substantial rainfall events (i.e. events that exceed 50-year Average Rainfall Intervals).

Was the performance objective met?

No units moved outside of the RAA area, and all repairable reefs were repaired. Therefore, all aspects of this performance objective were met, and no further action is necessary.

Supporting Evidence

No oyster restoration units moved beyond the RAA areas, and no units moved more than 1 m during either monitoring event (Table 3). Maps of each of the sites (Figures 5 to 18) are provided below to support this lack of movement of bags. High-resolution maps and csv files of the locations of the reefs at all three survey points (following installation, and at 6 and 12 month monitoring events) are available from USC upon request.

Table 3 List of reef site sites and reef units, their positions as given by the coastal surveyor, and the distance these units had moved from the initial installations (as recorded by the coastal surveyor) to the 6 and 12 month monitoring events. Distances measured are from the center points of oyster restoration units.

Site	Surveyor ID	Easting (GDA94)	Northing (GDA94)	Distance moved 6 months (m)	Distance moved 12 months (m)
2	2.1	504557.693	7081870.54	0.01	0.12
	2.2	504562.401	7081871.525	0.09	0.04
	2.3	504561.797	7081866.981	0.11	0.06
3	3.1	504297.232	7081482.809	0.05	0.17
	3.2	504300.191	7081487.149	0.21	0.08
	3.3	504302.058	7081482.224	0.30	0.03
4	4.1	504447.682	7080720.227	0.39	0.09
	4.2	504451.864	7080722.81	0.33	0.28
	4.3	504452.517	7080718.084	0.13	0.17
5	5.1	504977.921	7080596.146	0.20	0.02
	5.2	504980.268	7080598.985	0.08	0.11
	5.3	504983.03	7080596.309	0.28	0.37
6	6.1	505140.806	7080848.337	0.19	0.09
	6.2	505147.768	7080846.296	0.20	0.42
	6.3	505142.59	7080842.496	0.20	0.14
7	7.1	505475.222	7080728.716	0.02	0.21
	7.2	505481.921	7080724.223	0.06	0.07
	7.3	505476.882	7080722.755	0.20	0.20
8	8.1	506148.168	7080578.329	0.44	0.11
	8.2	506151.843	7080583.145	0.12	0.16
	8.3	506154.632	7080579.701	0.57	0.65
9	9.1	507047.3	7081174.147	0.24	0.22
	9.2	507052.487	7081172.727	0.46	0.12
	9.3	507048.33	7081169.39	0.03	0.15
10	10.1	507131.275	7081731.424	0.10	0.21
	10.2	507136.871	7081731.471	0.18	0.11
	10.3	507135.843	7081726.658	0.27	0.10
11	11.1	508035.278	7080213.498	0.03	0.17
	11.2	508040.293	7080216.237	0.15	0.14
	11.3	508038.955	7080212.182	0.23	0.07
12	12.1	507678.59	7079963.401	0.17	0.07
	12.2	507684.058	7079964.39	0.18	0.11
	12.3	507683.416	7079959.64	0.06	0.10
13	13.1	507103.328	7078792.463	0.20	0.12
	3.2	507107.243	7078796.008	0.16	0.08
	13.3	507107.661	7078790.417	0.06	0.15
14	14.1	507090.833	7078704.893	0.18	0.25
	14.2	507094.457	7078706.761	0.20	0.39
	14.3	507094.824	7078701.819	0.12	0.13
16	16.1	506199.719	7075595.579	0.21	0.07
	16.2	506204.963	7075595.325	0.18	0.04
	16.3	506200.595	7075590.153	0.16	0.19
			Mean	0.18	0.16
			StDev	0.12	0.12

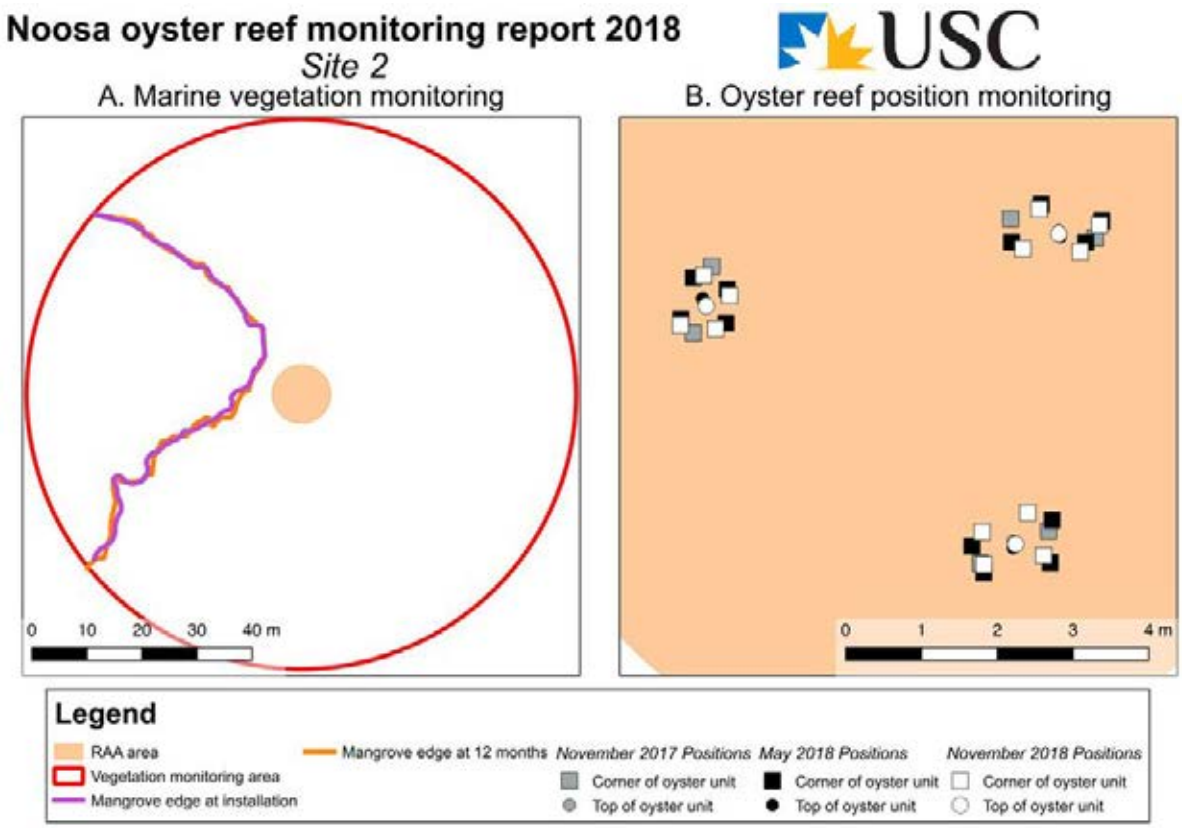

Figure 5 Map of (A) mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 2 in the Noosa River.

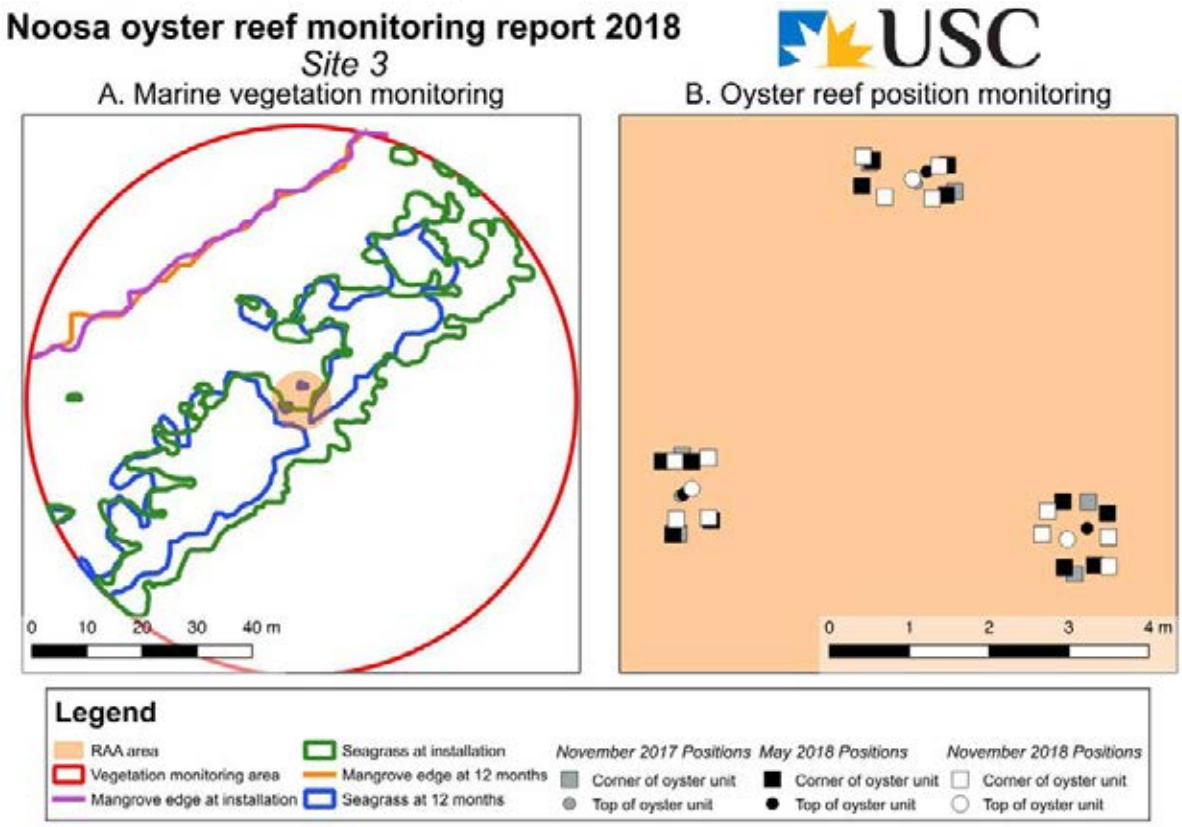

Figure 6 Map of (A) aerial extents of seagrass and mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 3 in the Noosa River.

