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Marine ecosystem restoration (MER) – challenges and new horizons

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Marine ecosystem restoration (MER) – challenges and new horizons

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Editorial: Marine ecosystem restoration (MER) – a call for a more inclusive paradigm

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Editorial on the Research Topic
Marine ecosystem restoration (MER) – challenges and new horizons

Widespread loss of coastal ecosystems and the important services they provide severely threatens both biodiversity and human health across the globe (Bayraktarov et al., 2015; He and Silliman, 2019; Saunders et al., 2020). To help combat this threat, the United Nations has declared 2021-2030 the Decade on Ecosystem Restoration. Demand for marine ecosystem restoration in many countries has subsequently increased at exponential rates (United Nations et al., 2020). For this demand to be met and for restoration to increase in efficiency and outcome success, the paradigm of marine restoration science, engineering, and application needs to expand to be more intellectually and socially inclusive of disciplines, sectors and stakeholders. Here, we highlight 10 key concepts that are essential for achieving such inclusivity. Widespread adoption of these concepts will advance the pace and scale of ecosystem restoration, as well as ensure higher and more equitable provisioning of user-inspired, social-ecological outcomes. For example, the restoration paradigm, with its solution-oriented focus, must rapidly factor in emerging technologies, advances in ecological and social science theory and application, diverse cultural and socioeconomic perspectives, broad stakeholder engagement, and advancements from established cultivation sciences and the private sector. Taken together, these concepts, highlight the urgent need to greatly broaden the marine restoration conceptual framework if we are to elevate and globally scale marine ecosystem restoration into an intervention that achieves real-world benefits in our lifetime.

The need to conserve marine ecosystems, biodiversity and habitat-forming species has become a broadly acknowledged societal goal, reflected in international frameworks and national and local policies (Bridgewater et al., 2019; Duarte et al., 2020; Ruckelshaus et al., 2020; Grorud-Colvert et al., 2021; United Nations et al., 2022). Beyond ethical or spiritual motivations, the focus on the tangible benefits marine biodiversity and habitats provide to humans in the form of ecosystem services (e.g., food provisioning and coastal protection) has emerged over the past 20 years as the other, key motivating factor for elevating marine conservation efforts (Saunders et al., 2020; Lester et al.; Bayraktarov et al., 2015; McAfee et al., 2021; Wittmer et al., 2021). Despite increased investments over the past few decades in traditional marine conservation interventions, such as protected areas, marine spatial planning, marine ecosystem management, pollution reduction from point and non-point sources, and fisheries management, the rate of marine ecosystem loss and marine biodiversity declines has continued globally (Saunders et al., 2020). While these traditional, conservation-focused interventions may be slowing the decline, they clearly are not enough. In many places, there remains an urgent need for bigger, more stable, and more productive marine ecosystems than presently exist that can generate multiple ecosystem services (Obura et al., 2023). There is also a need to deepen the inclusion of the communities that may benefit from such conservation and restoration efforts in the design, implementation and management of such interventions to enhance their value and long-term sustainability.

Inspired by the need to do more, and by The United Nations' declaration that 2021-2030 is the Decade on Ecosystem Restoration, national governments, the private sector and conservation agencies around the world have markedly increased their investment in marine ecosystem restoration over the past 5-10 years (Saunders et al., 2020). Their shared goal is to elevate marine ecosystem restoration so that it is a viable conservation intervention at large spatial scales relevant to achieving significant social, economic and ecological benefits. Increased investment alone, however, will not produce these results, as marine ecosystem restoration has traditionally been considered a less desirable intervention by practitioners because of its relatively high failure rates (62% seagrass, 35% coral, 35% salt marsh failures) and high costs (US $1,600,000 per restored hectare) (Bayraktarov et al., 2015). Instead, fundamental changes in how marine restoration is undertaken are required to achieve the gains that global communities now seek.

Despite the perception that marine ecosystem restoration is prone to failure, recent syntheses have revealed bright spots in marine habitat restoration and shown that restoration projects in marine systems can indeed be: 1) cost effective, 2) successful over large spatial and temporal scales, and 3) provide social and economic benefits to people (Bayraktarov et al., 2015; Saunders et al., 2020). This is especially true in coastal areas where the stressors that historically killed marine foundation species (e.g., pollution or overfishing) have been reduced and regrowth of habitat-forming species is limited by recruitment and presence of positive species interactions (e.g., Silliman et al., 2015; Temmink et al., 2021). Key to expanding these bright spots so that they become the rule rather than the exception is increasing successes in both organismal regrowth and ecosystem service outcomes in marine restoration efforts.

This Research Topic on Marine Ecosystem Restoration (MER) highlights key innovations and challenges that, if revised and overcome, cans greatly increase restoration success, its scale of application, and value to communities. To do so, however, the paradigm for marine ecosystem restoration must greatly expand and be more inclusive of disciplines, sectors and stakeholders not traditionally engaged in restoration planning, design, application and assessment. As a starting point, we highlight and discuss a non-exhaustive list of ten key concepts that should be incorporated into this emerging, new paradigm. The original papers in this Research Topic develop these concepts in more depth and raise many more important factors and issues that should be considered in the quickly evolving MER practice and paradigm. Adopting this expanded paradigm may require profound changes, including ethical and philosophical considerations that address the relationship and responsibility of humans to nature in the sea.

Concept 1. A comprehensive MER approach is a key condition for restoration success

Historically, comprehensive planning and evaluation have been missing from most restoration efforts in marine systems (Lester et al.) and, as a result, managers are less likely to adapt, expand and/or pivot their approaches (Domínguez-Tejo et al., 2016). Therefore, a comprehensive MER approach (Concept #1, or C1), which encompasses a sequence of three distinct phases, should be determined as a precondition of any MER project. The three phases are: 1) pre-launch assessment and planning, 2) restoration interventions, and 3) post-restoration monitoring and long-term adaptive management (Figure 1). The three phases are essential for a sound MER implementation and are designed to maximize the chance for success of any MER project.

The pre-launch assessment and planning phase includes site selection based on ecological and social factors (Abelson et al., 2016), as well as an assessment of the extent of the ecosystem degradation and the underlying conditions at restoration locations (Abelson et al., 2016; Gann et al., 2019). This phase should also include site specific spatial planning and in-depth understanding of specific goals in terms of habitat regrowth and increased provisioning of ecosystem services (Lester et al.). Information gained during this phase will be used to develop a site-specific MER plan that outlines the objectives (and identifies targets and baselines), and the feasible interventions required to restore the ecosystem to its pre-degradation healthy state. If a site is unable to be restored to its pre-degradation state or that goal is beyond reach due to local conditions or budget limits, then the ecosystem can be restored to achieve or provide better

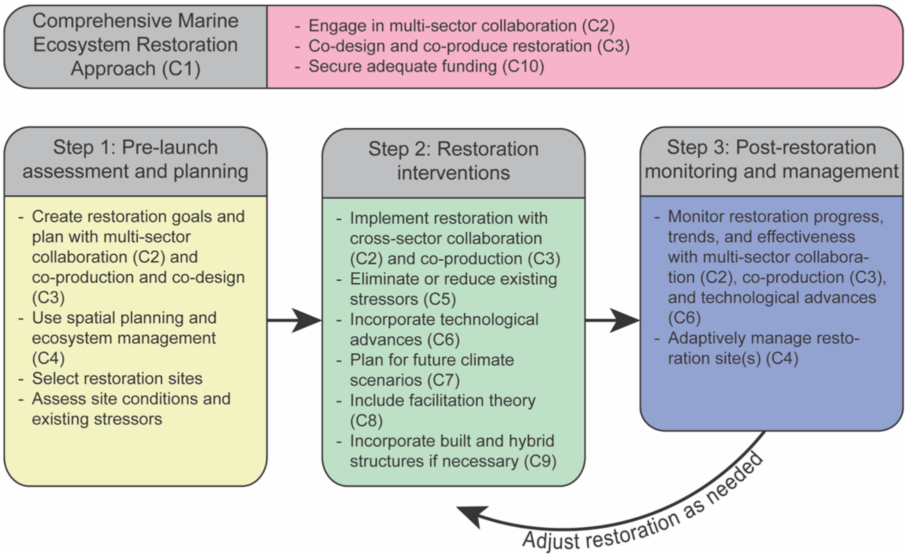

FIGURE 1
Comprehensive framework for marine ecosystem restoration. Framework incorporates key concepts. Each concept is labeled as "C" and the concept number. For example, Concept #2, which is multi-sector collaboration, is referred to as C2.

ecosystem services, although this may come with tradeoffs. The assessment should use various tools, such as ecological surveys, mapping, and modeling, and engage with local communities and stakeholders in multiple meetings to understand and incorporate their perspectives and concerns.

The restoration interventions phase is based on the planning outcomes of the first phase and may include one or more actions out of a wide range of active management tools of different levels of intervention (Abelson et al., 2016) along the "restorative continuum" (Gann et al., 2019). These include protection and elimination of exogenous stressors (e.g., land-based pollution sources like sewage outlets; Wear et al., 2021; Concept #5) and endogenous stressors (e.g., eradication of invasive or outbreaking species *via* culling; Guarnieri et al.), and habitat enhancement (e.g., artificial reefs; Paxton et al.; Concept #5), to diverse restocking tools of ecosystem engineers (Doropoulos et al.; Schmidt-Roach et al. et al.; Zhang et al.) and facilitating species (Hammann et al.; Zhang et al.; Concept #8).

The monitoring and long-term maintenance stage involves assessing the progress of the restoration interventions and evaluating the effectiveness of the restoration plan to ensure the sustainability of the restored ecosystem, and implementation of adjustments as needed. At present, monitoring is not typically funded sufficiently to cover the full life span of restoration projects (Bayraktarov et al., 2015; Saunders et al., 2020; Saunders et al., 2022). The long-term segment of phase 3 may be considered a management stage, which may include replenishment, trending, and maintenance that will accompany the restored ecosystem with no deadlines.

We believe that rigorous adoption of the MER comprehensive approach, beyond maximizing the chances of successful restoration outcomes, will prove to be cost-effective in the long-run by reversing degradation, reducing the need for ongoing restoration interventions and improving ecosystem services for local communities as well as national and global conservation entities.

Concept 2. Expanding multi-sector collaboration is essential for scaling-up restoration

For decades, MER has been carried out by a passionate consortium of organizations that vary in the degree to which they coordinate to meet society's demand for more expansive, productive, and resilient ecosystems. As highlighted in this Research Topic, both improving such coordination and activating the participation of sectors not yet engaged in restoration are vital to achieving major gains in rebuilding and creating marine habitats in the coming decade at large spatial extents (Eger et al.; Schmidt-Roach et al.). In short, large, well-coordinated teams that bring diverse expertise, resources, relationships, and values to bear are essential to pulling off large-scale, high impact restoration projects (Figure 2-C2).

For example, in Florida, USA, where coastal habitat mosaics of seagrasses, oyster reefs, coral reefs, dune systems, and vegetated intertidal wetlands are in decline to varying degrees statewide, projects to restore these systems to date have been championed by state agencies, non-governmental organizations (NGOs), city and county governments, engineering firms, and, to a lesser degree, academic institutions (e.g., Bersoza Hernández et al., 2018). Each entity has a unique mission, distinct jurisdictional boundaries and constrained financial capacity. For instance, city governments often oversee coastal wetland and dune restoration projects as a strategy to stabilize shorelines eroding adjacent to critical municipal infrastructure. In contrast, Florida Fish and Wildlife Conservation Commission, a state agency, and Ducks Unlimited, an NGO focused on conserving and restoring wetlands and associated habitats for waterfowl. These disparate approaches yield local, and often isolated, gains in restoring habitats, while comprehensive, region-wide gains in coastal habitat spatial extent, functionality, and service provisioning are not being achieved.

FIGURE 2
Key concepts to build a more inclusive paradigm for marine ecosystem restoration include: C2) Multi-sector collaboration, C3) Co-production, C4) Spatial planning, C5) Stressor reduction, C6) Technological advances, C7) Climate scenarios, C8) Facilitation theory, C9) Built ecosystems, and C10) Adequate funding. C2) Multi-sector collaboration, such as with artificial reef installation in the Philippines, can lead to successful restoration outcomes Photo credit: Avidgor Abelson. C3) Ellison et al. restored mangroves using co-production that incorporated values of multiple stakeholders and agents. Photo credit: Aaron M. Ellison, CC-BY-NC. C4) Spatial planning can be used to help design successful restorations. Image (s) used under license from Shutterstock.com. Rendering by Dan McDonald. C5) Removing stressors, such as seaweed from reefs, can achieve positive restoration outcomes. Photo credit: Avigdor Abelson. C6) Ridge and Johnston used aerial imaging technologies to monitor restoration outcomes. Photo credit: Duke University Marine Robotics and Remote Sensing Lab. C7) Incorporating climate scenarios, such as those related to coral reefs, can help generate restorations that may persist over longer timescales. Photo credit: Avigdor Abelson. C8)Incorporation of facilitation theory into salt marsh restoration (with mussels) can have positive outcomes. Photo credit: Chistine Angelini. C9) Paxton et al. found that built structures can be successful restoration tools. Photo credit: J. McCord/ECU-CSI. C10) Restoration efforts, such as oyster reef installation, require adequate funding not only for restoration implementation but also for planning, assessment, and adaptive management. Photo credit: Megan Saunders.

To meaningfully move the needle, entities currently engaged in restoration must coordinate their activities and investments so they systematically build off of one another. For instance, collaboration by restoration practitioners with decision makers and legislators is needed to create effective legislation and permitting that will aid in scaling up restoration (Saunders et al., 2022). Simultaneously, new entities need to be brought to the table, particularly those able to plan larger regional projects (e.g., urban and regional planners), curate long-term funding portfolios (e.g., the financial sector), manage the logistics (e.g., project management specialists), construct at scale (e.g., civil and industrial engineering industries), and assess the functionality of such projects (e.g., sensor technology companies).

Concept 3. Co-production is key for more equitable and relevant outcomes

There has historically been a divide between the generators of restoration knowledge (i.e., researchers) and the users of the knowledge (i.e., practitioners, policy-makers), with little discussion regarding how the transfer of information between these entities should actually take place. This has resulted in a theory-practice gap (alternatively referred to as a research-implementation gap or knowledge-action gap, among others; Cooke et al., 2021). As highlighted in Concept #2, the coordination and engagement of diverse entities will be imperative for scaling up MER practice, but in particular, it will be important to improve communication and break down barriers between groups that are traditionally thought of as knowledge producers versus knowledge users (Saunders et al., 2022; Figure 2-C3). Co-production rejects the idea that scientists alone should be the ones to identify and solve complex problems, but instead that this should be a collaborative process carried out by academics and non-academics alike (Norström et al., 2020). Co-production is context dependent, problem-oriented, and leverages the knowledge and priorities of diverse stakeholders. (e.g., local communities, non-governmental organizations, tribes, etc.).

While co-production has been used in agricultural research for decades (Rocheleau, 1991; Brown, 1996), its application has been relatively limited in ecosystem restoration projects, despite the fact that it can likely enhance implementation and project outcomes and help to focus MER on locally relevant priorities or desired species. For example, Aquatic Habitat Toronto (AHT) is a unique partnership among multiple diverse agencies that are conducting restoration work along the Toronto waterfront in Canada. It includes multiple diverse stakeholders, multiple jurisdictional boundaries, and three levels of government. AHT supports the planning and implementation of various restoration projects conducted for a variety of different reasons and they facilitate knowledge sharing through co-production. The co-production process used by AHT enables early communication among partners about impending projects, broad knowledge sharing, the incorporation of local knowledge, and ultimately more successful restoration projects that incorporate novel techniques and advances (Piczak et al., 2022). However, co-production is not without its potential challenges. If there are practical constraints to the restoration design, they might conflict with stakeholder goals, and unequal power dynamics can compromise the design and implementation process, ultimately resulting in outputs that do not sufficiently meet stakeholder goals (Hastings et al., 2020). Moreover, co-production often requires large time commitments and financial resources and, therefore, securing long-term and stable funding will be critical for ensuring that co-production approaches are feasible and successful (Piczak et al., 2022; see Concept #10).

Concept 4. Spatial planning and ecosystem management must inform restoration design

Scaling up MER must be done using principles from spatial planning (Figure 2-C4). At present, most restoration projects are uncoordinated and site selection is somewhat opportunistic; that is, a location is identified as biophysically suitable and then an opportunity presents itself from a social-governance perspective (e.g., there is political will, a willing landholder, or potentially a loop-hole in permitting which enables a project to proceed; Saunders et al., 2022). Scaling up restoration to larger spatial extents aimed at achieving widespread social, economic, and environmental outcomes will require more systematic approaches to site selection and stronger coordination among projects (Lester et al.; Gleason et al., 2021). Such approaches have been developed over decades for spatial conservation planning and ecosystem management. For example, the design and re-design of Australia's Commonwealth Marine Parks was done using science-based spatial planning approaches (Day et al., 2019).

Spatial planning involves clearly articulating stated goals and objectives, identifying actions that could be used to address those goals, and then estimating the benefits relative to the objective(s) which could be accrued for a given budget accounting for the likelihood that the project will succeed (Pressey et al., 2007; Gregory et al., 2012; Gleason et al., 2021). Spatial planning is informed by principles from the field of decision science and often includes cost-effectiveness or cost-benefit analyses. This approach is useful as it can help maximize benefits while minimizing costs and can help ensure that portfolios of benefits are accrued instead of all projects being conducted for the same outcome. Decision science can also help with identifying potential trade-offs, such as those between carbon sequestration vs. fisheries outcomes. In Lester et al., the authors review recent scientific peer-reviewed literature for several marine ecosystems to identify how site selection or spatial planning principles have been applied to MER over different spatial scales. Moving forward, there is an opportunity to advance the use and application of spatial planning principles to lead to better recovery of ecosystem function, benefit human communities, result in more efficient use of limited resources, and provide a platform for improved outreach and education.

Concept 5. The stressors that killed ecosystems must be reduced before restoring

Marine and coastal areas around the world are in decline because they are facing a consortium of stressors that are killing off foundational plants, animals, and algae as well as destabilizing food webs (Thomson et al., 2015; Borst et al., 2018). These stressors range from climate-related factors, such as higher water temperatures (Rosenberg and Ben-Haim, 2002; Collier and Waycott, 2014; Shields et al., 2019), more extreme drought (Silliman et al., 2005), more intensive storms (Greening et al., 2006), as well as human activity-related stressors, such as eutrophication (Smith, 2003; Burkholder et al., 2007), sewage pollution (Wear et al., 2021) overfishing (Eriksson et al., 2011), development (Bulleri and Chapman, 2010), boat wakes (Safak et al., 2021), industrial and emerging contaminants (Khan et al., 2022), and intensive recreational use (Hardiman and Burgin, 2010). Without exception, all of our coastal ecosystems are, to some extent, exposed to a suite of these climate- and human-related stressors (He and Silliman, 2019).

In order for coastal habitat restoration to be feasible, the portfolio of stressors must be constrained enough that the species we are seeking to restore can in fact survive, grow, and ideally reproduce (Figure 2-C5). Recent studies suggest that, if local, human-related stressors can be reduced through effective regulation, management, or infrastructure interventions, there is greater potential for habitats undergoing restoration to undergo succession, thereby regaining cover of foundation species and the food webs that depend on and facilitate them (Abelson et al., 2016; He and Silliman, 2019). For example, in coral reefs, experiments simulating the recovery of predatory fish and commensurate reduction in meso-predator snails can facilitate growth of resilience in corals (Shaver et al., 2018). In other regions, there is a huge need to reduce nutrient pollution and excessive sediment delivery to the coast before efforts to restore seagrasses are feasible. For example, Tampa Bay, Florida experienced a tremendous recovery of seagrasses after investments were made to reduce nutrient pollution to the bay, which resulted in increased water clarity and reduced incidence of hypoxia events, enabling seagrasses and their associated food webs to recover (Greening et al., 2011; Tomasko et al., 2018). In other instances, ecosystems can switch into alternative stable states because of the above-mentioned stressors or because of the loss of top-predators. For example, in the Mediterranean Sea, the expansion of urchin populations has changed the macroalgal dominated, rocky subtidal to a "barren" state and the restoration intervention of culling urchins has demonstrated promising results that can facilitate recovery and restoration success (Guarnieri et al.).

Thus, we call for a holistic, more inclusive perspective to MER that simultaneously considers restoration of target species and the systematic reduction of external stressors. However, we caution practitioners on waiting for the "ideal" conditions due to the rapid need for restoration and rather suggest joint efforts to improve conditions while restoring ecosystems. In some cases, environmental conditions, while in need of improvement, are not the limiting factors to successful restoration (see Orth et al., 2012 and Hughes et al., 2013) but rather an ecosystem wide approach that considers stock needs, trophic interactions, and environmental conditions can achieve cascading impacts that exceed handling singular issues at a time. Moving forward, decision science approaches and models (see Concept #4) can be used to assess where active marine restoration, protection, or mitigation of other stressors can best achieve coastal management objectives (Possingham et al., 2015; Saunders et al., 2017)

Concept 6. Technological advances must be rapid for MER to be a viable intervention

Rapid degradation of ecosystems shaped by habitat-forming species such as coral and bivalve reefs, vegetated coastal systems, and the increasing ambitions to halt and reverse these losses call for a rapid development and inclusion of technological advancements into restoration actions (Figure 2-C6). At present, restoration is failure-prone and expensive because the stability of ecosystems often hinges on self-facilitation generated by 'emergent traits' from habitat modifiers (Temmink et al., 2020). These are traits that are not expressed by an individual, but emerge at the aggregation level, causing self-facilitation (see Concept #9) to only work beyond certain minimum density thresholds. These emergent traits can be generated more rapidly when positive species interactions are incorporated (Shaver and Silliman, 2017; Reeves et al., 2020; Renzi et al., 2019; Valdez et al.; Zhang et al.). Technological advances using biodegradable structures that mimic valuable emergent traits can amplify restoration success while limiting the need for large amounts of donor material (Temmink et al., 2020; Temmink et al., 2021). For example, the artificial reef structures and built infrastructure in living shorelines can mimic and provide hard substrates needed for the restoration of mussel or oyster reefs (Dafforn et al., 2015; Mayer-Pinto et al., 2017; Temmink et al., 2021; Concept #9) or the facilitation of marsh or seagrasses (Temmink et al., 2020; Marin-Diaz et al., 2021). Additional examples of technologies that improve restoration techniques by ameliorating environmental stressors include the developments of bio-cements seeded with reef forming bivalves such as oysters or biodegradable matrices used to stabilize sediments for plant restoration (Marin-Diaz et al., 2021; Uddin et al., 2021). Moreover, recent work in coral reefs demonstrated how industry-scale restoration based on machinery and techniques derived from oil spill remediation, dredging operations, and aquaculture can yield effective harvesting, culturing, and outplacement of coral recruits (Doropoulos et al.). Another advancement in technology comes from the development and utilization of uncrewed systems. Uncrewed systems have the ability to assist in nearly every phase of a restoration project including site selection and planning, implementation, and monitoring (Ridge and Johnston). Combined, these recent advances highlight how inclusion of novel technologies allow for cross-scale improvements, from simple small-scale design changes to large-scale industry-derived approaches, paving the way towards effective low-cost restoration of marine ecosystems.

Concept 7. Future climate scenarios should permeate and inform restoration planning

It is beyond doubt that marine biodiversity will change in the future due to climate change. Impacts of climate change on marine ecosystems and the diversity they facilitate will occur in multifaceted ways, such as changes in CO2 concentrations, temperature, mixing regimes, and biogeochemical cycles of elements and organic compounds (Hillebrand et al., 2018). In addition, climate change driven modifications of marine organism performance, population size, and species inventory add up to the overall changes in marine biodiversity observed at the community and ecosystem level. For instance, temperature induced losses of a few marine species may cause a cascade of secondary extinctions up to a network collapse to half the initial network size (Jacob et al., 2011). Thus, to understand these causal relationships and their implications for ecosystem functioning, goods, and services, the response of the entire ecological network has to be analyzed (Woodward et al., 2010).

Projections of future climate change play a fundamental role in improving understanding of the climate system as well as characterizing societal risks and response options (Tebaldi et al., 2021). Indeed, modeling can help us to understand the biodiversity consequences of temperature change since range shifts alter regional marine diversity under altered temperature regimes. For example, we are currently observing a massive underwater "refugee crisis", as species are shifting habitats due to ocean warming (i.e., poleward range shifts; Fogarty et al., 2017). Thus, the early detection of climate-driven range-extending species is important for marine restoration schemes, given the potential for alteration of ecosystem structure and functioning, as well as economic impacts and opportunities (Robinson et al., 2015). Modeling approaches to detect impending range shifts can thus forewarn potential ecosystem changes, identify relevant conservation or restoration strategies, and adapt natural resource management to moderate or take advantage of these effects (Dawson et al., 2011). For instance, it could be shown that increased diversity enhanced ecosystem functions and had a positive impact on ecosystem recovery after climatic extremes (Worm et al., 2006).

All restoration planning must consider future climate conditions at a respective site in order to ensure that the central motivations for MER can actually be met and maintained over thelong-term (Figure 2-C7; Coleman et al). Based on the availability and reliability of future climate data, the MER plan (i.e., promoted adaptation) can be decided (Abelson et al., 2016) either *via* the "Predict-and-Prescribe" approaches (e.g., assisted evolution and designer reefs; Webster and Reusch, 2017; Darling and Côté, 2018), which are based on predicting future conditions or the "Portfolio" approach, which considers the range of uncertainty of future conditions (Schindler et al., 2015; Webster and Reusch, 2017). It should be noted that whilst the two strategies are distinct, they may serve as complementary tools, to be applied simultaneously to increase the chances of recovery (Abelson et al., 2016).

Concept 8. Inclusion of facilitation theory increases foundation species regrowth

Positive species interactions, such as mutualism and facilitation, are powerful relationships that allow marine foundation species to increase their tolerances to physical stress, resist biological suppression, and recover faster after disturbance. For instance, salt marsh grasses are protected from grazers by predators (Silliman and Bertness, 2002), experience increased resistance to climate change from mussel mounds (Angelini et al., 2016), are protected from wave stress by oyster reefs, and can overcome severe oxygen limitation in saturated soils by benefiting from the infusion of oxygen into the soil around their roots by neighboring plants (Silliman et al., 2015) or burrowing crabs (Bertness, 1985). Every marine foundation species has a list of positive species interactions that underlies their large-scale success over seascapes. These key positive interactions are highlighted for kelp forests (Eger et al.), seagrasses (Valdez et al.), oyster reefs (Reeves et al.), salt marshes (Renzi et al., 2019) and mangroves (Renzi et al., 2019) in this Research Topic, and for coral reefs (Shaver and Silliman, 2017) in previous work.

Despite an understanding of the key role that facilitation plays in the regrowth and sustained success of marine foundation species, MER does not systematically incorporate these beneficial relationships when outplanting foundation species. Indeed, the current paradigm in restoration narrowly focuses on systematically reducing stressors like competition and physical stress before planting (Silliman et al., 2015; Zhang et al.). Experimental work presented in this Research Topic, and in other recent studies, highlights the massive benefit that incorporating positive species interactions into restoration designs can generate. For instance, adding clams to seagrass seed plantings increases their growth and expansion by over ~300% (Zhang et al.). Similarly, planting marsh plants, seagrasses, and mangroves in clumps instead of dispersed designs increases their wave stress and low oxygen tolerance (Silliman et al., 2015; Zhang et al.), and regrowth of seagrasses in the presence of sea otters switches from 100% failure to 100% success (Hughes et al., 2013). There is now overwhelming evidence of the generality of this positive effect across all marine foundation species. Marine ecosystem restoration must immediately expand its paradigm to include systematic inclusion of positive species interactions, or pay an unnecessary penalty of missing out on massive gains in restoration success and decreased costs (Figure 2-C8).

Concept 9. Built and hybrid structures are key tools in the restoration tool chest

Reefs are vital marine habitats as their spatially complex hard structures attenuate current and waves, serve as attachment substrate, and provide shelter, foraging, and nursing grounds for myriad species. These ecological functions are particularly important in otherwise structurally homogeneous soft-sediment systems, where both rocky, geogenic reefs and biogenic reefs, made up of reef-building corals, bivalves, or tubeworms act as biodiversity hotspots. Over recent centuries, reefs have experienced massive losses worldwide (Eddy et al., 2021). Natural reefs declined due to habitat destruction, limiting the influx of natural substrates such as wood *via* rivers due to damming, pollution, and global warming-related extreme events. At the same time, the abundance of artificial hard substrates from shipwrecks, the construction of offshore oil platforms, dikes, and dams greatly increased (e.g., Petersen and Malm, 2006; Ruiz et al., 2009; Bugnot et al., 2021). Moreover, this growth is expected to continue as coastal defense issues increase due to sea level rise, and offshore windfarm numbers rise to support the renewable energy transition (Bugnot et al., 2021).

When marine ecosystems, such as reefs, are degraded, built and hybrid structures may be necessary to restore such ecosystems (Figure 2-C9). Recent analyses revealed that artificial reefs are generally successful in emulating ecological functions of natural reefs (Paxton et al.). Artificial substrates in many cases serve as suitable settlement surfaces for sessile species in ways similar to natural ones (e.g., Temmink et al., 2021; Dodds et al., 2022). Moreover, when employed based on proper scientific assessments, artificial reefs can also closely mimic natural ones in terms of their fish communities (Paxton et al., 2022), although there is mixed evidence on ecosystem-level effects (Layman and Allgeier, 2020). Hence, artificial reef structures may become a key tool in the marine restoration tool chest to mitigate natural reef declines.

In addition to artificial reef structures, nature-based infrastructure such as living shorelines that incorporate restoration with built infrastructure can incur benefits and improved ecosystem services (Smith et al., 2021), although the terminology and designs can vary widely (Smith et al.). As artificial ecological enhancements may be undesirable in many natural areas and can introduce ecological risks (Heery et al., 2017), we suggest they may become useful and effective as: 1) ecological enhancements as part of coastal defense (Morris et al., 2018) and offshore wind projects (Degraer et al., 2020) where introduction of hard substrates will be unavoidable, and 2) re-introduction of hard substrate in habitat-limited areas (Paxton et al., 2022) or woody substrates to compensate for losses from riverine input (Wohl and Iskin, 2021).

Concept 10. The need for adequate funding to safeguard MER success

It is common knowledge among conservation scientists and practitioners that prevention (i.e., conservation) is substantially better than the cure (i.e., restoration; Layton et al.). The cost of restoration typically far exceeds the cost of implementing protected areas per unit area (Possingham et al., 2015). However, even Marine Protected Areas (MPAs), the main marine conservation tool, fall below the minimal needed area for successful restoration outcomes (O'Leary et al., 2016). Moreover, many MPAs fail to meet thresholds for effective management practices, where the most common shortfalls are in staff and financial resources (Edgar et al., 2014; Gill et al., 2017), and currently, 70 percent of MPAs are underfunded (IMPAC5, 2023). That said, once damage to ecosystems has occurred the implementation of protected areas may not be able to return to the site to a highly functioning state, for instance, where propagule supply is limited, or where physical conditions are no longer suitable. In these instances, active restoration may be the only (and therefore most cost-effective, even if costly on a per ha basis) means of meeting objectives to recover coverage and functioning of the target habitat (See Concept #4, Possingham et al., 2015; Saunders et al., 2017). Due to the relatively high costs there is a need for institutional and financial support in order to overcome environmental and ecological barriers to restore at scale (Eger et al.; Figure 2-C10).

As earlier noted (Concept #1), for restoration projects to be successful they should include three stages. This obligatory MER comprehensive approach may infer that in cases of insufficient budget the proposed MER projects should be discarded. That is, if a restoration project has been approved but with limited funding (i.e., significantly below the required budget), there is a dilemma with three alternative decision-making options for how to proceed. First, to decline the project, as it is predestined to failure. Second, to apply whatever tools, which are not optimal, but fit the budget limitations. The third option, which is the recommended for better chances of improvement, is to start the first MER phase (pre-launch assessment and planning) as well as some basic actions that can alleviate local anthropogenic impact (e.g., MPA designation, sustainable alternative livelihood of local stakeholders, etc.; Abelson et al., 2016). During these initial steps, a plan can be tailored following the below suggested carbon and biodiversity credits.

Beyond the traditional means of fundraising (e.g., grant proposals, donations, and governmental funds), there are two relatively new ways that are in their nascency, but may prove to be gamechanger tools to raise funding for MER projects. The first approach is to adopt the concept of carbon offsetting and the use of carbon credits.This area is already a rapidly expanding concept, which may be relevant for mangrove forests, seagrass meadows and tidal marshes, which are the most effective carbon sinks (Mcleod et al., 2011; Macreadie et al., 2022). Second, a similar and more recent approach with promising MER implications for all marine ecosystems, is biodiversity offsetting and credits. The concept of biodiversity offsetting (and the use of biodiversity credits) is controversial (Droste et al., 2022) and bears some challenges (e.g., difficulties ensuring the offset projects are equivalent to the biodiversity losses; false sense of security that encourages further development and overall loss of biodiversity). However, practically, it is very likely that biodiversity credits, like carbon credits, are to become tools for financing the protection and restoration of marine coastal ecosystems. Taken together and as highlighted in C2 focused on multi-sector collaboration, it is clear that the future capacity to scale MER approaches requires the inclusion of expertise in financial planning to design the framework for funding that can support large-scale and long-term ecosystem rejuvenation efforts.

Concluding remarks

Here, we describe ten key concepts (Figures 1, 2) that together form key pillars of an 'inclusive MER paradigm.' These concepts may be categorized into two levels of necessity for success and application generality. The first, obligatory general concepts, refer to basic concepts, the adoption of which is critical to the success of all MER projects (e.g., the MER comprehensive approach [see Concept #1-3]). Second, particular concepts, which refer to concepts that may be essential to the success of certain MER projects under specific ecological and social circumstances and ecosystem types (e.g., "Built structures are a key tool in the MER tool chest;" see Concept #9). We argue that adopting the relevant key concepts for either further development of the scientific basis of MER, or as a general guide in applied projects, can help in accelerating the success of restoration projects as well as the image, and consequently the fundraising options, of MER as a major conservation management approach.

Author contributions

BS conceived the manuscript. BS led the manuscript draft with contributions from all coauthors. AP, JM, AA, and BS made the figures. All authors reviewed and edited the manuscript. All authors read and approved the final manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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METHODS
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Testing Industrial-Scale Coral Restoration Techniques: Harvesting and Culturing Wild Coral-Spawn Slicks

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Accelerating the recovery of marine coastal ecosystems is a global challenge that has been attempted on many systems around the world. Restoration efforts have shown varying levels of success at localized-scales, but developing techniques for large-scale application are still in their nascent stage for many systems. For seagrass meadows and marsh plants, large-scale successes have been realized by distributing seeds from moving boats or planes, respectively. Similarly for coral reefs, the harvesting, culturing and releasing of wild coral-spawn slicks to targeted reefs is anticipated to achieve cost-efficient, large-scale restoration of coral communities with low-impact technology. Yet, operational protocols for full-scale application still require development by practitioners. In this study we conducted a field trial to evaluate the actual feasibility of harvesting wild coral-spawn slicks for large-scale restoration activities, incorporating technologies used in oil spill remediation, dredging operations, and land-based aquaculture. Testing the potential for scalability to commercial vessels, our trial focused on concentrating and collecting wild coral-spawn slicks for culturing until settlement competency using an experimental 50,000 L aquaculture facility built on a tugboat. Five objectives were set and all were achieved successfully, with only one requiring further optimization. Overall, this restoration approach allows for long-distance translocation of genetically diverse coral assemblages, and may be combined with other larval conditioning techniques that are being developed to increase the resistance to stress and survival of coral recruits. Most importantly, it is fully scalable to produce billions of coral larvae for delivery to target reefs, with negligible impact to source populations.

Keywords: aquaculture, coral reef restoration, coral-spawn slick, eco-engineering, Great Barrier Reef, harvest, marine invertebrate larvae, reseeding

INTRODUCTION

Habitat degradation is one of the most pervasive global impacts of environmental degradation and threats to biodiversity loss in terrestrial, freshwater and marine ecosystems (Millennium Ecosystem Assessment, 2005; Butchart et al., 2010; Mazor et al., 2018). Habitat degradation occurs through direct human impacts such as land clearing (Foley et al., 2005), coastal development

(Lotze et al., 2006), and bottom trawling (Thrush and Dayton, 2002), as well as anthropogenic mediated climate change drivers (Intergovernmental Panel on Climate Change, 2014) that are typically larger in scale than direct human impacts. Globally, all coastal marine habitat providing organisms such as seagrasses, macroalgae, corals and other sessile invertebrates have been impacted by recent extreme warming events (Smale et al., 2019). Given the pervasiveness of habitat degradation, there is increasing recognition that active restoration interventions are necessary in order to ensure the viability of natural ecosystems and their services into the medium-term future (Bullock et al., 2011; Menz et al., 2013). The urgency of the situation is such that the United Nations recently declared the "UN Decade of Ecosystem Restoration 2021-30" that aims to massively scale-up the restoration of degraded and destroyed ecosystems (United Nations Environment Programme, 2019).

It remains unclear whether the current application of traditional coral restoration approaches can be operationalized to achieve effective ecosystem-scale restoration. Recent successes on coral reefs destroyed from dynamite fishing have shown the effective transplantation of fragments onto stable substrata made from steel rods to restore approximately 7,000 m^2 (Williams et al., 2019), and increases from 0 to 44% coral cover over 16 years when stable substrata from quarried rocks was provided in rubble fields in an area of reef with abundant larval supply from nearby reefs (Fox et al., 2019). Yet such 'gardening' or substrate stabilization approaches aren't viable options when donor colonies or natural larval supply are limited. In such circumstances, strategies of mass seeding have proven an effective large-scale approach in other coastal marine ecosystems. For example, the distribution of 38 million *Zostera* seeds from boats throughout a coastal bay system over a period of 11 years restored 1,700 hectares of seagrass habitat (Orth et al., 2012). In coastal saltmarshes, reseeding trials of *Spartina* using delivery from aeroplanes have also proven effective, with planting occurring at rates of 16 s per hectare (Utomo et al., 2016). Transportation of seeds or larvae derived from nurseries or distant habitats therefore provides a means of supplying degraded habitats with new propagules to aid recovery.

The direct release of vagile larvae from vessels to areas of reef that lack a sufficient supply of larvae provides a 'reseeding' approach for coral reefs equivalent to those applied with seeds in seagrass meadows and salt marshes. Recent modeling of industrial-scale harvesting, development, and release of wild coral-spawn slicks onto reef indicates that the approach has the potential to achieve large-scale restoration of coral communities with low impact technology at low cost per colony (Doropoulos et al., 2019). Yet while approaches for the collecting and culturing of coral-spawn slicks for use in coral reef restoration have been trialed using a variety of techniques (Heyward et al., 2002; Omori et al., 2007; Guest et al., 2014; Edwards et al., 2015; de la Cruz and Harrison, 2017), the scales at which they have been applied and their potential for large-scale applications and transportability are limited. Moreover, results from empirical studies using larval saturation techniques in highly localized areas of coral reefs have been mixed, providing nominal (Edwards et al., 2015) and positive (de la Cruz and Harrison, 2017) outcomes for coral recovery. Thus, the methods required to achieve restoration of reefs by harvesting wild spawn at an industrial-scale remain a critical information gap.

Scaling-up environmental restoration efforts to ecologically meaningful scales requires partnerships between scientists, engineers, and industry practitioners (De Vriend and Van Koningsveld, 2012; Gillies et al., 2015). For example, oil spill remediation routinely contains surface oil slicks with large booms that can also be used to contain wild coral-spawn slicks prior to collection (Doropoulos et al., 2019). Dredging operations use large vessels such as trialing suction hoppers dredgers that pump, contain, transport, and deposit fine particles at quantities > 20 ton (Laboyrie et al., 2018), which can be adapted for the industrial-scale collection of densely concentrated coral-spawn slicks. Land-based aquaculture industries culture billions of marine bivalve larvae in single facilities (Lucas et al., 2019) that can be applied to abundant coral-spawn slicks. Here, we incorporate these principles in a method to operationalize and test techniques required for the industrial-scale harvesting of coral-spawn slicks and culturing to settlement competency, enabling long distance transportation and release onto targeted reefs. To do so, we spotted coral-spawn slicks from a helicopter, contained them using an oil boom, and transferred them into a 50,000 L aquaculture facility built on the deck of a tugboat (**Figure 1**) using industrial scale pumps. We addressed the questions below that include 5 objectives to test the feasibility of the approach for further upscaling:

1. Concentration – can coral-spawn slicks be encountered and contained (obj. 1) in high enough concentrations to make collection viable?
2. Collection – can coral-spawn be pumped at high abundances (obj. 2) and survival rates (obj. 3) for rapid transfer?
3. Culturing and transportation – can larval culturing at large-scales in transportable containers using materials commonly found on commercial vessels occur at high survival rates (obj. 4) to competency (obj. 5)?

MATERIALS AND METHODS

Overall Study Approach

Prior to the field-testing component of the study, theoretical pump selection and initial testing and optimization of the pumping system were conducted in a controlled environment. Coral fecundity was then confirmed at Heron Reef in late-October 2019, and the field execution of the trial occurred in late-November 2019. Mass coral-spawning occurred on November 29 and 30, in the wild and by colonies housed on board the vessel. The concentration of live embryos was estimated from wild-slick coral-spawn slicks (n = 11). Four hand collected samples from wild spawn and four from colonies housed on board were pumped and survival estimated. An additional two samples of wild coral-spawn were skimmed and pumped directly from the water surface. All the pumped samples were cultured for up to 102 h in the aquaculture facility. During culturing,

FIGURE 1 | Testing the feasibility of operationalizing the spotting, containing, collecting, and culturing of coral-spawn slicks at industrial-scales. **(A)** View of a spawn slicks in the open ocean from a helicopter. **(B)** Containing coral-spawn slick in an oil boom for **(C)** collection onto the tugboat. **(D)** Overview of the back deck of the tugboat with the 4,500 L steel (*n* = 6) and plastic (*n* = 6) tanks.

larval concentration and survival were estimated every 24 h. At 72 h following spawning, settlement tiles were placed in each 4,500 L culturing tank, and coral settlement was estimated 48 h later. A methodological flow-diagram (**Figure 2**) presents the overall approach of the study, time-points, and replication at the different stages.

Pump Selection and Trialing

Different pumping principles and capabilities were initially compared to evaluate the potential of differing pump designs for safely and effectively pumping coral slicks. A short list of 17 potentially suitable pumps were ranked using a Multi Criteria Analysis (Statnikov and Matusov, 2002) by pump and dredging experts from Van Oord and Delft University of Technology. Theoretical criteria associated with shear stress, flow accelerations and pressure changes were included following Ulanowicz (1976). Four practical criteria were selected and included pump priming, availability, handling, and scalability. Following the Multi Criteria Analysis (**Table 1**), diaphragm and Hidrostal pumps ranked the highest and were selected for initial testing and optimization. Centrifugal pumps were included as a negative control.

Initial tests were conducted within a controlled setting to assess the damage on different particles used as proxies for coral embryos, including hydrogel balls, berries, and fish eggs. Trials indicated that increasing hose diameter and free passages (both of which decrease surface contact), as well as lowering flow velocity, all reduced particle damage. With these configuration principles incorporated in an optimized configuration of the pumping system, the diaphragm and Hidrostal pumps both incurred little damage on the particles, especially in comparison to the centrifugal pump (**Table 2**), so both were selected for testing on coral-spawn slicks during the field operation. For the field operation the two pumps with 100 mm intake diameter were capable of pumping >1 m^3 min^{-1}, with the diaphragm pump driven by air while the Hidrostal pump was electric and submersible.

Field Study Location and Timing

The field testing was timed to occur during the mass coral-spawning event after the full moon of November 23, 2018. Based on ecological monitoring data, we decided to base our work in the southern Great Barrier Reef where coral cover is presently the highest (Australian Institute of Marine Sciences, 2018). Other parts of the reef have recently been affected by crown-of-thorns starfish, cyclones, and bleaching mortality that have reduced overall coral cover, so higher coral cover in the southern region provided the best chance of the formation of coral-spawn slicks that could be harvested using pumps. While mass spawning of corals has been found to peak 4-5 nights after full moon on the central Great Barrier Reef (Harrison et al., 1984; Babcock et al., 1986), examination of records of spawning at Heron Island in the southern Great Barrier Reef indicated that the main night of spawning is slightly later,

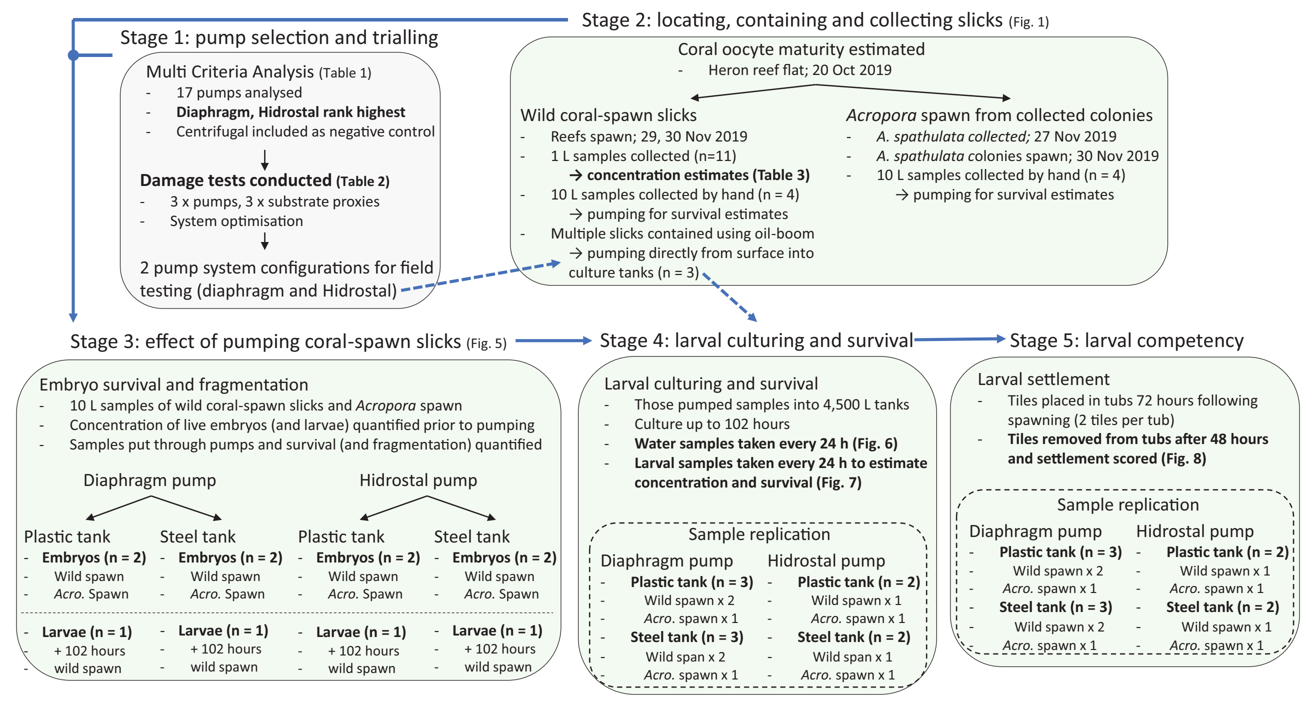

FIGURE 2 | Workflow diagram presenting the overall approach of the study, the five major stages, time-points of observations, and replication for each experiment.

TABLE 1 | Multi Criteria Analysis applied to initial pump selection.

			Criteria									
Pump type			**Shear**	**Turb.**	**Press. Diff.**	**Prim.**	**Head**	**Flow Acc.**	**Scal.**	**Avail.***	**Hand.¶**	**Total**
Archimedes	Jackscrew	Archimedes	4	5	5	5	4	4	5	1	2	39
Positive displacement	Continuous	Worm	3	3	3	5	2	5	4	1	4	36
		Gear	2	3	2	1	1	3	4	4	3	34
		Flexible vane	2	3	2	1	1	3	4	4	3	34
		Bulkhead	2	3	2	1	1	3	4	4	3	34
		Nutating	3	3	3	1	3	2	3	2	3	30
		Lobe	3	4	3	1	2	1	1	3	3	30
	Discontinuous	Piston	2	3	2	1	1	4	2	4	4	35
		Peristaltic	2	3	3	3	3	1	1	3	3	31
		Diaphragm	**3**	**2**	**2**	**5**	**2**	**4**	**2**	**5**	**4**	**43**
Centrifugal	Radial	Peripheral	1	1	1	1	1	3	2	3	3	25
		Centrifugal	*1*	*1*	*1*	*1*	*1*	*4*	*4*	*3*	*4*	*30*
	Ejector	**Hidrostal**	**3**	**3**	**3**	**2**	**4**	**4**	**4**	**5**	**4**	**46**
	Axial	Propeller and mixed flow	2	2	3	1	2	3	4	3	4	34
Injection	Injection	Venturi	1	1	1	3	1	3	4	1	3	23
Airlift	Airlift	Airlift	4	3	4	1	2	1	2	1	2	24
Bucket chain	Bucket chain	Bucket chain	3	2	4	5	3	3	1	1	1	26

*Worst scenario = 1; best scenario = 5. Diaphragm and Hidrostal pumps are boldfaced because they ranked the highest and were selected for the field trial. Centrifugal pump is shown in italics as it was selected as a negative control in the preliminary pump testing. *weighted by a multiplier of 3; ¶weighted by a multiplier of 2. Shear, low shear force; Turb., turbulence; Press. Diff., pressure difference; Prim., self priming; Head, hydraulic head capacity; Flow Acc., local flow accelerations; Scal., scalability; Avail., availability; Hand., handling.*

TABLE 2 | Summary of preliminary damage test outcomes using different pumps and substrates.

Pump type	Discharge ($m^3\ h^{-1}$)	Substrate	Replicates	Average number of particles pumped	Average proportion of particles broken
Centrifugal	17	Berries	6	117	0.45
	17	Hydrogel balls	6	60	1.00
	17	Fish eggs	0	NA	NA
Diaphragm	4.5	Berries	6	75	0.15
	4.5	Hydrogel balls	6	60	0.05
	4.5	Fish eggs	3	>500	0.00
Hidrostal	30	Berries	6	77	0.17
	30	Hydrogel balls	6	60	0.10
	30	Fish eggs	3	>500	0.00

most commonly between 6 and 8 nights after the full moon (Hock et al., 2019).

Locating, Containing and Collecting Slicks

Naturally occurring coral-spawn slicks were located using a hierarchy of temporal and spatial approaches. Colony fecundity and oocyte maturity was estimated at Heron Reef in late-October, and the majority of *Acropora* colonies were likely to spawn after the November 23rd full moon (pers. comm. Dr. Selina Ward).

A contingency plan was incorporated into the study so that pump testing and larval culturing could still be trialed in the event that wild coral-spawn slicks could not be located. Fecund colonies of *Acropora spathulata* were located on the reef and transferred to 4 basins on the deck of the tugboat. Each basin was 1 m^3 and contained up to 12 mature *A. spathulata* colonies that were supplied with constant water flow and aeration until they spawned. Colonies spawned in the basins from 22:00 to 22:30 on November 30, 2018. All egg-sperm bundles were stirred and agitated, left for 2 h to allow sufficient time for cross-fertilization, and used in trials thereafter.

Scientists working at Heron Island Research Station confirmed spawning by *Porites cylindrica* in aquaria on the night of November 27, with further spawning of some *Acropora* spp. in tanks on the night of the 28th. Weather on the night of the 28th was windy and no slicks were seen from the vessel on the water's surface during that night. However, signs of slicks were evident around Heron Island on the morning of November 29.

Further spawning occurred in tanks at Heron Island on the night of the 29th, and spawn slicks were also observed on the surface in Heron Island Channel at calm sea state conditions. Samples of these slicks were collected using 20 L buckets for use in pumping trials on board the vessel (see below "Pump selection and trialing"). From 06:45 to 07:30 am on November 30, aerial observations were made from a helicopter of multiple slicks along the south and east of Heron Reef (**Figure 1A**). GPS points were recorded and communicated so that the tugboat and support vessel could move to the slicks for sampling. On the evening of November 30, wild spawn slicks were evident on the sea surface, as well as on the following morning December 1. Wild slicks located on the sea-surface in daylight were contained with a 90 m long × 45 cm oil boom for direct pumping into the aquaculture tanks (**Figures 1B,C**).

To compare the concentrations of slicks to the only previous published account by Oliver and Willis (1987), 1 L samples were taken when slicks were encountered and concentrations of live embryos found in wild coral-spawn slicks estimated. Samples of slicks were conducted from the surface and in their center. A total of 11 samples were taken from November 29 to December 1. From each bulk sample, 1–3 × 1 mL subsamples were taken and the number of live embryos counted under a dissecting microscope. Bulk samples were well mixed prior to sampling.

Effect of Pumping Coral-Spawn Slicks

The level of impact of pumping coral-spawn slicks with the diaphragm and Hidrostal pumps was evaluated by comparing the total abundance of live embryos immediately before and after pumping. Total abundances of live embryos were estimated by sampling 50 mL of the harvested or pumped coral-spawn, immediately counting 1–3 × 1 mL subsamples for the number of live embryos under a dissecting microscope, and multiplying embryo density by the absolute volume. Bulk samples were well mixed prior to sampling.

Harvested coral-spawn was poured into a spare culturing tank on the tugboat, positioning the hose inflow inside the tank close to the water surface, and then pumped into a receiving tank. The total volume of actual coral-spawn poured through the pumps was 10.1 L per tank on average (min = 8.14 L, max = 12.0 L), with ca. 1 min of pumping per trial required to capture the full volume of gametes. Average discharge rates with the diaphragm pump were 38 $m^3\ h^{-1}$ (min = 16; max = 68) and with the Hidrostal pump 94 $m^3\ h^{-1}$ (min = 58; max = 128). An average of 4.8 million live embryos (min = 2,304,000; max = 8,884,400) were pumped per trial with the wild slicks from 00:30 to 01:30 on November 30, whereas an average of 660,000 live embryos (min = 456,064; max = 830,490) were pumped per trial using *A. spathulata* from 00:00 to 01:00 on December 1.

Four trials were conducted using the coral embryos derived from the wild coral-spawn slicks and four trials were conducted using the coral embryos derived from the *A. spathulata* spawn. Four additional trials were conducted using settlement competent larvae originating from the harvested wild coral-spawn slicks, at 11:00 on December 4, 4.5 days (108 h) following original collection. Trials were equally split between Diaphragm and Hidrostal pumps, resulting in 4 replicates per pump type for coral embryos, and 2 replicates per pump type for competent coral larvae.

Aquaculture Tank Construction and Water Quality Control

As a first-step of scaling-up prior to full-scale trials, we aimed to rear the wild coral-spawn slicks using a transportable 50,000 L system consisting of 12 tanks in total (6 × steel, 6 × plastic; **Figure 1D**). Previous studies have scaled the *in situ* rearing of wild coral-spawn slicks in floating ponds up to a total of 22,000 L (7 × 3,200 L, Omori et al., 2007), and in laboratory rearing up to 13,000 L (1 × 1,000 L fiberglass tank and 3 × 4,000 L inflatable pools, Edwards et al., 2015). We used 6 × 4,500 L steel rainwater tanks, as scaled equivalents of hoppers commonly used in commercial vessels, to investigate critical factors for coral larval survival. The insides of the steel tanks were sandblasted to remove the protective zincalume coating and mimic a raw steel surface equivalent to that in a dredger. In addition, 6 × 5,000 L capacity polyethylene (food grade) rainwater tanks were used as an inert control. Steel tanks measured 1900 mm diameter x 1500 mm height, while polyethylene tanks measured 1800 mm diameter x 2200 mm height. Tank replicates were randomly positioned and secured on the back deck of the tugboat (**Figure 1D**).

Water quality in the tanks was maintained by filtration (50 and 5 μm cartridge filters) and UV treatment (80Watt Emperor Aquatics UV) of seawater supplied to the tanks using a constant flow-through system (**Figure 3**). Cartridge filtration removes particles such as sediment, phytoplankton and zooplankton from the seawater, while UV filtration sterilizes the water from bacteria and viruses. No cleaning of the tanks was conducted throughout the entire culturing period, but water quality relied on the constant flow of filtered seawater.

Trace metal and physico-chemical properties of the seawater were characterized for the duration of the culturing period in the tanks. For total recoverable metals, three replicate steel and three replicate plastic tanks were sampled at 11:00 am on November 30th, December 2nd and 4th. At each time point, 150 mL of seawater was sampled, preserved with Nitric acid, and frozen. Seawater samples were sent to the Australian Government National Measurement Institute for analysis of total copper, iron, manganese, and nickel concentrations. Standard measurements of water quality including temperature, dissolved oxygen, salinity and pH were monitored using a YSI EXO1 Multiparameter Sonde. Water quality measurements were taken at 11:00 am, on November 30th, and December 2–4. Measurements were taken from the top and bottom of each tank, but no differences between depths was observed.

Larval Culturing and Survival

Pumped coral-spawn slicks were cultured in the steel and plastic rainwater tanks until competency was confirmed. Two approaches of collection were used to collect the coral-spawn slicks to test survival during culturing to competent larvae. Firstly, as described in “Pump selection and trialing”, collections by hand of wild slicks on November 30 and from the *A. spathulata* colonies housed on the tugboat on December 1 were poured through the pumps to estimate survival. Three additional samples were collected using a secondary approach by directly pumping wild slicks that had been concentrated and contained in oil booms from the sea-surface using the diaphragm pump (**Figures 1B,C**). Hence, a total of 7 replicates of competent larvae were pumped through the diaphragm pump – with 4 cultured in steel tanks and 3 cultured in plastic tanks; and a total of 4 replicates of competent larvae were pumped with the Hidrostal pump – with 2 cultured in steel tanks and 2 cultured in plastic tanks. All collected slicks were reared through to competency, with the concentrations of live embryos estimated every 24 h to test for differences in survival in the different tank types and following collection with the different pump types. Estimates of larval concentrations were conducted as described previously.

Larval Settlement Competency

To test the competency of larvae reared in the aquaculture facility, artificial tiles were placed in each rainwater tank at 72 h following slick collection. Ceramic tiles measured 5 × 5 cm, had an outer surface with fine-manufactured rugosity, with a hole drilled in the center for attachment (for further details see Doropoulos et al., 2014). The tiles were placed on the reef crest of Heron Island and preconditioned for 3 weeks. Upon collection, tiles were brushed to remove any fleshy algae and sediment, and placed in the rearing tanks. Two tiles were placed in each tank, with one tile laid flat on the bottom of the tank and the other tile left hanging at 10 cm above the bottom of the tank. The tiles were scored for larval settlement (i.e., attachment and metamorphosis) under a dissecting microscope 48 h after being placed into each tank.

Data Analyses

The effect of pumping stress was tested on the instantaneous survival of coral embryos and larvae. The proportional change of fertilized gametes was assessed by slick source (wild, *Acropora*), life phase (embryo, larvae), pump type (diaphragm, Hidrostal), and tank type (steel, plastic) using a linear model with Gaussian variance structure. Interactions among pump type, tank type, and slick source were specified in the model.

The concentration and survival of live gametes, from the embryo to larval phases, were both tested using generalized additive models with Gaussian variance structures for each model. Temporal trends of gamete concentration and survival were smoothed using natural splines (knots = 4), with pump type and tank type, and their interaction, incorporated as categorical predictors.

The abundance of settled larvae were tested using a generalized linear model using a quasi-Poisson variance structure due to overdispersion of the model residuals (Crawley, 2013). Settlement abundance was tested according to pump type, tank type, tile orientation (upwards, downwards), depth (flat, hanging), and their interactions.

All analyses were conducted in R (R Development Core Team, 2018), using the ‘lme4’ (Bates et al., 2015), ‘gamm4’ (Wood and Scheipl, 2013), ‘lsmeans’ (Lenth, 2016) libraries. All models were assessed by visualizing residual fits and normal distribution of the raw data. Statistical significance was based on comparison

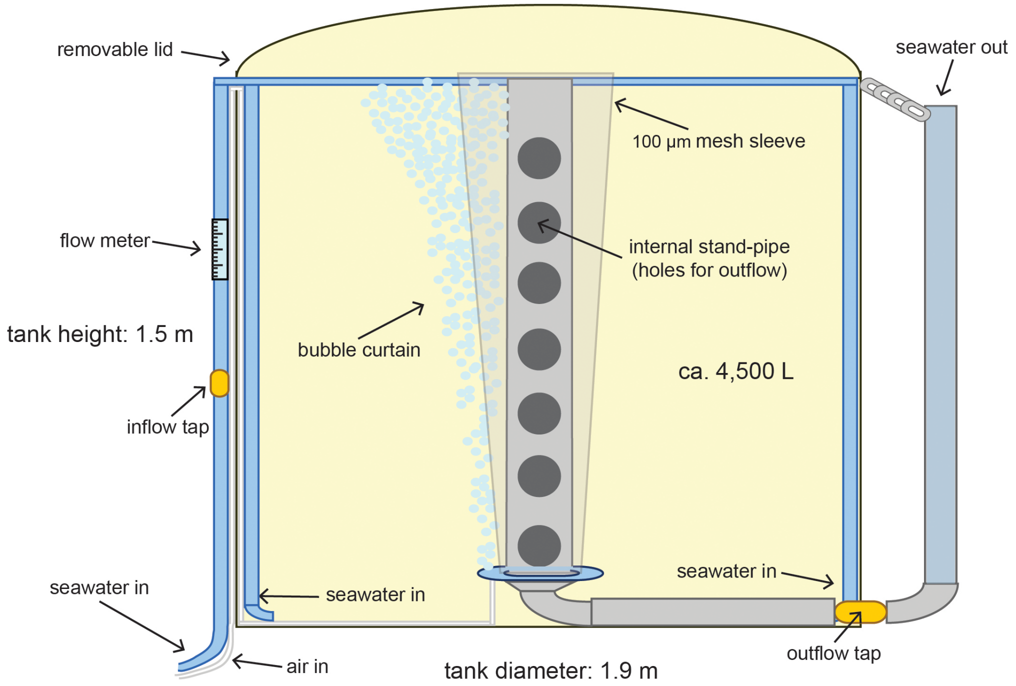

FIGURE 3 | Detail of tank design for flow-through rearing of the coral larvae. The water is circulated by the two opposing inflows and mixed from the flow of bubbles. The cone shaped mesh provides a large surface area that prevents larvae being lost to the outflow holes on the internal standpipe while the bubble curtain prevents them sticking to the mesh.

between the full model with reduced models using likelihood ratio test χ^2 P values for each term.

RESULTS

Very high concentrations of live embryos were consistently encountered in the naturally occurring coral-spawn slicks. Average densities revealed *in situ* concentrations of 169,330 live embryos L^{-1} (**Table 3**). These samples were collected by hand from a small boat and were composed of a variety of taxa based on sizes, color, and presence or absence of symbiotic zooxanthellae (**Figure 4**).

The boom was deployed multiple times to successfully surround coral-spawn slicks (**Figures 1B,C**), but attempts to move the slick met with mixed success. Occasionally, small wave action caused overtopping of the contained slick. Also, tidal flows in the area were substantial, meaning that even very low tow speeds resulted in loss of spawn-slick material below the weighted 45 cm depth of the boom skirt. Concentrations of live embryos collected by pumping these slicks from the sea surface were far lower than collection conducted by hand, averaging 44 live embryos L^{-1} ($n = 3$).

The total number of live coral embryos pumped was approximately 29 million – i.e., the amount in recipient tanks directly after pumping regardless of the collection or pumping method. "Survival" rates were often recorded to be greater than 100% following pumping, which includes embryos that fragmented and remained alive. Pumping live coral embryos <3 h following collection from a tank on deck to another tank on deck occurred with very high levels of survival (**Figure 5A**), averaging 131 ± 51% (stdev; $n = 8$). Occasional formation of vortices above the suction mouth did not appear reduce survival. It was also possible to pump 5-day old competent larvae (**Figure 5B**), with survival averaging 112 ± 88% ($n = 4$).

An interaction between pump type and tank type ($p = 0.029$) showed that the survival of embryos and larvae was higher when pumped with the Hidrostal pump into steel tanks compared to plastic tanks (steel 204% vs. plastic 92%, pair-wise $p = 0.0027$), whereas when embryos were pumped with the diaphragm pump

TABLE 3 | Concentrations of live coral embryos found in wild coral-spawn slicks.

Date	Slick sample	Subsample	L^{-1}	Stdev
November 29, 2018	1	1	196,000	NA
	2	1	192,000	NA
	3	1	804,000	NA
	4	1	468,000	NA
November 30, 2018	1	1	45,000	NA
	2	1	26,700	NA
	3	1	267	NA
December 1, 2018	1	3	12,333	3,786
	2	3	74,000	14,422
	3	3	13,000	1,732
	4	3	31,333	2,517
		Mean	169,330	5,614

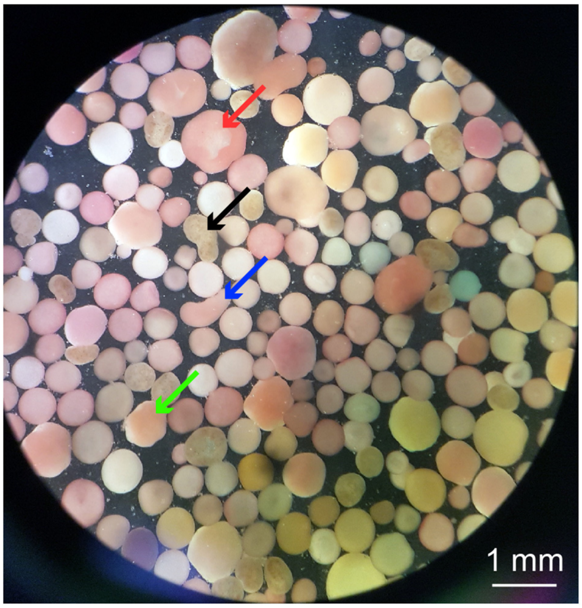

FIGURE 4 | Microscope image of a wild coral-spawn slick sample taken from one of the culture tanks approximately 36 h following spawning. The sample indicates a variety of coral species found in a wild coral-spawn slick, recognized through the range of sizes, colors, and those that have zooxanthellae already present (e.g., black arrow) or absent (e.g., red, blue and green arrows). Observed are a range of developmental stages of intact embryos to larvae, including: morula (e.g., green arrow), prawn chip (e.g., red arrow), and elongated planulae (e.g., black and blue arrows) (terms following Jones et al., 2015).

there was no statistical difference between steel tanks compared to plastic tanks (steel 116% vs plastic 87%, pair-wise $p = 0.426$). An interaction was also evident between pump type and slick source ($p = 0.035$), due to higher rates of survival when wild slicks were pumped with the Hidrostal pump compared to the diaphragm pump (161% vs 87%, pair-wise $p = 0.021$).

Flow rates in the aquaculture tanks were set to provide at least two full water changes per day within each tank, maintaining a high standard of water quality throughout the larval culturing period (**Figure 6**). Concentrations of trace metals were similar between steel and plastic tanks, were always below 1 μg L^{-1} for nickel and manganese, were slightly higher for copper at 1.5 μg L^{-1}, and averaged 11.7 μg L^{-1} for iron. Minor variations in salinity and water temperature were found between steel and plastic tanks. Seawater temperature averaged 26.8°C throughout the culturing period (min = 25.5°C, max = 28.8°C), with steel tanks on average 0.5°C warmer than plastic tanks. Oxygen saturation was always over 100%, and pH appeared to increase steadily over the period that larvae were cultured, rising from 8.24 to 8.30.

On collection of the coral-spawn slicks, initial stocking densities averaged 1272 live embryos L^{-1}, ranging from 14 to 8,000 L^{-1}. Differences in larval concentrations (**Figures 7A,B**) or survival rates (**Figures 7C,D**) throughout the culturing period were not affected by either pump type or tank type. The only significant factor influencing concentration and survival was time since collection, with overall concentrations ($p = 0.038$) and survival ($p < 0.001$) decreasing with larval age. By 4.5 days following spawning, coral-spawn pumped and reared in the aquaculture facility on the deck of the tugboat were fully competent, with a total of 5.6 million larvae remaining. Average survival of the initial stock from the coral-spawn slicks to larval competency was 14 ± 8% (stdev; $n = 11$).

High densities of settled coral larvae were found on conditioned tiles from both steel and plastic tanks, with an average of 7 settlers cm^{-2} on tile topsides (**Figure 8A**) and 15 settlers cm^{-2} on tile undersides (**Figure 8B**; settlement orientation $p = 0.014$). An interaction between pump type and tank type ($p = 0.007$) showed much lower settlement on tiles in steel tanks following pumping by the diaphragm pump (1.6 settlers cm^{-2}) compared to all other combinations (16.1 settlers cm^{-2}).

DISCUSSION

Industrial-scale collection, culturing, and transport of coral propagules may provide an important tool for the restoration of coral reefs. Prior to full scale application of our suggested approach (Doropoulos et al., 2019), considerations relating to containment, collection, and culturing needed empirical trialing. This field trial has demonstrated that harvesting and culturing of wild coral-spawn slicks for delivery to targeted reefs is achievable using a transportable 50,000 L aquaculture system built on-board a tugboat. To our knowledge, our study is the first to (1) harvest and culture coral-spawn at such a large volume, (2) use an aquaculture facility that can transport larval cultures 1000's of km's – distances relevant to the world's largest coral reef ecosystems, and (3) show that live coral embryos and larvae can be pumped for rapid collection and distribution, respectively, surviving the shear forces and turbulence generated by pumping. These outcomes suggest that further upscaling of coral-spawn harvesting and culturing to millions of liters for release onto reefs is feasible.

Mass coral spawning events occur on many reefs at predictable times of the year (e.g., Great Barrier Reef - Harrison et al., 1984; Babcock et al., 1986; Penland et al., 2003; north-western Australia - Gilmour et al., 2016), so, weather dependent, encountering coral-spawn slicks for harvest provides a reliable source of live embryos from a diverse mix of species. Given this periodicity of a known source of gametes, it is surprising that there was only one prior published account of the concentration of live embryos found in coral spawn slicks – i.e., 230 L^{-1} from the central Great Barrier Reef (Oliver and Willis, 1987). Following sampling from 11 slicks in our present study, the average concentration of live embryos found in the coral-spawn slicks was orders of magnitude higher than the concentration previously published. This information, in addition to previous *in situ* culturing of wild coral-spawn slicks (Heyward et al., 2002; Omori et al., 2007), show that wild coral-spawn slicks provide a highly abundant source of material that can be utilized for large-scale restoration efforts.

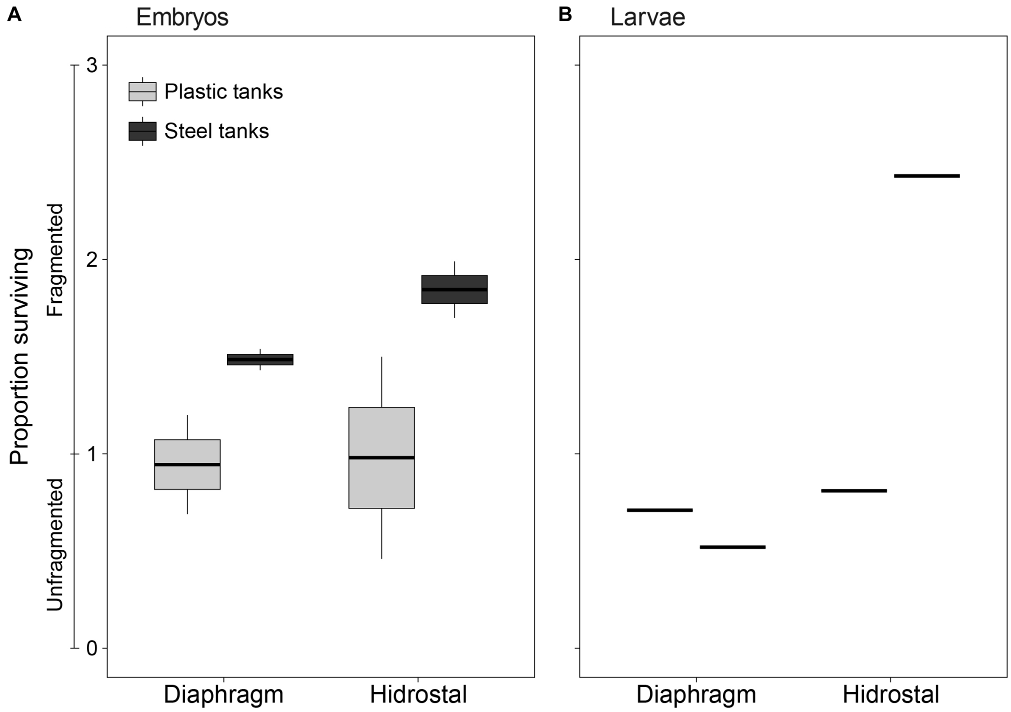

FIGURE 5 | Survival of coral **(A)** embryos and **(B)** larvae immediately following pumping by diaphragm and Hidrostal pumps in the plastic and steel tanks. Values ranging from 0 to 1 indicate unfragmented embryo survival, whereas values ranging 1–3 indicate the proportion of fragmented and surviving embryos. The middle line of each boxplot indicates the median value, upper and lower hinges indicate the 75 and 25% quantiles, upper and lower whiskers represent the maximum and minimum observations +1.5 × the inter-quartile range, and individual dots represent outliers (*n* = 2 per tank type × pump type for embryos; *n* = 1 per tank type × pump type for larvae).

Pumping coral-spawn slicks provides a means of collection for scaling-up coral reef restoration. Prior to conducting this field study, the potential for coral embryo survival during pumping was unknown and proportional survival estimated at 0.7–0.8 for modeling purposes (Doropoulos et al., 2019). Previous work has found size-dependent survival decreases as a linear function of increasing shear stress for eggs to juveniles of five fish taxa (Killgore et al., 2001), whereas our preliminary tests provided promising results with little to no damage on fish eggs and other proxies using the diaphragm and Hidrostal pumping systems (**Table 2**). When we applied these pumps to coral embryos in our field study, we discovered that coral embryos at two distinct developmental phases, i.e., fertilized eggs and competent larvae, could be pumped with high levels of survival that included fragmentation. That is, the overall average level of survival following pumping was >120%, indicating that fragmentation had occurred on the coral embryos. These smaller, fragmented embryos remained alive and continued to develop to fully competent larvae, a phenomena that has previously been demonstrated and hypothesized as a tool for clonal reproduction in corals (Heyward and Negri, 2012).

Survival of the pumped coral-spawn slicks to competent larvae following 4.5 days of culturing averaged 14% of the initial stock. Storage and culturing in 4,500 L steel and plastic rainwater tanks did not result in differences in survival. Steel tanks did have slightly higher temperatures than plastic tanks on average, a factor that may be related to lower rates of settlement. Overall however, the use of steel basins does not appear to pose a limitation to larval culturing in scaling to larger hoppers that are typically found in commercial vessels hoppers that typically use raw steel, such as those found in hopper dredgers of commercial vessels.

The larval-culturing survival rate of 14% using a 50,000 L facility with an average stocking density of 1,272 L^{-1} (range 18–8,000) in our study is among the highest found in the literature, demonstrating that the filtering system and flow rates provided water quality that is sufficient for larval culturing. In comparison, culturing of wild coral-spawn slicks using *in situ* ponds with a constant exchange of ambient seawater have found averages of ca. 17% survival using a 22,000 L capacity with initial stocking densities ca. 840 L^{-1} (Omori et al., 2007), and 5% survival using a 6,000 L capacity with initial stocking densities ca. 5,000 L^{-1} (Heyward et al., 2002). Such high initial stocking densities of ca. 5,000 L^{-1} in Heyward et al. (2002) likely resulted in such low proportional survival. Similarly in our study, while differences in larval concentrations between steel and plastic tank types were not statistically different, trends indicate that the initial reductions in concentration were steeper in the steel tanks than plastic tanks, caused by two steel tanks with much higher initial concentrations (**Figures 7A,B**). Work by Pollock et al. (2017) shows that density-dependent survival occurs when

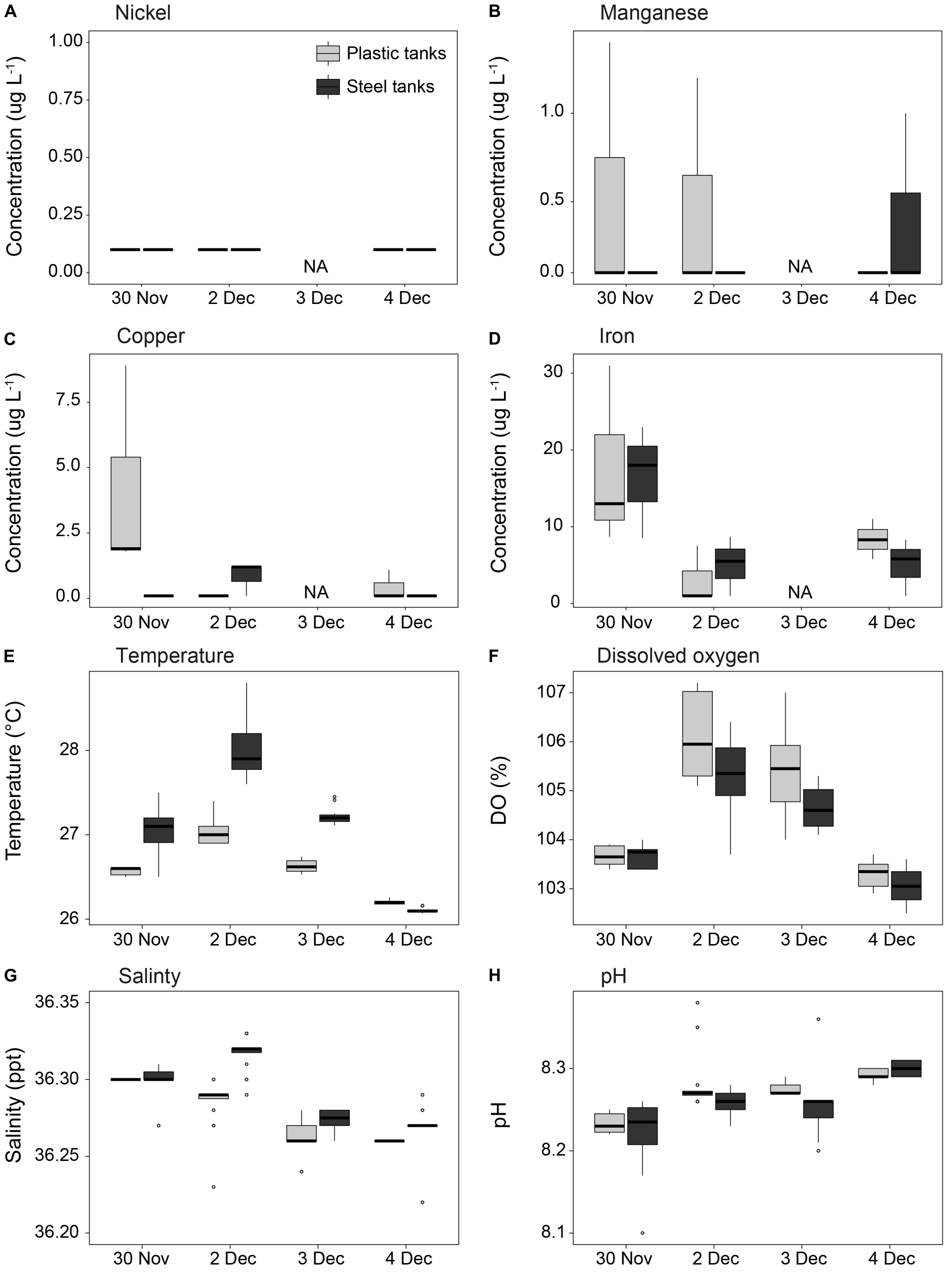

FIGURE 6 | Measurements of **(A–D)** dissolved metal concentrations and **(E–H)** water quality in the culture tanks throughout the duration of the coral larvae culturing period. The first batch of spawn slicks were pumped into the culture tanks at 00:30 am on Nov 30. Light gray = plastic tanks; dark gray = steel tanks (*n* = 3 per tank type for **A–D**; *n* = 6 per tank type for **E–H**; NA = no samples for **A–D**).

