

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

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Abstract

Global declines in oyster reefs have resulted in reduced habitat heterogeneity, extent and quality for some coastal finfish, potentially reducing fish populations and catches. It is well established that habitat restoration results in higher finfish biomass and diversity where oyster reefs replace bare substrata. Therefore, restoring oyster reefs with a view to also improving fish stocks is often a key goal of oyster restoration. However, the principles of habitat quality, ecological connectivity and broader ecosystem management are poorly integrated within oyster reef restoration ecology, but such principles may be instructive in enhancing the benefits of projects on fish populations throughout estuarine seascapes. This manuscript presents a framework for projects seeking to restore both oyster reef habitat and finfish communities. Structurally and biologically complex oyster reefs, comprising both oysters and other invertebrates, are required to provide shelter, food and nursery services to fish. By carefully considering site selection at seascape scales (km to 10s of km), restoration can enhance the network of habitat available to fish and potentially increase the overall carrying capacity of the estuary. Managers of estuaries that now include restored oyster reefs should implement fisheries management plans and consider the effects of management actions broadly throughout catchments; failing to do so may jeopardize gains in fish yields. Management decisions must be adaptable, responding to key criteria in thorough monitoring programs. Integrating these ecological and coastal management concepts into oyster reef restoration will enhance outcomes for fishes and increase stakeholder engagement and cost-effectiveness.

KEYWORDS

coastal management, habitat complexity, restoration, seascape, shellfish

1 | INTRODUCTION

Globally, 85% of oyster reefs have been lost, mainly due to over-harvesting, 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, Giotta, Luckenbach, & Breitbart, 1999; Peterson, Grabowski, & Powers, 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 & Luckenbach, 2000; zu Ermgassen, Grabowski, Gair, & Powers, 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, Boon, Brookes, & Sheaves, 2015; Humphries & La Peyre, 2015). Oyster reef restoration encompasses both categories of ecoengineering: Type A, the restoration of habitats thus allowing the desired species to colonize or expand; and Type B, which involves the direct increase in 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/m² of restored reef per year (Peterson et al., 2003). These effects of restoration on fish populations result from enhanced larval settlement and survival (Breitbart, Palmer, & Loher, 1995) and the immigration of adult fish to reefs, where they feed and take shelter (Gittman et al., 2016; Harwell, Posey, & Alphin, 2011). By enhancing fish biomass, restored oyster reefs can convey economic benefits of up to US\$4123 ha⁻¹ year⁻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., 2015), Europe (Farinas-Franco & Roberts, 2014) and Asia (Quan, Zhu, Ni, Shi, & Chen, 2009). While 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 stabilize 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 maximize stakeholder engagement, both locally and globally (La Peyre, Nix, Laborde, & Piazza, 2012).

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, Sheaves, Baker, & Connolly, 2015), and the degree to which these habitats are connected (Olds et al., 2016; Pittman, Kneib, & Simenstad, 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

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approach that accounts for how reefs interact with other structured habitats (Bostrom, Pittman, Simenstad, & Kneib, 2011). Advances in our understanding of how managing catchment water supply, sediment and nutrient run-off affects coastal ecosystems (Gorman, Russell, & Connell, 2009; Klein et al., 2012) and more effective fisheries restrictions (Gilby, Olds, Yabsley et al., 2017) can also improve the ecological condition of coastal habitats and modify the composition of fish assemblages. An increasing literature on ecohydrology with ecoengineering principles is 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 study, we analyse 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: (a) view oyster reefs as fish habitats; (b) recognize that oyster reefs are part of a wider seascape that includes other fish habitats; (c) consider the impact of other management interventions (e.g., fishing restrictions and catchment run-off reductions); and (d) 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 minimize their economic costs and maximize their ecological benefits for *both* oyster reefs and finfish fisheries.