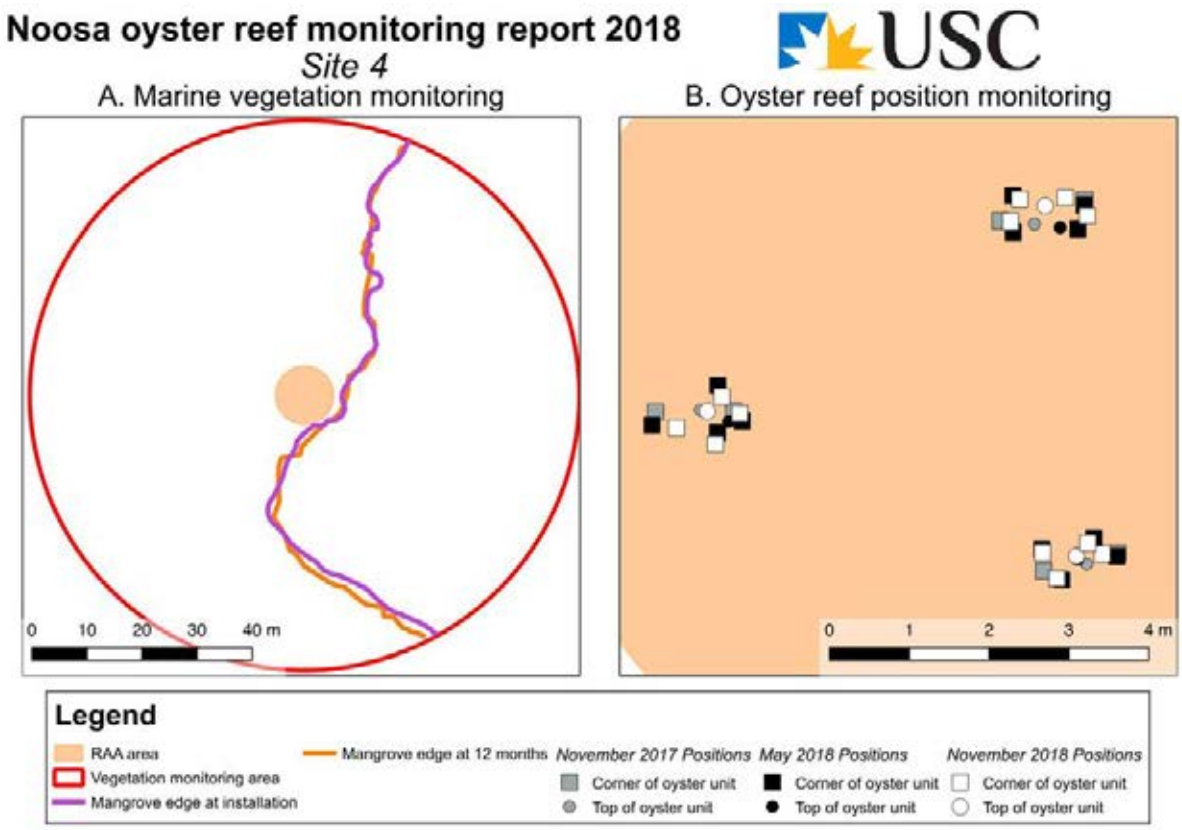

Figure 7 Map of (A) mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 4 in the Noosa River.

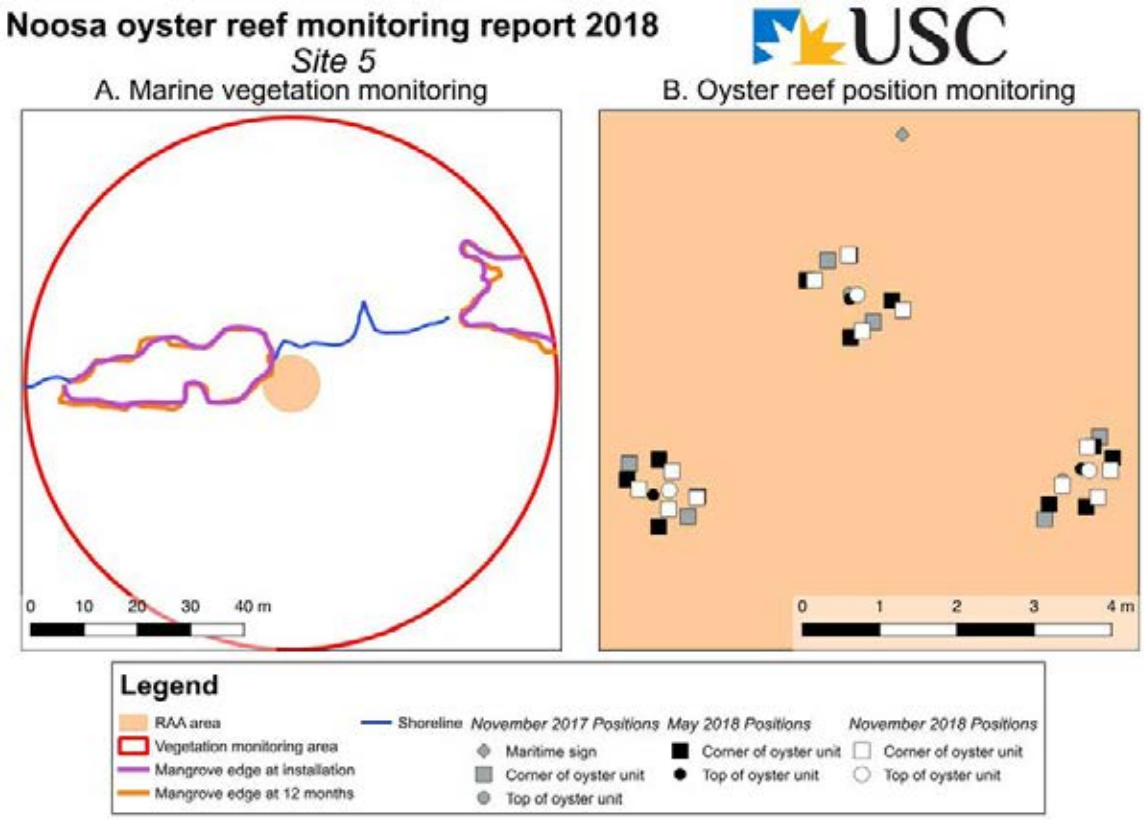

Figure 8 Map of (A) aerial extents of seagrass and mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 5 in the Noosa River.

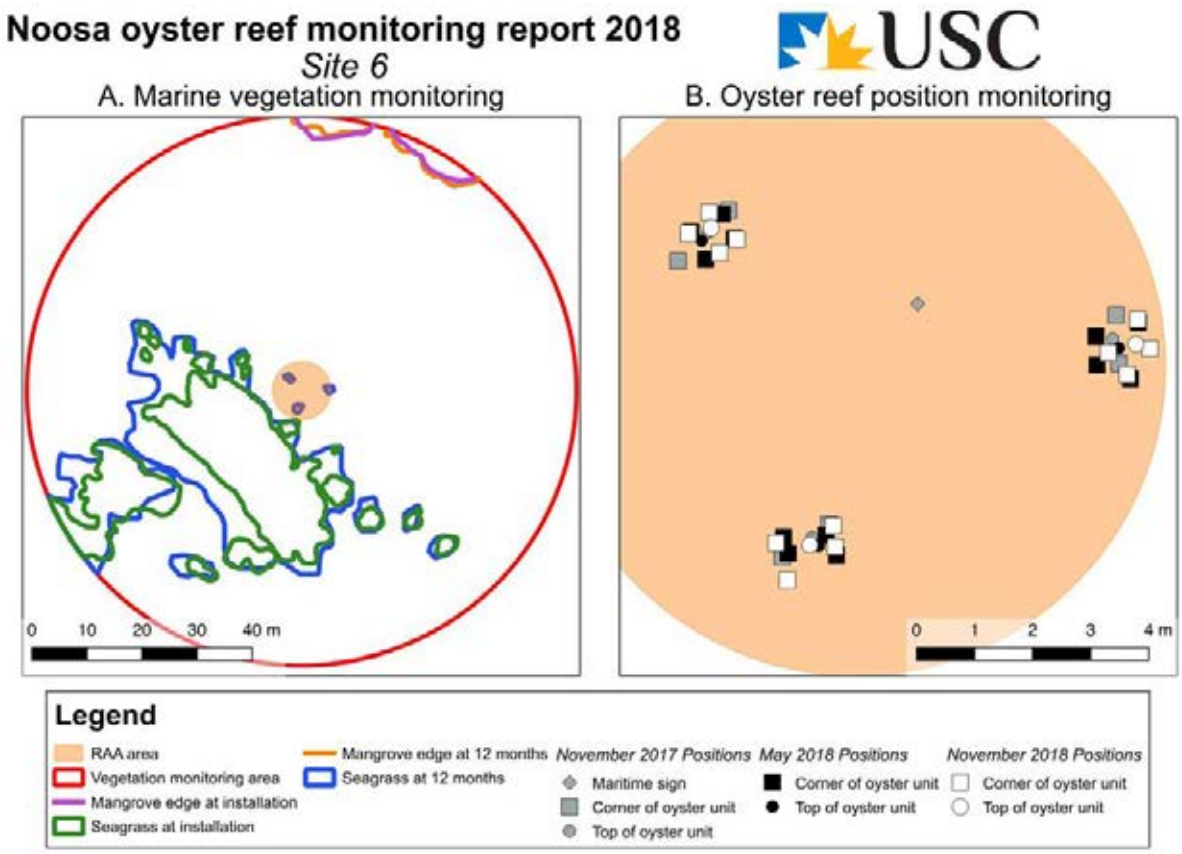

Figure 9 Map of (A) aerial extents of seagrass and mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 6 in the Noosa River.