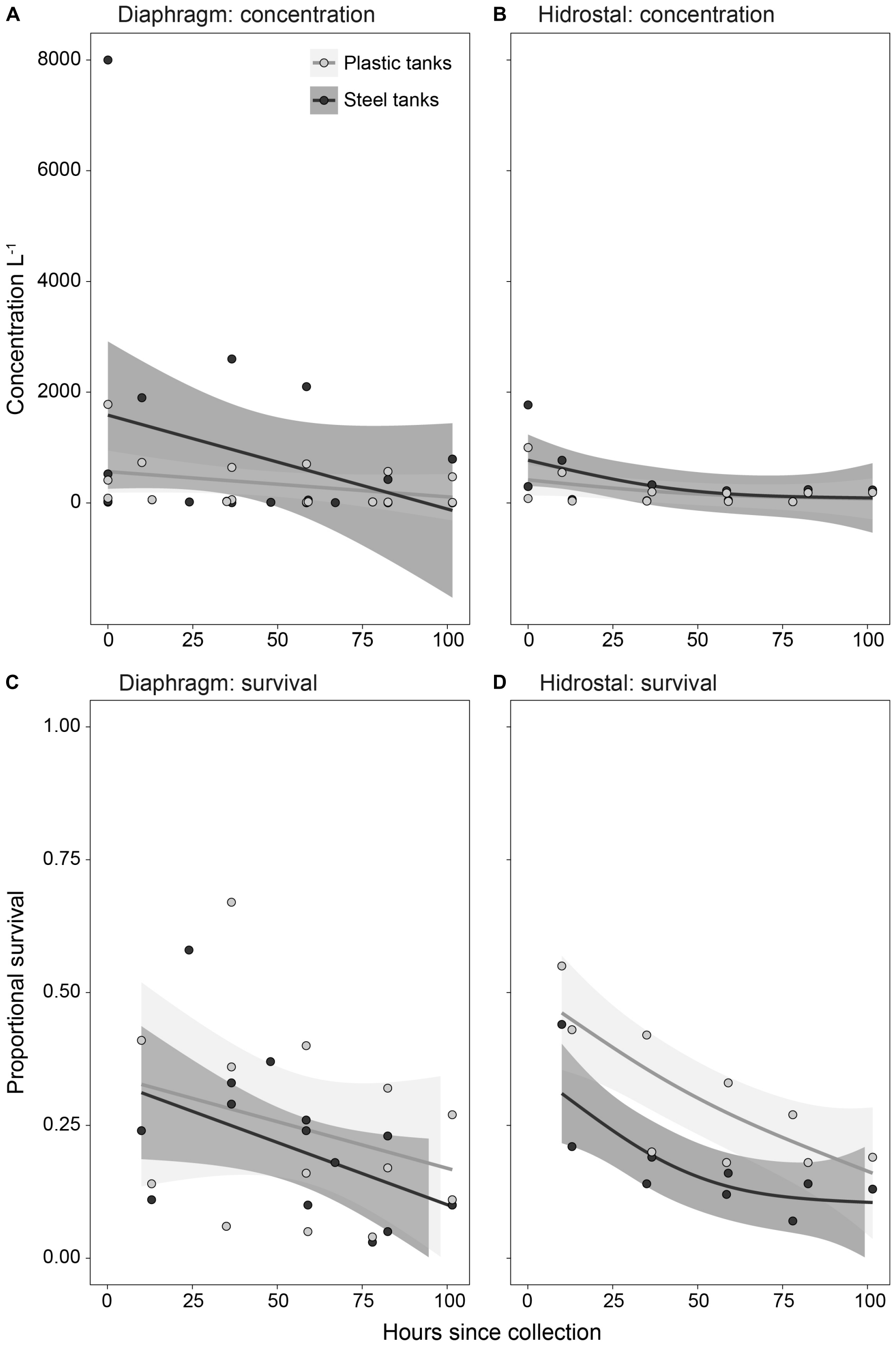

FIGURE 7 | Temporal trends in larval **(A,B)** concentration and **(C,D)** proportion survival following pumping by diaphragm and Hidrostal pumps in the plastic and steel tanks. Solid circles represent individual data points, solid lines represent mean of the generalized additive model fits, and shading is the 95% confidence interval of model fits (*n* = 3 per tank type for the diaphragm pump; *n* = 2 per tank type for the Hidrostal pump).

initial stocking densities are ≥500 larvae L^{-1}, and Edwards et al. (2015) suggested initial stocking densities of no more than 300 larvae L^{-1}. Thus, adjusting larval concentrations to 300–500 L^{-1} and increasing flow rates for steel tanks to keep water temperatures at ambient levels may help improve larval survival and competency.

While encountering, collecting, pumping, and culturing the coral-spawn slicks through to competency were realized

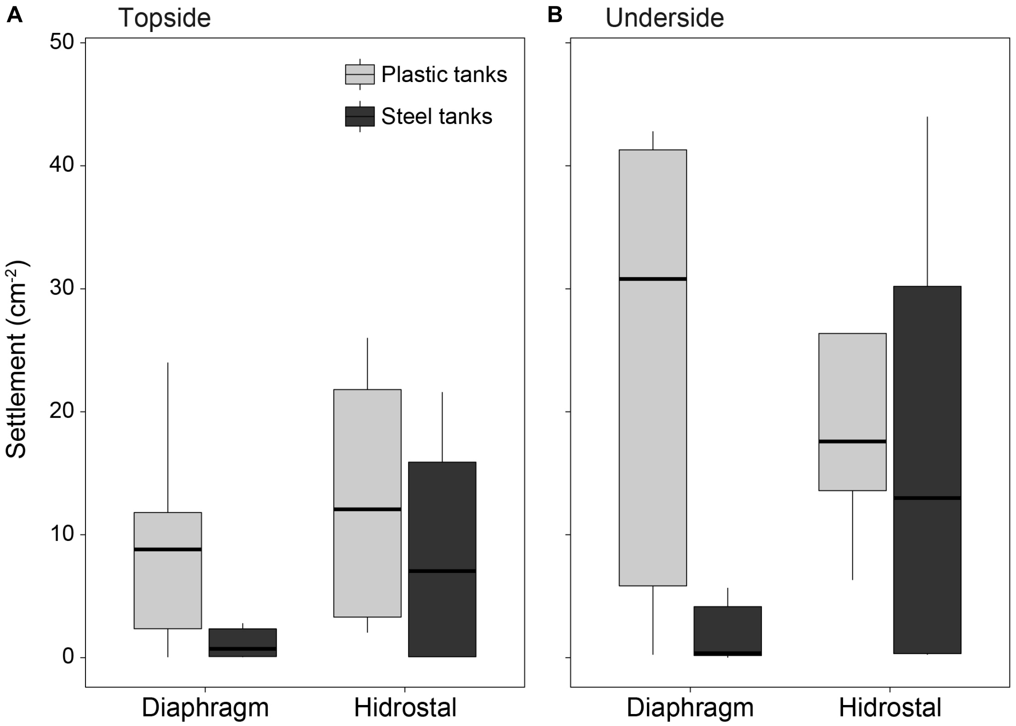

FIGURE 8 | Coral settlement density (cm^{-2}) on tile **(A)** topsides and **(B)** undersides placed in the plastic and steel culture tanks. Two 5 × 5 cm settlement tiles were placed in each tank and scored for settlement at 4.5 days following the introduction of embryos into the tanks (*n* = 6 per tank type × tile orientation for the diaphragm pump; *n* = 4 per tank type × tile orientation for the Hidrostal pump).

with great success during this study, containing the slicks in the oil booms and skimming the coral-spawn slicks directly from the surface of the seawater with the used pumping configuration was met with mixed outcomes that require further development. Additional tests are needed to improve the skimmer head design, such as configuring the skimmer to pass spawn slicks into the pump intake at depth. Optimizing this step of the collection phase will provide capacity for full-scale collection of wild coral-spawn slicks by minimizing any requirement of containment and manual handling. If containment of coral-spawn slicks on the sea surface is necessary, temporary collection into floating ponds could be an option prior to collection into the primary aquaculture facility on-board a vessel.

The type of pumping system for future large-scale implementation also requires consideration. While the Hidrostal pump has optimal flow control, pumps of this type require priming to enable a continuous water flow which can be time consuming and is likely to be problematic in rougher conditions since air may enter the pump resulting in partial or total loss of effectiveness. In contrast, diaphragm pumps do not require priming and are therefore easier to handle and quicker to deploy. Ultimately the choice of pump may need to be made taking into consideration the final design of the skimmer head, since diaphragm pumps will be more difficult to scale up further in terms of capacity, while this is more feasible with the Hidrostal design if priming and air intake issues can be overcome.

Of the upmost importance is that if harvesting is to be up-scaled and used as a common practice, initial characterizations of where excess material is located must be conducted to remove any possibility of over-harvesting that could reduce natural meta-population recovery (Doropoulos and Babcock, 2018). For example, based on demographic modeling from Doropoulos et al. (2019), only <0.0001% of the gametes spawned from Heron Reef slope alone were used in this current study. Moreover, coral-spawn harvesting should only occur where larval abundances are not degraded compared to historical levels, as has recently been found in the central to northern Great Barrier Reef (Hughes et al., 2019).

The potential for scalability of our approach is one of the key attributes that makes it an ideal candidate for use in addressing the challenge of coral restoration efforts at ecologically relevant scales. The number of embryos that could be harvested using our technique with a medium-sized trialing suction hopper dredger – volume 14,000 m^3 – was initially estimated at 1.6 billion, translating to >500 million competent larvae, and 11 million newly settled coral recruits onto reefs (Doropoulos et al., 2019). Opportunities using other vessels with the capacity to hold large volumes of water while maintaining high levels of water quality can also be utilized. Developing and moving this number of larvae is unprecedented and practically impossible using conventional approaches. However, following some optimization to the collection component of our approach, full-scale application of this restoration tool appears fully feasible.

We are now at the stage to scale further and pump competent larvae onto a degraded reef in an unconstrained manner to test whether this restoration approach is viable for routine and large-scale application.

DATA AVAILABILITY STATEMENT

The data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

CD, JE, FV, RH, MK, and RB contributed to the conception and design of the study. CD, JE, FV, RH, KS, MK, and RB conducted the study. CD organized the database, performed the analyses, and wrote the first draft of the manuscript. FV and RB wrote sections of the manuscript. All authors contributed to manuscript revision, and read and approved the submitted version.

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Kelp Forest Restoration in Australia

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Kelp forests dominate the rocky coasts of temperate Australia and are the foundation of the Great Southern Reef. Much like terrestrial forests, these marine forests create complex habitat for diverse communities of flora and fauna. Kelp forests also support coastal food-webs and valuable fisheries and provide a suite of additional ecosystem services. In many regions of Australia and around the world, kelp forests are in decline due to ocean warming, overgrazing, and pollution. One potential tool in the conservation and management of these important ecosystems is habitat restoration, the science and practice of which is currently undergoing substantial expansion. We summarize the present state of Australian kelp forests and emphasize that consideration of the initial drivers of kelp decline is a critical first step in restoration. With a focus on Australian examples, we review methods, implementation and outcomes of kelp forest restoration, and discuss suitable measures of success and the estimated costs of restoration activities. We propose a workflow and decision system for kelp forest restoration that identifies alternative pathways for implementation and acknowledges that under some circumstances restoration at scale is not possible or feasible. As a case study, we then apply the Society for Ecological Restoration's 5-star evaluation to Operation Crayweed, Australia's primary example of kelp forest restoration. Overall, no single method of kelp forest restoration is suitable for all situations, but outcomes can be optimized by ameliorating the driver(s) of kelp decline and achieving ongoing natural recruitment of kelp. Whilst scalability of kelp forest restoration to the seascape-scale remains a considerable challenge, the present review should provide a platform for future restoration efforts. However, it is also crucial to emphasize that the challenges of restoration place a high value on preventative conservation and protection of existing kelp forest ecosystems – prevention is invariably better than cure.

Keywords: canopy, Great Southern Reef, ecosystem, habitat-forming, macroalga, rehabilitation

THE ROLE OF KELP FORESTS

Kelp[1] dominate rocky coastal environments in temperate and subpolar latitudes around the world (Smale et al., 2013; Krumhansl et al., 2016; Wernberg et al., 2019). These habitat-forming macroalgae occur in intertidal and subtidal habitats and range in size from less than a meter to over 40 m in length. Much like terrestrial forests, kelp forests are complex three-dimensional habitats with modified sub-canopy conditions (Gaylord et al., 2007; Layton et al., 2019a) that support diverse communities of associated flora and fauna (Steneck and Johnson, 2014; Teagle et al., 2017; Miller et al., 2018). Kelp also act as the trophic foundation of coastal food-webs by providing food for a suite of grazers, detritivores, and microbes (Schiel and Foster, 2015; Wernberg et al., 2019) – the effects of which can reach to adjacent reef, seagrass, and sediment communities (Bustamente et al., 1995; Bishop et al., 2010), as well as to deep waters and beyond the continental shelf (Harrold et al., 1998; Thompson et al., 2011; Filbee-Dexter et al., 2018).

Most shallow (<30–50 m) rocky reefs in temperate Australia are dominated by kelp (**Table 1**; Marzinelli et al., 2015; Bennett et al., 2016; Coleman and Wernberg, 2017; Wernberg et al., 2019). Altogether, these kelp-dominated rocky reefs form an ~8,000 km long interconnected system known as the Great Southern Reef (GSR, Bennett et al., 2016), and sustain high levels of biodiversity and productivity (Ling, 2008; Bennett et al., 2016; Wernberg et al., 2019). One remarkable feature of biodiversity on the GSR is the high levels of endemism, and this is particularly true for macroalgae, with the GSR a global hotspot of macroalgal biodiversity and endemism (Womersley, 1987, 1994; Phillips, 2001; Kerswell, 2006). The GSR is also a global biodiversity hotspot for bryozoans, chordates, crustaceans, echinoderms, molluscs and sponges, with rates of endemism across these taxa ranging from ~20–60% (Bennett et al., 2016).

Australian kelp forests also have high economic value and support many fisheries, including the rock lobster and abalone fisheries that contribute >US$600 million p.a. to the national economy (ABARES, 2019). Beyond direct economic outputs, a lack of data makes it difficult to quantify the full value of ecosystem services provided by kelp forests in Australia. Notably, indirect commercial and social benefits arising from kelp forests are likely to be substantial, especially in coastal communities. These include indirect effects on fisheries (e.g., influence on coastal food-webs and prey species), recreational fishing, ecotourism, and other forms of marine recreation (e.g., scuba-diving) (Bennett et al., 2016). Despite their significant value, Australia temperate marine ecosystems are conspicuously underfunded and understudied relative to their tropical counterparts (Bennett et al., 2016).

STATUS OF AUSTRALIAN KELP FORESTS AND DRIVERS OF DECLINE

A strong rationale for considering restoration of Australia kelp forests is that they are in decline in many regions globally. In Australia, significant declines of kelp have occurred in Western Australia (Smale and Wernberg, 2013; Wernberg et al., 2016), South Australia (Connell et al., 2008), Tasmania (Ling, 2008; Johnson et al., 2011), Victoria (Kriegisch et al., 2016; Carnell and Keough, 2019), New South Wales (Andrew and O'Neill, 2000; Coleman et al., 2008; Vergés et al., 2016), and Southern Queensland (Phillips and Blackshaw, 2011). In these areas, and in many locations globally, drivers of kelp forest decline include both physical and biological factors (also see Krumhansl et al., 2016), and these must be understood for restoration efforts to be effective.

In Western Australia, an extreme marine heatwave over the 2010/2011 summer, in combination with southward range extension of subtropical herbivorous fishes associated with ocean warming, resulted in the loss of *Ecklonia radiata* (the dominant kelp across the GSR) and *Scytothalia dorycarpa* forests from ~100 km of coastline between Kalbarri and Geraldton (Smale and Wernberg, 2013; Wernberg et al., 2016). In South Australia, kelp forest losses have been mostly attributed to urbanization and increased runoff of sediments and nutrients (Connell et al., 2008; Gorman and Connell, 2009). Consequently, kelp forests within ~25 km of Adelaide, consisting mostly of *E. radiata*, have been largely replaced by less complex and less productive turf algae habitats (**Figure 1**). There has also been widespread loss of *E. radiata* in Port Phillip Bay, Victoria, particularly along the western and northern coastlines near the metropolitan areas of Geelong and Melbourne (Kriegisch et al., 2016; Carnell and Keough, 2019). Here, overgrazing by *Heliocidaris erythrogramma* urchins is the primary cause of kelp destruction, but subsequent proliferation of turf algae, in part due to high nutrient levels, also acts to inhibit kelp recruitment and recovery (Kriegisch et al., 2016; Reeves et al., 2018).

Destructive grazing by urchins is also a significant driver of kelp forest loss across Tasmania and the Bass Strait (Johnson et al., 2005, 2011; Ling, 2008), where urchin barrens formed by *Centrostephanus rodgersii* are now extensive and have replaced formerly lush kelp forests (Ling and Keane, 2018). This urchin, previously only abundant along the New South Wales coast, has undergone southern range extension over the last several decades due to increasing poleward penetration of the East Australia Current (EAC, Johnson et al., 2005, 2011; Ling, 2008). While warming waters and a strengthened EAC are responsible for the incursion of the urchin into southern waters, their local proliferation is linked to ecological overfishing of large southern rock lobster (*Jasus edwardsii*), which are the primary predator of *C. rodgersii* urchins in Tasmania (Ling et al., 2009; Johnson et al., 2011). While overgrazing by urchins has mostly affected *E. radiata* kelp forests, Tasmania has also suffered extensive losses of giant kelp (*Macrocystis pyrifera*) forests (Johnson et al., 2011). The loss of these iconic underwater forests (**Figure 2**) is mostly attributed to the increasing influence of the warm, nutrient-poor

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[1] Kelp are often defined as large, brown macroalgae belonging to the Order Laminariales, however this is a non-taxonomic term. Some authors (e.g., Steneck and Johnson, 2014; Bennett et al., 2016; Wernberg et al., 2019) argue for a broader functional definition that includes other large, brown habitat-forming macroalgae such as those from the Order Fucales. Here we adopt this broader functional definition, especially in light of the significant contribution of fucalean macroalgae to coastal ecosystems in Australia (**Table 1**; Coleman and Wernberg, 2017).

TABLE 1 | The primary genera/species of habitat-forming kelp in Australia. Unlike the northern hemisphere where kelp canopies primarily consist of "true" laminarian kelps, canopy-forming species in Australia constitute both laminarian and fucalean algae, with a larger diversity of fucoids than laminarians.

Species (order)	Common name	Australian distribution	Description	References
Cystophora spp. (Fucales)	cystophora	Sheltered to exposed reefs, 0–48 m. Nikol Bay, WA, to Port Stephens, NSW, and around TAS	Grows to 4 m. A widespread and diverse genus found only in Australasia. Can be locally abundant and dominant. May rise vertically (due to air-filled floats) or lay across the substrata	Huisman (2000), Edgar (2008), and Coleman and Wernberg (2017)
Durvillaea potatorum and *D. amatheiae* (Fucales)	bull kelp	Exposed reef, 0–30 m. Cape Jaffa, SA, to Tathra, NSW, and around TAS	Grows to 8 m. Massive, thick, and leathery kelp that lie prostrate across the substrata. The dominant species around low-tide level on exposed coastlines. Recently revised into two distinct species	Huisman (2000), Edgar (2008), Coleman and Wernberg (2017), and Weber et al. (2017)
Ecklonia radiata (Laminariales)	common kelp	Moderately exposed reef, 0–60 m. Geraldton, WA, to Brisbane, QLD, and around TAS	Grows to 1.5 m. Most widespread and abundant kelp in Australia, with a distribution that mirrors the extent of the GSR. Very often the dominant kelp on the reef. Has a long rigid "stipe" (i.e., stem) that holds the fronds above the substrata	Huisman (2000), Edgar (2008), and Wernberg et al. (2019)
Lessonia corrugata (Laminariales)	strapweed	Exposed reef, 0–20 m. Phillip Island, VIC, and around TAS	Grows to 1.5 m. Occasionally locally abundant and dominant, typically in shallower and more exposed locations than *E. radiata.* Typically lies across the substrata	Huisman (2000) and Edgar (2008)
Macrocystis pyrifera (Laminariales)	giant kelp, string kelp	Moderate to exposed reef, 0–28 m. Cape Jaffa, SA, to Walkerville, VIC, and around TAS	Grows taller than 35 m. Has air-filled floats and can form immense underwater forests, often with a floating surface-canopy. Can be locally abundant and dominant. Has a shorter ecotype (∼10 m, form *angustifolia*) that typically grows in shallower locations	Huisman (2000), Edgar (2008), and Schiel and Foster (2015)
Phyllospora comosa (Fucales)	crayweed	Moderate to exposed reef, 0–20 m. Robe, SA, to Port Macquarie, NSW, and around TAS	Grows to 3 m. Among the most common and dominant kelp on shallow and exposed sections of coastline. Has air-filled floats and typically floats just above the substrata. Often forms a dense band shallower than the zone dominated by *E. radiata*.	Huisman (2000), Edgar (2008), and Coleman and Wernberg (2017)
Sargassum spp. (Fucales)	sargassum	Sheltered to exposed reefs, 0–48 m. Australia-wide	Grows to 1.5 m. A diverse genus with global distribution that occur throughout tropical and temperate Australia. Can be locally abundant and dominant. May rise vertically (due to air-filled floats) or lay across the substrata	Huisman (2000), Edgar (2008), and Coleman and Wernberg (2017)
Scytothalia dorycarpa (Fucales)	western crayweed	Moderate to exposed reef, 0–44 m. Geraldton, WA, to Point Lonsdale, VIC	Grows to 2 m. Fulfils a similar role to *P. comosa*, especially in Western Australia.	Huisman (2000), Edgar (2008), and Coleman and Wernberg (2017)
Undaria pinnatifida (Laminariales)	Japanese kelp	Moderately exposed reef, 0–10 m. Port Phillip and Apollo Bays, VIC, and D'Entrecasteaux Channel to Coles Bay, TAS	Grows to 1 m. An introduced and invasive species. Occasionally locally common and dominant but highly seasonal, almost disappearing throughout summer and autumn. Has a short rigid "stipe" (i.e., stem) that holds the fronds above the substrata	Edgar (2008) and South et al. (2017)

waters of the EAC in Tasmania, although urchin overgrazing is likely to have exacerbated the problem (also see Ling, 2008; Ling and Keane, 2018) and be impeding recovery in some areas. Overall, more than 95% of Tasmania's surface canopy-forming giant kelp forests (which also occur to a lesser extent in parts of Victoria and South Australia) have been lost over recent decades, to be replaced by *E. radiata* forests or urchin barrens (Johnson et al., 2011; Ling and Keane, 2018). Consequently, in 2012 the giant kelp forests of southeast Australia became the first marine community listed as endangered under the Australian Federal Government *Environment Protection and Biodiversity Conservation Act* (Evans et al., 2017). There is still no Federal Recovery Plan prepared for this community.

The *C. rodgersii* urchin has also contributed to extensive barren formation across its historical range in New South Wales (Andrew, 1993; Andrew and O'Neill, 2000). Urchin barrens are estimated to extend across >50% of shallow rocky reef habitats along the central and southern coastlines of the state (Andrew and O'Neill, 2000), suggesting widespread losses of the two dominant kelp in the region, *E. radiata* and *Phyllospora comosa*. These urchin barrens likely formed over many decades – possibly due to overfishing of urchin predators such as eastern rock lobster (*Sagmariasus*

FIGURE 1 | Example of *Ecklonia radiata* kelp forests **(left)** replaced by turf algae **(right)**. Putative drivers include increased nutrients, and inhibition of kelp recruitment by the turf algae and entrained sediments. Photos by TW.

FIGURE 2 | Examples of healthy **(left)** and degraded **(right)** giant kelp (*Macrocystis pyrifera*) forests in Tasmania. Photos reproduced with permission of Matthew Ramaley **(left)** and Matthew Doggett **(right)**.

verreauxi) and eastern blue groper (*Achoerodus viridis*) (Ling et al., 2009; Ling and Johnson, 2012; Evans et al., 2017) – in conjunction with persistent declines in kelp cover associated with increasing urbanization and ocean warming (Andrew and O'Neill, 2000; Coleman et al., 2008; Mabin et al., 2013).

Urban development on the coasts of metropolitan Sydney, and in particular untreated sewage outfalls, were implicated in the local extinction of *P. comosa* forests throughout the 1980's (Coleman et al., 2008). Following improvements in wastewater infrastructure and water quality, these forests are now being restored under the aegis of Operation Crayweed (see below). Losses of *E. radiata* forests have also occurred on islands off northern New South Wales, toward the northern limit of the species' distribution, and have been attributed to warming waters and overgrazing by herbivorous subtropical fishes (Vergés et al., 2016). This poleward shift of sub/tropical species into temperate waters is referred to as tropicalization and is expected to increase in the future as oceans continue to warm (Vergés et al., 2016; Zarco-Perello et al., 2017). Indeed, it seems that increasing ocean temperatures – especially in southeast and southwest Australia, which represent global hotspots of ocean warming (Hobday and Pecl, 2014) – are likely to cause continued poleward range contractions of Australian kelp, to be replaced by smaller subtropical macroalgae (Wernberg et al., 2016; Coleman et al., 2017; Martínez et al., 2018) and substantially altering ecosystem functioning (Vergés et al., 2019).

BENEFITS AND VALUES OF KELP FOREST RESTORATION

Since kelp forests are the foundation of Australia's rocky reef ecosystems, it follows that maintaining or increasing the abundance and health of kelp forests via restoration could lead to concomitant benefits for production, biodiversity, and fisheries. Work has demonstrated that following urchin removal, small areas of recovered *E. radiata* kelp forests can support similar communities to natural *E. radiata* forests (Ling, 2008). However, this is not always the case and "recovered" kelp-dominated communities can be dissimilar to the pre-loss state (Valentine and Johnson, 2003). On artificial reefs in Tasmania, transplanting of adult *E. radiata* encouraged recruitment of economically and ecologically valuable invertebrates and fishes (including *Ostrea angasi* oysters and *J. edwardsii* rock lobsters), and facilitated development of diverse assemblages of flora and fauna (Layton et al., 2019a; Shelamoff et al., 2019). Whilst restoration of *P. comosa* forests by Operation Crayweed has had cascading benefits on epifaunal community composition, lags in system dynamics mean that restored communities can require time (i.e., years) to match natural *P. comosa* forests (Marzinelli et al., 2016).

Coastal macroalgal beds – of which kelp are the largest component by biomass – have also been identified as potentially important sinks of marine carbon (so called blue carbon) (Krause-Jensen and Duarte, 2016; Macreadie et al., 2019; Queirós et al., 2019). Recent work suggests that a significant portion of kelp forest biomass can be transported to coastal sediments and the deep ocean (Filbee-Dexter et al., 2018; Queirós et al., 2019). Furthermore, since macroalgal beds comprise such massive biomass, even conservative estimates of carbon transport/storage suggest that sequestration by kelp-dominated macroalgae beds can be a considerable contributor to blue carbon sinks (Macreadie et al., 2019; Queirós et al., 2019).

High biomass and fast growth rates ensure kelp forests also have critical roles in coastal nutrient-cycling (Smale et al., 2013; Bennett et al., 2016) and have great potential to absorb nutrients for bioremediation. Integrated multi-trophic aquaculture is a rapidly emerging field that might be able to utilize kelp to absorb excess nutrients associated with shellfish or finfish aquaculture (Buschmann et al., 2017; Hadley et al., 2018). Other emerging technologies and investments are also positioning kelp and macroalgae as a cornerstone of future blue economy applications, including as food for human consumption, livestock feed, biofuel, nutraceuticals, and pharmaceuticals (Buschmann et al., 2017; Froehlich et al., 2019). These high-value products represent market opportunities and economic incentives to help fund restoration efforts and thus contribute to the "restoration economy" (BenDor et al., 2015).

Kelp forests can also modify local hydrography and bolster coastal defenses by dampening ocean swell and decreasing erosion (Løvås and Tørum, 2001; Gaylord et al., 2007). This service should be given special consideration with regards to forecast increases in sea level and storm activity due to climate change (IPCC, 2014).

Kelp and associated macroalgae also play an important role in Indigenous Australian culture and tradition (reviewed by Thurstan et al., 2018). Uses include ceremonial activities, medicinal practices, clothing, food, shelter, and as domestic devices. Archival records of the use of bull kelp (i.e., *Durvillaea* spp.) are particularly numerous, and there is considerable contemporary use of this kelp by Indigenous practitioners in artistic and knowledge-sharing activities. Additionally, the culturing, outplanting and monitoring that large-scale kelp forest restoration efforts require, provides ideal opportunities for Indigenous employment, management and custodianship (also see McLeod et al., 2018), and to establish skills and knowledge that underpin macroalgae farming.

KELP FOREST RESTORATION ATTEMPTS: SUCCESSES AND FAILURES

The restoration of kelp forests globally has typically followed two broad strategies: assisted recovery and active restoration. Assisted recovery – where natural kelp recovery is facilitated by either the removal of the agent of decline (e.g., culling of sea urchins, Ling, 2008; House et al., 2018) or the installation of substrata for kelp colonization (e.g., artificial reefs, Carter et al., 1985; Ambrose, 1994; Terawaki et al., 2001) – has been successful at increasing kelp recruitment and development of a kelp canopy over the short-term. Results are nonetheless highly variable and site-dependent, and projects involving removal of the agents of decline have seemingly had greater success than those that only provide novel substratum. This may be due to the unsuitability of some artificial substrata for kelp colonization, and/or effects of other colonizing organisms (e.g., filamentous turf algae, mussel, and barnacles) on kelp recruitment. Critically, assisted recovery approaches are often hindered by resource constraints and by hysteresis and feedbacks in the ecological dynamic (see Scheffer et al., 2001; Marzloff et al., 2011), which impair kelp recruitment and reestablishment even after the initial driver of decline has been ameliorated (Gorman and Connell, 2009; Johnson et al., 2017). We are aware of only one example where assisted recovery in isolation has resulted in the long-term restoration of kelp forests (giant kelp in California, see Reed et al., 2006, 2017).

Active restoration efforts have typically had greater success, and typically involve transplanting adult or juvenile kelp from a donor site, or outplanting lab-cultured kelp (North, 1976; Hernández-Carmona et al., 2000; Perkol-Finkel et al., 2012; Zarco-Perello et al., 2017; Verdura et al., 2018). The long-term success of this approach is reliant on either continued transplantation of kelp – which can be cost-prohibitive and dependent on a healthy donor population (North, 1976; Devinny and Leventhal, 1979) – or adequate natural recruitment of juvenile kelp. In the latter case, recruitment could occur from nearby populations of kelp and/or from the transplanted kelp itself (see Operation Crayweed below). Notably, the planting of juvenile kelp (whether lab-cultured or otherwise) has had little success (but see Perkol-Finkel et al., 2012) unless it is combined with the outplanting of adult kelp (North, 1976; Devinny and Leventhal, 1979; Layton et al., 2019a). This may be due to increased herbivory, competition, or abiotic stressors that cause mortality of juvenile kelp in the absence of adults (Hernández-Carmona et al., 2000; Konar and Estes, 2003; Vergés et al., 2016; Layton et al., 2019a).

Within Australia there have been few attempts to restore kelp forests. The earliest reported work comes from the Seacare community group (Sanderson, 2003) who attempted to restore areas of giant kelp (*M. pyrifera*) in Tasmania. Multiple techniques were used, including transplanting juvenile kelp from donor populations; transplanting artificial substrata on which juvenile giant kelp were growing following natural recruitment; transplanting sporophylls (i.e., the reproductive fronds of giant kelp); and outplanting ropes seeded with small (∼5 mm) lab-cultivated juvenile kelp. *Centrostephanus rodgersii* urchins were also removed at some restoration sites and improved the likelihood of positive outcomes. Nonetheless, the project realized only marginal success and outcomes varied markedly across the 10 + sites. A single patch of giant kelp was established at one site but subsequently disappeared, in keeping with the ongoing decline of giant kelp in southeast Australia. The methods employed at the site of success did not differ from those at other sites (i.e., transplanting ∼100 juvenile kelp and 3 fertile sporophylls), but it did have the most similar community composition to the donor site and was the most exposed and southerly location of the restoration sites.

Operation Crayweed is the only other reported example of targeted kelp forest restoration in Australia of which we are aware (although there are several projects currently underway, as discussed below). This ongoing project began in 2011 and aims to restore crayweed (*P. comosa*) forests to metropolitan Sydney where the species was once abundant (Coleman et al., 2008; Campbell et al., 2014; Marzinelli et al., 2014, 2016). Adult crayweed are transplanted from donor populations outside of metropolitan Sydney to restoration sites, with the primary aim to establish sufficient adult individuals to promote recruitment of juvenile crayweed. Despite high variability among sites, survival of transplanted crayweed is typically comparable to natural mortality (Campbell et al., 2014) and, as of 2019, transplanted crayweed has reproduced in six locations such that multiple generations are now identifiable, often hundreds of meters from the original restored patches. These restored crayweed forests have become self-sustaining without the need for additional cost or maintenance, which is a rare result in marine restoration. This relatively small-scale intervention has translated into a large-scale impact/benefit, with crayweed populations continuing to expand and colonize substantial areas, and beginning to function as natural forests (Marzinelli et al., 2016).

Additional work has employed aspects of active restoration and assisted recovery to improve understanding of kelp forests and ecological restoration. Work by Valentine and Johnson (2005) found that even after the removal of urchins, heavy inoculation with *E. radiata* kelp spores was insufficient to achieve kelp reestablishment – presumably due to recruitment inhibition by the turf algae and sediments that had proliferated in the absence of the kelp (also see Layton et al., 2019b). However, Gorman and Connell (2009) showed that recovery of *E. radiata* kelp can naturally occur where turf algae are removed. Others have illustrated that urchin removal can facilitate natural recovery of kelp and other macroalgae on Australian temperate reefs when healthy kelp forests are nearby the denuded areas (Fletcher, 1987; Ling, 2008). Layton et al. (2019a) demonstrated successful transplanting of >500 adult *E. radiata* on artificial reefs in Tasmania. Survivorship of transplants was comparable to natural reefs, and abundant recruitment of juveniles (>750) ensured that many patches became self-sustaining. Crucially however, it was only patches above a certain size and density of adult kelp that facilitated adequate recruitment to maintain the kelp canopy; illustrating the importance of minimum patch sizes and densities when transplanting *E. radiata*, and likely other kelp species.

Given the rate of environmental change that is influencing coastlines worldwide, and that some drivers of kelp decline cannot be easily ameliorated (e.g., ocean warming), there is growing recognition of the need to plan adaptively and to “future-proof” marine restoration efforts, and potentially even consider the restoration of novel, more-suitable, species (van Oppen et al., 2015; Coleman and Goold, 2019; Wood et al., 2019). While we are aware of no published work implementing these strategies for kelp restoration, research in Australia is currently pioneering the identification of warm water-tolerant seaweed genotypes as the basis of future restoration efforts (IMAS, 2019; Gurgel et al., 2020).

ESTIMATION OF THE COSTS OF RESTORATION

Estimating the costs of implementing effective kelp forest restoration in Australia is difficult given the few examples to date. For Operation Crayweed, workers initially transplanted six 2 m^2 patches of *P. comosa* at each restoration site, with adult kelp densities of 15 m^{-2}. Initial transplanting efforts required ~5 days at each site and included site marking/preparation, securing of mesh mats for crayweed attachment, collection of adult crayweed from the donor population, and the transplanting itself. Costs of these efforts are estimated at ~US$6,850 per restoration site (i.e., ~$570 m^{-2}), which cover a 4-person team, boat and tow-vehicle, SCUBA tank fills, basic equipment and consumables. Project management and monitoring of the multiple Operation Crayweed sites is estimated at an additional ~US$18,500 p.a. Note that these costs do not include the science necessary to underpin decisions such as choice of donor site, size of patch, etc. Active restoration efforts typically occur at small to medium scales, and not the seascape scale at which kelp forest loss can occur. And so, while Operation Crayweed has demonstrated the translation of small-scale efforts into large-scale outcomes, efficient up-scaling of active restoration remains as a key ongoing consideration.

Assisted recovery techniques such as urchin culling are typically suited to tactical interventions at local spatial scales, such as reducing kelp loss to maintain/bolster the resilience of existing forests (Ling and Johnson, 2012; Layton et al., 2019a), remove incipient barrens (Ling, 2008; Tracey et al., 2015), or support active restoration efforts (Sanderson, 2003). Economic projections indicate that culling of *C. rodgersii* urchins from densities of 1.5 urchins/m^2 to 0.1 urchins/m^2 (i.e., the maximum density estimated to allow kelp recovery) across a 1 km^2 area of reef and from depths of 0–20 m would take two divers 685 days and cost ~US$980,478 or US$1,431 day^{-1} (Tracey et al., 2014). These projections are nonetheless conservative given that urchin densities on barrens are typically closer to 2 urchins/m^2 (Ling, 2008; Ling and Johnson, 2012). Novel technology is promising to improve the scalability and cost-effectiveness of urchin culling, and trials of autonomous underwater vehicles designed to locate and kill urchins are in planning. Other alternatives to enhance the value or reduce the costs of urchin-culling operations may involve working in partnership with fisheries/aquaculture industries (Pert et al., 2018) or enlisting the help of citizen scientists, as has been done in Japan (Watanuki et al., 2010) and the United States (House et al., 2018).

Overall, the impetus to consider kelp forest restoration would benefit greatly from environmental accounting to ascertain the (currently unknown) value of kelp forests to human society, and which could underpin rigorous benefit-cost analysis (e.g., Rogers et al., 2018). This is especially since the costs of restoration operations can likely be reduced by minimizing diver labor and increasing automation/efficacy of mass seeding techniques (e.g., mass dispersal of lab-cultured kelp propagules from boat-mounted pumps; North, 1976).

KELP FOREST RESTORATION: A WORKFLOW

The loss of kelp forests in Australia, and indeed the world, is complex due to high levels of geographic variation and the multitude of different stressors present in any given location. Accordingly, it is useful to apply a workflow and decision framework when approaching restoration (**Figure 3**), especially where this can also provide an indicator of potential local outcomes. Development and preliminary-testing of this workflow utilized examples of kelp loss from Tasmania, where local restoration interventions must consider two species of dominant kelp (i.e., *Ecklonia radiata* and *Macrocystis pyrifera*) and multiple drivers of kelp forest decline (e.g., ocean-warming, overgrazing by urchins).

Our novel workflow and decision support system illustrates multiple alternative pathways and endpoints of restoration, and critically, helps to identify circumstances where restoration is not possible or advisable (also see Johnson et al., 2017). This diversity of pathways and endpoints exists because of environmental factors that are beyond the control of practitioners, such as whether hysteresis is present in the system (e.g., Gorman and Connell, 2009; Johnson et al., 2017). The multiple pathways of kelp forest restoration are also reflective of the diversity of drivers of decline, variability in the resources available for restoration

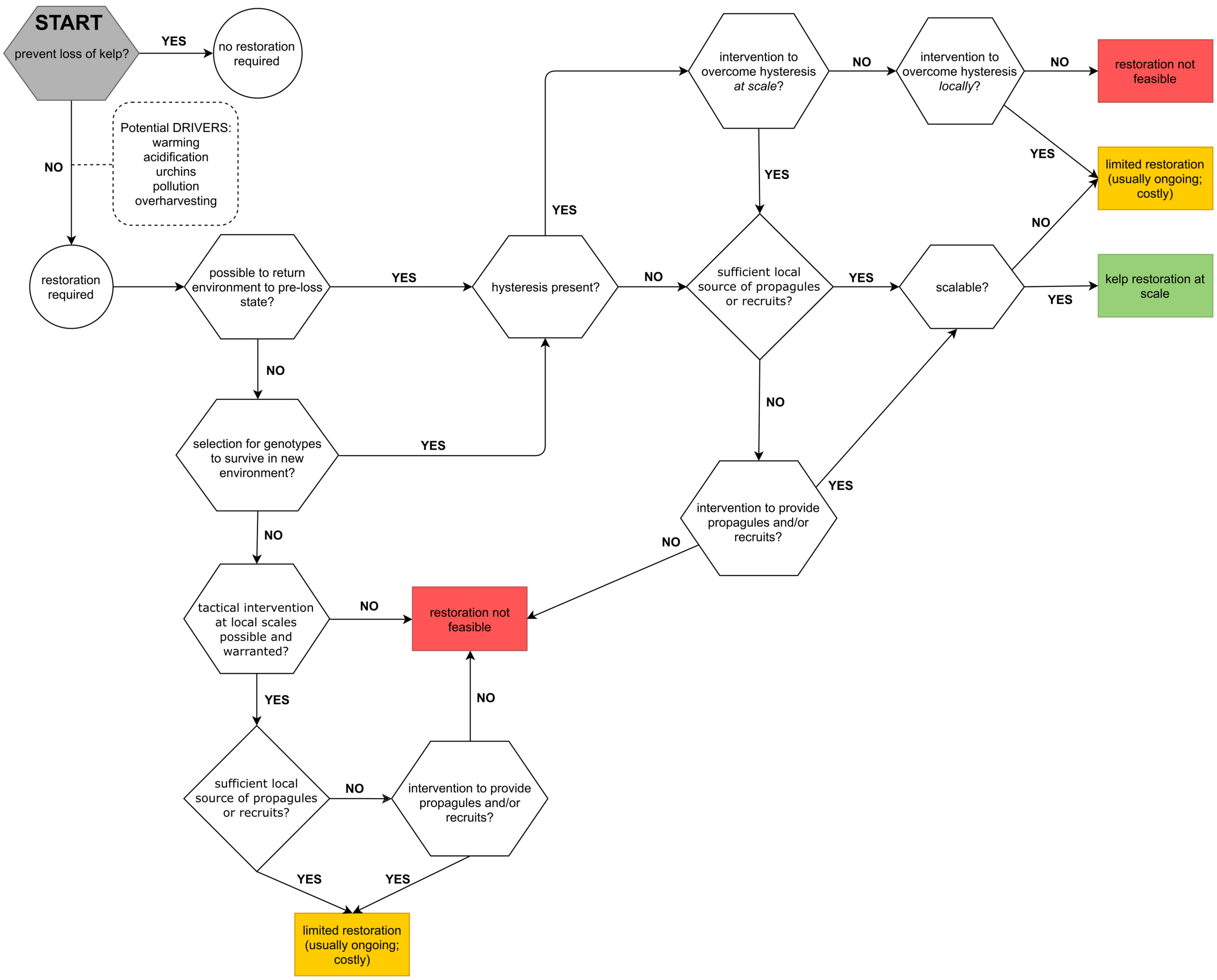

FIGURE 3 | Workflow and decision framework for kelp forest restoration.

efforts, and scalability of the intervention. For example, the efficacy of assisted recovery techniques is often hindered by resource constraints (e.g., Tracey et al., 2015), while active restoration efforts can be reliant on ongoing transplantation of kelp, which has limited scalability.

The workflow highlights that at each node, research is needed to inform decision making and progression to the next stage, and thus may also help identify knowledge gaps in baseline ecosystem knowledge. Using this workflow to plan restoration efforts should also help practitioners and managers to ensure that interventions are considered within resource constraints and that the driver(s) of kelp forest decline has been addressed.

Progressing through the workflow toward the point of successful kelp restoration incorporates several key questions as decision points. Firstly, is it possible to return the environment to its pre-loss state, such as the improvements in water quality that preceded Operation Crayweed? If not, it will be essential to select and facilitate kelp to survive in the new environmental state, for example, the selection for thermally tolerant kelp from remaining healthy individuals (see IMAS 2019). However, if it is not possible to ameliorate or adapt to the novel ecosystem state, restoration efforts will be, at best, limited to the local scale (**Figure 3**). Secondly, is there hysteresis present in the dynamics of the system? Knowledge of the capacity for hysteresis is critical since it can prove one of the biggest challenges to kelp forest restoration (see Gorman and Connell, 2009; Marzloff et al., 2011; Johnson et al., 2017). Lastly, for successful restoration to occur at scale, efforts to overcome hysteresis and/or provide a novel source of propagules must also be scalable, and ideally commensurate with the scale of the initial degradation (Steinberg et al., 2016; Johnson et al., 2017; Wood et al., 2019).

Overall, ensuring natural recruitment of juvenile kelp and the continuation of self-sustaining generations is critical to long-term restoration success. Thus, it is important that kelp forest restoration focus on restoring the positive feedbacks that initiate recruitment and facilitation cascades and which promote ecosystem stability (Halpern et al., 2007; Layton et al., 2019a). To this end, restoration actions should also be considered as tools to bolster resilience in existing and/or partially degraded kelp forests where smaller interventions may be adequate to conserve/restore these feedbacks.

MEASURING THE SUCCESS OF KELP FOREST RESTORATION

Since kelp are foundation species that support diverse ecological communities, comparison of community structure between restored and natural "reference ecosystems" can provide comparative indicators of restoration success at the community-level. However, in some instances reference ecosystems may not be identifiable or available, for example, when there are shifting baselines and poor understanding of ecosystem dynamics (Dayton et al., 1998; Johnson et al., 2017), or where ecosystem loss occurs prior to collection of adequate data (e.g., many Australian shellfish reefs, McLeod et al., 2018). Likewise, reference ecosystems may not be sensible targets for restoration when current/predicted environmental parameters (e.g., water temperature) are different to the historical state or community (Perring et al., 2015; Wood et al., 2019).

These diverse circumstances are acknowledged by the Society for Ecological Restoration (SER) who recognize that a reference ecosystem may instead be a conceptual model synthesized from numerous locations, indicators, and historical and predictive records (McDonald et al., 2016). SER have developed International Standards for the practice of ecological restoration, central to which is the "5-star recovery system" (see McDonald et al., 2016). This tool provides a consistent set of criteria against which key ecosystem attributes can be assessed, and acts as a conceptual framework for restoration practitioners, managers, and regulators. The 5-star system also provides a framework for habitat-specific indicators and metrics to be developed. Such indicators for kelp forest restoration might include transplant survival, growth rates, and condition (e.g., fouling, bleaching, and photosynthetic efficiency), genetic diversity, and recruitment. Certainly, recruitment of juvenile kelp is one of the greatest indicators of ongoing success and kelp forest resilience. In most cases, the ideal goal, as demonstrated by Operation Crayweed, is kelp forest recovery and reestablishment beyond the restoration footprint due to spill-over of natural recruitment.

OPERATION CRAYWEED – A CASE STUDY OF THE SER 5-STAR RECOVERY SYSTEM

Operation Crayweed has been the most successful kelp restoration program in Australia to date. It has evolved from pilot restoration attempts in 2011 (2 sites) through to restoration at the scale of loss in 2018 (11 sites across ~70 km) with further expansion ongoing. It provides an ideal opportunity to apply the 5-star recovery system to a kelp restoration project, especially since science was used to rigorously design and test restoration approaches, thus allowing objective assessment of some recovery attributes. While the recovery wheel is site, scale, and temporally specific, here we apply it to the overall Operation Crayweed initiative (~9 years following initial restoration began) (**Figure 4**).

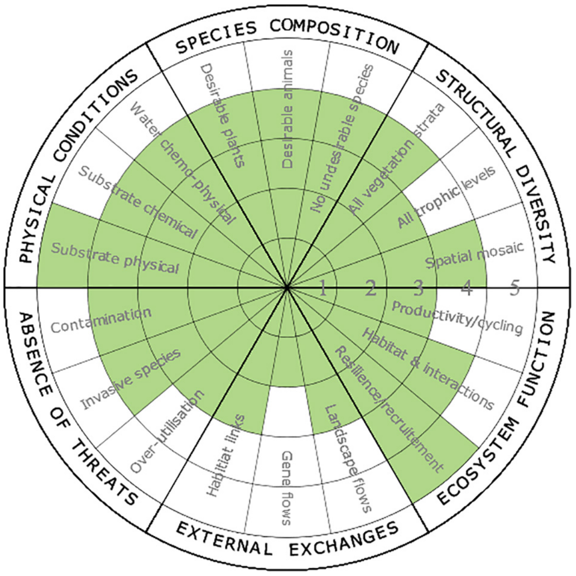

FIGURE 4 | Case study: Assessment of ecosystem recovery by Operation Crayweed using the SER 5-star recovery wheel. Average overall score is 3.7. Conducted by Operation Crayweed researchers (MAC, EMM, PDS, and AV). Individual attribute scores can range from 1 (e.g., biogenic structure restored, and ongoing deterioration prevented, but limited recovery of ecosystem attributes) through to 5 (e.g., restoration has re-established biota and functions that can continue a recovery trajectory without active interventions) (also see McDonald et al., 2016). Ratings are based on both monitoring and scientific publications, as well as expert opinion of the scientists and practitioners involved in restoration.

First, we know that some key aspects of ecosystem function (i.e., recruitment) in restored patches have reached levels found in natural areas (Campbell et al., 2014), warranting a 5-star rating for these attributes. Moreover, species composition of some associated organisms in restored crayweed forests is approaching that of natural forests (Marzinelli et al., 2016) warranting a rating of 4 for "habitat and interactions," Additionally, ongoing monitoring illustrates that the structural diversity of restored crayweed populations are approaching natural levels (Marzinelli et al., 2016; Steinberg et al., 2016), warranting ratings of 3–4. Whilst the physical conditions that likely precipitated the initial decline (i.e., poor water quality, Campbell et al., 2014) have dramatically improved (following improvements to wastewater infrastructure), given the highly urbanized nature of the restoration locations in metropolitan Sydney there are likely to be ongoing threats from contamination; and therefore warrant a rating of 4 for "absence of threats" (e.g., invasive species and contamination) and "physical conditions" (e.g., water chemo-physical). Moreover, these external attributes cannot be controlled within the restoration framework, but are managed and regulated by government.

Targets for other ecosystem attributes are less well defined, have not been measured, or cannot be measured within the temporal scale defined here (due to prolonged response times). Thus, the recovery rating for some attributes is subjective and based on expert opinion of the Operation Crayweed team (MAC, EMM, PDS, and AV). For example, it is premature to assess "external exchanges" (e.g., gene flow) between restored and pre-existing crayweed populations because insufficient time has passed to restore those connections. The collective scientific knowledge of these systems suggests however that restoration of external connections is occurring, since crayweed cover and extent is expanding at some sites without additional intervention (hence the 2–3 star rating). While recovery across multiple trophic levels is being monitored, it is possible that recovery of higher trophic levels may take decades (e.g., Babcock et al., 2010; Reed et al., 2017), especially for species with limited dispersal (e.g., abalone; Marzinelli et al., 2014). The long timescales over which some attributes respond to restoration may therefore be reflected as a low rating, but can still be indicative of an appropriate trajectory of recovery.

The Society for Ecological Restoration considers the mean attribute score as an appropriate measure of a project's progress along a trajectory of recovery. However, depending on project and ecosystem-specific requirements, certain criteria could be weighted to provide a more subtle assessment. For Operation Crayweed, the mean attribute score was 3.7, indicating that restoration of crayweed forests at the local of the initial loss is well under way, with high levels of recruitment and good progress toward development of associated communities and ecosystem functions that are on a self-sustaining trajectory. While the mean score and individual recovery attributes could be used as a tool to identify areas requiring ongoing active restoration to accelerate recovery, we believe that it is sufficient to restore populations to a point whereby they can continue on a recovery trajectory naturally, without additional intervention. This is not only cost effective but ensures that limited resources can be strategically directed to maximize restoration efforts across species and ecosystems in need. Regardless, recovery of restored crayweed populations will continue to be measured and assessment of the need for additional interventions will be re-examined on an ongoing basis. The SER recovery system provides assessment of the trajectory of ecosystem recovery but also identifies research gaps. For Operation Crayweed, areas that would benefit from future research include assessing whether crayweed restoration has resulted in recovery of broader ecosystem functions and services (e.g., productivity and recreational fishing) and whether there is increased connectivity among adjacent non-kelp forest habitats (e.g., seagrass).

CONCLUSION

While kelp forest restoration is not achievable or feasible in all situations, use of a decision framework and consideration of the initial drivers of decline should increase the likelihood of success and the appropriate use of resources. And while past examples of kelp forest restoration are as notable for the failures as the successes, it seems that under many circumstances, small to medium scale restoration is achievable. For example, Operation Crayweed has demonstrated positive ecological outcomes at a scale beyond their initial restoration intervention. However, increasing the scalability of kelp forest restoration to the seascape-scale remains a considerable challenge, as does restoration in response to climate change where drivers of decline cannot be readily ameliorated (e.g., ocean warming). Optimal results will be achieved via thorough planning of restoration interventions and where positive feedbacks in the dynamics of kelp forests can be harnessed to promote habitat resilience and recruitment of juvenile kelp.

It follows however that the challenges and costs inherent in restoring kelp forests ecosystems places a great emphasis on the importance of maintaining and conserving kelp habitats. The difficulty of restoring heavily degraded environments – such as expansive urchin barrens and turf algae habitats – reinforces the notion that "an ounce of prevention is worth more than a ton of cure." Ultimately, the management and conservation of Australian kelp forests should adopt policies that facilitate early warning and intervention for kelp environments under threat, with the aim to maintain and restore resilience in these critically important habitats.

AUTHOR CONTRIBUTIONS

CL and CJ conceived the initial idea for the review. CL prepared the manuscript with input from all other authors. All authors contributed to manuscript revision.

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REVIEW
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Positive Ecological Interactions and the Success of Seagrass Restoration

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Seagrasses provide multiple ecosystem services including nursery habitat, improved water quality, coastal protection, and carbon sequestration. However, seagrasses are in crisis as global coverage is declining at an accelerating rate. With increased focus on ecological restoration as a conservation strategy, methods that enhance restoration success need to be explored. Decades of work in coastal plant ecosystems, including seagrasses, has shown that positive species relationships and feedbacks are critical for ecosystem stability, expansion, and recovery from disturbance. We reviewed the restoration literature on seagrasses and found few studies have tested for the beneficial effects of including positive species interactions in seagrass restoration designs. Here we review the full suite of positive species interactions that have been documented in seagrass ecosystems, where they occur, and how they might be integrated into seagrass restoration. The few studies in marine plant communities that have explicitly incorporated positive species interactions and feedbacks have found an increase in plant growth with little additional resource investment. As oceans continue to change and stressors become more prevalent, harnessing positive interactions between species through innovative approaches will likely become key to successful seagrass restoration.

Keywords: coastal management, facilitation, positive species interactions, seagrass restoration, seagrass

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INTRODUCTION

Seagrasses are present on the coasts of all continents except Antarctica and are among the most productive ecosystems on Earth (Hemminga and Duarte, 2000; Green and Short, 2003). They provide habitat for multiple life stages of many commercially- and recreationally-important fishes, shellfish, and crustaceans, improve water quality, sequester carbon, stabilize sediment, and reduce coastal erosion (Nagelkerken et al., 2000; Jackson et al., 2001; Heck et al., 2003; Orth et al., 2006; Fourqurean et al., 2012; Duarte et al., 2013; James et al., 2019; Lefcheck et al., 2019). However, the total area covered by seagrass is estimated to have declined by 30–60%, including total loss in some places (Evans et al., 2018). Losses of seagrasses have been caused by anthropogenic influences including direct removal during coastal development (e.g., harbors, marinas, and channels), destructive fishing methods (such as trawling), run-off of nutrients and other pollutants from land-based sources, and climate change (Short and Wyllie-Echeverria, 1996; Orth et al., 2006;

Hughes et al., 2013; He and Silliman, 2019). The causal mechanisms typically involve increased frequency and intensity of stressors such as light reduction, extreme weather events (e.g., heat waves or cold snaps), high nutrient concentrations, and poor sediment conditions (e.g., high sulfide concentrations).

With recognition that seagrass habitats — together with the many ecosystem services they offer — are in decline globally (but see Santos et al., 2019), conservation and restoration of seagrass has renewed urgency. Historically, seagrass conservation has focused on decreasing environmental stressors (e.g., nutrients and sediment that affect water quality, Lefcheck et al., 2018). In addition, many restoration efforts have typically been conducted across small spatial extents limited to a few hectares. This is partly because of a perception that efforts would yield limited success (∼30%), and partly because of the time and money required for the methods used (Fonseca et al., 1998; Orth et al., 2006), which have included planting of shoots sourced from elsewhere (Cambridge et al., 2002) to broadcast of seeds (Orth et al., 2012), and deployment of substrata to enhance settlement of propagules (Tanner, 2015). Recent successes have demonstrated that active restoration of seagrass beds can be an important tool to facilitate recovery of seagrass meadows (Orth et al., 2012; Statton et al., 2014; van Katwijk et al., 2016; Statton et al., 2018).

Often, seagrass restoration is focused on reducing physical stressors (Bastyan and Cambridge, 2008) and or avoiding negative intraspecific interactions to enhance outplant growth (i.e., dispersed planting methods, Williams, 1987; Rose and Dawes, 1999; Worm and Reusch, 2000). However, positive interactions such as mutualism and facilitation are common in seagrass ecosystems (Peterson and Heck, 2001; Bruno et al., 2003; Van der Heide et al., 2007; Zhang et al., 2018). In tidal marshes, inclusion of positive interactions in restoration has shown recent success (Silliman et al., 2015). Whether such positive interactions might help improve seagrass restoration has rarely been explored. Given they are widespread, it is plausible that judicious inclusion of positive intra- and inter-species interactions into the design of restoration programs might also enhance seagrass restoration.

Amid growing international recognition of the importance of ecological restoration to return ecosystem services (e.g., the United Nations Decade of Ecological Restoration 2021–2030), restoration practices need to innovate to achieve increasingly ambitious goals. Positive interactions are worth examining to see if they can contribute to this innovation. In this paper, we review positive species interactions in seagrass ecosystems (**Figure 1**), and provide suggestions for research and restoration that, if implemented, has the potential to improve the outcomes of seagrass restoration.

POSITIVE DENSITY DEPENDENCE

Positive density dependence occurs when an increase in the density of conspecifics improves survival and reproductive success of an individual or population (Allee, 1931). Classic examples of positive density dependence include prey avoidance behavior in areas of high predation (i.e., nesting seabirds or schooling fish, Neill and Cullen, 1974; Oro et al., 2006). Alternatively, positive density dependence might be prevalent in areas where environmental stress is high and could be a mechanism to support ecosystem resilience (Bertness and Callaway, 1994; Callaway et al., 2002; Gross et al., 2010; Silliman et al., 2011, 2015; He et al., 2013). Restoration is potentially a high-stress scenario, as some sites are less than ideal for growth and survival. Overcoming restrictions to growth and survival (biotic or abiotic), can be challenging (Hobbs and Harris, 2001), but the limited evidence available suggests that positive density dependence might help.

For seagrasses, positive density dependence has been shown to be important for successful reproduction. Several seagrass species are pollen-limited (van Tussenbroek et al., 2016), leading to a prediction that restoration success might be improved if we are able to increase density of seeds or shoots, because this could eventually led to increased density of flowering shoots, and thus more seeds to facilitate natural recovery. Furthermore, positive density dependence has been observed in seagrass colonization and patch survival. In both *Zostera marina* and *Posidonia oceanica* beds, higher number of shoots in a patch increased survival and patch expansion (Olesen and Sand-Jensen, 1994; Almela et al., 2008). Indeed, van Katwijk et al. (2016) found, from a global meta-analysis, that seagrass restoration success increased by 20% when large enough numbers (<100000) of shoots or seeds are used. They hypothesized that this was because it spreads risk over time and space as well as allows for net positive feedbacks that promote growth and reproduction — mechanisms intrinsic to positive density dependence. Furthermore, recent restoration efforts support the idea of positive density dependence. Paulo et al. (2019) found larger transplant areas with more shoots had greater long-term survival and expansion than smaller plots. This is likely due to a breached threshold that confers protection from winter storms.

Although planting large numbers of seagrass shoots or seeds might initially be beneficial, the spatial arrangement need to be considered with caution as some work has shown negative effects of self-shading in meadows that are too dense (Ralph et al., 2007). Similar to salt marshes and mangroves, seagrass establishment likely also benefits from aggregated rather than dispersed planting arrangements under stressful conditions (**Figure 2**, Gedan and Silliman, 2009; Silliman et al., 2015).

Indeed, a growing body of literature suggests that positive density dependence is important to seagrass ecosystems as seagrasses can facilitate their own growth via multiple feedbacks. Moreover, theory suggests that such positive feedbacks can cause alternative stable states (Van der Heide et al., 2007; Maxwell et al., 2017). However, the ability to breach thresholds and achieve beneficial stable states is complex. In seagrass, there is the potential for several feedbacks that dictate ecosystem states and limiting factors are potentially nested within such feedbacks (Maxwell et al., 2017). Maxwell et al. (2017) suggests that identifying feedbacks such as positive density dependence in limited reproduction or stressful environmental conditions may aid seagrass recovery. The little work that has been done on positive density dependence in seagrass restoration illustrates the need for further exploration into how intraspecific facilitation may be harnessed to improve success and change stable states.

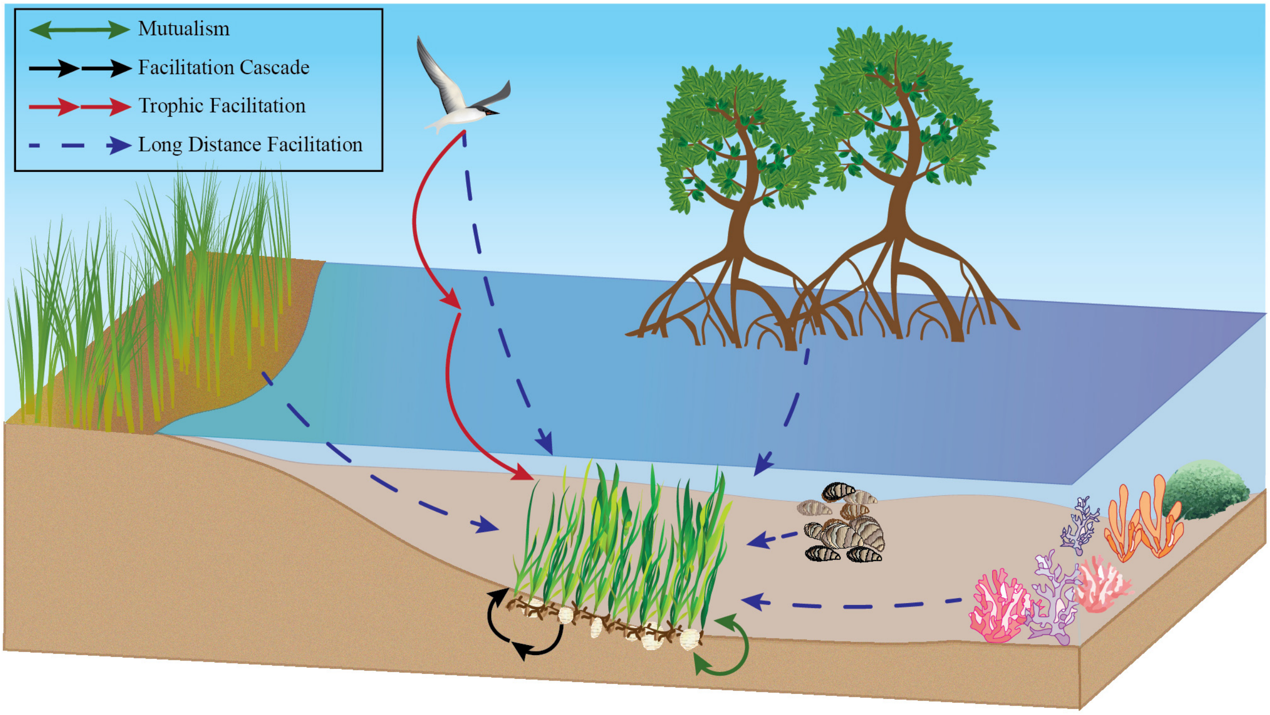

FIGURE 1 | Conceptual drawing of many positive interactions impacting seagrass. This includes but is not limited to long distance facilitation with corals, oysters, mangroves, seabirds, and salt marshes, mutualisms between seagrass and lucinid clams, and facilitation cascades of bivalves in seagrasses as examples.

SYMBIOTIC, INTERSPECIFIC MUTUALISMS

Interspecific mutualism is an interaction between two species that benefits both. Interspecific mutualisms have been well-documented in marine systems. For example, cleaner shrimp interactions with fish and the sea anemone interactions with clownfish (Mariscal, 1970; Bshary and Grutter, 2006). Likewise, in salt marshes, aggregates of mussels deposit nutrients into the soil, enhancing growth of smooth cordgrass (*Spartina alterniflora*) — in return the mussels receive a refuge from heat stress and predation (Angelini et al., 2015; Bilkovic et al., 2017).

Similarly, mutualism has been shown between seagrass and mussels. Peterson and Heck (2001) found that in the presence of filter-feeding mussels (*Modiolus americanus*) that likely transfer particulates and nutrients in the water column to the sediment, seagrass (*Thalassia testudinum*) growth rates and blade width increased, while epiphyte load decreased. Moreover, mussel survival rates increased in the presence of seagrass. Another mutualism occurs between seagrasses and the lucinid clams which harbor sulfide-oxidizing bacteria in their gills that limit toxic sulfide compounds (Van der Heide et al., 2012). While the lucinid clam and its associated bacteria benefit from nutrients sequestered by plant roots (Van der Heide et al., 2012). Seagrass shoot biomass increased 1.4–1.9 fold and root biomass increased 1.3–1.5 fold in treatments where lucinid bivalves were present. In treatments with sulfide addition and no lucinids, seagrass shoot biomass was half that of controls.

While recent work has documented the recovery of mutualisms in seagrass (e.g., recovery of seagrass and associated epifauna) after large-scale restoration in mid-Atlantic coastal bays (Lefcheck et al., 2017). There are no published examples of mutualisms incorporated into seagrass restoration. Restoration in salt marshes with mussel addition (Derksen-Hooijberg et al., 2018) and coral reef with sponge addition (Biggs, 2013) illustrated the creative ways in which mutualisms can be incorporated to enhance restoration. Given the common occurrence of mutualisms in seagrass, we believe there is a strong possibility that restoration outcomes would improve with their inclusion.

SEAGRASS- MICROBE INTERACTIONS

Microorganisms, which live within (endophytic) and on the surface of (epiphytic) plants, can profoundly influence plant health and productivity by inducing physiological or biochemical changes within their host (Bacon and White, 2016). They increase nutrient availability, by nitrogen fixation and mineralization of organic compounds, producing phytohormones that promote root and shoot development, and alleviate plant stress (Baligar et al., 2001; Vessey, 2003; Mantelin and Touraine, 2004). Some bacteria facilitate plants by actively detoxifying heavy metals (Lloyd and Lovely, 2001; De et al., 2008; Rajkumar et al., 2012) while others can assist and promote plant growth under high metal stress by directly

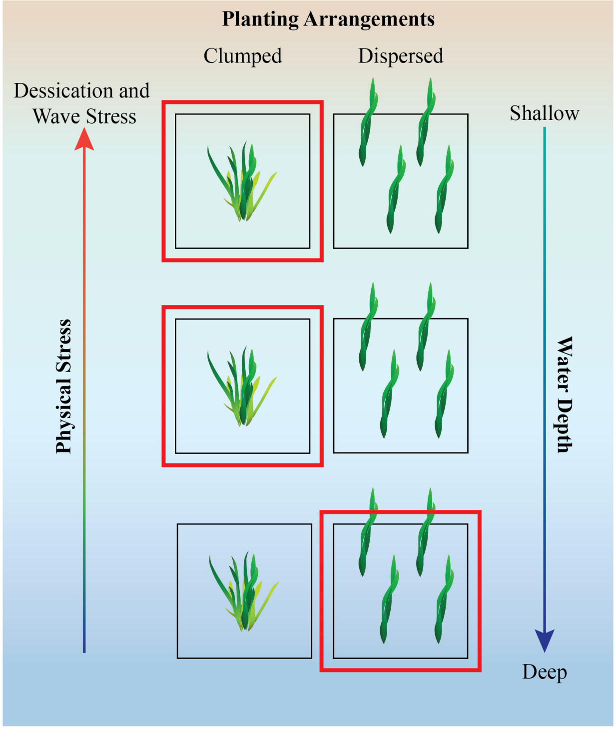

FIGURE 2 | Illustration of experimental design and hypothesis of planting design for seagrass along stress gradients. Hypothesized beneficial planting method is denoted by the red box. In a low stress environment, dispersed planting method may work well but in the face of environmental stress, clumped planting is likely to alleviate some stress via neighbor facilitation (Silliman et al., 2015). Figure inspired by a figure in Renzi et al. (2019).

providing nutrients, phytohormones, and enzymes (Burd et al., 2000; Sheng et al., 2008).

Yet, our knowledge of plant-microbial interactions in the marine environment is limited. However, recent work in salt marshes suggests they could be important. Daleo et al. (2007) showed that mycorrhizal fungi facilitates nutrient uptake in dense-flowered cordgrass (*Spartina densiflora*). Seagrasses also form symbiotic relationships with a variety of microorganisms (bacteria, archaea, and fungi) both above- and belowground (Venkatachalam et al., 2015; Garcias-Bonet et al., 2016; Tarquinio et al., 2019). For example, seagrass association with sulfide-oxidizing bacteria alleviates toxic sulfate accumulation (Cúcio et al., 2016; Martin et al., 2019). Sulfide-oxidizing bacteria associated with the seagrass rhizosphere have not only been linked with reduction of toxic soil conditions, but also with higher biomass and more complex rhizome structures (Welsh, 2000). Some bacteria (such as Actinobacteria and Cyanobacteria) present on leaves and roots of seagrasses synthesize a wide range of antimicrobial molecules. These bacteria may protect plants by releasing bioactive compounds that selectively target pathogens and biofouling organisms, as has been found in kelp (Egan et al., 2013). On the other hand, some species of sulfide-oxidizing bacteria could indicate poor environmental conditions for seagrass. Mat forming *Beggiatoa* have been associated with decline of seagrass (Elliott et al., 2006).

Given the limited, but potentially beneficial microbial interactions in seagrass, future research needs to be conducted before use in restoration. Research should test the types of interactions occurring between seagrass and microbes, the benefits or consequences seagrass accrues, and the methods for implementation into a restoration framework.

TROPHIC FACILITATION

Trophic interactions can facilitate survival and growth indirectly. For instance, herbivores can promote specific plant species by selectively feeding on their competitors. Plants can also be facilitated indirectly by consumers in simple three-level food chains via a trophic cascade. In these interactions, plants benefit from higher trophic levels that suppress the abundance or behavior of herbivores that would otherwise eat the plants (**Figures 1**, **3**). A classic example of a trophic cascade is sea otters' maintenance of kelp forests through the removal of kelp-eating sea urchins (Estes and Palmisano, 1974).

Prolific epiphytic macroalgae on seagrass blades can sometimes form aggregations that drift over meadows, negatively affecting seagrass (Silberstein et al., 1986; Drake et al., 2003; Heck and Valentine, 2006). Associated invertebrates often keep epiphyte abundance low (Heck and Valentine, 2006; Cook et al., 2011), which has shown to improve seagrass growth, production, and increase secondary production (Montfrans et al., 1984; Neckles et al., 1993; Duffy et al., 2003). Vertebrates such as great blue herons (*Ardea herodias*) and sea otters (*Enhydra lutris*) have also been shown to regulate biomass of seagrass epiphytes through trophic cascades, in which the consumption of fish and crustaceans increases the abundance of grazing invertebrates (Hughes et al., 2013; Huang et al., 2015). Alternatively, seagrass can be directly grazed upon. Seagrass herbivory by macrograzers (i.e., fish) and megagrazers (i.e., turtles and dugongs) are important to maintaining ecosystem function and reproduction in balanced ecosystems (i.e., systems with predators, grazers, and seagrasses) (Tol et al., 2017; Scott et al., 2018). With the loss of predators and conservation of large herbivores without habitat consideration, it is suggested that seagrass ecosystem functions could be lost from uncontrolled rates of grazing (Burkholder et al., 2013; Christianen et al., 2014; Heithaus et al., 2014; Scott et al., 2018).

Top predator introduction and herbivore management as methods for conservation is not a new idea. However, the generality of these chains of interactions, and how we might use them to benefit seagrass restoration, is not well-known. It is possible that predator introduction or recolonization might help stabilize or reverse seagrass decline in some places (Silliman et al., 2018). Predator addition is unlikely to be effective in areas where the cause of predator loss is unknown or seagrass has been completely lost, unless viable sources of propagules are nearby. Joint reintroduction of predators and seagrass restoration or consideration of sites with established predator populations might mitigate stressors in some conditions, especially where

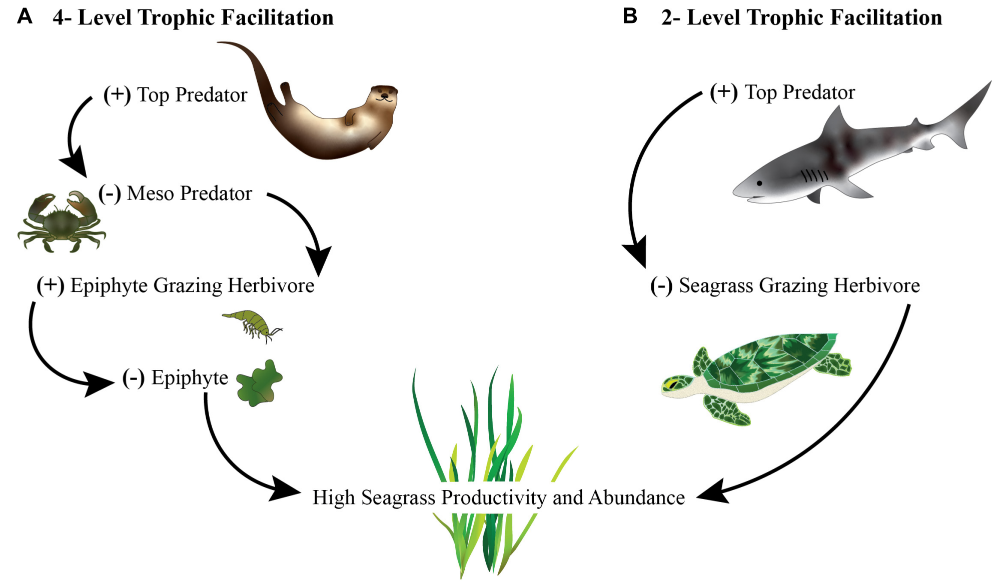

FIGURE 3 | Illustration depicting trophic facilitations where: **(A)** indirect consumption by top predators (sea otters) creates a cascade effect reducing mesopredators (crabs), increasing mesograzers (herbivorous invertebrates) that remove harmful epiphytes on seagrass that result in increased seagrass or **(B)** direct consumption or removal of seagrass eating herbivores (turtles) by top predators (sharks) maintains seagrass.

epiphyte consumers are uncommon, seagrass consumers are common, or nutrient concentrations are high.

LONG-DISTANCE FACILITATION

Interspecies, positive interactions are not limited to close proximity. Long distance facilitation occurs when a species is benefited by another that is not in direct physical contact (van de Koppel et al., 2015). This interaction is unique from the symbiotic mutualisms described above as physical contact between the interacting species does not occur and the positive effect is one-way, not requiring a feedback.

A recent review has shown long distance facilitations are important for maintaining stability and resilience in many marine ecosystems, including seagrasses. In this review, van de Koppel et al. (2015) describes how long-distance facilitations may mitigate light limitation, nutrient stress, and physical stress on seagrasses — which are all challenges in restoration. Light limitation can be reduced by non-sympatric bivalve reefs and mangroves that remove particulates from the water (Newell and Koch, 2004; Gillis et al., 2014; van de Koppel et al., 2015). Nutrient limitation can be improved in several ways by long distance facilitation as nutrient input from nearby but not overlapping mussel reefs (Reusch et al., 1994; van de Koppel et al., 2015), mangroves (Mohammed et al., 2001), bird colonies (Powell et al., 1991), and kelp forests (Wernberg et al., 2006; Hyndes et al., 2012) can improve plant growth. Alternatively, the negative effects of eutrophication on seagrass are diminished by the interception and burial of nutrients by salt marshes and mangroves (Valiela and Cole, 2002). Finally, physical stress on seagrass such as wave action can be reduced by coral and bivalve reefs (Moberg and Folke, 1999; Ferrario et al., 2014; van de Koppel et al., 2015). Incorporating long-distance facilitations into site selection for seagrass restoration is likely to benefit planting successes, but much more research is needed to understand context dependency of this type of interaction and the physical conditions under which it is likely to be most beneficial.

FACILITATION CASCADES

Facilitation cascades are indirect positive effects that emerge from direct facilitations. A non-trophic example is when a primary foundation species facilitates a secondary one which, in turn, enhance biodiversity (Altieri et al., 2007). This particular facilitation cascade is called a habitat cascade. A recent review, Thomsen et al. (2018) shows that these facilitation cascades occur across all ecosystems and their impacts on biodiversity is measurable.

The role of seagrasses as primary foundation species that facilitate other organisms suggests facilitation cascades might be widespread. For example, seagrasses can be epiphytized by a range of taxa including algae, bryozoans, and sponges (Borowitzka and Lethbridge, 1989), which in turn have been shown to provide food and shelter for a range of small invertebrates (Jernakoff et al., 1996). Interactions in *Zostera muelleri* meadows found that razor clams, *Pinna* sp. formed a complex array of positive and negative interactions culminating in a net increase in overall diversity when live clams were present (Gribben et al., 2017). Another study found that density of pen clams (*Atrina rigida* and *Atrina serrata*) were positively associated with eelgrass (*Z. marina*) and that in the presence of pen clams, diversity of animals in the meadow increased (Zhang and Silliman, 2019). Although these studies did not observe a change in seagrass growth and production during the study period, others have found that an increase in overall biodiversity can lead to more stable and productive seagrass habitat as well as buffer ecosystems from changing conditions (Duffy, 2006).

As facilitation cascades are a research frontier, their importance and occurrence in seagrasses is mostly unexplored. However, given the effect size they have in other systems, their importance could be high. Future research should test generality and impacts of facilitation cascades in seagrass systems, and, if found, systematically test how addition of secondary foundation species impacts seagrass restoration success, both in terms of plant growth and increased overall system functioning (e.g., provisioning of biodiversity).

BIODIVERSITY AND ECOSYSTEM FUNCTION

Biodiversity can refer to genetic, species, and functional diversity of an ecosystem. Increased biodiversity can facilitate healthier, more productive ecosystems that are resilient to disturbance and stable due to a repetition in functional groups (Chapin et al., 2000; Reed and Frankham, 2003; Hooper et al., 2005; Hughes et al., 2008; Hensel and Silliman, 2013). Given these findings, ecosystem restoration is likely to benefit from inclusion of similar intra- and interspecies diversity facilitations.

Globally, there are 72 seagrass species, ranging from temperate to tropical climates with many of them co-occurring (Orth et al., 2006). Traditional ecological theory suggests that the presence of co-existing species would create competitive interactions (McGilchrist, 1965; Hassell and Comins, 1976). However, some studies suggest that the co-existence of seagrass species is beneficial, especially in areas of frequent disturbance where interspecies diversity increases ecosystem resilience (Williams, 1990). Williams et al. (2017) found that increased species richness of seagrasses also increased transplant success. They hypothesized that the mechanism underlaying this effect was niche partitioning of resources and a diversity of growth patterns. Restoring multiple species, if originally present, could restore function and self-reliance in the system (Duffy, 2006). To make our knowledge about seagrass diversity more impactful in restoration more research in multispecies conditions is needed.

Species diversity is not the only means of diversity to consider for seagrass restoration. Genetically diverse populations are often more productive in stressful environments (Hughes and Stachowicz, 2009). Unlike previous topics in this paper, genetic diversity has been studied and even considered in seagrass restoration. The studies that implemented genetic diversity into their restoration scheme observed increased restoration

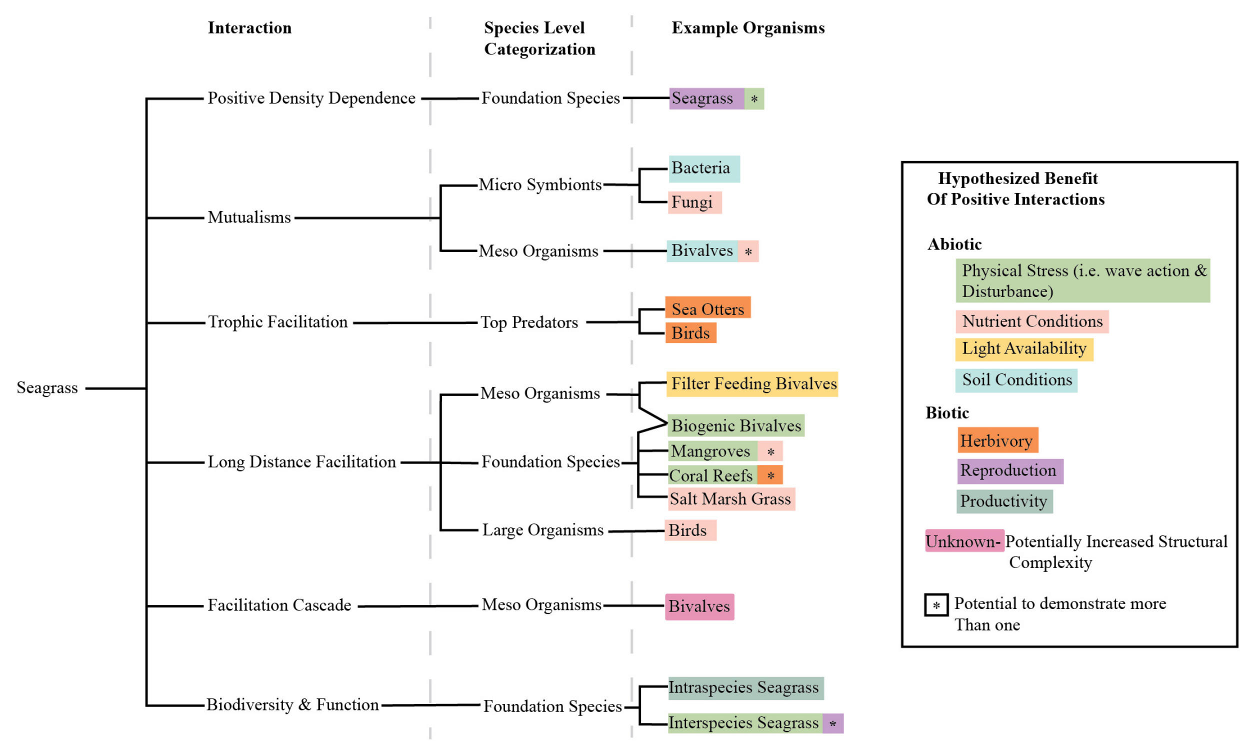

FIGURE 4 | Tree diagram of interactions discussed in this paper, organismal level at which we think they are prevalent, and examples of organisms that have been observed having these interactions with seagrasses. Organisms are color coded by the alleviation they likely have on seagrasses. In some cases, organisms can demonstrate many beneficial roles denoted by an asterisk color coded by another effect. The primary and secondary coloration of the word and asterisk are arbitrary and do not denote strength of the effect.