2 | 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 areas where they are to be restored might be because the area 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, for example, 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., overharvesting and 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, Hughes, Kimbro, & Dolan, 2005). Thus, there are three important considerations (Figure 2) for oyster reef restoration projects that seek to enhance fish and fisheries:

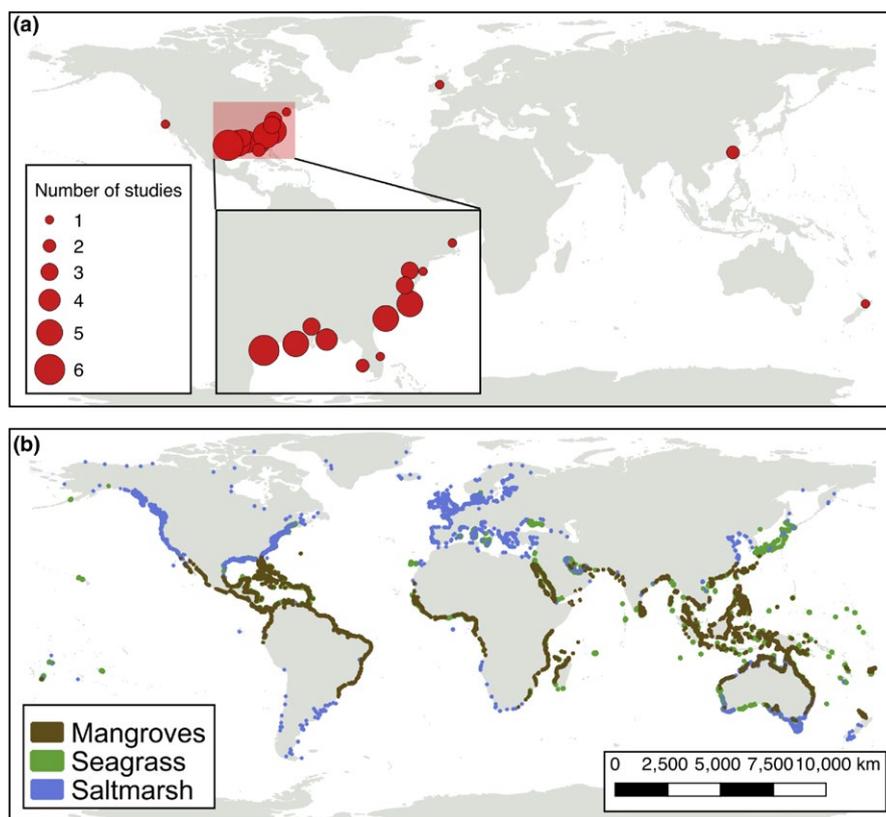
1. Evidence for the historical occurrence of oyster reefs in the target region;
2. Causes of oyster reef decline must be reversed, and modern-day conditions are suitable for oyster growth; and
3. New nonreef habitats support fewer fish than oyster reefs.

3 | KEY CONCEPTS TO IMPROVE RESTORATION OUTCOMES FOR FISH AND FISHERIES

3.1 | 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 colonize these reefs.

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)



3.1.1 | 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 & 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 emphasizing the need for a good understanding of ecophysiology principles (Wolanski & 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, that is, 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 & Quintino, 2007), but are nevertheless also susceptible to extreme water temperatures (Marshall & Elliott, 1998), salinity levels (Bachman & Rand, 2008; Marshall & Elliott, 1998)

and low dissolved oxygen concentrations (Stevens, Blewett, & Casey, 2006) that are beyond their physiological limits. To minimize 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, Micheli, Shelton, & Peterson, 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 (Kimbrow, Byers, Grabowski, Hughes, & Piehler, 2014; Lenihan, 1999; Tamburri, Luckenbach, Breitburg, & Bonniwell, 2008). High turbidity levels can also be harmful to some estuarine fish species (Benfield & Minello, 1996), particularly visually orienting predators (Lunt & Smee, 2015). While 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, Humphries, Casas, & La Peyre, 2014; Newell & 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 colonized by fish. Many estuaries, especially macrotidal ones, have strong erosion-deposition cycles which need incorporating into the assessment of risk to the beds.