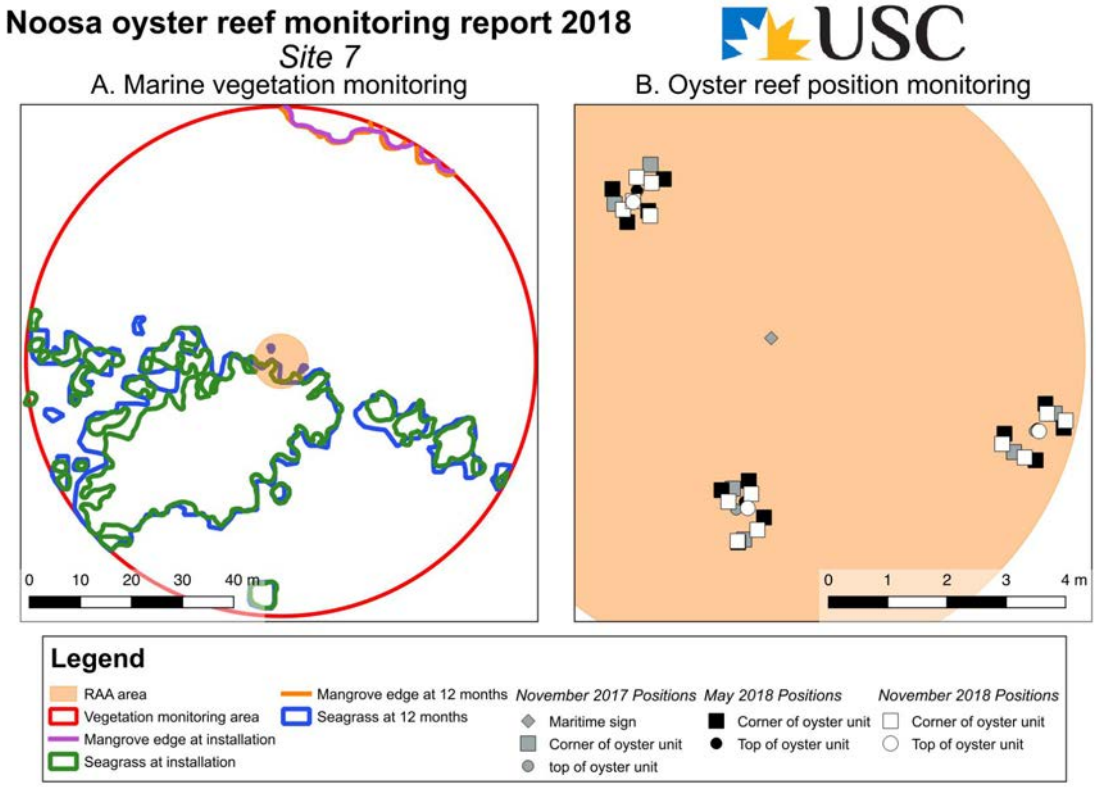

Figure 10 Map of (A) aerial extents of seagrass and mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 7 in the Noosa River.

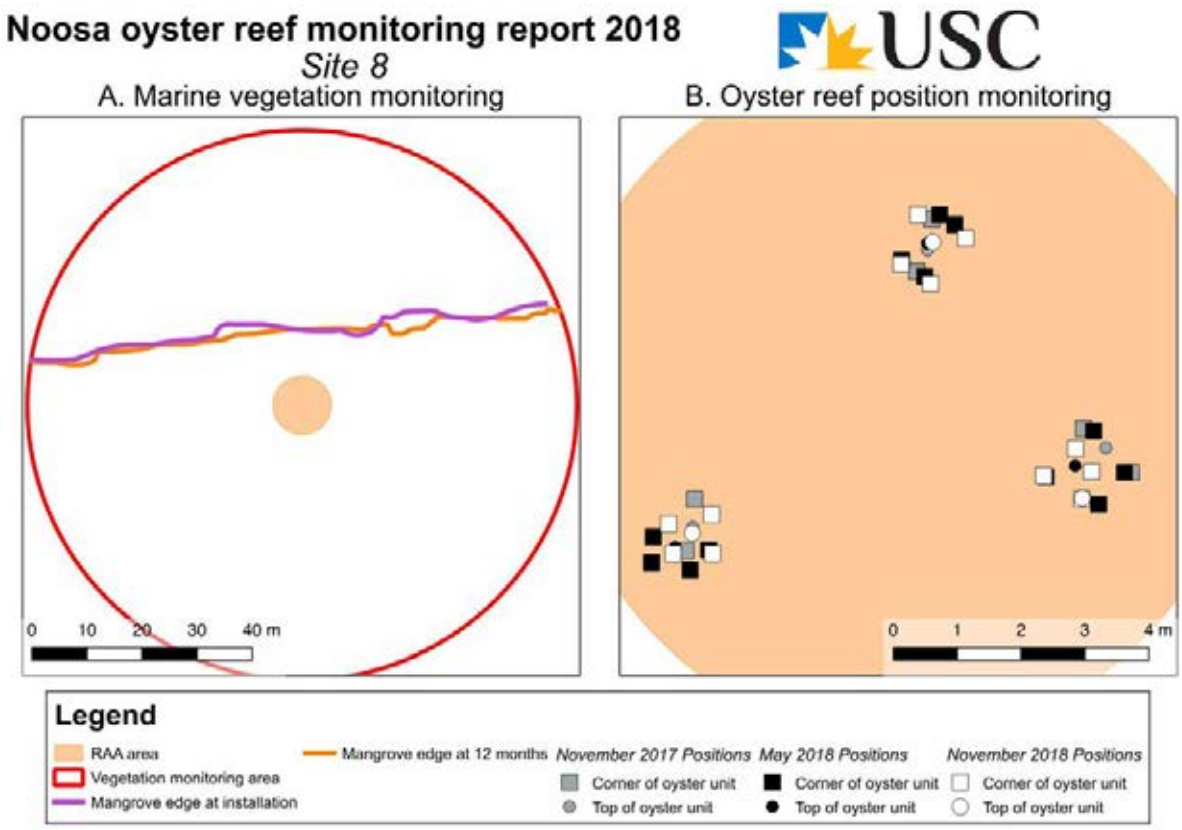

Figure 11 Map of (A) mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 8 in the Noosa River.

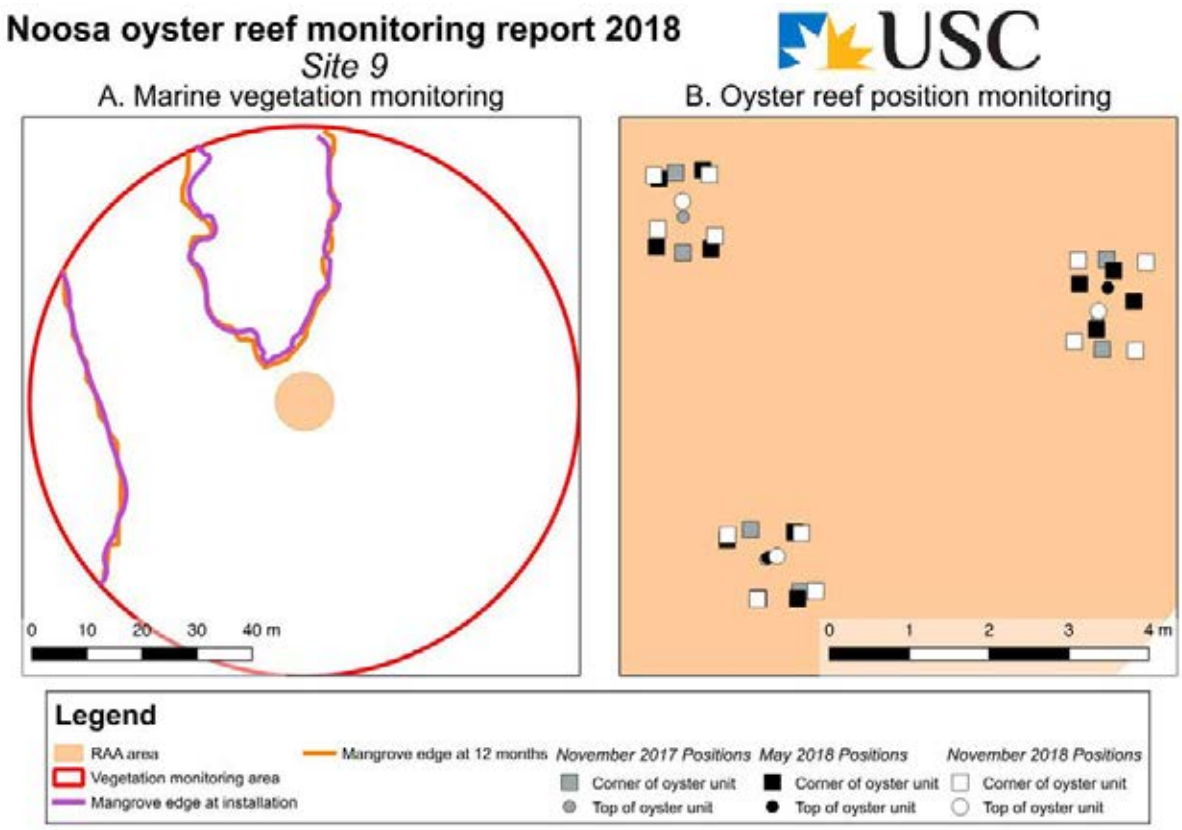

Figure 12 Map of (A) mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 9 in the Noosa River.