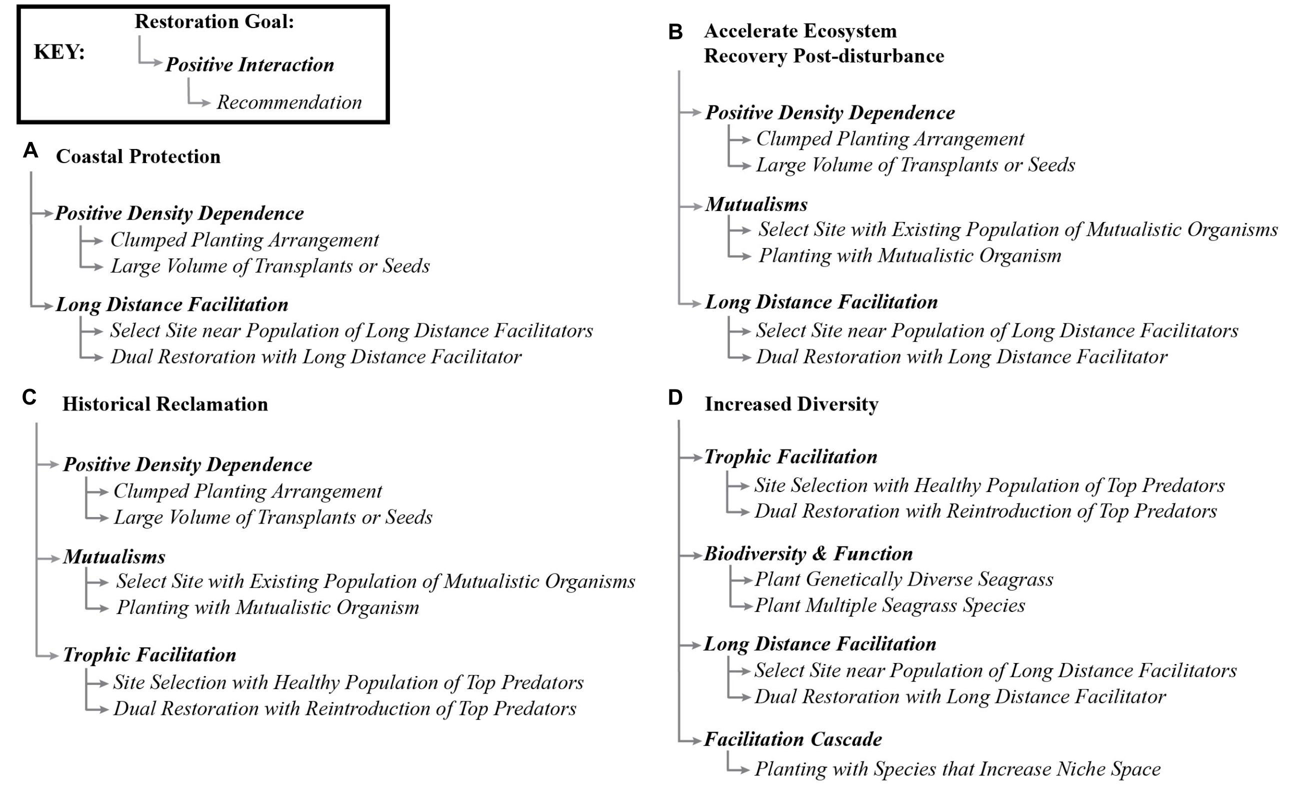

FIGURE 5 | Conceptual map of some common restoration goals (Yap, 2000) and the positive interactions that could be used to accomplish such goals, and brief recommendations of how to explore the positive interactions as a starting point for researchers and practitioners.

success (Williams, 2001; van Katwijk et al., 2009; Reynolds et al., 2012). It is thought that donor populations from already stressful environments will be better adapted to restoration site conditions (Franssen et al., 2014; Marín-Guirao et al., 2016; Tutar et al., 2017). As well, diverse populations spread the risk of complete collapse by a single stressor (van Katwijk et al., 2009). Considering genetic variation in donor populations that have similar habitats to restoration sites and account for a variety of stressors could be valuable in restoration planning.

CONCLUSION AND RECOMMENDATIONS

Restoration is increasingly becoming an important component in conservation. Restoration of seagrass has mostly been limited in extent with generally low success (Statton et al., 2018). As seagrass restoration continues to mature, practices will improve. We suggest that incorporation of knowledge gained through ecology will help accelerate improvement. Incorporating positive interactions into restoration methods appears to be a promising avenue for restoration research and practice. However, positive interactions are likely not a shortcut to restoration success but rather a complimentary method to traditional methods.

Traditionally, marine restoration has focused on systematically reducing stressors. Here, we propose to expand the perspective on seagrass restoration to also include systematic reduction of physical stressors, but to also methodically incorporate positive species interactions (**Figure 4**). This means that efforts to improve water and sediment conditions should be continued and that positive interactions should be additionally included in such efforts. Of course, the expression of positive and negative interactions in a system vary depending on the organisms available, environmental conditions, and site characteristics (He et al., 2013), and this will be reflected in restoration approaches that are sensitive to these contexts. However, our review shows that seagrasses participate in many potential positive interactions that could be usefully harnessed to enhance restoration success. Many studies have considered the balance between positive and negative interactions and the layering of human and biological interventions, but none have discussed the potential to harness these in seagrass restoration (Bertness et al., 1999; Maestre et al., 2003; Cheong et al., 2013). We suggest that researchers and restoration practitioners should consider positive interactions as an untapped resource with potential to enhance seagrass restoration goals (**Figure 5**). Progress will be facilitated if researchers and practitioners work in tandem to test the potential of a range of positive interactions to improve restoration.

Many positive interactions are not fully understood — for example the role of microbes and facilitation cascades — so we encourage researchers to develop an understanding of such interactions so that they can be effectively applied in restoration. This is not without challenges in these complex, sometimes distant interactions, especially where ecosystems develop slowly. The inclusion of positive interactions into restoration will not occur simultaneously but should be considered as research progresses. In this paper, we have outlined a broad suite of positive interactions, shown how they are expressed in seagrass ecosystems, and offered some ideas about how they might be used to enhance restoration. Below, we outline a restoration and research framework that deserve further consideration to enhance future seagrass restoration:

(1) State clearly restoration goals — this will help understand whether positive interactions are applicable and which ones.
(2) Test whether planting arrangements (e.g., dispersed versus clumped) and number of units (plants, shoots, seeds, or other units) improve survival, growth and reproduction in a variety of contexts.
(3) Include bivalves (such as lucinid clams or mussels) when planting seagrass to help improve survival and growth, and test different arrangements and methods of including them.
(4) Determine sites near established mangroves, coral reefs, or oyster that generate potential long-distance facilitations.
(5) Identify sites with intact assemblages of seagrass facilitating herbivores and predators.
(6) Design restoration projects with initial cohorts that are genetically diverse, selecting transplant units (such as whole plants or seeds) from several distinct parent populations to increase resiliency.
(7) Test whether restoration using multiple species of seagrasses, in different arrangements, improves restoration success in places where seagrass diversity is naturally high.
(8) Consider restoring ecosystems rather than single, target species.

AUTHOR CONTRIBUTIONS

BS conceived the idea for the manuscript. SV wrote the manuscript with additions from FT on microbial interactions. SV created all figures. BS, TH, YZ, FT, MV, and RO provided comments and improvements.

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POLICY AND PRACTICE REVIEWS
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Habitat Features and Their Influence on the Restoration Potential of Marine Habitats in Europe

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To understand the restoration potential of degraded habitats, it is important to know the key processes and habitat features that allow for recovery after disturbance. As part of the EU (Horizon 2020) funded MERCES project, a group of European experts compiled and assessed current knowledge, from both past and ongoing restoration efforts, within the Mediterranean Sea, the Baltic Sea, and the North-East Atlantic Ocean. The aim was to provide an expert judgment of how different habitat features could impact restoration success and enhance the recovery of marine habitats. A set of biological and ecological features (i.e., life-history traits, population connectivity, spatial distribution, structural complexity, and the potential for regime shifts) were identified and scored according to their contribution to the successful accomplishment of habitat restoration for five habitats: seagrass meadows, kelp forests, *Cystoseira* macroalgal beds, coralligenous assemblages and cold-water coral habitats. The expert group concluded that most of the kelp forests features facilitate successful restoration, while the features for the coralligenous assemblages and the cold-water coral habitat did not promote successful restoration. For the other habitats the conclusions were much more variable. The lack of knowledge on the relationship between acting pressures and resulting changes in the ecological state of habitats is a major challenge for implementing restoration actions. This paper provides an overview of essential features that can affect restoration success in marine habitats of key importance for valuable ecosystem services.

Keywords: degraded habitats, restoration success, recovery, seagrass, macroalgae, coralligenous assemblages, corals

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INTRODUCTION: DEGRADATION AND RESTORATION OF HABITATS IN EUROPEAN SEAS

For centuries humans have been reliant upon the ocean as a source of food, transport, and leisure. As resources become increasingly scarce and populations continue to grow, we are progressively turning to the coasts and oceans to drive the global economy and stimulate innovation and growth (EC, 2018). The potential for economic opportunities in the coastal region is great, resulting in convergence of different activities, such as shipping, tourism and energy production, alongside traditional resource-based activities, such as coastal fisheries, seaweed harvesting, and aquaculture. There is now ample evidence that such opportunities come with significant environmental risk and costs (e.g., Ramirez-Llodra et al., 2011; Halpern et al., 2015). Human activities exert considerable pressure on ecosystems and resources through pollution, over-exploitation of resources, introduction of invasive species and habitat clearance and fragmentation (Dailianis et al., 2018; Gerovasileiou et al., 2019). Together, such activities are resulting in a decline in biodiversity, a reduction in the capacity of the oceans to provide ecosystem goods and services (Worm et al., 2006; EEA, 2015) and increased vulnerability of marine ecosystems to additional pressures such as climate change and ocean-acidification stressors (Folke et al., 2004).

In an attempt to reverse the current level of degradation within European seas, the EU Biodiversity Strategy 2020 aims to restore at least 15% of degraded ecosystems by 2020, in accordance with the 2010 Aichi targets and the UN 2030 Agenda for Sustainable Development[1]. However, whilst marine restoration actions are common in many areas of the world, their success rate is highly variable. For instance, whilst 65% of tropical coral reef and salt marsh restoration projects successfully achieved their goals, seagrass restoration has had a success rate of only 38% (Bayraktarov et al., 2016; van Katwijk et al., 2016). Variation in restoration success stems from different sources, including the inherent biology and ecology of species, including their interactions (Kilminster et al., 2015) and how, where and when restoration is conducted (Montero-Serra et al., 2018a). This variation leads to uncertainty in terms of conservation outcomes and economics. Consequently, there is a need to develop robust methodologies to effectively restore habitats and deliver the full range of conservation and socioeconomic benefits that can be derived (Elliott et al., 2007).

Historically, research on restoration best practices and methods has mainly focused on terrestrial, rather than on marine, ecosystems. Even though several of the basic principles developed in terrestrial systems can be used in the marine realm (van Dover et al., 2014; Da Ros et al., 2019), the knowledge on which factors are enhancing or limiting restoration success is very limited for the marine environment. The H2020 MERCES project[2] aims to enhance the European Union's capacity to restore degraded marine ecosystems and habitats and the ecosystem services they provide. As part of this effort, the present paper seeks to structure and discuss the existing knowledge amongst leading European experts on the restoration potential of some important marine habitats within Europe. The discussion includes the biological and ecological features that determine the habitats' sensitivity to human pressures and thereby modulate the success of restoration actions. This information will provide the basis for knowledge-based guidelines of how to advance marine ecosystem restoration and increase the political and management willingness to initiate restoration actions.

THE APPROACH

A total of 25 experts representing 11 European countries, from Norway and Finland in the north to Crete in Greece in the south, was part of a MERCES initiated workshop to discuss habitat restoration activities. The group had expertise on species biology and ecology, covering key habitats found within the Mediterranean Sea, the Baltic Sea, and the NE Atlantic Ocean. A set of focal habitats were selected (section Selection and Description of the Target Habitats), and the experts were asked to suggest and agree on a set of key biological and ecological features (section Selection of Habitat Features and Assessment ("Scoring") of the Restoration Potential) that were important to the recovery of these habitats. Following this discussion, each feature was discussed in terms of their relevance to the recovery potential, in general and for each habitat separately. The agreed-on features and characteristics were based on knowledge from both past and ongoing restoration efforts, within the European seas. The aim was to provide a consensual judgment (a "scoring," section Selection of Habitat Features and Assessment ("Scoring") of the Restoration Potential) on how different biological and ecological features impact restoration success and the recovery of habitats.

Throughout this paper, the term "restoration" refers to an intentional activity (i.e., active intervention or manipulation) that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity, and sustainability (SER, 2004). Active approaches, also referred to as assisted regeneration (McDonald et al., 2016), include seedling of spores, transplantation, the removal of grazers, etc. The recovery of the ecosystem is defined as the reinstatement of ecosystem attributes, such as composition, structure, and function, back to a level identified for a reference ecosystem (McDonald et al., 2016). We do not include passive restoration (natural re-generation), where restoration goals are achieved by allowing the ecosystem to recover once the source of disturbance has been removed.

Selection and Description of the Target Habitats

The five marine habitats chosen for this paper were selected by the expert group at the workshop because they are considered to be highly ecological and economic important, are sensitive to human activities and are relevant in conservation. Different directives and list were used as guidance when making the agreed-on list of target habitats: EU Habitats Directive 92/43/EEC, OSPAR List of Threatened and/or Declining Species

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[1] https://undocs.org/A/RES/70/1

[2] www.merces-project.eu

and Habitats (OSPAR, 2008), HELCOM List of Threatened and/or Declining Species and biotopes/habitats in the Baltic Sea (HELCOM, 2007), UNEP/MAP-SPA/RAC 2018 Annex II List of Endangered or threatened species. The selected habitats cover shallow and deep areas and soft and hard substrates in the Mediterranean Sea, the Baltic Sea and NE Atlantic Ocean (see **Figure 1** for habitat examples).

Seagrass meadows are found on soft bottoms down to a maximum depth of 50 m (Duarte, 1991b). Seagrasses are important ecosystem engineers, i.e., they create, modify and maintain habitats (Boström et al., 2014; Jahnke et al., 2016), and provide multiple ecosystem services through stabilizing sediments, sequestering carbon, filtering nutrients and providing food and shelter for invertebrates, fish and birds (Hemminga and Duarte, 2000). Different human pressures are responsible for the decline of seagrasses in Europe (Airoldi and Beck, 2007). Whilst seagrass loss has been accelerating through decades (Waycott et al., 2009), recent assessment demonstrates a more positive trend in Europe (de los Santos et al., 2019).

Kelp forests are found on rocky seabed down to a depth of about 30 m, with single individuals (i.e., not forests) growing even deeper. Kelps are habitat-forming species, providing food, shelter and habitat for many species (Christie et al., 2009; Leclerc et al., 2013). They play a major role in the carbon cycle (Krause-Jensen and Duarte, 2016) and coastal protection, along with a long list of other ecosystem services (Gundersen et al., 2016). The kelp forest distribution is decreasing in many areas around the world (Filbee-Dexter and Wernberg, 2018) but is also showing increasing trends in some parts (e.g., recovering in the Norwegian NE Atlantic, Araújo et al., 2016; Krumhansl et al., 2016).

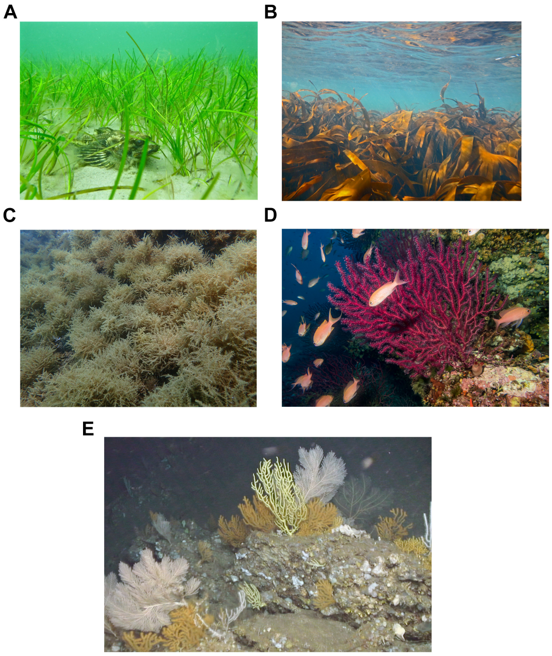

FIGURE 1 | Examples of the selected marine habitats assessed in this paper: **(A)** *Zostera marina* seagrass meadow, **(B)** *Laminaria hyperborea* kelp forest, **(C)** *Treptacantha elegans* macroalgal bed, **(D)** Mediterranean coralligenous assemblage, and **(E)** Cold-water coral habitat, dominated by the octocorals *Callogorgia verticillata*, *Acanthogorgia* sp. and *Dentomuricea* aff. *meteor* in the Azores. Photos by Christoffer Boström **(A)**, Janne K. Gitmark **(B)**, Alba Medrano **(C)**, Cristina Linares **(D)** and EMEPC, ROV Luso (EMEPC/Luso/Açores/2009) **(E)**.

Cystoseira macroalgal beds are found down to a maximum depth of 50 m. *Cystoseira* spp. are habitat-forming species found in rocky intertidal and subtidal coastal areas and are recognized as hot spots for biodiversity. They provide food and habitat to diverse assemblages of understory species and enhance coastal primary productivity (Ballesteros, 1990; Ballesteros et al., 1998; Cheminée et al., 2013). Shallow beds (mainly down to 10 m depth) have a different community composition and different life history traits than deeper ones (10–50 m depth, Capdevila et al., 2016). The decline in *Cystoseira* over vast areas has been documented in many regions (Bianchi et al., 2014; Thibaut et al., 2015) and natural recovery has been recorded only occasionally (Perkol-Finkel and Airoldi, 2010; Iveša et al., 2016).

Coralligenous assemblages can be found down to maximum depth of about 120 m (Laborel, 1961). Coralligenous outcrops are mainly produced by the accumulation of calcareous encrusting algae. This habitat supports high biodiversity (approximately 10–20% of the Mediterranean species) and structural complexity (Ballesteros, 2006), and the most abundant species are long-lived algae and sessile invertebrates with an important role as habitat-formers (Linares et al., 2007; Cerrano et al., 2010; Teixidó et al., 2011). Coralligenous assemblages have been lost or degraded in several areas across the Mediterranean Sea (Bevilacqua et al., 2018; Ingrosso et al., 2018).

Cold-water coral habitats are major ecosystem engineers in the deep sea, mostly occurring in the depth range of 200–1500 m, where they can form large and extensive habitats, such as coral reefs formed mostly by Scleractinia species (stony corals) and coral gardens primarily composed by octocorals and black corals (Roberts et al., 2009; Buhl-Mortensen and Buhl-Mortensen, 2018). They create a complex three-dimensional habitat and support high levels of biodiversity, providing refuge, feeding opportunities, and spawning and nursery areas for a wide range of organisms (Buhl-Mortensen et al., 2010). Cold-water corals grow extremely slowly (a few to several mm per year) and can live for hundreds or thousands of years (e.g., Roberts et al., 2009; Watling et al., 2011; Carreiro-Silva et al., 2013). The limited knowledge on the distribution and extent of cold-water coral habitats makes it difficult to assess changes. Nevertheless, cold-water coral habitats have been defined as Vulnerable Marine Ecosystems (VMEs, FAO, 2009) and international management and conservation policies (e.g., FAO, OSPAR) are expected to contribute to the recovery of impacted sites and the protection of the remaining pristine coral communities.

Selection of Habitat Features and Assessment ("Scoring") of the Restoration Potential

The recovery potential of habitats depends upon their resilience, which is strongly influenced by the biology and ecology of their component species. The expert group identified and agreed on the biological and ecological features of greatest relevance through discussion and by structuring information from literature reviews (Perkol-Finkel and Airoldi, 2010; Abelson et al., 2016a,b; McDonald et al., 2016). This resulted in the selection of five features most relevant to restoration success, namely: life-history traits, population connectivity, spatial distribution, structural complexity, and the potential for regime shifts. The features' general relevance to the recovery potential of habitats is described in **Table 1**.

By using the features, the expert group assessed the restoration potential of the selected habitats based on (1) evidence in the published literature, (2) experiences obtained from ongoing restoration projects and actions, and (3) expert knowledge of the habitats' or species' biology and ecology. The discussion ended up with agreed-on characteristics of the biological and ecological features for each habitat (**Table 2**). Based on these characteristics, each feature was given a score from 1 (low) to 5 (high), according to its potential contribution to the successful accomplishment of restoration for each of the habitats (**Table 3**). We chose five levels to ensure that enough variability could be included in the assessment to distinguish restoration potential amongst habitats, but that did not have too many levels that would hide emerging patterns. This number of levels have also been considered suitable for defining conservation status of habitats and species (from favorable to unknown under the EU Habitats Directive) and ecosystem health status of marine waters (from high to bad under the Water Framework Directive). When a feature may lead to both restoration failure and success, the scoring was given as a range or a set of values, rather than one single score. As shallow *Cystoseira* beds have a different community and different life history traits than deeper beds, these communities were scored separately.

THE ASSESSMENT OF THE HABITAT FEATURES AND THE RESULTING "SCORING"

The characteristics of the biological and ecological features relevant for assessing the recovery potential is described in sections Seagrass meadows to Cold-Water Coral Habitats and summed up in **Table 2**. **Table 2** provides the information needed for the agreed-on scoring in **Table 3**, in which the features of the different habitats are considered according to their contribution to successful restoration.

Seagrass Meadows

As life-history traits of seagrass may lead to restoration failure or success, depending on the species in question, it is difficult to assess this feature‘s importance for habitat restoration in general (Kilminster et al., 2015). For example, *Posidonia oceanica* is a slow-growing species (Duarte, 1991a) forming enduring meadows (Kilminster et al., 2015), while *Cymodocea nodosa* and *Zostera marina* exhibit faster clonal growth (Olesen and Sand-Jensen, 1993; Cancemi et al., 2002), forming more transient meadows (Kilminster et al., 2015). As slow-growing species will need more time to recover than fast-growing species (Montero-Serra et al., 2018a), the time scale needed for recovery should be assessed carefully depending on the species in question. In general, populations with high connectivity (dispersal and gene flow) have higher genetic diversity, which makes them more resilient to environmental perturbations (Reusch et al., 2005; Jahnke et al., 2018). However, especially at the extreme ends of the geographical range of eelgrass, clonal growth dominates, creating vulnerable and isolated populations with limited connectivity (Olsen et al., 2004). Several species may spread both asexual (clonal) and through seed production (McMahon et al., 2014). Thus, different geographical regions and species naturally possess different capacities for local and large-scale dispersal (gene flow), from less than 15 m to up to 1000 km (Orth et al., 1994; Källström et al., 2008; Jahnke et al., 2018). The distribution of the species is also crucial, as a wide spatial distribution implies easier access to donor populations during restoration, which increases the probability of recovery success. In general, large-scale planting has been identified as an important method for increasing restoration success (van Katwijk et al., 2016).

Seagrass meadows are extremely vulnerable to anthropogenic pressures, such as habitat destruction, eutrophication, pollution, and climate change (Orth et al., 2006). It is important that pressures, such as eutrophication (which limits light availability and growth, Burkholder et al., 2007; Moksnes et al., 2018) and habitat destruction (Erftemeijer and Lewis, 2006), are removed and appropriate sediment conditions are re-established, as sediment conditions tend to become unsuitable for re-establishment following seagrass loss (de Boer, 2007; Carr et al., 2016; Moksnes et al., 2018). Seagrass meadows are prone to regime shifts (Maxwell et al., 2016; Moksnes et al., 2018), characterized by a transition into an algal dominated or a barren state. Understanding drivers, interactions and thresholds in these regime shifts is crucial before any restoration action can take place.

After restoration action has taken place, seagrass meadows should be sustained in the long-term through positive feedback mechanisms (Maxwell et al., 2016; Suykerbuyk et al., 2016). As part of restoration it is therefore important to ensure (and possibility reintroduce) healthy populations of associated species, especially top predators, which can control algal (over)growth through trophic cascades (Moksnes et al., 2008, 2018; Jahnke et al., 2018).

Kelp Forests

All of the selected features associated with kelp forests promote successful restoration. Fertile kelp produces a high number of propagules that can be dispersed for several days with coastal currents (Reed et al., 1992; Andersen, 2013), and the release is relatively synchronous among populations (Andersen et al., 2011). Connectivity between kelp populations is reinforced by reproductive synchrony because higher abundance of spores in the currents increases the probability of long-distance dispersal (Reed et al., 1997), which also facilitates recovery. Kelp colonizes hard substrate such as bedrock, boulders, and rocks, forming forests with a wide spatial distribution. Kelp forests are structurally very complex, with a heterogeneous understory of younger plants and associated flora and fauna. Kelp forests

TABLE 1 | Description of the key features assessed for the habitats included in this paper and their relevance to the recovery potential.

Key features	Description	Relevance to the recovery potential	References
Life history traits	Reproduction potential, larval biology, age at first maturity, growth rate, longevity, generation length.	Species with low reproductive output, delayed maturity, slow growth, and high longevity take longer to recover from impact.	McMahon et al., 2014; Capdevila et al., 2016; Montero-Serra et al., 2018a
Population connectivity	Dispersal and gene flow.	Populations with high connectivity/gene flow have higher genetic diversity, which provides resistance to disturbance and high potential for natural recolonization of disturbed areas from nearby sites.	Pascual et al., 2017; Jahnke et al., 2018
Spatial distribution	Spatial extent, distribution patterns.	Populations in fragmented habitats are more vulnerable to environmental impact and genetic stochasticity, and therefore face a higher risk of local extinction.	Gera et al., 2013; Giakoumi et al., 2013
Structural complexity	Three-dimensional complexity.	Increased habitat complexity supports higher biodiversity and thus associated food webs, thereby enhancing recovery through various ecosystem processes, including facilitation, and positive feedbacks between coexisting species.	Kovalenko et al., 2012
Regime shift	The potential for regime shift.	Habitats that experience variation in extent, coverage and status, but that don't experience regime shifts, will recover more easily than habitats that show regime shifts	Hughes et al., 2013; Maxwell et al., 2016

generally support food webs with a high number of species at different trophic levels (e.g., Steneck et al., 2002; Smale et al., 2013; Krause-Jensen and Duarte, 2014) contributing to ecosystem resilience.

Restoration actions may be implemented at large spatial scales and transplanted or recovered kelp plants can quickly become spore donors to adjacent barren areas. The major threats for kelp (reviewed in Filbee-Dexter and Wernberg, 2018) are eutrophication, temperature increase (in the North Sea, Bekkby and Moy, 2011; Moy and Christie, 2012) and grazing by sea urchins (in the Norwegian and Barents Sea, Araújo et al., 2016), but kelp forests show high level of recovery when these pressures are removed. Consequently, removing pressures, such as sea urchins and nutrients, should be the priority before any additional actions (such as planting kelp or seeding spores). Despite the documented regime shift and widespread collapse of kelp forests (Ling et al., 2015), such as for the *Laminaria hyperborea* forests, some forests have had a back-and-forth shift between kelp and turf algae, without it being a regime shift (e.g., *Saccharina latissima*, Christie et al., 2019). Before any restoration action can take place, an in-depth understanding of the drivers, feedback effects and critical thresholds for the shifts is needed, including knowledge of the interaction with predators (such as sea urchins), turf algae and local and global stressors.

Cystoseira Macroalgal Beds

Cystoseira macroalgal beds display relatively high reproduction, growth rate and longevity (Ballesteros, 1989), with a considerable variation in life history traits at different depths (Capdevila et al., 2016). The shallow beds have, in general (but with exceptions), wide spatial distribution and are dominant habitat-forming species in rocky intertidal and subtidal habitats, while deeper beds are more fragmented. *Cystoseira* beds have a high structural complexity, providing food and shelter to diversified assemblages of understory species. *Cystoseira* beds are vulnerable to various anthropogenic pressures (such as eutrophication, chemical pollution, coastal development, sedimentation) as well as being at risk due to climate change and outbreaks of grazers (Fraschetti et al., 2001; Airoldi et al., 2014). Overgrazing due to sea urchin outbreaks is responsible, along with other local and global stressors, for the loss of *Cystoseira* beds and the subsequent community shifts toward turf-forming algae or barren grounds (Pinnegar et al., 2000; Airoldi et al., 2014).

The high level of fragmentation often found for this habitat and the low connectivity (Thibaut et al., 2016) suggest that restoration actions should be considered over a local scale (meters). Restoration should focus on structural species that provide habitat for associated species. Shallow beds have high growth and fast dynamics (Ballesteros, 1989) and may be easier to restore compared to deeper beds (e.g., below 30 m depth). Restoration actions should include large adult organisms. However, in cases where the natural and donor populations are in a critical state, manipulation should be avoided, and restoration must rely on recruitment enhancement and the growth of juveniles (Verdura et al., 2018; De La Fuente et al., 2019). In these situations, a longer time (possible decades) for restoration must be accepted (Mangialajo et al., 2012; Capdevila et al., 2016; Thibaut et al., 2016). Anthropogenic pressures (such as eutrophication, chemical pollution, coastal development, sedimentation) should be reduced. Restoration practitioners have found that a combination of two approaches (sea urchin eradication to control their impact, and recruitment enhancement techniques) was the best technique to enhance *Cystoseira* forestation from a shallow degraded barren ground (Medrano et al. unpublished data).

TABLE 2 | The characteristics of the five selected key features for each habitat.

Habitat		**Habitat features**				
		Life history	**Population connectivity**	**Spatial distribution**	**Structural complexity**	**Regime shifts**
Seagrass meadows		Both slow and fast-growing species, both low and high reproductive output	Generally high dispersal and high gene flow, but some populations are clones	Relatively fragmented populations, depending on the species	High 3D complexity	Prone to regime shifts
Kelp forests		High recruitment, growth rate and longevity	High connectivity, number of propagules and dispersal distance	Wide distribution	High 3D complexity	Prone to regime shifts
Cystoseira macroalgal beds	(Shallow, i.e., at 0–10 m)	Fast or medium growth and recruitment rate	Medium or poor dispersal ability	Wide distribution, but might occur in patches	High 3D complexity	Prone to regime shifts
	(Deeper, i.e., at 10–50 m)	Slow growth and recruitment rate	Poor dispersal ability	Fragmented	High 3D complexity	Prone to regime shifts
Coralligenous assemblages		Slow growth and low recruitment rate, long life span	Low connectivity, disconnected populations and limited larval transport	Fragmented	High 3D complexity	Likely, but unclear
Cold-water coral habitats		Slow growing, long life spans, low reproductive output and low recruitment rate	Low fecundity and larval dispersal for most species	Fragmented	High 3D complexity	Unclear

Shallow Cystoseira macroalgal beds have a different community and different life history traits than deeper ones and are thus treated separately.

TABLE 3 | The agreed-on expert scoring of the habitat features according to their contribution to the successful accomplishment of habitat restoration; 1 – low contribution, 5 – high contribution.

Habitat		Habitat features				
		Life history	**Population connectivity**	**Spatial distribution**	**Structural complexity**	**Regime shifts**
Seagrass meadows		1–5	5 (1)	2	5	Prone to regime shifts
Kelp forests		5	5	5	5	Prone to regime shifts
Cystoseira macroalgal beds	(Shallow, i.e., 0–10 m)	4	3	4	5	Prone to regime shifts
	(Deeper, i.e., 10–50 m)	3	2	2	5	Prone to regime shifts
Coralligenous assemblages		2	1	1	5	Likely, but unclear
Cold-water coral habitats		1	1	1	5	Unclear

The habitat features are presented in general in ***Table 1****.* ***Table 2*** *provides the information used for the agreed-on scoring here. Seagrass meadows are difficult to score when it comes to life history, as the life history of the different seagrass species may lead to both restoration failure and success. Also, some seagrass populations have extremely low connectivity (leading to the score 1 in brackets). Shallow Cystoseira macroalgal beds have a different community and different life history traits than deeper beds, and scores are therefore given separately.*

Coralligenous Assemblages

Coralligenous assemblages form through the growth of organisms on dead skeletons of previous generations, creating high structural complexity. Most are calcareous algae, sponges, bryozoans, and octocorals, which are relatively slow-growing and long-lived species, with limited recruitment (Coma et al., 1998; Garrabou and Harmelin, 2002; Linares et al., 2007; Teixidó et al., 2011). In addition, populations of different coralligenous species, such as the octocorals *Paramuricea clavata* and *Corallium rubrum*, are most likely far apart, and larval supply may be limited (Costantini et al., 2007; Ledoux et al., 2010; Arizmendi-Meija et al., 2015).

Restoration through transplantation would require low initial effort due to high survival of transplants. As coralligenous species are slow-growing and long-lived, with limited recruitment, it takes a long period of time to restore the full complexity of the habitat through transplantation, probably at decadal timescales (Linares et al., 2008; Montero-Serra et al., 2018a). This would be the case for most of the key coralligenous groups, such as sponges (e.g., *Petrosia fisciformis, Spongia lamella, S. officinalis*) and octocorals (e.g., *Paramuricea clavata*, *Corallium rubrum*) (Teixidó et al., 2011; Montero-Serra et al., 2018b). However, there are other groups, such as bryozoans, mainly *Pentapora fascialis*, which can display higher growth rates, and recovery of structural complexity could be achieved in short time scales (5–10 years, Pagés et al. unpublished data). As the habitats are generally fragmented and the population connectivity low, restoration actions need to be performed at very local scales.

Coralligenous assemblages are presently threatened by a combination of nutrient enrichment, invasive species, increase of sedimentation and mechanical impacts, mainly from fishing activities, as well as climate change (Ballesteros, 2006; Balata et al., 2007; Garrabou et al., 2009; Cebrian et al., 2012; Piazzi et al., 2012). Reduction of pressures should be a priority before starting restoration actions. The slow population dynamics of coralligenous assemblages make it difficult to detect regime shifts, which could be eventually detected after longer time periods exposed to stressors. However, experimental and observational evidences show that extreme warming events can replace a structurally complex habitat with fast-growing and turf-forming species, which can indicate regime shifts (Ponti et al., 2014; Di Camillo and Cerrano, 2015; Verdura et al., 2019).

Cold-Water Coral Habitats

Cold-water coral habitats have among the lowest recovery potentials. This is related to coral life-history traits such as slow growth, high longevity and low fecundity, which makes their recovery dynamics extremely slow, particularly for octocorals and black corals. Bypassing sensitive early-life stages, by transplanting adult and reproductive colonies of key coral species, may accelerate the initial recovery of the ecosystem (e.g., Linares et al., 2008; Montero-Serra et al., 2018a). However, the life-history traits of the species will condition the slow recovery of the ecosystem, including its full biodiversity, structure and functioning, which will likely require several decades to centuries. This is because individual native species will regenerate naturally at different time scales and because transplantation may be feasible only for a limited number of species (and if donors are available). Therefore, the appropriate choice of species to transplant may be important, giving priority to species with relatively fast growth rates, so that they can more easily recover and create the three-dimensional structure needed for associated species. The slow population dynamics of the cold-water coral habitats makes it difficult to really know if they are prone to regime shifts, as it would take long-lasting studies.

Cold-water coral habitats are sensitive to a range of human activities, including commercial bottom fisheries, hydrocarbon exploration and extraction, and if developed, deep-sea mining (Ramirez-Llodra et al., 2011; Ragnarsson et al., 2017). The bottom fisheries are considered to be the major pressure, often resulting in the removal of entire communities, with little evidence of recovery (Clark et al., 2019). An important challenge in the restoration of deep-sea coral habitats is the remoteness of these habitats, which makes restoration actions highly dependent on technological means (e.g., large ships and ROVs), being costly in comparison with shallow-water habitats (van Dover et al., 2014; Da Ros et al., 2019). This may reduce the capacity to restore large areas using coral transplants. Thus, a combination of restoration approaches will likely be necessary, with assisted regeneration at small scales and natural regeneration (through fisheries closures, marine protected areas) at large scales.

CONCLUSION AND FUTURE PERSPECTIVES ON RESTORATION

Active restoration is required where the impact of human pressures goes beyond a point where no passive (unassisted) recovery may take place or does not proceed at the desired speed. Undertaking active restoration may provide conservation outcomes (Possingham et al., 2015) and should be used in combination with other management practices, such as protected areas (Barbier et al., 2014; van Dover et al., 2014; Da Ros et al., 2019).

Based on the discussions and scoring of the biological and ecological features and their contribution to the successful accomplishment of habitat restoration, the expert group concluded that most of the kelp forest features facilitate successful restoration (high score in **Table 3**), while the features for the coralligenous assemblages and the cold-water coral habitat did not promote successful restoration (low score). For seagrass meadows and *Cystoseira* macroalgal beds the conclusions were much more variable. Life-history traits of seagrass may lead to restoration failure or success, depending on the species (**Table 2**), which makes it difficult to score this feature according to its contribution of the successful accomplishment of habitat restoration.

The success of restoration actions depends upon the inherent ecology and biology of the species and habitats being restored. Life history and population connectivity impact restoration success, while structural complexity typically is a feature that will affect the habitat's vulnerability against perturbations (see **Table 2**). This means that restoration actions should mainly undertake two different activities. The first step should be to protect and maintain structural complexity and diversity, the second should be devoted to enhancing the conditions crucial for those features that make the success uncertain (i.e., life history and population connectivity). The protection and maintenance of structural complexity and diversity may be achieved by coupling the restoration action with management measures to significantly reduce stressors at the restoration site (van Dover et al., 2014). Close proximity of the restoration site to more pristine habitats improves restoration potential as the unaffected populations can provide offspring to support re-colonization and population connectivity, increasing genotypic diversity, if no other limiting factors (e.g., current directions, topographic barriers) are present.

Based on the experiences from ongoing restoration projects and actions, the expert group suggests that four factors should be considered to obtain the greatest chances of success for restoration:

(1) *The choice of the donor and recipient sites* – to ensure that the restoration site has suitable physical conditions and biological characteristics, as similar as possible to that of the donor site.
(2) *The identification of the best transplantation methodology* – a multitude of transplantation techniques exists for different species and habitats. The choice of the right technique (or combination of techniques) requires reviewing existing literature and outcomes of previous restoration projects.
(3) *The influence of positive species interactions* – the presence of species could improve survival by for instance providing habitat or refuge, which may speed up the recovery. Instead of only minimizing competition and predation, restoration actions should also focus on positive, including co-restoration of several habitats.
(4) *The potential for regime shifts* – if the habitat is prone to regime shifts, in-depth understanding of the drivers, feedback effects and critical thresholds for the shifts, including the interaction between species (positive and negative) and local and global stressors, is needed.

Point 3 in the list above, which is also relevant for point 4, needs some elaboration. Even though positive interactions between species are highly recognized in ecology, it is not commonly integrated in conservation or restoration efforts. Often, the negative interactions (competition and predations) are easier to identify and is therefore more often included as part of the restoration effort (Silliman et al., 2015). Considering positive interactions are more common in terrestrial (and to a certain degree freshwater) restoration projects. However, Halpern et al. (2007) provide some guidelines on why and when positive interactions should be considered, including for marine habitats. In general, physically or biologically stressful systems benefit more from positive interactions than mild habitats (Halpern et al., 2007; Silliman et al., 2015). It is therefore important that the degree of stress in the system is assessed as part of planning the restoration action. Silliman et al. (2015) shows that doing small adjustments in the restoration design to enhance positive interactions increases the restoration success.

Often, the challenge of marine restoration is that it can require long timescales (from several years to decades) before the success of the restoration methods can be evaluated, and it requires substantial funding and high-technology equipment, particularly in deep-sea habitats (Bayraktarov et al., 2016; Verdura et al., 2018). The cost of restoration is a crucial issue, both in terms of its estimation, for example through the transparent reporting of costs, and also the efficiency of actions (Bayraktarov et al., 2016). Efficiency can be increased by structuring restoration action across several partners (Bodin and Crona, 2009) and by thinking creatively, for example using deep-sea corals from fisherman's by-catch in transplantations. In addition, for habitats such as cold-water corals, which recover slowly, short-term monitoring (i.e., a few years) cannot be expected to be a good indication of restoration trajectory or success. In these cases, management measures should be taken to ensure the long-term monitoring of the area under restoration, which may be beyond the typical lifetime of a restoration project. Often (as experienced in kelp forest restoration), maintaining long-term restoration actions is also a prerequisite for success (e.g., continuous sea urchin and turf algae removal).

An additional challenge in marine restoration is that in many cases (at least for the deep sea) we have limited knowledge on key features that support restoration success or can promote resilience. The lack of knowledge of pre-disturbance baselines, which may have shifted along with climate change (Pauly, 1995), is also a challenge. Ultimately, this hampers a proper evaluation of the impact of anthropogenic activities, the actual degree of degradation and therefore the choice of the restoration goals.

In conclusion, this work provides an overview of the essential biological and ecological features for a range of marine habitats (ecosystem engineers) that can affect restoration success, highlighting the key factors for a successful restoration. Moreover, we provide some best practice guidelines to improve restoration success. Even though habitat restoration is much more complicated than that which has been discussed here, it is hoped that our discussions and recommendations will be useful when designing and executing future marine restoration.

AUTHOR CONTRIBUTIONS

As part of the MERCES WP1 work, an expert group selected the marine habitats and features to be included in this manuscript. TB, NP, and CS lead the focus workshop of experts. TB, CG, CL, NP, CS, TM, DF, KG, SF, CM, EB, and EC were all part of this process and earlier analyses. At a later stage, more people were added to the expert group in order to ensure expertise on all habitats and regions, and to support the new analyses. ER, GA, CF, and HG were included in the work on the kelp forests, CB on seagrass meadows, MC-S, TM, and MB on cold-water coral habitats, CC and SK on the coralligenous assemblages, RD and ER-L on deep-sea habitats, and JK and HO on habitat ecology in general. TB, NP, DF, CM, ER, CB, MC-S, and CL were responsible for the **Table 3** "scoring," but all authors listed have contributed to the discussions and conclusions, and in writing of the manuscript.

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REVIEW
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Restore or Redefine: Future Trajectories for Restoration

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Global habitat deterioration of marine ecosystems has led to a need for active interventions to halt or reverse the loss of ecological function. Restoration has historically been a key tool to reverse habitat loss and restore functions, but the extent to which this will be sufficient under future climates is uncertain. Emerging genetic technologies now provide the ability for restoration to proactively match adaptability of target species to predicted future environmental conditions, which opens up the possibility of boosting resistance to future stress in degraded and threatened habitats. As such, the choice of whether to restore to historical baselines or anticipate the future remains a key decision that will influence restoration success in the face of environmental and climate change. Here, we present an overview of the different motives for restoration – to *recover* or *revive* lost or degraded habitats to extant or historical states, or to *reinforce* or *redefine* for future conditions. We focus on the genetic and adaptive choices that underpin each option and subsequent consequences for restoration success. These options span a range of possible trajectories, technological advances and societal acceptability, and represent a framework for progressing restoration of marine habitat forming species into the future.

Keywords: assisted adaptation, provenance, kelp, climate change, evolution, synthetic biology

INTRODUCTION

Habitat deterioration and destruction threaten global ecological functions and result in significant loss of social and economic values (Hoffmann et al., 2010; Venter et al., 2016; Powers and Jetz, 2019). Recognizing this threat, the UN has declared 2021–2030 the "decade of restoration" (FAO, 2019) with the aim to restore 350 million hectares of degraded ecosystems, and massively scale up restoration efforts to promote resilience to climate and anthropogenic change and reverse biodiversity loss. In particular, there is an urgent need for marine restoration initiatives to combat and reverse existing habitat loss (e.g., Krumhansl et al., 2016; Filbee-Dexter and Wernberg, 2018), and even pre-empt future habitat loss (Gattuso et al., 2015; Hughes et al., 2017). As such, both preventive (passive) and adaptive (active) restoration measures are globally supported as viable options under future climates (IPCC, 2019).

Successful, large scale restoration efforts will require robust, science-based practices that consider the fundamental question: "to what time point should we restore?" Historically, restoration has sought to replicate what was lost and to recover properties of populations or communities (species, structure, ecosystem services) to historic states that are putatively adapted to extant environmental conditions. However, ongoing habitat deterioration and climate change is outpacing the ability of many species to adapt, challenging the assumption that restoration to historic states will be sufficient to ensure persistence into the future (Hobbs et al., 2009; van Oppen et al., 2015; Perring et al., 2015; Breed et al., 2018, 2019; Gurgel et al., 2020). Instead, improving or redesigning properties of lost habitats to withstand predicted future conditions may confer greater restoration success. Moreover, restoration could also include anticipatory actions (prior to loss) to proactively boost resilience and adaptive capacity of extant populations to predicted future conditions (assisted adaptation, Aitken and Whitlock, 2013; van Oppen et al., 2017). Thus, the decision whether to restore to extant or historical baselines, versus some predicted but uncertain future state is likely to be central to restoration success into the future.

Given that habitat resilience (the capacity to resist or recover from perturbation) and adaptive capacity to cope with environmental change will be influenced by underlying genetic properties of populations (genetic diversity, composition of genes and alleles; Wernberg et al., 2018), determining provenance (the origin and diversity of donor individuals) and thus, choosing an historic versus unknown future genetic baseline is a key consideration in contemporary restoration science (Breed et al., 2018). Although genetic baselines are not static and change through time, here we define a genetic baseline as the level of the genetic diversity and structure chosen and initially replicated in a restoration program through provenance decisions. Current best practice recommends local provenance for restoration, that is, that donor adults or propagules are sourced within contemporary extant genetic boundaries to maintain locally adapted genotypes and avoid maladaptation and genetic pollution (e.g., SERA, 2017). Moreover, characterizing and replicating extant levels of genetic diversity and structure is recommended to ensure sufficient diversity for adaptation (Bischoff et al., 2010; Wood et al., in review). Unfortunately, restoration, particularly in marine systems, has historically been conducted in the absence of formal genetic assessments, which may contribute to poor outcomes to date (McKay et al., 2005; Mijangos et al., 2015; Crouzeilles et al., 2016). Although current restoration efforts are increasingly incorporating empirical assessments of genetic provenance into practice[1] (e.g., Evans et al., 2018; Wood et al., in review), the extent to which this will confer success under future scenarios of climate and anthropogenic stress remains a critical uncertainty (Weeks et al., 2011; Perring et al., 2015).

Predicted increases in climate and anthropogenic stress have prompted calls for "future-proof" restoration practices that reinforce or even redesign historic and extant genetic baselines to confer increased resilience to future conditions and stressors in restored populations (van Oppen et al., 2017; Breed et al., 2018, 2019; Ralls et al., 2018; Wood et al., 2019; Sgrò et al., 2011). Critically, both reinforcing and redefining existing genetic baselines can be applied similarly through traditional restoration programs after loss or degradation, or as a preventative measure prior to any impact occurring. Reinforcing genetic baselines could be achieved via increasing genetic diversity in restored populations to provide sufficient adaptive capacity to cope with future change. Another strategy involves matching predicted environmental and anthropogenic conditions to the ability of individuals and populations to adapt through addition of resilient genotypes identified through experimentation (Breed et al., 2019) or genome wide association studies (GWAS; van Oppen et al., 2015; Rinkevich, 2019). Completely redefining genetic baselines and population resilience is now possible with emerging genetic technologies (Popkin, 2018). For example, synthetic biology and gene editing using tools such as CRISPR/CAS9 can be harnessed to create or spread novel or engineered beneficial genetic elements within restored or vulnerable populations (Coleman and Goold, 2019) and allow bespoke restoration or assisted adaptation programs to be designed for specific stressors of interest.

Here, we focus on kelp forests, critical marine habitats in decline, to present a framework to guide the design of restoration initiatives as a function of four possible motives: *Recover, Revive, Reinforce*, and *Redefine* (**Figure 1**). Importantly, this framework does not only apply to kelp forests but to restoration efforts more broadly. *Recover* and *revive* center on contemporary, reactive restoration practices that seek to return already degraded habitat to historic or extant baselines. In contrast, *reinforce* and *redefine* seek to proactively anticipate future conditions and boost resilience in lost, degraded or vulnerable habitats. This framework spans a range of possible trajectories, technological advances and societal acceptability and represents a platform for progressing marine restoration into the future. We discuss techniques for estimating appropriate genetic provenance in cases where prior genetic data is limited and pathways to develop preventative strategies that anticipate and boost resilience to future stress.

KELP FORESTS – CRITICAL HABITATS IN DECLINE

Kelp forests are highly productive seascapes dominated by large brown seaweeds (Wernberg and Filbee-Dexter, 2019). They are particularly prominent in temperate to polar environments where they are the foundations for immense biodiversity and valuable ecological services such as important recreational and commercial fisheries (Wernberg et al., 2019b). The best available evidence suggests that 40–60% of the world's kelp forests have been in decline over the past 50 years (Krumhansl et al., 2016; Wernberg et al., 2019b) as a consequence of a variety of direct

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[1] http://www.operationcrayweed.com

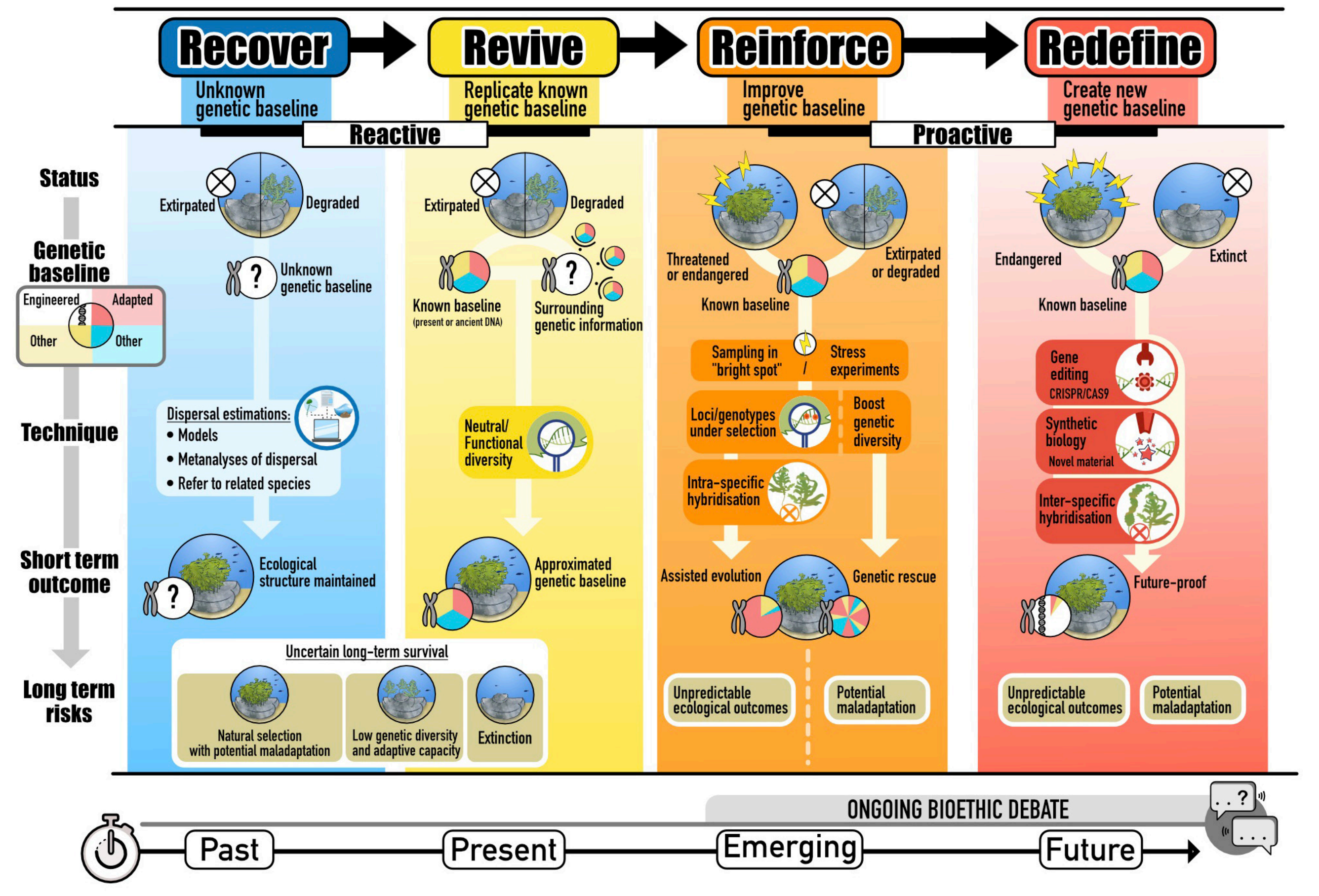

FIGURE 1 | Different motives for restoration. Whether to *recover* or *revive* historic and extant genetic baselines or *reinforce* and *redefine* to unknown baselines for future conditions, is a critical choice in restoration programs that determines possibilities for adaptability and persistence under future environmental conditions and climates.

and indirect stressors including warming, marine heatwaves, eutrophication and increasing herbivory from range-shifting warm-water herbivores (Vergés et al., 2014; Filbee-Dexter and Wernberg, 2018). For example, in Australia, kelp forests of laminarian kelp and fucoids (e.g., *Ecklonia radiata*, *Scyothalia dorycarpa*, *Phyllospora comosa*) are found throughout the Great Southern Reef along the southern coastline of the continent (Coleman and Wernberg, 2017; Wernberg et al., 2019a). In recent decades, almost every part of this unique large-scale ecosystem has experienced localized to regional decline and loss of kelp forests due to a range of processes including eutrophication, over grazing, warming, and marine heatwaves (Coleman et al., 2008; Connell et al., 2008; Ling et al., 2009; Vergés et al., 2016; Wernberg et al., 2016; Carnell and Keough, 2019). In almost all cases in Australia and globally, kelp loss has been persistent with no signs of natural recovery. Instead, kelp forests have been replaced by alternate habitats including turf algae (Filbee-Dexter and Wernberg, 2018) or urchin barrens (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015) which create strong reinforcing feedbacks that prevent natural recovery of kelp. This provides strong impetus and motivation to apply interventions such as restoration, especially where the initial stressor no longer occurs (e.g., Coleman et al., 2008) or can be controlled (e.g., Sanderson et al., 2015; Layton et al., 2020).

The first published studies on kelp forest restoration stem from the 1960s–1970s in Japan and North America (Carlisle et al., 1964; North, 1976; Kuwahara et al., 2006). Although the number of kelp restoration attempts has increased exponentially since then, such efforts are generally of limited duration (<2 years), small in scale (<0.1 ha) and have had limited success (Eger et al., 2019). Moreover, these efforts have generally lacked empirical data of underlying patterns of genetic diversity and structure (particularly functional genetic diversity), and often have not considered demographic history and ecological processes influencing kelp populations, all of which may have contributed to poor restoration outcomes. There are however some notable ongoing projects that address some of these concerns. For example, the Wheeler North Reef in southern California has successfully established a giant kelp forest community at a large scale (70 hectares of artificial reef structure) to compensate for the loss of natural giant kelp forests due to impacts from a nuclear power station (Schroeter et al., 2018). The Korean government has also developed a major marine seaweed foresting program and has already restored over 3,000 hectares of seaweed forests since 2009 (Lee, 2019). In Sydney, Australia, a project is also ongoing that aims to re-establish lost forests of *P. comosa* at the scale of the initial degradation −70 km of metropolitan coastline[1] (Campbell et al., 2014; Wood et al., in review). The projects that have seen sustained success have generally been well financed, have often been coordinated by regulatory bodies, carried out over a sustained periods of time, or harnessed the power of local community engagement to deliver lasting results (Eger et al., 2019; DeAngelis et al., 2020; Layton et al., 2020). While these projects are currently in the minority, interest in kelp restoration is accelerating and we are at the point where we can adequately learn from our past mistakes and enhance restoration of our underwater forests (Eger et al., 2019). Central to the success of these future efforts, however, is determining which environmental conditions to restore to and, therefore, whether to recover or revive genetic baselines, or reinforce and redefine them. These issues are common not only to kelp forests restoration but also to marine and terrestrial restoration more broadly.

RECOVER – RESTORATION THAT REPLICATES UNKNOWN GENETIC BASELINES

Marine restoration initiatives have historically operated in the absence of empirical genetic data, instead focusing on restoring community and habitat structure, functions and biodiversity (e.g., Campbell et al., 2014; Marzinelli et al., 2016; Verdura et al., 2018). This is partly a reflection of the historically high costs, complexity and inaccessibility of genomic techniques to assess baseline genetic diversity and structure using high throughput methods. Nonetheless, restoration practices have typically informally considered genetic baselines through available scientific literature on related taxa, knowledge of direct dispersal distances where measurable, incorporation of general genetic principles into practice (e.g., mixing populations to avoid inbreeding and ensure diversity) or through expert opinion. For example, global metanalyses for marine algae have shown that scales of dispersal and population connectivity are generally limited to ∼50 km (Durrant et al., 2014), which can be used as a general rule of thumb for provenance when empirical data for the species of interest is lacking. Alternatively, estimates of oceanographic dispersal distance relative to properties of propagules (Gaylord et al., 2006) can sometimes be used to infer appropriate provenance in the absence of data (e.g., Coleman et al., 2011b; Coleman et al., 2013), with consideration of potential barriers to dispersal or genetic breaks (e.g., Coleman and Brawley, 2005; Coleman and Kelaher, 2009; Alberto et al., 2010; Durrant et al., 2018).

The risk associated with restoring populations in the absence of empirical genetic knowledge is that restored populations will inadvertently lack diversity or appropriate adaptive capacity to cope with extant or future conditions (e.g., Williams, 2001), which may be particularly pertinent for species that exhibit small scale dispersal and are therefore susceptible to reduced gene flow, increased inbreeding or asexual propagation (e.g., Guillemin et al., 2008; Coleman et al., 2011a, 2019; Coleman and Wernberg, 2018; Miller et al., 2019). This risk is exacerbated given increasing habitat fragmentation and deterioration often characterizes the seascapes from which donor adults or propagules must be sourced for restoration (Coleman and Kelaher, 2009). Inadvertently sourcing donor plants from outside locally adapted populations could cause maladaptation and decreased fitness relative to appropriate provenance (Sexton et al., 2011), which may contribute to the general lack of successes in marine restoration to date (e.g., see Rinkevich, 2014 for a coral example). Obtaining genetic baselines is, however, now within reach of most restoration programs due to the increasing sophistication and reduced cost of modern genetic techniques (e.g., sequencing) that allow for assessments of population genetic structure without lengthy development stages (Narum et al., 2013). We argue that such assessments should now be planned and budgeted for prior to implementation in future restoration initiatives by adapting existing frameworks (e.g., Hoffmann et al., 2015).

REVIVE – RESTORING EXTANT OR HISTORIC GENETIC BASELINES

Contemporary restoration programs should aim, at a minimum, to replicate natural genetic baselines informed by empirical genetic data. Given that "before" data collected prior to loss rarely exist (Grant et al., 2017), population genetic diversity and structure should be assessed within surrounding, putatively non-impacted populations. This can then be replicated within restored populations through careful selection of donor populations and individuals (**Figure 2**). Such genetic assessments can now be done with less cost and effort than previously with the advent and accessibility of high throughout sequencing and should be included as "best-practice" in restoration programs. Moreover, modern genomic techniques (e.g., genotyping by sequencing of single nucleotide polymorphisms; SNPs) allow both neutral and functional or adaptive genetic diversity to be characterized simultaneously, an advance that is set to improve restoration outcomes through refined provenance decisions. While there are no current examples of its use in the literature in the context of restoration, genotyping by sequencing of tens of thousands of SNP loci, along with reference genomes to identify functions, is providing detailed extant baselines for key foundation species of kelp (e.g., *E. radiata*), that will soon allow replication (or bespoke manipulation, see section "*Reinforce* – Improving Genetic Baselines for Future Conditions") of neutral and functional diversity and structure in restoration programs.

Restoration informed by underlying patterns of genomic diversity and structure was recently implemented for one of the largest kelp restoration programs globally, Operation Crayweed[1] (Wood et al., in review). Prior to restoration, population genetic diversity and structure of the endemic crayweed (*P. comosa*) was characterized throughout its entire distribution and within

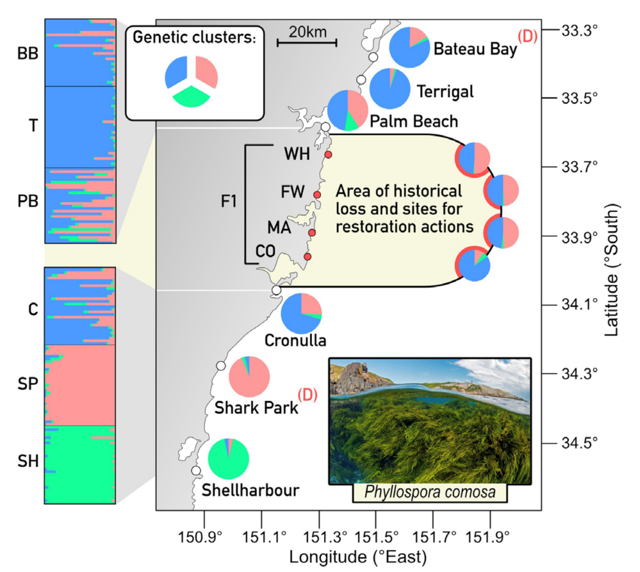

FIGURE 2 | Restoration of crayweed (*P. comosa*) at four sites within the 70 km gap in distribution where it was locally extinct (shaded area), was informed by genetic structure of six extant surrounding populations. Restored sites were a mix of plants from two donor populations (D) and the resulting F1 generation mimicked natural, extant genetic baselines. Adapted from Wood et al. (in review).

180 km either side of the intended restoration areas (**Figure 2**; Coleman et al., 2008; Coleman and Kelaher, 2009; Wood et al., in review). Natural level of genetic diversity and structure were mimicked in restoration programs by sourcing and mixing adult donor plants from two sites that represented the genetic clusters that occur within an 80 km radius of where *Phyllospora* was lost (**Figure 2**; Wood et al., in review). This avoided mixing distant genetic clusters that were not representative of the region and was also a practical distance to ensure donor plant survival during transplantation. The success of this approach was evidenced by rapid recruitment and an F1 generation that had near identical genetic properties to donor plants and sites (**Figure 2**; Wood et al., in review). This is among the most successful restoration programs globally and there are now self-sustaining crayweed populations with likely F3–4 generations in some restored sites.

To ensure empirical genetic data is utilized to facilitate informed provenance decisions, data on genetic diversity and structure and their links to environmental conditions should be made publicly available to stakeholders and non-experts including community groups and governments who often implement restoration programs. For example, the restore and renew website for terrestrial plants[2] (Rossetto et al., 2019) allows users to define a site to be restored, choose appropriate provenance within defined genetic populations and even provides provenance options to improve resilience (see "*Revive* – Restoring Extant or Historic Genetic Baselines"). No such platforms exist for marine systems but development of new marine restoration methods that will increase accessibility of marine restoration to diverse user groups and over large scales, will necessitate similar initiatives to ensure scientifically informed provenance decisions are made within the decade of restoration.

DYNAMIC BASELINES – WHY WE SHOULD NOT REPLICATE WHAT WAS LOST

In rare cases baseline genetic data from lost or vulnerable populations are available and can theoretically be replicated. For example, rare "before" and "after" data has revealed massive change in baseline levels of genetic diversity and structure in three species of kelps that were impacted by a heatwave off Western Australia (Coleman et al., 2011b; Wernberg et al., 2018; Gurgel et al., 2020). Under a scenario of restoration that seeks to replicate what was lost, such "before" estimates can be used as a guide for provenance. This may be desirable where legislation dictates the necessity for a baseline (McAfee et al., 2019) or there are concerns surrounding genetic pollution (Potts et al., 2003). However, these studies have also revealed that genetic "baselines" are not static but are naturally dynamic properties of populations that can change rapidly (within a few months), due to redistribution of existing genetic variants through dispersal or selection (Torda et al., 2017; Gurgel et al., 2020).

This raises the important question of whether it is desirable to replicate exactly what was lost, or to embrace the dynamic nature of baselines and make informed decisions to reinforce or redefine them to an unknown future state (**Figures 1**, **3**). Kelp loss and change in genetic baselines may naturally enhance resilience to future stress through selection. Thus, restoring kelp forests using past genetic baselines may, therefore, actually create populations that are more vulnerable to the events or stressors that caused loss in the first place providing a mechanistic basis and impetus for reinforcing as a restoration goal. Predicting future genetic response can be enhanced by the incorporation of neutral and functional genetic variation into species distribution models under projected future environmental scenarios (Bay et al., 2017; Razgour et al., 2019). Given naturally shifting baselines and environmental changes that are increasingly overwhelming the intrinsic capacity of organisms to adapt and survive in parts of their range (Deutsch et al., 2015; Segan et al., 2016) it is imperative to explore the potential to enhance or reinforce the resilience of ecosystems through restoration (Hobbs et al., 2017) as well as proactively reinforce resilience in habitats that will be threatened under future scenarios of change.

REINFORCE – IMPROVING GENETIC BASELINES FOR FUTURE CONDITIONS

Often termed "assisted adaptation" or "assisted evolution," the idea of reinforcing genetic baselines is to introduce diversity or genotypes that will enhance resilience to future stressors in restored or threatened populations. While there are scientific and ethical challenges to adoption of such approaches (Coleman and Goold, 2019; Filbee-Dexter and Smajdor,

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[2] restore-and-renew.org.au

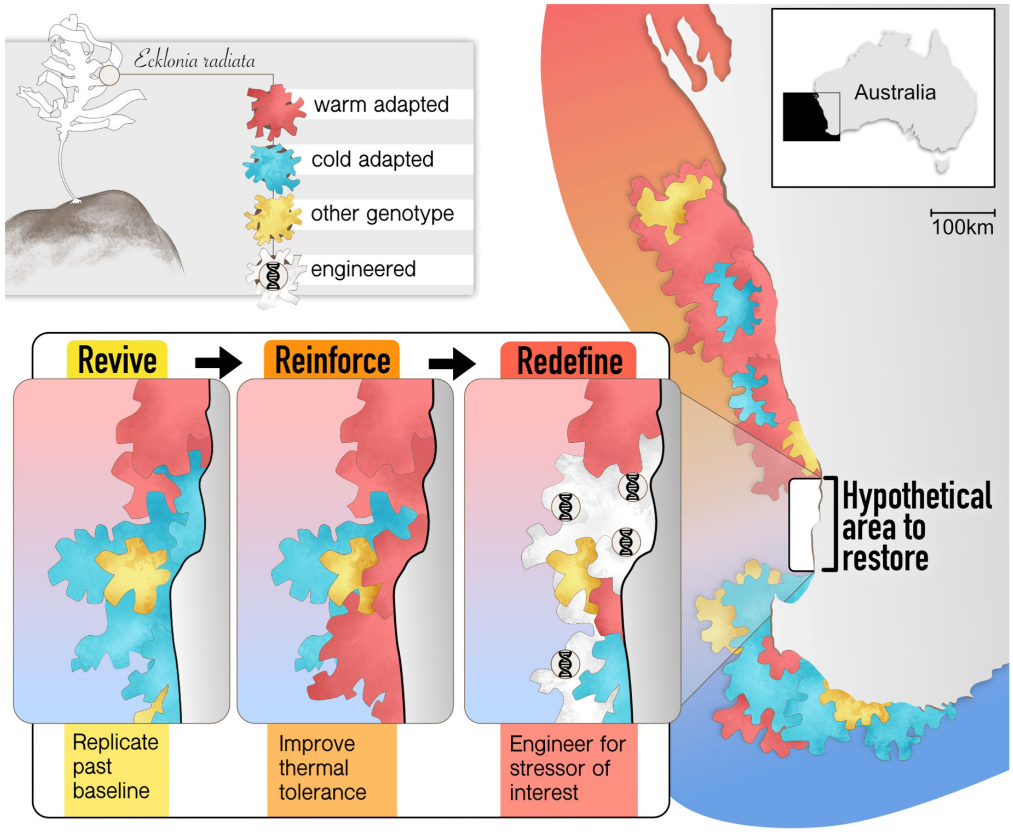

FIGURE 3 | Potential scenarios for kelp restoration for a hypothetical area to be restored off Western Australia. Frequencies of putative warm (red) and cool (blue) adapted genotypes have been identified along a gradient of ocean temperature (shaded background) which could be utilized to revive or reinforce kelp forests against future thermal stress. Kelps with engineered genetic elements could one day be used to redefine the genetic baseline.

2019), the continued anthropogenic alteration of habitats and emergence of novel ecosystems place such interventions firmly at the forefront of restoration science.

The terms assisted adaptation or evolution capture numerous approaches for manipulating natural genetic properties of populations in order to increase their ability to adapt to changing environmental conditions. Such measures include moving resilient individuals to vulnerable populations to increase their capacity to resist or recover from disturbances (known as assisted gene flow or assisted migration; **Figure 3**). This could be achieved through targeted sourcing of donor plants using laboratory selection experiments or through identification of natural selection in the field (Zhang et al., 2011; Robinson et al., 2013; Gurgel et al., 2020). Another proposed strategy is "genetic rescue" whereby genetic diversity is enhanced in populations that have limited adaptive capacity, rather than entirely new genotypes introduced. Opting for boosting genetic diversity also reduces risks of negative fitness trade-offs by increasing the overall range of responses to various environmental conditions without aiming at improving one specific function. This approach has enhanced seagrass restoration success with greater productivity and biodiversity in experimental plots with increased genetic diversity (Reynolds et al., 2012). Similarly, higher genetic diversity in kelp forests may also confer greater resilience to climate stressors (Wernberg et al., 2018). Finally, resilience may be increased by utilizing intra-specific hybrid vigor or heterosis whereby crossing individuals from different populations (often not connected by contemporary gene flow) increases fitness relative to pure breds (e.g., Sexton et al., 2011), although this idea may be underpinned by mechanisms including increase in genetic diversity *per se*, addition of more resilient genes or epigenetic responses (Fujimoto et al., 2018).

Given the controversial nature of restoration strategies that seek to reinforce or improve extant genetic baselines, prioritization and careful selection of candidate species or sites is vital, as is experimentation to provide proof of concept that such strategies will work under a range of current and potential future stressors. It may be most appropriate to consider assisted adaptation in areas where species are already threatened or endangered, where projections of loss are severe or where impacts of loss will have widespread economic and ecological effects (e.g., foundation species; Baums, 2008; Aitken and Whitlock, 2013). Australian kelps meet all these criteria because a lack of poleward landmasses and warm currents along both coastlines create a unique scenario whereby species are locked into an ever narrowing thermal niche (Coleman et al., 2011b, 2017; Martínez et al., 2018). Projections for Australian kelps under climate change scenarios reveal an average loss of 78% of current distributions under the immediate RCP 6.0 scenario (Martínez et al., 2018), which may present logical targets for assisted adaptation and improving extant genetic baselines. This could be done through genomic identification of heritable loci under selection for certain stressors combined with manipulative stress experiments using multiple stressors that test the resilience of genotypes possessing such loci and assess potential trade-offs. Genotypes that perform well can then be cultured for enhanced seeding into restored populations (**Figure 2**; Weeks et al., 2011; Webster et al., 2017; Fredriksen et al., 2020). Given that such approaches, however, could lead to detrimental trade-offs (maladaptation) and decreased resilience to non-target stressors (Hereford, 2009; Anderson et al., 2014), a portfolio approach whereby assisted adaptation is paired with other approaches including enhancing diversity or connectivity, protecting a wide range of seascapes and minimizing stressors (Webster et al., 2017) may provide more security in uncertain futures.

REDEFINE – CREATE A NOVEL GENETIC STATE

Scientific advances are providing never-before imagined solutions to emerging environmental problems, with synthetic biology and CRISPR/CAS9 gene editing tools among the fastest developing and transformative scientific fields (Lin and Qin, 2014; Wang et al., 2016; Piaggio et al., 2017). These technologies involve the creation of novel and engineered genetic variation that could be utilized in a restoration context to redefine extant genetic baselines and future resilience of species and populations to change (**Figure 3**; Coleman and Goold, 2019). The potential application of such technologies is vast, at times controversial, and technological advances have outpaced social, ethical and practical considerations. Here, we discuss some of the potential applications of synthetic biology and gene editing in restoration. Rather than advocate or oppose their use, we identify where and when they may play a role in restoration science. Regardless of whether these techniques will ever be socially acceptable or even necessary, this is a discussion that must be had early on.

Synthetic biology, or the engineered creation of novel genetic variation, is a fast developing and transformative scientific field. It can involve both genetic and metabolic engineering to create new functions in living cells or the creation of entirely new cells with synthetic components. Synthetic biology has been enabled through the decreasing costs of sequencing and synthesis of DNA, availability of extensive databases including information on sequences and functions, and the standardization of parts (genetic elements, proteins, organisms) which allows for increasing predictability in biological organisms, facilitating their use in a more designed approach as biological devices (Canton et al., 2008). Synthetic biology has also been enabled by development of the CRISPR/Cas9 genome editing tool (Pretorius, 2017) that cleaves viral double stranded DNA and allows for very precisely targeted changes to be made in a genome, as long as an organism is genetically tractable (Doudna and Charpentier, 2014). Examples of the use of CRISPR/Cas9 range from introducing a point mutation in a species genome to affect the quantity of metabolites (Shih et al., 2016), engineering speciation through designer karyotypes (Luo et al., 2018), or creating sequence specific anti-microbials through microbiome engineering (Bikard et al., 2014).

In conjunction with the availability of vast metagenomic data, it should be possible for scientists to map the genetic characteristics of resilient species or entire populations that are thriving despite stress, through natural and manipulative experiments. Resilient genetic elements could then help guide synthetic biology/genome engineering design principles. For example, traits from populations of marine organisms which have adapted to adverse conditions (e.g., polluted areas or warm range edges) could be introduced into related species or impacted populations to improve resilience to those stressors. The nature of these genetic elements could range from advantageous single nucleotide polymorphisms (SNPs; Doudna and Charpentier, 2014), to different genetic alleles/genes or even foreign/synthesized DNA (Williams et al., 2017), to larger duplications, inversions or deletions of entire chromosome arms (Luo et al., 2018). Synthetic biology could even be applied to restore extinct species. Such approaches are being considered in terrestrial contexts, with various groups attempting to resurrect extinct species (known as “de-extinction”), such as the great auk and the woolly mammoth (Corlett, 2017). Indeed, by extensive and rigorous bio-banking it may be possible, in the long term, to attempt to partially recreate extinct species and biomes using synthetic biology and store adaptive potential (Hodgins and Moore, 2016). Thus, to enable future restoration, bio-banking and *ex situ* conservation approaches should be promptly considered to allow the possibility for habitat recreation into the future.

Another technique that constitutes redefining extant genetic baselines is assisted evolution through inter-specific hybridization or heterosis. This utilizes the phenomenon of hybrid vigor, whereby species F1 hybrids display greater fitness than pure breds and is an emerging idea that has been suggested as a tool to enhance survival and persistence of foundation species under future climates (Rinkevich, 2014; van Oppen et al., 2015; Wood et al., 2019). In an assisted evolution context, inter-specific hybridization would be facilitated where it would otherwise not occur spatially, temporally (e.g., reproductive isolation) or within evolutionary time frames that would match the rapid pace of climate change. For example, hybrids of both kelp and coral have been shown to have greater thermal tolerance (Chan et al., 2018; Martins et al., 2019) which could be utilized in a restoration or assisted adaptation context that accepts redefining genetic baselines by mixing species gene pools.

At present, redefining extant genetic baselines in natural ecosystems is perhaps most palatable and ethically acceptable in the extreme case of stopping species extinction. Given the transformative nature and unpredictability of creating new genetic states, we suggest a starting point may be to prioritize species with little chance of persistence under future climate conditions. Again, Australian kelps provide the perfect example of such a situation because rapid warming, a narrowing thermal niche combined with high endemism (Phillips, 2001) create conditions that will see many species extinct within the next century (Martínez et al., 2018). For example, the endemic fucoid *P. comosa* (Coleman and Wernberg, 2017) is predicted to be completely lost by 2100 under future scenarios of climate change given extant temperature tolerances. Moreover, this species possesses a shallow history with low genetic diversity and structure (Coleman and Kelaher, 2009; Coleman et al., 2011a; Durrant et al., 2015), likely limiting its possible responses to change. Given that no other extant species seem to provide the same functions as *P. comosa* (Marzinelli et al., 2014, 2016), this warrants prompt discussion on the potential for genetic engineering of novel elements to boost thermal resilience as well as limit the effects of additional stressors (Coleman and Goold, 2019). Without such interventions, this key foundation species may be lost forever.

Assisted adaption, gene editing and hybridization raise complex ethical issues, which largely center on whether we should be deliberately introducing new genetic entities into natural ecosystems. From an ethical perspective, this shift in restoration focus from "*revive*" to "*redefine*" is significant (Camacho, 2010). Redefining genetic baselines can create problematic value judgments, such as prioritizing some species or properties over others, effectively deciding the winners and losers of the Anthropocene. These strategies to alter populations to withstand future stress also transform our role from *guardians* to *engineers* and *designers* of natural systems, which we do not fully comprehend, and can move ecosystems toward states that they have never been in before. As a result, we are determining the value of species and ecosystems based on the degree to which they match our current ideals of how things should be – targeting a more intact, familiar ecosystem that has been genetically manipulated to resist certain types of environmental stress, instead of an unpredictable and unfamiliar ecosystem that is transforming due to human activity. The use of adaptive or assisted evolution is also complicit with a worldview of environmental manipulation and commodification of natural systems that could perpetuate the damaging habits and dispositions which have caused the habitat loss in the first place (Sandler, 2013). Even if not morally wrong itself, adapted or assisted evolution may increase reliance on biotechnological intervention or even be used to justify continuing harmful practices in the future.

Conversely, inaction or passive decisions (i.e., not using all available tools to potentially save a species or habitat from disappearing) may also be unethical. If we have reason to predict that not acting will cause more harm than acting, then intervention seems to be the best course of action available. In an ideal world, we would reduce emissions and mitigate human impacts in time to remain in the "revive" space of conservation. Yet, we are in a state of crisis that we know will severely impact our environment and future generation (Gattuso et al., 2015). In light of this pressing reality, it could be argued that we have a moral responsibility to take risks we can reasonably predict will help to repair human-caused damage – as long as we are not reckless or negligent in doing so (Douglas, 2003). At a minimum, we should seek to thoroughly understand the potential impact of using all the tools available to us now, so that we will be in a position to choose these options should some catastrophic scenario arise in the future (e.g., "arm the future argument" outlined by Gardiner, 2010).

At a more practical level, there are several first steps we can take toward including ethical considerations in decisions to use assisted evolution tools. First, we can ensure that a minimum standard of risk assessment of potential impact on the environment is conducted. This could include controlled manipulative experiments on novel or engineered genotypes to assess their performance and interactions in natural settings. Second, that informed consent of stakeholders is obtained and that no conflicts of interest exist in the relationships between researchers/managers and local communities. Finally, we can develop policy and guidelines for the use of these tools in specific systems. Regardless, there is a pressing need for prompt collaboration and dialogue among geneticists, synthetic biologists, ecologists, and conservationists to identify opportunities for use of these transformative technologies and ensure that extant research directions are set on trajectories to allow these currently disparate fields to converge toward practical restoration solutions. While the application of such techniques to natural settings is currently controversial (Filbee-Dexter and Smajdor, 2019) they should remain at the forefront of discussions to future-proof marine ecosystems and restoration practices (Coleman and Goold, 2019).

RESTORE OR REDEFINE: A BROADLY APPLICABLE FRAMEWORK

While we have focused here on kelp forests, the framework presented is broadly applicable to any marine or terrestrial restoration program. Indeed, it may even be more easily applied and adopted for restoration of species that are more genetically tractable than kelps. Genomic techniques might be more rapidly developed in taxa for which DNA extraction and subsequent sequencing techniques are more easily applied. Further, genomic resources are more developed for key model species such as corals, making progress toward *revive* and *redefine* more tangible. Indeed, genetics and provenance are emerging considerations in coral reef restoration guidelines (Baums et al., 2019) and standard practices that are easily accessible to managers and practitioners (e.g., www.reefresilience.org). For such taxa, progress toward empirically incorporating appropriate genetic baselines to restoration programs should be more rapid. The goal to redefine genetic baselines in restoration programs may also be more tangible for taxa that have direct economic value (e.g., harvested species), where breeding programs often involve detailed genomic assessments linking performance and traits to environmental conditions. Regardless, restoration of foundation macrophytes (e.g., saltmarsh, seagrass, mangroves) and animals (e.g., oyster beds, corals) that underpin vast biodiversity of marine systems is gaining increasing traction, funding and sophistication with great potential toward achieving the aims of the United Nations decade of restoration.

CONCLUSION

Whether to recover and restore historic and extant genetic baselines, or reinforce and redefine them to some unknown future state, will fundamentally affect the resilience and adaptive capacity of restored populations (Hobbs et al., 2009; van Oppen et al., 2015; Breed et al., 2018, 2019; Wood et al., 2019) but is largely untested for marine systems. Here, we discuss the application of both traditional and modern genomic tools for characterizing (e.g., genotyping by sequencing) and manipulating (CRISPR/Cas9) the genetic composition of lost or degraded marine habitats. The increasing accessibility of these genomic techniques means that future marine restoration efforts can, and should, proceed with the best available genetic data and technologies. At a minimum, baseline empirical genetic data should inform provenance decisions and, where acceptable, incorporate assisted adaptation strategies.

More broadly, it is clear that restoration in the traditional sense of returning a system to a past state, is unlikely to be sufficient or effective under future climates (van Oppen et al., 2017). Instead, restoration should seek to reinforce and perhaps even redefine populations and species to withstand future environmental conditions and stressors. However, this raises profound and challenging management (to what baseline should we “restore?”), technical (how do we achieve that baseline in a practical sense?) and ethical (what right do we have to introduce novel genetic entities into the marine environment?) questions that will determine our ongoing relationship with nature. We argue for a worldwide move among marine managers and scientists toward prompt consideration of more interventionist approaches. The failure to consider and prepare for such approaches, despite ethical debates, is also an ethical decision with potentially serious environmental consequences of inaction.

Marine restoration will benefit from learnings from the history of biomedical fields, where technological developments and associated benefits have often outstripped the social and ethical dialogue necessary for implementation. Prompt dialogue is thus required among scientists, policy makers and the broader community on setting restoration targets, including the increasing need to restore for future conditions and the implications of using novel or engineered genetic entities (Coleman and Goold, 2019). Scientific agendas should be set on trajectories to provide the underpinnings for such decisions. Only then can we ensure that our valuable marine habitats continue to deliver ecosystem goods and services in the face of increasing environmental change.

AUTHOR CONTRIBUTIONS

MC and AM conceived the idea and led the manuscript. All authors wrote sections and edited the manuscript. AM produced the figures.

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Meta-Analysis Reveals Artificial Reefs Can Be Effective Tools for Fish Community Enhancement but Are Not One-Size-Fits-All

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Approaches toward habitat conservation and restoration often include supplementing or enhancing existing, degraded, or lost natural habitats. In aquatic environments, a popular approach toward habitat enhancement is the introduction of underwater human-made structures or artificial reefs. Despite the nearly global prevalence of artificial reefs deployed to enhance habitat, it remains debated whether these structures function similarly to comparable natural reefs. To help resolve this question, we conducted a literature review and accompanying meta-analysis of fish community metrics on artificial reefs within the coastal ocean and made comparisons with naturally-occurring reference reefs (rocky reefs and coral reefs). Our findings from a synthesis of 39 relevant studies revealed that, across reef ecosystems, artificial reefs support comparable levels of fish density, biomass, species richness, and diversity to natural reefs. Additional analyses demonstrated that nuances in these patterns were associated with the geographic setting (ocean basin, latitude zone) and artificial reef material. These findings suggest that, while artificial reefs can mimic natural reefs in terms of the fish assemblages they support, artificial reefs are not one-size-fits-all tools for habitat enhancement. Instead, artificial reefs should be considered strategically based on location-specific scientific assessments and resource needs to maximize benefits of habitat enhancement.