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)

3.1.2 | 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, Furlong, Brown, Piazza, & Brown, 2014), (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 and mussels) that grow on oyster reefs or use reefs as habitats (Johnson & Smee, 2014; Lehnert & 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 individual bivalve size can make the organisms protrude above the bed boundary layer and 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 & 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 & Allen, 2002). While these intertidal reefs, like many other intertidal habitats (e.g., mangroves and intertidal flats), might provide rich feeding opportunities during high tide, the structure of the fish assemblage that utilizes them often depends on the composition of the surrounding seascape that fish use during low tide (Olds, Connolly, Pitt, & Maxwell, 2012a; Pittman, McAlpine, & Pittman, 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 postlarvae (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 than those that are submerged permanently (e.g., Baker, Sheaves, & Johnston, 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, Connolly, Pitt, & Maxwell, 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 historical extents of oysters in the target estuary. The size of a restoration site has two complementary facets: (a) the area of seabed covered by living and nonliving

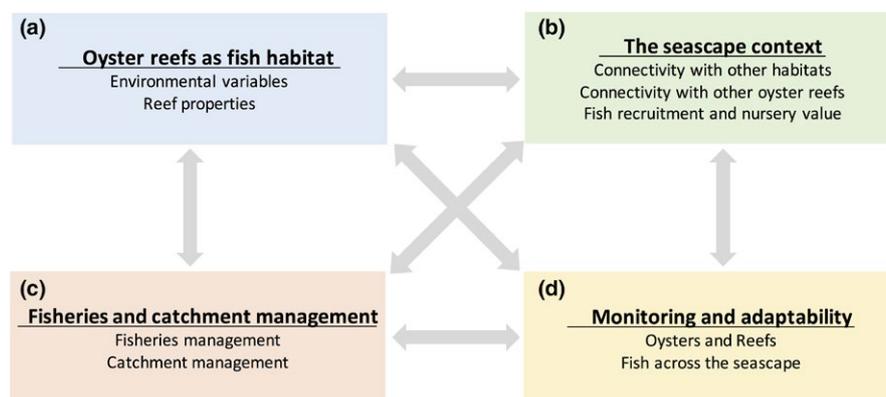


FIGURE 3 Key concepts to improve restoration outcomes for fish and fisheries. (a) Oyster reefs must be healthy and complex biogenic habitats that are positioned within the physicochemical niche of both oysters and fish. (b) Oyster reef restoration projects should be positioned to improve connectivity (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 and 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

oyster shells and (b) the total aerial dimensions of the project footprint, including any nonreef 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) emphasized that fish diversity increased with habitat heterogeneity, then size and then productivity. Habitats that are structurally complex (e.g., reefs, mangroves and seagrass) typically harbour higher fish biomass and diversity than habitats that are simpler (e.g., sand and mud flats; Grabowski et al., 2005; Gratwicke & Speight, 2005a; Sherman, Gillian, & Spieler, 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 & 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, Alvarez-Filip, & Mumby, 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 & Elliott, 2009), but require further investigation for oyster reefs (Table 1).

3.2 | Recognize 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 physicochemical 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 & Elliott, 2009). Following this, biology–biology relationships create the ecological functioning from the structure, and then the biota starts 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 colonization from elsewhere in the seascape; therefore, seascape positioning is a vital consideration when restoring oyster reefs for fish.

3.2.1 | 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, Pittman, Caldwell, Kendall, & Frazer, 2009; Olds et al., 2018; Potter, Tweedley, Elliott, & Whitfield, 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., 2018; 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

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	<p>1. <i>Food for fish</i>: 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)</p> <p>2. <i>Protection from predators</i>: What attributes of oyster reefs (i.e., area, height, architecture) provide fish with the best protection from predators? (e.g., Sherman et al., 2002)</p>
B. Oyster reefs as part of wider seascapes	<p>3. <i>Connectivity</i>: 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?</p> <p>4. <i>Fish movement</i>: 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)</p>
C. Fisheries and catchment management	<p>5. <i>People and oyster reefs</i>: What are the effects of fishers and fishing on the restoration of fish biomass? (e.g., Powers, Peterson, Grabowski, & Lenihan, 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, Hyder, & Skov, 2017)</p>
D. Monitoring and adaptability	<p>6. <i>Indicator species and processes</i>: 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)</p>

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., 2018).