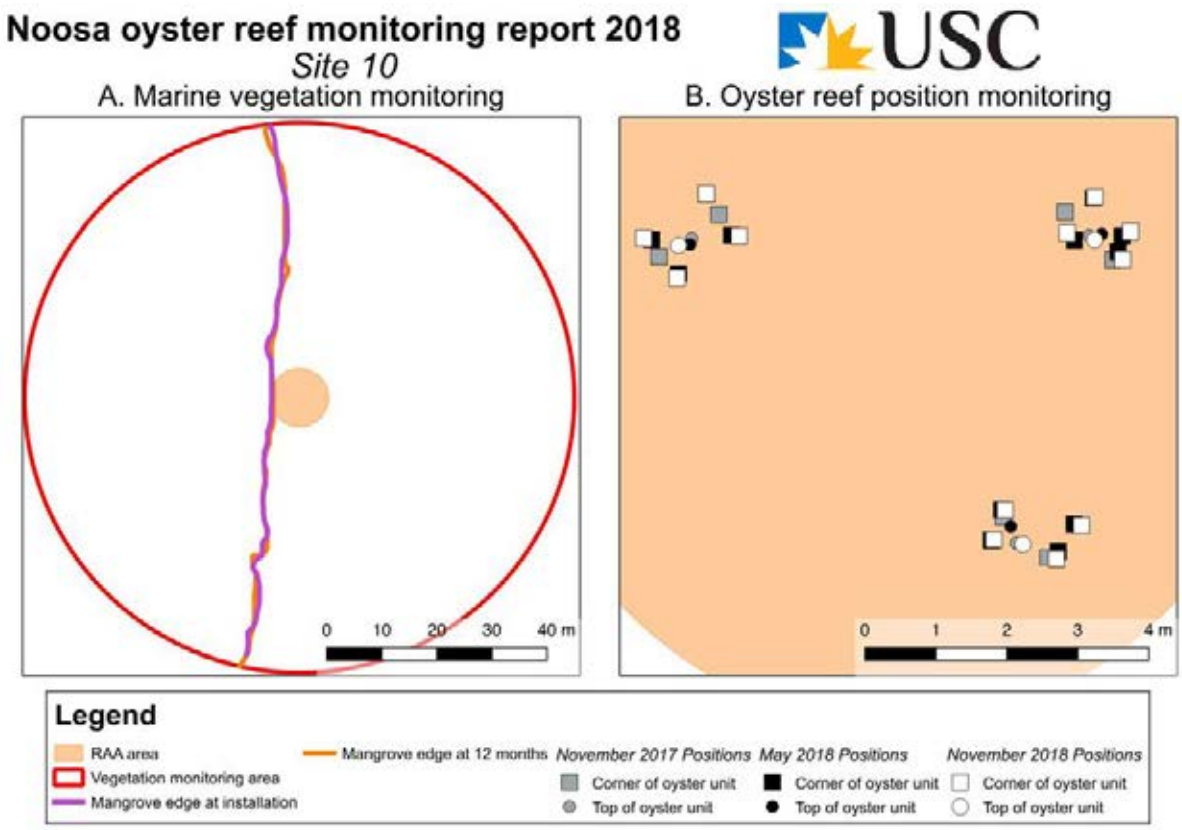

Figure 13 Map of (A) mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 10 in the Noosa River.

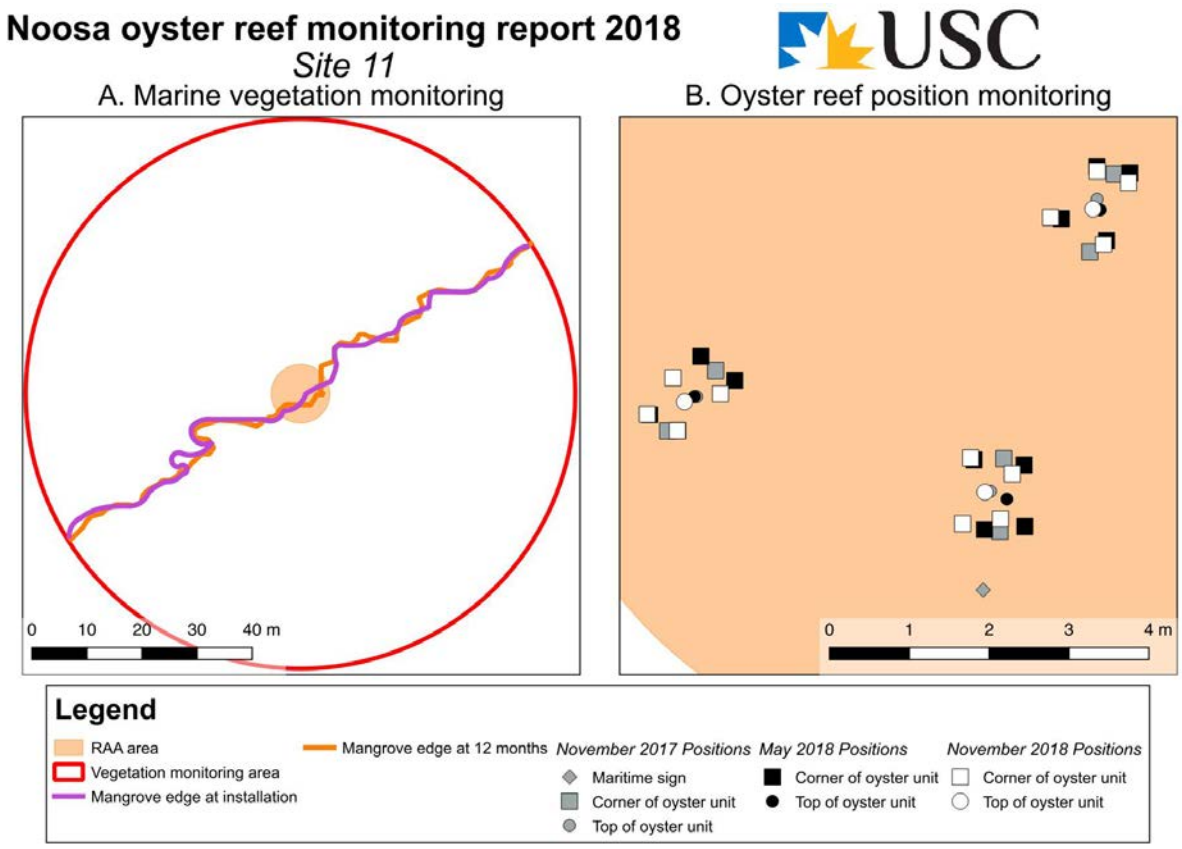

Figure 14 Map of (A) mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 11 in the Noosa River.

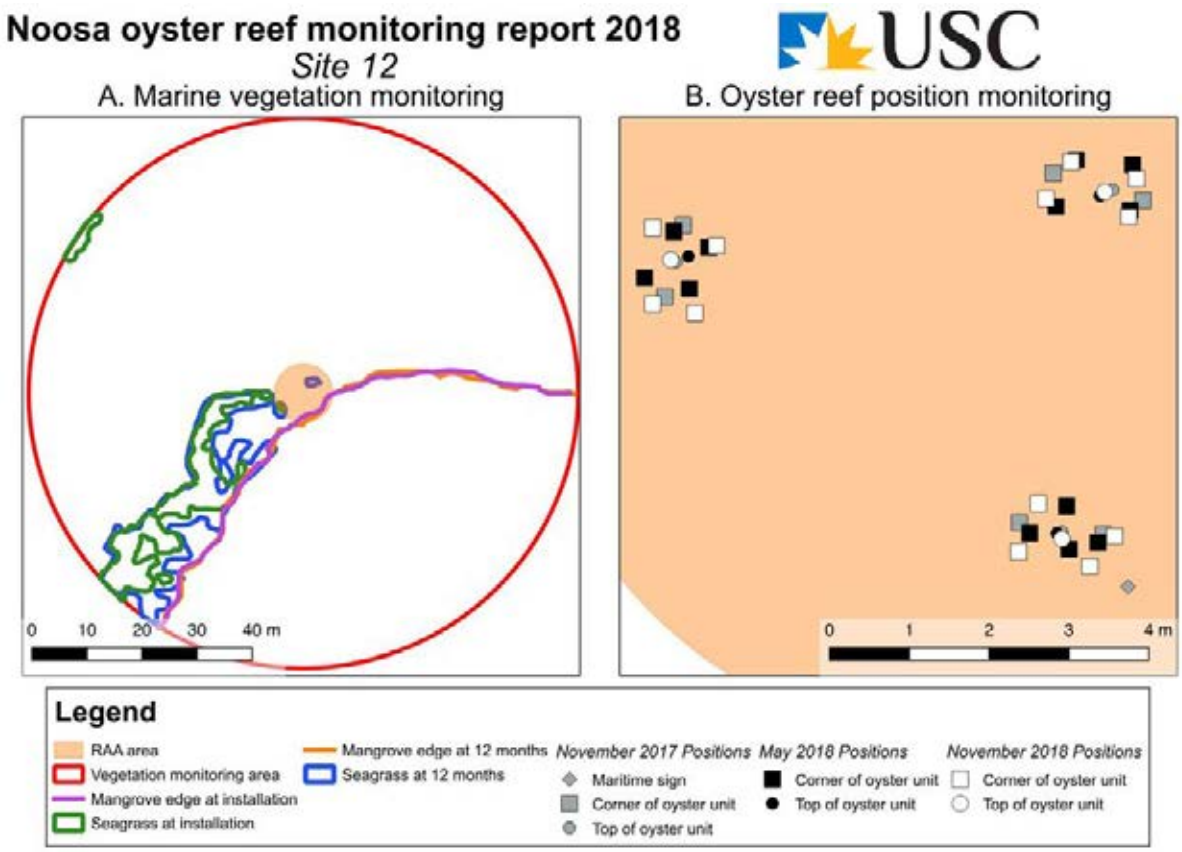

Figure 15 Map of (A) aerial extents of seagrass and mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 12 in the Noosa River.