Keywords: artificial reef, habitat enhancement, habitat creation, marine restoration, habitat supplementation, reef fish, fish community, meta-analysis

INTRODUCTION

Coastal reef habitats face diverse and varied threats, including overharvesting, habitat destruction, pollution, and climate change (Millennium Ecosystem Assessment, 2005; Lotze et al., 2006). For example, extensive habitat degradation and loss has been documented on coral reefs (Burke et al., 2011; McClenachan et al., 2017). Foundation species (e.g., kelp) associated with rocky reefs have also declined (Filbee-Dexter and Wernberg, 2018). Even when reefs are not actively facing degradation, the value of ecosystem services that reefs provide (Hughes et al., 2017; Townsend and Lohrer, 2019) often prompt managers to enhance the existing reefs (Seaman, 2007; Becker et al., 2018). A popular approach toward reef habitat enhancement is the introduction of underwater human-made, artificial structures (Seaman, 2007). Human-made artificial structures, such as metal vessels and concrete modules, are frequently deployed as artificial reefs on the seafloor to create reef habitats (Becker et al., 2018), and decommissioned energy platforms are dismantled and converted to artificial reefs (Macreadie et al., 2011).

Artificial reefs are defined as "submerged structure[s] deliberately constructed or placed on the seabed to emulate some functions of a natural reef, such as protecting, regenerating, concentrating, and/or enhancing populations of living marine resources" (United Nations Environment Programme, 2009). Artificial reefs have a long history, with the first recorded use in Japan during the 1600s when rock and rubble from former buildings were deployed to aggregate fish and grow kelp (Stone et al., 1991). In the United States, the first documented use of artificial reefs occurred in the 1830s when small wooden structures (log huts) were deployed off South Carolina to facilitate fishing (McGurrin et al., 1989). More widespread reef construction in the open ocean began in the United States in 1935 but then lulled during World War II (McGurrin et al., 1989). During the 1950s artificial reefs surged in popularity, as fishermen deployed disposable objects, such as tires and concrete, to enhance their fishing opportunities, eventually leading to commonplace government-led artificial reef programs (McGurrin et al., 1989). In the modern era since the environmental movement in the 1960s and 1970s, artificial reefs have garnered increasing attention as a tool for habitat restoration and enhancement of fisheries resources.

Artificial reefs are widespread globally across temperate and tropical systems (Seaman, 2002; Ilieva et al., 2019). In the United States, for example, artificial reefs are established and maintained by state-run artificial reef programs with national guidance (National Oceanic Atmospheric Administration, 2007). Artificial reefs are also prevalent in Europe (Jensen, 2002; Fabi et al., 2011), Africa (Lechanteur and Griffiths, 2001; Seaman, 2002), South America (Honório et al., 2010; Hackradt et al., 2011), Asia (Nakamura, 1985; Chou, 1997), and Australia (Branden et al., 1994; Mills et al., 2017). The goals of artificial reef programs vary geographically, yet common goals across regions are to support fisheries management, increase fishing yield, provide fishing and diving opportunities, mitigate habitat loss, and to restore habitats, such as kelp forests and coral reefs, by providing substrate (Becker et al., 2018).

Despite the popularity of deploying artificial reefs to enhance habitat, it remains debated whether these reefs function similarly to comparable natural reefs (Carr and Hixon, 1997; Simon et al., 2013; Granneman and Steele, 2015). Artificial reefs are known to facilitate abundance of tropical fish at their range edges (Paxton et al., 2019), enhance nursery grounds (Mercader et al., 2017), and host elevated predator densities (Paxton et al., in revision), but also facilitate invasive species (Airoldi et al., 2015) and increase biotic homogenization (Dafforn et al., 2015). Evidence for whether artificial reefs support similar fish communities to natural reefs is mixed. In some systems, artificial reefs have been demonstrated to support equivalent amounts and types of fish as natural reefs (Stone et al., 1979; Lemoine et al., 2019). However, in other instances, artificial reefs have been documented to hold greater (Bohnsack et al., 1994; Arena et al., 2007; Paxton et al., 2017) or fewer (Carr and Hixon, 1997; Froehlich and Kline, 2015) fish and fish species. Given the differing evidence, knowledge gaps remain in whether fish community metrics are similar on artificial reefs relative to natural reference habitats. Resolving this question requires a global synthesis of artificial reefs, natural reefs, and their associated fish communities.

Here, we conducted a literature search and meta-analysis to test whether artificial reefs host similar fish community metrics to comparable natural reefs. We focused our synthesis on four fish community metrics—density, biomass, species richness, diversity—reported on marine artificial reefs and naturally-occurring habitats (rocky reefs and coral reefs) at depths shallower than 150 m. Specifically, we asked: (1) Do fish community metrics differ between artificial reefs and natural reefs and (2) What potential mechanisms (e.g., geographic setting and artificial reef material) explain differences in fish community metrics on artificial vs. natural reefs?

METHODS

Literature Screening

We conducted a literature search of fish communities associated with artificial reefs vs. natural reefs in the coastal ocean using Web of Science and Google Scholar. In addition to artificial reefs, other structures, such as shipwrecks (Hoyt et al., 2014) and oil and gas infrastructure (Macreadie et al., 2011), also reside on the seafloor. In this study, we collectively refer to these structures (artificial reefs, shipwrecks, energy infrastructure) as artificial reefs. We conducted the Web of Science search on 5 November 2019 using the advanced search function with Boolean logic with the search query: TS = (artificial reef* OR artificial habitat* OR man-made reef* OR shipwreck* OR oil rig* OR oil platform*) AND TS = (fish*) AND TS=(rocky reef* OR coral reef* OR hardbottom* OR hard-bottom* OR hard bottom* OR livebottom OR live-bottom* OR live bottom* OR natural reef*) AND TS = (abundance* OR biomass* OR densit* OR richness* OR diversity*) (note that the * acts as a wildcard, so a string such as densit* would represent density or densities). This search for the dates 1900 to present yielded 524 potentially relevant articles. We imported the title and abstract of each article into Colandr (Cheng et al., 2018) and screened each article according to specified inclusion criteria (**Table 1**). Briefly, we included field-based studies that reported fish community metrics on artificial habitats and comparable reference reef habitats in the coastal ocean through direct observations, such as diver surveys, video surveys, and net tows at depths shallower than 150 m. This initial screening revealed that 103 of the 524 articles were candidates for inclusion; we then conducted a full-text screening of these 103 articles based on the inclusion criteria. Of these studies, 32 met our criteria and were retained for data extraction.

To ensure that additional relevant papers were not overlooked, we completed a complementary search with a more basic search query (fish assemblage OR fish community AND artificial reef AND natural reef) from 1900 to present in Google Scholar on 6 November 2019. Since this was a complementary and intentionally broader search, it returned 23,600 articles sorted by

TABLE 1 | Study inclusion components and criteria for literature review.

Inclusion component	Inclusion criteria
Subject(s)	Reef-associated fish
Comparator	Artificial habitats vs. natural reference habitats in coastal marine systems globally. Artificial habitats can include artificial reefs, oil platforms, wind turbine bases, and shipwrecks. Shoreline habitats (e.g., jetties and breakwaters), aquaculture enclosures, pipelines, and estuarine artificial habitats were excluded. Artificial habitats were excluded if they were deployed on healthy or degraded natural habitat. Natural habitats include rocky reefs and coral reefs. Depth <150 m
Response(s)	Density (or abundance), biomass, species richness, or diversity of fishes on artificial habitats vs. natural reference habitats. Studies that reported on metrics for only a subset of fishes, such as planktivorous fishes, demersal fishes, resident fishes, or fish families, were excluded
Study type	Primary research studies reporting field observations of fish assemblages or communities on artificial habitats and natural reefs from visual surveys (e.g., diver surveys, video surveys, and net tows)

relevance. We screened the titles and abstracts of the first 200 articles sorted in order of relevance in Google Scholar, conducted a full text-screen on 24 potentially relevant articles, and found 7 that met our inclusion criteria. Thus, 39 papers (32 Web of Science, 7 Google Scholar) in total were targeted for data extraction. Both the Web of Science and Google Scholar searches were for peer-reviewed literature (**Table S1**).

Data Extraction

We built a relational database in Microsoft Access to facilitate data extraction. During data extraction, we recorded identifying information for each study: author, title, publication date, and journal information. We then extracted metadata related to geographic location [continent, country, state (if applicable), ocean basin, local water body, latitude, and longitude], survey approach (method, year), natural reef descriptions (natural reef type, depth, complexity, and description), artificial reef descriptions (artificial reef type, depth, complexity, description, material, date of deployment, and substrate deployed on), and any additional notes that might be important for understanding conditions of the study. If a range of depths were provided, we used the mean of the upper and lower range values as the depth. We categorized complexity as low (<2 m vertical relief), medium (2–4 m vertical relief), or high (>4 m vertical relief). If multiple sites were surveyed with differing complexities, we categorized complexity according to the highest relief reef. If complexity values were not provided, we used typical values (e.g., patch reef = low relief, concrete modules = low relief, shipwreck = high relief). We converted latitude to a factor called "latitude zone," where 0–23.5° N/S is tropical, 23.5–35° N/S subtropical, 35–50° N/S temperate, and 50–70° N/S subarctic. There were no studies with latitudes >70° N/S. We coded artificial reefs composed of more than one material (e.g., concrete, metal, boulders, and tires) as "mixed."

Next, we extracted data for each fish community metric (i.e., density, biomass, richness, and diversity) reported in a given study. For each fish community metric, we recorded the units, and if units were not explicitly provided, we determined them based on methodological information, such as the transect dimensions for diver surveys. We then recorded the mean value of the metric reported on artificial reefs and natural reefs, as well as the accompanying precision and noted the type of precision (none, standard error, standard deviation, 95% confidence intervals). We extracted the sample size per reef type and the location within the paper where data were extracted (e.g., table number, figure number, or paragraph location). For several papers, data on fish metrics were only available from figures, so we used the "digitize" package (Poisot, 2011) in R (R Core Team, 2019) to extract the relevant values.

While data extraction was straightforward for most publications, others required us to make decisions about which data were most relevant. In such cases, we made these decisions on the basis of comparability. As an example, in several studies, mean values were reported for one artificial reef and for multiple natural reefs but without information necessary to calculate a pooled group mean for natural reefs. In these cases, we extracted the metric value from a single natural reef that most closely matched the single artificial reef in location (e.g., geography, depth). If studies reported metrics for multiple artificial reef materials separately (e.g., metal vessel and concrete pipes), then these values were recorded as different entries (rows) in the database and associated with the same natural reef data. If a study included only a segment of the fish community (e.g., only resident species or excluded certain fish families), then it was omitted according to our inclusion criteria (**Table 1**) since it did not report on the entire community.

Effect Size Calculations

To calculate effect sizes (e.g., outcome representing relationship between fish community metrics for artificial vs. natural reefs), we required standard deviation (*SD*), sample sizes (*n*), and mean values (*X*) for each community metric and each study on both artificial and natural reefs. Computations or conversions were necessary to obtain the required values for some studies. When standard error (*SE*) was presented but not *SD*, we calculated *SD* as:

$$SD = SE\sqrt{n} \tag{1}$$

(Higgins et al., 2019). Similarly, when 95% confidence intervals (*CI*) were provided, we calculated the *SD* as:

$$SD = \frac{\sqrt{n}\left(CI_{upper} - CI_{lower}\right)}{3.92} \tag{2}$$

where CI_{lower} and CI_{upper} represent the lower and upper bounds of the 95% confidence interval (Higgins et al., 2019). When multiple groups were presented for a reef type (e.g., three artificial reefs of the same material with metrics reported separately), we pooled the means and weighted by the sample size following:

$$\overline{X} = \frac{\sum_i n_i x_i}{\sum_i n_i} \tag{3}$$

where X_i is the value of the ith group, n_i is the sample size of the ith group, and $\overline{X}$ is the weighted mean (Borenstein et al., 2009; Higgins et al., 2019). We calculated pooled SD as:

$$SD_{pooled} = \sqrt{\frac{\sum_i (n_i - 1)\, SD_i^2}{\sum_i n_i - N}} \tag{4}$$

where N is the number of groups and SD_i is the SD of the ith group (Borenstein et al., 2009).

We calculated effect size as a standardized mean difference. Specifically, we used Hedges' g because it contains a correction factor that reduces bias. Using the sample means, standard deviation, and sample size for artificial (AR) and natural reef (NR) groups, we then calculated the Hedges' g effect size as:

$$g = \frac{\left(\overline{X_{AR}} - \overline{X_{NR}}\right) * J}{s} \tag{5}$$

(Borenstein et al., 2009), where J is a bias correction factor calculated as:

$$J = 1 - \frac{3}{4\,(n_{AR} - n_{NR}) - 9} \tag{6}$$

(Koricheva et al., 2013), and where s is the standard deviation pooled across reef type as:

$$s = \sqrt{\frac{(n_{AR} - 1)SD_{AR}^2 + (n_{NR} - 1)SD_{NR}^2}{n_{AR} + n_{NR} - 2}} \tag{7}$$

(Borenstein et al., 2009). We calculated the variance of Hedges' g as:

$$v_d = \frac{n_{AR} + n_{NR}}{n_{AR} n_{NR}} + \frac{g^2}{2\,(n_{AR} + n_{NR})} \tag{8}$$

(Borenstein et al., 2009). For one study, fish community metric means on artificial and natural reefs were unavailable, but ANOVA results examining the effect of artificial vs. natural reefs on metrics were available. We used the reported F value to calculate Hedges' g as:

$$|g| = \sqrt{\frac{F\,(n_{AR} + n_{NR})}{n_{AR} n_{NR}}} \tag{9}$$

and ensured that g was positive if the metric was higher on artificial than natural reefs and negative if the opposite (Koricheva et al., 2013). Similarly, for another study we used the reported t-value to calculate Hedges' g as:

$$g = t\sqrt{\frac{n_{AR} + n_{NR}}{n_{AR} n_{NR}}} \tag{10}$$

(Koricheva et al., 2013).

Imputation of Missing SD

For studies that did not report measures of precision ($n = 10$ density, $n = 4$ biomass, $n = 17$ richness, $n = 5$ diversity), we imputed SD by fitting a linear model between the known mean and SD, both log transformed, from the other studies (Marinho et al., 2003; Higgins et al., 2019). It is generally preferable to impute missing values than to exclude those studies with missing values from the meta-analysis (Batson and Burton, 2016; Weir et al., 2018). We then used the fitted model to impute the unknown SD values for the studies that reported means but not SD. For the one study that provided a t-value and the one study that provided an F-value that permitted calculation of Hedges' g but not the variance in Hedges' g, we used the mean variance in Hedges' g from the other studies for the same community metric and applied it (Batson and Burton, 2016). We later verified that our model outcomes were robust to imputation, as described below.

Meta-Analysis

We used the extracted data to explicitly test whether fish community metrics differ between artificial reefs and natural reefs using random effects models. We fit these meta-analytic models with the "metaphor" package (Viechtbauer, 2010), providing the Hedges' g effect size and variance in Hedges' g for each study. We used random effects meta-analysis models because of their assumption that there may be different effect sizes underlying different studies (Borenstein et al., 2009). For each fish community metric, we first fit a base model without moderators (i.e., independent predicator variables). We then fit a series of mixed models using categorical moderators: ocean basin (Atlantic, Pacific, Mediterranean), latitude zone (tropical, subtropical, temperate, subarctic), and artificial reef material (metal, concrete, boulders, mixed, tires). We chose not to include depth as a moderator since our inclusion criteria specified that all studies were shallower than 150 m. We also did not include reef complexity as a moderator because reef complexity closely relates to reef material. For example, metal ships are usually high complexity, whereas concrete structures are usually low complexity. We fit models for each combination of one, two, or three moderators (ocean basin, latitude zone, artificial material), resulting in eight total models per fish community metric.

We selected the final model from each of the eight candidate models per fish community metric using Akaike Information Criteria (Burnham and Anderson, 2004), with the lowest AIC value indicating the best performing model. We also examined the heterogeneity metrics associated with each model to verify our model selection (Borenstein et al., 2009). These included several metrics: T^2 (tau^2), the estimated total amount of heterogeneity (or residual heterogeneity if moderator included in model); I^2, the percent of total variability due to heterogeneity; H^2, the total variability divided by the within-study variance, and R^2, the proportion of true variance explained by the moderators relative to the base model without moderators. Model selection aimed to pick low T^2, I^2, H^2, values and high R^2 values (Borenstein et al., 2009). We additionally examined effect sizes for the models. When models contained moderators, we obtained the effect sizes of each moderator level by subtracting the model intercept. To then test for effects of moderators, we conducted omnibus tests of moderator significance (yielding QM*p* values, which provide a *p*-value for the moderator associated with the residual heterogeneity test). We also conducted likelihood ratio tests (LRTs) between the full and reduced versions of the model to examine the effect of each moderator. We visualized model results by plotting mean effect sizes and associated 95% confidence intervals, as well as by creating forest plots to visualize the effect sizes and confidence intervals of individual studies.

To verify that our final model results for each of the four fish community metrics were not dependent upon the imputation of the missing SD values, we bootstrapped the imputation procedure 1,000 times. In each bootstrap iteration, we generated a new log-log linear model, with model coefficients drawn from a 95% truncated multivariate normal distribution using the "tmvtnorm" package (Wilhelm and Manjunath, 2015). We tested how many times the significance of the moderators in each of the final models changed relative to the original fits. We also tested how many times the Hedges' *g* value was positive vs. negative for the base models without predictors to provide a supplementary test of the robustness of our overall results. To examine potential effects of publication bias in the final models, we created funnel plots, which help visually diagnose publication bias, and quantitatively tested for funnel plot asymmetry using regression tests (Viechtbauer, 2010). Specifically, we tested whether the observed outcomes for models without moderators or the residuals for models with moderators were related to their standard error values.

RESULTS

Our meta-analysis of 39 studies (**Figure 1**; **Table S1**) revealed that metrics describing fish communities are equivalent on artificial and natural reefs (**Figure 2**). The studies included in the meta-analysis span all continents except Antarctica and include artificial reefs in three ocean basins (Atlantic, Pacific, and Mediterranean). The artificial reefs were composed of metal, concrete, boulders, mixed materials (>1 material), and tires. Across the studies, density metrics were reported on 30 occasions, biomass 15, richness 34, and diversity 10. This general pattern of similar communities on artificial and natural reefs was robust to imputation for all community metrics, as the effect size and associated confidence intervals always overlapped zero during the bootstrap procedure.

Below, we detail our findings and detected nuances for each of the fish community metrics. When reporting the Hedges' *g* effect size, positive values indicate that a fish community metric is higher on artificial reefs than natural reefs. In contrast, a negative Hedges' *g* effect size represents a community metric that is higher on natural than artificial reefs. If 95% confidence intervals overlap with zero, then the difference between artificial and natural reefs is considered to not be statistically significant.

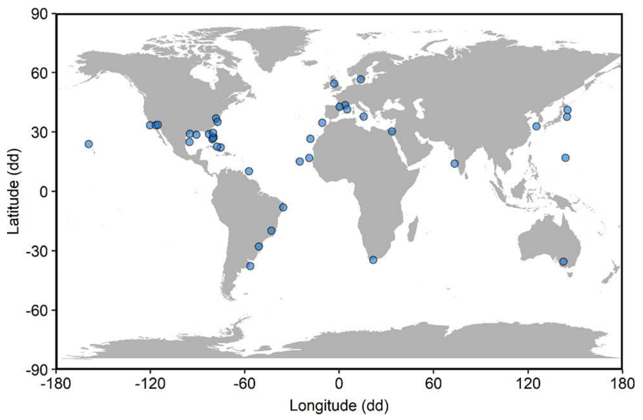

FIGURE 1 | Locations of 39 studies included in global synthesis of fish community metrics on artificial reefs relative to nearby natural reefs. Locations, in decimal degrees (dd), have been offset to avoid visual overlap of points.

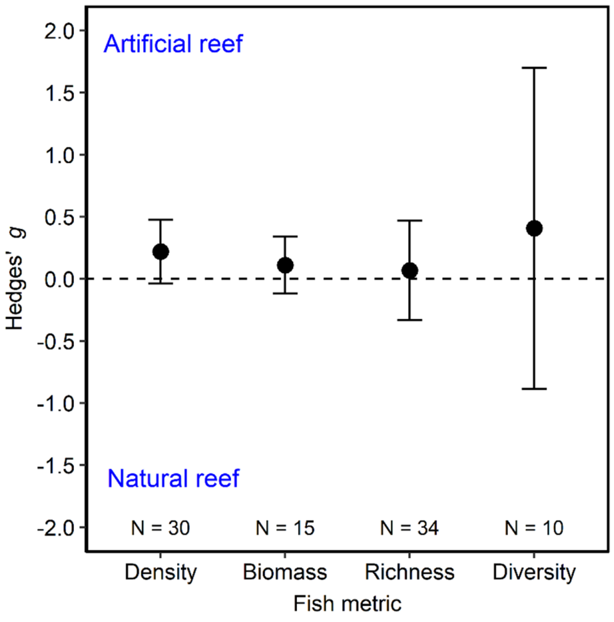

FIGURE 2 | Fish community metrics on artificial vs. natural reefs. Shown are mean Hedges' *g* effect size estimated with random-effects models without moderators for fish density, biomass, species richness, and diversity. Positive *g* indicates the fish community metric is higher on artificial than natural reefs, and a negative *g* means the opposite. Error bars represent 95% confidence intervals. If error bars overlap with zero, then the fish community metric is not significantly different on artificial vs. natural reefs. *N* represents the number of studies.

Density

Artificial reefs hosted similar fish densities to natural reefs (**Figure 2**). When we examined how fish density by reef type differed as a function of moderator variables, we discovered nuances to this pattern (**Figures 3**, **4**). Although ocean basin was not significantly related to fish density, artificial reefs in the Atlantic Ocean but not the Pacific Ocean or the Mediterranean Sea tended to host higher density than natural reefs (**Figure 3A**; LRT $\chi^2 = 4.13$, $p = 0.13$). Fish density on artificial and natural reefs was associated with the latitude zone that the reefs were located in **Figure 3B** (LRT $\chi^2 = 10.76$, $p = 0.01$). Artificial reefs

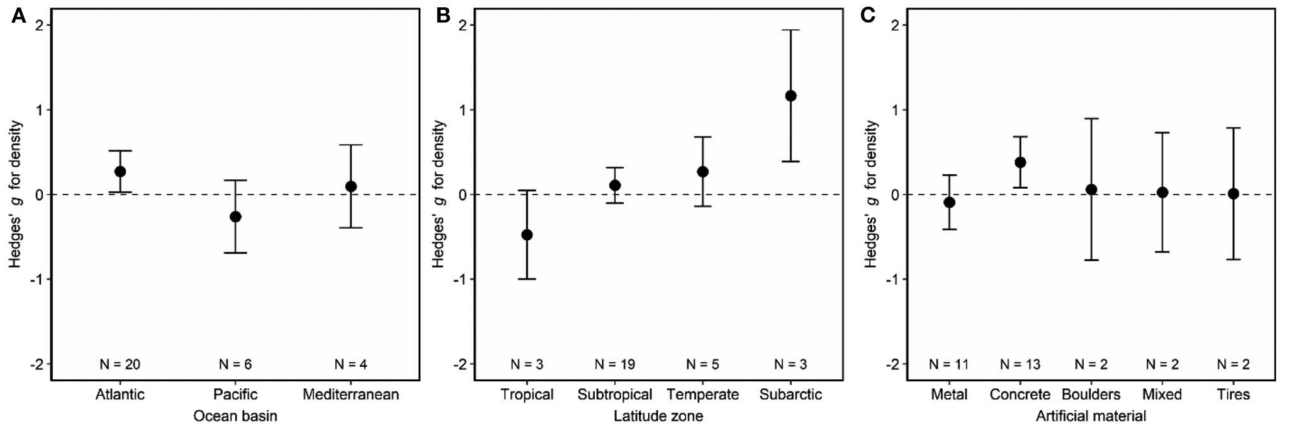

FIGURE 3 | Effects of **(A)** ocean basin, **(B)** latitude zone, and **(C)** artificial material on fish density associated with artificial and natural reefs. Shown are mean Hedges' *g* effect size estimated with mixed-effects models including either **(A)** ocean basin, **(B)** latitude zone, or **(C)** artificial material as a moderator. Positive *g* indicates density is higher on artificial than natural reefs, and a negative *g* means the opposite. Error bars represent 95% confidence intervals. If error bars overlap with zero, then density is not significantly different on artificial vs. natural reefs. *N* represents the number of studies.

in subarctic (50–70° N/S) zones supported higher fish density than natural reefs, whereas artificial reefs in tropical regions tended to support lower density, although this latter pattern was not statistically significant (**Figures 3B**, **4**). Additionally, reefs composed of concrete tended to have higher density than natural reefs (**Figure 3C**), but material was not significant overall (LRT $\chi^2 = 6.34$, $p = 0.18$). These patterns were represented in the final model selection that included latitude zone as a moderator (QM$p < 0.001$), which explained 45.97% more variance than the base model without the moderator (**Table S2**). These results were not influenced by the imputation of standard deviation, as all 1,000 bootstraps of the final model imputation yielded p-values for the moderator that remained significant. Additionally, the regression test for publication bias indicated no asymmetry in the funnel plot, suggesting there was not significant publication bias (**Figure S4A**; $p = 0.79$).

Biomass

Fish biomass did not differ on artificial and natural reefs (**Figure 2**, **Figure S1**). Biomass remained similar on artificial and natural reefs regardless of the ocean basin (**Figure 5A**; LRT $\chi^2 = 0.33$, $p = 0.85$) and latitude zone (**Figure 5B**; LRT $\chi^2 = 2.36$, $p = 0.31$). However, biomass was higher on artificial materials of mixed composition relative to natural reefs (**Figure 5C**, **Table S3**; LRT $\chi^2 = 15.30$, $p = 0.004$). The final model including artificial reef material as the moderator (QM$p < 0.0001$) explained 100% more variance than the base model without the moderator (**Table S3**). The funnel plot (**Figure S4B**) and bootstrapping procedure both verified that these results were robust to imputation, and the regression test suggested no asymmetry (publication bias) in the funnel plot (**Figure S4B**; $p = 0.91$).

Richness

Species richness was similar on artificial vs. natural reefs (**Figure 2**, **Figure S2**). Neither ocean basin (**Figure 6A**; LRT $\chi^2 = 2.86$, $p = 0.24$), latitude zone (**Figure 6B**; LRT $\chi^2 = 4.53$, $p = 0.10$), artificial material (**Figure 6C**; LRT $\chi^2 = 0.41$, $p = 0.98$), nor imputation affected this outcome. Although not statistically significant, artificial reefs located in the Mediterranean tended to have lower species richness than natural reefs (**Figure 6A**), and artificial reefs located in subtropical latitudes tended to have higher species richness than natural reefs (**Figure 6B**). The final model, therefore, did not include moderators (**Table S4**). The regression test indicated asymmetry in the funnel plot (**Figure S4C**; $p < 0.01$), suggesting the possibility that studies with small or non-significant findings were not published and thus not included in this analysis. If so, such a publication bias could influence our results.

Diversity

Artificial and natural reefs exhibited similar fish diversity (**Figure 2**, **Figure S3**). Nuances emerged with both ocean basin (**Figure 7A**; LRT $\chi^2 = 6.61$, $p = 0.04$) and latitude zone (**Figure 7B**; LRT $\chi^2 = 12.46$, $p = 0.006$) influencing diversity (QM$p < 0.0001$). In general, artificial reefs in the Mediterranean or in tropical or temperate locations seemed to have higher diversity than natural reefs, although the difference was not statistically significant. Artificial material did not influence the similarity in diversity on artificial and natural reefs (**Figure 7C**; LRT $\chi^2 = 0.08$, $p = 0.78$). The final model with both ocean and latitude included as moderators explained 78.25% more variance than the base model without these moderators (**Table S5**). The imputation procedures did not affect the model outcome, and funnel plot asymmetry was not significant, per the regression test (**Figure S4D**; $p = 0.72$).

DISCUSSION

Our findings from synthesis of 39 relevant global studies demonstrate that artificial reefs exhibit similar fish density, biomass, richness, and diversity to natural reefs. Further analyses revealed nuances in these patterns with geography and artificial

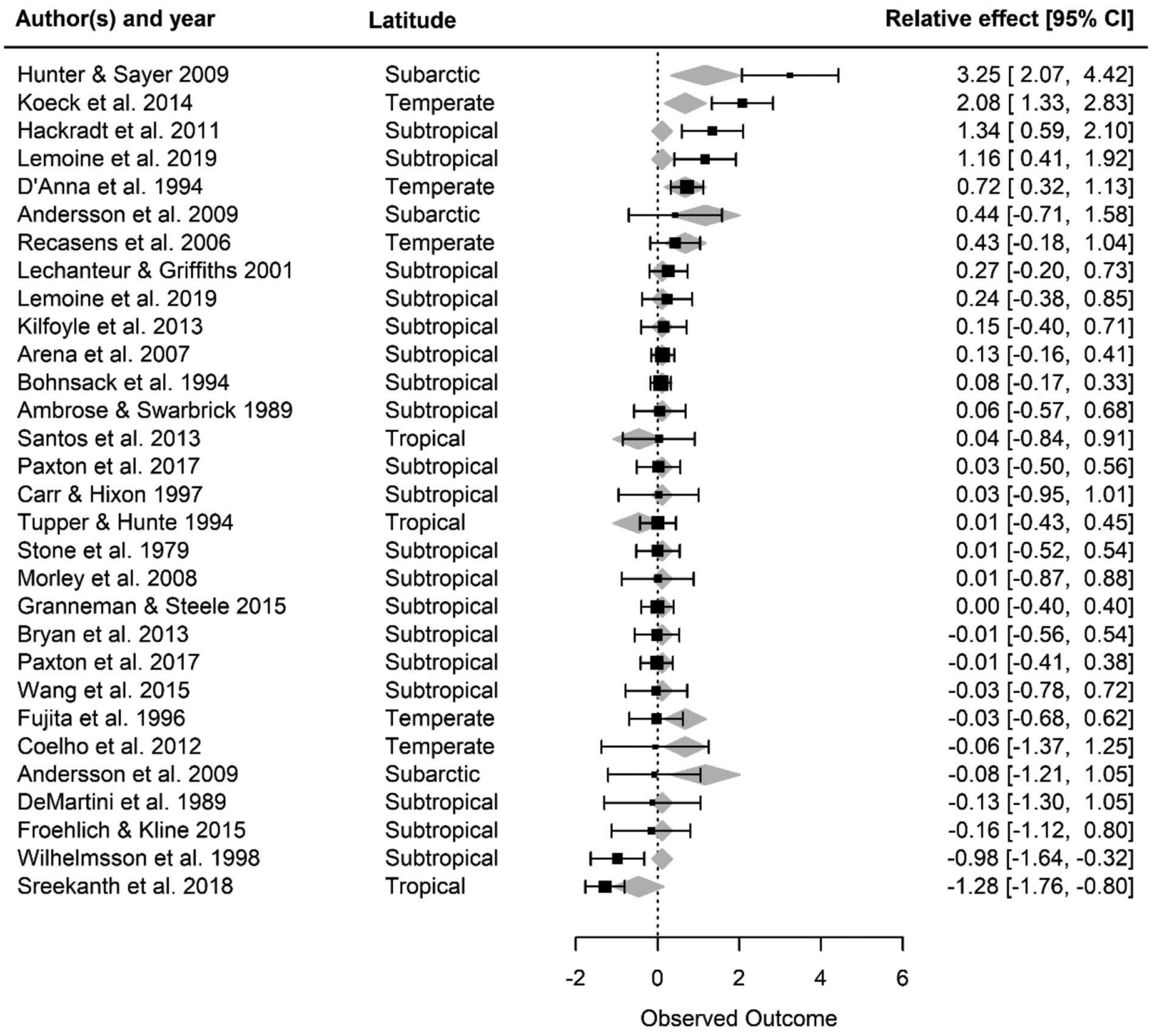

FIGURE 4 | Forest plot of observed outcome (Hedges' *g* effect size) for the final fish density model with latitude included as a moderator. For each study, the effect size and its 95% confidence intervals are provided, along with the latitude zone. Gray diamonds represent the mean effect size of latitude zones; the width of the diamonds corresponds to the confidence interval limits for the fitted value. Positive effect sizes (Hedges' *g*) indicate that fish density is higher on artificial than natural reefs, and a negative value means the opposite. If the 95% confidence intervals overlap with zero, then density is not significantly different on artificial vs. natural reefs.

material. For example, artificial reefs located in the Atlantic Ocean or composed of concrete hosted higher fish densities than natural reefs. These findings suggest that artificial reefs are effective tools for fish habitat enhancement because they can support fish communities similar to those found on natural reefs. Yet differences in fish communities with geography and reef material indicate artificial reefs are not one-size-fits-all tools for habitat enhancement, and deployment strategies should be location-specific to address specific objectives, such as those related to fisheries management or habitat enhancement. We explore the implications of our findings with regards to deployment of artificial reefs to enhance or restore habitats.

The evidence that artificial and natural reefs can host similar fish community metrics stems from our synthesis of peer-reviewed publications from North America, South America, Europe, Asia, Africa, and Australia in coastal oceans up to 150 m deep. Our meta-analysis models revealed that, even with variation in studies, artificial and natural reefs tend to host similar density and biomass of fish, as well as species richness and diversity, to neighboring rocky or coral reefs. This is reassuring since many artificial reef deployments aim to enhance or restore natural reef habitats (Becker et al., 2018). Our meta-analysis adds a quantitative synthesis to the body of literature on the efficacy of artificial reefs for fish habitat enhancement and in some cases, restoration of degraded habitats (Pickering et al., 1999; Seaman, 2007; Dupont, 2008).

Despite the overall evidence garnered in our synthesis that artificial and natural reefs perform similarly as fish habitat,

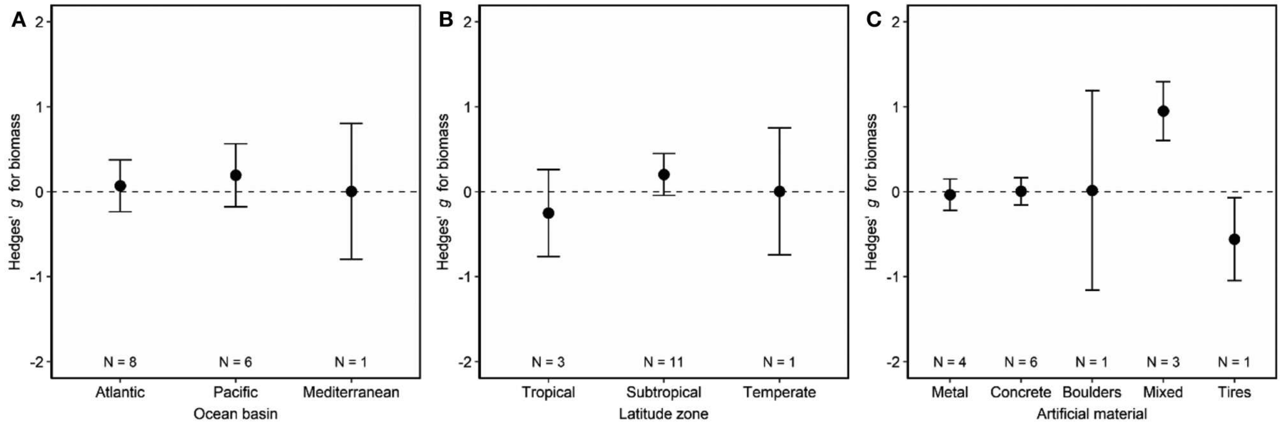

FIGURE 5 | Effects of **(A)** ocean basin, **(B)** latitude zone, and **(C)** artificial material on fish biomass associated with artificial and natural reefs. Shown are mean Hedges' *g* effect size estimated with mixed-effects models including either **(A)** ocean basin, **(B)** latitude zone, or **(C)** artificial material as a moderator. Positive *g* indicates biomass is higher on artificial than natural reefs, and a negative *g* means the opposite. Error bars represent 95% confidence intervals. If error bars overlap with zero, then biomass is not significantly different on artificial vs. natural reefs. *N* represents the number of studies.

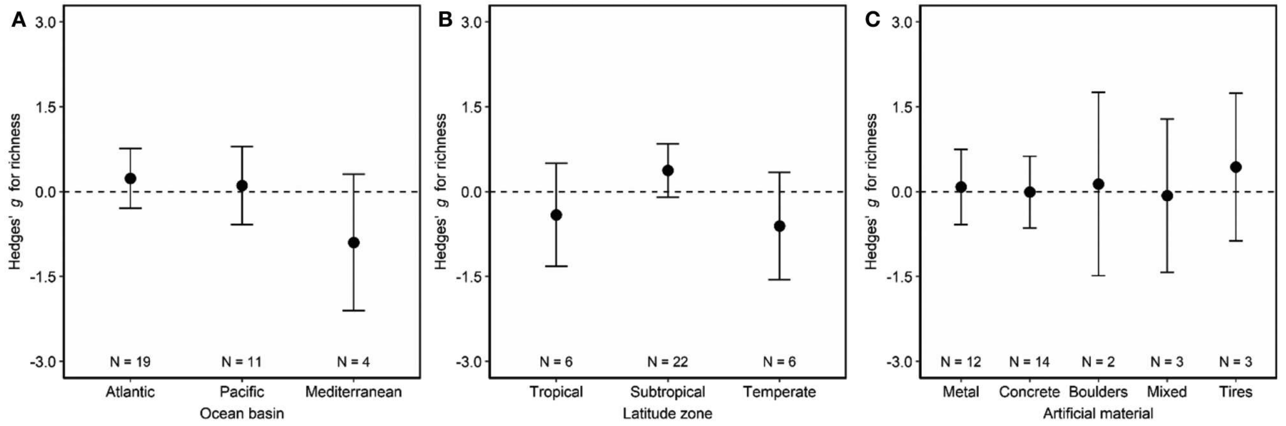

FIGURE 6 | Effects of **(A)** ocean basin, **(B)** latitude zone, and **(C)** artificial material on fish species richness associated with artificial and natural reefs. Shown are mean Hedges' *g* effect size estimated with mixed-effects models including either **(A)** ocean basin, **(B)** latitude zone, or **(C)** artificial material as a moderator. Positive *g* indicates species richness community metric is higher on artificial than natural reefs, and a negative *g* means the opposite. Error bars represent 95% confidence intervals. If error bars overlap with zero, then species richness is not significantly different on artificial vs. natural reefs. *N* represents the number of studies.

artificial reefs in certain locations may perform better than others relative to natural reefs. We discovered these distinctions may be attributed to the ocean basin—Atlantic, Pacific, or Mediterranean, as well as the latitudinal zone—tropical, subtropical, temperate, or subarctic. These findings are logical since previous studies have found that deployment location of an artificial reef can affect the reef's performance (Baine, 2001). For example, local factors linked to reef function include the surrounding habitat characteristics, current, waves, water temperature, turbidity, and depth (Baine, 2001). Spacing of artificial reef structures relative to one another can also influence fish communities (Strelcheck et al., 2005). In particular, the pattern of lower fish density in tropical latitudes, where natural reefs are largely coral reefs, suggests that it may be hard for corals to recruit to and propagate on artificial reefs at rates similar to natural reefs. In contrast, subarctic latitude reefs, which are mainly rocky and often lack slow-growing, hard corals, hosted higher fish density, perhaps because artificial reefs at these higher latitudes may mimic natural reefs more quickly. Interestingly, artificial reefs in the Mediterranean exhibited lower species richness yet higher species diversity than natural reefs, which may reflect upon evenness of the fish communities. Our findings of broad-scale patterns in artificial reef function coupled with previous knowledge that fine-scale patterns affect reef function support the notion that artificial reefs should be evaluated on case-by-case bases according to location-specific parameters and needs (Dupont, 2008).

Fish community metrics on artificial vs. natural reefs are also associated with artificial reef material. In our synthesis, we found higher fish density on artificial reefs composed of

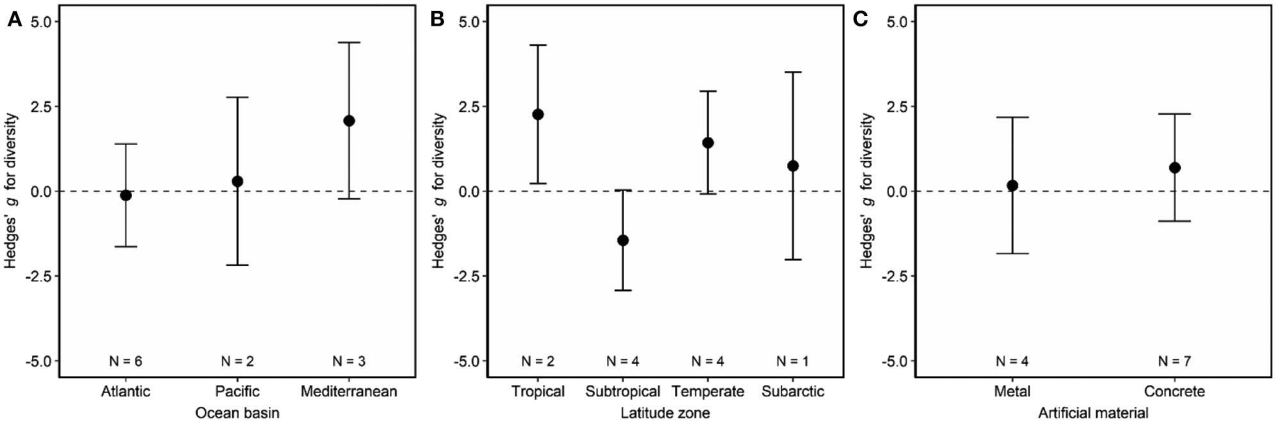

FIGURE 7 | Effects of **(A)** ocean basin, **(B)** latitude zone, and **(C)** artificial material on fish diversity associated with artificial and natural reefs. Shown are mean Hedges' *g* effect size estimated with mixed-effects models including either **(A)** ocean basin, **(B)** latitude zone, or **(C)** artificial material as a moderator. Positive *g* indicates diversity is higher on artificial than natural reefs, and a negative *g* means the opposite. Error bars represent 95% confidence intervals. If error bars overlap with zero, then diversity is not significantly different on artificial vs. natural reefs. *N* represents the number of studies.

concrete than natural reefs but that reefs of other materials hosted similar amounts of fish to natural reefs. Interestingly, when we examined fish biomass, we found higher biomass on mixed-material artificial than on natural reefs. We know that material can affect fish community metrics from prior studies examining the performance of different types of artificial materials relative to one another. For example, in the Atlantic Ocean, two studies have documented higher densities and biomasses of fish on large, high-relief metal structures as opposed to on smaller, low-relief concrete structures (Paxton et al., 2017; Lemoine et al., 2019). This directly contrasts with the meta-analysis findings that concrete hosts higher fish densities than metal, which we interpret as another indication of the necessity of location-specific decisions on artificial reef deployments.

Given the association of geographic setting and artificial material with changes in fish community metrics on artificial vs. natural reefs, we consider location-specific siting of artificial reefs to be both wise and necessary. For example, if an artificial reef mimics a natural reef in the Pacific Ocean, we cannot assume that it will in the Atlantic Ocean. Therefore, while our global meta-analysis indicates that artificial reefs can be effective at supplementing natural reefs, artificial reef deployment strategies should be guided on local contexts, rather than global or regional generalities. Additionally, even though artificial reefs tended to host similar fish communities as natural reefs, the amount of heterogeneity detected among studies and the strong influence (weight) of select studies further stress the importance of place-based artificial reef deployment strategies.

We caution that while artificial reefs exhibit similar fish community metrics to natural reefs in the 39 studies included in our synthesis, our conclusions are limited to four specific metrics—density, biomass, species richness, and diversity. Other metrics, such as fish community composition or metrics specific to functional groups, may behave differently. For example, studies report that the trophic structure differs between artificial and natural reefs for fishes (Simon et al., 2013), as well as for invertebrates (Page et al., 2007). Additionally, we do not know whether the food support that fish receive differs between artificial and natural reefs, nor whether there are species-specific patterns or differences related to reef size. The age of artificial reefs may also have an influence on community metrics, especially as water-column associated fish seem to occupy artificial reefs soon after deployment, followed by demersal species (Paxton et al., 2018). It is also plausible that the survey gear and design (scuba survey type, net type, etc.) may relate to fish detectability and thus influence patterns by reef type. Disentangling such questions may contribute to our understanding of how artificial reefs perform relative to natural reefs, which could provide insight into traits of artificial reefs that can best maximize fish habitat enhancement. Lastly, we acknowledge the debate on whether artificial reefs aggregate fish from nearby natural reefs or produce fish (Bohnsack, 1989; Layman et al., 2016; Smith et al., 2016). Whether aggregation or production occurs is likely system- or species-specific, and we do not attempt to address this debate with our meta-analysis. Instead, we simply document and synthesize snapshots of fish community metrics reported in global studies.

In conclusion, our synthesis revealed that artificial reefs, when evaluated on the bases of fish community density, biomass, richness, and diversity, perform similarly to natural reefs. This suggests that artificial reefs can be effective habitat enhancement tools for reef-associated fish communities. We caution that, given patterns in fish community metrics on artificial vs. natural reefs that emerged with geography and artificial material, location-specific siting, and evaluations of artificial reefs will be critical for maximizing the likelihood of reef success.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

AUTHOR CONTRIBUTIONS

AP conducted the literature search and screening, and wrote the manuscript. AP and KS extracted and analyzed the data. All authors assisted with data extraction, discussed and interpreted the results, edited the manuscript, and conceptualized this research.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00282/full#supplementary-material

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Mangrove Rehabilitation and Restoration as Experimental Adaptive Management

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Rehabilitated and restored mangrove ecosystems have important ecological, economic, and social values for coastal communities. Although a *sine qua non* of successful mangrove rehabilitation or restoration projects is accurate attention to local hydrology and basic biology of mangrove trees and their associated fauna, their long-term success depends on far more axes, each with their own challenges. Rehabilitation projects: are planned, designed, executed, and managed by people with diverse backgrounds and different scientific and socio-political agendas; need to be responsive to these multiple stakeholders and agents who hold different values; are often influenced by laws and treaties spanning local to international scales; and must be able to adapt and evolve both geomorphologically and socioeconomically over decades-to-centuries in the context of a rapidly changing climate. We view these challenges as opportunities for innovative approaches to rehabilitation and restoration that engage new and larger constituencies. Restored mangrove ecosystems can be deliberately designed and engineered to provide valuable ecosystem services, be adaptable to climatic changes, and to develop platforms for educating nonspecialists about both the successes and failures of restored mangrove ecosystems. When mangrove rehabilitation or restoration projects are developed as experiments, they can be used as case-studies and more general models to inform policy- and decision-makers and guide future restoration efforts. Achieving this vision will require new investment and dedication to research and adaptive management practices. These ideas are illustrated with examples from mangrove restoration and rehabilitation projects in the Indo-West Pacific and Caribbean regions, the two hotspots of mangrove biodiversity and its ongoing loss and degradation.

Keywords: Belize, designed ecosystems, ecological mangrove restoration (EMR), ecosystem services, landscape architecture, Singapore, socio-ecological systems (SES)

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1. INTRODUCTION

We are living in the era of ecosystem rehabilitation and restoration (Wilson, 1992). Restoration ecology has progressed rapidly from its initial, unrealistic "ecocentric" goal of eliminating or compensating for human influences on ecosystems (Jordan and Lubick, 2011) to its current "meliorative" framework of creating and maintaining sustainable socio-ecological systems (e.g., Ostrom, 2009; Kibler et al., 2018; Krievins et al., 2018). Methods and approaches for rehabilitating and restoring coastal and marine ecosystems have progressed especially rapidly. It is now realistic to envision that, with concerted effort and careful attention to climatic change, many coastal and marine ecosystems could be "substantially to completely" rebuilt by the middle of this century (Duarte et al., 2020). In this review, we discuss approaches to rehabilitation and restoration of mangroves that integrate ecocentric and meliorative approaches. We use two contrasting case studies to show how mangrove rehabilitation and restoration can be seen as an adaptive management tool for mangroves considered as socio-ecological systems.

Throughout this review, we use the contemporary definition of "ecological restoration" as *any* ***activity*** *with the goal of achieving substantial ecosystem recovery relative to an appropriate* ***reference model****, regardless of the time required to achieve recovery* (Gann et al., 2019, emphasis in original). In this context, "restoration" is distinguished from "rehabilitation" in that the former aspires to *substantial recovery* of the native biota and ecosystem functions (Gann et al., 2019, emphasis in original), whereas the latter strives not to recover an entire ecosystem formed only of native species but only to reinstate a level of ecosystem functioning sufficient to provide ongoing, defined ecosystem services. In this sense, a rehabilitated ecosystem may include nonnative components (see also Miller and Bestelmeyer, 2016; Zimmer, 2018). Although Elliott et al. (2007) suggested that "restoration" be used to describe any activity (including restoration, rehabilitation, and reclamation) aimed at promoting any type of ecosystem recovery in coastal and estuarine environments (including mangroves), we follow Field (1998), Abelson et al. (2016), and Gann et al. (2019) in distinguishing rehabilitation from restoration in mangrove ecosystems. Rehabilitation and restoration also are at one end of the spectrum of management interventions that support recovery of ecosystems from damaged, degraded, or destroyed states (Ounanian et al., 2018). Stages preceding rehabilitation and restoration include protection, remediation, and recreation (Abelson et al., 2016; Ounanian et al., 2018).

2. BACKGROUND

2.1. What Are Mangroves?

Mangroves are a taxonomically diverse group of ±70 tree, shrub, and fern species (in at least 25 genera and 19 families) that grow in anoxic and saline peaty soils on sheltered, tropical coasts. Mangroves share a suite of genetic, morphological, physiological, and functional traits that provide one of the most convincing cases for convergent evolution among diverse taxa in response to similar environmental constraints (Polidoro et al., 2010; Tomlinson, 2016; Xu et al., 2017). Mangroves can be found throughout the tropics, with representatives of the major mangrove genera *Rhizophora* and *Avicennia* present in both the Indo-West Pacific (IWP) and the Atlantic, Caribbean, and Eastern Pacific (ACEP) realms (Ellison et al., 1999; Tomlinson, 2016). Mangrove species diversity is much lower in the ACEP, where it reaches a maximum of 8–9 species at any given site, than in the IWP, where 30 or more species from the regional pool of at least 46 can co-occur (Ellison et al., 1999). At least 16% of mangrove species worldwide are currently considered to be of conservation concern (Polidoro et al., 2010).

Where they grow, mangroves can form dense, often monospecific stands whose species composition is determined in large part by tidal elevation (Ellison and Farnsworth, 2001). Mangroves are thought to be one of the few good examples of foundation tree species in the tropics (Ellison et al., 2005; Ellison, 2019). They create habitats for many terrestrial, intertidal, and marine species, stabilize shorelines, and modulate nutrient cycling and energy flow through the forests they define (Ellison and Farnsworth, 2001). Mangrove forests have some of the highest reported net primary productivity of any ecosystem on the planet, and their loss or deliberate removal leads to rapid build-up of acid sulfides in the soil, increased shoreline erosion and sedimentation onto offshore coral reefs, and collapse of intertidal food webs and inshore fisheries (Ellison and Farnsworth, 2001).

A recent fine-scale analysis of global mangrove forest cover yielded an estimate of $\approx 84,000\text{km}^2$ spread across 105 countries (including special administrative areas and French overseas provinces: Hamilton and Casey, 2016). In the latter decades of the twentieth century, FAO (2007) and Spalding et al. (2010) estimated mangrove deforestation rates approaching $1\% \cdot \text{yr}^{-1}$, but during the first dozen years of the twenty-first century, only $\approx 2\%$ of global mangroves were lost, corresponding to a much lower rate of $\approx 0.16\% \cdot \text{yr}^{-1}$ (Hamilton and Casey, 2016). Thus, there is a strong imperative to rehabilitate or restore mangroves to offset continued losses of mangroves around the world, and the number of mangrove restoration and rehabilitation projects worldwide has nearly tripled in the last 20 years (Duarte et al., 2020). The majority of these projects have been in Southeast Asia and Brazil (Duarte et al., 2020).

2.2. Ecosystem Services and Human Uses of Mangroves

Mangroves provide a wide range of benefits—*a.k.a.* ecosystem services (*sensu* Millenium Ecosystem Assessment, 2005)—to human populations (e.g., Ellison, 2008; Barbier et al., 2011). Coastal communities have long relied on the provisioning services of mangroves, such as the extraction of construction materials and fuel wood (Dahdouh-Guebas et al., 2000; Chow, 2018), and the capture of food sources such as shellfish and finfish (Ellison, 2008; Carrasquilla-Henao et al., 2019). Coastal communities also derive cultural ecosystem services from mangroves, including tangible services such as recreation and intangible services such as aesthetic appeal and spiritual values (e.g., James et al., 2013; Thiagarajah et al., 2015; Spalding and Parrett, 2019). Mangroves also provide a range of regulating services, including coastal protection (Horchard et al., 2019; Ranjan, 2019), pollutant assimilation (Tam and Wong, 1995), and macroclimate regulation and mitigation of global climatic change through carbon (C) storage and sequestration (Adame et al., 2018). Some regulating services (e.g., coastal protection) accrue directly to co-located coastal communities, whereas others (e.g., regulation of macroclimate) benefit the global commonwealth.

2.3. A Brief History of Mangrove Rehabilitation and Restoration

Rehabilitation and restoration of mangroves has been practiced for decades (salient reviews are provided by Lewis, 1982, 2005, 2009; Field, 1998; Ellison, 2000; Lewis et al., 2019). The rationales for rehabilitating or restoring mangroves reflect specific ecosystem services, including creation or maintenance of forest stands for "sustainable" high yields, coastal protection, landscaping, conservation of biodiversity, or because laws require it (e.g., local regulations mandating "No Net Loss" of wetlands following development projects). Broad classes of rehabilitation and restoration methods include: (1) incorporation of mangroves into engineered hard coastal defense structures (Cheong S.-M. et al., 2013; Lai et al., 2015; Mayer-Pinto et al., 2017; Morris et al., 2018, 2019); (2) monoculture plantations (e.g., Chan, 1996; Field, 1998; Ellison and Farnsworth, 2001; Matsui et al., 2012; Chow, 2018); and (3) "ecological mangrove restoration" (EMR) approaches, in which the intertidal zone is manipulated (e.g., regraded, dredged, filled) so that biophysical conditions (particularly inundation) are within tolerable limits for mangrove establishment, growth, and reproduction (e.g., Lewis, 2005; Lee et al., 2019; Lewis et al., 2019; Suman, 2019). Zimmer (2018) has proposed an additional method, (4) "mangrove ecosystem design," which foregrounds people and their needs, and then uses those needs to define the set of ecosystem services to be included in the project. Subsequent rehabilitation or restoration activities are then focused on meeting those needs and services, given biophysical constraints. Mangrove ecosystem design is described in more detail in section 2.6.

For example, in terms of regulating ecosystem services, growth rates and biomass accumulation tend to be greater in young plantations than in older ones, but recruitment of saplings may increase with plantation age or be completely absent (Bosire et al., 2008). Rehabilitated mangroves sequester more C than the land-use cover-types they replace (Sasmito et al., 2019). Successful rehabilitation has led to rapid accumulation of biomass C stocks, and over longer time scales can increase soil carbon stocks by 83 (Matsui et al., 2012) to 96 Mg C/ha (Cameron et al., 2019a). Rehabilitated mangroves on previously abandoned and exposed aquaculture ponds emit substantially less CO_2 from their soils than do the abandoned, exposed ponds themselves (Cameron et al., 2019a). In parallel, rates of peat accumulation in constructed mangrove forests can exceed that of natural stands (Osland et al., 2020). Carbon is a traded commodity, and the selling of C credits provides financial incentives for mangrove rehabilitation through Payments for Ecosystem Services (PES). PES has been promoted for its potential to offset greenhouse gas emissions while providing livelihood opportunities to local communities (Locatelli et al., 2014). The high rates of C accumulation and positive impact on baseline soil C fluxes in mangrove ecosystems means that they provide more cost-effective PES than most terrestrial ecosystems (Cameron et al., 2019b).

Rehabilitated mangroves also provide provisioning ecosystem services that local communities benefit from and appreciate. These include construction materials and fuel wood, non-timber products such as natural dyes, and nursery grounds for molluscs collected for food (Rönnback et al., 2007; Ellison, 2008). Following mangrove rehabilitation, fish catches by artisanal fishers often increase and positive influences on offshore commercial fish catches also have been observed (Das, 2017).

2.4. The Socioecology of Mangrove Rehabilitation and Restoration

Mangrove rehabilitation and restoration projects almost always are conceived and executed as "one-off" projects with surprisingly little attention paid to transference of valuable information about previous successes, failures, or technical knowledge that could guide successful projects (Field, 1998; Ellison, 2000; Lewis, 2005, 2009; Lewis et al., 2019). Unsurprisingly, the failure rate of mangrove restoration and rehabilitation projects remains unacceptably high (Brown, 2017; Kodikara et al., 2017; Lee et al., 2019).

Technically, rehabilitation or restoration of mangroves can be surprisingly easy: [*T*]*he single most important factor in designing a successful mangrove restoration project is determining the normal hydrology (depth, duration and frequency, and of tidal flooding) of existing natural mangrove plant communities* ([i.e.,] *a reference site*) *in the area in which you wish to do restoration* (Lewis, 2005, p. 409). Actual planting of mangrove propagules is often used but rarely needed (Field, 1998), except perhaps when the goal is a monoculture or forest plantation, or when stem-density targets need to be achieved more quickly than natural regeneration would allow (Field, 1998; Ellison, 2000; Lewis, 2005).

However, rehabilitation and restoration projects do not succeed on technical grounds alone (Gann et al., 2019; Lovelock and Brown, 2019), and, as noted above, most mangrove restoration or rehabilitation projects have failed. Follow-up monitoring has been sporadic and, at best, short-term. Most failures result from the lack of community involvement, appropriate governance structures, and alignment of objectives and goals of external agents (including scientists) and local stakeholders (Field, 1998; Mazón et al., 2019). Cormier-Salem (1999) argued that interacting dynamics of natural and social systems was a *sine qua non* of effective long-term management of mangroves, but that social scientists had not been included in mangrove restoration projects. Similarly, Walters (1997, 2000) found that socio-economic factors including peoples' traditional knowledge about trees and tree planting; patterns of land use and ownership; perceived economic costs and benefits; and community social organization interacted were far more important than ecological factors in determining success of mangrove reforestation in the Philippines. Unfortunately, the advice and insights of these authors have been notably absent from subsequent major reviews of mangrove rehabilitation or restoration (Lewis, 2005, 2009; Bosire et al., 2008; Lewis et al., 2019); Dale et al. (2014) is a useful counter-example.

The last few years has seen a resurgence in interest in bringing ideas and theories about socioecological systems to bear on restoration and rehabilitation of mangroves (e.g., Biswas et al., 2009; Brown, 2017; Ranjan, 2019). Ounanian et al. (2018)

identified four "restoration discourses" applicable to marine (including mangrove) ecosystem restoration that are based on the degree of human intervention (the *how* of restoration) and the motivation for action (the *why* of restoration) (**Figure 1**). The goal of mangrove rehabilitation (rarely restoration) projects prior to the early 1980s—afforestation for silviculture (Ellison, 2000)—reflected the idea that mangroves should support people (lower left quadrant of **Figure 1**). Lewis (1982) and Field (1998) moved the discourse up the ecocentric axis of **Figure 1**, "Putting Nature first" and bringing biological diversity, habitat creation, and food sources for near-shore and pelagic food webs into the discussion. EMR approaches moved the needle toward the upper-right, "Bringing Nature back" quadrant of **Figure 1**, but most ecocentric approaches continue to place people outside of "nature" and squarely within the classic ecocentric framing of ecological restoration (Jordan and Lubick, 2011). In contrast, Community Based Ecological Mangrove Rehabilitation (CBEMR) has adapted EMR to include local communities and bring people back into nature (Brown et al., 2014; Mantrove Action Project, 2019).

For example, rehabilitation and restoration activities are linking ecological integrity ("Bringing Nature Back") with actions to mitigate negative effects of climatic change ("Helping Nature Support Humans") while building local capacity in island ocean states (Wilson and Forsyth, 2018). At the same time, methods to better monitor and assess social and ecological status of coastal habitats are being developed (Cáardenas et al., 2017; Wongbusarakum et al., 2019). In any project, participants and stakeholders are unequal and weak or asymmetric relationships among them—differences in capacity, power, or ideologies—can lead to gaps in policies, project design, and implementation (Vaughn, 2017; Thompson, 2018). These asymmetries can be overcome through long-term commitments to funding and monitoring, stronger collaborations between the funders and individuals carrying out the restoration projects, and resolution of conflicts between bottom-up (local) environmental initiatives and top-down (governmental) legislation (Sa'at and Lin, 2018; Thompson, 2018). Clarification of ownership and title to mangrove-covered areas can limit deforestation, encourage environmental stewardship, and maintain rehabilitated or restored areas (Lovelock and Brown, 2019; Suman, 2019).

2.5. The Potential of and for Adaptive Management of Rehabilitated and Restored Mangroves

Adaptive management, a structured, iterative process of "learning-by-doing" and decision-making in the face either of continuous change (environmental, social, cultural, or political)

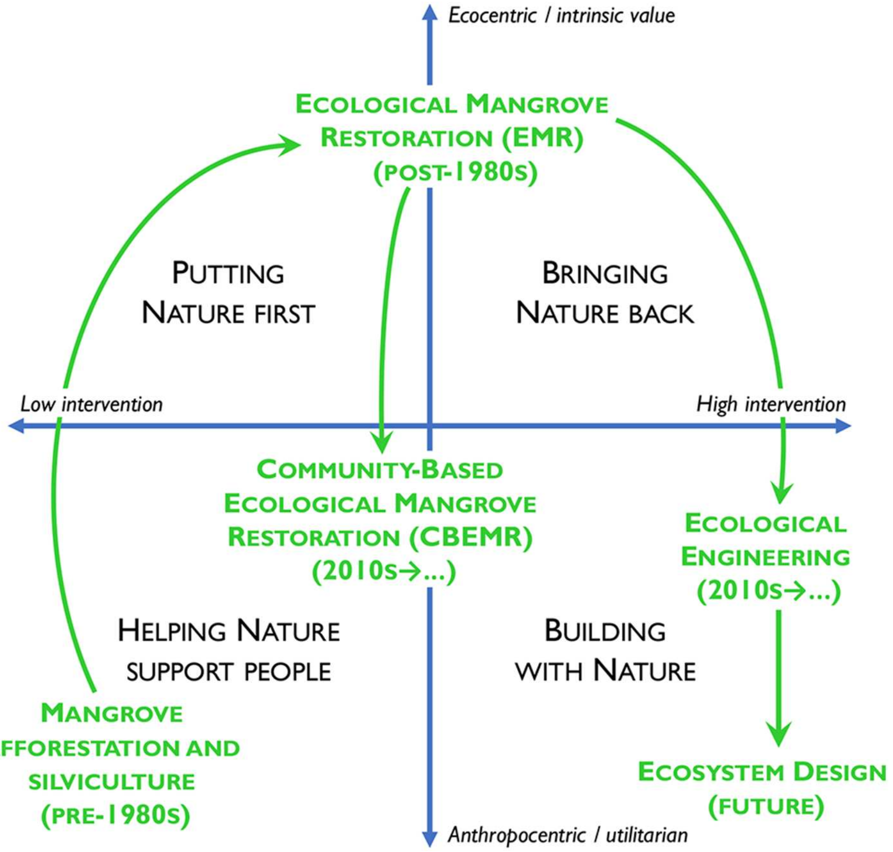

FIGURE 1 | Four discourses for marine ecosystem restoration, after Ounanian et al. (2018), with placement of major types of mangrove rehabilitation and restoration overlain in appropriate quadrants.

or uncertainty (Holling, 1978), *can and should be the standard approach for any ecological restoration project, irrespective of how well-resourced that project may be* (Gann et al., 2019, p. S16). Not only does adaptive management require regular monitoring of key indicators to determine if the objectives and goals of a rehabilitation or restoration project are being met, it also requires clear triggers or decision-points for appropriate intervention and action if the objectives or goals are not being met (Gann et al., 2019). For mangrove rehabilitation and restoration projects, long-term monitoring is uncommon (e.g., Mazón et al., 2019), and adaptive management is rarely applied. However, Eriksson et al. (2016) showed clearly that adaptive management of an "ecosystem approach" improved outcomes associated with managing mangroves for small-scale fisheries in Indonesia (Lombok), the Philippines, Solomon Islands, and Tanzania. They used the Participatory Diagnosis and Adaptive Management framework (Andrew et al., 2007) with participants who represented the interests of natural ecosystems, the livelihood of people (economic drivers), institutions and governance, and external drivers including macroeconomic instability, climatic change, and environmental uncertainty. Their goal was to determine stakeholder priorities and identify key interventions to support the transition from purely exploitative to more sustainable fisheries. One key conclusion of Eriksson et al. (2016) was that strengthening governance was as important as mangrove rehabilitation, economic improvement, and other technical and data-driven aspects of management. This conclusion is not restricted to fisheries management (Eriksson et al., 2016), but applies more broadly to any mangrove protection, conservation, rehabilitation, or restoration project (Lovelock and Brown, 2019; Suman, 2019).

2.6. Experimentation Plus Deliberate Design as an Integrating Framework for Mangrove Rehabilitation and Restoration

Observational monitoring of key indicators is necessary to evaluate success of goals and objectives of rehabilitation or restoration projects and to guide adaptive management and decision-making. Formal experiments, either within an observational before-after-control-impact (BACI) framework (e.g., Stewart-Oaten et al., 1986) or using manipulations with appropriate controls and adequate sample sizes, could improve causal interpretation of observed patterns and identify key processes (Gann et al., 2019). Restoration and rehabilitation projects provide ideal opportunities and sites for "real-world"-scale experiments to determine whether, for example, particular engineering solutions, planting patterns, or facilitative (positive) interactions among species could improve restoration success (Halpern et al., 2007; Gedan and Silliman, 2009), but these have yet to be integrated into any mangrove restoration or rehabilitation project (Renzi et al., 2019).

At the same time, intentional design of ecosystems with functional characteristics to provide particular services has been proposed as an alternative to rehabilitation or restoration projects with high costs or low likelihoods of success; to take advantage of nonnative species with equivalent functionality; or to be effective in rapidly changing environmental conditions (Hobbs et al., 2006; Morse et al., 2014; Miller and Bestelmeyer, 2016). Such designed ecosystems foreground people, societies, and the ecosystem services that support them, and use engineering principles and technical knowledge to assemble a group of taxa into appropriate environments (Zimmer, 2018). More deliberately designed or engineered mangrove systems have been tried in Bangladesh and Singapore (Cheong S.-M. et al., 2013). A more complete designed mangrove landscape that provides stormwater management, flood protection, and recreational opportunities, was constructed in the Fengxinglong Ecological Park at the junction of the Sanya and Linchun Rivers in China's southern Hainan Province (Nengshi et al., 2018).

Ecological, socioeconomic, and governance issues come together in discourses that define rehabilitation and restoration of ecosystems. Adaptive management, including monitoring and triggers for intervention and modification of management require participation of individuals with technical expertise and those who can make culturally-informed decisions. Including manipulative experiments with appropriate attention to sample size and scope of inference could permit more rapid conclusions about how a system is actually working, and provide additional guidance for adaptive management. All of these threads come together in designed ecosystems that foreground needed ecosystem services, specify them as project goals or deliverables, and assemble groups of species that can provide said services in a given environmental context that is treated as a long-term experiment in rehabilitation and restoration.

In the next section, we use case studies of mangrove rehabilitation and restoration projects in Singapore and Belize to illustrate these principles (**Figure 2**). We chose case studies from these two countries because Singapore and Belize are in different mangrove realms and have different sociopolitical and economic histories and contexts, but they also face similar challenges in rehabilitating, restoring, and managing mangroves. Belize is 30-fold larger than Singapore and has more a 1,000-fold greater mangrove cover but only 1/300th of Singapore's GDP (The World Bank, 2018). Conservation and preservation of large areas of extant mangroves is still possible in Belize, but not in Singapore. People and the governments in both countries recognize the value of the ecosystem services that mangroves provide. At the same time, coastal zones in both countries are being engineered, and their mangrove rehabilitation projects are mostly small-scale and driven primarily by ecocentric goals.

3. CASE STUDY 1: SINGAPORE

Singapore (1.290270 °N, 103.851959 °E) is a 721-km^2 city-state in Southeast Asia. Its equatorial climate and biophysical environment is well-suited to supporting minerogenic mangrove systems. Singapore is located close to the epicenter of mangrove species diversity and diversification (Ellison et al., 1999); 35 of the ≈ 46 mangrove species found in the Southeast Asian region of the IWP mangrove realm, including the critically endangered *Bruguiera hainesii*, have been recorded from Singapore (Yang et al., 2011).

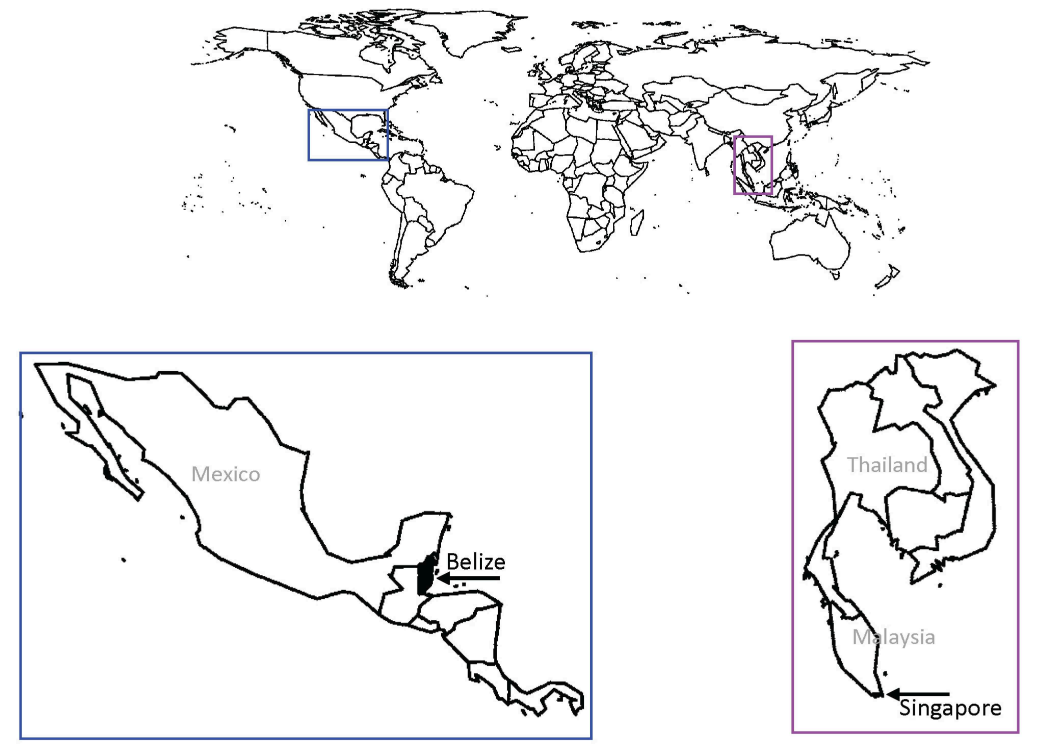

FIGURE 2 | World map showing locations of Singapore (in magenta inset) and Belize (in blue inset). Additional details about each country are given in each of the case studies; the extent of mangroves in each country is illustrated in **Figures 3**, **6**.

Since it became an independent state in 1965, Singapore has lost > 90% of its mangrove forest extent as land has been reclaimed for industrial development and aquaculture, freshwater reservoirs have been constructed in previously mangrove-fringed estuaries, and the shoreline has eroded and been increasingly polluted (Lai et al., 2015; Friess, 2017). Mangrove coverage in Singapore was estimated at only 0.81 km^2 in 2018 (**Figure 3**; Gaw et al., 2019).

3.1. Socioeconomic and Sociopolitical Context

Although Singapore's historical economic and sociopolitical drivers provided large incentives to destroy mangrove forests, the present-day sociopolitical context has opened up possibilities for mangrove rehabilitation or restoration. Some mangrove areas now are protected as Nature Parks or Nature Reserves, and protected area coverage continues to increase in the country (Tay, 2018). In 2019, the Singapore Government announced that preparing for and dealing with the impacts of climatic change are key government priorities; measures to protect the country and adapt to sea-level rise are estimated to cost at least US $74 billion over the next century (Prime Minister's Office, 2019); US $5 billion is allocated in next year's budget. The government has highlighted nature-based solutions, especially mangrove rehabilitation, as key adaptive responses to sea-level rise (Tan and Fogarty, 2019).

3.2. Mangrove Rehabilitation and Restoration Activities in Singapore

3.2.1. Bringing Nature Back: Recreating Biophysical Conditions

Because much of Singapore's highly urbanized coastline is on reclaimed land in the intertidal zone, large spaces within appropriate biophysical bounds for successful mangrove establishment and growth do not exist. Thus, the first step for mangrove rehabilitation projects in Singapore has been to "Bring Nature Back" (upper right quadrant of **Figure 1**) by recreating the necessary biophysical conditions to support mangroves and their associated biota.

3.2.2. Types of Mangrove Rehabilitation Efforts in Singapore

Previous and current rehabilitation efforts in Singapore can be classified into three broad tiers that correspond to the three standard methods of mangrove rehabilitation and restoration: ecological engineering, plantations, and EMR approaches (**Figure 4**; Friess, 2017). All of these efforts have been opportunistic, and have occurred in response to individual development projects or specific management concerns. Most fall into the "Bringing Nature Back" or "Building with Nature" paradigms of **Figure 1**.

An example of the first (smallest) tier is on Pulau Tekong, an island off Singapore's northeast coast, where mangrove saplings have been planted within new and existing hard

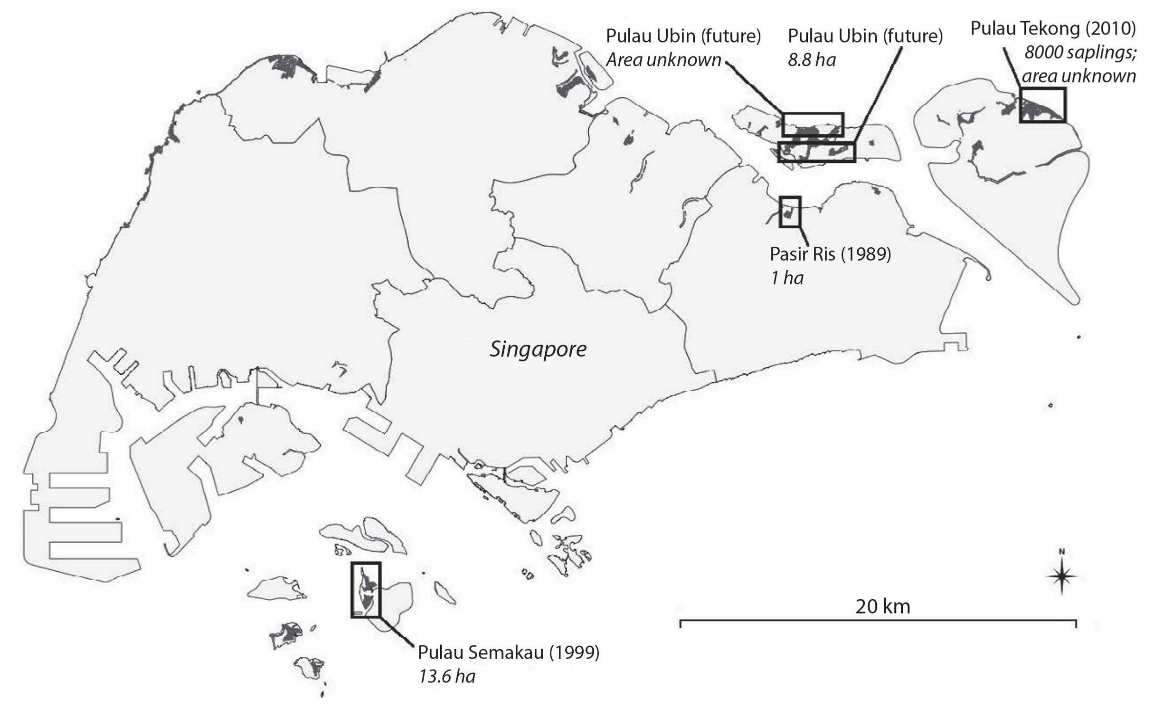

FIGURE 3 | Distribution of mangrove forests (black) in Singapore in 2014 with locations of major rehabilitation projects. Redrawn from Friess (2017).

coastal defense structures. This mangrove area was experiencing substantial shoreline erosion from storms, ship wakes, and changing hydrodynamic conditions resulting from nearby land reclamation (Cheong K. H. et al., 2013; Cheong S.-M. et al., 2013). Because the intertidal zone was eroding, simple planting would have been insufficient to rehabilitate a mangrove forest. Instead, an artificial rock wall was built, sediment was introduced into the system in biodegradable bags, and multi-species plantings were done inside 8,000 plastic planting tubes placed between the rocks (Yang et al., 2011; Cheong S.-M. et al., 2013).

The second-tier rehabilitation approach of planting monocultures has been done on Pulau Semakau. At this site, 13.6 ha of mangrove forest were cleared during the construction of a landfill. After construction, a rehabilitation project was initiated to ensure no net loss of habitat. Reclaimed land was overlain with a layer of mangrove mud at an elevation of 1.8–2.2 m above chart datum low water, and as many as 400,000 propagules of *Rhizophora apiculata* and *R. mucronata* were successively planted across the site at a density of 1,900 propagules per hectare. This density was required to account for the $\approx$ 94% mortality rate of the planted propagules (Tatani et al., 2001; Yang et al., 2011; Friess, 2017). Such high mortality is uncommon in long-term, multiple-rotation mangrove forestry plantations (Chan, 1996) but common in monoculture rehabilitation projects more broadly (Kodikara et al., 2017).

Two rehabilitation sites in Singapore have implemented principles of EMR (Tier 3). The first, at Pasir Ris, was designed to allow mangrove seedlings to naturally colonize a 1-ha area that had been reclaimed previously; the goal here was to make connections with other mangrove patches along this coastline (**Figure 5**; Lee et al., 1996). The reclaimed land was regraded to a lower elevation that allowed flooding up to 50 times per month. Once tidal exchange had been re-established, the site was rapidly colonized by *Avicennia alba* and *Sonneratia alba*, two key mangrove pioneer species that can survive in the lower intertidal zone. After 20 years, a high diversity of mangrove species, molluscs, crustacea, and snakes had established at Pasir Ris (Lee et al., 1996; Karns et al., 2002). Fish diversity, but not abundance, has been higher at Pasir Ris than in adjacent constructed shorelines (Jaafar et al., 2004; Benzeev et al., 2017). Pasir Ris also provides valuable cultural ecosystem services, including spiritual/religious ("sense of peace"), inspirational ("connecting with nature"), and recreation/tourism ("recreation" and "enjoying time with family") (Thiagarajah et al., 2015).

The second, and most recent EMR project is ongoing within 8.8 ha of abandoned aquaculture ponds on Pulau Ubin. This project differs from other mangrove rehabilitation projects previously undertaken in Singapore in that it has been a community-based initiative, organized by local NGOs, community groups, and academics, and strongly supported by government agencies responsible for nature conservation (Friess, 2017; RUM, 2017). The first phase of this project has required extensive mapping of biophysical conditions across the site and neighboring natural mangroves, particularly tidal flows and elevations relative to tidal conditions, to ensure that subsequent construction works modify physical site conditions to approximate as closely as possible those within surrounding "baseline" mangroves. The second phase

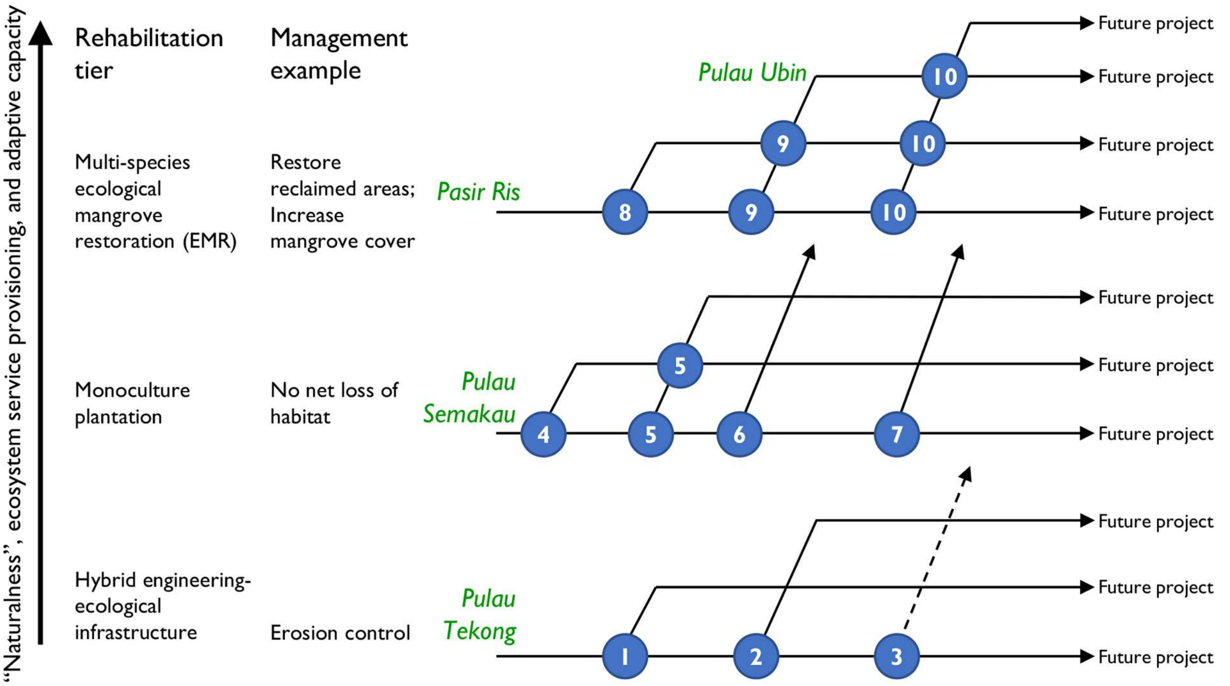

FIGURE 4 | Conceptual mangrove rehabilitation trajectories and key decision points (white numbers in blue circles) where each trajectory can be changed to improve project outcomes. The decision points are: (1) Improve success with better selection of species; (2) Shift from gardening to greater inclusion of mangrove ecosystem services; (3) Improve biophysical conditions (unlikely without extensively engineered works or ongoing maintenance); (4) Plant at correct intertidal elevation; (5) Plant multiple species; (6) Improve pre-rehabilitation planning of all biophysical parameters with an eye toward future ecological mangrove restoration (EMR); (7) Identify new areas for rehabilitation (to improve beyond no net loss); (8) Extensive site and community assessments prior to initiating rehabilitation; (9) Ensure participation of local communities and stakeholders; (10) Scale up size of pilot projects and full projects. The projects at Pulau Tekong, Pulau Semakau, Pasir Ris, and Pulau Ubin are all discussed in text (section 3.2.2).