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- vs. marsh-dominated seascapes), should therefore be a priority for research (research priorities 3 and 4, Table 1).

While it can be generalized broadly across coastal ecosystems, that higher connectivity with alternate habitats is positive for fish assemblages (Olds et al., 2018), 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, Powers, Heck, & Cebrian, 2009; Grabowski et al., 2005). On the contrary, 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. Thus, further studies which seek to determine the optimal distance for the isolation are an important requirement for optimizing future restoration projects (research priorities 3 and 4, Table 1).

The scale of patch connectivity effects between habitats is usually between 100 and 1,000 m in most coastal seascapes (Bostrom et al., 2011) and is dictated by the following: (a) fish mobility; (b) the type of migration being undertaken (e.g., feeding and reproductive); (c) the composition of seascapes; and (d) hydrology (Edwards, Elliott, Pressey, & Mumby, 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 and 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., 2018). 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., 2018; Nagelkerken et al., 2015; Table 1).

3.2.2 | 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 & Gardner, 1996; Soons, Messelink, Jongejans, & Heil, 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, Johnson, & Powers, 2009). While the “optimal” distance that maximizes 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, Powers, & Heck, 2008; Steppe, Fredriksson, Wallendorf, Nikolov, & Mayer, 2016), but also sufficiently far apart to provide additional reef nodes in the network of oyster reefs that are linked by fish movement (Gustafson & 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). Thus, several smaller restored reefs that are well connected to each other (within the 100 to 1,000 m range) across a seascape, therefore, are more likely to be 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 & Williams, 1998) and the probability of visitation by adults (Connolly & Hindell, 2006; Henderson et al., 2017). Fish employ tidal excursion currents to traverse large distances between inshore habitats (e.g., feeding areas and juvenile nursery habitats) and offshore habitats (e.g., spawning areas and 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 among restored and protected environments (D'Agostini, Gherardi, & Pezzi, 2015; Planes, Jones, & Thorrold, 2009).

3.2.3 | Enhancing fish recruitment and nursery value

Oyster reefs are important sites for fish spawning (Tolley & Volety, 2005), attract fish larvae (Breitburg et al., 1995) and function as nursery areas for many fish species (Coen, Luckenbach, & Breitburg, 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 interrelated factors: (a) the likelihood that fish larvae settle on reefs; (b) the abundance, growth and survival, of juveniles; and (c) the level of success that juvenile fish have in migrating from oyster reefs to their adult habitats (*sensu* Beck et al., 2001).

Fish larvae often enter estuaries through passages to the open sea (e.g., estuary mouths, coastal bays and 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, Molony, & Tobin, 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, Gray, Broadhurst, Spach, & Nagelkerken, 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 & Elliott, 2015).

The growth and survival of juvenile fish depend on the availability of quality food and protection from predation (Blaber, 2008). This in turn relies on the presence and creation or loss of habitats, which again are influenced by habitat change through restoration or anthropogenic pressures (Amorim, Ramos, Elliott, Franco, & Bordalo, 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 postsettlement 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, Caldow, Hile, & Monaco, 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).

3.3 | Consider the impact of fisheries and catchment management

Anthropogenic stressors such as run-off from altered catchments (Gilby, Maxwell, Tibbetts, & Stevens, 2015; Lerberg, Holland, & Sanger, 2000) and overharvesting both in the catchment and at sea (Pauly, Watson, & Alder, 2005; Pauly et al., 2003) 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, run-off 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.