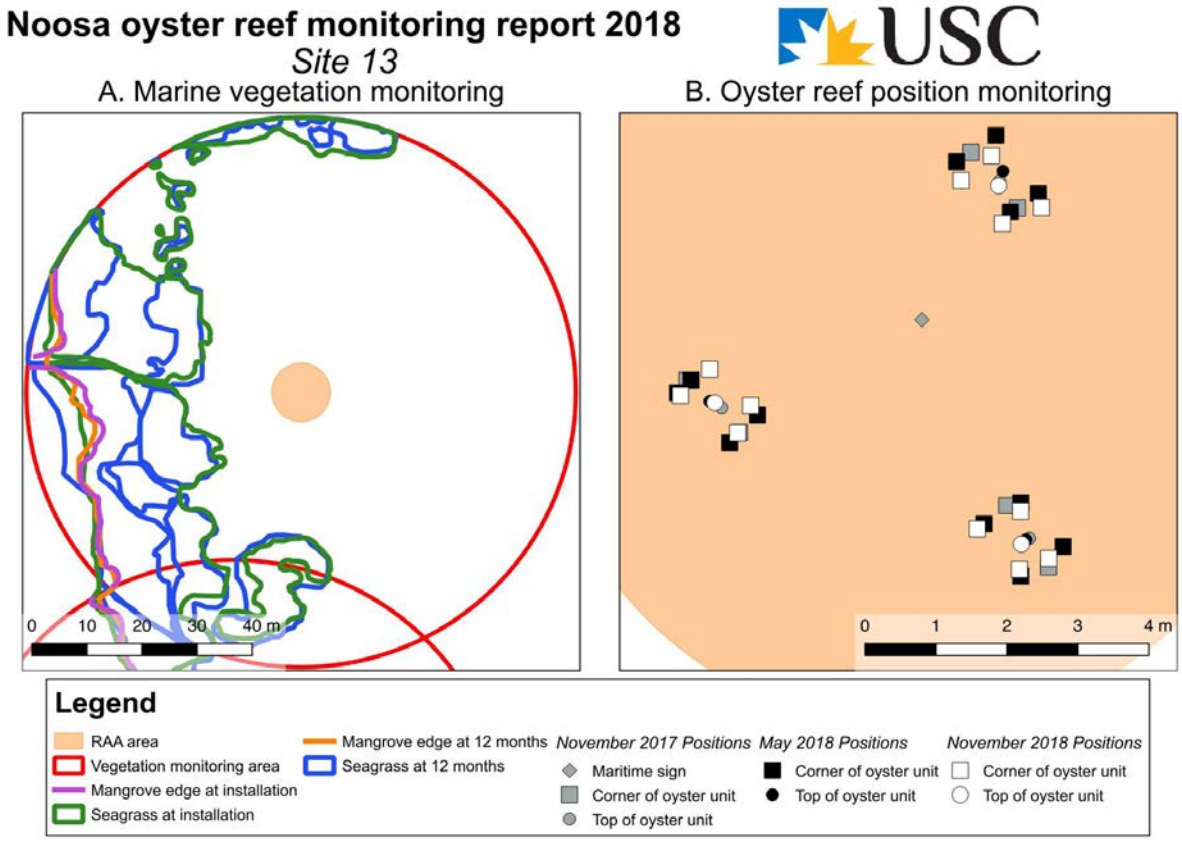

Figure 16 Map of (A) aerial extents of seagrass and mangrove edges and (B) oyster reef

unit positions (at installation, and at 6 and 12 months post installation) at site 13 in the Noosa River.

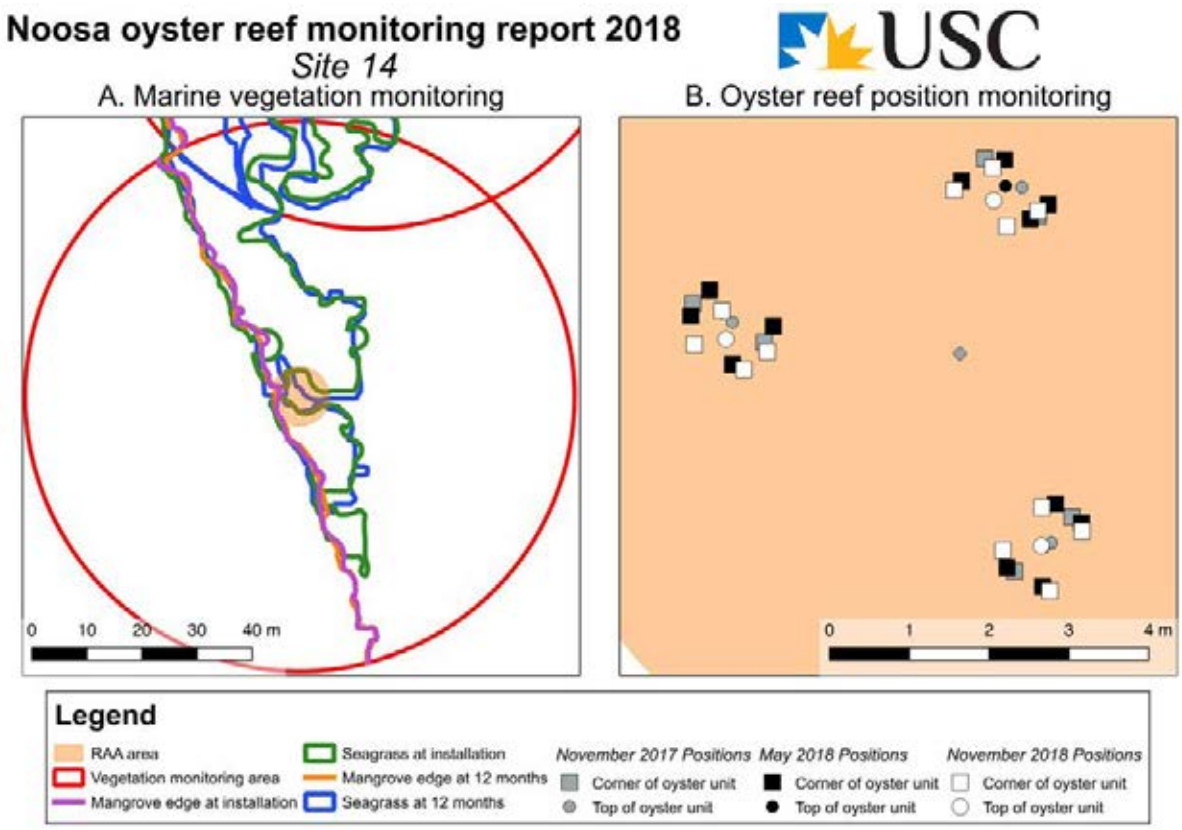

Figure 17 Map of (A) aerial extents of seagrass and mangrove edges and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 14 in the Noosa River.

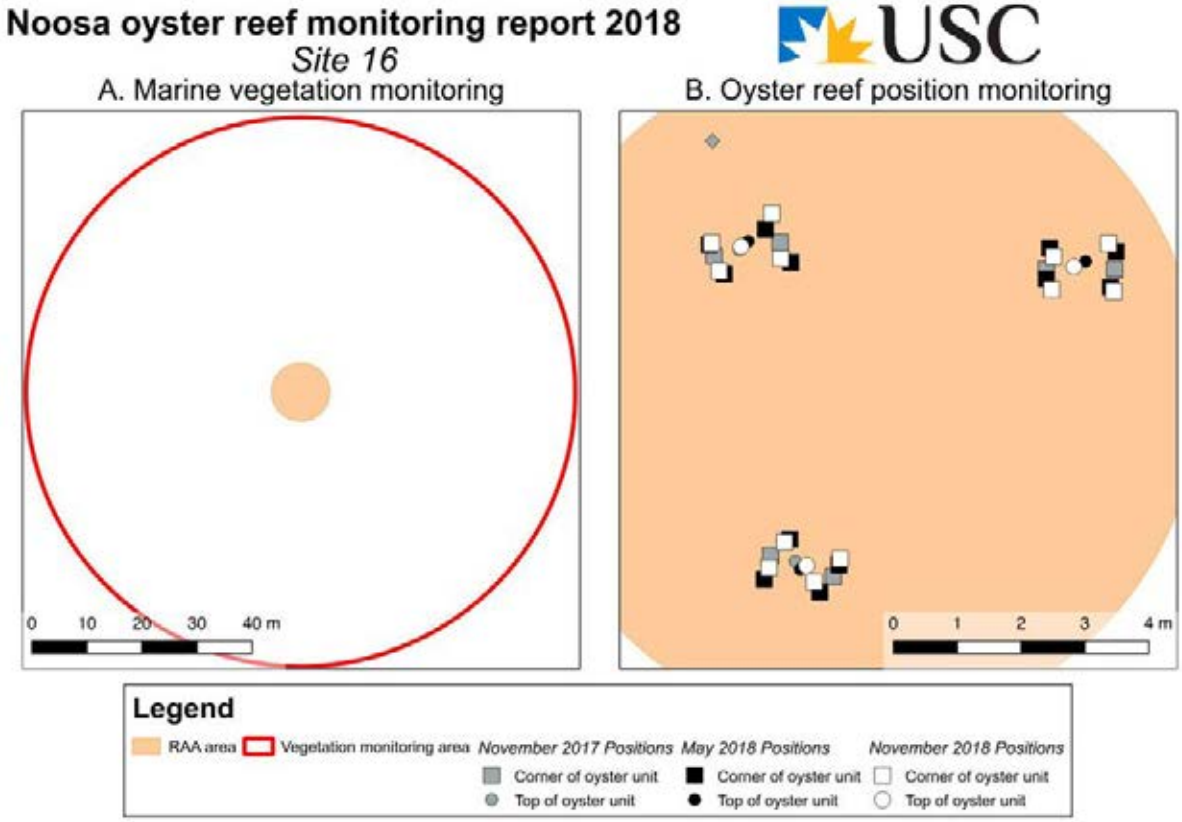

Figure 18 Map of (A) vegetation monitoring area (note there was no seagrass or mangroves at this site) and (B) oyster reef unit positions (at installation, and at 6 and 12 months post installation) at site 16 in the Noosa River.

Monitoring criteria 2- Natural recruitment processes

Performance objective: Oysters and other sessile benthic invertebrates recruit to reef restoration units to establish a biogenic matrix, which binds oyster shells in place, prior to degradation of coir material. The Key Performance Indicators for this are:

1. **Oyster recruitment**: successful recruitment of oyster spat in at least 1 out of the 3 years (i.e. 33% of the time) post deployment (following international best practice of 40%: Baggett et al. 2015);
2. **Cover of oysters and other sessile benthic invertebrates**: an upward trend in the cover of sessile benthic invertebrates growing on restoration units; and
3. **Establishment of stable biogenic matrix**: structural rigidity of oyster restoration units, denoting a stable biogenic matrix after 3 years post deployment, which is sufficient to hold oyster shells in place.