FIGURE 5 | Restored mangroves at Pasir Ris. **(A)** Channels are maintained to allow for tidal exchange; **(B)** A boardwalk was constructed through the mangrove to facilitate access while minimizing impacts to the forest; **(C)** Fringing mangrove provides habitat for juvenile fish and birds; **(D)** Interpretive and exhortative signs for education, engagement, and outreach are widespread along the boardwalk. White numbers in blue circles correspond to restoration and rehabilitation decision points illustrated in **Figure 4**. Photographs by Aaron M. Ellison.

will begin the reconstruction of appropriate hydrological conditions and sediment infilling to support natural or augmented regeneration.

Data as yet are unavailable to assess the long-term success of Singapore's two EMR projects because reference stands have not been systematically monitored; natural regeneration at Pasir Ris cannot be compared to the observed self-thinning of planted stands; and the ongoing mangrove restoration at Pulau Ubin is still in its early stages. However, EMR projects in other countries generally have been more successful in terms of seedling survival than planted monocultures (Djamaluddin, 2007). There is, however, some evidence that EMR has been ecologically more successful in Singapore than lower-tier rehabilitation approaches. The multi-species, natural regeneration at Pasir Ris has led to faster tree growth and biomass accumulation than at other mangrove rehabilitation sites in Singapore (Lee et al., 1996; Friess, 2017).

3.3. Lessons to Inform Adaptive Management

Mangrove rehabilitation in Singapore has yielded key lessons in how to enhance ecological diversity and ecosystem services in an urbanized coastal setting. The Pulau Tekong hybrid engineering project illustrated how to incorporate mangrove vegetation into traditional coastal defense structures and has built competency in large-scale coastal ecological engineering (Friess, 2017). This project also highlighted the importance of planting multiple species and matching species traits to prevailing environmental conditions (Lewis, 1982; Field, 1998). To achieve target tree densities in the monoculture plantation on Pulau Semakau, successive replantings of up to 400,000 *Rhizophora* propagules were required because of high seedling mortality rates resulting from suboptimal biophysical conditions at the site for the planted species. The ongoing rehabilitation project on Pulau Ubin also has highlighted the importance of increasing project scope to include community engagement and involvement, which secured community support and buy-in for the restoration works (see also Damastuti and de Groot, 2017; Sa'at and Lin, 2018; Powell et al., 2019; Ranjan, 2019).

Rehabilitation projects at all sites have shown the importance of recreating the correct biophysical conditions to allow mangrove seedlings to grow, including creating artificial structures to protect seedlings from hydrodynamic energy or using EMR to create site elevations suitable for mangrove establishment (see also Lewis, 1982, 2005; Ellison, 2000). All projects also have highlighted the challenges needed to scale them up to larger areas. Thus far, mangrove rehabilitation sites in Singapore have ranged from < 1 to just under 14 ha in size. These small sizes reflect a legacy of executing rehabilitation projects along urban shorelines with severe space constraints and for which there are conflicting coastal management priorities. However, larger rehabilitation sites may be able to support higher levels of biodiversity and provide a greater number of ecosystem services.

Analysis of mangrove rehabilitation projects in Singapore has identified ten key decision points within an adaptive management framework that provide opportunities to improve restoration trajectories in this coastal setting (**Figure 4**). These decision points can be categorized broadly as: diversifying target species for rehabilitation (decision points 1 and 5); stronger incorporation of key biophysical thresholds that determine mangrove survivorship (decision points 4, 6, and 8); and increasing the scope and scale of rehabilitation (decision points 2, 7, 9, and 10). In some instances it may be possible to jump between rehabilitation tiers at these decision points. For example, planted monocultures could incorporate aspects of EMR such as identification and mapping of biophysical constraints on mangrove establishment that may be used to encourage natural recruitment of mangrove propagules. This could be done at existing sites (decision point 6) or along an entire coastline to identify suitable areas for future rehabilitation (decision point 7). In other situations, it may not be possible to jump to a higher rehabilitation tier. For example, hybrid engineering approaches are used in eroding areas where mangrove planting or natural recruitment would never be successful because of biophysical constraints.

Although the small number of restoration sites in Singapore has limited the opportunities to take advantage of these lessons or use the proposed adaptive management framework (**Figure 4**), possibilities abound for the future. More than 63% of Singapore's 319 km coastline is armored (Lai et al., 2015) and new coastal rehabilitation projects could take advantage of lessons learned in hybrid engineering at Pulau Tekong. Ecological enhancement of sea walls for corals and associated fauna has been a strong, focused area of basic (Loke and Todd, 2016) and applied research (Loke et al., 2019; Morris et al., 2019). Mangrove rehabilitation on sea walls would benefit from a similar research focus. An additional 75 ha of previously abandoned aquaculture ponds in Singapore potentially are available for restoration to their original mangrove cover (Friess, 2017). If these areas were restored successfully, the mangrove extent in Singapore would increase by up to 10%, with appreciable, positive gains in provisioning of ecosystem services by Singapore's mangroves.

4. CASE STUDY 2: BELIZE

Belize (17.49952 °N, −88.19756 °W) is small country (land area = 22,963 km^2) on the eastern side of Central America, bordered by Guatemala to the west, Honduras to the south, Mexico to the north, and the Caribbean Sea to the east. The varied topography and geology of Belize include two physiographic regions: the Maya Mountains in the south and west and the northern lowlands in the north and east. The latter form broad coastal plains with sandy soils underlain by limestone bedrock. Vegetation types of the northern lowlands include semi-deciduous forests and savannas, and extensive wetlands, swamps, and coastal lagoons, mangroves, and seagrass meadows (**Figure 6**; Hartshorn et al., 1984; Ellison, 2004; Cherrington et al., 2010a). Offshore, the 300-km Belize barrier reef is the largest continuous section of the 900-km Mesoamerican reef system (Rützler and Macintyre, 1982) and a designated UNESCO World Heritage site (UNESCO, 1996). Belize still has substantial intact

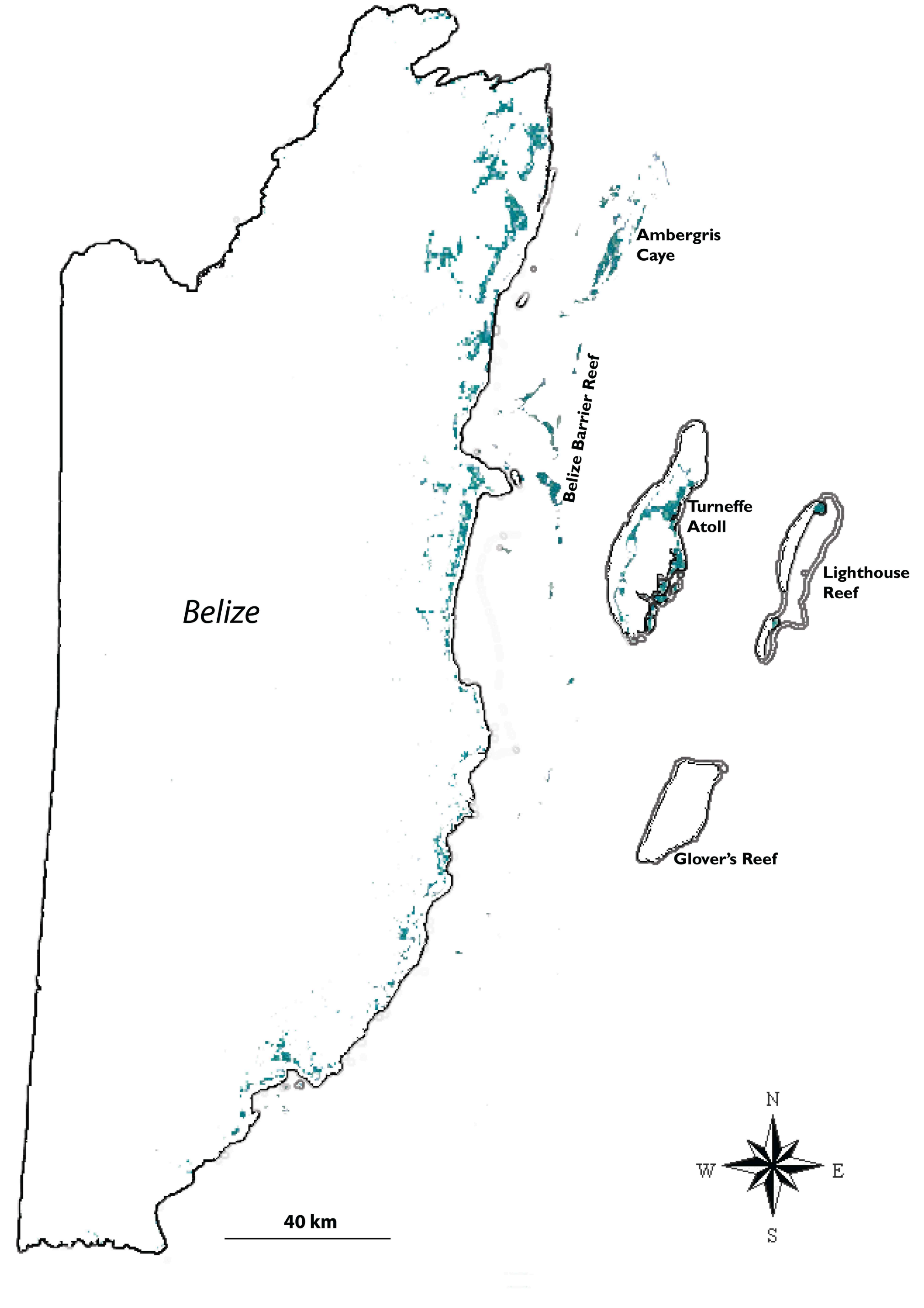

FIGURE 6 | Map of Belize, showing areas of mangrove cover in teal. The offshore mangrove forests include dozens of mangrove-covered cays along the Belizean barrier reef complex, and on two of the three atolls further east. Occasional mangrove seedlings have been seen at Glover's Reef, but they have failed to survive. Location of mangroves based on map in Meerman and Sabido (2001).

mangrove habitat covering ≈ 747 km^2 along its 386 km of marshy coastline and many of its ≈ 300 coral cayes (islands). The four most common mangrove species in the ACEP mangrove realm—*Rhizophora mangle, Avicennia germinans, Laguncularia racemosa*, and *Conocarpus erectus*—grow in Belize (Murray et al., 2003; Neal et al., 2008).

4.1. Socioeconomic and Sociopolitical Context

Mangroves are legally protected under Belize's Forests Act (Government of Belize, 2003) and remain mostly intact in Belize. At least 60% of the population of Belize depends directly or indirectly on ecosystem services from coastal and marine habitats (Belize Tourism Industry Association, 2010), but foreign ownership and recent trends in land-use change, development, wastewater management, and tourism (especially a rapid increase in arriving cruise ships) all put pressures on mangroves and other coastal habitats. Approximately 70% of Belize's coastline is privately owned, mostly by foreign entities, and mangrove cover has declined by $\approx$ 2% since 1980 (Brooksmith Consulting, 2011). Burgeoning aquaculture operations for rearing prawns and tilapia along the coast are constructed in mangrove estuaries. Following deforestation for their construction, increased nutrient loading from their operations into adjacent wetlands and waterways drives additional mangrove loss (Government of Belize, 2002).

The Belizean barrier reef complex, with its cayes, mangroves, seagrasses, and coral reefs, is an important component of Belize's tourism economy. Mangroves alone contribute $\approx$ US $174–249 million each year to the country's economy (Cooper et al., 2009). Ongoing climatic change negatively impacting coastal ecosystems across the Caribbean will lead to an estimated reduction in tourism revenue by 2,100 of $>$ 25% of total GDP across all countries in the Caribbean Basin (Bueno et al., 2008) and $\approx$ US $28 million in Belize alone (Richardson, 2009). Ironically, the expanded tourism and fisheries that drive the economy of Belize also threaten the ecosystems that support these activities. Trends in expansion of tourism and fisheries coupled with climatic change raise serious concerns for future conservation and management of mangroves in Belize (Ellison and Farnsworth, 1996; Farnsworth and Ellison, 1997; Clarke et al., 2012).

Recent legislation has continued to reform and amend mangrove clearance laws in Belize, and includes higher fines and stronger regulations (Government of Belize, 2018). However, developers routinely work around these restrictions. Mangrove clearance often occurs without proper permits and enforcement of mangrove regulations is rare. Although recent losses of mangroves in Belize overall have averaged $0.9\% \cdot \text{yr}^{-1}$ (Hamilton and Casey, 2016), in urban and urbanizing areas (e.g., in and around the capital, Belize City), mangrove cover has declined by as much as $> 3\% \cdot \text{yr}^{-1}$ as stands have been cleared for housing, industry, farming, and septic and wastewater systems (Furley and Ratter, 1992). In these areas, conservation or management of mangroves is rare, and occurs mostly on small scales. Mangroves also are used in urban areas to extend septic systems and treat wastewater; the main sewage treatment system in Belize City is a constructed lagoon. More rural areas also are developing rapidly and along similar trajectories. For example, the 30-km Placencia Peninsula in southeast Belize has extensive mangroves along the western "lagoon" side and white-sand beaches with housing and substantial resort development on the eastern side facing the Caribbean Sea. While much of the lagoon's intertidal zone remains mangrove-covered, the mangrove stands are being degraded by coastal development for real estate and tourism, aquaculture and agriculture, sedimentation from upland deforestation and mangrove removal, and diverse impacts of dredging and armoring the coast with bulkheads and other hard infrastructure (Ellison and Farnsworth, 1996; Murray et al., 2003; Coastal Zone Management Authority & Institute, 2014; Dale et al., 2014).

4.2. Mangrove Rehabilitation and Restoration Activities in Belize

4.2.1. Putting Nature First: Preserving Extant Mangroves Comes First

Because extensive and intact stands of mangroves still remain throughout Belize, their preservation, protection, and sustainable management or explicit inclusion in development projects will be the most effective and efficient means of maintaining mangrove ecosystem functions in Belize. To foster mangrove preservation, the Mangrove Challenge contest was established in 2010–2011 (Brooksmith Consulting, 2011). The Mangrove Challenge not only helped to identify individuals involved in effective mangrove conservation and restoration across Belize, but also fostered creation of networks among them by awarding small cash prizes (US $250–500). Awards were made to: conservation organizations that were maintaining mangrove reserves; building projects that were maintaining substantial mangroves in place; formal landscaping and design proposals for resorts or homes that incorporated mangrove hedges and aesthetic trimming; educational opportunities created by boardwalks through mangrove forests city parks with mangroves; and docks built along mangroves rather than removing mangrove shorelines. The Mangrove Challenge also highlighted locations where substantial contiguous habitat patches existed or had been protected. A positive outcome of the Mangrove Challenge has been the expanded recognition of mangroves and various spin-off projects from the original competition (Brooksmith Consulting, 2011).

4.2.2. Mangrove Protection in Belize Involves Governmental and Non-governmental Organizations

Addressing issues contributing to mangrove degradation and loss in Belize are being addressed through both bottom-up (grass-roots) and top-down (governmental) approaches. For example, the Government of Belize recently has enacted new laws to support of mangrove conservation (Government of Belize, 2018). Instituting effective zoning policies guiding development and enforcing regulations need to be communicated better and more effectively, especially to foreign property-owners (Flomenhoft et al., 2007). The Belize Coastal Zone Management Authority & Institute (CZMAI) has recognized that protection and preservation of existing extant stands of mangroves will continue to be a high priority. CZMAI is working to increase awareness and oversight of existing mangroves to maintain their spatial and functional integrity, and seeking to develop institutional stability for organizations that create and monitor mangrove reserves. For example, an action item in the Belize Integrated Coastal Zone Management Plan of 2016 is to establish a national water quality monitoring program and a long-term national strategy for monitoring the health of reef, seagrass, mangroves, and other coastline habitats (Cherrington et al., 2010b; Coastal Zone Management Authority & Institute, 2016). They proposed to develop an annual State of the Coast Report and to develop a centralized data repository that will include baseline ecological data and information on coastal uses. Most stakeholders now recognize that legal support from real-estate lawyers to address issues around mangrove removal, encroachment, and ownership disputes, and methods for enforcing the current regulations around mangrove conservation is essential. Crafting a system of incentives to back this legal support, funded, and implemented by the Government of Belize is one way forward.

In parallel, the Belize Association of Private Protected Areas (BAPPA) and the Belizean Mangrove Conservation Network encourage land owners to work toward conservation and restoration of mangroves and other natural areas. Another local NGO, Friends of Placencia Lagoon, has documented impacts of nearby shrimp-farm effluent disposal on the local water quality. In general, active participation in mangrove management and conservation by individuals and experts who use coastal resources on a day-to-day basis will increase understanding and awareness of the ecosystem services provided by Belize's mangroves and coastal waters.

4.3. Lessons to Inform Adaptive Management

At ≈ 6 m above sea level, Belize City and its population are extremely vulnerable to coastal effects of ongoing climatic change: rising seas, increases in flooding frequency and duration, sediment deposition, and erosion. Because the pace and scope of climatic change continues to vary, adaptive management solutions can address immediate concerns while creating flexibility to respond to longer-term dynamics (Holling, 1978). A key aspect of adaptive management is the revision of management actions in response to new observations or environmental conditions. But adaptive management responses can be accelerated if additional information is available from designed experiments focused on outcomes of management interventions.

4.3.1. Observations Driving Adaptive Management in Belize

Crucial ecosystem services that mangroves provide for Belize include water filtration and treatment and coastal defense (Barbier et al., 2011; Horchard et al., 2019) and mangrove rehabilitation and restoration projects in and around Belize City may mitigate some effects of climatic change (**Figure 7**). Working with CZMAI and co-author Alex Felson, Coryelle Pondy (*unpublished data*) gathered and geospatially analyzed data on drainage and flood risk associated with storm events, current regulations and practices, predicted sea-level rise, water quality and wastewater infrastructure, and current projects and future plans for Belize City. She studied existing infrastructure and critical needs of Belize City (**Figure 7**), focusing on adaptions to sea-level rise and stormwater discharge into and from wastewater and septic systems, drainage networks, and roadways.

Opportunities for both preservation and rehabilitation of mangroves could take advantage of these valuable ecosystem services. For example, the 1,620 ha Bolton Bank parcel on the western side of Belize City is currently on the market for US $12M (**Figure 7B**). Mangrove preservation coupled with "smart" development in this area could provide significant civic benefits with extensive flood water storage capacity and habitat value.

The many canals in Belize City provide critical drainage but they overflow during heavy rains and floods, sending contaminated water into the city. Dredging and clearing trash from the canals is essential to optimize their flood management function. A recent International Development Bank project will dredge and install a pump and sluice gates to the canal outlets to manage flow and siltation (Interview with Belize Water Services 2017-06-16; see also Grau et al., 2013).

The Belize Water Services (BWS) runs the lagoon sewage processing facility, which is located adjacent to a low-income neighborhood on the south side of Belize City (**Figures 7C,D**). The sewage system drains ≈ 18% of the city and treats the ≈ 5.5 million L of sewage per day generated by ≈ 65% of the city's population (Silva, 2013); the rest of the city's inhabitants and those in neighboring communities either have private septic systems or discharge wastewater directly into adjacent mangroves. A facultative lagoon system (**Figure 7C**) operating as cells in series treats the sewage; each cell provides 10 days of hydraulic retention time. The sewer ponds are divided into three zones with the outfall being discharged through two pipes and into an excavated drain that connects to the Caribbean Sea. The collection systems are interconnected with Zone 1 flowing into Zone 2 and Zone 2 into Zone 3. On occasions, one of these zones fails and the wastewater is directly discharged into a canal, the river, or the sea through a series of outfalls designed as a fail-safe mechanism to deal with overflows, malfunctions, or power outages (Silva, 2013). Otherwise, treated effluent flows through canals cut through a mangrove wetland and is discharged into the Caribbean Sea (Belize Water Services, 2013). BWS engineers have raised concerns about salt intrusion while sea-level rise is pressuring them to raise the elevation of the berms around the lagoons (Interview with Belize Water Services 2017-06-16). There are additional conflicts between nearby low-income populations and the BWS, which wants to expand the lagoon system.

4.3.2. Designing Experiments With Management in Mind

With mangrove restoration and conservation as goals, we identified an additional critical parcel of mangroves that has undergone substantial land-use changes (**Figures 7A**, **8**). This parcel now presents opportunities for mangrove rehabilitation that could provide ecosystem services including natural habitat, storm surge and wave attenuation, drainage, and erosion control (i.e., EMR with decision points 8–10 in **Figure 4**). Because the parcel is located on land owned by St. John's Junior College, it also provides additional opportunities for education, outreach, and community engagement. In addition to buildings, the site includes mangroves and land connecting freshwater runoff to the sea; other than the BWS sewage lagoon and Bolton Bank, the "St.

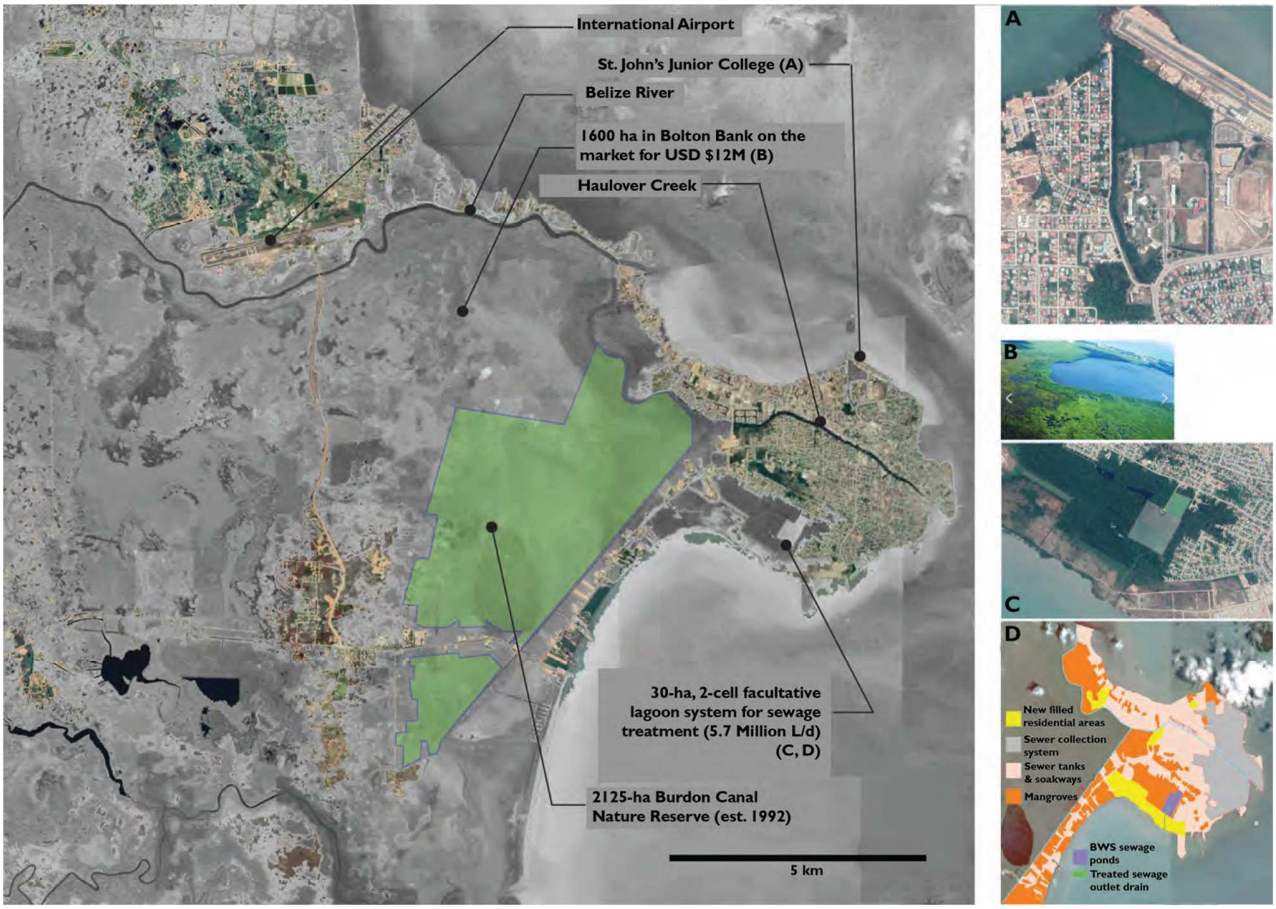

FIGURE 7 | Belize City (large aerial photograph) is located just south of the mouth of the Belize River on a delta surrounded by mangrove forests and the Caribbean Sea. The four insets illustrate key sites discussed in the case study of mangroves impacted by past development and proposed for rehabilitation These sites include **(A)** Saint John's Junior College (see also **Figures 8**, **9**); **(B)** the Bolton Bank land for sale; **(C)** the sewage lagoon system managed by the Belize Water Services; and **(D)** the overall sewered and mangrove areas of Belize City.

John's" parcel is the most valuable extant mangrove within Belize City to target for conservation and rehabilitation.

Based on a preliminary assessment of St. John's campus, and through discussions with CZMAI and a review of Belize's Integrated Coastal Zone Management Plan (Coastal Zone Management Authority & Institute, 2016), we have developed a concept-design proposal to combine nature-based infrastructure development with mangrove ecosystem management for Belize City. The project also proposes experimental research and monitoring (**Figure 9**) in an educational setting to work with students and faculty interested in learning about ecosystem functions and services of natural, rehabilitated, and restored mangroves, and best management practices to sustain them.

As with any EMR-based project, the St. John's project will start with gathering baseline biophysical data. Given its location in a human-dominated landscape, these biophysical data will be linked climate-change scenarios and ongoing development plans. To effectively develop these strategies, we defined a set of experimental zones (**Figure 9**) in which we will use observations and manipulative experiments to understand relationships between reconstructed tidal hydrology, connections within the existing mangrove systems, natural regeneration, and deliberate plantings (Felson and Pickett, 2005).

Proposed experiments take advantage of several environmental gradients at the site. Experiments 01 and 02 (**Figure 9**) would include plots sited on fill above highest high water adjacent to the airstrip, and within an existing mangrove stand, coastal uplands, and inland of the latter. These experiments would evaluate plant physiological responses and seedling or sapling growth and population dynamics as a function of inundation rate and frequency, water quality, and hydrological changes imposed by airstrip construction. Plots within Experiment 03 (**Figure 9**) would be used to study responses of seedlings and saplings to disturbance along a gradient from existing, intact mangroves to parts of the campus that are mown and fertilized.

Plots within Experiment 04 (**Figure 9**) would be used as test plots to develop nursery stock of appropriate species for restoration and rehabilitation efforts onsite and elsewhere in Belize. The primary driver variables here would be species

FIGURE 8 | Land-use changes at St John's Junior College illustrate **(left)** preserved mangroves and existing structures built from when the campus was located there in 1952 until 2006 and new changes resulting from the 2012 to 2016 extension of the Belize City Municipal Airstrip **(center, right)**. The series of panels illustrates conditions before (2006), during (2014), and after airstrip construction was completed (2019). This US $8.5M extension required clearing of ≈ 8.5 ha of intact mangroves.

identity and, to a lesser extent, water quality and soil nutrients that differ with distance from the existing mangrove stand onsite. Finally, Experiment 05 would be sited within the existing tidal wetland. This area would be used to explore diversity of mangrove-associated flora and fauna across a tidal range and associated impacts of the adjacent airstrip.

We also propose to construct a boardwalk in this mangrove stand to provide access to the restoration project and create opportunities for education and outreach (cf. **Figure 5**). Embedding the rehabilitated and restored stands on campus also will establish a stronger research-based identity for the campus landscape designed as an experiment while securing the remaining natural mangrove stands and improving the public understanding of the benefits of mangrove restoration (Felson et al., 2013a; Felson, 2016). The ultimate goal of this project is to change public awareness of the coastal management areas of Belize City and shift perceptions so that everyone recognizes the responsibility of inhabitants and institutions to share management and governance of Belize City's environmental assets.

5. DISCUSSION

Mangroves are socio-ecological systems whose functions provide a wide range of ecosystem services (e.g., Barbier et al., 2011, and section 2.2). Although mangroves, like other wetlands, have been undervalued, cut over, and converted to other uses for millenia, their anthropocentric and ecocentric values increasingly are appreciated. Technical needs for successful mangrove rehabilitation and restoration have been understood for at least fifty years (Lewis, 1982; Ellison, 2000, and section 2.3), but knowledge transference between mangrove restoration projects remains the exception (Lewis, 2009). At the same time, long-term success of any rehabilitation or restoration project must use bring together ecology, sociology, economics, and governance through community involvement to define, measure, monitor, and update project objectives and goals (e.g., Ounanian et al., 2018; Gann et al., 2019, section 2.4 and **Figure 4**). The case studies of mangrove rehabilitation and restoration in Singapore and Belize that we presented above illustrate these ideas and provide directions for future work.

In countries such as Belize that still have extensive, intact mangrove forests, large-scale experiments (e.g., **Figure 9**) can be designed and implemented to yield general results. Benchmarks for, and adaptive management of, rehabilitation and restoration projects can be guided by experimental results and observations of co-located "reference" stands. Management authorities in urban areas can partner with NGOs focused on conservation and preservation in rural areas to build ecological functions (e.g., biodiversity, habitat structure) and ecosystem services into rehabilitation and restoration efforts in city-based projects. Urban rehabilitation efforts, such as those proposed for the St. John's College campus will be visible to large audiences and can create new constituencies interested in cooperative governance of the broader environment. In contrast, in countries such as Singapore where little intact mangroves remain, rehabilitation and restoration projects will be opportunistic and constrained by local conditions and constituencies. Although large-scale ecological experiments are unlikely in these localities, social dynamics and key decision points (e.g., **Figure 4**) will define project objectives and goals while informing or accelerating adaptive management.

As climatic change continues to accelerate, key biophysical characteristics determining mangrove survival, growth, and reproduction—notably local sea-level, salinity, and temperature—will change in tandem. Thus, biophysical optima for specific mangroves in particular locations will change, altering patterns of local species diversity (Record et al., 2013).

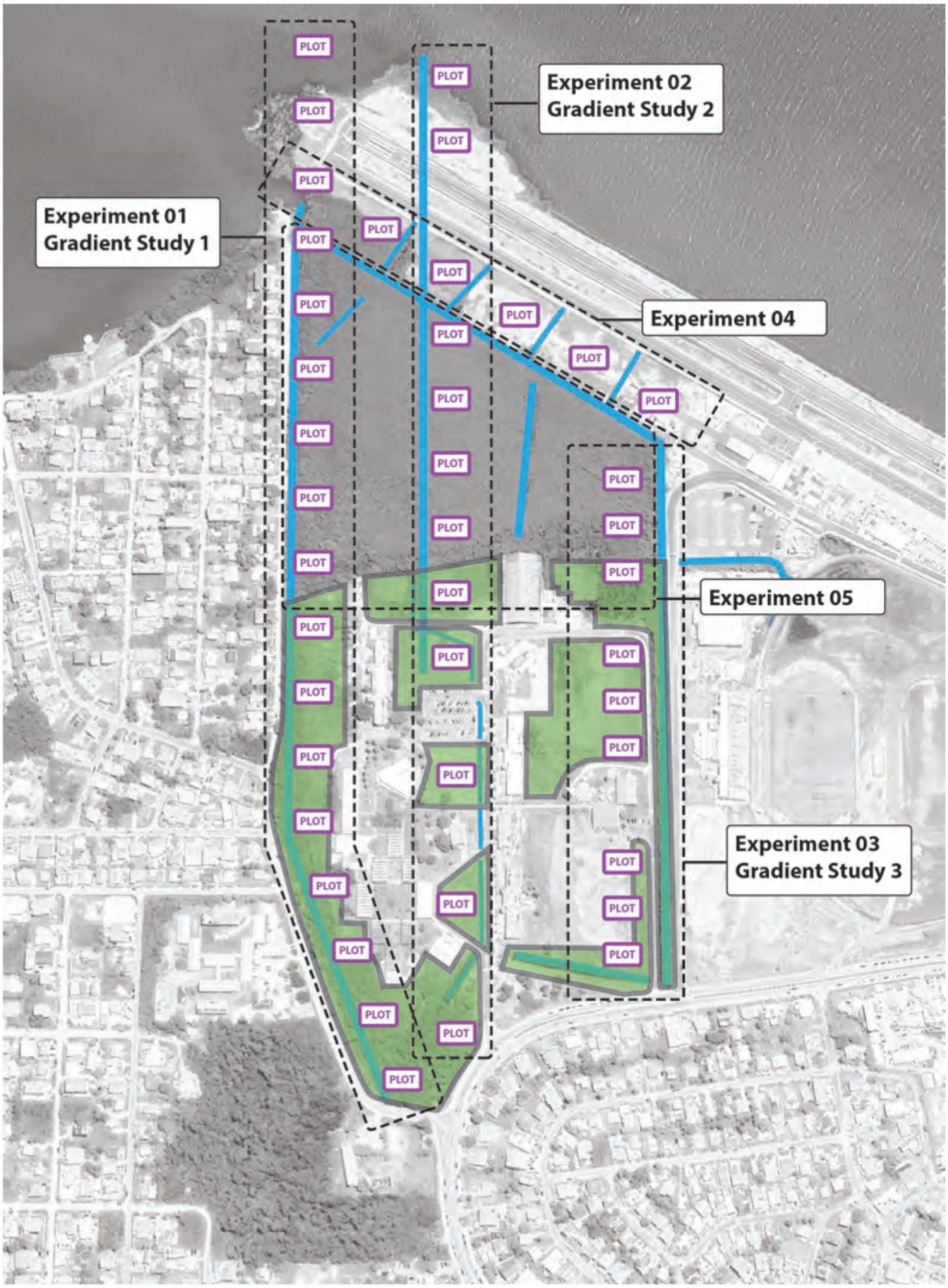

FIGURE 9 | Saint John's Junior College is hydrologically interconnected with channels and low-lying wet areas and includes multiple existing (degraded) habitats. Our proposed mangrove rehabilitation and restoration plan for the campus will establish five designed experiments (identified on the figure and described in detail in section 4.3.2) to develop research and encourage education-based restoration to improve the campus identity and inform smart land-use decisions and conservation practices.

Intentionally designed and engineered ecosystems that include novel combinations of species (Hobbs et al., 2006; Miller and Bestelmeyer, 2016) may be more resilient to ongoing and future climatic changes while providing a broad suite of desirable ecosystem services (Cheong S.-M. et al., 2013; Zimmer, 2018). Such designed mangroves should be guided by proven EMR and

CBEMR approaches in Singapore (**Figures 4**, **5**) and elsewhere (Brown et al., 2014; Lewis et al., 2019), deliberate experimental infrastructure in educational settings being developed in Belize (**Figure 9**), and integration of participatory adaptive management frameworks used throughout the world (Felson et al., 2013b; Eriksson et al., 2016; Brown, 2017).

AUTHOR CONTRIBUTIONS

AE was invited by the editors of this special issue to organize this article, He defined its conceptual framework. AE, AF, and DF together wrote and edited the article.

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REVIEW
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Spatial Planning Principles for Marine Ecosystem Restoration

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Coastal and marine ecosystems characterized by foundation species, such as seagrass beds, coral reefs, salt marshes, oyster reefs, and mangrove forests, are rich in biodiversity and support a range of ecosystem services including coastal protection, food provisioning, water filtration, carbon sequestration, recreational opportunities, cultural value, among others. These ecosystems have experienced degradation and a net loss of total area in regions around the world due to a host of anthropogenic stressors, resulting in declines in the associated ecosystem services they provide. Because of the extensive degradation in many locations, increasing attention has turned to ecosystem restoration of these marine habitats. Restoration techniques for marine and coastal ecosystems are generally more expensive when compared to terrestrial ecosystems, highlighting the importance of carefully selecting locations that will provide the largest return on investment, not only for the probability and magnitude of restoration success, but also for ecosystem service outcomes. However, site selection and spatial planning for marine ecosystem restoration receive relatively little attention in the scientific literature, suggesting a need to better study how spatial planning tools could be incorporated into restoration practice. To the degree that site selection has been formally evaluated in the literature, the criteria have tended to focus more on environmental conditions beneficial for the restored habitat, and less on ecosystem service outcomes once the habitat is restored, which may vary considerably from site to site, or with more complex landscape dynamics and spatial patterns of connectivity. Here we (1) review recent (2015–2019) scientific peer-reviewed literature for several marine ecosystems (seagrass beds, salt marshes, and mangrove forests) to investigate how commonly site selection or spatial planning principles are applied or investigated in scholarly research about marine ecosystem restoration at different spatial scales, (2) provide a conceptual overview of the rationale for applying spatial planning principles to marine ecosystem restoration, and (3) highlight promising analytical approaches from the marine spatial planning and conservation planning literatures that could help improve restoration outcomes. We argue that strategic site selection and spatial planning for marine ecosystem restoration, particularly applied at larger spatial scales and accounting for ecosystem service outcomes, can help support more effective restoration.

Keywords: restoration, spatial planning, site selection, conservation planning, spatial prioritization, seagrass, mangrove, salt marsh

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INTRODUCTION

Coastal and marine ecosystems characterized by foundation species, such as seagrass beds, coral reefs, salt marshes, oyster reefs, and mangrove forests, support a range of ecosystem services important to society including storm protection, food provisioning, water filtration, erosion control, carbon sequestration, recreational opportunities, cultural value, among others (Barbier et al., 2011). All of these ecosystems have experienced degradation and a net loss of total area in regions around the world because of a host of anthropogenic stressors, with associated declines in the ecosystem services that they provide (Valiela et al., 2001; Waycott et al., 2009, IPBES, 2019). Ecosystem degradation is so widespread that is it no longer sufficient to focus just on traditional approaches to ecosystem conservation (e.g., protected areas, threat reduction). In addition to preventing further declines, it will be necessary to restore ecosystems in locations where they have been lost. However, funding for restoration is often inadequate, raising challenging questions about how to best allocate scarce resources.

Traditionally, ecosystem restoration was primarily motivated by protecting biodiversity and restoring the natural character of systems degraded by human development (Hughes et al., 2018). However, in parallel with the growing appreciation for the importance of the ecosystem services provided by natural and properly functioning ecosystems, there is increasing policy focus on restoration efforts that protect or enhance ecosystem services (Bullock et al., 2011). For example, the Convention of Biological Diversity (CBD)'s Aichi Target 14 calls for the restoration and protection of ecosystems that provide essential services by 2020 (CBD, 2010). More recent initiatives, such as the United Nations Sustainable Development Goals (UNGA, 2015) and the zero draft of the CBD post-2020 global biodiversity framework (CBD, 2020), highlight that ecosystem services are a key motivation for ecosystem protection and restoration. Consistent with this policy attention, increasingly many restoration projects focus on ecosystem service objectives (e.g., Allan et al., 2013; Kittinger et al., 2016; Hagger et al., 2017). As pointed out by Bullock et al. (2011), this shift in focus from biodiversity conservation to ecosystem services creates both opportunities and challenges for restoration. A focus on ecosystem services provides an important motivation for funding and executing restoration projects (De Groot et al., 2013; Matzek, 2018). Furthermore, markets for services and specifically payment for ecosystem services schemes could provide an important funding stream to support restoration activities (e.g., Bonn et al., 2014; Hejnowicz et al., 2015; Matzek et al., 2015). However, there could also be tension between these two management goals; although biodiversity and ecosystem services are often positively correlated (Benayas et al., 2009; Nelson et al., 2009), that is not always the case and the relationship between the two can be complex (Tallis et al., 2008).

Given that a key driver of many restoration projects going forward will be recovering the ecosystem services provided by the restored habitat, the impact of many restoration projects is likely to be measured based on the services that are provided. Restoration techniques for marine and coastal ecosystems are generally very expensive (Bayraktarov et al., 2016), particularly compared to terrestrial ecosystem restoration costs, highlighting the importance of selecting locations that will provide the largest return on investment. Poor siting decisions can contribute to failed restoration projects (Fonseca, 2011; Bayraktarov et al., 2016), and indeed many marine and coastal systems have low success rates that contribute to their high average costs (e.g., van Katwijk et al., 2016). Furthermore, return on investment can be assessed as the value that people place on the resulting ecosystem services, suggesting that restoration in areas where people rely on the benefits provided by those systems may be more worthwhile investments.

While restoration projects involve decisions about where to target restoration, it is not clear how often such decisions are based on analyses that explicitly consider alternative sites, or whether such decisions are occurring at appropriate spatial scales and accounting for ecosystem service outcomes. This is surprising given the increasingly wide array of spatial planning tools that are being applied in other fields of conservation and management (such as marine protected area design and marine spatial planning). While the scientific literature on marine ecosystem restoration is rich with studies comparing alternative restoration techniques within a single site, there has been less attention paid to the potentially equally important impacts of decisions about where to conduct restoration in the first place. When site selection is considered, there is often a focus on environmental conditions beneficial for the restored habitat (e.g., Pollack et al., 2012; Valle et al., 2015; Hotaling-Hagan et al., 2017), key threats that need to be avoided or mitigated for restoration to succeed (e.g., Hotaling-Hagan et al., 2017), and/or the historical distribution of the species or habitat as an indicator of whether restoration is likely to be effective (e.g., Braje et al., 2016). For example, Pollack et al. (2012) developed a restoration suitability index model for oysters based on abiotic conditions such as salinity, temperature, turbidity, dissolved oxygen, and depth, and a reef quality index that accounted for the abundance of live oysters, dead shells and spat. These types of approaches are useful, but they overlook the likely spatial variation in ecosystem service outcomes once the habitat is restored.

In this paper we seek to catalyze the wider adoption of quantitative spatial analyses from the closely related fields of marine spatial planning, conservation planning, and spatial ecology into the science and practice of marine ecosystem restoration. Our first step is to present a structured review of the peer-reviewed scientific literature from 2015 through 2019 for three key marine ecosystems, seagrass beds, salt marshes, and mangrove forests. With this comprehensive survey of a limited set of years and ecosystems, we were able to document how site selection is being incorporated into recent restoration research for these representative ecosystems. Examining this literature, we investigate whether and how site selection and spatial planning principles are being applied at different spatial scales. We then provide a conceptual overview of the rationale for applying spatial planning principles to marine ecosystem restoration, highlighting important issues that may not be adequately considered in the current literature. We then discuss specific analytical approaches from other literatures, summarizing how each is used in related conservation and management fields and illustrating how they could improve outcomes in marine ecosystem restoration. Strategic spatial planning for marine ecosystem restoration, using the approaches and tools discussed in this paper, can help support more successful, cost-effective restoration that maximizes desired ecosystem service outcomes.

LITERATURE REVIEW

Methods

We reviewed studies published in the scientific literature between January 2015 and November 2019. Publications were selected based on a topic search in the Web of Knowledge's Web of Science Core Collection database using specific search terms and keywords for restoration, site selection or spatial planning, and the ecosystem type (**Table 1**). We focused our search on three ecosystems: seagrass beds, salt marshes, and mangrove forests, evaluating 146, 220, and 206 papers, respectively (see **Supplementary Reference Lists**). These ecosystems were selected to be illustrative and representative, recognizing that important restoration research and practice is happening in other coastal and marine ecosystems (e.g., oyster reefs, coral reefs). This literature review was more narrowly focused in terms of ecosystem type and publication dates than the rest of the paper.

We reviewed all papers returned by our searches to identify those that examined site selection for restoration and/or applied spatial planning principles to ecosystem restoration. We defined spatial planning for restoration as making strategic decisions using available data and/or models about site selection, spatial extent (i.e., size of area to be restored), or spatial configuration (i.e., landscape attributes including patch shape, connectivity, fragmentation). Only studies that examined site selection for restoration or applied spatial planning principles to restoration in the focal systems were analyzed further (**Table 1**, "Spatial planning papers" and **Supplementary Table S1**). We did not further analyze articles that did not meet these spatial planning criteria, including those that focused on a different ecosystem or were not about restoration site selection or spatial planning for restoration (e.g., ecology focused papers examining the impact of restoration on species abundance or ecosystem function). In some cases, a paper did not meet our spatial planning criteria because it was not directly about site selection or spatial planning for restoration, but the results of the paper could have implications for spatial planning for restoration, and we noted this (**Table 1**, "Additional papers with implications for spatial planning"), although it was a more subjective assessment and we did not further analyze these papers.

For those papers that met our spatial planning criteria ($n = 7$ for seagrass, 3 for salt marsh, and 3 for mangroves; **Table 1**), we recorded:

(1) Scale of the study, categorized based on the length of the coastline under consideration:
  (a) "local" if the study spanned less than 10 km
  (b) "regional" if the study was between 10 and 100 km
  (c) "larger regional" if the study was between 100 and 1000 km
  (d) "large ecosystem" for studies spanning a region longer than 1000 km

(2) Motivation(s) for site selection (not mutually exclusive):
  (a) improve restoration success (e.g., identify locations with appropriate environmental conditions or where survival or growth is likely to be higher; identify historical distributions of the target ecosystem; identify areas without stressors that would hinder restoration success)
  (b) enhance ecosystem services that could be provided by the restored ecosystem
  (c) minimize the financial costs of restoration
  (d) minimize conflict with human uses

(3) Analytical technique or approach(es) used for spatial planning (not mutually exclusive):
  (a) experimental techniques (e.g., restoration experiments in different locations to inform site selection)
  (b) habitat suitability models (HSM) for the habitat targeted for restoration, including statistical models relating vegetation occurrence to environmental factors, and index-based models that rank the relative habitat suitability of different locations
  (c) mapping and spatial analysis (including mapping of ecological or social survey data and remotely sensed

TABLE 1 | Search strings used for each ecosystem type, number of papers published between January 2015 and November 2019 that were returned by each search and thus reviewed, number of papers that met our spatial planning criteria, and number of papers that did not meet our spatial planning criteria but could have implications for spatial planning.

Ecosystem	Search terms for all ecosystems	Ecosystem-specific search terms	# of papers (*n*)	Spatial planning papers (*n*)	Additional papers with implications for spatial planning (*n*)
Seagrass	*restor* AND (spatial* OR siting OR "site selection" OR seascape*)*	*AND (seagrass* OR eelgrass OR surfgrass)*	146	7	16
Salt marsh		*AND (saltmarsh* OR "tidal marsh*" OR spartina OR salicornia OR phragmites)*	220	3	24
Mangrove		*AND (mangrove*)*	206	3	13

See ***Supplementary Material Section 1.2*** *(****Supplementary Reference List****) for a complete list of all papers reviewed, including those that met the spatial planning criteria and those that could have implications for spatial planning.*

data, with mapping conducted by hand or using software like ArcGIS)
   (d) spatial prioritization algorithms (e.g., Marxan, Zonation)
   (e) social surveys (e.g., participatory mapping; stakeholder preferences)
   (f) other modeling techniques (e.g., ocean circulation models)

(4) Parameter(s) for site selection used in the analysis (not mutually exclusive):
   (a) environmental and biological factors (e.g., light attenuation, water quality, temperature, growth rate)
   (b) current or historical presence of the habitat
   (c) proximity to the habitat
   (d) stressors (e.g., water quality or shoreline alterations)
   (e) ecosystem services expected to be enhanced from habitat restoration (e.g., coastal protection, biodiversity enhancement, etc.)
   (f) human use (e.g., boating)

We also evaluated whether the study was aiming to inform a real restoration decision or focused on more hypothetical or theoretical aspects of site selection or spatial planning.

Results and Discussion

Our review of scientific literature published between 2015 and 2019 on seagrass, salt marsh, and mangrove restoration suggests that site selection and spatial planning are rarely a research focus. Despite ~150–220 papers per ecosystem type being returned by the focused searches we conducted, <5% of papers either examined site selection for restoration or applied spatial planning principles to ecosystem restoration (**Table 1** and **Supplementary Table S1**). A somewhat larger number of papers, while not specifically focused on site selection or spatial planning, had potential implications for spatial planning for restoration based on their analysis and findings (**Table 1**). As examples, some papers conducted experiments to determine the optimal level of a limiting environmental factor(s) (e.g., Sloey et al., 2016; Xu et al., 2016), developed a species distribution model (Adams et al., 2016), or established spatial patterns of population structure and connectivity (Jahnke et al., 2018; Triest et al., 2018), results that could be used to inform site selection. Thus, information that can improve restoration site selection is actively being produced, but most restoration research is not directly evaluating spatial variability in likely restoration outcomes. An additional class of papers mentions the importance of site selection or spatial planning, but do not perform any type of analysis or suggest an approach to make spatial restoration decisions (e.g., Kodikara et al., 2017; Macreadie et al., 2017; Wegscheidl et al., 2017); these papers did not meet any of our criteria, but highlight that there is a need for analytical approaches that can be used to inform spatial planning for restoration.

For the small number of studies that met our spatial planning criteria, motivations for site selection or spatial planning varied across ecosystem type (**Table 2**). The most common motivation was improving restoration success, an objective of all seagrass and saltmarsh papers, while minimizing conflict with human uses and enhancing ecosystem services were relatively uncommon motivations (**Table 2**). Minimizing restoration costs was a motivation in about a third of the papers overall, but was not a motivation in any of the seagrass papers, despite the fact that seagrass restoration has a higher per area cost than the other two systems (Bayraktarov et al., 2016). The few papers on salt marsh and mangrove restoration included a variety of motivations, but seemed to have more emphasis on minimizing restoration costs. Enhancing ecosystem services was only mentioned as a motivation for two papers (both about mangrove restoration), a surprising result given that the ecosystem service benefits of all three habitats are a focal point of many management and conservation efforts (Needles et al., 2015; Cullen-Unsworth and Unsworth, 2018; Romañach et al., 2018). In general, social, political and cultural motivations for restoration were often not highlighted explicitly, although these drivers are required for restoration to occur. Over two-thirds of the papers were aiming to inform real restoration decisions, as opposed to studies focused on more hypothetical or theoretical cases.

The vast majority (85%) of the studies that met our spatial planning criteria were focused specifically on site selection, as opposed to other aspects of spatial planning, like spatial scale or spatial configuration of restoration areas (**Table 3**). The two studies that were not focused on site selection (one seagrass study and one salt marsh study) examined spatial scale, specifically determining the minimum spatial scale or patch size required for successful restoration (Adams et al., 2018; Gittman et al., 2018). No studies examined spatial configuration of restored

TABLE 2 | Number (and percent) of papers meeting our spatial planning criteria that specified the aims and reasons/motivations for site selection or spatial planning for restoration.

System	Aims to inform real decisions, *n* (%)[1]	Motivation for site selection or spatial planning, *n* (%)			
		Improve restoration success	Enhance ecosystem services	Minimize restoration costs	Minimize conflict with human use
Seagrass	5 (71%)	7 (100%)	0	0	1 (14%)
Salt marsh	2 (67%)	3 (100%)	0	2 (67%)	0
Mangrove	2 (67%)	1 (33%)	2 (67%)	2 (67%)	1 (33%)
Overall %	**69%**	**85%**	**15%**	**31%**	**15%**

Studies could be motivated by more than one reason, and all studies had at least one of the motivations listed here. [1]Those papers not aiming to inform real decisions were hypothetical or theoretical studies.

TABLE 3 | Number (and percent) of papers meeting our spatial planning criteria that were focused specifically on site selection (those that did not focused on spatial scale), and methodological approaches used in each study.

System	Focused on site selection, *n* (%)[1]	Methodological approach or technique, *n* (%)					
		Experi-mental	Habitat suitability models	Mapping/spatial analysis	Spatial prioritization	Social surveys	Other models
Seagrass	6 (86%)	4 (57%)	5 (71%)	4 (57%)	0	1 (14%)	1 (14%)
Salt marsh	2 (67%)	2 (67%)	1 (33%)	0	0	0	1 (33%)
Mangrove	3 (100%)	0	1 (33%)	3 (100%)	1 (33%)	1 (33%)	0
Overall %	**85%**	**46%**	**54%**	**54%**	**8%**	**15%**	**8%**

Studies could employ more than one methodological approach, and all studies employed at least one of those listed here. [1] *Those papers not focused on site selection examined spatial scale (n = 1 each for seagrass and salt marsh systems).*

sites or patterns of connectivity, although one study did account for proximity to existing habitat patches (Pirrotta et al., 2015). Furthermore, some of the studies that did not meet our criteria could have implications for approaching restoration at a seascape scale that considers habitat or population connectivity (Howe and Simenstad, 2015; Gillis et al., 2017; Taylor et al., 2017; Jahnke et al., 2018; Olson et al., 2019). Our findings are consistent with those of Gilby et al. (2018) who found, looking across terrestrial and aquatic systems, that landscape context was rarely (<15% of cases) used as a criterion for site selection for habitat restoration aimed at benefitting animal populations. They argue that more consideration of landscape attributes like habitat configuration and population connectivity could help enhance animal populations dependent on the restored habitat because of the importance of colonization dynamics (Gilby et al., 2018). This logic would apply to the valuable nursery habitat function that seagrass, mangrove, and salt marsh systems provide for many marine species, and yet none of the studies that met our spatial planning criteria looked at these types of factors.

The most common methodological approaches employed were habitat suitability models (HSMs) and mapping/spatial analysis (**Table 3**). Slightly less than half of the studies included an experimental study. Use of spatial prioritization algorithms, such as the conservation planning tools Marxan and Zonation, was rare (<10% of studies) despite the fact that such tools could be directly applicable to site selection analyses. Social surveys or participatory research was also relatively rare, perhaps because the motivations for site selection were often not explicitly focused on the human dimensions of ecosystem restoration (e.g., they were focused on improving restoration success rather than minimizing conflicts with human uses). The parameters most commonly used in site selection and spatial planning (**Table 4**) largely follow from the methodological approaches and motivations for site selection. Environmental factors predominate (85% of studies), which is consistent with the use of HSMs, experimental approaches, and mapping and spatial analysis. Expected ecosystem services were only used as a site selection parameter in a single study, and stressors and human uses were only used in less than a handful of studies, aligning with the fact that enhancing ecosystem services and reducing conflict with human use were not common motivating factors among these studies.

Across the three systems studied in the spatial planning papers, a majority (67%) examined a "regional" spatial scale (10–100 km along a coastline), with a couple operating at smaller (<10 km) or much larger (>1000 km) spatial scales (**Figure 1**). The presence of such large scale studies was somewhat surprising given that many actual restoration projects for these habitats are occurring at much smaller scales (Bayraktarov et al., 2016), and given that no study was focused on scales between 100 and 1000 km. On the other hand, site selection and spatial planning become more important and relevant when making decisions over larger scales, and so it makes sense that spatial planning research has a larger scale focus. Finally, the results of our literature search may not reflect the size distribution of actual restoration projects, many of which are not discussed in the peer reviewed scientific literature.

WHY SPATIAL PLANNING FOR MARINE ECOSYSTEM RESTORATION?

Spatial planning for restoration – broadly defined here as making strategic decisions using available data and/or models about site

TABLE 4 | Number (and percent) of papers using different types of parameters for site selection.

System	Environmental factors	Current/historical habitat presence	Proximity to habitat	Stressors	Ecosystem services	Human use
Seagrass	7 (100%)	4 (57%)	1 (14%)	1 (14%)	0	1 (14%)
Salt marsh	3 (100%)	0	0	0	0	0
Mangrove	1 (33%)	2 (67%)	0	1 (33%)	1 (33%)	2 (67%)
Overall %	**85%**	**46%**	**8%**	**15%**	**8%**	**23%**

Studies could use multiple types of parameters, and all studies employed at least one of those listed here.

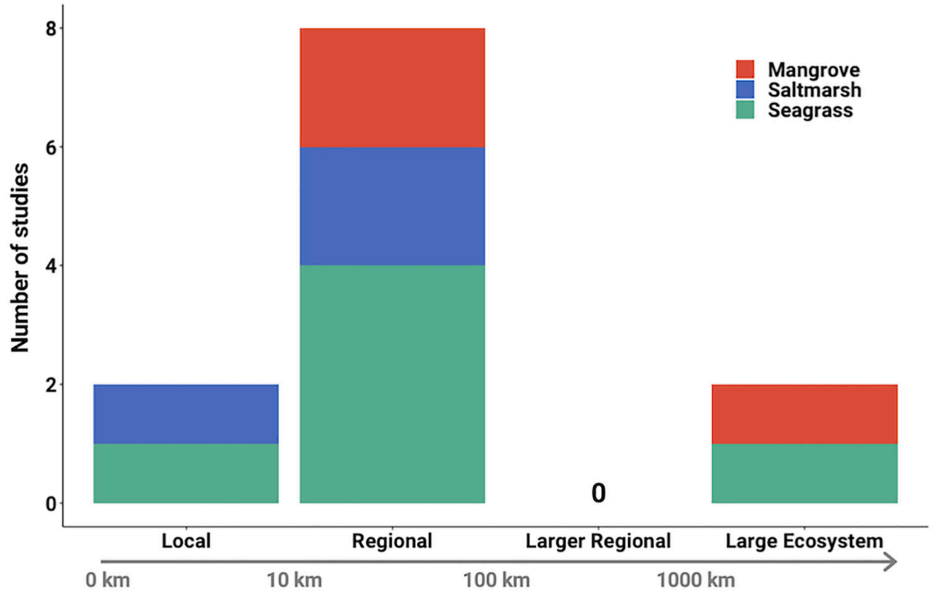

FIGURE 1 | Spatial scale of spatial planning restoration studies (*n* = 12 because scale was not applicable in one modeling study).

selection, spatial extent (i.e., size of area to be restored), or spatial configuration (i.e., landscape attributes including patch shape, connectivity, fragmentation) – has the potential to improve return on investment for marine ecosystem restoration projects (**Figure 2**). Marine environments are spatially heterogeneous at a range of spatial scales and levels of biological organization; spatial variation in environmental conditions underlies spatial variation at the ecosystem, community, population and individual levels. This creates spatial variability in ecosystem function and processes, and therefore in the ecosystem services that are provided by natural ecosystems (Koch et al., 2009; Townsend et al., 2018). The human communities that depend on marine resources and ecosystem services are also not distributed uniformly along the coast, and anthropogenic impacts can be highly variable across space. Admittedly, in some cases it might be more expedient or practical to implement a restoration project at a site without taking a step back to consider spatial planning or site selection. But in many others, accounting for this tapestry of spatial variation within restoration decision-making could pay important dividends.

Expected restoration success, whether defined as the target habitat persisting following the restoration intervention for some minimum time, or as germination success, or as survival rate of a foundation species, will vary across the seascape. This is because environmental conditions that influence survival, growth, and reproduction of the target species vary across space. Furthermore, restoration success can be influenced by positive and negative species interactions (e.g., Gómez-Aparicio, 2009; Silliman et al., 2015) and these interacting species are likely patchily distributed. Connectivity with existing areas of the target habitat can also be important for successful establishment of the restored habitat (van Katwijk et al., 2016), either by ensuring supply of recruits undergoing long-distance dispersal or through migration of adults of mobile species. Such connectivity might be inferred from simple proximity or estimated from more sophisticated genetic or oceanographic analyses. Finally, spatial variation in the stressors that lead to losses necessitating restoration can impact success (Allan et al., 2013), as avoiding these stressors minimizes the chance of restoration failure.

There will also be spatial variation in the value of ecosystem services, or the benefits of economic, social or cultural value to people, that are provided by the ecosystem if successfully restored. This variation may not simply mirror the spatial pattern of restoration success. That is because while the supply of a potential service is dictated by ecological functions and biophysical aspects of the ecosystem, the use of that supply by people is what defines it as an actual ecosystem service, and peoples' preferences for different services further define their value (Tallis et al., 2011). Thus, the supply of potential ecosystem services will vary across the seascape as a function of the factors discussed in the previous paragraph – environmental conditions impacting the growth or productivity of foundation species, species interactions, ecosystem structure and function, and connectivity between and among habitats – in addition to other biophysical aspects of the system (e.g., wave energy for coastal protection services; fish populations for fishery services). But then the use or utility of those potential services will depend on the spatial distribution of human communities along the coast or spatial patterns of human activity (e.g., fishing, recreation), and assessments of service value will further depend on human values which can vary along the coast depending on factors such as social preferences and norms, socioeconomic status, and social vulnerability to environmental threats (Tallis et al., 2011; Townsend et al., 2018).

For example, restoration of mangroves, coral reefs, and oyster reefs can be motivated by the coastal protection service provided

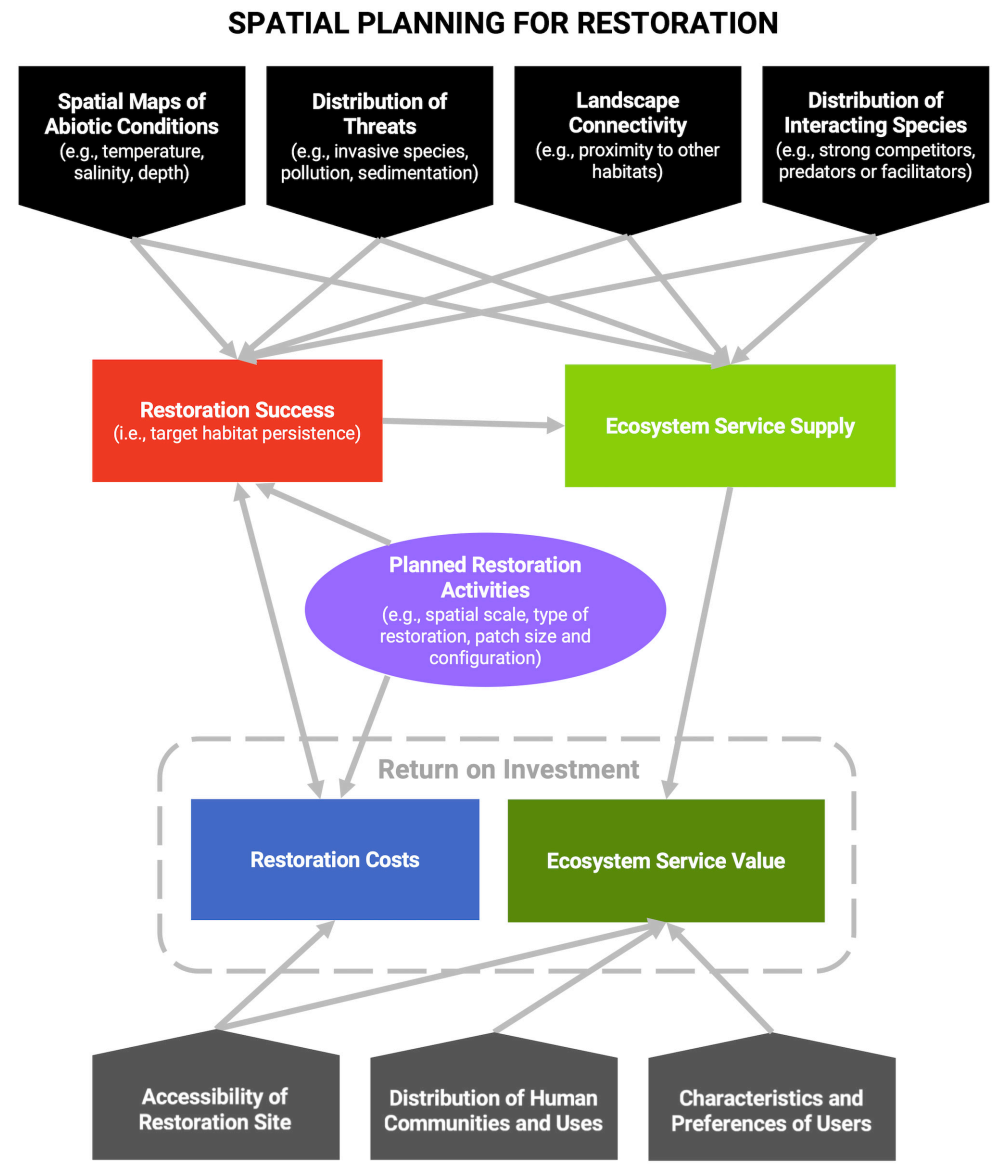

FIGURE 2 | Conceptual figure of sources of spatial variation that influence restoration success, ecosystem service supply and value, and restoration costs. Accounting for these sources of spatial variation in restoration planning and site selection has the potential to improve return on investment, which we use here broadly to refer to the ecological and ecosystem service benefits (i.e., return) and the financial and social costs (i.e., investment) of restoration.

by these biogenic habitats dampening wave energy before it reaches the coast (Barbier et al., 2011; La Peyre et al., 2015). The supply of that potential service will vary along the coastline as a function of local oceanographic conditions, wave energy, and characteristics of the ecosystem (e.g., mangrove tree height and density, live coral cover) (Koch et al., 2009). Its value as a service will vary based on where people are living along the coast, and its spatial pattern of value will be further modulated by community preferences and socioeconomic factors, including accessibility to inland shelters during major storm events, ability to rebuild properties following storm and inundation damage, preferences or resources for building artificial protective structures (e.g., seawalls), among others. Service value will not be the same for all people and can be measured for different dimensions of value. For example, the value of coastal protection could be assessed based on property value along the coast or based on the number of people impacted by storm surge, which could yield very different assessments of value (Arkema et al., 2013; Pascal et al., 2016). Collectively, these diverse dimensions of ecosystem services, which couple the social and ecological components of the system, can create rich spatial patterns that could inform restoration priorities across space.

Lastly, there may also be spatial variation in the costs associated with implementing a restoration project. This can include the actual financial costs of the project, but also the social and financial opportunity costs of pre-empting other uses of that space (e.g., restoring a mangrove forest rather than using that area for shrimp farming). Financial costs could depend on the level of ecosystem degradation in different areas, the proximity to existing areas of the ecosystem that could allow for natural recruitment, proximity to ports and other infrastructure, and the existence of stressors that need to be mitigated prior to restoration. For example, Allan et al. (2013) mapped stressors relative to ecosystem services for the Great Lakes and suggested that return on investment should be high where ecosystem services are high and stressors are low or absent because stressor mitigation will not be required. Given the high average cost of restoring even a single hectare of a marine ecosystem, it is crucial that we consider spatial variation in likely restoration success, benefits from ecosystem services, and restoration costs when setting restoration priorities.

The concepts reviewed in this section apply to all coastal and marine ecosystems and to a range of spatial scales. Restoration decision-making includes two scales: the spatial extent of the actual project (i.e., how large of an area will be restored) and the scale of site selection (i.e., how large of an area is under consideration when deciding where to do the project). Weighing the costs and benefits of different scales of restoration projects is useful (Iftekhar et al., 2017), but here we are particularly focused on the benefits from spatial planning and site selection decisions. Although the scale of decision making is often determined by jurisdictional constraints, considering larger areas is likely to include more variation in levels of expected restoration success, predicted ecosystem service benefits, and estimated restoration costs, enhancing the likelihood of identifying sites that provide the best benefit to cost ratio. We thus argue that it is useful to conduct a spatial planning analysis at the largest scale practical within existing constraints.

APPROACHES AND TOOLS TO SUPPORT SPATIAL PLANNING FOR MARINE ECOSYSTEM RESTORATION

Spatial planning for marine ecosystem restoration can be advanced by formal quantitative approaches. Fortunately, this does not require the creation of new methodological approaches and analytical tools, but can build on extensive work on spatial planning tools being done in related fields of marine conservation and management. Restoration can adopt existing methods from these fields with rather modest modifications, and can take lessons from how those tools have been applied to similar problems. Here we review several classes of approaches and tools that are particularly applicable to spatial planning for restoration. We borrow heavily from the conservation planning and marine spatial planning literatures, especially the former, with its established history of using spatial analysis to improve the efficiency and biodiversity outcomes of conservation projects. Some tools may fit in more than one of the categories outlined below, and the approaches we describe are not necessarily mutually exclusive. There are examples of all of these approaches being applied to ecosystem restoration as described below, although sometimes just for terrestrial systems, and these examples are often too few and far between. We hope to catalyze more widespread research and adoption of these tools for marine ecosystem restoration.

Mapping and Spatial Analysis

Geographic information systems (GIS) offer powerful and versatile tools for storing, mapping, and analyzing spatial data. As a result, GIS is already used for a variety of purposes associated with spatial planning and site selection for activities like wind farms, aquaculture, and marine protected areas (Gimpel et al., 2015; Brown et al., 2016; St-Pierre and Gagnon, 2020). In these contexts, assembling a GIS database of relevant environmental, biological, and socio-economic data layers is often a critical first step in defining the spatial domain and identifying important information gaps for a study region (Stamoulis and Delevaux, 2015). When key datasets are missing, spatial analyses and models can be used to fill the gaps using analysis platforms like ArcGIS or R (Caldow et al., 2015; Stamoulis and Delevaux, 2015), thereby enabling pixel by pixel comparisons of features across a broad spatial scale. For example, geostatistical approaches (like kriging) are commonly used to interpolate spatial patterns of environmental conditions and potential threats at unsampled locations over various spatial and temporal scales (Gimpel et al., 2015). Classification techniques applied to remote sensing imagery are also widely used to produce habitat maps (e.g., coral reefs, seafloor habitats, and kelp; Roelfsema et al., 2018; St-Pierre and Gagnon, 2020) because direct observation is usually impractical. Furthermore, many HSMs (described below) can be implemented and visualized in a GIS environment, such as those available through the Marine Geospatial Toolbox and the SDM Toolbox[1,2]. Ecosystem service models (described below) are also frequently implemented and visualized in a GIS platform to map the spatial distribution of potential service outcomes (Guerry et al., 2012). Lastly, participatory mapping in GIS is increasingly used to gain insights into stakeholders' patterns of use and preferences for different planning options (Brown et al., 2016). All of these types of datasets can be combined, visualized and analyzed in a GIS program. For example, using an overlay analysis, the relative suitability of different locations for restoration can be assessed based on criteria such as environmental and physical conditions (e.g., Hogg et al., 2018), expected species distributions (e.g., Theuerkauf et al., 2019), ecosystem services, fixed constraints (e.g., regulatory boundaries) and stakeholder input.

Many of these GIS mapping and analysis techniques are readily applicable to spatial planning and site selection for marine ecosystem restoration, as demonstrated by studies analyzed in our literature review (**Supplementary Table S1**). For instance, GIS classification techniques applied to historic and current habitat imagery can be used to identify potential restoration sites, such as areas that previously supported seagrass habitats (Pirrotta et al., 2015) or currently support degraded mangrove habitats (Adame et al., 2015). Further, geostatistical interpolation can be used to create spatial layers for environmental and

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[1] https://mgel.env.duke.edu/mget/

[2] http://www.sdmtoolbox.org/

anthropogenic factors that could become barriers to successful restoration of target species (e.g., light availability and boating disturbance in the case of seagrass beds; Hotaling-Hagan et al., 2017). Habitat maps and interpolated layers can then be used as inputs to HSMs for identifying the best locations for successful restoration of target species (e.g., Pirrotta et al., 2015; Puckett et al., 2018) or can be overlaid with maps of expected ecosystem services (e.g., Adame et al., 2015) or participatory maps indicating preferred restoration sites (e.g., Rakotomahazo et al., 2019) to assess potential restoration options. The reliability of spatial data layers visualized in GIS will depend on the nature and quality of input datasets and on the degree of gap filling or interpolation required, and it is important to account for potential sources of uncertainty and error, as with any modeling and data synthesis exercise (Caldow et al., 2015).

Habitat Suitability Models

Habitat suitability models, sometimes referred to as environmental niche models and including some types of species distribution models, aim to predict the suitability of a location for a species, based on environmental variables that limit its distribution, by using observed relationships between species occurrences and environmental conditions (Rushton et al., 2004; Elith and Leathwick, 2009; Franklin, 2013; Thuiller and Münkemüller, 2017). These models range in sophistication from correlative (e.g., generalized additive models) and machine learning approaches (e.g., MaxEnt; Linhoss et al., 2016), down to simple index models that ask whether locations meet a set of minimum criteria for the species to thrive. In each case, the models generate maps of suitability based on current or predicted environmental conditions. Thus, besides explaining and inferring current distributions, they can be used to predict how suitable habitat for a species could change under different environmental scenarios, such as with predicted climate change (Heikkinen et al., 2006) or threat reduction. Indeed, HSMs have been used to inform marine ecosystem restoration projects, including for seagrass meadows (e.g., Adams et al., 2016), salt marshes (Heuner et al., 2016), mangrove forests (Petrosian et al., 2016), and oyster reefs (Barnes et al., 2007; Theuerkauf et al., 2016; Chowdhury et al., 2019). The reliability of these models, however, depends on the availability and quality of data on species' distributions and environmental parameters. Furthermore, in heavily degraded systems, current distributions may not accurately reflect where a species could survive if threats were mitigated as part of the restoration project.

The benefit of using HSMs to inform restoration site selection is that they can preemptively identify locations where restoration is likely to be more (or less) successful before costly projects are implemented. For example, for seagrass meadows, HSMs have been used to select locations where restoring is predicted to be successful (Adams et al., 2016; Hotaling-Hagan et al., 2017; Zhou et al., 2017; Thom et al., 2018). Some studies also validate these predictions by performing *in situ* transplants that resulted in successful seagrass restoration, suggesting that HSMs are useful decision tools for restoration projects (Pirrotta et al., 2015; Valle et al., 2015). Although simple HSMs can be useful, HSMs can also be combined with physical models (e.g., oceanographic modeling projections) and data on species behavior (e.g., animal movement such as dispersal) to provide more dynamic predictions. With these modifications HSMs have been used to identify candidate locations for restoration in oyster and mussel reefs (Barnes et al., 2007; Pollack et al., 2012; Elsäßer et al., 2013). Furthermore, HSMs can also be used to identify locations for restoration that will enhance the provision of ecosystem services. For example, Theuerkauf et al. (2019) combined a habitat suitability index for oysters with abiotic data (e.g., dissolved oxygen, chlorophyll a, water flow) to identify restoration areas that would maximize the water filtration service provided by oyster reefs, while Zellmer et al. (2019) used stacked-species distribution models to identify sites for artificial reefs that would enhance reef fish distributions and richness and the services they support (e.g., fisheries, recreation).

Ecosystem Service Models

Ecosystem service models are increasingly used to describe potential benefits from nature to inform conservation and spatial planning (Nelson et al., 2009; White et al., 2012; Lester et al., 2013; Arkema et al., 2015). These models capture the linkages between ecosystems and people, and assess how service supply and value could be impacted by proposed management actions, human activities, and environmental degradation. Ecosystem service models can range from simplified approaches based on expert opinion or on the assumption that values documented for that ecosystem in one location apply to other locations (e.g., benefit transfer methods; Brander et al., 2012); to complex spatial models that require more data but can account for multiple sources of spatial variation in both service supply and value to people (e.g., production function models; Chan and Ruckelshaus, 2010; Guerry et al., 2012; Townsend et al., 2018).

The development of ecosystem service models for marine systems has lagged behind models for terrestrial and freshwater systems (Townsend et al., 2018), and thus applications to marine ecosystem restoration are somewhat rare. This is understandable given data limitations for marine systems, the complexity of processes controlling the supply and value of ecosystem services, and the uncertainty associated with predicting potential restoration outcomes. Where poor theoretical understanding or data limitations exist, it may be necessary to rely on more simplified approaches (e.g., benefit transfer), knowing there could be greater spatial variation in service outcomes than is captured by these techniques. In this case, relying on generalized ecosystem service models, global databases, and web interfaces for acquiring model parameters and inputs can be useful (like those offered by the InVEST suite of models; Guerry et al., 2012; Sharp et al., 2016). GIS mapping and spatial analysis (described above) can also generate local datasets that can be used in generalized modeling frameworks (e.g., La Peyre et al., 2015; Gilby et al., 2020).

Despite challenges with modeling marine ecosystem services, the growing number of cases where ecosystem service models have been used in spatial planning for conservation illustrate how they could guide marine ecosystem restoration. For example, Arkema et al. (2013) developed a model to quantify coastal protection services associated with different nearshore habitats in the U.S. to evaluate the potential impact of habitat conservation on various measures of social vulnerability to climate change. Arkema et al. (2015) developed models to quantify ecosystems services associated with coral reefs, mangroves, and seagrasses in Belize and used the outputs along with stakeholder preferences to inform a spatial planning process. Both of these analytical approaches could be expanded to inform restoration site selection and planning. Adame et al. (2015) and Theuerkauf et al. (2019) are good examples of this type of approach, showing how ecosystem service models can inform site selection and spatial planning for restoration of oyster reefs and mangroves, respectively.

Spatial Prioritization Analysis

Spatial prioritization is the process of identifying and selecting the best locations to take action. This is perhaps the most well-developed aspect of the field of conservation planning (Groves and Game, 2016), where it is used to select locations for conservation action, most commonly protection (Ban et al., 2013). Spatial prioritization can be done at a range of complexity levels, from applying simple heuristic rules where sites are ranked according to some objective (e.g., species richness or presence of rare species) to using more sophisticated optimization algorithms or approximations (Moilanen et al., 2009). These algorithms, although themselves varying in complexity, essentially aim to identify a site or collection of sites that achieve a set specified objectives (e.g., protecting some percentage of biodiversity, maximizing habitat representation, or minimizing the total amount of area protected) (Camm et al., 1996). There are a variety of software tools available for this purpose, with the most prominent being Marxan (Ball et al., 2011) and Zonation (Lehtomaki and Moilanen, 2013). A common use of these tools in conservation planning is to identify a site or collection of sites that meet specified targets for various conservation objectives while minimizing "costs." Costs can be actual financial costs or social costs such as prohibiting human activities in areas, and costs are commonly operationalized as the smallest total amount of area, with the implicit assumption that less area protected will be less objectionable to society (Ban and Klein, 2009). Site selection can also demand certain configuration requirements, such as the minimum size of areas, clustering, or site connectivity (Beger et al., 2010). In cases where prioritization tools select sites to meet multiple criteria (e.g., representation of different habitat types while minimizing costs or area protected), they also fall into the tradeoff analysis category described below as they are selecting a site or collection of sites to minimize tradeoffs.

Many of the same fundamental concepts and tools used to prioritize sites for protection can be used to identify and select locations for restoration. In fact, in many cases, spatial prioritization analyses that select areas that are a high priority for conservation do not specify what type of conservation action should take place in those areas (Groves and Game, 2016), and restoration may be critical when ecosystems have been degraded to the point where protection alone will not lead to recovery. There are a few key considerations when applying prioritization analysis to identifying sites for protection versus restoration. For one, in the case of restoration, sites are prioritized based on where the target conservation feature no longer exists or has been severely degraded, typically because of anthropogenic threats, as opposed to prioritizing sites that are often the least impacted locations (Yoshioka et al., 2014). This increases the importance of either historical data, for example to identify potential restoration sites based on differences between current and past distributions (Yoshioka et al., 2014), or predictive models such as species distribution models and HSMs (described above) that can be used to identify sites where restoration is likely to be successful. Costs may also need to be conceptualized differently, as minimizing the area to be restored may not be an objective. Costs can be assessed as the actual financial cost of the restoration project, the feasibility of the project, the cost of removing threats that might hinder restoration success, and the compatibility of other land or sea uses with the target habitat (Yoshioka et al., 2014). Lastly, because restoration projects are increasingly motivated by a desire to protect or enhance ecosystem services, ecosystem service outcomes will often need to be included among the objectives that are being maximized within the optimization algorithm. Again, this requires predictive models because restoration will provide services in new locations, but, as described above, there are spatial ecosystem service models that can be parameterized using hypothetical habitat distributions, such as the array of InVEST models (Sharp et al., 2016).

While it is less common to apply prioritization analyses explicitly to selecting priority restoration sites, particularly at larger spatial scales (Tobon et al., 2017), useful examples do exist (e.g., Crossman and Bryan, 2006; Adame et al., 2015; Vogler et al., 2015; Singh et al., 2019). Tobon et al. (2017) used a heuristic multi-criteria analysis to rank the priority of terrestrial sites for ecosystem restoration throughout Mexico based on the biological importance of sites, the restoration feasibility, and different weightings of the two objectives. Yoshioka et al. (2014) used Marxan to conduct what is known as a complementarity analysis, which assigns high priority to sites with more unrepresented features (in this case, sites that have lost endangered bird species) balanced by costs (in this case, restoration infeasibility measured as the levels of urbanization and farming), for Japan to identify priority restoration sites to benefit birds. There are also a growing number of examples that focus on ecosystem services as key outcomes. For example, Singh et al. (2019) used an optimization algorithm to prioritize locations for wetland restoration at a regional scale using an ecosystem service model of phosphorous retention and restoration costs. Adame et al. (2015), the only study in our literature review analysis that used spatial prioritization, selected priority areas for mangrove restoration in the Mexican Caribbean using Marxan. In this analysis, the authors examined scenarios where they fixed the percentage of area restored, and prioritized sites based on the expected provisioning of three ecosystem services (carbon storage, water depuration, coastal protection) and minimizing costs (assuming costs increase as a function of ecosystem degradation and inaccessibility). This study nicely demonstrates how spatial prioritization tools from conservation planning can be readily adapted to spatial planning for marine ecosystem restoration.

Tradeoff Analysis

Tradeoff analysis is an analytical tool for evaluating alternatives that could be quite useful in spatial planning and site selection for marine ecosystem restoration, although it has not been widely used in this context. The approach borrows from economic theory and multi-objective decision analysis, and provides an explicit and systematic assessment of tradeoffs, for example, among competing management objectives. In the context of spatial planning, where different planning options will have different outcomes for various management objectives, the goal is to identify which planning options best balance those objectives (i.e., maximize a joint objective) (Lester et al., 2013). Therefore, the outcome for each management objective from each possible spatial plan must be quantified, whether through empirical data, quantitative models, or conceptual models. For example, if the goal of a restoration project is to improve water quality and storm protection, and five candidate sites are under consideration, predictive spatial models of water quality and storm damage can be used to determine the outcome for these two objectives under each of the five restoration scenarios. Often the most intuitive way to assess the possible tradeoffs is to visualize them on a multidimensional graph, where the axes represent the objectives and each point corresponds to the outcomes from each spatial plan or restoration scenario. In some cases, there may be obvious win-win options where all objectives are high, and in other cases there will be clear tradeoffs, providing a starting point for a more explicit discussion about how those tradeoffs should be balanced (Lester et al., 2013).