3.3.1 | 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 reserve (Edgar et al., 2014) or by implementing size and bag limits (Bartholomew & 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, Gaines, & Warner, 2004; Lédée, Sutton, Tobin, & De Freitas, 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, Pine, Allen, & Ahrens, 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 & Stevens, 2014), and in some cases, enhance surrounding fisheries (Halpern, Lester, & Kellner, 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). Thus, 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 seascares (Bostrom et al., 2011; Micheli & 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). On the

contrary, reefs open to unsustainable oyster harvesting will likely be quickly degraded (Kirby, 2004; Rothschild, Ault, Gouletquer, & Heral, 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, Pollack, & Stunz, 2014; Table 1).

3.3.2 | Catchment management

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

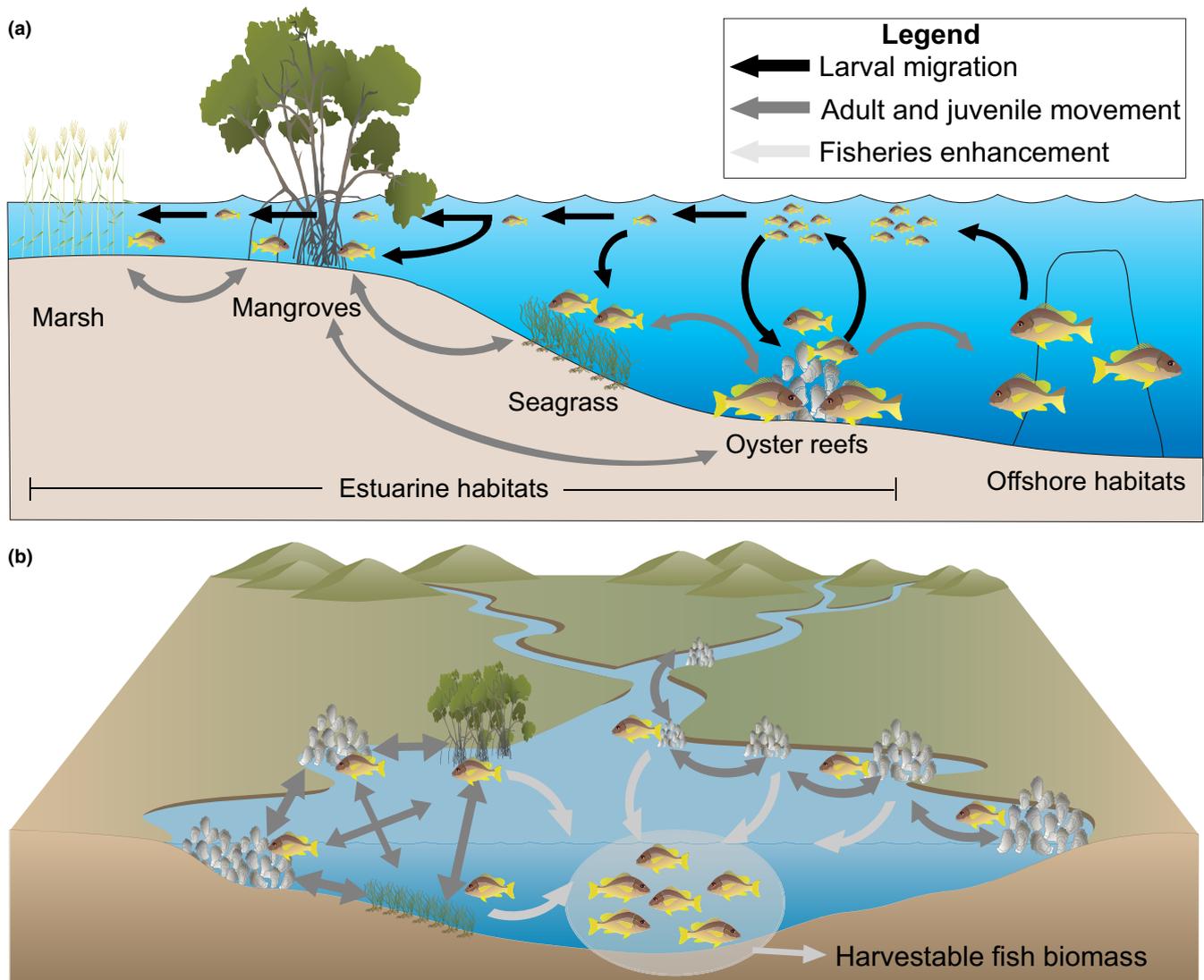


FIGURE 4 Oyster reefs are one type of fish habitat in coastal seascares and are functionally linked to other habitats by fish movement. (a) Most fish move among multiple habitats during their lives (dark grey arrows). These movements link adult and juvenile habitats, feeding and spawning habitats, and ecosystems that are used as stepping stones during migrations and are enhanced when habitats are closer together (i.e., higher connectivity). Many species spawn over offshore coral or rocky reefs, and their larvae are washed into estuarine nursery habitats (black arrows). (b) Fish use oyster reefs and other complex habitats, in coastal seascares as stepping stones during migrations among estuarine habitats, or from estuarine to offshore habitats (dark grey arrows). By restoring oyster reefs at key locations in estuaries, we might enhance the numbers, and quality, of stepping stone habitats and therefore improve the habitat values, productivity and carrying capacity of coastal seascares for fish and fisheries (light grey arrows and ellipse). Symbols courtesy of the Integration and Application Network, ian.umces.edu/symbols/

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
<i>Prerequisites</i>	
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?
<i>A- Oyster reefs as fish habitats</i>	
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?
<i>B- The seascape context</i>	
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?
<i>C- Fisheries and catchment management</i>	
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?
<i>D- Monitoring and adaptability</i>	
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?

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 & 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 and 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 maximized only when management minimizes 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 & Schaafsma, 2015). These include: (a) improving water quality by reducing excess nitrogen (Piehler & Smyth, 2011; Smyth, Piehler, & Grabowski, 2015) and filtering particulates, which increases the level of sunlight reaching the seabed (Wall, Peterson, & Gobler, 2008); (b) the fertilization of benthic habitats from pseudofaeces (Peterson & 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 & Schaafsma, 2015).