Monitoring method: Quantify the recruitment of oysters and other sessile benthic invertebrates to reef restoration units, and measure changes in the cover of oysters and other sessile benthic invertebrates over time (following international best practice)(Baggett et al., 2015). The monitoring methods for each Indicators are:

1. **Oyster recruitment**: marked oyster shells will be fastened to the outside of restoration units. These shells will be harvested at regular intervals (15 oyster shells per location on each event – i.e. 5 shells per unit) and the density and size of recruits recorded;
2. **Cover of oysters and other sessile benthic invertebrates**: photographs of ten quadrats (25 cm x 25cm), distributed in a stratified random design, across each oyster reef restoration unit will be taken at regular intervals to quantify the change in cover of oysters and other sessile benthic invertebrates (Baggett et al., 2015).
3. **Establishment of stable biogenic matrix**: assess the structural integrity of each oyster reef restoration unit and monitor the degradation of coir material. Structural integrity will be quantified by measuring the proportion of oyster shells (from 10 shells that are selected at random at each location), which can be removed easily by hand manipulation. The rate of coir degradation will be measured by monitoring changes to the condition of coir mesh over time from the ten photo-quadrats, which are collected twice per year to assess changes in the cover of benthic invertebrates at each oyster reef restoration unit.

Frequency: Every 6 months for a minimum of three years, unless otherwise detailed within corrective actions

Was the performance objective met?

We identified significant oyster spat settlement and growth at all oyster reefs. Whilst this has not yet proliferated to cover of oysters on the outside of the restoration units, or to fully cementing shells within the units together, these positive spat fall and growth results indicate that these performance criteria are likely to be met in the coming years. Therefore, no further action is necessary at this early stage of the project.

Supporting evidence

Oyster recruitment

We collected shells from two sources;

1. 5 shells collected from within the coir bags at each oyster restoration unit (henceforth 'bags'), and
2. 5 shells collected from 'oyster necklaces' which were strings of drilled oyster shells tied together with fishing line and then affixed to the top of the oyster restoration units during installation (henceforth 'necklaces').

All live oysters growing on the shells were identified to species, counted, and their height measured, and the density of oysters calculated as number of oysters per square meter of shell (as recommended by Baggett et al., 2015).

We identified significant oyster settlement during both monitoring events on both necklaces and in the oyster restoration unit bags (Figure 19, Figure S1, Table 4, Table 5). Overall, we identified an average of 387.5 spat/m^2 in May 2018, 306.1 oysters/m^2 in November 2018, and 349.9 oysters/m^2 across both monitoring events (Table 4). Whilst we identified some changes in the densities of oysters at specific restoration sites (Figure S1, Table 5), with some sites showing increased oyster density between sampling events, and others lower oyster density, the overall pattern was for a reduction in oyster density between monitoring events 1 and 2 (Table 4). This change was, however, offset by a significant change in the size-frequency distribution of oyster shells on the reefs (Figure 20, Figure S2). Here oysters increased in size from 14.3 mm (+/- 6.5 mm SD) in May 2018, to 19.1 mm (+/- 8.9 mm SD) in November 2018. Consequently, it is likely that intermediate sized oysters (6-15 mm in length) in May 2018 grew to the larger sizes (i.e. <30 mm) by November 2018, and that the smaller oysters (<6mm) either grew to an intermediate size, or did not survive the winter. Consequently, despite a reduction in overall average density, this was offset by a larger average oyster size during the second monitoring event.

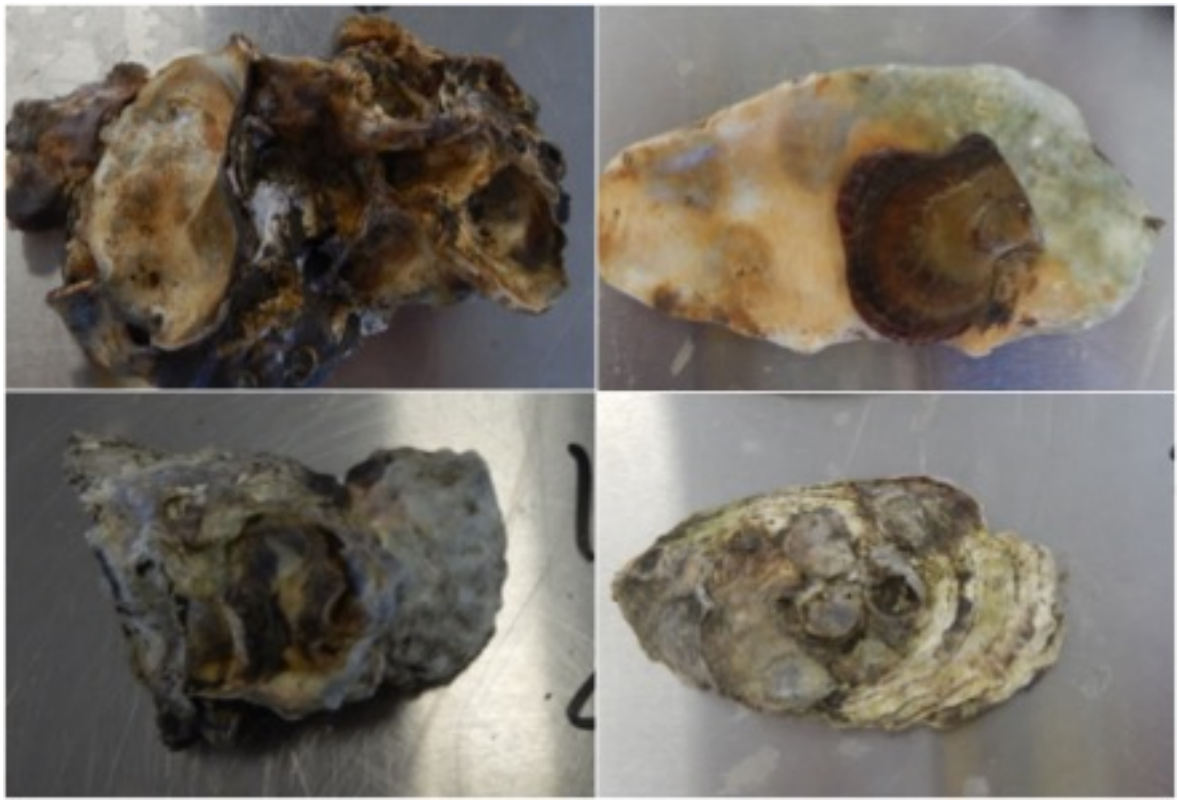

Figure 19 Example images of juvenile oysters growing on shells collected from within the oyster reef restoration units.

Table 4 List of oyster quantification methods, and the average densities (with standard deviations) of oysters during both monitoring events, and for all monitoring events in 2018.

	Monitoring event 1		Monitoring event 2		Overall (both events)	
	Average (spat/m^2)	StDev	Average (spat/m^2)	StDev	Average (spat/m^2)	StDev
Necklaces	543.7	643.5	493.9	513.4	525.8	599.3
Bags	272.9	413.3	230.9	438.2	251.9	425.9
All	385.7	537.7	306.1	475.1	349.9	511.7

Table 5 Summary of average oyster density (with standard deviation) across all oyster restoration sites. Note that all sites recorded significant spat settlement. Necklaces were unrecoverable from three sites in November 2018 sue to anchor damage.

	May 2018				Nov 2018			
	Bags		Necklace		Bags		Necklace	
Site	Avg (spat/m^2)	StDev	Avg (spat/m^2)	StDev	Avg (spat/m^2)	StDev	Avg (spat/m^2)	StDev
2	114.7	153.4	159.9	413.5	135.7	153.3	212.5	316.4
3	131.5	132.8	217.9	219.4	37.9	82.4	320.2	364.6
4	49.6	75.1	229.0	274.9	72.4	92.7	317.6	305.0
5	544.8	307.4	1399.2	961.6	473.1	315.7	550.5	601.5
6	165.8	181.3	475.0	562.5	282.8	323.9	No shells recoverable	
7	191.1	279.7	664.4	363.3	94.5	195.3	No shells recoverable	
8	810.0	944.4	1229.5	527.7	1101.2	984.6	0.0	0.0
9	300.5	374.0	611.7	861.9	57.8	172.3	672.9	278.2
10	145.7	156.9	842.1	722.7	82.1	131.5	No shells recoverable	
11	279.8	321.7	409.9	377.3	178.6	277.4	666.1	764.4
12	340.5	308.6	825.5	548.3	86.5	126.6	758.9	511.0
13	589.8	527.2	551.3	316.8	475.4	518.8	1056.5	425.7
14	142.0	178.3	428.7	675.4	117.2	164.2	793.7	468.3
16	15.5	60.0	0	0	37.8	79.2	45.5	150.8

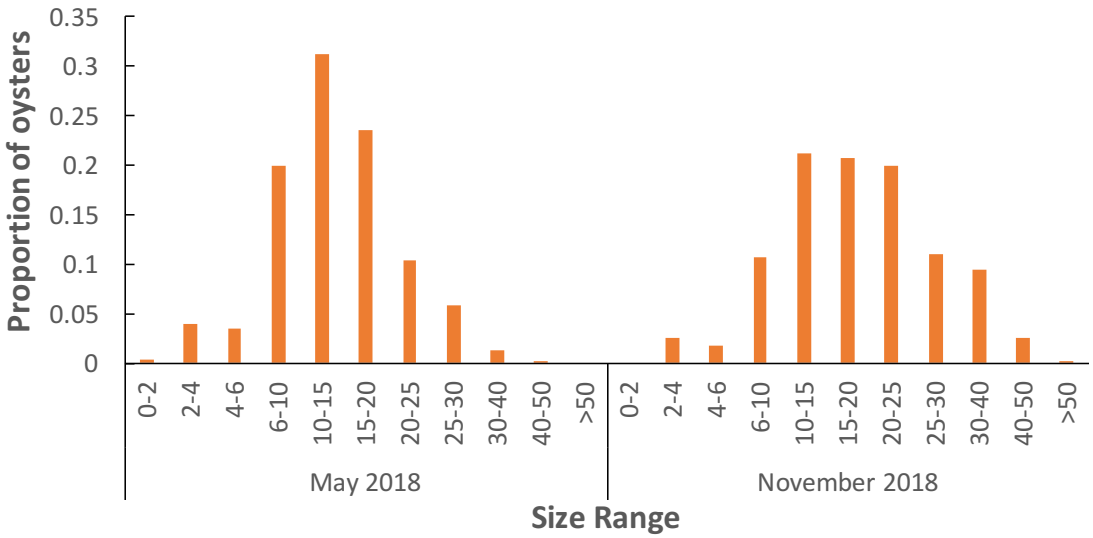

Figure 20 Size frequency distribution of oyster shells across all samples taken in May and November 2018.