The most useful application of tradeoff analysis assesses all (or many) of the theoretically possible restoration options. In the simple two objective case, the outer bound of all points (those further up and to the right on the graph) is the "efficiency frontier" comprised of "Pareto optimal options," to use the economics terminology, whereby one objective cannot be further increased without a loss to the other objective. All options on the frontier represent options that differently prioritize objectives across which there are unavoidable tradeoffs. Which option on the frontier is "best" depends on the relative preference for the objectives among society or decision-makers (Lester et al., 2013). The points interior to the frontier are poor options, assuming all of the important management objectives have been included in the tradeoff analysis, because at least one objective could be improved with no cost to the others. The analysis is easiest to visualize with only two objectives, but the logic applies to any number of dimensions. An analytically defined objective function can explicitly evaluate the response of different management objectives to different possible spatial plans, considering different weighting factors for each objective (as not all objectives may be equally important), and specify spatial plans that are on the frontier (e.g., Lester et al., 2018).

This approach has been applied to marine spatial planning and particularly the challenge of siting new ocean uses (White et al., 2012; Lester et al., 2018), and for evaluating tradeoffs in the context of implementing marine protected areas (Brown et al., 2001; Rassweiler et al., 2014), including using prioritization analyses as described above (e.g., Klein et al., 2013). There are also numerous examples of how this approach can be useful in land use planning for evaluating tradeoffs and identifying scenarios that would increase the provisioning of multiple ecosystem services (Polasky et al., 2008; Nelson et al., 2009; Goldstein et al., 2012), which is analogous to the goal of restoring marine habitats to improve ecosystem service outcomes. While there are some examples of tradeoff analysis being applied in the context of restoration (Zheng and Hobbs, 2013; Vogler et al., 2015; Martin et al., 2016; Singh et al., 2019), or for comparing the effects of different types of management actions including restoration (Needles et al., 2015), research that evaluates different site selection options for marine ecosystem restoration using this approach is rare or nonexistent. We argue this approach could be an important tool in spatial planning for restoration, particularly in making site selection decisions that account for spatial variation in restoration costs, likely restoration success, and ecosystem service outcomes. The major challenge with implementing such an approach is access to fine resolution spatial data and spatially explicit models that predict restoration success and ecosystem service delivery if the ecosystem is restored at different locations across the seascape. Nevertheless, when these data and models are available, tradeoff analysis could be used to improve restoration return on investment.

CONCLUSION AND WAYS FORWARD

Because of the high cost and importance of restoration for marine ecosystems, and the limited resources often available for such efforts, pursuing restoration projects that are effective and efficient is essential. Here we have provided a case for how restoration outcomes, particularly for ecosystem services, could be improved by applying spatial planning principles. Despite this strong rationale, our review of recently published (2015–2019) peer-reviewed papers on restoration for three high profile ecosystems (seagrass beds, salt marshes, and mangrove forests) reveals that site selection and spatial planning are rarely incorporated into restoration research. Those studies that do examine site selection or spatial planning for restoration focus most commonly on environmental conditions required for the restored habitat, and rarely include an explicit analysis of ecosystem service outcomes. However, because we focused on peer reviewed literature and did not include gray literature in our search, our results may not capture the current state of restoration practice and we acknowledge that there could be important differences between activities occurring as part of actual restoration efforts and scholarly research about restoration. Nevertheless, we expect that if spatial planning principles were commonly incorporated into restoration practice, these themes would appear more commonly in the scientific literature. Furthermore, their rarity in the literature highlights a missing avenue for their dissemination and adoption. Therefore, to try to facilitate a new wave of research and practice that fills this gap, we provide a conceptual overview of why and how to apply spatial planning principles to marine ecosystem restoration (**Figure 2**).

Accounting for spatial variation in expected restoration success, the supply and value of ecosystem services, and the cost of restoration projects has the potential to improve return on investment for restoration. While abundant spatial data exist in many cases, the challenge of connecting these data with decision-making may seem daunting or not worth the effort. We aim to dispel this concern by providing an overview of existing analytical tools available to support restoration site selection and spatial planning. These tools, which include GIS and spatial analysis, habitat suitability models (HSMs), ecosystem service models, spatial prioritization algorithms, and tradeoff analyses, have been applied extensively within conservation planning, and more recently, marine spatial planning. There are also examples of all of these approaches being applied to ecosystem restoration, although the scientific literature suggests that applications to coastal and marine ecosystems may still be rare.

The tools described in this paper can be applied for restoration planning at any spatial scale and resolution, and are limited mainly by the availability and quality of spatial data. Although these tools can be employed individually, multiple tools can also be integrated within a single restoration spatial planning analysis. For example, the output of a HSM that makes spatial predictions for restoration success – and thus can identify candidate areas for restoration – could be used within multiple ecosystem service models that predict outcomes if a habitat was restored in those areas. These ecosystem service predictions could then be visualized in a tradeoff analysis that plots different possible siting options for restoration. Alternatively, the ecosystem service predictions can serve as inputs to a prioritization algorithm that suggests the best sites for restoration.

We expect that as spatial planning approaches and principles are applied more frequently to marine ecosystem restoration, there will be improvements made to these tools that allow them to be more readily applied to future restoration projects. Further, as the field matures, more sophisticated planning approaches that account for climatic and other major directional changes will be imperative. As ecosystems move into states for which there is no historical analog, it will be useful to combine climate projections of environmental conditions (e.g., sea level rise, temperature, pH, etc.) and expected changes to human communities (e.g., population density, food insecurity, coastal vulnerability) with predictive models of habitat suitability and ecosystem services to facilitate planning for climate-robust restoration projects. Fortunately, climate model outputs are increasingly available at appropriate spatial resolutions to be integrated into these types of analyses (e.g., Assis et al., 2018). Looking forward, there could also be benefits of including cross-ecosystem connections into spatial planning analyses given that connectivity among adjacent ecosystems, including nutrient exchange, trophic connections, and impacts on physical conditions, can affect restoration success (Gillis et al., 2017). Many marine species use multiple habitat types, either during different life stages or for feeding and shelter over daily time scales, and therefore restoration should account for these linkages. This will require conducting analyses and making coordinated restoration decisions at landscape scales.

Although application of spatial planning tools has substantial potential to improve the probability of restoration success and resulting outcomes for ecosystem services, there are costs to the planning as well. These include the direct costs of doing the planning (salaries for analysts, costs of acquiring or collecting data, etc.), but also the implicit costs associated with a delay in the start of restoration. If a site selection process adds 6 months to the planning stage, this can be viewed as a loss of the ecosystem services that would otherwise have been provided by an earlier start to restoration activities. Analyses of whether formal site selection should be undertaken are vanishingly rare. While the costs of planning can be estimated, the benefits cannot be known until the analysis is undertaken. As a general rule, benefits are likely to be larger when candidate sites are spread across the landscape with relatively high variation either in environmental or social factors, a circumstance which could result from a large potential planning area, or from high local variation within a smaller area. However, even when variation is modest, the high cost of marine restoration projects means that even a small percentage improvement in outcomes is likely to dwarf the direct financial costs of planning, and if the restored habitat has a long expected lifetime, any delay in implementation should be easily outweighed by the improved long-term outcomes.

Marine ecosystem restoration will only become more important as we attempt to halt the degradation of nature and recover the ecosystem services society relies on. As the human population grows and climate change impacts increase, ecosystem restoration projects will increasingly require large scale and costly interventions. By investing some resources and time in strategic spatial planning, restoration can better recover ecosystem function and benefit human communities. Spatial planning can also provide a useful platform for improved outreach and education about restoration aimed at the general public, policy makers and funders, as spatial planning analyses can make important tradeoffs more explicit and can illustrate the benefits of more investment in restoration.

AUTHOR CONTRIBUTIONS

SL designed the research with input from all co-authors. AD, SL, and GH compiled and analyzed the data. SL, JM, AR, and GH wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00328/full#supplementary-material

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frontiers in Marine Science

SYSTEMATIC REVIEW
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Coming to Terms With Living Shorelines: A Scoping Review of Novel Restoration Strategies for Shoreline Protection

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In an era of rapid coastal population expansion and habitat degradation, restoration is becoming an increasingly important strategy for combating coastal habitat loss and maintaining ecosystem services. In particular, techniques that use habitat restoration alone or restoration in combination with built infrastructure to provide coastal protective services are growing in popularity. These novel approaches, often called living shorelines, have the potential to expand the reach and applicability of coastal restoration projects. To understand how living shorelines research has expanded over time, we conducted a scoping review of English-language peer-reviewed articles. We included papers that self-identified as living shorelines research, as well as studies that used other related terminology, to investigate trends in publication rates, geography, site characteristics, and outcomes measured. Using a systematic search protocol, we compiled a database of 46 papers; the earliest study was published in 1981, and the earliest study to use the term living shoreline was published in 2008. Eighty-three percent of studies were conducted in North America, followed by 11% in Asia, and 7% in Europe, but the use of the term living shoreline was almost exclusively restricted to North America. Saltmarshes, oyster reefs, mangroves, and freshwater vegetation were used in living shoreline designs, but 91% of studies also incorporated structural materials like oyster shell and rock. Most living shorelines research was conducted at sites that were <5 years old. The vast majority of studies exclusively reported on ecological outcomes (89%), and of those, ecological processes were measured in 74% of studies. Processes related to coastal protection were measured most frequently (52% of ecological studies), followed by biological interactions, water filtration, nutrient cycling, and carbon sequestration. Altogether, our data suggest that living shorelines research is on the rise, but there is a need for more long-term data, socio-economic research, further consensus on the terminology used to describe different types of projects, and research on the types of living shorelines that are most effective in different environmental contexts. Future long-term and interdisciplinary research will help to elucidate the full effects of living shorelines.

Keywords: natural infrastructure, nature-based solution, coastal protection, habitat degradation, ecosystem service, ecological engineering, hybrid infrastructure

INTRODUCTION

Coastal habitats provide ecologically and economically important ecosystem services—they protect shorelines, cycle nutrients, support fisheries, promote tourism, and sequester carbon (Barbier et al., 2011; Mcleod et al., 2011; Scyphers et al., 2011; Silliman et al., 2019). These habitats and associated services, however, are under threat from a variety of human impacts including climate change (Hoegh-Guldberg and Bruno, 2010; He and Silliman, 2019), urbanization (Bertness et al., 2004), land reclamation for aquaculture and development (Lee et al., 2006), and overexploitation of key species (Coleman and Williams, 2002). In the two decades between 1980 and the turn of the century, 35% of mangroves were lost worldwide and mangrove cover is projected to continue declining (Valiela et al., 2001). Similarly, human impacts destroyed 67% of wetlands in 12 major estuaries across Europe, Australia, and the United States (Lotze et al., 2006). Finally, in the most extreme ecosystem-specific case, 85% of historic oyster reefs have been lost and many remaining reefs are in poor condition (Beck et al., 2011). In response to these widespread declines, conservation practitioners are turning to restoration in an effort to slow and potentially reverse coastal ecosystem loss.

The number of scientific articles published annually on coastal restoration has increased dramatically in recent years (Zhang et al., 2018), and diverse restoration projects are being implemented worldwide (Bayraktarov et al., 2016). The original intent of restoration was to return an ecosystem to a close approximation of its original condition (NRC, 1992), but this may not be widely feasible going forward because of climate change, widespread human impacts, conflicting uses, and ecosystems that have been forced into alternate stable states (Hobbs and Norton, 1996). As such, the field of ecological engineering has emerged over recent decades with the goal of sustainably restoring habitats in a way that benefits both humans and the environment, especially in areas that are experiencing ongoing human pressure (Mitsch, 2012). In particular, there is rising interest in ecological engineering alternatives for traditional coastal protection infrastructure (Cheong et al., 2013; Sutton-Grier et al., 2015).

The proliferation of coastal defense structures is likely as coastal populations grow and hazards intensify (Scyphers et al., 2011; Hinkel et al., 2014); however, common coastal armoring strategies (e.g., seawalls, revetments, groins) can drive habitat loss (Titus, 1998), lower floral and faunal biodiversity (Gittman et al., 2016a), and depress socio-economic resilience by requiring frequent and expensive maintenance (Smith et al., 2017, 2018). Accordingly, ecosystem-friendly alternatives to traditional coastal defense structures are becoming more prevalent in areas where maintaining a natural shoreline is not possible. These techniques rely on some combination of natural or living materials and built infrastructure; they can meet a socio-economic need, by providing enhanced shoreline protection, and they can also expand the reach of restoration projects into urbanized areas. The terminology used to refer to these projects is diverse and includes (but is not limited to): natural and nature-based infrastructure (Sutton-Grier et al., 2018), nature-based solutions (Nesshöver et al., 2017), hybrid infrastructure (Sutton-Grier et al., 2015), ecosystem-based coastal defense (Temmerman et al., 2013), soft ecological engineering (Strain et al., 2019), and living shorelines. Non-standardized terminology can cause miscommunication and lead to flawed or reduced information sharing among scientists, practitioners, managers, and coastal residents (Bilkovic et al., 2017).

The term "living shoreline" is quickly becoming one of the primary terminologies used by practitioners, management agencies, and policy makers in the USA to refer to novel restoration projects for shoreline protection (e.g., Maryland's Living Shorelines Protection Act of 2008, the United States Army Corps of Engineers Nationwide Permit for Living Shorelines, and the Living Shorelines Act of 2019). The term living shoreline is not consistently defined, but generally refers to a suite of shoreline protection schemes that incorporate habitat restoration alone or in combination with some type of built infrastructure to provide coastal protective services to humans (NOAA, 2015). Living shoreline designs are often categorized along a green to gray spectrum, spanning from vegetative plantings for coastal protection on the green end to habitat restoration in conjunction with structural materials on the gray end (**Figure 1**). Living shorelines are touted for their potential to provide triple-bottom line returns (i.e., ecological, social, and economic benefits) by enhancing coastal habitat function (Currin et al., 2008; Davis et al., 2015; Gittman et al., 2016b) and increasing community resilience to storms (Manis et al., 2015; Smith et al., 2018), while requiring less maintenance and fewer repairs than traditional coastal armoring infrastructure (Smith et al., 2017, 2018). States within the USA have instituted local-level policies to encourage the installation of living shorelines, and on a national level, the US House of Representatives passed the Living Shorelines Act of 2019 to assist local and state governments and non-profits with living shoreline creation.[1] High-level interest in living shorelines may indicate an increased appreciation for the services that coastal habitats provide, but there are still unknowns related to the design and functionality of living shorelines in different environments. To increase the likelihood that living shorelines are successful at protecting coastal property and infrastructure, as well as delivering other ecosystem services, we need to ensure that restoration practice is based on the most up-to-date science and that the services most desired by coastal residents are being measured. Unfortunately, restoration practice is often based on anecdotal information rather than the systematic review of existing evidence (Pullin et al., 2004). For example, in a survey of managers of one of the most highly-protected wetlands in England, Sutherland et al. (2004) found that 77% of management actions were based on personal experience and only 2% were based on primary scientific literature. This is problematic, as common practices and assumptions based on personal experience are not always supported (Pullin and Knight, 2001).

To ensure that limited research and restoration funds for living shorelines are optimally allocated, and to reduce duplication of research efforts as well as information gaps, we

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[1] Living Shorelines Act of 2019 (2019). U.S. House of Representatives.

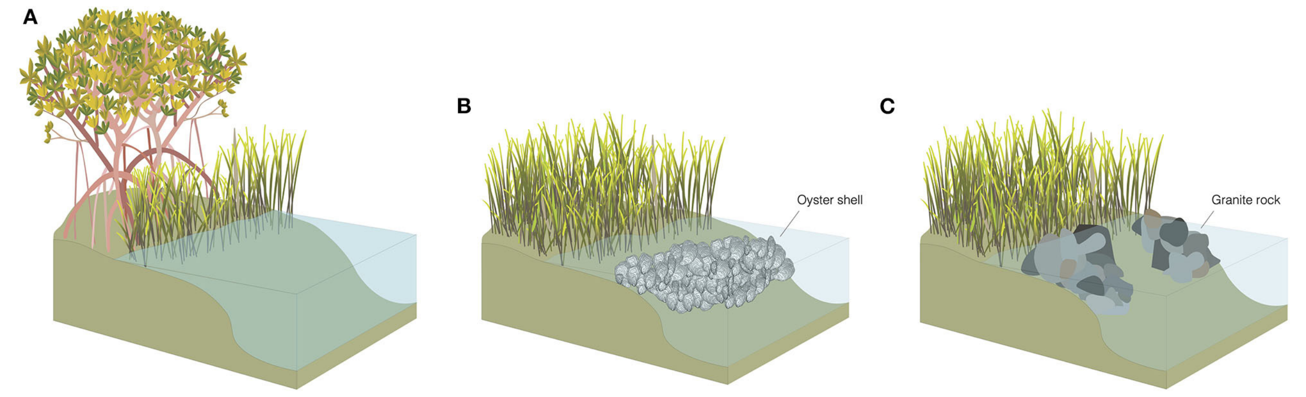

FIGURE 1 | Living shoreline spectrum illustrating three broad categories of living shorelines, including **(A)** vegetation plantings only, **(B)** restoration with soft materials (e.g., oyster shell, coir fiber), and **(C)** restoration with hard materials (e.g., granite rock, marl, concrete).

need a better understanding of which living shoreline practices and impacts are backed by scientific studies. The overarching goals of this scoping review were to: (1) characterize the English-language living shorelines literature; and, (2) identify research gaps and areas of concentrated research. In particular, we were interested in the following questions: (i) where has living shorelines research been conducted?; (ii) which types of living shorelines have been studied?; (iii) what is the disciplinary scope of the research that has been conducted and which outcomes have been measured?; and, (iv) what other terms are commonly used to refer to living shoreline projects?

METHODS

Literature Search

A challenge for reviewing living shorelines research is that the term itself is relatively new and is often used synonymously with other terminology. To fully characterize the field, we included papers that self-identified as living shorelines research (i.e., included the term in the text of the paper) as well as research that used alternate terminology, but that met our criteria for inclusion. We performed a preliminary search of the term "living shoreline" in Scopus and Web of Science to identify other terminology commonly used to refer to living shoreline projects. Synonyms identified during this search, along with terms compiled by the authors and terms suggested by external experts, were used to formulate the final search string.

We systematically searched Web of Science and Scopus in October 2019, using the search string: ("living shoreline*" OR "bioengineer* hybrid technique*" OR "blue engineering" OR "blue infrastructure*" OR "build* with nature*" OR "created wetland*" OR "eco engineering" OR "ecosystem friendly engineering" OR "engineer* with nature" OR "green engineering" OR "green infrastructure*" OR "hybrid infrastructure*" OR "hybrid restoration technique*" OR "hybrid shoreline*" OR "hybrid stabilization*" OR "hybrid technique*" OR "natural infrastructure*" OR "nature based coastal management" OR "nature based feature*" OR "nature based infrastructure*" OR "nature based protection" OR "nature based saltmarsh restoration" OR "nature based shoreline*" OR "nature based solution*" OR "nature friendly bank protection*" OR "riprap mangrove habitat*" OR "soft engineering" OR "soft shoreline*" OR "soft stabilization*" OR "stabilized salt marsh*" OR "sill*") AND ("shoreline*"). Additionally, we used a snowball approach and searched the bibliographies of the papers included from the database search and the bibliographies of several relevant literature reviews (Bilkovic et al., 2016; Gittman et al., 2016a; Dugan et al., 2018; Morris et al., 2018, 2019; Mitchell and Bilkovic, 2019). A full diagram of the search flow can be found in **Figure 2** (Moher et al., 2009).

To be included in our database, all papers had to be English-language, peer-reviewed (no government reports, theses, etc.), and primary literature (no syntheses, conceptual papers, etc.). Additionally, each study had to include a physical living shoreline intervention (though it did not need to specifically be called a living shoreline) that: (1) included the restoration of a biogenic shoreline habitat; (2) mentioned that erosion control, sediment stabilization, or shoreline protection was a motivation for the project (or studied the same sites as another paper that mentioned that erosion control, sediment stabilization, or shoreline protection were project motivations); and, (3) maintained the land/water continuum (Bilkovic et al., 2017). Requiring a physical living shoreline intervention likely excluded some social and economic analyses from our database, but it was impossible to evaluate whether a project contained an appropriate living shoreline intervention when there were no project descriptions. We also excluded beach restoration projects from this synthesis, though they are sometimes considered living shorelines (Bilkovic et al., 2016, 2017), as living shorelines tend to be best suited for low to moderate- energy areas (United States Army Corps of Engineers, 2016), and beach-front projects are often subject to a different set of management and permitting regulations. Finally, the coastal protective services and ecosystem benefits of natural habitats as compared to hardened shorelines have been thoroughly reviewed elsewhere (Gittman et al., 2016a), and accordingly we focus on living shorelines where habitats were being actively restored. Going forward, all studies are referred to as living shorelines research, regardless of whether that term explicitly appeared in the text of the paper.

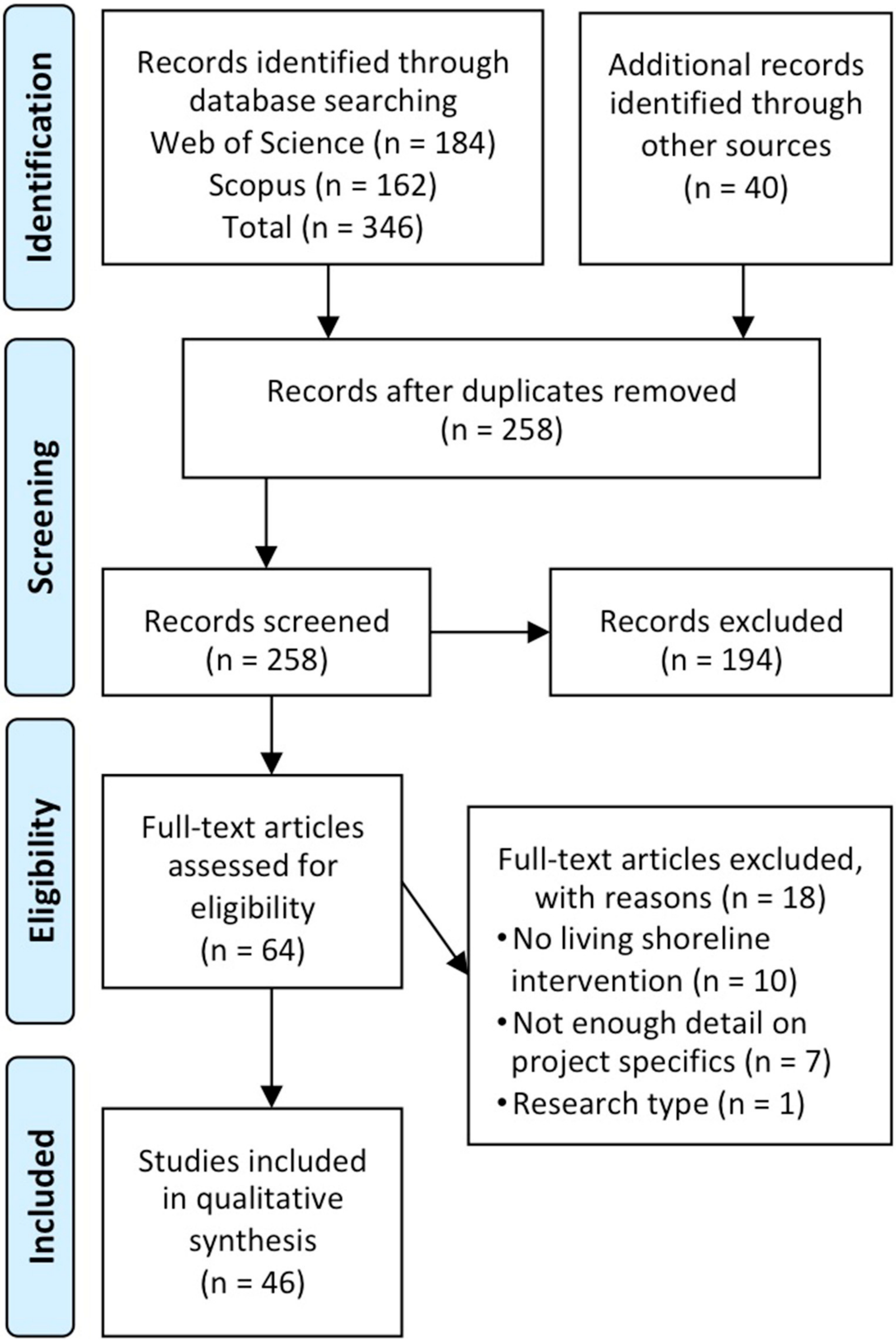

FIGURE 2 | PRISMA flow diagram for article selection.

Data Extraction

To ensure consistency, two independent reviewers conducted abstract screening and full-text data extraction. From each included study, we extracted bibliographic details (i.e., journal name, date of publication, and author affiliations), project descriptions (i.e., location, habitats restored, age, materials included in project design), metrics of study design (i.e., study type and comparators), and measured outcomes. Additionally, we noted whether or not the term "living shoreline" was included in the text of each paper and any relevant synonyms used to refer to the projects. When project age was reported, we recorded the age of each project at the time of the final sampling event; for papers looking at multiple projects, we report on the oldest living shoreline included in each study. For projects that had more than one type of non-living material incorporated into their designs (e.g., a rock breakwater in combination with coir logs) we categorized the project based on the grayest component of the design (e.g., rock). To characterize project outcomes, we first noted whether papers were reporting ecological or socio-economic outcomes. We further categorized ecological outcomes as focusing on foundation species structure (e.g., density, biomass, percent cover of the foundation species being restored), diversity and community abundance (i.e., community level metrics), and/or ecosystem processes (*sensu* Wortley et al., 2013). To evaluate the different terminology used to refer to living shoreline projects, we extracted synonyms from the title and abstract of each paper. We were interested in high-level terminology that could be applied to most living shoreline projects, thus we only included non-habitat specific synonyms (e.g., "restored oyster reef" and "stabilized saltmarsh" were not included). When an individual paper used the same word in multiple synonyms (e.g., "hybrid stabilization" and "hybrid shoreline protection"), the repeated word was only counted once in the frequency plot. The experimental unit for this synthesis is the individual paper rather than each living shoreline project, as multiple papers may have reported on the same project. All data are presented descriptively.

RESULTS

Our final database included 46 studies (**Table 1**). The earliest study was published in 1981 and the earliest study that included the term living shoreline was published in 2008 (i.e., Currin et al., 2008). The number of papers increased dramatically over time. Overall, 57% of studies included the term living shoreline (**Figure 3A**). Fifty-nine percent of studies had authors affiliated with only one sector (i.e., academic, governmental, non-governmental, or other/unknown), 35% had authors that were affiliated with two sectors, and 6% had authors affiliated with three sectors. Academic affiliations were the most common (87% of papers), followed by governmental (43%), non-governmental (9%), and other or unknown (9%) (**Figure 3B**). Fifteen percent of all 1st authors had cross-sector affiliations; 83% of 1st authors were affiliated with academic institutions, followed by 24% affiliated with governmental organizations, 4% with non-governmental organizations, and 4% with other types of organizations. Sixty-one percent of studies used a field survey approach (e.g., observational studies), followed by field experiments (33%), modeling (4%), stakeholder interviews (4%), and lab experiments (2%) (**Figure 3C**); two studies used multiple approaches. Fifteen percent of studies had no comparator and 35% of studies had multiple comparators. Eighty-three percent of studies included a reference (natural or degraded) shoreline as a comparator, 20% compared to a hardened shoreline, 13% compared among different types of living shorelines, and 9% used another type of comparator (such as before-after or space-for-time design) (**Figure 3D**). The studies were published in 26 different journals, with *Ecological Engineering* ($n = 7$) and *Estuaries and Coasts* ($n = 5$) being the most frequent (**Table 1**). Thirty percent of all studies were open access.

Studies were heavily concentrated in North America ($n = 38$), followed by Asia ($n = 5$), and Europe ($n = 3$), with no studies included from other continents. The term living shoreline was used in the majority of North American studies (66%), only used in one European study, and not used in any studies in Asia (**Figure 4A**). Within the continental United States, we found examples of living shorelines research in all Gulf States, most Atlantic coast states, and only one Pacific coast state, California. North Carolina had the highest number of studies ($n = 14$), followed by Florida ($n = 7$), Louisiana ($n = 6$), Maryland ($n = 5$), Virginia ($n = 5$), and Alabama ($n = 4$) (**Figure 4B**).

Forty-five of the 46 articles in our database investigated living shorelines that were built in the field and one study built living shorelines in a laboratory setting (Manis et al., 2015). Of the 45 field studies, 27% reported on a single living shoreline site and 78% included five or fewer living shoreline sites. Of the field studies that provided information about the age of any of the structures sampled ($n = 41$), 56% of the oldest structures sampled were younger than 5 years old and 76% were younger than 10 years old (**Figure 5A**). Four studies included sites that were more than 25 years old, and the oldest project was 52 years old (i.e., Knutson et al., 1981). Four of the 46 studies included living shorelines where different habitats were being restored at different sites. Thirty-five percent of papers included a site where saltmarsh was the only habitat restored, vs. 30% for oysters, 11% for mangroves, and 4% for freshwater vegetation. Twenty-two percent of articles included sites where saltmarsh and oysters were restored together vs. 0% for saltmarsh and mangroves, 2% for oysters and mangroves, and 4% for all three habitats (**Figure 5B**). Only 13% of studies included living shoreline sites/designs where only vegetation was planted, whereas 91% of studies included sites that used soft or hard structural materials in addition to habitat restoration. Nine of the 46 studies investigated more than one living shoreline design (e.g., one site had a rock sill and another site had an oyster sill). Forty-eight percent of studies investigated sites that used shell, including loose shell, bagged shell, shell mats, and shell in gabion boxes. Only 4% of studies used coir logs as the only structural component. Nine percent of studies looked at sites with wooden breakwaters, 13% with concrete structures (e.g., oyster castles), and 33% investigated sites with rock materials (**Figure 5C**).

Most studies in our database reported on purely ecological outcomes (89%), with few studies reporting on socio-economic outcomes (**Figure 6A**). Within the ecological studies, foundation species structure was often measured (61% of studies) but rarely as the only metric (5%). Diversity and community abundance metrics were also often measured (49% of studies), but rarely on their own (12%). Of the 21 studies that measured diversity and community assemblage metrics, 24% only measured floral diversity, 62% only measured faunal diversity, and 14% measured both. Twelve of the 16 faunal studies measured diversity and

TABLE 1 | Bibliographic information for included studies with location of study, habitats restored, and synonyms used to describe projects.

No.	References	Journal	Country	Habitat type(s)	Synonyms	LS?
1	Chowdhury et al. (2019)	*Scientific Reports*	Bangladesh	Oyster reef	Nature-based solution	
2	Kibler et al. (2019)	*Sustainability*	USA	Saltmarsh; Oyster reef; Mangrove		✓
3	Wiberg et al. (2019)	*Estuaries and Coasts*	USA	Oyster reef		
4	Davenport et al. (2018)	*Estuaries and Coasts*	USA	Saltmarsh		✓
5	Herbert et al. (2018)	*Sustainability*	USA	Oyster reef		✓
6	Josephs and Humphries (2018)	*Journal of Environmental Management*	USA	Saltmarsh	Nature-based coastal management	✓
7	Onorevole et al. (2018)	*Ecological Engineering*	USA	Saltmarsh; Oyster reef	Nature-based solution	✓
8	Palinkas et al. (2018)	*Estuaries and Coasts*	USA	Saltmarsh		✓
9	Polk and Eulie (2018)	*Estuaries and Coasts*	USA	Saltmarsh; Oyster reef		✓
10	Smith et al. (2018)	*Ecological Applications*	USA	Saltmarsh, Oyster reef	Nature-based solution; rock sill	✓
11	Donnelly et al. (2017)	*Hydrobiologia*	USA	Saltmarsh; Oyster reef; Mangrove		✓
12	Balouskus and Targett (2016)	*Transactions of the American Fisheries Society*	USA	Saltmarsh	Riprap-sill	✓
13	Gittman et al. (2016b)	*Ecological Applications*	USA	Saltmarsh; Oyster reef		✓
14	Sharma et al. (2016)	*Ecological Engineering*	USA	Saltmarsh; Oyster reef	Hybrid shoreline stabilization; bioengineering hybrid technique; hybrid restoration technique	✓
15	Walles et al. (2016)	*Journal of Sea Research*	Netherlands	Oyster reef		
16	Casas et al. (2015)	*Marine Ecology Progress Series*	USA	Oyster reef		
17	Davis et al. (2015)	*PLoS ONE*	USA	Saltmarsh; Oyster reef	Natural infrastructure; hybrid infrastructure	✓
18	De Roo and Troch (2015)	*River Research and Applications*	Belgium	Freshwater vegetation	Nature-friendly bank protection	✓
19	Humphries and La Peyre (2015)	*PeerJ*	USA	Oyster reef		✓
20	Kochnower et al. (2015)	*Ocean and Coastal Management*	USA	Saltmarsh	Natural infrastructure	✓
21	La Peyre et al. (2015)	*PeerJ*	USA	Oyster reef	Sustainable shoreline protection	✓
22	Manis et al. (2015)	*Journal of Coastal Conservation*	USA	Saltmarsh; Oyster reef		✓
23	Milbrandt et al. (2015)	*Ecological Engineering*	USA	Oyster reef; Mangrove	Multiple habitat restoration strategy	
24	Peters et al. (2015)	*Bulletin of Marine Science*	USA	Mangrove		✓
25	Scyphers et al. (2015b)	*Environmental Management*	USA	Oyster reef	Submerged breakwater	✓
26	Van Cuong et al. (2015)	*Ecological Engineering*	Vietnam	Mangrove	Soft coastal engineering	
27	Gittman et al. (2014)	*Ocean and Coastal Management*	USA	Saltmarsh	Alternative shoreline protection approach	
28	La Peyre et al. (2014)	*Ecological Engineering*	USA	Oyster reef		
29	Lawless and Seitz (2014)	*Journal of Experimental Marine Biology and Ecology*	USA	Oyster reef		✓
30	Motamedi et al. (2014)	*The Scientific World Journal*	Malaysia	Mangrove	Ecofriendly coastal protection scheme	
31	Bilkovic and Mitchell (2013)	*Ecological Engineering*	USA	Saltmarsh	Hybrid stabilization	✓
32	De Roo and Troch (2013)	*Journal of Waterway, Port, Coastal, and Ocean Engineering*	Belgium	Freshwater vegetation	Environmentally friendly bank protection	
33	Moody et al. (2013)	*Marine Ecology Progress Series*	USA	Oyster reef		✓

(Continued)

TABLE 1 | Continued

No.	References	Journal	Country	Habitat type(s)	Synonyms	LS?
34	Balouskus and Targett (2012)	*Estuaries and Coasts*	USA	Saltmarsh	Riprap-sill	
35	Naohiro et al. (2012)	*International Journal of Ecology*	Thailand	Mangrove		
36	Kamali and Hashim (2011)	*Ecological Engineering*	Malaysia	Mangrove		
37	O'Connor et al. (2011)	*Wetlands Ecology and Management*	USA	Saltmarsh	Sill	✓
38	Scyphers et al. (2011)	*PLoS ONE*	USA	Oyster reef	Natural breakwater	✓
39	Stricklin et al. (2010)	*Gulf and Caribbean Research*	USA	Oyster reef		
40	Currin et al. (2008)	*Wetlands Ecology and Management*	USA	Saltmarsh		✓
41	Piazza et al. (2005)	*Restoration Ecology*	USA	Oyster reef	Sustainable shoreline protection strategy	
42	Meyer and Townsend (2000)	*Estuaries*	USA	Saltmarsh; Oyster reef	Habitat creation technique	
43	Meyer et al. (1997)	*Restoration Ecology*	USA	Saltmarsh; Oyster reef		
44	Broome et al. (1986)	*Estuaries*	USA	Saltmarsh		
45	Benner et al. (1982)	*Wetlands*	USA	Saltmarsh	Vegetative erosion control	
46	Knutson et al. (1981)	*Wetlands*	USA	Saltmarsh	Vegetative stabilization	

LS, indicates whether the term living shoreline was included in the full-text of the paper.

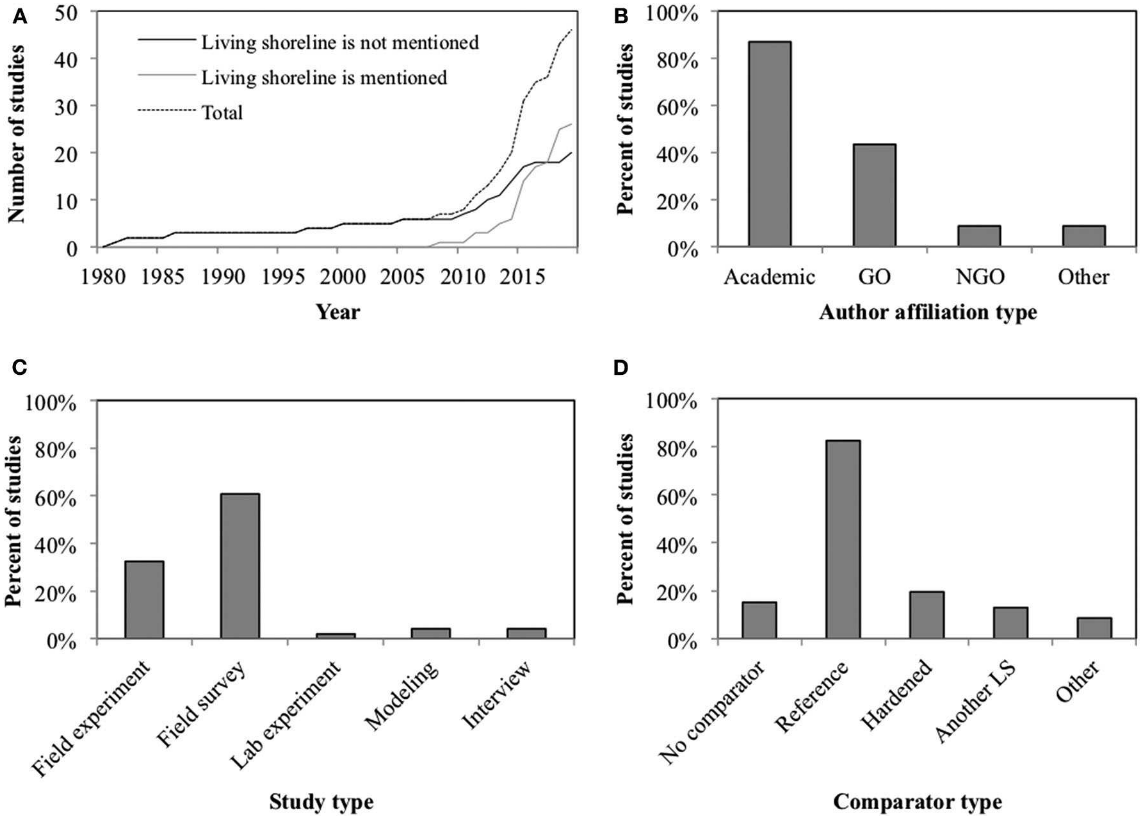

FIGURE 3 | Bibliographic information from studies, including **(A)** number of studies published over time, **(B)** author affiliations, **(C)** study type, and **(D)** comparator types. The bars in figures **(B–D)** do not add up to 100% as some studies had multiple author affiliations, study types, and comparators.

abundance within invertebrate and vertebrate communities, and the remaining four studies only measured within the invertebrate community. Ecological processes were the most common outcomes measured, with 74% of studies reporting on an ecosystem process (**Figure 6B**). More than half of all ecological studies (52%) measured a process related to the

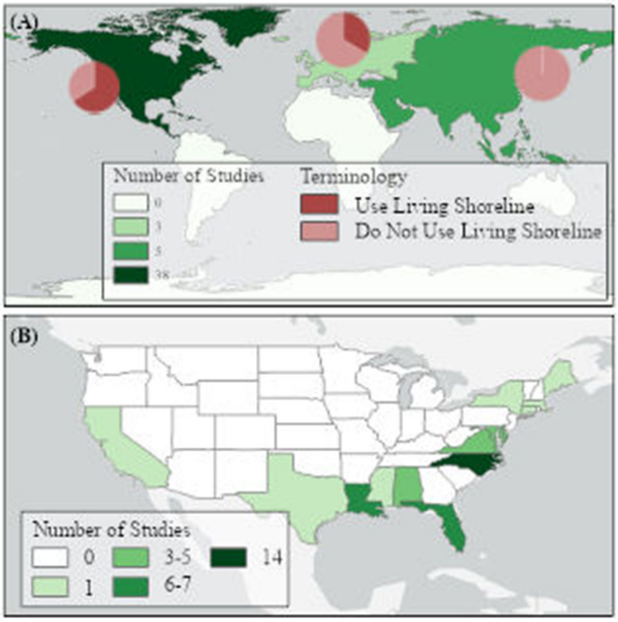

FIGURE 4 | Map of study distributions **(A)** globally and **(B)** in the continental United States. The global distribution indicates the number of studies from each continent and the proportion of studies within each continent that included the term living shoreline. Studies that included sites from multiple states count toward the total of each state.

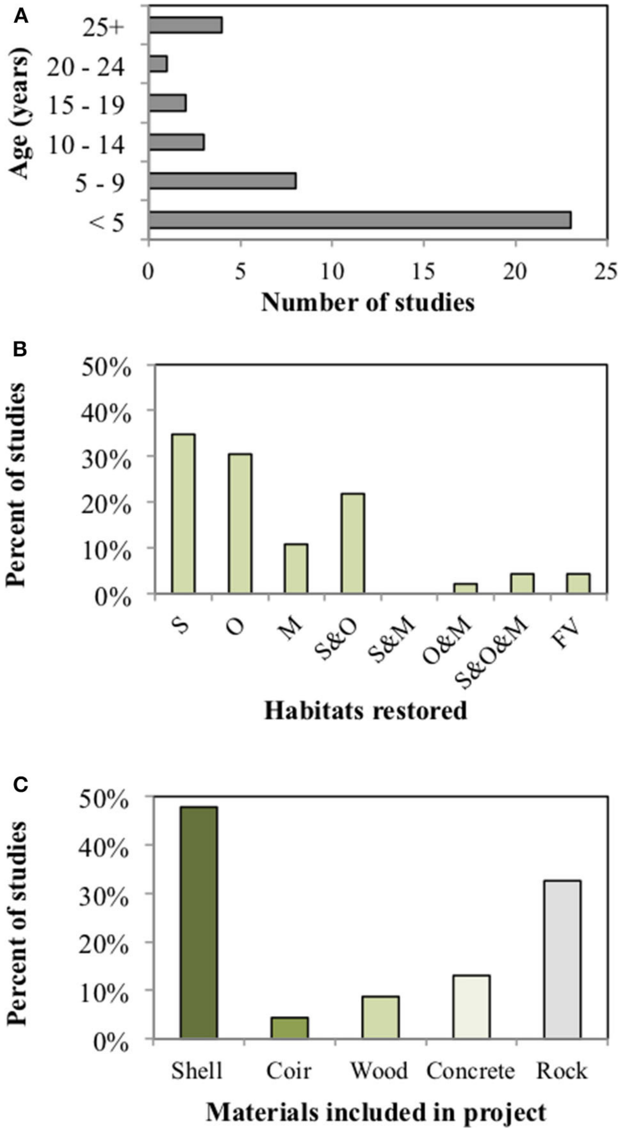

FIGURE 5 | Living shoreline project characteristics, including **(A)** maximum age of living shoreline projects when they were sampled, **(B)** habitat types restored within a single living shoreline site, and **(C)** materials used within a single living shoreline site. When there were multiple living shorelines in a single study, we report on the oldest living shoreline at the time of the last data collection. For **(B,C)**, the bars do not add up to 100% as some articles investigated multiple types of living shorelines. In **(B)**, S, saltmarsh; O, oyster; M, mangroves; FV, freshwater vegetation; & indicates that the habitats were restored together within a single site.

coastal protection services of living shorelines (i.e., sediment stabilization, wave attenuation). Other measured ecosystem processes were biological interactions ($n = 9$), water filtration ($n = 3$), nutrient cycling ($n = 1$), and carbon storage ($n = 1$) (**Supplementary Material**).

The terminology used to refer to living shoreline projects was extremely diverse (**Table 1**). The most common words used in living shoreline synonyms were protection, nature, sill, based, and shoreline (**Figure 7**).

DISCUSSION

The number of living shorelines papers increased substantially over time, as did the proportion of studies specifically using the term living shoreline. This supports the idea that living shorelines are gaining momentum as a practice and research topic. Further, the term living shoreline has become a primary term used by the research community to refer to restoration projects that have a principal goal of providing coastal protective services. Interest in living shorelines has similarly increased within the practitioner and policy realm in the United States. For example, Restore America's Estuaries, a conservation non-profit, maintains a living shorelines community of practice, through which practitioners and managers can network, access training modules, and view relevant webinars on the most up-to-date research. Since its creation in 2016, this community of practice has grown 4-fold, with training modules and the companion website experiencing steady and constant traffic (*personal communication* H. Stevens). Moreover, the recent passage of the Living Shorelines Act of 2019 within the US House of Representatives as well as a 2017 Nationwide Permit for the construction of living shorelines (United States Army Corps of Engineers, 2016), illustrate high-level interest in the promotion and construction of living shorelines. Nevertheless, for living shorelines to scale to a meaningful level, enthusiasm needs to be met by interdisciplinary evaluations of efficacy in different contexts.

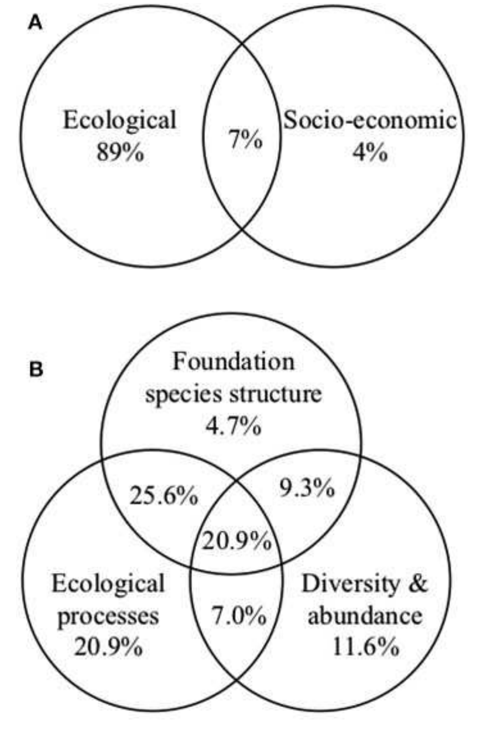

FIGURE 6 | Venn diagrams showing **(A)** the percentage of papers that reported ecological and socio-economic outcomes, and **(B)** the percentage of ecological papers that reported outcomes related to foundation species structure, diversity and community assemblage, and/or ecosystem processes and functions.

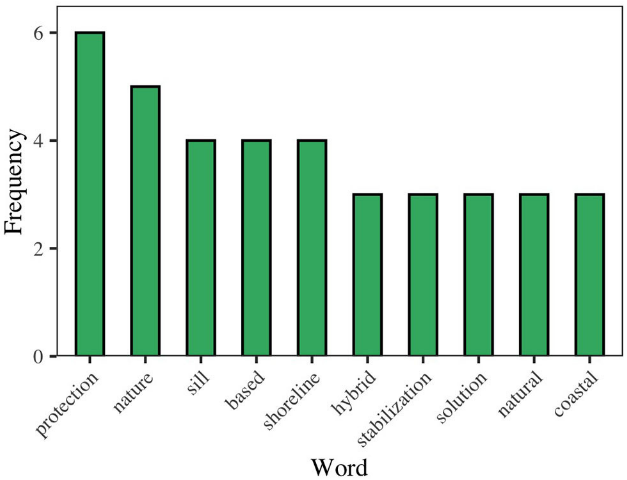

FIGURE 7 | Bar graph showing the 10 most common words used in synonyms to describe living shoreline projects (all other words were used fewer than three times). Frequency also corresponds to the number of papers that used each word in at least one synonym.

Our results show that the vast majority of living shoreline studies had an ecological focus, with very few papers reporting socio-economic outcomes. These results are congruent with similar studies looking at habitat restoration in terrestrial (Wortley et al., 2013) and marine biomes (Bayraktarov et al., 2019). Historically, restoration was aimed at replacing habitat that had been lost in order to restore ecological structure and function (NRC, 1992). These relatively narrow objectives and outcomes could be stated and measured by ecologists; now, however, there is increasing investment in restoration with broadened objectives that include maximizing the delivery of ecosystem services. As the breadth of desired restoration outcomes has expanded well beyond what can be measured by ecologists alone, so too must our assessments of these projects expand to include social and economic metrics (Eden and Tunstall, 2006; Martin, 2017). Living shorelines are fairly unusual because they have a high potential for private investment, as they provide an alternative to hardened shorelines that homeowners and municipalities are already accustomed to paying for (Sutton-Grier et al., 2018). As such, a deeper understanding of why and in which types of communities living shorelines are being built could help to elucidate the factors that influence their social acceptability and implementation.

Nearly three quarters of the ecological studies in our database measured a process, rather than exclusively reporting on foundation species structure or diversity. In contrast, similar reviews of terrestrial restoration projects reported that ecosystem processes were measured less frequently than diversity metrics (Ruiz-Jaen and Aide, 2005; Wortley et al., 2013); the authors attributed these findings to the time and cost required to take multiple measurements over time rather than a one-time measurement of diversity or ecosystem structure. Unlike traditional restoration projects, living shorelines are designed and promoted as restoration techniques that provide explicit services to humans, namely coastal protection. This reflects a growing trend involving a shift away from the restoration of an ecosystem and toward the restoration of ecosystem services (Palmer et al., 2014). To measure an ecosystem service, it is necessary to measure whether the underlying process has been restored, which may explain why the studies in our database focused heavily on processes. Moreover, waterfront property owners in the United States prioritize effectiveness over all other attributes when choosing how to stabilize their shorelines (Scyphers et al., 2015a; Smith et al., 2017); appropriately, >50% of all ecological studies in our database investigated a process related to the coastal protective services of living shorelines.

Living shoreline studies were heavily concentrated in the United States, with no studies from the Southern Hemisphere. At a global level, many of the most at-risk geographic regions have seen little research regarding living shorelines. For example, Asia is home to eight of the top ten countries with the largest populations in low-elevation coastal zones (McGranahan et al., 2007), yet only five of the living shoreline studies in our database took place in Asia. This finding may be due in part to: (1) an English-language publication bias; (2) fewer research institutions and lower funding in other countries; or, (3) different terminology than what was included in our search terms. Regardless, more studies from diverse locations could expand our understanding of which techniques and habitats can successfully be incorporated into coastal defense plans at a global scale. Within the continental United States, the largest concentration of research was in North Carolina. It can take time for new technology to gain momentum and familiarity among users, practitioners, and managers; thus, it is probably not coincidental that the earliest study in our database and the earliest study to use the term living shoreline were both conducted in North Carolina. Moreover, North Carolina was one of the earliest states in the country to issue a general permit for living shorelines (i.e., the General Permit for the Construction of Marsh Sills in 2005), which streamlined the process for constructing projects. As information about living shorelines continues to disseminate and management and policy avenues improve, we are likely to see an increase in research on a global scale. Nevertheless, the amount of primary research may not correlate with the prevalence of actual living shoreline projects. For example, while North Carolina has been a leader in peer-reviewed living shorelines research, according to our database, it is likely that there are fewer living shorelines projects in North Carolina vs. other areas (RAE's Living Shorelines Academy). Furthermore, North Carolina has certainly lagged behind on understanding and acknowledging the negative ecological effects of shoreline hardening relative to other areas, such as the Chesapeake Bay (see Seitz et al., 2006; Bilkovic and Roggero, 2008; Patrick et al., 2016 for a few examples), which has policies specifically identifying living shorelines as a preferable alternative to hardened shorelines (i.e., the Living Shorelines Protection Act of 2008). Further research into the distribution and characteristics of living shoreline projects themselves would be useful for characterizing the socio-ecological factors that influence their construction.

Currently, in the United States, the relative difficulty of completing the permitting necessary for installation of a living shoreline, as opposed to conventional shoreline protection structures (e.g., bulkheads), incentivizes construction of the latter. This differential burden stems partly from a desire by permitting agencies, and therefore property owners, to avoid projects that might encroach into public waters (National Research Council, 2007) or that have unknown or unproven effects. Research has been conducted on the ecological effects of shoreline hardening more broadly (Gittman et al., 2016a), but studies focused on the alternatives when maintaining a natural shoreline is not possible have lagged behind. Thus, a hurdle for the adoption of living shorelines as opposed to artificial protection is evaluation of the relative efficacy of both (Morris et al., 2018). While coastal protective services in general were well studied, only 20% of the studies in our database directly compared living shorelines to hardened shorelines. If living shorelines are to become a feasible alternative to hardened shorelines, we need research not only demonstrating that they actually work at stabilizing sediments, attenuating waves, and protecting property, but also demonstrating that they are as effective or more effective than the status quo (i.e., traditional engineering approaches). Furthermore, research on the relative costs of different living shoreline interventions is extremely limited (Gittman and Scyphers, 2017), though there is promising data from the wider field of nature-based infrastructure (Narayan et al., 2016). One significant advantage that living shorelines have over hardened shorelines is the potential to self-repair and adapt over time without continued human intervention. While this potential is promising, the majority of the projects in our database were young (<5 years old) at the time of sampling and only provided a short-term snapshot of performance. Many ecosystem services require time to fully develop after restoration (La Peyre et al., 2014; Manis et al., 2015; Gittman et al., 2016b) and therefore long-term monitoring data will be critical to fully evaluate the functionality of living shorelines, particularly in the context of rising sea levels.

Given sustained interest in living shorelines among researchers, practitioners, and policy makers, the need for common terminology is particularly pressing. The terminology used to refer to living shorelines in this study was extremely diverse; even the same authors used different terms to refer to the same projects (see De Roo and Troch, 2013, 2015; Gittman et al., 2014, 2016b). This could be because some papers pre-date the common use of the term living shoreline or it could reflect the fact that different terminology is used to appeal to different audiences (e.g., the term living shoreline is often used by non-governmental organizations, whereas the term marsh sill is commonly used by permitting agencies in the United States). Regardless, lack of a shared definition may hinder efforts to incorporate living shorelines into large-scale coastal initiatives and policies (such as those described by Sutton-Grier et al., 2015). A secondary challenge associated with terminology is that living shorelines come in a variety of different forms, each of which may be associated with different terminology. For example, studies in our database used four different habitat types, alone and in combination, and 90% of papers included sites that also had structural components, ranging from shell and natural fibers to eco-concrete and rock. Standardized terminology is essential to future performance and dissemination of living shorelines research and therefore, implementation. Though a shared definition would not be a panacea, providing a unifying description of living shorelines to local and national policy makers could promote further rulemaking regarding living shorelines, and allow inter-jurisdictional cooperation and sharing of lessons learned. Moreover, an assessment of the relative performance of different structural materials in different environmental contexts is needed to improve best practices.

One of the biggest challenges for translating basic science to practice and policy is that research is currently buried in a growing number of interdisciplinary journals, many of which are locked behind pay walls where practitioners and coastal managers cannot access them (Fuller et al., 2014). The studies in our database were published in 26 unique journals, spanning many sub-disciplines within the environmental sciences. Nearly one third of the papers were open access, compared to the 9% rate of open access articles that has been noted in other restoration syntheses (Zhang et al., 2018). This may reflect the general growth of open access publishing or may alternatively reflect the highly applied nature of living shorelines research and a push within the community to make research accessible to restoration practitioners and managers that can use the data. Future support for open access publishing should be permissible from granting agencies, universities, and organizations to encourage the transference of knowledge between sectors.

Recommendations for Future Research

Our review highlights some important areas of concentrated research as well as gaps in the peer-reviewed literature surrounding living shorelines. Going forward, more studies might be included in a synthesis if the search was expanded beyond peer-reviewed and English-language literature. In regards to research foci, a large proportion of the papers in this review measured processes related to the coastal protective services of living shorelines. Accordingly, it may be possible going forward to conduct a targeted synthesis or meta-analysis to determine whether or not living shorelines can provide superior coastal protection. In terms of research gaps, we suggest that the study of living shorelines could benefit from directed research in the following areas:

- The socio-economic dimensions of living shorelines, particularly relating to their social acceptability among homeowners and municipalities, as well as their installation and maintenance costs over both short and long time scales.
- Long-term performance of living shorelines, which could be achieved by revisiting older sites that have been sampled in previous studies and publishing longer-term data sets to understand how living shoreline functionality changes over time, and how it may change with accelerated sea level rise.
- Direct comparisons between living shorelines and traditional hard infrastructure, to better understand the tradeoffs between different coastal protection strategies.
- The impacts of different living shoreline designs and materials on the delivery of ecosystem services to maximize the functionality of living shorelines in different environmental contexts.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

CS, MR, and BS conceived of the project. CS, MR, EM, VP, JR, and EW extracted the data. CS, JR, EM, VP, and RG assisted with figure creation. CS wrote the manuscript with help from JR, EW, and EM and critical input from all authors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00434/full#supplementary-material

Supplementary Table 1 | Database of living shorelines papers and extracted data used to generate figures and tables for the manuscript.

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REVIEW
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Unoccupied Aircraft Systems (UAS) for Marine Ecosystem Restoration

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Assessing, implementing and monitoring ecosystem restoration can be a labor intensive process, often short term (<3 years), and potentially destructive to the habitat. Advances in remote sensing technology are generating rapid, non-destructive methods for siting, executing and monitoring restoration efforts, particularly in fragile marine environments. Unoccupied aircraft systems (UAS), or drones, are a highly flexible method for accessing and remote sensing ecosystems with on-demand capabilities, greater resolution than sensors from satellites and occupied aircraft, and the ability to cover large areas quickly. With the variety of platforms and payloads available, UASs are providing a suite of tools for conservation practitioners to properly plan marine ecosystem restoration projects and evaluate their success. Both conventional and specialized sensors coupled with image processing techniques can be used to gauge impact to and recovery of entire ecological communities. For example, high-resolution, multispectral imaging allows for discernment of population changes across trophic levels, concurrent with the discrimination of species (including rare) across a landscape, and detection of vegetation stress. Structure from Motion photogrammetric processing provides centimeter-scale three-dimensional models of habitat structure to measure ecologically significant aspects like rugosity and assess their change through time. Water quality around a broad impacted area can be remotely monitored via a number of payloads before and after restoration. Additionally, specially designed payloads can be used to manually disperse seeds or materials for restoration applications without disturbing the habitat. UASs have increasing potential to reduce the costs (both time and money) associated with restoration efforts, making site assessment and long-term, broad-scale monitoring more achievable. Here we present a review of the applications of UASs in marine ecosystem restoration with an overview of the special considerations of using this technology in the marine environment.

Keywords: UAS, drones, marine ecosystem, restoration, conservation, living shoreline

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INTRODUCTION

Much of the world's coastal and marine habitats are threatened by climatic changes and anthropogenic modifications (Adam, 2002; Halpern et al., 2008), driving an increased focus on marine ecological conservation and restoration over the past several decades. The biogenic habitats that exist across the margins of our coastal seas (e.g., coral reefs, seagrass, saltmarsh, oyster reefs, mangroves, etc.) provide numerous benefits to the surrounding environment (Barbier et al., 2011). As the quantity and quality of these habitats have declined in the last few centuries, we are now struggling to mitigate losses in the ecosystem services they can provide (Halpern et al., 2008). Restoration of marine and coastal habitats is now occurring on many scales, spatially and temporally, and these efforts consist of a series of multifaceted stages of planning, implementation, and ultimately monitoring restored sites to determine how they respond over time. Having adequate information to guide the stages of restoration projects is essential, and accessing efficient and affordable tools to implement necessary actions during each of these phases will help ensure the success of marine ecosystem restoration (MER) projects.

Remote sensing of environments for assessment purposes, most often from orbiting satellites or occupied aircraft, has been rapidly developing in the last several decades. Remote sensing methods offer a way to monitor fragile environments, like biogenic coastal habitats, with minimal to no disturbance (Shuman and Ambrose, 2003). This is an important consideration for restoring delicate ecosystems when long term monitoring practices can have potentially lasting negative impacts on a habitat through impacts such as trampling (Goldman Martone and Wasson, 2008) (**Figure 1**). Traditional remote sensing methods (satellite and occupied aircraft operations) are increasingly powerful for environmental monitoring but have certain limitations including prohibitive costs, inadequate temporal resolution or timing of sensing, and insufficient spatial resolution of the data (Turner et al., 2015; Windle et al., 2019). That being said, advances in satellite sensor and data processing technologies have vastly expanded the types and quality of data products that can be generated through remote sensing while also promising increased affordability and immediacy (Pettorelli et al., 2014).

The past decade has seen a surge of research using unoccupied aircraft systems (UAS) for conservation applications (Klemas, 2015; Marvin et al., 2016; Manfreda et al., 2018; Harris et al., 2019; Jiménez López and Mulero-Pázmány, 2019; Johnston, 2019). While these platforms are referred to with many names (e.g., drone, unmanned aerial vehicle, UAV, or remotely piloted aircraft, RPA), the aircraft itself represents one part in a system of components, which includes the ground control and communication systems between the remote pilot, aircraft, and the payload sensor on board. The range of platforms (i.e., fixed-wing, rotary-wing, and hybrid) and plethora of modular sensors (e.g., multispectral, hyperspectral, lidar, etc.) makes UAS a highly versatile tool for science and conservation missions, operating on-demand to sample at previously unobtainable temporal and spatial scales, transforming the way we can examine a range of organisms and their ecosystem interactions (Anderson and Gaston, 2013; Chabot and Bird, 2015; Pimm et al., 2015). Furthermore, developments in photogrammetric methods [e.g., Structure from Motion (SfM), spectral analysis, machine learning algorithms] allow users to extract even more information (e.g., three-dimensional structure and vegetation health) from UAS remote sensing data (Mancini et al., 2013; Ballari et al., 2016; Kalacska et al., 2017; Doughty and Cavanaugh, 2019).

As the number, complexity, and scale of coastal restoration projects grow, the application of new technological approaches, including the use of UAS-based tools, is essential. This article provides perspectives on how UAS technology is being applied to restoration tasks, and more specifically, details how they can be further integrated into important components of MER efforts. To give the reader a more comprehensive understanding of UAS capabilities and their potential applications, we first provide a brief overview of current and developing UAS technology, with reference to specific works that cover greater details of UAS equipment, operational workflows, and the data they produce. We then delve into ways UASs can be, or are, applied to various aspects of three key MER stages: planning, implementation, and monitoring (**Table 1**). These example applications focus primarily on how UAS-based methods can be applied to a living shoreline project, with additional examples supplied in other marine environments. **Table 1** presents examples of each these use cases, providing details on the aircraft employed, it's sensor/payload, the analytical workflow and the citation for that case study.

A PRIMER ON UAS AND THEIR PRODUCTS

Platforms

There are a number of UAS platforms that can or have been incorporated into MER practices. Based upon their airframe configuration, these aircraft generally fit within three broad categories: rotary wing or multirotor, fixed wing, and transitional (or hybrid). The suite of aircraft distributed among these categories provide different utilities related to their maneuverability, payload capacity, flight endurance, and their launch and recovery needs. Within each category, airframes are available that encompass the spectrum of consumer-grade to professional-grade setups, with varying levels of onboard Global Navigation Satellite System (GNSS) accuracy ranging from several meters horizontal and vertical (consumer-grade) to centimeter accuracy when equipped with a survey-grade real-time kinematic (RTK) GPS (Seymour et al., 2018). Furthermore, almost all UAS are capable of autonomous operation, programmed through mission planning software. While this article focuses on how UAS are employed in MER-related activities, a more thorough discussion on UAS components, best practices and platform considerations for a broad array of missions can be found in González-Jorge et al. (2017), Joyce et al. (2018), Manfreda et al. (2018), Harris et al. (2019), and Johnston (2019).

Payloads

A variety of passive and active sensor options as well as engineered mechanical payloads enable UASs for a multitude of mission objectives. While some UASs come pre-equipped with integrated payloads, many have swappable or modular payloads, sometimes enabled through a modification kit. Passive sensors are most commonly used in restoration work, relying on solar reflectance dynamics, an organism's thermal radiation,

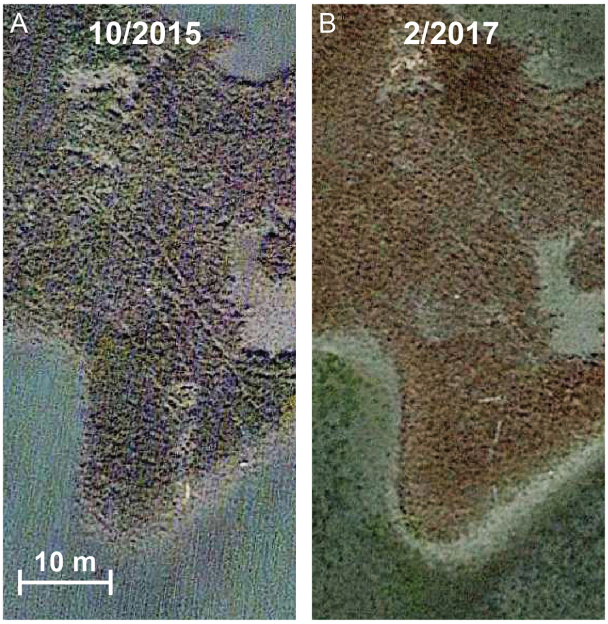

FIGURE 1 | Vegetation sampling transects conducted in 2015 **(A)** in a North Carolina saltmarsh that are still visible in 2017 **(B)**. Imagery obtained from Google Earth Pro V 7.3.3.7699 (October 25, 2015 and February 19, 2017) Middle Marsh, North Carolina, USA. 18S 351935.66 m E 3839950.94 m N. Eye alt 951 feet. Maxar Technologies 2020. [Accessed May 28, 2020].

or non-solar generated light. Passive sensors include the basic camera RGB (Red, Green, and Blue) sensors used for digital imaging along with more complex multispectral and hyperspectral cameras that are able to obtain wide and narrow-band information across other sections of the visible and near-visible electromagnetic spectrum. While some of these multispectral sensors are geared to obtain RGB along with the wider-band spectra of near infrared and red edge, some are more directly engineered to obtain just the necessary spectral bands to calculate specific environmental health indices, such as the normalized difference vegetation index (NDVI) that compares red and near-infrared reflectance. Active sensors can include compact lidar systems and certain types of radar, like ground penetrating radar (Wu et al., 2019). Finally, mechanical payloads have been engineered to enable UASs to collect water samples (see review by Lally et al., 2019), deliver herbicides and pesticides (Rodriguez et al., 2017), and even disperse seeds (Stone, 2017).

Data Types and Uses

The variety of payload options and rapidly developing image processing technology allows for the generation of rich, temporally explicit data products that range from basic observational data to more involved environmental mapping. Basic RGB sensors provide high resolution streaming video and still photography to monitor and measure organisms and their behavior (Linchant et al., 2015; Krause et al., 2017; Gallagher et al., 2018) and determine habitats of importance. When UAS are used to conduct a mapping survey of image transects, photogrammetric software (e.g., Pix4D, Metashape, and Drone2Map) can generate high-resolution orthomosaics of study sites (**Figure 2A**). This can be completed with basic RGB imagery as well as with more advanced multispectral and narrow-band hyperspectral imagery. In the case of these more advanced sensors, the data products are generally in the form of reflectance indices tied to specific bands captured from 5 to 10 wider bands (10–40 nm) with multispectral to 100–1,000 narrow bands (5–15 nm) with hyperspectral, which can then be used to create false color orthomosaics or combined to produce a variety of spectral indices useful to detect specific habitat components and, in some cases, their health.

Unoccupied aircraft systems-generated 3D models provide accurate topographic information, which can inform efforts to restore species that are tidally dependent, as with many of our coastal biogenic habitats (i.e., oysters, saltmarsh, and mangroves). Drones equipped with lidar units can generate highly accurate 3D data of scanned environments (Resop et al., 2019), and simple overlapping imagery from most sensors can also be used to generate 3D products through the SfM process. Indeed, the advancement of SfM techniques provides for incredibly accurate (cm-scale error) 3D data products in coastal environments, especially with the incorporation of ground control practices (Seymour et al., 2018; Casella et al., 2020). From both lidar and SfM, 3D point clouds (**Figure 2B** and **Supplementary Video S1**) can be used to create digital surface models, and digital elevation models (**Figure 2C**) when data are georectified within a vertical datum. UAS-derived 3D modeling has been conducted in a variety of environments including shorelines (Gonçalves and Henriques, 2015; Seymour et al., 2018; Lowe et al., 2019; Seymour et al., 2019; Casella et al., 2020), several shallow-water/tidal habitats (Long et al., 2016; Ventura et al., 2016; Casella et al., 2017; Kalacska et al., 2018; Windle et al., 2019), and to study hydrological dynamics in wetlands (Capolupo et al., 2015; de Roos et al., 2018; Harvey et al., 2019).

A range of UAS data applications and post-processing software systems (e.g., ArcGIS and eCognition) can be used to extract or derive a variety of measurements and habitat condition variables that may be key for restoration efforts. Environmental health indices can be calculated using specific combinations of spectral bands, such as the NDVI mentioned previously (**Figure 2D**) as well as other indices that have been used in coastal vegetation health assessments (e.g., Normalized Difference Red-Edge Index, Soil-adjusted Vegetation Index, etc.). In a restoration context, these vegetation indices cannot only assess habitat health, but also help delineate habitats and differentiate species (Yaney-Keller et al., 2019). Open source software tools for UAS imagery are becoming more prevalent, enabling users to quickly conduct measurements on photographed organisms to assess their body condition and health (Torres and Bierlich, 2020). Advanced machine learning algorithms are now being widely used to classify UAS data based on spectral and 3D characteristics. Object-based image analysis (OBIA) has been used to effectively classify UAS-based maps of shallow water environments such as seagrass meadows and hard bottom habitats (Chabot et al., 2018; Ventura et al., 2018). Many of these algorithms are now established tools within geospatial

TABLE 1 | Representative use cases with associated aircraft, payloads, and primary data analysis tools.

Example use cases	Unoccupied aircraft system (UAS)	Payloads	Data analysis tools	Sources
Marine ecosystem restoration (MER) site suitability, baseline data, and monitoring				
Spatial context: elevation and landscape	Fixed wing (senseFly eBee)	RGB (senseFly S.O.D.A.)	SfM, GIS*	Seymour et al., 2018
	Multirotor (DJI Phantom series)	RGB (on board)		Marteau et al., 2017
Mangrove percent cover and canopy height	Multirotor (DJI Phantom series)	RGB (on board) Multi** (Sentera NDVI)	NDVI, SfM, GIS/OBIA	Yaney-Keller et al., 2019
Map invasive species	Fixed wing (Precision Hawk Lancaster)	Multi (MicaSense RedEdge)	NDVI+***, SfM, GIS	Samiappan et al., 2017
Wetland health	Fixed wing (senseFly eBee)	Multi (Parrot Sequoia)	NDVI+, GIS	Díaz-Delgado et al., 2018
Animal populations				
Seals	Fixed wing (senseFly eBee)	Thermal (senseFly ThermoMap)	GIS	Seymour et al., 2017
Turtles	Multirotor (DJI phantom series)	RGB (on board)	GIS	Schofield et al., 2017a
Birds	Multirotor (3DR Iris+)	RGB (Sony Cybershot RX100 III)	ImageJ, Machine Learning	Hodgson et al., 2018
Environmental quality				
Groundwater discharge	Multirotor (DJI Matrice 100)	Thermal (ICI 9640)	GIS	Harvey et al., 2019
Water quality data mule	Multirotor (DJI 450)	Receiver		Potter et al., 2019
Surveillance	Multirotor	RGB Thermal	Photo/video observation	See Nowlin et al., 2019
MER design				
3D modeling	Multirotor (DJI Phantom series)	RGB (on board)	SfM, GIS	Allen and McLeod, 2017
Flow modeling	Multirotor (DJI Phantom series)	RGB (on board)	ImageMagick	Powers et al., 2018
MER implementation				
Vegetation planting	Multirotor (Dendra Systems)	Seed gun		Peters, 2019
Fire ignition	Multirotor (Ascending Technologies Firefly)	Ignition sphere dropper		Beachly et al., 2017
Herbicide treatment	Multirotor (Octacopter)	Herbicide sprayer		NCDOT, 2019

**Structure from Motion (SfM) denotes the use of photogrammetric software packages (e.g., Pix4D, Agisoft, etc.) and Geographic Information System (GIS) denotes the use of analyses within GIS software packages. **Multispectral sensor. ***NDVI+ indicates the use of additional spectral indices calculated from multispectral data.*

software packages, but some habitat classifications may require more complex applications of machine learning such as neural networks to train a computer how to identify target habitats or metrics (Casado et al., 2015; Ridge et al., 2020). In this context, UAS can be applied to the development of training data for machine learning systems, as well as for conducting rapid validation sampling that reduces human impacts on restored systems (Gray et al., 2018). Regardless of programming complexity, increasingly active data and script sharing, facilitated through standard open source licensing, is making these tools more accessible to the general user.

PLANNING AND INITIAL MONITORING

The use of UASs during the planning stages of MER projects provides heightened situational awareness of the targeted location and the larger environmental context it is embedded within. In many cases, data generated through UAS surveys of a proposed restoration site can help researchers and practitioners locate and target critical habitats (e.g., coral reefs, seagrass, mangroves, etc.) or provide maps and geospatial information needed to identify and assess specific ecosystem dynamics (predator/prey relationships) or environmental conditions (e.g., hydrological functions). With all the considerations necessary to planning, there are many avenues for incorporating UASs into this process. The major applications during project planning revolve around assessing site suitability (determining whether a location is amenable to a particular MER practice), gathering baseline data and using UAS products to guide MER design (**Figure 3**).

Site Suitability and Baseline Data

From the air, users can obtain a perspective on a potential restoration site to gather data with little to no disturbance to the actual environment. With the ability to collect high resolution imagery and 3D environmental data, planners can better place a MER within the boundaries of ecological and regulatory frameworks. In this context, UAS can be applied as survey instruments to establish exactly where restoration efforts can and should be conducted, based on existing property limits or ecotones. In the example of a living shoreline, planners generally have to consider the restored wetland's setting within the general environment (e.g., tidal range, landward boundary, etc.) as well as proximity to limiting factors, such as breakwaters to navigational channels or beds of submerged aquatic vegetation.

Accurate baseline data at restoration sites are essential to determine if MER efforts are successful. Many MER

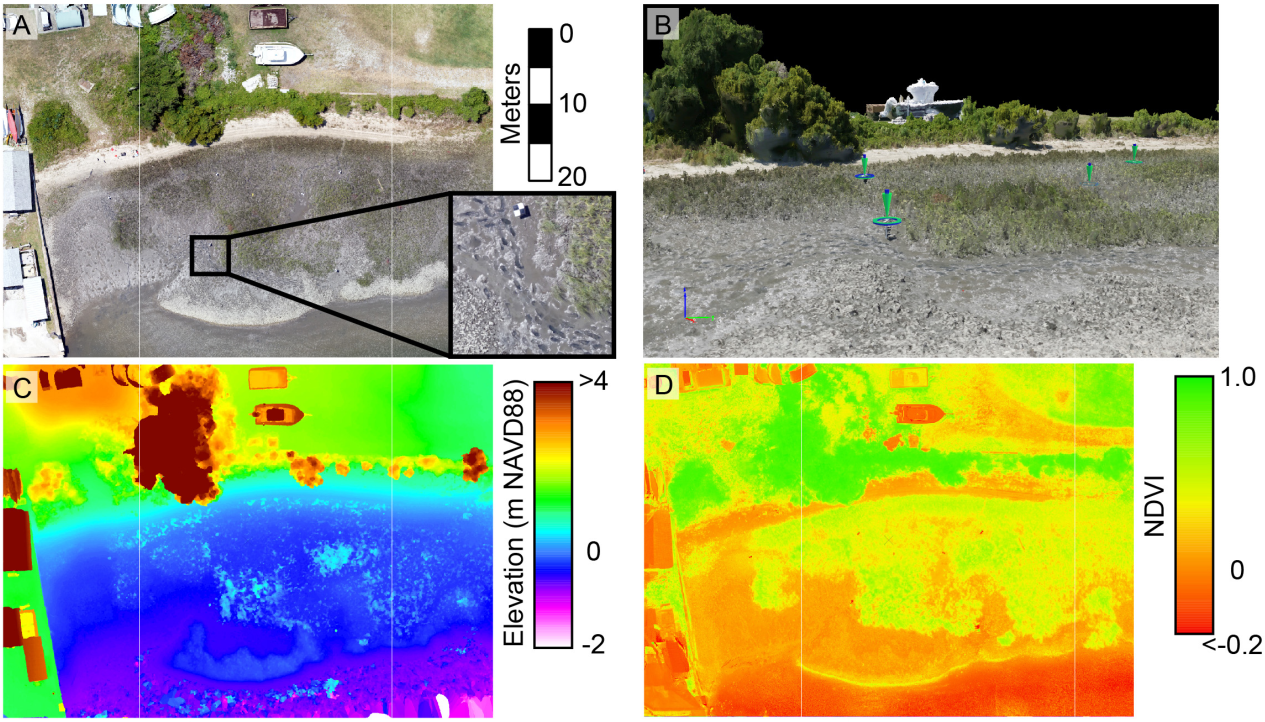

FIGURE 2 | Stitched orthomosaic of a living shoreline (saltmarsh and oyster reef) situated on Pivers Island, North Carolina **(A)**. Densified point cloud of the site with ground control points designated by green arrows **(B)**. Digital elevation model of the site with water artifacts along the bottom edge **(C)**. Normalized difference vegetation index of the site obtained from concurrent multispectral UAS imagery **(D)**.

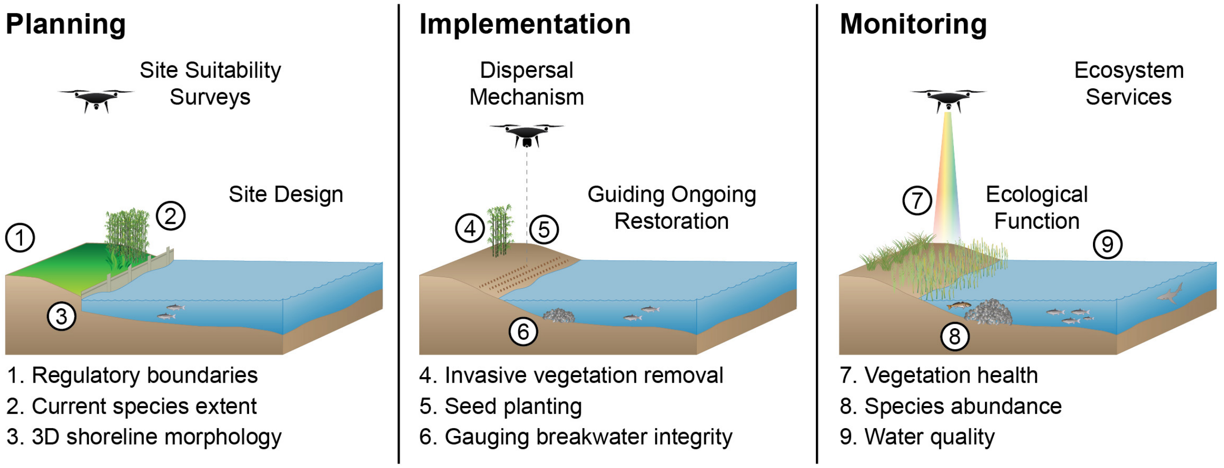

FIGURE 3 | Synopsis of unoccupied aircraft system (UAS) applications in Marine Ecosystem Restoration (MER) projects at the three major stages with select examples provided. The Planning stage includes collecting baseline data to establish regulatory and ecological boundaries (Site Suitability) and generation of visuals and models help determine MER success criteria (Site Design). In the Implementation stage, UASs can be applied for vegetation planting, fire ignition, herbicide or pesticide treatments as well as helping direct ongoing restoration activities. During the Monitoring stage, UASs can collect data on vegetation health, wildlife abundance and behavior (Ecological Function) and data on topography, hydrology, and water quality of the surrounding landscape (Ecosystem Services). Some of the symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols).

projects implement a before-after-control-impact design for assessment purposes, where obtaining pre-restoration conditions is paramount. For a living shoreline MER, this could involve mapping the current extent of specific species and their percent cover (Marcaccio et al., 2015; Husson, 2016; Yaney-Keller et al., 2019), invasive or non-native organisms (**Figure 4A**; Samiappan et al., 2017), and signs of degradation (Chirayath and Earle, 2016) (e.g., reef loss, marsh die off, and shoreline erosion).

FIGURE 4 | Examples of UAS data products capturing the presence and locations of non-native coconut palms among mangroves in Belize **(A)**, the migration of thousands of cownose rays in a North Carolina estuary **(B)**, shark behavior **(C)**, and the thermal signatures (white dots) of a penguin colony **(D)**. All images obtained by Duke University Marine Robotics and Remote Sensing Lab, collected under permit.

Similarly, Nahirnick et al. (2019) used UAS imagery to map eelgrass and were able to differentiate between eelgrass and macroalgae based on image textural differences that may not be as apparent in lower resolution imagery (>m). Additional use of specialized sensors can offer an even more detailed perspective of habitat condition through generation of health indices. NDVI can aid the classification process by using the values to isolate coastal vegetation through masking (Ballari et al., 2016), and UAS-derived NDVI values correlate strongly with aboveground biomass in a California saltmarsh (Doughty and Cavanaugh, 2019). Similarly, Díaz-Delgado et al. (2018) used UAS-based multispectral data to assess indicators of ecological integrity of wetlands in Spain. Hyperspectral sensors could be used to further discriminate species (Silvestri et al., 2003) and refine vegetation index results by removing background spectral noise in these habitats (e.g., oversaturation in dense vegetation, sediment reflection – see Hladik et al., 2013). Parsons et al. (2018) used UAS-obtained RGB and hyperspectral imagery in combination with in-water surveys to help identify areas of degradation in coral reefs. Specialized multi and hyperspectral sensors can also help determine turbidity and sediment flow (Vogt and Vogt, 2016; Díaz-Delgado et al., 2018) as well as concentrations of chlorophyll in the surface water (Kislik et al., 2018). Thermal sensors can identify groundwater discharge (Willms and Whitworth, 2016; Harvey et al., 2019), which can impact the salinity dynamics of a site or the potential input of contaminants from affected groundwater.