3.4 | 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 & Pressey, 2000; Wiens & 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 revision 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 & 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, Jonson, & Dixon, 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 reference sites or remnant habitats of the type which the restoration effort is aspiring to recreate (Grayson, Chapman, & Underwood, 1999; McDonald et al., 2016). The physicochemical 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, Rochet, Jennings, Field, & Gislason, 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, Cornwell, Owens, & Paynter, 2013), are intimately linked with the abundance of fishes in coastal ecosystems and so are increasingly used as measures of ecosystem health (Havstad & Herrick, 2003). The use of indicators of ecosystem condition and functioning (e.g., indicator species and umbrella species) is increasing for estuaries

globally (e.g. Gilby, Olds, Connolly et al., 2017; Montagna, Estevez, Palmer, & Flannery, 2008; Valesini, Cottingham, Hallett, & Clarke, 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). Otherwise, 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. Likewise, 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.

4 | 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 stabilization 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 maximize 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 and eutrophication), and monitored over time to maximize the accumulation of fish biomass and the benefits of restoration for fisheries (Margules & Pressey, 2000; Wiens & Hobbs, 2015). Oyster reef restoration projects that account for the reef designs or placements that might serve to maximize the utility of

seascapes for fish will lead to greater fish diversity, abundance and harvestable fish biomass throughout coastal ecosystems. As shown in this manuscript, 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 optimizing 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 maximize their accessibility (Kingsley-Smith, Stone, Keppler, & Leffler, 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 stabilization 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 optimize the habitat values, seascape context and ongoing monitoring and management of restored reefs.

The restoration of habitats and biodiversity is valued by society and can convey significant psychological benefits to users (Fuller, Irvine, Devine-Wright, Warren, & Gaston, 2007; Rey Benayas, Newton, Diaz, & Bullock, 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 and 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 & 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 optimize 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 emphasize that the effectiveness of oyster reef restoration projects for fish and fisheries can be improved by optimizing the habitat values and seascape context of individual reefs, by managing other impacting processes and through adaptive monitoring with appropriate indicators of restoration performance.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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