Cover of oysters and other sessile invertebrates

At this stage, we were not able to identify any significant settlement of invertebrates on the outside of the coir bags. This is unsurprising as significant growth of invertebrates on the outside of the coir mesh bags was not expected within the first year, and therefore not a compulsory success criteria for the first year in the monitoring program. We anticipate, however, that given the positive indications of spat recruitment and oyster growth, that it is likely that this target will be achieved fully in the coming years. We were, however, able to use the quadrat samples (see figure 21) to show that there has been no significant degradation of the coir mesh, that it is still strong, and that the gauge of the rope has not been narrowed by any natural decomposition as yet. Similarly, we not that there is minimal macroalgal coverage on the bags (<1% in all cases), meaning that there is no significant fouling occurring that would limit the settlement of oysters either on, or into, the oyster restoration units into the future.

Establishment of stable biogenic matrix

The development of the reefs is in the early stages, therefore 100% of randomly selected oyster shells were still easily moved during both monitoring events. This is unsurprising as the development of stable biogenic matric was not expected within the first year. We

anticipate, however, that given the positive indications of spat recruitment and oyster growth, that this performance criteria will likely will be achieved in the coming years.

Figure 21 Example images of quadrat photos taken on oyster reef restoration units, here at reefs 13 (top row) and 16 (bottom row). We did not identify any significant growth of invertebrates on the outside of the oyster reef units, but there was also no significant degradation of the coir mesh noted.

Monitoring criteria 3- Community use and enjoyment of the declared fish habitat area

Performance objective: Oyster restoration units do not significantly impair community use and enjoyment of the declared Fish Habitat Area, particularly fishing activities.

Monitoring method: Maintain records of community feedback, evidence of vandalism, and vessel strikes on the trial oyster reef restoration units. Records will be comprehensive and include, as a minimum set:

1. the number and type of complaints received (also, to allow the Department to gauge the success, any positive comments should also be provided);
2. the type, nature, and severity of any acts of wilful vandalism; and
3. the type and severity of any vessel strike.

Frequency: Annual reporting of all complaints, cases of willful vandalism, and instances of vessel strike received for the three-year trial period.

Was the performance objective met? Noosa Council holds the data / information on any complaints from the public. We did not identify any willful vandalism of the reefs, but we did identify several instances of boat propeller and anchor strikes in the November 2018 monitoring event.

Supporting Evidence

Noosa Council is the designated contact for comments regarding the oyster reef restoration project in the Noosa River, and of how this project affects the use and enjoyment of the declared fish habitat area by the community. This is clearly stated on the signage at each oyster reef restoration site (Figure 22).

We identified some damage to oyster reefs during the monitoring events (summarized in Table 6). During the monitoring event in May 2018, only one reef required repairs. In November 2018, most reefs required repair, and some coir bags were unrepairable. It is likely that the majority of damage to the oyster reefs is caused by being struck by boat propellers (especially at sites where bags were torn), and/or poorly placed or dragging boat anchors (especially at sites where bags were torn and/or moved from their position on the reef). During the November 2018 monitoring event, four of the reefs were also badly fouled by fishing line and/or abandoned crab pots. This fishing gear was removed from the reefs and disposed of. Combined, this damage resulted oyster spat necklaces being impossible to retrieve from some reefs (see monitoring criteria 2, Table 5).

Members of the USC team have conducted several surveys on the fish fauna associated with the oyster reefs in the Noosa River, beyond the monitoring events detailed here. In association with these surveys, team members have taken note of the number of reefs where fishing activities have been occurring (Table 7). Whilst this is simply a snapshot view of the types of activities taking place around the reefs, it is indicative of the potential damage occurring to the reefs. The key observation is a general increase in the number of fishing boat at the reefs with time since installations. This is likely due to 1) the general public becoming increasingly familiar with the locations and benefits of the reefs, 2) media reports of the positive results regarding fish assemblages coming to light, and 3) the timing of September school holidays.

Whilst we did not identify any acts of willful vandalism of the oyster reef restoration units during our monitoring events, many marker buoys (placed on the corner of the reef units; a compulsory condition of the development approval) were missing during monitoring events. These were immediately replaced by the USC team. Some buoys were, however, removed from sites the night after being reinstalled, thereby indicating very regular removal of reef

hardware by members of the public at some sites. This lack of buoys on the corner of the oyster reefs is likely a contributor to some of the reefs being hit by boat propellers etc. No site signage was damaged or modified during the past year, so no maintenance or replacement has been necessary (Figure 22).

Figure 22 Oyster reef restoration signage being installed at an oyster reef restoration site in the Noosa River, with text on the sign indicating the contact details at Noosa Council for comments on the broader oyster restoration project.

Table 6 List of recorded damage and repairs to oyster reefs during both monitoring events

Site	Damage May 2018	Repairs conducted	Damage November 2018	Repairs conducted
2	None	NA	All top bags torn. Buoy missing.	Repairs to bags completed where possible. Replaced buoy.
3	None	NA	All top bags torn. Buoy missing.	Repairs to bags completed where possible. Replaced buoy.
4	None	NA	Bottom right, and top right bag torn. Middle reef unit covered by significant sand. Right hand reef unit and nearby buoy tangled with crab pot.	Repairs to bags completed where possible. Crab pot removed.
5	Reef struck by boat which broke mooring, one buoy missing	Reef repaired and put back in place. Replaced buoy.	All top bags torn. Buoy missing.	Repairs to bags completed where possible.
6	None	NA	Middle top bag ripped.	Repaired bag.
7	None	NA	Middle top bag ripped.	Repaired bag.
8	Right hand bag moved and torn, 1 buoy missing	Repaired and put back on reef. Replaced buoy.	Right hand top bag torn. Buoy missing.	Repaired bag, replaced buoy.
9	Right hand bag moved and torn, 2 buoys missing.	Repaired and put back on reef. Replaced buoys.	Left hand top bag torn, right hand reef significantly covered by sand, middle top bag ripped.	Repaired bags.
10	One buoy missing.	Replaced buoy.	Top middle bag destroyed, significant covering by sand. Buoy missing.	Repaired bag, replaced buoy.
11	Two buoys missing.	Replaced buoys.	Top middle bag torn.	Repaired bag.
12	None	NA	Right top bag torn.	Repaired bag.
13	None	NA	None	NA
14	None	NA	None	NA
16	None	NA	None	NA

Table 7 List of days USC team members have surveyed the reefs, and the number of reefs upon which fishing activities have been noted during these surveys.

Date of field work	Number of days	Sites visited	Activity being completed	Sites with boats present
25-26 November 2017	2	3-8	Ecological function study	0
27-30 November 2017	4	All	Fish surveys	0
29-30 December 2017	2	All	Fish surveys	2
29-30 January 2018	2	3-8	Ecological function study	0
15-16 February 2018	2	All	Fish surveys	1
26-27 March 2018	2	3-8	Ecological function study	2
29-30 March 2018	2	All	Fish surveys	1
31 May, 1 June 2018	2	3-8	Ecological function study	0
15-18 May 2018	4	All	Fish surveys	2
20-22 May 2018	3	All	6 month monitoring	3
27-28 June 2018	2	All	Fish surveys	4
16-17 August 2018	2	All	Fish surveys	2
1-2 October 2018	2	All	Fish surveys	2
19-20 November 2018	2	All	Fish surveys	3
26-27 November 2018	2	All	12 month monitoring	1

Monitoring criteria 4- Other potential effects

Performance objective

Oyster reef restoration units do not cause a decline in the extent of marine plants within a 50 m radius of the restoration units, and are not attributed to erosion of adjacent shorelines or other ambient environmental impacts.

Monitoring method

Map the area of marine plant habitats (seagrass, mangroves) in the immediate vicinity (i.e. with a 50 m buffer) of each oyster restoration area, using high-resolution GPS (cm scale) and field-validated aerial imagery (sourced from Nearmap) (NearMap, 2018). Monitor changes in the composition coverage and condition of seagrass within 50 m radius around the oyster reefs. Map the location and condition of estuarine shorelines that occur in the immediate vicinity (i.e. with a 50 m buffer) of each oyster reef, using high-resolution GPS (cm scale) and field-validated aerial imagery (sourced from Nearmap).

Frequency

Annually for a minimum of three years, or until any failed restoration units have been removed.

Was the performance objective met?

All aspects of this performance objective were met, so no further action is necessary.

Supporting evidence

Mangroves and seagrasses were successfully mapped at each site using the described methods (Figures 8-21). We identified no significant change in the distribution of mangroves or seagrasses within the 50 m monitoring area (Table 8; t test, P>0.9), or any erosion to nearby shorelines. Whilst the footprint of seagrass was lower at some sites, there was no loss of seagrass attributable to the installation of the reefs (i.e. significant decline of seagrass away from the reefs, especially within the RAA areas). Photographs of the mangrove fringe and shoreline within the 50 m monitoring area both before the installation, and during the 12 month monitoring event are available from USC upon request.

Table 8 Extent of seagrass and length of mangrove edge at within 50m of each oyster restoration site at installation and 12 months post installation.

Reef	Mangroves at installation (m)	Mangroves at 12 months (m)	Seagrass at installation (m^2)	Seagrass at 12 months (m^2)
2	113.9	119.4	0	0
3	92.0	87.9	1995.9	1443.6
4	135.6	133.8	0	0
5	162.3	175.2	0	0
6	39.4	43.6	1372.1	1590.0
7	43.1	48.2	1480.8	1913.5
8	108.8	112.0	0	0
9	180.8	181.8	0	0
10	110.7	114.4	0	0
11	138.5	137.5	0	0
12	114.4	116.9	151.9	499.0
13	81.7	82.3	2105.0	1707.5
14	134.5	136.2	854.6	765.5
16	0	0	0	0

No change to seagrass composition or density was identified at any restoration sites. All sites were dense (>70% cover) and long (>20 cm) eelgrass (*Zostera capricorni*) (except for sites 13 and 16- see below). During the 12 month monitoring event, we identified small (leaf height <1 cm), low coverage (<5%) growth of dugong grass *Halophila ovalis* inside the RAA area at site 13, and some small patches within the rocky shore adjacent to site 16. This seagrass was not present at the sites during installation (Table 1). The growth of seagrass at these sites is likely due to lower runoff in Lake Weyba and Weyba Creek over the past yeah, and especially in the past 6 months, and the stabilizing and baffling effects of the reefs on surrounding sediments (especially at site 13). Further monitoring will be required on these growing seagrasses.