The use of UASs in MER is not limited to baseline habitat assessments. For example, UASs have been used to observe a variety of coastal and marine species including fish (Kiszka et al., 2016; Raoult et al., 2018; Rieucau et al., 2018; Benavides et al., 2019; Gore et al., 2019), birds (Hodgson et al., 2016, 2018; Han et al., 2017), reptiles (Elsey and Trosclair, 2016; Schofield et al., 2017a,b; Sykora-Bodie et al., 2017; Bevan et al., 2018; Rees et al., 2018), and mammals (Durban et al., 2015; Johnston et al., 2017; Krause et al., 2017; Seymour et al., 2017; Ramos et al., 2018). In some cases this is focused observation of an individual/group (**Figures 4B,C**), as seen with whale behavior studies (Torres et al., 2018), or orthomosaic products that can be used to enumerate congregations of organisms such as nesting birds (**Figure 4D**; Hodgson et al., 2016) or seal colonies (Johnston et al., 2017). UASs equipped with thermal infrared sensors can help quantify wildlife in an area, and thermal imagery has been particularly useful for examining marine mammal populations (Seymour et al., 2017) and nesting birds (Christie et al., 2016). Willms and Whitworth (2016) used UAS thermal imaging to identify temperature dynamics of spawning waters for salmon. For a projected living shoreline, these data could provide a before-restoration reference for wildlife use of the site. There continues to be major efforts ensuring that UASs for wildlife monitoring are operated at safe and non-invasive altitudes, which has produced some very promising results indicating that UASs can still collect high-resolution data without disturbing wildlife (see Arona et al., 2018 and reviews in Christie et al., 2016; Mulero-Pázmány et al., 2017).

Finally, baseline data on pollution factors at proposed restoration sites can also be facilitated with UAS. For example, UAS can be used to monitor marine debris in coastal and marine environments. UAS imagery coupled with machine learning algorithms have proven efficient at identifying and classifying litter (Martin et al., 2018), and Hengstmann et al. (2017) were able to use a UAS to geolocate marine debris and help identify the major factors influencing its distribution as part of a large beach marine litter monitoring effort in Germany. Similar work has been conducted in areas of the United States, examining marine debris dispersal across an estuarine landscape to locate hot spots for targeting clean ups and considering litter source mitigation (Newton et al., unpublished data).

Marine Ecosystem Restoration Design

Once baseline imagery is captured and processed, the maps and models generated can become instrumental for designing restoration projects. As with the living shoreline example, a restored saltmarsh may include a fringing oyster reef sill. Oysters thrive within very specific zones of the tidal range (Morris et al., 2002; Ridge et al., 2015), and the 3D models of restoration sites can help planners quickly calculate the possible extent of a MER as well as distributional guidance for vegetation and volumetric information for oyster material. Comparably, Fodrie et al. (2014) spent several days walking GPS transects across extensive sandy shoals to plan where to site their oyster restoration study, which could have been achieved in the course of just a few hours with a UAS.

Unoccupied aircraft systems-obtained data on environmental variables can help MER designers make process-driven decisions about how to structure restoration efforts. Basic RGB sensors can be used in conjunction with rhodamine applications to track flow dynamics (Powers et al., 2018) through the landscape. A UAS could be outfitted with ground penetrating radar to measure soil moisture (Wu et al., 2019), an important factor for wetland vegetation health. Soil type, quality and moisture are essential components for planning where and how to plant wetland vegetation. Understanding these dynamics can help shape a MER, allowing planners to take advantage of natural processes to maximize the success of the project.

The creation of MER site maps and model visualizations have manifold utility. The site map and 3D model could be ingested into design software for advanced viewshed analysis, rendering what the proposed project would look like when finished. These can be useful materials when approaching potential funding agencies and gaining community interest and support for restoration efforts. Finally, these initial surveys will ultimately serve as the baseline reference for establishing and eventually assessing project success metrics.

IMPLEMENTATION

Restoration efforts can be a massive undertaking, potentially requiring restructuring of the landscape and the deployment of materials (e.g., shell, seedlings, and corals). Considering the manual nature of many MER efforts, it is unfeasible for UASs to replace many current methods. However, UAS can assist MERs in the form of an actual dispersal mechanism for various materials (**Figure 3**). Within the last several years, drone-based solutions for planting trees and grasses have emerged, and are being implemented on a large scale (10s of hectares) to restore mangroves in Myanmar (Peters, 2019). In this case, a UAS was equipped with a payload that fires seed bullets, essentially biodegradable pods with a germinated seed and nutrients, into the ground. This highly successful application has resulted in the germination of millions of mangrove plants, potentially revolutionizing large scale mangrove restoration efforts. It is possible that with the right packaging of nutrients and germinated seeds this method could be expanded to other MER efforts, like saltmarsh plantings. In other dispersal methods, UASs are now being used for targeted management in the form of fire ignitions and herbicide treatments. In the case of wetland restoration, fire has been a traditional tool for inhibiting woody species (Nyman and Chabreck, 1995), and UASs have been developed with an integrated ignition sphere dispenser that is programmed to drop the spheres at specific intervals to initiate a controlled burn (Beachly et al., 2017). Some restoration efforts face encroachment by non-native species, like the common reed *Phragmites australis*. Restoration work in a *Spartina alterniflora* marsh showed that herbicide treatment of *Phragmites* allowed the native *S. alterniflora* to bounce back in under 5 years (Gratton and Denno, 2005). Recently, UASs have been outfitted with herbicide dispensers and have become part of *Phragmites* control initiatives in North Carolina (NCDOT, 2019). These types of uses extend beyond addressing plant species. For example, UAS can now be used to drop poison baits targeting invasive species of rodents (Island Conservation, 2019).

While some MER activities are discrete one-time efforts, many are multiyear programs where UASs can be a significant boon by guiding subsequent actions and interventions. Periodic surveying and follow up plantings, invasive or unwanted vegetation treatments, or the need to secure or augment stabilization structures like an oyster reef sill are examples of these extended use-cases. The use of multispectral and hyperspectral sensors can provide vegetation index information during MER implementation to gauge the health of the restored vegetation and identify whether or not additional actions need to be taken to ensure restoration success (e.g., fertilizer treatments, grazer removals, etc.).

MONITORING SUCCESS

The autonomous nature of UAS surveys makes for an efficient, repeatable tool for monitoring an ecosystem. Many of the UAS applications for monitoring success of MERs are extensions of the applications discussed earlier for the planning phase (**Figure 3**). However, the temporal context becomes even more important with restoration monitoring, since understanding how these systems are changing through- or as a result of MER efforts is essential for gauging project outcomes. Furthermore, UAS-derived data can help achieve specific monitoring metrics established by restoration funding agencies (e.g., US Fish and Wildlife Service, National Fish and Wildlife Foundation), which will serve as an added frame of reference in the sections below.

Ecological Dynamics

Subsequent UAS mapping missions using simple RGB or combined multispectral and/or hyperspectral can assess changes to areal habitat extent through time. This process can elucidate changes in the extents of the restored species in conjunction with other possible notable factors, like invasive species (**Figure 4A**). As an example application for meeting funding requirements, measuring percent cover by species is one of the National Fish and Wildlife Foundation's (NFWF) primary monitoring metrics for both wetland and living shoreline restoration projects under their Coastal Resilience Fund (NFWF, 2019), and includes the total areal footprint of oyster reef restored. Under NFWF guidance, both of these restoration activities also require a metric for shoreline position (NFWF, 2019), which can be obtained from UAS-derived orthomosaics with cm-level accuracy.

Repeatable visual transects, through RGB and/or thermal infrared, can provide population estimates of organisms or behavioral insights of species across trophic levels, essentially measuring the use and ecological functions of restored habitats as compared to the pre-restoration conditions. For example, Rieucau et al. (2018) conducted UAS video transects along fringing reefs to examine habitat-dependent shark behavior, providing a baseline for possible future disruptions to that habitat. Sykora-Bodie et al. (2017) used UAS image transects perpendicular to the beach to identify and count sea turtles in areas that may result in interactions with fisheries, and Gray et al. (2019) went a step further by using a deep learning algorithm to automate sea turtle detection. These methods can be applied to understanding if a MER is benefiting local wildlife and providing desired ecosystem services.

Structure from Motion (SfM) technology continues to transform the role UASs can play in assessing ecosystem structure. Instead of measuring oyster reef growth through time using terrestrial lidar (Rodriguez et al., 2014; Ridge et al., 2015, 2017) UAS-derived approaches (e.g., Windle et al., 2019), could assess a greater number of oyster reefs during narrow low tide windows across larger coastal landscapes. The development of structural metrics in vegetated environments has been greatly enhanced by the addition of UAS tools. Multiple studies have used SfM products to measure canopy heights and estimate biomass in mangroves (Warfield and Leon, 2019; Yaney-Keller et al., 2019). Yaney-Keller et al. (2019) actually used a dual band NDVI sensor (no RGB) in conjunction with SfM to measure canopy heights and percent cover in mangroves, and differentiate species in the estuaries of Pacific Costa Rica. Boon et al. (2016) also combined SfM products with orthophotos to greatly enhance wetland delineation and health assessment.

Ecosystem Services

In addition to monitoring ecological recovery, UASs have a vast potential for monitoring how MER efforts benefit the surrounding landscape, both natural and anthropic. Many MER projects have implications for shoreline stabilization and coastal resilience, and assessing how adjacent landscapes are sheltered by these marginal habitats is a metric for evaluating success. One way to monitor this is through assessing elevation, a primary metric often included in restoration monitoring for wetlands and living shorelines (NFWF, 2019) as it represents the habitat's vulnerability to – and ability to keep pace with – sea level rise. Elevations are easily obtained for non-vegetated surfaces using SfM, like oyster reefs (Windle et al., 2019) and beach environments (Seymour et al., 2018), but may need a more strategic approach in densely vegetated environments, potentially using dormant season flights, fine scale mapping (low altitude), or other references like water level. Working in a coastal wetland, Meng et al. (2017) developed a workflow to help estimate the terrain in these densely vegetated environments. While not serving as a replacement for finite sediment surface measurements like those obtained from saltmarsh Surface Elevation Tables (SETs, Cahoon, 2015), UAS-derived elevation data could help determine the overall scalability of SET measurements over a larger area. UASs have been used to track changes to barrier islands and other coastal environments over the course of months to years capturing morphological changes to the landscape (Seymour et al., 2019). Similarly, Marteau et al. (2017) used these methods to track geomorphic change of a restored riverine environment to assess restoration outcomes.

As mentioned previously, UAS payload configurations can be used to sample water quality either directly or through remotely sensed data processes to monitor how well a MER is benefiting water quality. Considering the repetitive nature of monitoring, a rising concept in UASs for environmental observation is the idea of drones as data mules (Palma et al., 2017). This relies on a coupled system with *in situ* sensors and a UAS equipped with data retrieval hardware that will remotely link to these sensors and download the data (Potter et al., 2019). For the purposes of MER, the deployed equipment could be a network of autonomous water quality samplers across a site (Trevathan and Johnstone, 2018). Instead of physically extracting the data from the samplers, a UAS could be flown over with a datalink to retrieve the data wirelessly, never requiring managers to have to enter the site. Potter et al. (2019) demonstrated the use of this coupled system with a network of sensors collecting water temperature, pH, and conductivity that transmitted the data to a UAS that hovered above the central node. The system could be adapted to collect any number of environmental variables and would be especially useful in remote locations that do not have existing wireless communication networks.

Another major benefit of UAS-based monitoring is the fine temporal scale afforded by its on-demand nature. A combination of sensor payloads can provide an abundance of multidimensional data over a landscape in a relatively short period of time. This readily enables the surveying of MER sites before and after storms, or other predictable disturbances, to assess impact on the MER as well the benefits a MER may be offering adjacent habitats. In the case of a living shoreline restoration project, UAS provide significant opportunities to assess how natural systems dampen storm energy compared to artificial or unstructured shorelines. Recognizing this advantage, UASs are incorporated into post-storm monitoring in coastal systems internationally (Turner et al., 2016; Seymour et al., 2019; Casella et al., 2020). Studies conducted on living shorelines to assess their resilience and shoreline protection against storm impacts (e.g., Smith et al., 2018) would benefit from the incorporation of UASs, which would expedite field sampling and reduce unintentional, but inevitable, impacts of direct sampling within the habitat (**Figure 1**).

Enforcement and Protection

While highly dependent upon the legal restrictions governing an area, UASs have been used as a tool to protect conservation areas. With limited personnel resources, UASs could provide a periodic mobile watchtower over a MER site to deter poaching (Mulero-Pázmány et al., 2014) and other illegal or unpermitted acts. A review of UAS use for conservation in protected areas touted the benefits of using drones for enforcement while also acknowledging that there are still some ethical considerations left to work out (Jiménez López and Mulero-Pázmány, 2019). In general, though, UAS surveying of public use of a managed land can be a viable option, and Nowlin et al. (2019) provide best practices for this use case in some coastal contexts.

CAVEATS

As with any developing technology, caveats to its integration emerge as we test limits and determine best practices. Unfortunately for some entities drone usage may be periodically restricted, as has been seen while governments navigate cybersecurity issues (e.g., grounding of some United States federal agency drone fleets –U.S. Department of the Interior [USDOI], 2020). While the UAS research community has begun to harmonize methods, standards, procedures, and reporting (Joyce et al., 2018; Barnas et al., 2020), there remains work to be done (Buters et al., 2019). Some key caveats for UAS MER applications are related to image acquisition methods. For example, image quality of submerged landscapes from UAS is highly dependent on a number of environmental conditions including (but not limited to) sun angle, cloud cover, surface disturbance by wind, and turbidity (Joyce et al., 2018; Nahirnick et al., 2019). This may also prove true in areas with uniform image texture (e.g., smooth sand) that may generate artifacts in the point clouds (Seymour et al., 2018). When imaging forest canopies, like mangroves, higher altitudes and more overlap may be necessary because of the greater potential for the foliage to move with even just a small amount of wind (Fraser and Congalton, 2018). NDVI assessments of certain species, like emergent vegetation, can be affected by inundation (Kearney et al., 2009) or high soil water content (Ballari et al., 2016) affecting attempts to estimate biomass (Byrd et al., 2014). In some cases, these problems can be mitigated with specific mission planning insights, like adjusting UAS altitude, orientation of acquired imagery (away from sun), or understanding the limitations of the data collected for a certain habitat. Further consideration must also be made to the cost-benefit of using UAS technology for specific applications. While costs of aircraft and sensors continue to drop, the pricing can range from \$1,000 (USD) for consumer-grade to \$10K–\$20K (USD) for professional-grade aircraft and sensor packages, with the more advanced packages (e.g., hyperspectral, lidar, etc.) reaching \$50K–\$100K (USD). The software (e.g., Pix4D, Agisoft Metashape, etc.) may add another cost on the order of \$1K–\$5K (USD). This may make adoption of UASs cost-prohibitive for outright purchase for some restoration managers, but the data could still be obtained by contracting an institution equipped with appropriate resources. It is worth noting that many of the studies within this review used a consumer-grade drone on the order of \$1,000–\$2,000 (USD), indicating a lot of work can still be accomplished at that technology tier. There are also well-funded UAS and spatial analysis programs that help train and equip natural resource managers in developing regions, like the growing Flying Labs program (WeRobotics, 2020). This program has fostered the development of local UAS capacity in 27 countries spread across South America, Africa, Asia, and Europe that, in part, seek to overcome this challenge. Though technical and regulatory hurdles exist (Hardin and Jensen, 2011), progress made within the last decade to alleviate these hurdles is quite promising for the further development and application of this technology (Hardin et al., 2019).

CONCLUSION

As drone platform and sensor technology continues to advance, UAS-based approaches to MER will further bridge the scale between *in situ* sampling and remote sensing from occupied aircraft and satellites. Innovations in platforms, sensors, engineered payloads, and image processing have proven to be a valuable addition to the MER toolbox, across all stages of a project. UAS offer unparalleled flexibility in temporal and spatial resolution for environmental monitoring, enabling access to hard-to-reach areas with little to no disturbance. While UAS can be applied successfully in most restoration projects, these operations must be conducted within local legal and ethical frameworks (e.g., pilot certifications, airspace authority, and permitting) and with consideration of potential disturbance impacts to non-target species. Limitations in UAS flight time, operational conditions, and payload capacity will continue to diminish, as will airspace restrictions and other regulatory hurdles. As these challenges fade, UAS-based approaches to marine restoration projects will increase and diversify, establishing UAS as a fundamental and versatile tool for enhancing planning, implementation, and monitoring of marine restoration efforts globally.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00438/full#supplementary-material

VIDEO S1 | Densified point cloud created from unoccupied aircraft system imagery (standard RGB) over a living shoreline constructed by the National Oceanic and Atmospheric Administration Beaufort Lab (Pivers Island, Beaufort, North Carolina, USA). The restored shoreline consists of planted saltmarsh and oyster reef.

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frontiers in Marine Science

SYSTEMATIC REVIEW
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Priorities and Motivations of Marine Coastal Restoration Research

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Active restoration is becoming an increasingly important conservation intervention to counteract the degradation of marine coastal ecosystems. Understanding what has motivated the scientific community to research the restoration of marine coastal ecosystems and how restoration research projects are funded is essential if we want to scale-up restoration interventions to meaningful extents. Here, we systematically review and synthesize data to understand the motivations for research on the restoration of coral reefs, seagrass, mangroves, saltmarsh, and oyster reefs. We base this analysis off a published database of marine restoration studies, originally designed to estimate the cost and feasibility of marine coastal restoration, derived from mostly scientific studies published in peer-reviewed and some gray literature. For the present study, the database was updated with fields aimed at assessing the motivations, outcomes, and funding sources for each project. We classify restoration motivations into five categories: biotic, experimental, idealistic, legislative, and pragmatic. Moreover, we evaluate the variables measured and outcomes reported by the researchers and evaluate whether projects adhered to the Society for Ecological Restoration's (SER) standards for the practice of ecological restoration. The most common motivation of the scientific community to study restoration in marine coastal ecosystems was experimental i.e., to seek experimental data to answer ecological research questions or improve restoration approach, as expected since mostly peer-reviewed literature was evaluated here. There were differences in motivations among the five coastal ecosystems. For instance, biodiversity enhancement was the most common case for a biotic motivation in mangrove restoration projects. The most common metrics evaluated were growth/productivity, survivorship, habitat function, physical attributes, and reproduction. For most ecosystems, ecological outcomes were frequently reported, with socio-economic implications of the restoration rarely mentioned, except for mangroves. Projects were largely funded by governmental grants with some investment from private donations, non-governmental organizations, and the involvement of volunteers. Our findings and database provide critical data to align future research of the scientific community with the real social, economic and policy needs required to scale-up marine coastal restoration projects.

Keywords: marine coastal restoration, motivations for ecological restoration, conservation funding, restoration success, restoration metrics, restoration outcome, standards for the practice of ecological restoration

INTRODUCTION

Despite the goods and services that marine coastal ecosystems provide to humans (UNEP, 2006), ecosystems such as coral reefs, seagrass, mangroves, saltmarsh, and oyster reefs are being lost at alarming rates worldwide mainly due to unsustainable land use, coastal development and climate change (Orth et al., 2000; Valiela et al., 2001; Pandolfi et al., 2003; Duke et al., 2007). Protection alone cannot solve this problem, as many areas have little natural habitat left to conserve, are facing extinction (Aronson and Precht, 2001) or have already become functionally extinct globally (Beck et al., 2011). Ecological restoration or "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2004) is urgently needed to assist ecosystems where natural recovery is hindered or impeded (Perrow and Davy, 2002). Ecological restoration principally seeks to recover the functioning of degraded ecosystems, however restoration of marine and coastal habitats can provide a range of ecological and socio-economic benefits, such as coastal protection from flooding and erosion, fisheries habitat, water quality improvements, and carbon sequestration and storage (Duarte et al., 2013; Fodrie et al., 2017; Macreadie et al., 2017; Abrantes et al., 2019; Gilby et al., 2020). The United Nations General Assembly recently declared the "UN Decade on Ecological Restoration" for 2021–2030 and ecological restoration is on the rise as a component of the solution to ameliorate ecosystem degradation (Possingham et al., 2015). For example, the United Nations Sustainable Development Goals call for restoration of marine coastal ecosystems (Goal 14). Marine coastal restoration plays a paramount role in the current focus on nature-based solutions to address global societal challenges (e.g., climate change adaptation and mitigation, supporting fisheries) (Cohen-Shacham et al., 2016) that are presently being advocated across government and industry and will feature as a key topic at upcoming global forums (e.g., UN Oceans Conference, Lisbon in 2020; Post-2020 global biodiversity framework for the UN Convention on Biological Diversity). Despite these high-level goals, a synthetic picture on what motivates people on the ground to undertake restoration in marine coastal ecosystems is lacking.

Restoration is a human undertaking; therefore, it is critical to understand the motivations of individuals and organizations to conduct restoration, and how those motivations relate to project outcomes or funding sources. Understanding motivations, defined as "a reason or reasons for acting or behaving in a particular way" (oxford dictionary), has been well-assessed in various fields of socio-ecological research, for instance, to assess the reasons for people to engage in community-based conservation (Nilsson et al., 2016), to conserve urban biodiversity (Dearborn and Kark, 2010), or to volunteer in marine conservation programs (Kitney et al., 2018). The reasons or motivations why terrestrial ecosystems are restored have been described as "numerous, disparate, generally understated, and commonly underappreciated" (Clewell and Aronson, 2006). Little is known about the motivations of individuals or organizations to undertake restoration in marine and coastal environments. When we understand people's motivations, we can engage them toward achieving common goals. Therefore, understanding the motivations of individuals and organizations to restore are essential to better align these with the desired project outcomes, funding sources, and to overcome the barriers to scaling-up marine coastal restoration practice.

Motivations for a particular restoration project may be complex, as there are likely multiple agents, governance structures, and funding sources involved. For instance, marine coastal restoration projects form part of many government and non-government environmental programs, which are being implemented by a range of stakeholders including community and Indigenous groups, conservation groups, not-for-profit organizations, and private companies. Scaling-up restoration efforts to meet international commitments (UNEP, 2019), necessarily involves a larger number and variety of stakeholders, which requires consideration of multiple motivations (Wyborn et al., 2012; Menz et al., 2013). It also requires stronger government policy, sustained funding, improving the relationships with existing restoration networks and community engagement (Gillies et al., 2015). This is particularly important for designing large-scale restoration programs which are carried out by multiple stakeholders. Recognizing and integrating different motivations in setting restoration goals and evaluating outcomes against these goals, can allow projects to deliver multiple benefits, help resolve stakeholder conflict, and sustain stakeholder commitments to restoration in the long-term (Hagger et al., 2017). Furthermore, customizing incentives to cater for diverse stakeholder motivations can also encourage restoration projects (Jellinek et al., 2019).

Motivations for restoration can be categorized into five broad categories: *biotic* (motivations aligned with the desire to recover lost aspects of local biodiversity), *idealistic* (personal and cultural expressions of concern or atonement for environmental degradation, reengagement with nature, and/or spiritual fulfillment), *heuristic* (attempts to elicit or demonstrate ecological principles and biotic expressions), *technocratic* (restoration that is conducted by government agencies or other large organizations to satisfy specific institutional missions and mandates) and *pragmatic* (recover or repair ecosystems for their capacity to provide a broad array of natural services and products upon which human economies depend and to counteract extremes in climate caused by ecosystem loss) (Clewell and Aronson, 2006). This framework was applied by Hagger et al. (2017) to evaluate the reasons why people restore terrestrial habitats and how this influences planning and monitoring approaches to achieve desired outcomes. So far, in a marine context, the framework has only been used to understand the reasons of the scientific community to restore coral reefs, which were largely focused on improving the restoration approach and answering questions of ecological concern, i.e., heuristic/experimental motivations (Bayraktarov et al., 2019). Little is known about the reasons of scientists to restore other marine coastal habitats and whether these motivations differ among coral reefs, seagrass, mangroves, saltmarsh, and oyster reefs.

The Society for Ecological Restoration (SER) was founded in 1988 to "advance the science, practice and policy of ecological restoration to sustain biodiversity, improve resilience in a changing climate, and re-establish an ecologically healthy relationship between nature and culture" (SER, 2020)[1]. The International Standards for the Practice of Ecological Restoration (first edition released by SER, 2016) contain a number of best practice guidelines developed over decades of research and practice from well-established restoration of terrestrial habitats, however is aimed to be transferrable to marine and freshwater ecosystems (McDonald et al., 2016). SER have developed many tools to help restoration practitioners track their progress toward a full ecosystem restoration, such as the "recovery wheel" used to assess advancement based on metrics categorized under the attributes: absence of threats; ecosystem function; external exchanges; physical conditions; species composition; and structural diversity (McDonald et al., 2016). In addition to best practices and metrics, the outcomes from a restoration project can be categorized into ecological, social and economic or a combination thereof following the framework by Wortley et al. (2013). For marine coastal restoration, we do not currently know: (1) whether the best practice standards toward a full ecosystem recovery proposed by SER have been applied; (2) which metrics have been measured to assess recovery; and (3) what the intended outcomes for the restoration projects were.

Allocation of funding may be considered a metric of an organization's level of interest in a subject, therefore, assessing funding sources in relation to motivations for marine restoration helps us to discern the motivations of organizations. Reported marine coastal restoration costs range from USD \$9,000 ha^{-1} for mangrove restoration where large contributions of effort by communities and volunteers are common (Bayraktarov et al., 2016a) to USD \$400,000 ha^{-1} for coral reefs which often involve logistical constraints to reach the restoration sites (Bayraktarov et al., 2019). While investment in conservation of biodiversity continues to be limited and is simply not enough to meet global biodiversity targets (James et al., 1999; McCarthy et al., 2012), it has to be carefully evaluated in its effectiveness to actually make a change for biodiversity (Ferraro and Pattanayak, 2006).

Information on restoration projects can be obtained from either the scientific process of examining peer-reviewed papers, or through gray literature such as newspaper reports, newsletters, targeted interviews, or government reports. The knowledge from the former source can be accessed through systematic literature review while the latter is more difficult to synthesize. It is not known what the motivations to restore marine coastal ecosystems from either of these sources are and whether they are aligned with the broader needs to reach restoration at scales. These are: to build a business case and awareness that restoration is feasible, develop a policy framework that enables restoration, to build skills and experience in restoration practitioners and to learn from the expertise of terrestrial restoration and adopt best practices (Gillies et al., 2015). Here we focus on the scientific community, their priorities and motivations to restore marine coastal ecosystems.

We systematically review empirical results from the published literature, with the inclusion of some gray literature and personal communications, to elucidate the reasons why (mostly) scientists engage in the field of marine coastal restoration. We specifically answer the questions: (1) what priorities and motivations do scientists have to engage in marine coastal restoration; (2) do motivations to engage vary between different ecosystems; (3) what are the metrics measured and which restoration attributes did they assess; (4) were best practices for ecological restoration applied; and (5) what is the nature of funding to carry out restoration projects? We answer these questions by expanding and updating a global systematic review focused on cost and feasibility assessments of marine coastal restoration (Bayraktarov et al., 2016a), to compare the results across five ecosystems: coral reefs, seagrass, mangroves, saltmarsh and oyster reefs.

METHODS

This paper assesses the motivations underpinning marine coastal restoration as reported primarily by scientists in peer-reviewed scientific literature. The analysis builds off a published database of 235 papers on marine coastal restoration projects which was developed using search criteria aimed at quantifying the cost and feasibility of marine coastal restoration (Bayraktarov et al., 2016a,b). For the purpose of this study the database was updated with more recent literature and expanded to include information on the motivations, outcomes, and funding sources of the research. We used a modified version of the framework by Clewell and Aronson (2006) as adopted by Bayraktarov et al. (2019) for corals reefs to categorize the motivations of the restoration projects. Coral reef data presented in this paper was previously published (Bayraktarov et al., 2019) and is included here as a comparison to four other ecosystems.

Database

The database of Bayraktarov et al. (2016a) which included publications up to 2014, was expanded for the present study using the following methods: The database was updated to include publications until 2018. This involved a systematic literature search using Web of Science (Core collection; Thomson Reuters, New York, New York, U.S.A.) and Scopus (Elsevier, Atlanta,

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[1] Available online at: https://www.ser.org/

Georgia, U.S.A.) and the title search terms "(ecosystemA* OR ecosystemB*) AND restor*," as well as "(ecosystemA* OR ecosystemB*) AND rehab*." The terms ecosystemA and ecosystemB were used as placeholders for two different words describing the same ecosystem (e.g., coral and coral reef, mangrove and mangal, saltmarsh and salt marsh, shellfish, and oyster). For consistency with Bayraktarov et al. (2016b), an EndNote (Version X8.1; Thomson Reuters.) search was then performed within the full text using the search terms "(cost* OR feasib* OR surviv*)." Additional information was gathered by following citations, personal communications, and inspecting diverse restoration databases and webpages. Reports included in the database were mostly from the published literature but also included some information from webpages and personal communications. English was the primary language in which the restoration projects were described with a few exceptions in Spanish. The updated database consisted of 275 studies of which 64% were scientific papers published in journals and 36% included other reports (e.g., books, book chapters, conference proceedings, reports, webpages, and personal communication).

Data were extracted from each primary study (publications describing original research) where each study described one restoration project. The first observation representing a study in the database was used for analyses. An exception was the study by Edwards and Gomez (2007), which contained information on five independent restoration projects which were sufficiently described to enable data extraction from the same source for multiple projects. Secondary sources, reviews or guideline papers were excluded because these studies usually lack the level of detail required for data extraction to inform motivations, variables measured or restoration outcomes.

For the present study, 275 primary (original research) and secondary (research referring to original research e.g., reviews) restoration studies across the five ecosystems—coral reefs (87), seagrass (57), mangroves (64), saltmarsh (33), and oyster reefs (34)—met the above search criteria. These were further refined to 186 primary studies (75 coral reefs; 30 seagrass; 38 mangrove; 23 saltmarsh; 20 oyster reefs) to determine motivations, variables measured, outcomes reported, funding sources and alignment with the six standards for the practice of ecological restoration described by McDonald et al. (2016) (see methods, below). Projects were carried out in 57 countries (**Figure 1**), of which 27 had high-income economies, 17 had upper-middle income economies, 10 had lower-middle income economies and two were from countries with a low income economy as defined by The World Bank (2014).

Motivations for Engaging in Marine Coastal Restoration

For each entry in the database, the motivations of the authors to engage in marine coastal restoration were assigned to five categories adopted from Clewell and Aronson (2006). For example, enhancing or increasing biodiversity is a *biotic* motivation to restore coral reef habitat and improve resilience to ocean warming and acidification (McLeod et al., 2019). Other examples for biotic motivations are an increase in the number of native species (e.g., for saltmarsh), habitat creation, ecosystem connectivity, and increasing the ecological resilience of the ecosystem (**Table S1**). Improving the approach to restore coral reefs by harvesting and culturing wild coral-spawn slicks to apply at large, industrial scales (Doropoulos et al., 2019) is an *experimental* (or heuristic) motivation. Building community awareness, involvement, a shared responsibility for the restoration site, and creating jobs through restoration activities is an *idealistic* motivation for the restoration of coral reefs (Kittinger et al., 2016). Marine ecosystem restoration required to offset biodiversity in order to comply with an environmental policy (Jacob et al., 2018) is a *legislative* (or technocratic) motivation. The provision of ecosystem services is an important *pragmatic* motivation worldwide, for example community-based restoration of mangroves in Indonesia for storm protection (Brown et al., 2014), and oyster and coral reef restoration for fisheries production (Gilby et al., 2018).

To identify motivations or reasons for restoration we screened for key words like *objective, purpose, goal, success, intent, aim, focus, intention, aspiration, direction, target*. Motivations for each marine coastal restoration project were classified as *biotic*; *experimental*; *idealistic*; *legislative*; and/or *pragmatic* (see examples for motivations in **Table S1**) following Clewell and Aronson (2006) and Bayraktarov et al. (2019). These five categories are not necessarily mutually exclusive but comprise a categorization that facilitates their systematic description (Clewell and Aronson, 2006).

Variables Measured

The methods of each study were inspected to extract variables measured during monitoring of the restoration sites. Variables were grouped to specific "sub-attribute categories" (e.g., survivorship) which were nested within broader "attribute categories" (e.g., ecosystem function) (**Table S2**) modified from the International Standards for the Practice of Ecological Restoration (McDonald et al., 2016). Following these standards, the variables survival, growth and productivity were categorized under the attribute "ecosystem function." These variables have been categorized as variables measuring the biological response of the ecosystem to the restoration interventions in other studies e.g., Hein et al. (2017).

Variables measured during monitoring of the restoration sites included those related to ecosystem function and processes (e.g., survival, reproduction, growth, and productivity), but also the physical environment of the site (e.g., temperature, turbidity, and pH), the level of threats (e.g., invasive species, predators, and physical damage), as well as social and socio-economic variables (**Table S2**).

Restoration Outcomes

The type of restoration outcome was described after searching the abstract, results, and discussion of each study. We categorized the reported outcomes of each restoration project as ecological, economic, social, or as a combination thereof following Wortley et al. (2013).

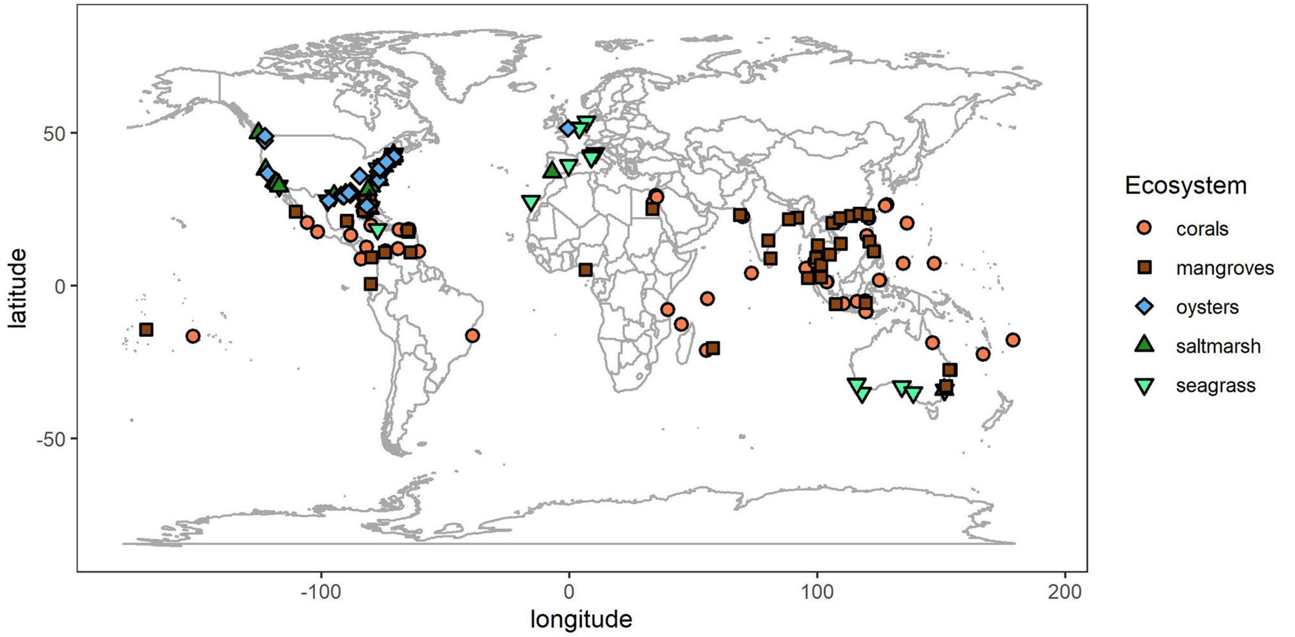

FIGURE 1 | Locations of all marine coastal restoration projects in the database.

Standards for Ecological Restoration

Each project was searched for whether it aligned (fully or partially) with any or all of the six standards for the practice of ecological restoration (McDonald et al., 2016). We modified the six standards for practical reasons to: (1) having a reference ecosystem to compare restoration progress against a reference; (2a) having clear targets and goals, as well as SMART (specific, measurable, adequate, repeatable, and time-bound) restoration objectives; (2b) having specific and measurable indicators to evaluate targets, goals, and objectives; (2c) employing adaptive management of the restoration site; (3) assessing the capacity for natural recovery of the ecosystem prior to restoration intervention; (4) aiming for full ecosystem recovery; (5) drawing from all relevant knowledge including science, practice and traditional knowledge; and (6) having early and ongoing stakeholder engagement with communities and end-users. Active adaptive management incorporates uncertainty and the process of iterative learning about the system being managed, which leads to better decisions (McCarthy and Possingham, 2007). We added the adaptive management component to complement the SER standards which did not include this principle. Because of the differences in time periods between SER standards (2016) and studies assessed (1974–2018), we did not search for wording of the six standards verbatim but the "philosophy" or scientific "intent" behind them. A full list of all categories and extraction rules are included in the (**Table S3**). Primary studies were categorized into whether they addressed each of the standards by SER, only addressed them partially and whether they have not addressed them at all. "Partially" often means that a certain component was missing in order to fully address the specific standard. For instance, studies that only partially addressed the standard of "having clear targets and goals, as well as SMART restoration objectives" often had clear restoration objectives, but those objectives were not time-bound.

Financial Contributors of Marine Coastal Restoration Projects

Following the methods by Bakker et al. (2010), we extracted data from the acknowledgments section of each primary study and identified the funding sources as a combination of: (1) government funding, (2) non-government funding, (3) private investments by businesses, individuals or philanthropy, and (4) projects supported by volunteer labor.

RESULTS

Motivations of Scientists to Engage in Marine Coastal Restoration

The most common primary motivation to engage in restoration across all five ecosystems was experimental i.e., to further ecological knowledge and improve restoration techniques. Sixty-seven percent (50 studies out of 75) of the primary studies investigating coral reef restoration followed this rationale with 63% for seagrass (19 out of 30 studies), 24% for mangroves (9 out of 38 studies), 48% for saltmarsh (11 out of 23 studies), and 85% for oyster reefs (17 out of 20 studies) (**Figure S1a**). The second most predominant motivations were biotic, i.e., to enhance biodiversity, and legislative, i.e., to restore the ecosystem after environmental impact such as ship grounding or oil spill as well as for biodiversity offsets. Only a small number of studies followed the pragmatic motivation to enhance ecosystem services. Six mangrove studies were motivated by enhancing coastal protection through restoration, while three studies on

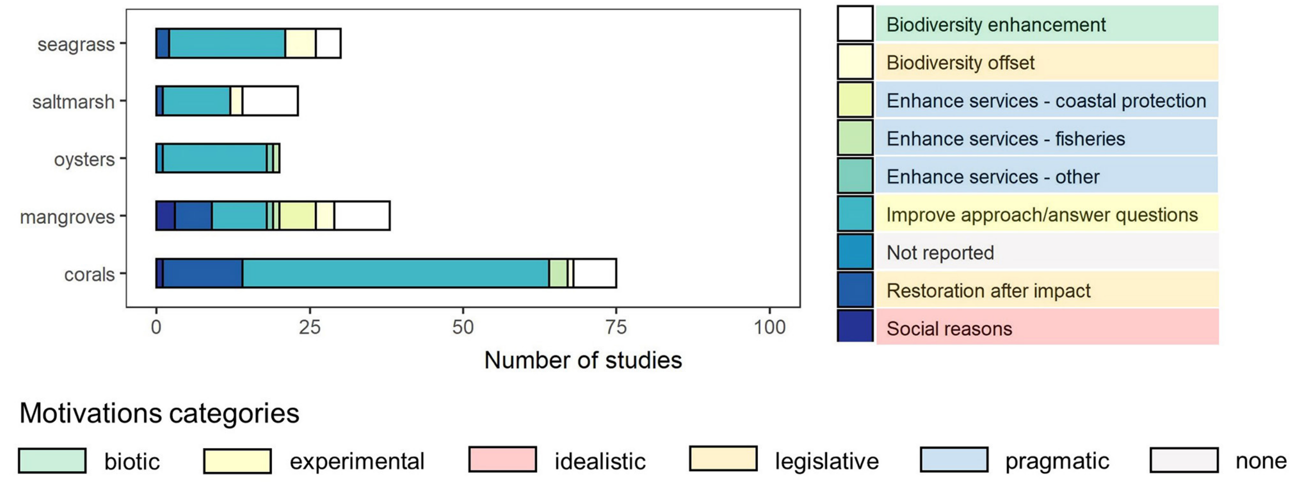

FIGURE 2 | Primary motivation for marine coastal restoration aggregated by ecosystems for restoration studies. The total number of primary studies: $n = 186$. The motivation categories biotic, experimental, idealistic, legislative, and pragmatic are color coded.

coral reefs, one oyster reef restoration study and one mangrove study aimed to increase fisheries production from restoration.

Primary motivations varied among ecosystems, with the most common motivations in mangrove projects being biotic (i.e., biodiversity enhancement) while in oyster, coral, saltmarsh and seagrass studies, projects were most often motivated by the experimental rationale (i.e., improving restoration approaches, technology and methods and answering ecological research questions) (**Figure 2**). Restoration projects of coral reefs had the largest proportion of studies with experimental motivations. Projects for oyster reefs were the only projects that did not include biotic motivations. These were largely motivated by the experimental rationale, as well as pragmatic (e.g., ecosystem services), and to a lesser degree idealistic (e.g., social) reasons. Note that only the primary motivations are described here, while also information on secondary and tertiary motivations are available in the database as well as an analysis in (**Figure S1**).

Alignment With Standards for Ecological Restoration

We identified a mismatch between the six standards proposed by McDonald et al. (2016) and the characteristics of the projects, implemented between 1974 and 2018. None of the projects (which were implemented between 1974 and 2018) aligned with all six standards proposed by McDonald et al. (2016). Only the standards of having a reference site; clear, SMART targets and goals; and specific and measurable indicators to track progress were recorded in the studies (**Figure 3**).

Variables Measured

The most common attribute category of variables measured was "ecosystem function" (**Figure 4**), which mostly described the sub-categories growth/productivity (assessed 387 times); survivorship (151 times); habitat function (130 times); but also physical attributes (79 times); and reproduction (75 times) were often assessed (**Table 1**).

Restoration Outcome

Ecological outcomes were the most commonly reported outcomes (79.0% of all primary studies, **Figure 5**). Some studies reported an ecological and social outcome (10.2%). Only 2.2% of the overall studies reported a combined ecological, social and economic outcome. Mangrove ecosystems were the only ecosystem for which all types of outcomes i.e., ecological, social and economic as well as combinations thereof were reported. Studies of the other ecosystems reported predominantly ecological outcomes; seagrass (93.3%), saltmarsh (91.4%), oyster reefs (85.0%), and coral reefs (77.3%) (**Table 2**).

Financial Contributors

Restoration projects were primarily funded by government agencies (92 of 186 studies) or government agencies in combination with other funding institutions (149 studies). Few studies were funded exclusively by non-government organizations (NGO) (four studies) or private organizations (10 studies), and no studies were supported exclusively through volunteer effort. Sixty-four studies reported multiple funding types and 16 studies did not acknowledge any funding (**Figure 6A**). Government funding was the largest contributor to restoration for each individual ecosystem, funding 83% of coral projects (62 of 75 studies), 82% of mangrove projects (31 of 38 studies), 90% of oyster projects (18 of 20 studies), 78% of saltmarsh projects (18 of 23 studies), and 67% of seagrass projects (20 of 30 studies). Coral reef restoration projects also had a large contribution of funding by NGOs (19 studies) and by donations and investments from private businesses (15 studies). The investment by NGOs vs. unpaid volunteers was equivalent for mangrove restoration projects (11 studies each). For oyster reef restoration projects volunteer-funded projects (11 studies) exceeded NGO (eight studies), and private funding (five studies). Saltmarsh and seagrass had only a few NGO and volunteer-based projects. Seagrass had a relatively small proportion of investment by private donations or businesses (seven studies) (**Figure 6B**).

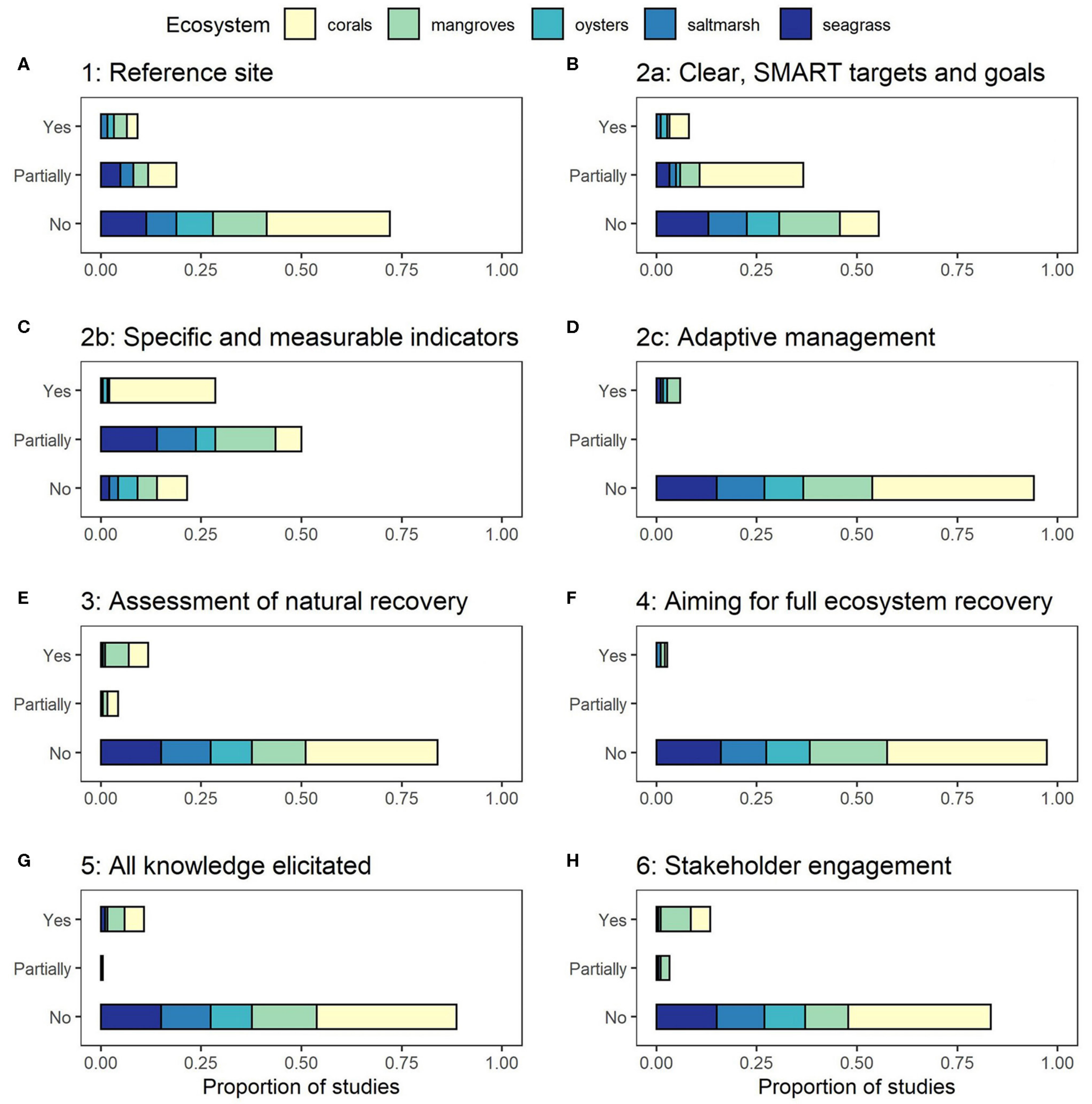

FIGURE 3 | Proportion of studies following the six standards for the practice of ecological restoration proposed by the Society for Ecological Restoration (SER) (McDonald et al., 2016). Studies were assessed based on the standard categories: **(A)** Reference site, **(B)** Clear, SMART targets and goals, **(C)** Specific and measurable indicators, **(D)** Adaptive management, **(E)** Assessing of natural recovery, **(F)** Aiming for full ecosystem recovery, **(G)** All knowledge elicited, and **(H)** Stakeholder engagement.

DISCUSSION

Based on a published database of primarily published literature, we found that scientists who engaged in marine coastal restoration globally were mainly motivated by experimental reasons i.e., to improve the restoration approach and/or answer ecological questions. This differs from the survey results obtained from terrestrial restoration practitioners across Australia, who were mainly motivated by biodiversity enhancement and also biodiversity offsetting, water quality improvements, and social reasons (Hagger et al., 2017). It is yet to be explored whether surveying marine coastal practitioners would lead to similar results. Our results based on the scientific literature may reflect a lag in development of the field, where restoration

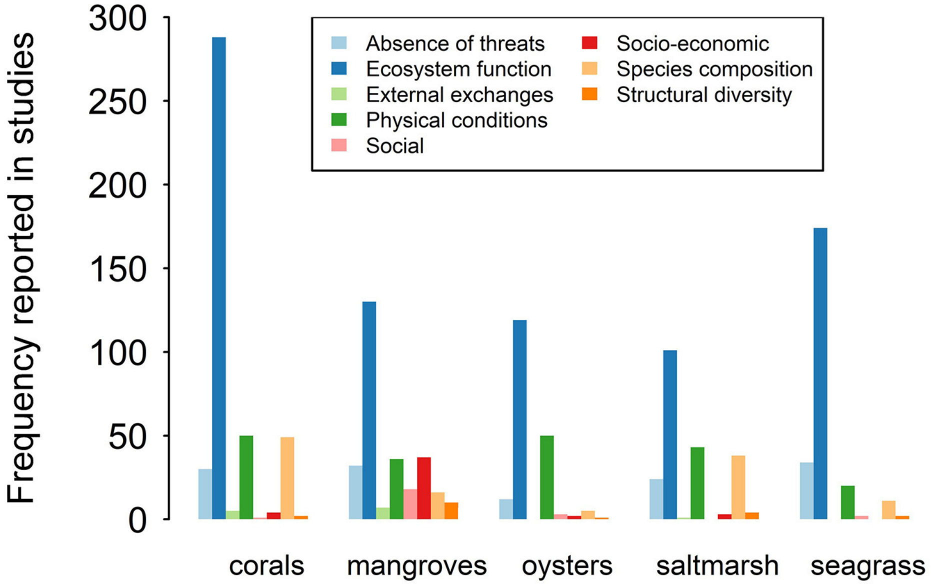

FIGURE 4 | Attribute categories of the variables measured to assess the restoration studies.

approaches for coral, kelp and seagrass in particular are still in the proof-of-concept phase, focused at small-scale experimental interventions (Bayraktarov et al., 2016a) and not yet (widely) aiming to maximize biodiversity or the provision of ecosystem services. This finding might also be biased by the difference in motivation of those who do research with publication as a key motivation (i.e., scientists and students), vs. those involved in the practice and operationalization of large-scale restoration projects (NGOs, natural resource management bodies, community groups, governments, consultants, developers etc.). For example, a study that used a systematic review to assess the global literature of marine coastal restoration found that ca. 84% of published studies included an author affiliated with a university (Zhang et al., 2018).

It is also questionable whether restoration for the purpose of methodology development should be considered "restoration" *sensu stricto* as per definition of the Society for Ecological Restoration (SER). Projects aiming at an improvement of the restoration approach are typically carried out at small scales (Bayraktarov et al., 2016a) and do not aim to achieve a full ecosystem recovery (this study). We observed that restoration of coral reefs in low income and lower-middle income countries followed the experimental rationale, however, this was only the case for seven studies on mangrove restoration. In countries with low and lower-middle income economies, mangrove restoration was motivated by pragmatic, biotic, social and legislative reasons, potentially due to the growing interest in carbon storage, livelihood creation and nature-based solutions (Grabowski and Peterson, 2007; Greiner et al., 2013; Cohen-Shacham et al., 2016; Macreadie et al., 2017). All records on the restoration of seagrass, saltmarsh and oyster reefs in our database were from countries with a high or upper-middle income economy and cases from countries with low and lower-middle income economies remain unknown to the published literature.

Motivations of scientists to engage in marine coastal restoration vary among ecosystems. While the restoration of most ecosystems described here were motivated by an experimental rationale, mangrove restoration differed in that projects were equally motivated by biotic, experimental, and pragmatic rationales. Mangrove restoration projects also deviated in the type of outcomes reported. While projects for most ecosystems reported a purely ecological outcome, mangrove restoration research often considered socio-economic implications of the restoration intervention and had the highest proportion of social and socio-economic variables included as metrics of achieving outcomes. Many of the published studies recommended greater efforts to incorporate social, economic, and cultural factors in assessing the effectiveness of ecological restoration e.g., Ruiz-Jaen and Mitchell Aide (2005), indicating that this is a priority for future marine restoration practice. Restoration of mangroves is less expensive, has been accomplished over larger areas, and it has higher survival of restored organisms than the other coastal ecosystems (Bayraktarov et al., 2016a). Failures of mangrove restoration have occurred, but this has been largely associated with poor site selection, often driven by social factors (Lee et al., 2019). The feasibility of mangrove restoration may be due to being practiced for a relatively long duration (since at least 1977, with reforestation of mangroves dating back to the early 1900s, Primavera and Esteban, 2008) and has efficient methods, while restoration of other marine coastal ecosystems may need to mature. The maturity of mangrove restoration was evident in the reduced focus on improving methods compared to the other ecosystems. There also

TABLE 1 | Number of primary restoration projects reporting on variables grouped under the following sub-attribute categories.

Sub-attribute category	Coral reefs	Mangroves	Oyster reefs	Saltmarshes	Seagrasses
Growth, productivity	140	53	54	43	97
Survivorship	66	27	23	10	25
Habitat function	52	18	16	29	15
Physical attributes	19	10	14	21	15
Reproduction	13	21	11	10	20
Biological threats	23	8	6	11	8
Physico-chemical variables (water)	18	3	26	5	3
Physical disturbance	4	8	6	8	21
Physico-chemical variables (soil)	0	20	5	14	0
Socio-economic attributes	0	34	2	0	0
Species make-up, diversity and distribution	6	5	1	12	5
Growth, productivity of species	8	4	0	15	1
Survivorship of species	22	3	0	3	0
Nutrient cycling	3	3	0	3	13
Engagement	1	14	3	0	2
Recruitment/succession of species	11	4	0	4	1
Health/condition	1	3	6	5	2
Rate of sedimentation	13	0	2	0	0
Response to environmental stress	14	0	1	0	0
Contamination	3	9	0	1	0
Strata diversity	1	6	1	4	1
Physico-chemical threats	0	3	0	1	5
Environmental variables	0	2	3	3	0
Hydrological connectivity	0	7	0	1	0
Species composition (non-target ecosystem flora)	0	0	0	4	4
Restoration costs	4	0	0	3	0
Awareness	0	7	0	0	0
Coastal protection	0	5	2	0	0
Diversity of growth forms	1	4	0	0	1
Growth, productivity (adjacent ecosystem)	0	0	6	0	0
Genetics/gene flow	5	0	0	0	0
Anthropogenic threats	0	3	0	2	0
Environmental threats	0	1	0	1	0
Species composition (adjacent ecosystem)	0	0	2	0	0
Species composition (non-target ecosystem fauna)	0	0	2	0	0
Potential nutrient enrichment	0	0	0	0	2
Sediment trapping	0	0	0	0	2
Species composition (non-target ecosystem flora or fauna)	1	0	0	0	0
Health/Condition	0	1	0	0	0
Physico-chemical variables	0	1	0	0	0
Growth, reproduction	0	0	1	0	0
Genetic relationships	0	0	0	1	0

The numbers correspond to times a sub-attribute was recorded by the studies (i.e., a single study can report multiple variables belonging to the same sub-attribute). The sub-attributes are ordered from most frequently recorded to least frequently recorded across all five ecosystems.

tended to be higher levels of involvement of communities and support by volunteer labor in mangrove restoration (Brown et al., 2014) which may also contribute to successful projects at larger spatial scales. Greater accessibility to the restoration sites by communities may also contribute to enhanced success of mangrove restoration which can be carried out by fishermen and small boats, in comparison to ecosystems like coral reefs, oyster reefs and seagrass which require underwater activities and other logistics (e.g., divers, SCUBA equipment).

This analysis included three main biases inherent in the database: (1) a large number of papers in the field of research

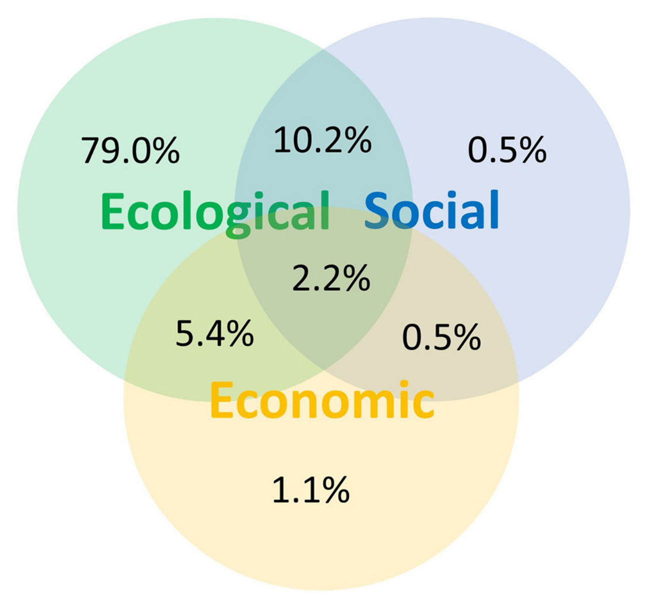

FIGURE 5 | Breakdown of outcomes reported by studies on the restoration of coral reefs, seagrass, mangroves, saltmarsh, and oyster reefs.

of marine coastal restoration are omitted due to a relatively narrow scope provided by the original search terms ("cost," "feasibility," and or "survival"); (2) much of the knowledge from practitioners who conduct restoration, and whom have less incentive to publish in the literature, are omitted; (3) the database is comprised of records mainly in English and a few entries in Spanish. Despite these limitations, the analysis is systematic and repeatable, and the biases are consistent across the five ecosystems. Therefore, while the results may not paint a complete picture of the motivations for marine ecological restoration in general, and do not canvass the full body of literature in the field, the results can be used to compare general trends for scientists studying restoration across the five coastal ecosystems. A more comprehensive search that goes beyond the publication bias, capturing newspaper articles, newsletters, social media posts, blogs, YouTube videos, and incorporates targeted interviews with marine coastal restoration practitioners may yield different results because it would represent the motivations of the wider restoration community.

The focus of restoration on experimental motivations may not be surprising when data are assessed from the published scientific literature. Many restoration practitioners may not publish results because of limited resources, and thus their motivations for restoration may differ from what we have found in our assessment of the scientific literature. This is a general trend in conservation where there is still a gap between conservation science and practice (Sunderland et al., 2009; Milner-Gulland et al., 2010). Studies where motivations were gleaned by surveying restoration practitioners have found primarily biotic, pragmatic or social rationales for restoration, e.g., Bernhardt et al. (2007) and Hagger et al. (2017). Information on large-scale restoration and in countries where English is not the main language is often not published, with only few exceptions, e.g., Bayraktarov et al. (2020), and we may be missing out on more than 35% of the knowledge in conservation if peer-reviewed literature searches are restricted to English (Amano et al., 2016). Another caveat is that funding provided by the research institution in terms of salaries and facilities are rarely acknowledged in a scientific publication. The results presented here may largely ignore the contributions of academic institutions and academics who often volunteer their time to carry out the research.

The most common metrics recorded in marine coastal restoration research were growth/productivity, survivorship, habitat function, physical attributes and reproduction. This is in line with plant survival being the most commonly used metric in terrestrial restoration practice, followed by absence of weeds or pest animals, plant species diversity, and vegetation cover (Hagger et al., 2017). Assessments based on peer-reviewed literature show that restoration progress is commonly reported by variables related to biodiversity, vegetation structure or ecological functions (Ruiz-Jaen and Mitchell Aide, 2005; Basconi et al., 2020). Expanding the variables monitored in marine coastal restoration (e.g., monitoring ecosystem function or ecosystem services more effectively than simply assessing growth/productivity and survival) is an important step toward capturing socio-economic outcomes, to improve the effectiveness of restoration and alignment with the motivations of stakeholders sectors such as fishing, aquaculture, governments, tourism and water utilities/managers (Fonseca et al., 2000; Paling et al., 2009; Basconi et al., 2020).

Restoration projects presented here were primarily funded by government agencies, either alone or in combination with other funding contributors. Restoration forms part of many government and non-government environmental programs, and is implemented by a diverse range of stakeholders, from community groups and not-for-profit organizations, to private companies and government agencies (Hobbs, 2017; Maron and Louis, 2018). Increased diversification of financing will be required to enable wider adoption and scaling-up of marine coastal restoration, to meet ambitious recent targets (e.g., increasing the global mangrove area by 20% by 2030 within the 'Global Mangrove Alliance' – a coalition of global conservation organizations Waltham et al., 2020). Opportunities such as market-based mechanisms to fund marine coastal restoration, including payment for ecosystem services (e.g., carbon storage or nutrient cycling) may increase resources available for restoration (Basconi et al., 2020). Additionally, a combination of government funding in conjunction with supportive policy has been found to leverage substantial private funding for large-scale marine coastal restoration in the USA, an approach which could be more widely implemented (Waltham et al., 2020). For example, the "Mangroves for the Future" program, established under the International Union for the Conservation of Nature (IUCN) and the United Nations Development Program, and involving many institutional partners, have promoted large-scale planting of mangroves throughout Southeast and South Asia.

Most of the projects we assessed did not address the six key standards of the International Standards for the Practice

TABLE 2 | Percentage of outcome categories reported.

Outcome	Coral reefs	Seagrass	Mangroves	Saltmarsh	Oyster reefs
Ecological	77.3	93.3	60.5	91.4	85.0
Social	0	0	2.6	0	0
Economic	0	0	5.3	0	0
Ecological & social	13.3	6.7	15.8	0	5.0
Ecological & economic	8.1	0	5.3	4.3	5.0
Social & economic	0	0	2.6	0	0
Ecological & social & economic	1.3	0	7.9	0	0
None	0	0	0	4.3	5.0

The number of studies used for analysis was n = 75 for coral reefs, n = 30 for seagrass, n = 38 for mangroves, n = 23 for saltmarsh and n = 20 for oyster reefs.

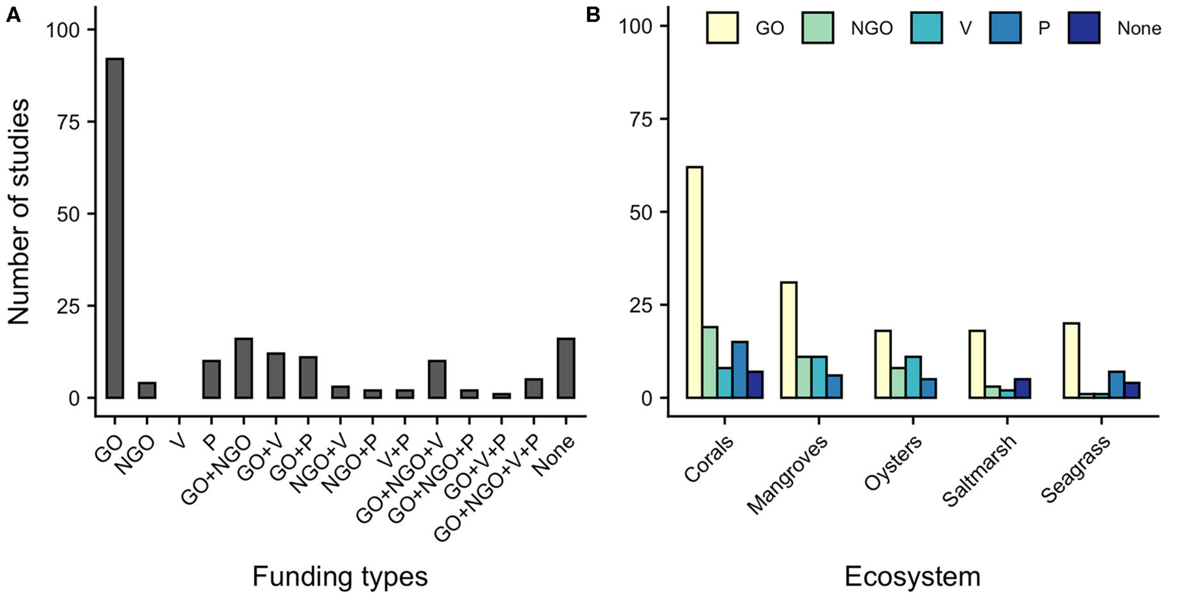

FIGURE 6 | Type of financial contributors to marine coastal restoration projects extracted from the acknowledgments of each primary study. **(A)** Shows the combination of funders across all studies (*n* = 186). **(B)** Shows the number of studies by ecosystem that had support from each funding type (note: a single study can be represented in multiple bars if it received funding from multiple sources). Abbreviations: GO, governmental; NGO, non-governmental; V, supported by volunteers; P, supported by private organizations or businesses, and None, no funding reported.

of Ecological Restoration by McDonald et al. (2016). This is not necessarily surprising, given that the standards were first released in late 2016, while the restoration projects described here were implemented between 1974 and 2018, and that two thirds of the studies were motivated by experimental reasons. The earliest studies in our database were published in 1974 by seagrass, followed by 1977 for mangroves, 1988 for saltmarsh, 1991 for coral reefs and 1999 for oyster reefs. While the limited number of projects and studies prevented us from assessing changes in adoption of the SER concepts embedded in projects over time, our study provides a baseline assessment from which future studies can assess changes in the application of best practices in restoration projects, which are key to scaling-up restoration of marine coastal ecosystems and achieving economies of scale (Gillies et al., 2015; Bayraktarov et al., 2016a; McDonald et al., 2016; van Katwijk et al., 2016). Nevertheless, it should be noted that there are other, equally valuable reasons for restoring marine and coastal habitat that go beyond SER's goal of reaching full ecosystem restoration, which may expand future restoration initiatives. Examples include restoration for socioeconomic and cultural benefits (Kittinger et al., 2016), building/engineering with nature for green infrastructure and urbanization control (Vargas-Hernández and Zdunek-Wielgołaska, 2020) or to explore the value of reconstructed novel ecosystems (Hobbs et al., 2006) as nature-based solutions for climate change mitigation and adaptation (e.g., for costal protection, Reguero et al., 2018).

The hurdles that many marine coastal restoration practitioners experience are typically not related to the restoration approach or technique but rather deal with finding agreements between the different stakeholders involved, having a policy framework which allows for the implementation of the restoration projects, a clear legislation related to biodiversity offsets, and competition between different organization carrying out restoration (Menz et al., 2013; Gillies et al., 2015; Waltham et al., 2020; Stewart-Sinclair et al. submitted). To increase access to information on practitioner-led restoration activities and showcase how barriers to marine coastal restoration can be overcome, we recommend that practitioners connect with existing coastal ecosystem networks, such as the Global Mangrove Alliance or Seagrass Watch, and encourage data sharing (Worthington et al., 2020). Better guidance for data gathering and monitoring would assist in disseminating information and evaluating outcomes to support future funding.

CONCLUSION

Our work based on systematic literature review suggests that the restoration of marine coastal ecosystems is a developing field of conservation, with the scientific community still largely motivated by evaluation of experimental approaches. While the restoration of some ecosystems (e.g., coral reefs, seagrass, saltmarsh, and oyster reefs) may still be in a rapidly developing proof-of-concept phase, the scientific community carrying out mangrove restoration has begun to be motivated by, and engage in, a broader consideration of socio-economic and other benefits, similar to motivations reported for restoration of terrestrial ecosystems. We found that government funding supports most projects with matching involvement from a range of other sectors. Increased involvement from other sectors could increase resources available for marine and coastal restoration which may push restoration science along a developing trajectory beyond small-scale experimental studies. We show that marine coastal restoration research is still much focused on experimental work, while it requires a better alignment with the real needs for scaling-up future efforts such as counteracting the biodiversity decline, solving issues around biodiversity offset policy, reaching resilience goals by providing ecosystems services for climate change adaptation and mitigation to humans, and achieving community acceptance and participation. More science on the socio-economic benefits from restoring marine coastal ecosystems is needed to be able to connect restoration research to policy and people.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the Dryad Digital Repository: https://datadryad.org/stash/share/MKbsS4eQh7w5RjXK4_wXZJawc-gAvdA_FhGvJk0VlPE.

AUTHOR CONTRIBUTIONS

EB, SB, VH, and KW conceived and designed the research. EB and SB carried out data extraction from the published literature. EB, CS, and VH analyzed the data. EB, SB, VH, CS, CL, KW, CG, AS, and MS wrote and edited the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00484/full#supplementary-material

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Playing to the Positives: Using Synergies to Enhance Kelp Forest Restoration

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Kelp forests are highly productive foundation species along much of the world's coastline. As a result, kelp are crucial to the ecological, social, and economic well-being of coastal communities. Yet, due to a combination of acute and chronic stressors, kelp forests are under threat and have declined in many locations worldwide. Active restoration of kelp ecosystems is an emerging field that aims to reverse these declines by mitigating negative stressors and then, if needed, introducing biotic material into the environment. To date, few restoration efforts have incorporated positive species interactions. This gap presents a potential shortcoming for the field as evidence from other marine ecosystems illustrates that the inclusion of positive species interactions can enhance restoration success. Additionally, as the climate continues to warm, this approach will be particularly pertinent as positive interactions can also expand the range of physical conditions under which species can persist. Here, we highlight how practitioners can use positive density dependence within and amongst kelp species to increase the chances of restoration success. At higher trophic levels, we emphasize how co-restoring predators can prime ecosystems for restoration. We also investigate how emerging technologies in genetic and microbial selection and manipulation can increase the tolerance of target species to warming and other stressors. Finally, we provide examples of how we can use existing anthropogenic activities to facilitate restoration while performing alternative purposes. As kelp forests continue to decline and the field of kelp restoration continues to develop, it is also important that we monitor these potential advancements and ensure they do not have unintended ecosystem effects, particularly with untested techniques such as genetic and microbial manipulations. Nevertheless, incorporating positive species interactions into future restoration practice stands to promote a more holistic form of restoration that also increases the likelihood of success in a shifting seascape.

Keywords: kelp, restoration, positive species interactions, facilitation, synergy

INTRODUCTION

Significance, Threats, and Declines of Kelp Forests

Kelp, defined here in the broad sense as large brown seaweeds from the orders Laminariales, Fucales, Desmarestiales (Wernberg and Filbee-Dexter, 2019), are habitat-forming marine macroalgae that form the basis for some of the most productive ecosystems in the world's sub-tropical, temperate and polar seas (Dayton, 1975; Coleman and Wernberg, 2017; Smale et al., 2019; Wernberg et al., 2019). These habitat formers provide a complex three-dimensional habitat (Miller et al., 2018; Layton et al., 2019) that support other macroalgal species (Melville and Connell, 2001; Wernberg et al., 2005), fish, and invertebrates many of which are commercially valuable, e.g., abalone, and lobsters (Graham et al., 2007; Marzinelli et al., 2014; Teagle et al., 2017; Olson et al., 2019). Kelp is also a valuable food source, both through the production of live tissue and of detritus that is often exported to other ecosystems (Dayton, 1985; Bustamante et al., 1995; Bishop et al., 2010). Exportation of carbon into deep sea sediments, combined with their high productivity means kelp can act as a valuable carbon sink (Chung et al., 2013; Filbee-Dexter et al., 2018; Queirós et al., 2019). Other ecosystem services include wave attenuation and reductions in coastal erosion, services that are increasingly important under climate-mediated sea level rise and increases in extreme storm events (Smale et al., 2013). Many kelp species are also part of a wild or farmed harvest economy (Vásquez et al., 2014), are efficient nutrient cyclers (Graham et al., 2007), and provide recreational and cultural value (Smale et al., 2013). Based on these services, kelp ecosystems are currently valued at ~1 million USD per kilometer of coast per year, though these values are considered underestimates (Wernberg et al., 2019).

Given the great ecological and economic importance of kelp forests, there is growing concern about their disappearance from the world's oceans. Krumhansl et al. (2016) found that laminarian populations in 38% of studied ecoregions had declined over several decades. Compounding the global average decline, several regions have experienced range contractions and near total losses of their kelp populations in the last 5–10 years (Bennett et al., 2015; Ling and Keane, 2018; Rogers-Bennett and Catton, 2019). These dramatic losses of kelp have already led to severe socioeconomic consequences and resulted in declines, closures or limitations of major fisheries, such as abalone fisheries in eastern Japan and California (Kiyomoto et al., 2013; Rogers-Bennett and Catton, 2019) and rock lobster fisheries in Australia (Hinojosa et al., 2014). An analogous synthesis does not exist for fucoid species, but there have also been notable local declines of *Phyllospora, Fucus, Sargassum,* and *Cystoseira* species throughout the world (Thibaut et al., 2005; Coleman and Wernberg, 2017). Natural recovery is not common and is not anticipated at a significant scale (Wernberg et al., 2019; Layton et al., 2020) so without intervention, the loss of kelp and their associated services will likely continue (Smale et al., 2019).

The causes of kelp forest decline and disappearance are complex and range from local, often mitigatable impacts, to global, irreversible changes over the course of decades (Smale et al., 2013; Schiel and Foster, 2015; Wernberg et al., 2019). At local scales, nutrient and contaminant inputs from untreated sewage and agricultural runoff can distribute toxic materials (Burridge et al., 1996; Coleman et al., 2008), increase abundances of competitors (Connell et al., 2008), and cause high turbidity that can prevent kelp from photosynthesizing (Reed and Brzezinski, 2009; Tait, 2019). Construction can also physically remove kelp from the seafloor (Cheney et al., 1994). Local biotic stressors can also play an important role in reducing kelp forest distributions. Overgrazing by herbivores has resulted in the marked decline of kelp forests in many locations around the globe (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015). The main actor, sea urchins, are a natural part of the kelp ecosystem, but their populations can increase in numbers when, for example, their predators (e.g., otters, fishes, lobsters) disappear from an ecosystem (Shurin et al., 2010), or when altered environmental conditions, such as warmer temperatures result range expansion to a new location (Ling et al., 2009). Furthermore, warm water herbivorous fishes have expanded their ranges in many parts of the world in response to ocean warming, causing declines in kelp populations (Vergés et al., 2014, 2019). Climate change poses a major threat to kelp forests, as most kelp are cool water species, and warming temperatures can push them beyond their physiological limit and either kill juvenile or adult plants or prevent further recruitment by killing the spores (Smale et al., 2019).

Ocean warming and other climate-related stressors cannot be mitigated over short time scales and may cause a re-evaluation of which populations are manageable under changing conditions (Coleman and Goold, 2019). For example, along the warm edge of the distribution of many species, management of kelp forests may entail supporting the expansion of naturally warm-adapted genotypes or even alien species. Alternately, management could work to expand the niche of native species, through more interventionist approaches such as introduction of new genotypes via assisted evolution (Coleman and Goold, 2019; Wood et al., 2019) or the introduction of species which are involved in positive species interactions.

Traditional Management Interventions in Kelp Forests

Kelp conservation has a long history and managers across the world have been working to conserve kelp forests since the 1800s (Fujita, 2011), mostly focusing on eliminating the causes of kelp decline such as kelp overharvesting (Buschmann et al., 2014) or water pollution (Coleman et al., 2008). Overharvesting can be a straightforward fix in systems that contain wild harvest industries (e.g., Chile, France, Japan), and appropriate management that regulates kelp extraction can allow for populations to return (Fujita, 2011; Buschmann et al., 2014; Frangoudes and Garineaud, 2015). Enhancing the water quality in an area can also slow kelp loss or sometimes allow it to return (Hawkins et al., 1999). While kelp restoration is not usually a focal motivation for implementing marine protected areas (MPAs) (Woodcock et al., 2017), MPA restrictions may limit the harvest of certain marine predators that can help control herbivore population and thus their installation may promote the resilience of kelp ecosystems (Ferrari et al., 2018). Only some MPAs and harvest restrictions have had success in restoring kelp populations, particularly where food webs are less complicated and there is no nutrient limitation or other stressors present, whereby increases in the populations of urchin predators such as sea otters or lobsters have had a positive cascading impact on kelp (Shears and Babcock, 2002; Watson and Estes, 2011; Caselle et al., 2018; Eger and Baum, 2020). Where kelp does not re-establish following such interventions (Barrett et al., 2009; Campbell et al., 2014a), restoration should be considered.

Restoration of Kelp Forests

Many attempts at preventing further losses of kelp have failed, accelerating the interest in both different forms of kelp forest restoration (Eger et al., 2020a). Successful kelp restoration projects are rare and costs have been high (Bayraktarov et al., 2016; Eger et al., 2020a; Layton et al., 2020). The majority of the work conducted thus far is at spatial scales of less than one hectare and over durations of less than 2 years, and the costs have often exceeded hundreds of thousands of US dollars per hectare (Eger et al., 2020a). Despite these limitations, there is an emerging interest in large scale kelp restoration from universities, non-governmental organizations, governments, and industries. Active efforts to restore kelp forests include the addition of kelp transplants, seeds, or habitat (via artificial reefs) to the marine environment (Basconi et al., 2020), but can also involve the removal of kelp consumers such as urchins and fishes (Terawaki et al., 2001; Tracey et al., 2015; Layton et al., 2020). The main techniques used in these early kelp restoration efforts have been a combination of passive restoration via first eliminating threats and active efforts that focus on supplementary activities such as transplanting (Wilson and North, 1983; Campbell et al., 2014a; Verdura et al., 2018). While these techniques will remain relevant, it is important to consider what further elements might enhance the chances of success and lower the costs of kelp forest restoration, which can be significant (Eger et al., 2020b).

Positive Species Interactions, Stress, and Kelp Forests

One promising method to complement previous ecosystem restoration methods is to incorporate positive species interactions and other synergies into the process. Positive species interactions occur between organisms where at least one individual benefits and the other individual is not harmed (e.g., mutualism, commensalism, facilitation, Bruno et al., 2003) and are increasing documented across almost all marine ecosystems (Thomsen et al., 2018; Gribben et al., 2019). There is now evidence from coastal marine ecosystems (coral reefs, salt marshes, mangroves, seagrasses) that positive interactions can work to enhance restoration success and reduce costs (Silliman et al., 2015; Shaver and Silliman, 2017; Renzi et al., 2019; Valdez et al., 2020). For example, Silliman et al. (2015) showed that enhancing positive interactions, and not suppressing competition was key to coastal wetland recovery. Not only did their facilitation focused planting orientation increase growth by 1–200% but it also reduced oxygen stress and increased resistance to wave erosion. Other examples are found in mangroves whereby clumping saplings also reduces oxygen stress (Gedan and Silliman, 2009). There are also some examples of facilitation between species, as ascidians and sponges growing on mangrove roots, can protect mangroves from isopod grazing (Ellison and Farnsworth, 1990).

According to the Stress Gradient Hypothesis, the frequency of positive interactions should increase with greater levels of stress (Bertness and Callaway, 1994). Positive interactions may thus become more important in the future as conditions become more stressful due to multiple, interactive abiotic (physical disturbance, temperature) and biological (e.g., predation) stressors (He et al., 2013; Wright and Gribben, 2017; Uyà et al., 2019). In particular, positive interactions can influence the physical conditions under which species persist, and thus have the potential to mitigate the effects of warming, drought or acidification on the distribution of species (Silliman et al., 2011; Angelini et al., 2016; Bulleri et al., 2016, 2018). For example, positive species interactions can help biogenic habitats such as salt marsh survive acute abiotic stresses such as drought (He et al., 2017) and might increase the thermal tolerance of some species such as corals to otherwise lethal warming events (Shaver et al., 2018). In intertidal systems, canopies of the fucoid *Ascophyllum nodosum* can reduce maximum summer rock temperatures in New England by up to 8°C (Leonard, 2000). The presence of such canopies also influences biotic processes and interactions of key grazers in the system (Marzinelli et al., 2012), which in turn can affect kelp recruitment (Hawkins and Hartnoll, 1983). Recognizing and encouraging these interactions may aid in successful restoration of kelp forest ecosystems, especially as ecosystems become more stressed and variable. While these interactions are not regularly considered in a kelp restoration context, there are some well-known positive interactions from ecological literature on kelp forests that may aid restoration efforts.

Interest in kelp restoration is increasing and it is important that managers consider the best available options for developing successful and cost-effective restoration. Incorporating positive species interactions into kelp restoration could help kelp recovery, but also accelerate the re-establishment of associated biodiversity (Angelini et al., 2016) and ecological processes (Thomsen et al., 2018). Given that kelp restoration is an emergent and fast-growing field, the opportunity exists to incorporate positive interactions into the development of management interventions and improve the likelihood of success of future efforts and their cost-effectiveness. The aim of this paper is to catalog known and potential positive interactions in kelp forests and provide context about how future kelp restoration efforts can use these interactions. Our work uses a combination of a structured literature review and expert knowledge to identify several different positive interactions under current and future conditions. These are: (1) facilitation between primary producers; (2) indirect trophic effects; (3) genotypic and microbial interactions; and (4) anthropogenic synergies. For each interaction, we review the existing knowledge for kelp forests and provide advice on how current and future restoration efforts can apply these.

METHODS

We first conducted a literature search using SCOPUS on July 12th, 2019, with the following search terms:

> kelp* OR seaweed* OR macroalga* OR Laminariales OR Fucales OR Desmarestiales
> AND
> species interact* OR biotic OR connect* OR link*
> AND
> positiv* OR benefic* OR facilitat* OR density dependen* OR mutalis* OR synerg* OR c
> ommensal* OR cascad*

The search returned 156 results. We then conducted a preliminary assessment for suitable papers that might (1) involve a species of seaweed from the order Fucales or Laminariales or Desmarestiales and (2) involve positive interactions (e.g., mutualism, synergism, commensalism). This process refined the initial search results down to 92 possible papers (**Figure 1**). We then read these papers to ensure they met the same two criteria, and if so, classified the positive interaction detailed in each paper to create a table of all identified positive interactions (**Supplementary Table S1**). We then created a final list of 14 interactions by combining the returned topics with suggestions from the authors (**Supplementary Table S1**). Each author then identified which six interactions they thought were most relevant to include. We created a final list of topics by selecting the interactions that had three or more votes; this process resulted in a final list of nine interactions (**Supplementary Table S2**). We removed the topics on facilitation cascades and settlement because insufficient material exists for kelp and we incorporated the topic "hypothesized interactions from other ecosystems" into the main text.