Conclusions

In this report, we show that;

5. Oyster restoration units have not moved from the RAA area, nor have they moved greater than 1 m within the RAA area.
6. There has been significant spat settlement and oyster growth at all oyster reef restoration sites. Whilst this has not yet proliferated to coverage of invertebrates on the outside of the coir bags, or to the proper stabilisation of shell within the bags (i.e. cementing of the biogenic reef matrix), these oyster growth results are a positive sign for the likely success of the reefs in achieving these performance criteria in the near future.
7. Whilst we did not identify any wilful damage to the oyster restoration units, we did identify that marker buoys were regularly removed from the oyster restoration sites, and there have been several instances of boat propeller and anchor strikes on the reefs. This was repaired where possible.
8. There has been no significant change to the distribution, composition or quality of seagrass or mangroves around the oyster reef sites. Similarly, there has been no shoreline erosion at oyster reef sites.

Consequently, two of the four monitoring targets reported on here have been fully met, the third relating to oyster and invertebrate growth is tracking very favorably with the criteria likely to be met in the coming years, and the final relating to community usage may require closer monitoring.

We identified some damage to the oyster reef units from boating activities (principally anchor and prop damage) at many sites during the November 2018 monitoring event. We have some evidence to suggest that the use of oyster reefs by fishers has increased over time, and that some of the ecological benefits of the reefs might therefore be being offset by fishing. The three reefs more distant from the main boating activities in Lake Weyba and Weyba Creek (due to the combined effects of limits on access to hire boats, and difficulty of access due to shallow waters) are the most intact oyster reefs, with no damage recorded in either 2018 monitoring events. Whilst these reefs do not necessarily have the highest rates of settlement (the exception being reef number 13, which has the highest average live oyster density), their success might be the most guaranteed as they are less likely to be damaged by the sorts of impacts occurring on reefs in the central stretch of the river.

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Appendices

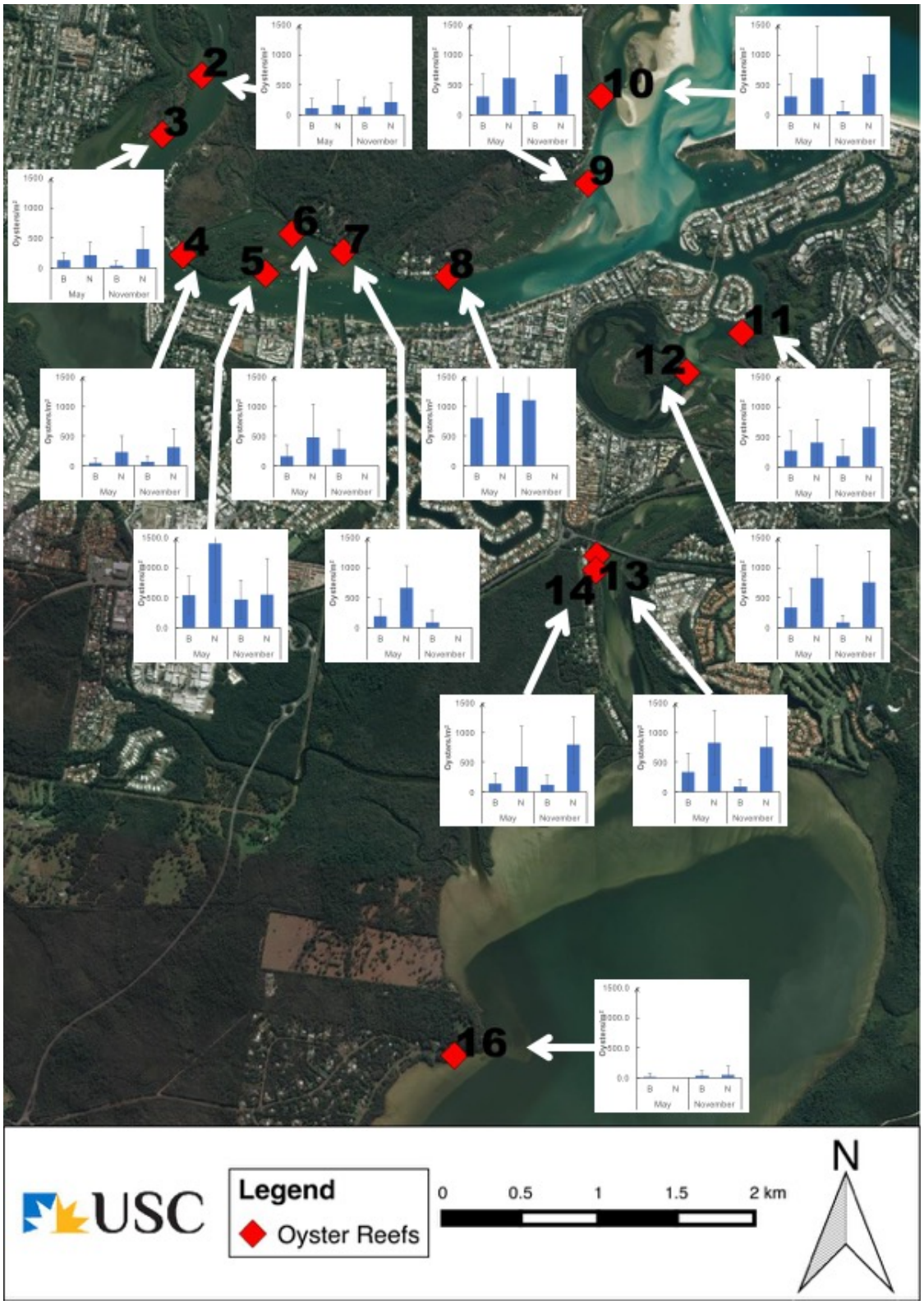

Figure S1 Map of oyster reef restoration sites with average (+/- SD) values for oyster density during May and November 2018 monitoring events in the oyster reef bags (B) and on the oyster necklaces (N).

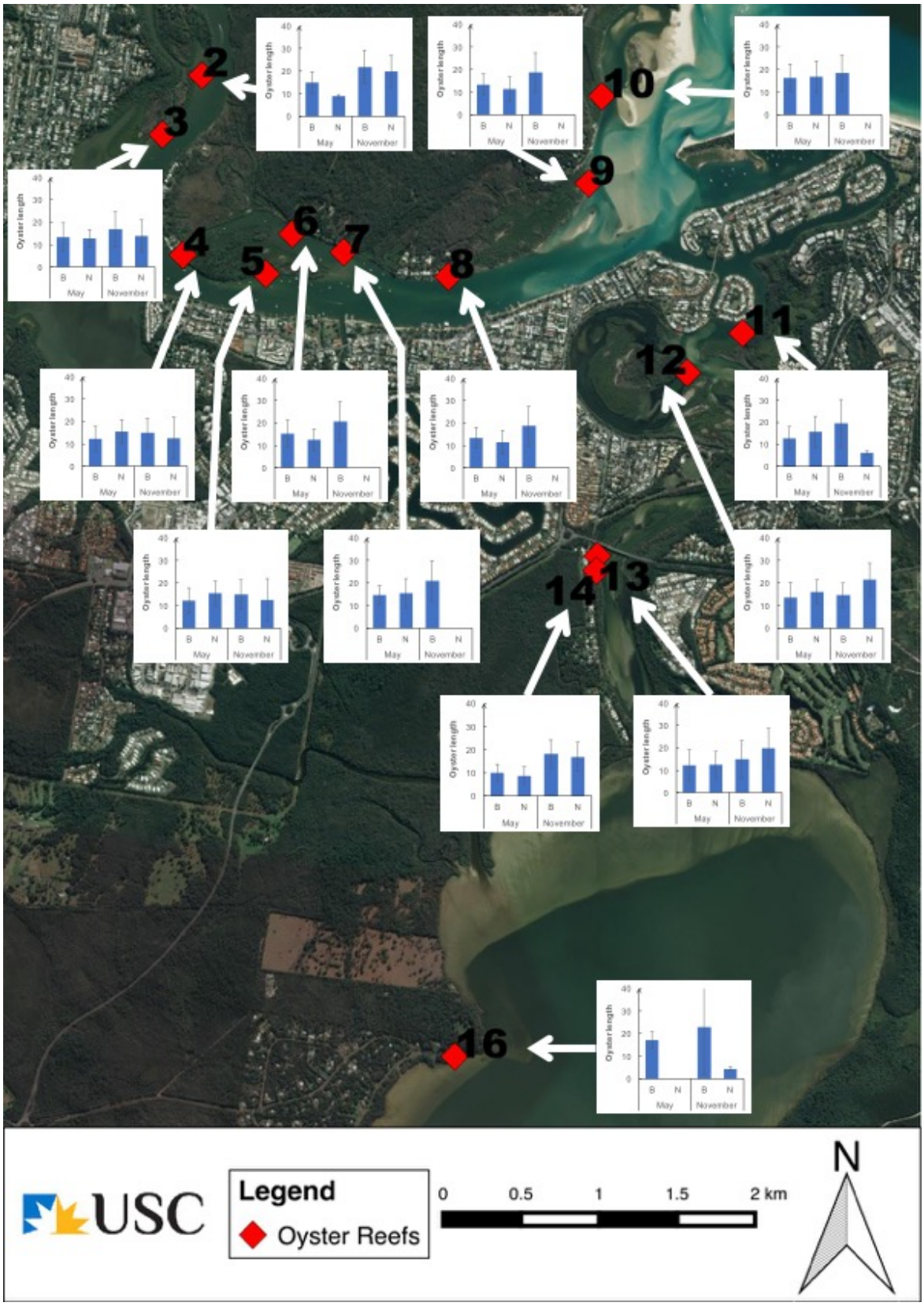

Figure S2 Map of oyster reef restoration sites with average (+/- SD) values for oyster length during May and November 2018 monitoring events in the oyster reef bags (B) and on the oyster necklaces (N).