SYNERGIES IN KELP FOREST RESTORATION

Intraspecific Facilitation – Figure 2-1

There is strong evidence for positive density dependencies in kelp forests, with numerous studies showing that kelp populations have density thresholds that alter the environment and support future generations (Dayton, 1985; Harrold and Reed, 1985; Schiel, 1985; Pearson and Brawley, 1996; Anderson et al., 1997). Indeed, the slow recovery of kelp after large-scale losses (Kirkman, 1981; Toohey et al., 2007; Connell et al., 2008) is often attributed to the breakdown of these positive 'environment-engineer feedbacks' (Cuddington et al., 2009; Jones et al., 2010). Likewise, a failure to re-establish this intraspecific facilitation may explain the limited success of some previous kelp restoration efforts (Layton et al., 2019, 2020).

One pathway by which this feedback manifests is via the supply and dispersal of reproductive propagules in the environment. In general kelp species, across all three orders considered here, are poor dispersers and only have single generation dispersal ranges of 0.1–10 km (Chan et al., 2013; Schiel and Foster, 2015; Luttikhuizen et al., 2018). Additionally, populations need very high densities of adults to supply propagules to future generations (Dayton, 1985), which, in turn, can enhance fertilization (Pearson and Brawley, 1996). As a result, the lack of a local adult populations limits the unassisted range expansion of a single population as well as the regular long-distance dispersal of buoyant species such as Sargassum. Without adequate propagule supply to enhance recruitment success, the survival of those offspring is thus likely limited (Schiel and Foster, 2006).

The modification of the local physical and chemical environment by the adult kelp canopy can also facilitate the survival and development of juvenile conspecifics within the sub-canopy (Schiel and Foster, 2006; Layton et al., 2019). Degraded kelp canopies (e.g., reduced patch sizes or densities) lower the ability of the canopy to engineer the sub-canopy environment and can cause a reduction or break down of the positive feedback processes (Layton et al., 2019). In turn, this loss can lead to disruption and even collapse of the demographic processes of micro- and macroscopic juvenile kelp and can result in a total loss of habitat stability and resilience.

The importance of intraspecific facilitation, especially for juvenile kelp, might be greater in more stressful environments (Bertness and Callaway, 1994). At local scales, for instance, the importance of facilitation may relate to depth gradients in light, ice scour, or wave exposure (Kitching, 1941; Wood, 1987; Chapman and Johnson, 1990). At larger scales, gradients of abiotic stress across latitudinal gradients, due to changes in water temperature and irradiance, may be more important (Wernberg et al., 2011). Ultimately, the presence of adult kelp in stressful conditions can expand the realized niche of juvenile conspecifics beyond their fundamental niche, thus allowing juveniles to thrive in areas where they would otherwise perish in isolation (Bruno et al., 2003; Layton et al., 2019). This is likely to become more important in the future given projections suggest that the marine environment will become more stressful (Frölicher et al., 2018; Smale et al., 2019).

As we continue to improve and refine active restoration interventions, there are several ways to better harness and re-establish the internal processes that promote the stability of kelp forests. Given the importance of intra-specific facilitation for kelp patch expansion and dispersal (Schiel and Foster, 2006), future restoration attempts might be most successful when they occur nearby intact kelp forests, thus ensuring there is an adequate supply and exchange of propagules between neighboring populations. If new patches are being created, it would be prudent to orient them such that there is connectivity with nearby forests as to enhance the contributions of local propagule supply. Effective dispersal distances vary amongst species, with distances less than 1–2 km in genera such as *Saccharina, Alaria, Ecklonia, Sargassum,* and *Undaria* (Norton, 1992; Forrest et al., 2000; Serisawa et al., 2005; Chan et al., 2013; Akino et al., 2015; Luttikhuizen et al., 2018) but up to 10 km in *Macrocystis* (Reed et al., 2006). Smaller distances between populations may further enhance the likelihood of propagule exchange and restoration success.

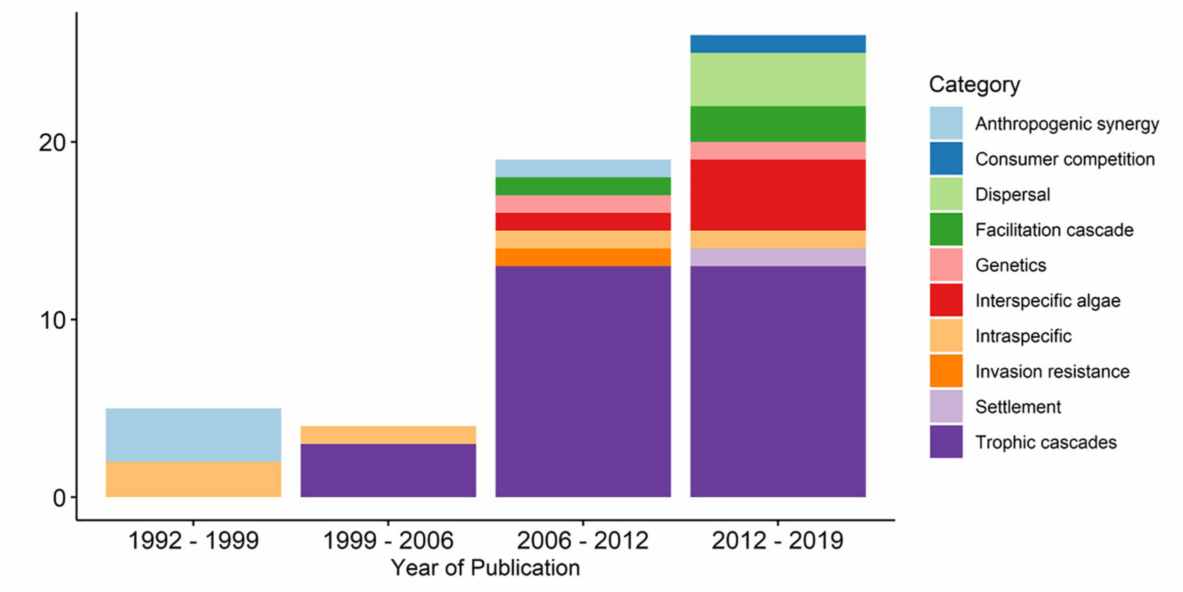

FIGURE 1 | Number of publications identified in the literature search by year and by category.

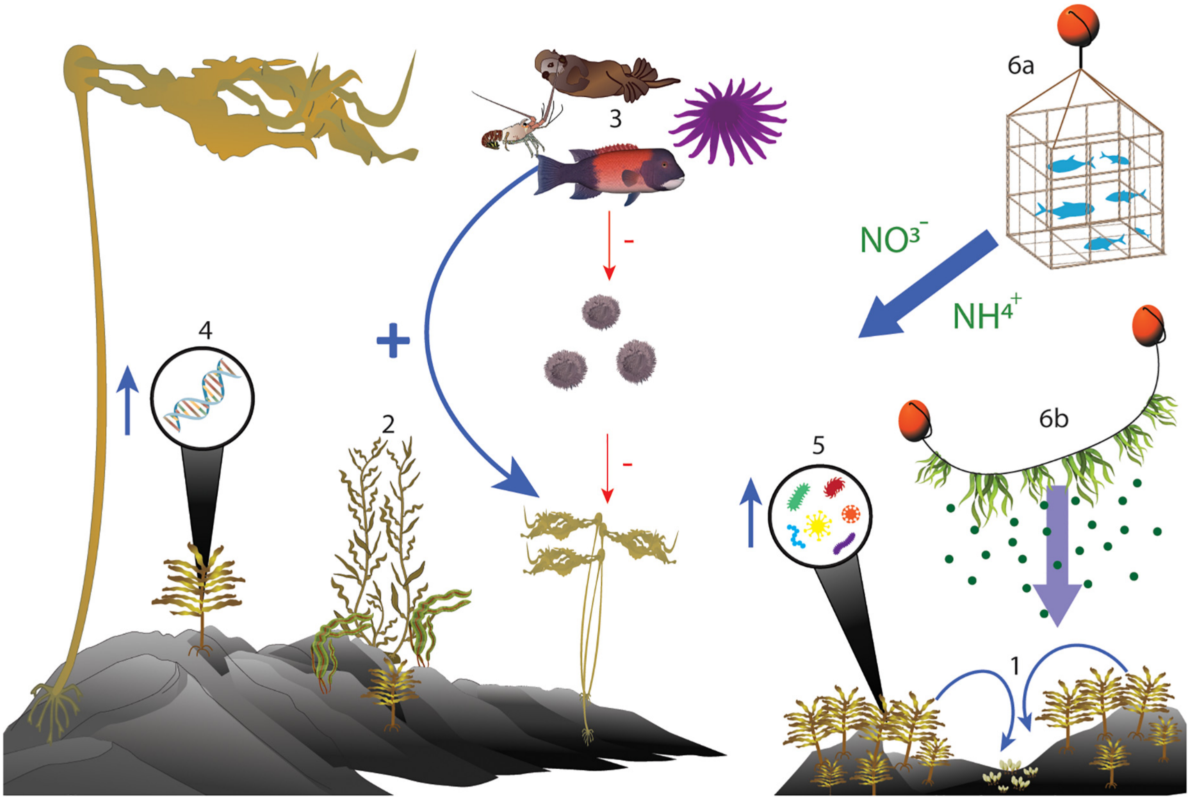

FIGURE 2 | Ecosystem diagram of different positive interactions that may be used in kelp forest restoration. 1: Intraspecific facilitation. 2: Interspecific foundation species facilitation. 3: Trophic cascades. 4: Genetic manipulation. 5: Manipulation of microbial communities. 6a: Fish farms and nutrient cycling. 6b: Kelp farms and spore supply.

Existing kelp canopies can be used in several different ways to facilitate restoration projects. For instance, managers can transplant kelp individuals or propagules to enhance existing but declining kelp populations and help re-establish positive density-dependent processes before they disappear. If successful, this approach avoids a phase shift to a barren or turf-dominated state, after which it may be more difficult to restore (Gorman and Connell, 2009; Johnson et al., 2017; Filbee-Dexter and Wernberg, 2018), and aids dispersal. In restoration attempts using propagules or juveniles, it may also be helpful to transplant (or outplant cultured) adult individuals to help prime the environment for the new recruits, though this step adds additional upfront cost. However, if it leads to increased survival, it can be more cost effective in the long term. Indeed, it seems for some species and locations that juvenile kelp do not recruit nor survive (if transplanted) in the absence of adult conspecifics (Layton et al., 2019). It is unlikely that enhanced intraspecific facilitation alone will be enough to help vulnerable populations survive water temperatures above their physiological threshold and these approaches may need to be applied along with the genetic techniques described in section "Genetics in Kelp Restoration – **Figure 2-4**."

Interspecific Facilitation – Figure 2-2

Facilitation cascades, whereby a habitat-forming species promotes a secondary habitat-former with positive effects on associated biodiversity, occur in almost all marine ecosystems (Thomsen et al., 2018; Gribben et al., 2019). Most studies on facilitation cascades have focused on synergistic effects of positive interactions among habitat-forming species on the overall biodiversity they support. In contrast, few studies have explored how interactions between different habitat-forming species influence their own performance (Bulleri, 2009; Gribben et al., 2019), despite such positive interactions being potentially critical for restoring or increasing the resilience of kelp forests.

For instance, in the absence of established kelp beds to facilitate recruitment, other habitat-forming species may be critical recruitment habitats that reduce abiotic (e.g., wave action) or biotic (e.g., herbivory) stress (Bulleri et al., 2011). As an example, recruitment of the habitat-forming fucoid *Scytothalia dorycarpa* is facilitated by the canopy of the kelp *Ecklonia radiata* (Bennett and Wernberg, 2014). Interestingly, a similar positive effect is found on recruits of the fucoid *Sargassum* spp., but only under partial *Ecklonia* canopies, whereas dense canopies had a negative effect on recruitment of *Sargassum* (Bennett and Wernberg, 2014). This result suggests that we need to better understand the context and species specifics of positive interactions between habitat-forming kelp before they can be incorporated in management interventions to avoid undesired outcomes.

Experimental tests with artificial kelp blades show that the motion or "whiplash" from frond movement can help deter urchin grazing and facilitate the growth of juveniles (Vasquez and McPeak, 1998). Though this example used artificial blades, the presence of other kelp species nearby could play a similar role, but further testing is required to determine the efficacy. Some kelp species may be better at deterring grazing through such mechanisms and thus outplanting adults of these species alongside focal restoration species or transplanting the focal species near to extant canopies of the grazing-deterrent species, could enhance effective restoration. Working to transplant multiple species requires additional considerations as they may have different environmental requirements and thus necessitate separate cultivation chambers or storage units; however, the additional investment could prove worthwhile if success rates are increased.

There is also some evidence that habitat-forming species can facilitate other spatially distant habitat-formers, that is, facilitation often occurs at larger, seascape scales (Gribben et al., 2019). For example, in soft-sediment environments, beds of mussels can promote the high abundances of other bivalves by altering hydrodynamic regimes at distances of 100s of meters away from the mussel beds (Donadi et al., 2013), and clams provide a hard substratum for fucoid settlement thus extending their distribution from their natal habitat (rocky shore) to a connected novel habitat (Lanham et al., 2020). Therefore, kelp restoration may only succeed if the habitat is made more amenable for growth by the presence of another habitat-forming species (e.g., another kelp species) in the local seascape. It is predicted that these types of interactions will have larger positive seascape-scale effects on habitat-forming species and may thus provide the biggest benefits in ecosystem services and function, but for kelp forests such effects remain unknown. Pragmatically, reinstalling these types of interactions may be more difficult than utilizing other habitat-formers to facilitate restoration of a focal kelp species at smaller scales.

Harnessing positive interspecies interactions has the potential to aid kelp restoration efforts. But before managers can achieve this goal, we require a better understanding of how other species enhance kelp populations, under what conditions do positive interactions perform best. Notably, the target kelp or the facilitative species may eventually experience negative feedbacks as the relationship maybe positive at one life stage or given density and negative at a differing life stage or density (Gribben et al., 2019).

Trophic Cascades – Figure 2-3

Trophic cascades where predators impact the health of foundation species are well documented across many marine ecosystems and often positively affect foundation species (Eger and Baum, 2020). Tri-trophic cascades in which predators promote foundation species by suppressing populations of their grazers are powerful examples and include blue crabs and fish protecting salt marsh plants (Silliman and Bertness, 2002; Altieri et al., 2012) and sharks promoting seagrass growth by deterring turtle grazing (Burkholder et al., 2013). Trophic cascades are particularly relevant in the context of kelp restoration as the loss of predators such as sea otters (Estes and Duggins, 1995), sea stars (Burt et al., 2018), lobsters (Ling et al., 2009), and predatory fish (Caselle et al., 2018), and later expansion of consumers such as sea urchins, is often linked to the initial loss of the kelp habitat. Therefore, controlling herbivore populations and re-establishing predator populations, along with the kelp, may not only be an additional step to increase the success of kelp restoration but a requisite step, without which long term restoration success may never be possible.

Two interventions that have been successful in elevating predator populations are the establishment of strict harvest limits on predators and the creation of MPAs. For example, installing limits on predator harvest has resulted in large scale returns of kelp habitat in Alaska (Estes and Duggins, 1995), California (Caselle et al., 2018), British Columbia (Watson and Estes, 2011), and New Zealand (Shears and Babcock, 2002). MPAs are a common marine management tool to help restore animal populations (Boonzaier and Pauly, 2016). Since both fisheries limits and MPAs are gaining momentum, used in governmental policy (Watson et al., 2014), and are often politically viable (Jones et al., 2013), these two methods have great promise as key mechanisms to help kelp recovery. To date, however, management of kelp through the management of predators has tended to stop at the predator level and have not typically considered kelp populations in the marine planning process (Woodcock et al., 2017). As a result, future MPA designs should consider how their placement can also suit the restoration of primary producers, instead of solely focusing on high trophic levels. For example, restoration efforts can occur within MPAs or managers can situate new MPAs to ensure population connectivity among kelp populations (Coleman et al., 2017). Through these planning adjustments, restoration efforts could also benefit from the increased predator populations.

Often, the restriction or elimination of a harvest pressure is not enough to allow for the return of predators, and in turn, kelp. For example, after the end of the fur trade, and following legal protection as an endangered species, sea otters (*Enhydra lutris*) failed to return to parts of their previous range. To resolve this problem, managers translocated otters and reintroduced them into parts of the United States and Canada (Bodkin, 2015). Though these efforts were costly, difficult, and resulted in significant otter mortality (VanBlaricom et al., 2015), they have been successful at restoring kelp beds at large scales and maintaining those restored populations (Filbee-Dexter and Scheibling, 2014). To date, no captive breeding program exists for restoration purposes (VanBlaricom et al., 2015) and if otters require introduction, scientists instead advocate for additional otter translocations to help connect the populations and restore kelp ecosystems (Davis et al., 2019). Despite their success, translocating otters or other predators (Hayward and Somers, 2009), can be contentious because they are very likely to interact with humans, eat recreationally and commercially harvested species, and opportunities for development can disappear because of their endangered status and legal protection (Booth, 1988). Additionally, otters can sometimes avoid using urchin barrens as feeding grounds because urchin barrens contain nutritionally poor urchins, and instead hunt in nearby kelp forests, which defeats the purpose of their reintroduction (Hohman et al., 2019). Thus, introduced otters may be most effective at maintaining kelp forests rather than promoting their recovery. As a result, managers are currently hesitant to introduce more otter populations in the Eastern Pacific (Hohman et al., 2019). Potentially, the restoration of a diversity of predators may be needed to control herbivore populations (Katano et al., 2015) and other species could be introduced alongside or in place of otters.

Artificial stock enhancements of marine fishes and invertebrates, often for harvest, have been successful in augmenting the wild populations of many species worldwide (Bell et al., 2008; Lorenzen et al., 2010). As a result, programs focused on other species that consume urchins may prove to be a more cost-effective and politically tenable alternative or supplement to sea otter introduction. In areas such as Tasmania, Australia, where overharvest of the Southern Rock Lobster (*Jasus edwardsii)* has contributed to increases in urchin populations and declines in canopy-forming algae (Ling et al., 2009), managers could release cultured *J. edwardsii* into the environment. Although lobsters are unlikely to revert declines (Layton C, Johnson C, personal communication), they can complement other restorative actions and aid in conserving extant kelp forests. While *J. edwardsii* is not currently used to restore kelp populations, researchers are successfully culturing the species (Hooker et al., 1997; Ritar, 2001; Kittaka et al., 2005) and managers could redirect this practice to a restoration focus. Similar species such as the Eastern rock lobster (*Sagmariasus verreauxi*), a key predator of *Centrostephanus rodgersii*, are also cultivable (Jensen et al., 2013) and are candidates for wild enhancement programs.

Other species which are not as developed from an aquaculture standpoint, but that also positively affect kelp ecosystems are the predatory crabs (red king crab, *Paralithodes camtchaticus* and brown crab *Cancer pagurus*) in Norway (Christie et al., 2019), the California sheephead (*Semicossyphus pulcher*) in the Eastern Pacific (Caselle et al., 2018), and sea stars, such as the carnivorous *Pycnopodia* spp. along the Pacific Coast of North America (Burt et al., 2018). Little work has assessed the feasibility of culturing these species, but preliminary results on other analogous species suggest that it could be feasible (Stevens, 2006; Brooker et al., 2018). For example, large scale cultures of *Paralithodes camtchaticus* supplement wild fishery populations (Epelbaum et al., 2006; Daly et al., 2009) and maybe adjusted for restoration purposes. In California, the sheephead is a popular target for sports fishers and preliminary work part of a breeding program showed that they can spawn in captivity (Jirsa et al., 2007). However, their social structure, feeding requirements, and hermaphroditism make them difficult to culture and further efforts by the "Hubbs-Seaworld Research Institute and the Ocean Resources Enhancement and Hatchery Program" in California, United States are no longer under investigation (Stuart, Personal communication, 2019). Following the sea star wasting syndrome die off in the Eastern Pacific (Eisenlord et al., 2016; Harvell et al., 2019), scientists at the University of Washington and The Nature Conservancy California are beginning to experiment with culturing wild sea stars *Pycnopodia* spp., spawning them, and raising the juveniles to maturity, and determining their impact in the ecosystem. If the trials are successful, they plan to scale up the results, incorporate genetic diversity into the breeding program, and work to develop a recovery plan for the species (Eddy, Personal communication, 2020).

The restoration of an ecosystem through restored trophic interactions has been and will continue to be the subject of much debate (Seddon et al., 2007; Lorimer et al., 2015; Svenning et al., 2016). As this conversation continues, any attempt at restoring kelp forests in parallel with one of the prior mentioned species must consider: the ecosystem effects of that species, the genetic diversity of the introduced population, potential disease transmission, actual and opportunity costs, and public perception, and will for reintroduction along with other societal issues. Other authors (McCoy and Berry, 2008; Lorenzen et al., 2010) consider these barriers elsewhere, but this is beyond the scope of our review.

As oceans continue to warm, species ranges and territories will change, and new trophic interactions will form. For example, the tropical rock lobster (*Panulirus ornatus*) is currently mass cultured for commercial sale (Petersen and Phuong, 2010) but the species is currently restricted from most of South Australia by temperature. As oceans get warmer, there may be the opportunity to introduce *P. ornatus* into these now habitable areas to help control urchin populations. Such considerations and novel interactions may become important in any attempt to assist in future kelp restoration efforts (Wood et al., 2019).

Genetics in Kelp Restoration –Figure 2-4

Over the past few decades, it has become clear that genetics are an influential component of an individual's, population's, or wider ecosystem's health. For example, genetic diversity and provenance can affect establishment rates and population fitness in many plants and animals (Hughes and Stachowicz, 2004; Forsman and Wennersten, 2016). Restoration efforts can thus benefit by incorporating the mechanisms responsible for these positive health effects (McDonald et al., 2016; Gann et al., 2019). The positive population and ecosystem effects from enhanced genetic diversity may be achieved through the restoration of diverse genotypes or phenotypes or individuals (Gann et al., 2019). The case is particularly strong for foundation species, where enhanced genetic diversity has benefitted not only the survival of the target species but also other components of the ecosystem, such as primary productivity and rates of decay and flux of nutrients (Whitham et al., 2006; Hughes et al., 2008; Reynolds et al., 2012; Kettenring et al., 2014; Gribben et al., 2020).

Although genetic approaches are only now being considered in the context of kelp restoration (Coleman and Goold, 2019), the kelp or broader seaweed aquaculture industry has long used techniques to genetically manipulate kelp, such as selected breeding or strain selection and manipulation to increase yield and flavor (Dai et al., 1993; Liu et al., 2006; Bast, 2014). Phycologists in the industry have used chimeras in *Laminaria sp*. populations to insert traits for increased tolerance to irradiance, seawater temperatures, and tissue rot (Li et al., 2007, 2008; Robinson et al., 2013). Further work to increase the genetic heterogeneity of seaweeds may potentially allow for increased resistance to abiotic stressors (Medina et al., 2015) and may also confer adaptive capacity to climate stress (Wernberg et al., 2018).

The selection of donor biological material (reproductive tissue, individuals, populations) that contain desirable traits such as tolerance to thermal stress may also be necessary to future-proof populations (Wood et al., 2019). This process might involve sourcing biological material for restoration from warm-adapted populations, breeding under specific conditions designed to achieve "super strains" or even implementing synthetic biology techniques, e.g., using CRISPR-Cas9 genome editing tool to edit the genomes of kelp species to bring out desirable traits (Coleman and Goold, 2019; Wood et al., 2019). Such future-proofing concepts are in development for terrestrial (Aitken and Whitlock, 2013) and coral reef systems (van Oppen et al., 2015), and are now being explored in the context of seaweed restoration as well (Wood et al., 2019).

While the explicit incorporation of genetics in marine restoration is rare (Mijangos et al., 2015), the techniques exist in industry (Robinson et al., 2013) which when coupled with the advancement of other genetic and genomic tools, e.g., rapid DNA sequencing technologies, can enable scientists to understand how to further advance restoration (Mijangos et al., 2015; Wood et al., 2019). For example, Wood et al. (2020) recently demonstrated that genetic diversity and structure of restored *Phyllospora comosa* (order Fucales) populations mimicked that of a mixture of local extant populations and this provides a platform to effectively "design" populations of this species as desired. While the application of seaweed genetic diversity in a restoration/management context requires further research, there is encouraging evidence for its future application to seaweed restoration programs. As these programs continue to develop, it is important that they proceed with caution and consider the potentially deleterious effects of introducing new genes or altering existing genes within a population (Filbee-Dexter and Smajdor, 2019).

Microbial Interactions and Kelp Restoration – Figure 2-5

Another aspect that may enhance effective restoration and management is the incorporation of kelp–microbiome interactions. Evidence from multiple systems suggests that microorganisms play fundamental roles in the life and performance of their eukaryotic hosts (McFall-Ngai et al., 2013). This knowledge has led to the proposal of the "holobiont" concept (Margulis and Fester, 1991), which argues that 'macrobial' hosts and their associated microbiota form a coherent biological entity and we need to considered them together to understand the biology and ecology of hosts (McFall-Ngai et al., 2013). In marine systems, this concept was first applied to reef-forming corals (Rohwer et al., 2002), but recent work highlights its applicability to other marine macroorganisms, including seaweeds (Egan et al., 2013). For instance, surface-associated microorganisms can influence the development, growth, photosynthesis, and reproduction of seaweeds (see review by Egan et al., 2013), and recent work suggests that microbes may even influence interactions between seaweeds and other macroorganisms such as grazers and epiphytes (Campbell et al., 2014b; Marzinelli et al., 2018).

Most studies of kelp-associated microorganisms are, however, descriptive, showing relationships between environmental conditions and/or kelp performance and condition, and the structure of the associated microbiota (Lachnit et al., 2011). Often, the focus is on the negative effects of microbes on kelp

(Marzinelli et al., 2015), for example, changes in abundances of several bacterial taxa can cause a bleaching disease of the Australian kelp *Ecklonia radiata*, and experiments manipulating warming and acidification show that future environmental conditions are likely to exacerbate this (Qiu et al., 2019). Some studies have gone beyond establishing relationships to show causation in seaweed systems via isolation and subsequent experimental inoculation of target microorganisms (Matsuo et al., 2005; Case et al., 2011; Kumar et al., 2016). Despite the focus on negative/harmful interactions, experimental inoculations and similar experimental approaches (e.g., via selective removal of microbial taxa, Singh and Reddy, 2014) are potential techniques to determine positive interactions and isolate microbial taxa that may enhance kelp performance and/or confer resistance or resilience to future environmental conditions (see Rosado et al., 2019 for corals). Microbial communities associated with macroorganisms in marine systems are a "soup" of microbes and this presents manipulation challenges. However, recent work in corals has demonstrated that coral-associated microbiomes are influenceable and can develop in distinct directions following inoculations at early larval stages in experimental conditions (Damjanovic et al., 2017). Thus, focusing microbially guided restoration efforts on early life stages may enhance the feasibility of using such solutions in seaweed systems, either to enhance recruitment or growth, or resilience to abiotic (e.g., temperature) or biotic (e.g., grazing, fouling) stressors. For example, managers could grow kelp zygotes or recruits in the lab and inoculate them with specific taxa until they achieve a desired microbial community and then outplant them as normal.

Finally, host genetics can influence associated microbial communities (Org et al., 2016). Understanding the relative importance of host characteristics versus the environment in shaping the kelp microbiota is critical, as this may have implications on how we design restoration and/or future-proofing programs (Wood et al., 2019). If the environment influences microbial communities or important taxa, attempts to harness microbial interactions to improve restoration or future-proofing outcomes may fail as local microbial taxa swamp the microbial communities (but see Campbell et al., 2015). Alternately, if host specific traits influence microbial communities, harnessing positive microbial interactions may be as simple as including genotypes (or phenotypes) with beneficial microbiota. Another approach could be to tailor microbial manipulations to specific host types, as is in human medicine (Benson et al., 2010; Bonder et al., 2016). Our knowledge of kelp–microbiota interactions is still in its infancy and more experimental work aimed at understanding mechanisms is necessary in order to develop methods that successfully harness the power of beneficial microorganisms in the context of kelp restoration.

Anthropogenic Synergies – Figure 2-6

It is likely that kelp forest restoration can receive ecological and environmental benefits from kelp aquaculture and marine harvest efforts. The use of cultivated populations of kelp as concentrated sources of spores seems particularly promising, especially given that extensive localized losses of kelp in some areas combined with short dispersal distances and Allee effects can slow natural recovery of kelp populations. But these applications require availability of suitable local substratum nearby and that the kelp not be harvested before it is reproductive, two conditions that require additional consideration. The aquaculture of kelp also has direct economic outputs, and this may help incentivize and contribute to the funding of local 'restoration economies' (BenDor et al., 2015). Kelp aquaculture would also help to ease pressure on kelp forests (restored or otherwise) that may be the target for wild harvest operations. In addition, kelp cultivation may also be a cost-effective method of trialing whether an area is suitable for kelp growth and re-establishment, especially where local conditions have improved/degraded relative to the established trend.

Another innovative solution is the removal of sea urchins by divers who then sell them as a food product, known as *uni* in Japanese restaurants (Hohman et al., 2019; Sea Urchin Harvest, 2020). In many instances, however, the edible part of the urchin (the roe) is of poor quality due to limited food availability in the urchin barren (Claisse et al., 2013). Companies are working to solve this problem by establishing land-based aquaculture facilities that take urchins collected from barrens, feed them an adequate diet, improve the quality of the gonads, and then sell the urchins on the market (Urchinomics, 2020). As conservation considers market-based solutions (Huwyler et al., 2016), this approach to kelp restoration holds significant promise and may be especially useful in areas where predators are unable to revert urchin barrens from an alternate stable state while also creating jobs and contributing to local economies.

Kelp forests are especially efficient nutrient cyclers and are thus recognized as sustainable and positive solutions to nutrient loading in aquaculture farms (Chopin et al., 2001; Stévant et al., 2017). While kelp forests do not directly benefit from this relationship (unless nutrient-limited), their services could motivate aquaculture facilities to restore kelp forests next to their operations, thus helping reduce the financial load on other organizations. While these solutions will not be applicable in all circumstances, these practices contribute to the broader idea behind 'restorative aquaculture' (Theuerkauf et al., 2019) and might provide a beneficial accompaniment to restoration activities.

Incorporation of Positive Interactions in Kelp Forest Restoration

As managers continue to work to restore kelp forests, they will need to consider novel and adaptive approaches in a bid to achieve success while also crafting cost-efficient solutions. We posit that incorporating facilitative interactions and other synergies into traditional forms of restoration may help achieve these two purposes. Many of the solutions described above, need little to no further research to inform new restoration projects and can be used once the initial causes of decline have been mitigated or removed. To take advantage of intraspecific processes, managers can pair juvenile and adult outplants or combine adult transplants with seeding efforts. We also suggest that future restoration locations be closely spaced to each other or in close vicinity to extant kelp beds. Or, if kelp beds are declining but have not yet disappeared, restoration efforts can instead focus on augmenting existing beds and eliminating the need for future restoration. Depending on the species involved, managers could look for algal species, or genotypes, that promote each other and look to outplant polycultures instead of monocultures. Managers can further consider the benefits of restoring additional elements of the ecosystem in addition to the kelp itself. For example, where urchins are a problem, restoring species like otters, lobsters, crabs, or sea stars incurs a high upfront cost but can likely offset the cost of continual, manual urchin removal in the long term. Additionally, by adopting this approach to restoration, we are advancing the establishment of ecosystem functions beyond those provided by foundation species, an implicit goal in most all ecosystem restoration projects. Kelp and aquaculture farms also provide exploitable synergies to not only restore ecosystems but provide profits for their operators. Working to situate kelp farms near restoration sites can help seed barren grounds and once populations have become established, the kelp itself can work to offset nutrient pollution from aquaculture farms. It is also possible that kelp restoration could be profitable with new companies looking to remove, culture, and sell the urchins from barrens, thus letting the kelp regrow. Future permitting could be contingent on the company adopting best ecosystem practices and restorative aquaculture certifications can incentivize companies to restore kelp forests as part of their business.

Other approaches, namely incorporating genetic adaptation, interactions between specific genotypes and beneficial microbes are not as established, but steady progress is being made on understanding how future efforts can use these approaches. Because these approaches will initially be more costly than traditional restoration, it will be important to consider the added benefits of incorporating them into restoration practices. While this analysis is not completed, it is possible that with rapidly shifting environmental conditions, microbial and genetic approaches will be requisites to future restoration operations.

Managers can start integrating these interactions into restoration during the planning process, first by describing the known or plausible interactions in their system, determining which ones are feasibly included, carefully considering adverse outcomes, experimentally testing them at small scales, and then putting them into practice. As with any new conservation or restoration intervention, it is vital that we pair these approaches with adequate monitoring programs to evaluate them against goal-dependent performance criteria (Basconi et al., 2020; Eger et al., 2020b), and work to determine the marginal gains in success and the associated costs. Additionally, caution should be used whenever manipulating the environment, most notably when introducing foreign or novel species, genotypes, or microbiomes. While the interactions described above carry many potential benefits, they may also cause unintended harm to the ecosystem as novel introductions could replace elements of the ecosystem beyond those intended. Therefore, an essential part of the planning process is the small-scale experimentation and trialing of the proposed methods. In all cases, the precautionary principle should be applied and we do not promote the blind application of these methods. Rather we suggest a careful, case-specific consideration of application of proven methods while also considering the need to make conservation decisions with incomplete information (Grantham et al., 2009).

More generally speaking, kelp restoration efforts would benefit from positive remediation of the environment and other preventative conservation measures. For example, a decrease in land-based nutrient inputs that benefits turf algae or a decrease in sediment deposited in coastal ecosystems which interferes with the recruitment of kelp populations. As alluded to the positive species interactions section, it may indeed be most effective to restore kelp populations on the periphery of existing natural populations. Therefore, any efforts to conserve extant kelp populations may indeed be facilitating future restoration efforts. These efforts are also tied to improvements in water quality but also related to the destruction of rocky reef habitat, overfishing, overharvesting, or introduced species (Wernberg et al., 2019).

While we document the reported positive interactions that are feasibly useable to enhance kelp restoration, there are several other interactions from marine ecosystems that are not yet described. For instance, facilitation cascades (a set of positive species interactions) are well described and hypothesized to apply to salt marsh and coral restoration, but we are unaware of applicable analogs in kelp restoration. Further, as kelp species are typically limited dispersers, any interaction that worked to enhance the dispersal range of kelp forests would be a great aid to restoration efforts as established, restored populations could act as a source population for other areas. Even among the topics included in our review there is very little empirical evidence for most subjects. Of the 54 papers found in our literature search, over half were about trophic cascades and no other topic had more than five papers on that subject. Additionally, aside from trophic cascades, the concepts outlined here, have only been tested at small scales and stand to be trialed at larger, more ecologically relevant scales. Both the topics included and excluded from this literature review require additional research.

The importance of these positive interactions should increase with additional anthropogenic stressors related to coastal development in climate change. Unfortunately, there is little empirical evidence, and these remain theoretical improvements to restoration. Therefore, we encourage scientists and managers not only to attempt to incorporate these approaches into their projects but work to test their efficacy and allow for restoration to act as both an experiment and a conservation outcome. By doing so, we can quickly and efficiently work to determine how to best restore our underwater forests in the face of mounting pressures.

AUTHOR CONTRIBUTIONS

AE and BS conceived the manuscript concept. All authors contributed to narrowing the scope and selecting the final topics to be covered. AE conducted the literature review and created the figures and tables. AE incorporated comments from all authors and wrote the first draft. All authors read the draft, provided comments, and approved the manuscript for submission.

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SUPPLEMENTARY MATERIAL

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Know Thy Anemone: A Review of Threats to Octocorals and Anemones and Opportunities for Their Restoration

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In studies of habitat-forming species, those that are not spatially dominant are often considered "non-primary" habitat and may be overlooked. This is despite the fact that minority habitat formers can provide critical complexity, food, and other services that underpin ecosystem biodiversity. Octocorals and anemones are found in marine and estuarine habitats across all climate zones. Despite their potentially important ecological roles, to date there have been few studies of their specific threats and stressors or attempts at their restoration. Here we review studies of the ecology of octocorals and anemones with a focus on threats and restoration. We identify many threats including habitat damage, collection and trade, disease, predation, pollution, and the most wide-spread – climate change. While evidence suggests that some octocorals and anemone populations may be more resilient to disturbances than stony corals because they often recruit and grow quickly, resilience is not guaranteed. Instead, resilience or susceptibility within this large group is likely to be site and species specific. We find that the loss of octocorals and anemones has been difficult to quantify as most species have no hard structures that remain following a mortality event. Only through long-term monitoring efforts have researchers been able to document change in these populations. Due to the increasing extent and severity of human impacts in marine ecosystems, restoration of habitat forming species is becoming increasingly necessary after disturbance events. To illustrate the challenges ahead for octocoral and anemone restoration, we present two examples of ongoing restoration efforts assessed against the International Standards for the Practice of Ecological Restoration. Restoration planning and implementation progress are documented for the Mediterranean red coral *Corallium rubrum* and the temperate Australian cauliflower soft coral, *Dendronephthya australis*. This review and the detailed case studies demonstrate that while some octocorals and anemones can provide resilient habitat within reef systems, a greater research focus on their ecology, threats, and restoration potential is urgently required.

Keywords: alcyonaceae, octocoral, soft coral, sea anemone, tropical, temperate

INTRODUCTION

In many ecosystems, studies of habitat-forming species often focus on those believed to support the greatest mobile species diversity, such as seagrass in shallow coastal water and kelp in temperate rocky reefs (Duffy, 2006; Nagelkerken et al., 2008; Teagle et al., 2017). This can lead to an unresolved understanding of the role of non-primary (or spatially sub-dominant) habitat formers and an underestimation of the ecosystem services they provide (Coleman and Wernberg, 2017). In seagrass ecosystems, mixed macroalgae-seagrass stands have significantly higher vegetative surface area than seagrass alone, leading to a proportional increase in epifaunal densities (Stoner and Lewis, 1985; Parker et al., 2001). In addition, the loss of non-primary habitat formers can negatively impact mobile species, such as in Florida Bay seagrass systems, where the loss of sponges resulted in declines of juvenile commercially important lobster species that required human intervention (Butler Iv, 1995). In temperate rocky reefs, fucoid algaes are often overlooked in favor of kelps, but fucoids support unique and abundant assemblages of macroinvertebrates (Coleman and Wernberg, 2017). In tropical coral reef ecosystems, it is often assumed that octocorals and anemones are not the primary habitat used by the majority of mobile species and as such they have tended to be overlooked relative to their stony counterparts (Norström et al., 2009; Ferrari, 2017; Epstein and Kingsford, 2019). In deeper marine ecosystems, aposymbiotic octocorals can be more prominent but these systems are less well-studied (Sánchez et al., 1998; Cerrano et al., 2009; Wareham, 2009; Baillon et al., 2012). When studied in detail, octocorals and anemones are revealed as structurally complex animals that are used as habitat, food sources, and foraging substrate by a variety of mobile fauna across the world (Fautin and Allen, 1997; Heifetz, 2002; Epstein and Kingsford, 2019; Schweitzer and Stevens, 2019).

Octocorals and anemones have a world-wide distribution in marine and estuarine habitats, with species inhabiting all climate zones and habitat types (Verselveldt and Alderslade, 1982; Dinesen, 1983; Fautin, 1992; Sánchez et al., 1998; Heifetz, 2002; Fautin et al., 2013). Reefs in the same climatic zones can also have very different patterns of octocoral distribution depending on location. For example, in tropical climates, Great Barrier Reef (GBR) octocorals are much more abundant on reef slopes than on shallow reef flats, while in the Caribbean octocorals are abundant in both shallow reefs and deep, wave exposed reef terraces (Dinesen, 1983; Sánchez et al., 1998). In the GBR, octocorals can also comprise up to 45% of coral cover on individual reefs, while in the Caribbean, octocoral abundance and density can be even higher (Sánchez et al., 1998; Australian Institute of Marine Science [AIMS], 2018; Epstein and Kingsford, 2019). Octocorals are also widely distributed in depth range, and are found in deep water reefs from temperate to arctic waters (Verselveldt and Alderslade, 1982; Heifetz, 2002). Since octocorals and anemones have varying degrees of structural complexity, they can provide important structural habitat for many species in all climate zones (**Figures 1b–e**; Heifetz, 2002; Poulos et al., 2013; Ferrari, 2017; Richardson et al., 2017).

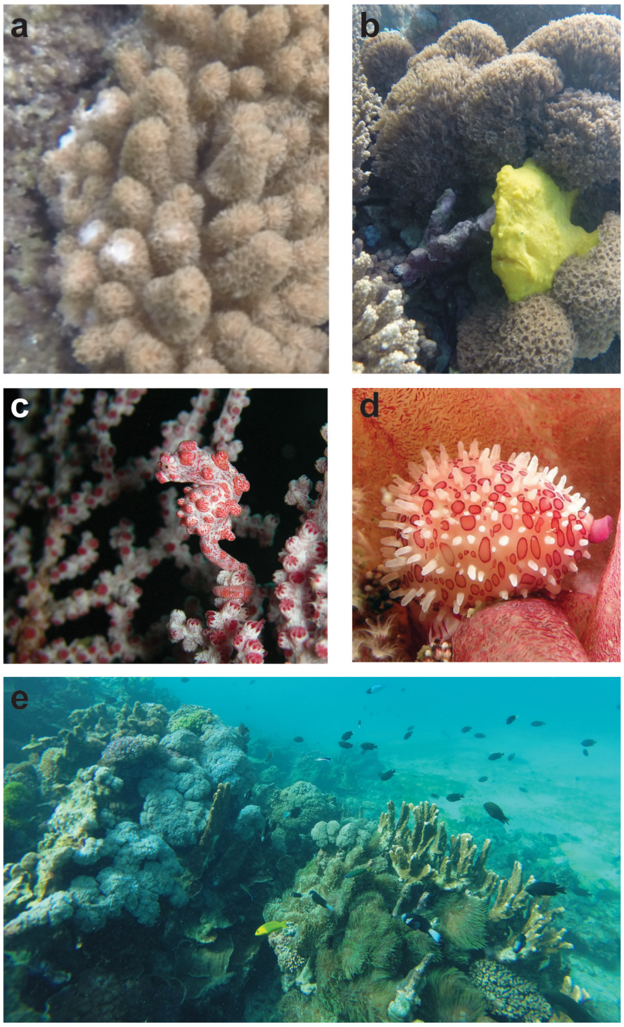

FIGURE 1 | Use of soft corals and anemones as food and habitat. **(a)** Bite marks in *Aldersladum* sp. soft coral, **(b)** use of *Anthelia* sp. as habitat by frogfish, **(c)** obligate symbiont *Hippocampus bargabanti* in its gorgonian host, **(d)** corallivorous cowrie in *Dendronephthya australis*, and **(e)** use of mixed stony coral, soft coral, and anemone habitat by anemonefishes, damselfishes, wrasses, and other fish species. Photo credits – **(a,b,e)** Rosemary K. Steinberg, Lord Howe Island. **(c)** Steve Childs, https://www.flickr.com/photos/steve_childs/2643195469, d) John Turnbull, MarineExplorer.org.

Octocorals and anemones are benthic Cnidarians that share a wide variety of physical traits, most prominently that neither form solid skeletal structures, and both have strong defense mechanisms. Octocorals and anemones are soft-bodied, although octocoral tissues do contain calcified spicules and/or axes that increase tissue stiffness (Koehl, 1982; Fabricius and Alderslade, 2001; Sethmann and Wörheide, 2008; Fabricius, 2011). Octocorals primarily rely on secondary metabolites for defense, rendering them unpalatable and sometimes toxic, while anemones employ painful stings from venomous nematocysts (Changyun et al., 2008; Frazão et al., 2012). Octocorals are primarily colonial anthozoans that possess polyps with eight tentacles, often fringed with pinnules (Fabricius and Alderslade, 2001; Fabricius, 2011). Examples include photosynthetic Xeniid octocorals, also known as pompom corals, which are commonly found in tropical and subtropical shallow reefs (**Figures 1b,e**), and non-photosynthetic *Dendronephthya* sp. octocorals, also known as carnation corals, which are usually found in deep water from temperate to tropical zones and come in a wide variety of colors (**Figures 1c,d**; Fabricius and Alderslade, 2001). Anemones are generally solitary, though they can also form colonies, with some species employing both life histories (Francis, 1979). The most well-known group of anemones are the host anemones, which associate with anemonefish. The bubble-tip anemone *Entacamaea quadricolor* is particularly popular both as a tourist attraction and in home aquaria (**Figure 1e**; Jones et al., 2008; Scott et al., 2011; Thomas et al., 2015). In addition, octocorals and anemones have similar ecological roles as soft benthic habitat formers.

Across the world, octocorals and anemones provide shelter and food for a wide variety of mobile species, including endangered species and habitat specialists (**Figures 1a–e**). For example, gorgonians are famous for hosting habitat-specialist pygmy seahorses amongst other less charismatic fauna (**Figure 1c**; Lourie and Randall, 2003; Cerrano et al., 2009; Harasti, 2016; Epstein and Kingsford, 2019). In temperate waters, octocorals are critical habitat for the endangered White's Seahorse and host epibenthic food sources such as amphipods for other protected sygnathids (Harasti et al., 2014; Harasti, 2016; Corry et al., 2018). In the subarctic, sea pens and other octocorals provide nursery habitat for larvae of commercially important fisheries species (Baillon et al., 2012). In tropical and subtropical systems, anemones can form aggregations that house large anemonefish populations – North Solitary Island and the surrounding region have the highest density of anemones in the world, leading to very high anemonefish densities (Richardson et al., 1997; Scott et al., 2011). Additionally, anemones support other species of macro-symbionts including *Dascyllus* sp. damselfishes, anemone shrimps, and anemone crabs and are food sources for other fish species, such as butterflyfishes (Ates, 1989; Fautin et al., 1995; Valdivia and Stotz, 2006). Though examples of specific mobile fauna species utilizing octocoral and anemone habitat have been recorded, few general studies exist. Recently Epstein and Kingsford (2019) reported for the first time that fish species richness in Orpheus and Pelorus Islands on the central GBR increases with octocoral – *but not stony coral* – cover. Similarly, in temperate waters off the eastern United States fish abundance was significantly positively correlated with sea whip coral cover, but not to any other benthic habitat group (Schweitzer and Stevens, 2019).

Hard and soft benthic cnidarians are under increasing threat from both natural and human-induced disturbances, including climate change, disease, anchor and boat damage, and commercial collection (Loya et al., 2001; Precht et al., 2001; Santangelo and Abbiati, 2001; Goldberg and Wilkinson, 2004; Garrabou et al., 2006; Bruno et al., 2007; Jones et al., 2008; Poulos et al., 2013; Thomas et al., 2015; Erni Cassola et al., 2016). Many threats facing octocorals and anemones are similar to those facing stony corals, although some responses are unique (e.g., Loya et al., 2001). Additionally, both octo- and stony corals are commercially harvested for the commercial aquarium trade, but some species of octocoral are also harvested for jewelry – a threat unique to octocorals and black corals (Grigg, 2001; Santangelo and Abbiati, 2001). Conversely, some destructive stony coral predators such as the Crown of Thorns seastar, whose populations are understood to benefit from agricultural runoff, rarely ingest octocorals, creating possible opportunities for octocoral population expansion (Endean and Stablum, 1971; Fabricius, 1997; Kayal et al., 2012).

Although vulnerable to anthropogenic threats (Loya et al., 2001; Santangelo and Bramanti, 2010; Harasti, 2016), there is also evidence that octocorals and anemones possess traits that may increase their ability to recover naturally and make them amendable for restoration projects. Octocorals and anemones generally do not form calcium carbonate skeletons, and therefore do not build long term reef structures. As such, soft-bodied habitat-forming organisms can often recruit and grow faster than hard-bodied ones. For example, on the GBR the octocoral *Sinularia flexiblis* and the fast-growing stony coral *Acropora hyacinthus* grow at estimated average rates of 128 $\pm$ 7 cm^2y^{-1} and 41.22 $\pm$ 9.5 cm^2y^{-1}, respectively, following bleaching-induced population declines (Bastidas et al., 2004; Linares et al., 2011). The soft coral *Efflatounaria* sp. uses clonal reproduction to reach pre-disturbance abundance (but not percent cover) within 109 days of a disturbance event (Karlson et al., 1996). Additionally, in the Florida Keys, recruitment dynamics vary significantly between stony and octocorals after temperature disturbance. In recruitment surveys only three species of opportunistic or hardy stony coral were recorded, while a wide range of octocoral genera recruited (Bartlett et al., 2018). Though octocorals generally recover quickly after disturbance events, recovery times vary. For example, rocky-wall octocoral communities in the Tropical Eastern Pacific are expected to take 21–34 years to recover their full suite of octocoral species after disturbances (Gomez et al., 2018). In total, on tropical reefs octocoral communities can reach pre-disturbance densities in 10–15 years, whereas the full suite of stony corals can take up to 100 years (Rinkevich, 2005). It should be noted that stony coral can recover to pre-disturbance cover much more quickly, though community composition may not be the same (e.g., Robinson et al., 2019). After disturbances that deplete stony coral populations and cover, a phase-shift to octocoral-dominated reefs can occur, quickly increasing species and habitat diversity (Norström et al., 2009). Octocorals and anemones are also adept at colonizing novel habitats and can quickly increase both structural and species diversity in an area (Brace and Quicke, 1986; Perkol-Finkel and Benayahu, 2005; Perkol-Finkel et al., 2005; Hiscock et al., 2010). This has resulted in some species becoming particularly successful invaders (Concepcion et al., 2010; Hancock et al., 2017). Anemones grow relatively slowly, but can reproduce asexually, leading to relatively rapid local population expansion (Brace and Quicke, 1986; Veale and Lavery, 2012; Scott et al., 2014; Scott, 2017). Though the lack of skeletal structure likely facilitates rapid recovery, it also means that their initial loss can be difficult to quantify because octocorals and anemones leave no obvious traces of population declines or extirpations. Understanding soft coral ecology likely requires a finer temporal scale of sampling than necessary for habitat formers that leave a skeleton or shell. Due to certain inherent biological characteristics such as rapid growth and reproduction, benthic soft-bodied cnidarians may become an increasingly dominant component of future reefs and a focus on their biology, ecology, and restoration is dearly warranted.

In this review, we apply the international and regional frameworks provided by the Society for Ecological Restoration (SER) to assess current knowledge of octocoral restoration (McDonald et al., 2016a,b). As the first necessary step, we identify previous and/or ongoing damage and threats to octocorals and anemones and identify critical knowledge gaps. Second, we examine the information needed to successfully restore octocorals and anemones and link current knowledge gaps to potential novel restoration approaches. These goals will be different for each target species and may or may not involve returning the restoration site to pre-disturbance diversity and abundance, depending on the type and severity of the initial disturbance (McDonald et al., 2016a). Finally, we present two case studies of ongoing restoration efforts to highlight the difficulties in setting specific restoration targets and identifying successful replanting techniques.

WHAT ARE THE THREATS FACING OCTOCORALS AND ANEMONES?

The most wide-spread threat to habitat-forming cnidarians is climate change (Sokolow, 2009; Cheal et al., 2017; Hughes et al., 2017). In fact, reefs around the world are experiencing unprecedented warming-induced bleaching events (Hughes et al., 2017). Although bleaching is widely studied, most research is focused on reef-building stony corals, but zooxanthellate octocorals and anemones also bleach, which can lead to stress, disease and mortality (Loya et al., 2001; Lambo and Ormond, 2006; Hill and Scott, 2012; Hobbs et al., 2013; Scott and Hoey, 2017). For example, in the tropics the majority of recorded octocoral and anemone loss has been attributed to climate-change induced bleaching (Loya et al., 2001; Lambo and Ormond, 2006; Harrison et al., 2011; Thomas et al., 2015). These bleaching events are caused by increased sea surface temperature of as little 1°C above the physiological upper limit of the symbiosis, and coral bleaching is predicted to be the summer norm by 2050 (Harrison et al., 2011; Van Hooidonk et al., 2016).

On the GBR coral reefs have recently been subjected to repeated mass bleaching events which have caused coral mortality and significantly impacted coral species assemblages, 3D reef structure, and ecological functions, but the impact on octocorals and anemone cover has not been quantified in this period (De'ath et al., 2012; Hughes et al., 2017, 2018; Australian Institute of Marine Science [AIMS], 2019). Conversely, recent monitoring from the Australian Institute of Marine Science shows that octocoral cover is fairly stable in shallow waters of the GBR (Australian Institute of Marine Science [AIMS], 2018). In Japan after the prolonged 1998 heatwave at Sesoko Island, bleaching mortality was greater in octocorals than stony corals, with a 99% decrease in overall octocoral cover vs. 73% in stony corals (Loya et al., 2001). In the Houtman Abrolhos Islands in Western Australia, anemone cover dropped from 70% in 1992 to 0% in 2012, at least partially due to the 2011 marine heat wave (Thomas et al., 2015). Because of the loss of the obligate anemone hosts, anemonefishes were also extirpated from the area (Thomas et al., 2015). Bleaching can also have severe long-lasting, sub-lethal effects on octocorals. Laboratory experiments on *Lobophytum compactum* found that egg fertilization success, fecundity, and offspring viability were all significantly impacted for at least 20 months post-bleaching (Michalek-Wagner and Willis, 2001).

Ocean acidification is expected to significantly impact reef ecosystems worldwide by reducing the calcification ability of reef-building organisms (Kleypas and Yates, 2009). Though octocorals do not build reef structure, they produce calcified spicules and/or axes for tissue stiffening and structural support and can be negatively impacted by increased oceanic CO_2 (Koehl, 1982; Watabe and Kingsley, 1992; Kleypas and Yates, 2009; Gómez et al., 2015). These impacts have been studied *in situ* using natural CO_2 gradients associated with volcanic vents, and vary between study locations – For example, in Milne Bay, Papua New Guinea soft coral cover and richness were both significantly reduced in high CO_2 environments, while in waters off Iwotorishima Island, Japan, community composition shifted from stony coral dominated in low CO_2 environments to being dominated by a single species of octocoral in moderately acidified water (Fabricius et al., 2011; Inoue et al., 2013). At Shinkine Island in the subtropical-temperate transition zone in Japan, both octocorals and anemones were only found at the lowest concentrations of CO_2 (Agostini et al., 2018). Unlike octocorals, anemones are non-calcifying, and as such, may be more resilient to ocean acidification (Doherty, 2009; Ventura et al., 2016). In fact, the host-symbiont relationship of temperate anemones shows remarkable resilience to the effects of acidification. When pH was reduced to as low as pH 7.4, zooxanthellae densities in several anemone species were either unimpacted, or zooxanthellae densities were reduced while chlorophyll concentration and photosynthetic yield per cell were increased (Doherty, 2009; Jarrold et al., 2013; Ventura et al., 2016). Though effects on tropical anemones are not as well-characterized, ability of larval anemonefish to find anemones is reduced in acidified environments and could negatively impact both anemone and anemonefish populations (Munday et al., 2009; Frisch et al., 2016).

Cyclones can have devastating effects on coral reefs that can take centuries to recover (Harmelin-Vivien, 1994), and cyclone intensity and effects on reefs are expected to rise with increasing global temperatures (Cheal et al., 2017). Cyclones can impact octocorals and anemones through wave-induced tearing or shearing and inundation with fresh water from rains (Van Woesik et al., 1995; Fabricius and De'ath, 2008). Cyclone "Joy" flooded sections of the GBR in late 1990 and early 1991, impacting several nearshore reefs. Six groups of octocorals were surveyed during this event, with only one group unimpacted, four groups partially impacted, and one group totally bleached or dead (Van Woesik et al., 1995). Although bleaching and increased cyclone intensity are major effects of climate change, elevated ocean temperatures can also contribute to other problems for corals, such as disease (Sutherland et al., 2004; Bruno et al., 2007; Sokolow, 2009).

Disease is a major threat to stony corals, especially in the Caribbean, but less is known for octocorals (Ruiz-Moreno et al., 2012; Slattery et al., 2013). Though octocorals do suffer from diseases like aspergilliosis, black and red band diseases, gorgonian labyrinthulomycosis, and at least 15 others, information on their susceptibility to and effect from these diseases is limited (Slattery et al., 2013; Weil et al., 2015). In the Caribbean, outbreaks of disease have caused mass mortality events in several species of gorgonians (Garzon-Ferreira and Zea, 1992; Geiser et al., 1998; Sutherland et al., 2004). Surveys in Arrial do Cabo, Brazil found that approximately 48% of surveyed colonies were dead, and 75% of living colonies showed signs of disease with ongoing tissue loss over time (Erni Cassola et al., 2016). In the Mediterranean, mass mortality (likely disease induced) of *Eunicella singularis* had long-lasting effects, with 59% of live colonies still exhibiting damage 4 years after the event (Garrabou et al., 2006). Though these examples have not been explicitly linked to climate change, they exemplify why temperature driven increases in disease prevalence could be devastating to octocoral communities. Octocorals and anemones are not only vulnerable to global disturbances such as ocean warming, they also face threats from more local sources.

Octocorals and anemones are especially vulnerable to habitat damage, both natural and anthropogenic. Mooring blocks and boat anchors can easily tear and uproot soft bodied organisms from the benthos. In Port Stephens, a single mooring block scoured over 1300 m^2 of *Dendronephthya australis* soft coral habitat (Harasti, 2016). This species was particularly impacted because of its shallow benthic attachment and soft sediment habitat preferences (Davis et al., 2015). Other human activities, such as dredging, shift sediment and can damage corals by smothering colonies or reducing photosynthetic ability and exacerbating the effects of bleaching (Erftemeijer et al., 2012; Appeldoorn et al., 2016; Jones et al., 2016; Bessell-Browne et al., 2017). In the GBR octocorals are much less abundant in areas of high nutrients and turbidity, suggesting that dredging and industrial agricultural runoff will likely have negative effects on octocoral abundance and species richness (Fabricius and De'ath, 2001; Fabricius et al., 2005). On the other hand, some species of octocorals in South Africa were more tolerant of sedimentation than stony corals at the reef-sediment interface (Schleyer and Celliers, 2003). Additionally, one species of anemone, *Mesactinia genesis*, increased both its photosynthetic ability and stinging efficacy against stony corals in high nutrient and turbidity environments (Liu et al., 2015). Understanding the mechanisms behind how turbidity and sedimentation affect octocorals and anemones in different parts of the world is critical to understanding how these corals will react to threats such as dredging.

Other activities such as fishing, especially trawling, can damage benthic environments and have previously damaged both octocoral and anemone populations and their ecosystem functions (McConnaughey et al., 2000; Thrush and Dayton, 2002; Kaiser et al., 2006). In heavily trawled waters, soft bodied habitat builders can be damaged as bycatch in nets and can take years to recover (McConnaughey et al., 2000; Kaiser et al., 2006). Octocorals are especially vulnerable since many species grow in or near soft sediments and often prefer the deep water habitats also frequented by trawlers (Schleyer and Celliers, 2003; Wareham, 2009; Baillon et al., 2012; Poulos et al., 2016). Though dredging and trawling cause more widespread damage, octocoral colonies can also be destroyed by entanglement in recreational fishing gear, as the filaments and hooks can become easily entangled in soft tissue (Poulos et al., 2013; Erni Cassola et al., 2016).

Like stony corals, octocorals and anemones are commercially traded and often harvested from the wild (Dee et al., 2014). Unlike stony corals, the majority of octocorals are not listed in the Convention on International Trade in Endangered Species (UNEP-WCMC (Comps.), 2014) and therefore trade is largely unmonitored (Bruckner, 2001). In fact, no octocorals in the orders Alcyonacea, Gorgonacea, or Pennatulacea are CITES Appendix II listed, and only four species in Gorgonacea are CITES Appendix III listed (Bruckner, 2001; UNEP-WCMC (Comps.), 2014). Collection of octocorals and anemones is often unrestricted in contrast to restrictions on the scleractinian coral trade, such as in Tonga and Indonesia (Dee et al., 2014). In other areas, such as the Maldives and Australia, export of octocorals and anemones is not regulated explicitly, but is included in aggregate export limits (Dee et al., 2014). Some species of octocoral are also harvested for other commercial purposes. For example, *Corallium rubrum* is harvested for jewelry making, and has been significantly overharvested in the Mediterranean. This species is now considered endangered by the IUCN (Santangelo and Abbiati, 2001; Bruckner, 2009, 2016; IUCN, 2016). Like octocorals, no anemones are listed in CITES (UNEP-WCMC (Comps.), 2014). Despite this, anemones are widely traded in the aquarium industry and anemonefish host anemones are especially susceptible to overharvesting because of their popularity (Shuman et al., 2005).

There are several well-known stony coral threats that have not been well-examined in octocorals and anemones. For example, industrial runoff can have many negative impacts on coral reefs, including increased turbidity, deposition of pesticides and herbicides, and nutrient enrichment, but only the effects of turbidity have been examined in octocorals and few studies have examined both turbidity and nutrient enrichment in anemones (Fabricius, 2005; Brodie et al., 2012; Liu et al., 2015).

Although octocorals and anemones are generally more susceptible to physical disturbances than stony corals, some disturbances that strongly impact stony corals seem to have little to no impact on octocorals. For example, crown-of-thorns seastars (COTS) can devastate stony coral populations over large spatial scales, but often leave octocorals relatively unaffected (Fabricius, 1997; Kayal et al., 2012). This is likely because COTS preferentially predate on stony corals and only eat octocorals when their preferred prey are scarce (De'ath and Moran, 1998). In addition, octocorals produce a plethora of chemical defensive secondary metabolites that deter predators and protect colonies from fouling, which may give them an advantage over their stony cousins during COTS outbreaks (Coll, 1992; Changyun et al., 2008). In fact, octocorals may take advantage of the opportunity by growing on exposed coral skeleton left behind by such outbreaks, and this may result in a phase shift to octocoral dominated state (Endean and Stablum, 1971; Norström et al., 2009). In the Caribbean, octocorals are also less susceptible to population declines due to commercial diving activities and physical disturbances than stony corals, with some species seeming to prefer highly impacted sites (Tratalos and Austin, 2001). This may be due, in part, to their soft and flexible bodies; though a detriment when entangled, they will bend instead of break when kicked or touched. Thorough understanding of the unique threats facing soft corals as well as those common to soft and stony corals is needed to assist effective recovery efforts after a disturbance event.

WHAT INFORMATION DO WE NEED TO SUCCESSFULLY RESTORE OCTOCORAL AND ANEMONES?

First, we need to understand how the target species will cope with a changing climate or other large scale, unavoidable human impacts (van Oppen et al., 2017; Bellwood et al., 2019). If the species is not resilient enough for restoration to be a long-term solution, alternatives may need to be considered. For example, if a temperature-sensitive species has been extirpated from a reef that regularly experiences heat waves, restoration to this area would be risky. Instead, protection of remaining populations or restoration efforts in less impacted environments (or different temperature envelopes) may be viable alternatives. This may be considered as a form of "assisted migration" and is a contentious approach as it may be akin to deliberately introducing a species to a new area with all of the potential risks that entails (van Oppen et al., 2017; Mayer-Pinto et al., 2019). However, if long-term impacts, such as climate change or recurring port dredging cannot be avoided, then a shift in approach must be considered. Management interventions, such as genetic, reproductive, physiological, population/community, and environmental interventions, can be used to great effect in conservation and restoration efforts, though these techniques are not without complications (van Oppen et al., 2017; National Academies of Sciences Engineering and Medicine, 2019). For example, assisted evolution may be a viable method for increasing within-species resistance to ongoing pressures, and should be considered when trying to mitigate the effects of long term, unavoidable disturbances in conjunction with other short term methods (van Oppen et al., 2015, 2017; Ainsworth et al., 2019). As the topic of assisted evolution is beyond the scope of this review, please see van Oppen et al. (2015, 2017) for further discussion.

Next, to choose appropriate restoration sites, we must identify the preferred habitat of the target species of octocoral or anemone. Many species are associated only with certain substrates or associate strongly with other benthic species. For example, the octocoral *Dendronephthya australis* is strongly associated with sponge gardens and soft substrates, and restoration would likely fail outside of these habitats (Poulos et al., 2016). To develop restoration targets, it is important to try and determine previous range and densities. This can be particularly difficult for soft-bodied organisms. Ideally, historical or reference surveys should be consulted for this information, but other, more anecdotal sources may also be necessary. For example, reports from research organizations such as the AIMS long term monitoring program (Australian Institute of Marine Science [AIMS], 2018) or CSIRO South East Marine Protected Areas Seamounts project (CSIRO, 2019) can provide rigorous insights into recent distributions in Australia, while less quantitative historical accounts, such as those of Darwin (1889) may be needed to give insight into historical distributions. The state of the area to be restored should also be examined. If the previous habitat is no longer suitable for the target species (for example, there have been irreversible changes to flow or sediment regimes), then it needs to be decided whether restoring the abiotic substrate or other habitat factors is worth the time and effort involved or whether alternative areas should be considered.

The presence and effect of predators, grazers, and competitors – both native and introduced – should also be considered in the planning of restoration efforts and choice of restoration site. For example, restoration of lake trout (*Selvelinus namaycush*) in Lake Ontario has been hampered by predation of trout fry by alewives (*Alosa pseudoharengus*; Krueger et al., 1995). In plant restoration ecology, the roles of herbivory and competition are widely studied, and have significant – and often manageable – impacts on restoration of both species and habitats (e.g., Llewellyn and Shaffer, 1993; Opperman and Merenlender, 2000; Sweeney et al., 2002; Midoko-Iponga et al., 2005). In tropical coral reef systems, algae and coral compete for space which can affect the size and distribution of coral colonies (McCook et al., 2001; Sandin and McNamara, 2012). Algal competition may also affect mortality of stony coral transplants, especially in shallow waters (Yap et al., 1998). Understanding the individual roles of competition, herbivory, predation, and environmental factors in transplantation success (e.g., Johnston and Clark, 2007) will help restoration efforts focus on solutions to common setbacks and increase efficacy of restoration efforts.

Once it is decided whether restoration is feasible in the long term and where to restore, we need to decide which kind of restoration is necessary. According to the SER framework, there are three major restoration approaches – (1) natural regeneration, (2) assisted regeneration, and (3) reconstruction (McDonald et al., 2016a). These restoration approaches can be used in conjunction for multiple species occupying the same area. The restoration approach required in each case may depend on several factors, including the level of population degradation and connectivity to other sites. Given that there are many variables that may impact restoration success, treatments should be piloted before full-scale regeneration or reconstruction are implemented (McDonald et al., 2016a). This is a requirement of current restoration activities proposed for the Great Barrier Reef Marine Park (GBRMPA, 2018).

The simplest form of restoration is *natural regeneration*, where recolonization is allowed to happen naturally after the removal of threats and disturbances (**Figure 2**). This works well for species that have had limited population degradation and/or are have a strong supply of larvae. As this method is not resource intensive, it can be scaled up more easily than more direct interventions (Bellwood et al., 2019). *Assisted regeneration*

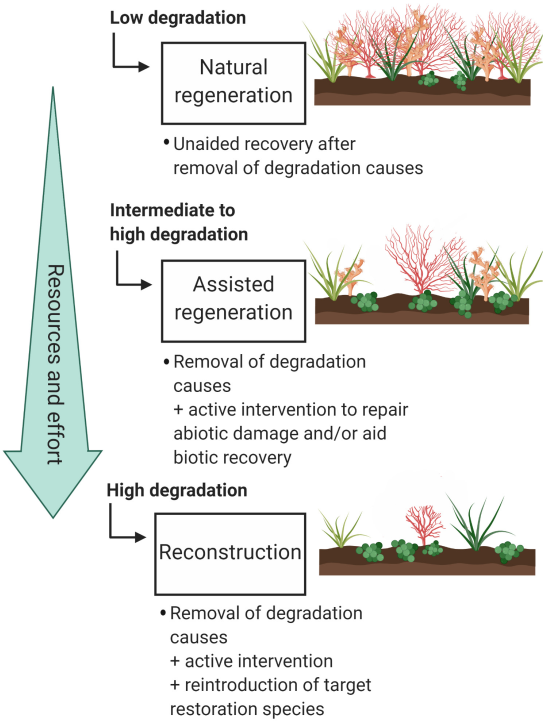

FIGURE 2 | The three types of restoration as described by the Society for Ecological Restoration (SER). Types are listed in order of increasing resources and effort. Examples of different soft coral habitat degradation levels are illustrated on the right hand side of the figure. Figure created in BioRender (biorender.com).

is the support of natural regeneration without transplanting organisms to the restoration site (**Figure 2**). The most common type of assisted regeneration is restoration of degraded abiotic habitat to facilitate natural regeneration of populations. In stony coral restoration this technique is commonly used when rubble fields are formed due to mining, blasting, or boating incidents (e.g., Clark and Edwards, 1994; Edwards and Clark, 1999; Precht et al., 2001; Lindahl, 2003; Rinkevich, 2005). Some species of octocorals are adept at colonizing new environments, making assisted regeneration an ideal option for these species. Adding artificial structures for octocoral recruitment can increase regional diversity and improve octocoral population densities (Perkol-Finkel et al., 2006; Perkol-Finkel and Benayahu, 2007, 2009; Mayer-Pinto et al., 2019). This technique is a viable option for mitigating the impact of necessary underwater infrastructure, especially if the structures are designed to increase coral recruitment (e.g., Burt et al., 2009). Care should be taken in design and construction of artificial structures to minimize the risk of structures being dominated by invasive, non-native, or nuisance species (Dafforn et al., 2012; Geraldi et al., 2014; Dafforn, 2017).

Regeneration can also be facilitated by use of naturally occurring positive feedback systems (Shaver and Silliman, 2017). For example in anemones, survivorship increases when they are inhabited by anemonefish (Frisch et al., 2016). Anemone survivorship could be increased by regulating anemonefish removal by the aquarium trade or by releasing cultured juvenile anemonefishes into existing anemone populations, as aquaculture techniques are well-established (Moorhead and Chaoshu, 2010). In the Florida Keys, predation on gorgonian octocorals by predatory snails was significantly increased when the snails were released from predation pressure (Burkepile and Hay, 2007), suggesting that strategic conservation of predatory fishes can reduce predation and improve octocoral populations in this and related systems (Shaver and Silliman, 2017). Positive feedbacks can also be used to increase coral cover through natural larval settlement, as diverse herbivore populations reduce height of settlement-inhibiting turf algae and indirectly increase density of settlement-promoting crustose coralline algae (Burkepile and Hay, 2008; Shaver and Silliman, 2017). Single species facilitation dynamics can also be exploited to increase efficacy of restoration efforts. For example, saltmarsh restoration efforts in both Florida and the Netherlands exploited natural facilitation by planting *Spartina* sp. plugs in close proximity. This increased yields by an average of 107% compared to when they were planted further apart (Silliman et al., 2015). Understanding and exploiting positive feedbacks naturally occurring in target systems could be an effective method for increasing efficiency and impact of restoration efforts (Shaver and Silliman, 2017).

The third type of restoration, *reconstruction*, is the most resource intensive (**Figure 2**). It involves transplanting organisms to the restoration target area, either by moving them directly from one area to another or by growing them in either aquaculture or mariculture. For corals, this method is usually implemented when natural recruitment is expected to be slow or to fail, even though the water quality, substratum, and other factors are appropriate for the target species (Edwards and Clark, 1999). To simplify the decision-making process related to which types of interventions are appropriate, a simple decision tree has been provided (**Figure 3**).

If reconstruction is necessary, the first step is to decide how to procure individuals. There are two main methods used for soft corals – sexual (use of larvae) or asexual (cut nubbins) propagation (Edwards et al., 2010). In stony coral restoration, sexual propagation is generally preferred because it increases genetic diversity through recombination, though this can reduce the frequency of locally adapted genotypes (Baums, 2008; Edwards et al., 2010). Unfortunately, little is known about octocoral propagation by this method, so feasibility must be assessed species by species. For restoration via sexual propagation to be viable, we need to understand the method and timing of reproduction, settlement method, preferred settlement substrate, and growth rate of the target species (Edwards et al., 2010). Similar information would be required for anemones that have been successfully grown in captivity from fertilized eggs, but grew extremely slowly (Scott et al., 2014; Scott, 2017).

On the other hand, octocorals and anemones are usually relatively simple to propagate asexually (from cuttings) due to their soft bodies. Anemones can be cut in halves or quarters, and will close the wound within 24 h and have a fully formed mouth in as little as 1 month (Scott et al., 2014; Scott, 2017). The greatest drawback to this method is that is reduces genetic

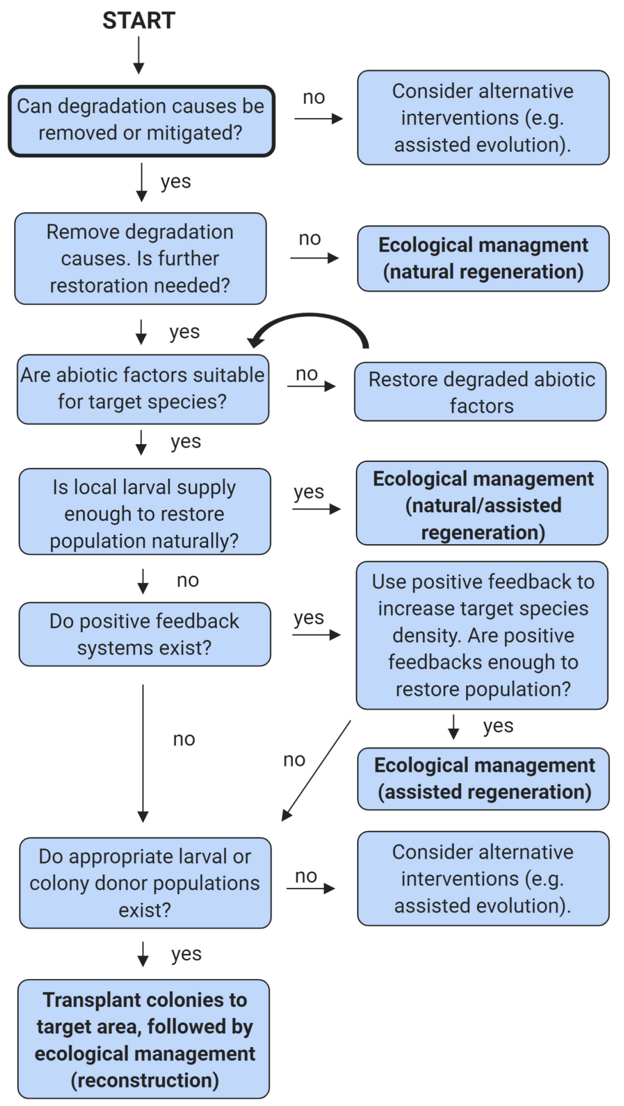

FIGURE 3 | A simple decision tree to inform soft coral restoration efforts. For multiple species occupying the same area, begin the tree anew for each species. This tree does not consider all possible scenarios, please see the section entitled "What information do we need to successfully restore octocoral and anemones?" for further details. Figure created in BioRender (biorender.com).

diversity due to the clonal nature of fragments, which can affect future population genetic structure and breeding success, though this can be mitigated by collecting fragments from multiple genetically distinct colonies (Baums, 2008; Shearer et al., 2009). Despite this, some octocorals and anemones naturally grow by clonal means, including budding and fission, and this method may result in naturally low diversity and an increased proportion of locally adapted genotypes and increase local adaptations (McFadden, 1991; Dahan and Benayahu, 1997; Barneah et al., 2002; Baums, 2008; Sherman and Ayre, 2008; Scott et al., 2014; Scott, 2017). Overall, the reproductive method (sexual vs. asexual), local adaptations, and genetic diversity of source populations should be considered when choosing how to source propagules for restoration (Baums, 2008; Edwards et al., 2010).

Once this has been decided, the juvenile/cut octocorals or anemones can be kept in aquaculture or mariculture systems until they are large enough for transplantation (Edwards et al., 2010; Leal et al., 2017). Fragments can be transplanted directly after collection, though mortality may be high (Weinberg, 1979; Linares et al., 2008). Similarly, some studies are now releasing stony coral larvae directly after collection (dela Cruz and Harrison, 2017). Anemones are highly sought after in the aquarium trade, and therefore aquaculture techniques are well-established for many species (Scott, 2017). Some species of octocoral are also grown for the ornamental aquarium trade, but many restoration target species are too difficult for the average home aquarist due to habitat and feeding requirements. Many species of both octocorals and anemones are non-photosynthetic, which may create difficulty for restoration projects as these need to be fed regularly (Leal et al., 2017). This leads to a more complex aquaculture technique than generally needed for stony coral restoration.

Finally, individuals must be transplanted to the restoration area, which can be challenging. Stony corals can be attached to substrate by placing adhesive material on the inner skeletal areas and using these to anchor colonies to the restoration substrate (Rinkevich, 2005; Edwards et al., 2010). Because octocorals and anemones do not have any stony, non-living surfaces, glues and epoxies do not work in the same way. Many octocorals, anemones, and sponges are sensitive to concretes, cyanoacrylates, and other materials commonly used to anchor stony corals to substrates, making attachment more difficult and labor intensive (Rinkevich, 2005; Ng et al., 2015). Therefore, alternative strategies are needed. Though clamps, clothes pegs, or other physical restraints may seem logical, these often are not strong enough to handle high-energy environments and do not encourage attachment of fragments to the benthos (Weinberg, 1979). One effective strategy that has been discovered is transplanting individuals attached to rock instead of free-living coral or coral cuttings (Weinberg, 1979; Oren and Benayahu, 1997; Ng et al., 2015). Individuals can either be collected with their attachments still in place, or can be physically attached using wire, string, or other physical material (e.g., Oren and Benayahu, 1997; Ng et al., 2015).

Because of these difficulties, attachment techniques must be developed that are appropriate for specific octocoral and anemone groups. For example, restoration of a wide range of gorgonians can be informed by trials done in the Mediterranean on *Paramuricea clavata*. During restoration trials, it was found that large *P. clavata* transplants created a lot of drag against their attachment putty media due to their surface area in the current and were easily lost, while smaller transplants remained attached (Linares et al., 2008). This team also tested different attachment methods, which included attaching fragments to putty with no support, supported within a short piece of plastic tubing, and tied to a plastic stick. The stick treatment showed the greatest survival rate despite being in direct contact with putty. These simple preliminary experiments are extremely important to long term success or failure of restoration efforts, as they inform future efforts and promote successful attachment, and can improve restoration efficacy of this and other species.

EXAMPLES OF ONGOING RESTORATION

To place restoration of octocorals and anemones in the context of the SER framework, here we present two examples of ongoing restoration of the red coral *Corallium rubrum* and the cauliflower soft coral *Dendronephthya australis*. *C. rubrum* is a Mediterranean coral that grows from 10 to 300 meters depth and prefers dark environments (**Figure 4a**; Weinberg, 1979). *Dendronepthya australis* is a cold water coral found off the coast of temperate New South Wales, Australia (NSW) and is critical habitat for the endangered White's seahorse, *Hippocampus whitei* (**Figures 4b,d**; Harasti et al., 2014; Harasti, 2016). The examples are presented against the International Standards for the Practice of Ecological Restoration Section III: Standard Practices for Planning and Implementing Ecological Restoration Projects. All headings from this section and whether information pertaining to this heading is available as presented in **Table 1** and expanded upon in this section. In summary, for *C. rubrum* in areas where threats have been mitigated or removed but natural recolonization is expected to take decades, reconstruction is a feasible solution for speeding population recovery. On the other hand, more difficulties have been encountered in *D. australis* restoration efforts, and while reconstruction will likely be beneficial to recovering populations, more information is needed on feasibility for this species.

These species were chosen for several reasons. Firstly, significant literature exists against which to assess restoration efforts following the SER framework. Furthermore, the species have different life history traits, have experienced different causes and severity of declines, and are in different stages of restoration, all of which allow for a more complete picture of challenges that can arise in octocoral restoration. Finally, C. rubrum was chosen because of the extensive time frame of both impacts and protections, and breadth of literature. D. australis was chosen because of the recent nature of impacts and the apparent restricted distribution of this species which provides an urgency to any potential restoration projects. Literature was sourced using Web of Science and Google Scholar databases using the keywords "*Dendronepthya australis*" and "*Corallium rubrum*" paired with "restor*," "impact*," "declin*," "protect*," and "recover*." Asterisks were used to denote different forms of words, for example "restor*" returned "restored," "restoring," and "restoration." If information on a topic was not found during searches, it is reported in **Table 1** as "no peer-reviewed published information found."

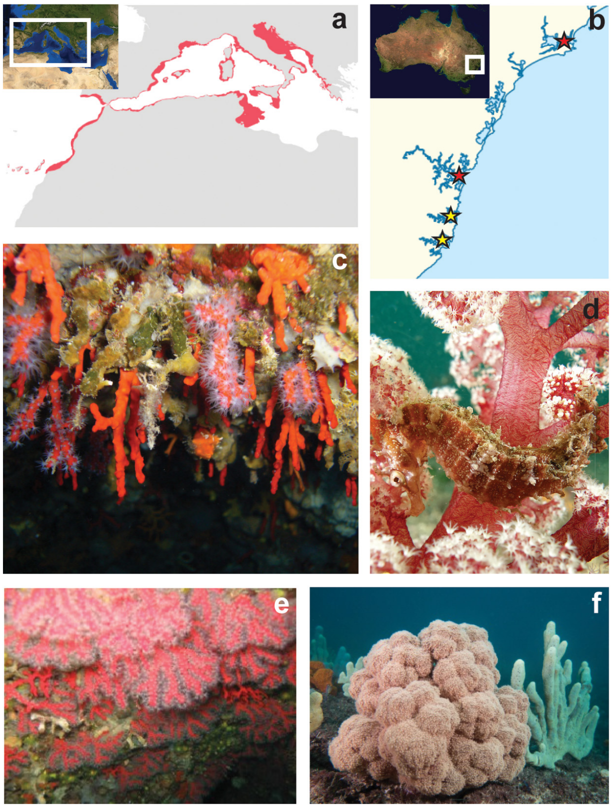

FIGURE 4 | Distribution and identification of case study species. **(a)** Distribution map of *Corallium rubrum*, map of Mediterranean inset, **(b)** distribution map of *Dendronephthya australis*. Populations with known population declines marked in red, map of Australia inset. **(c)** Small, immature *C. rubrum* colonies in the Mediterranean, **(d)** the endangered White's seahorse, *Hippocampus whitei*, in *D. australis*, **(e)** large, mature *C. rubrum* colonies, **(f)** mixed sponge and *D. australis* habitat. Photo credits – **(a)** modified from © FAO Fisheseries and Aquaculture Department, 2016. Aquatic Species Distribution Maps. FAO aquatic species distribution map of Corallium rubrum. In: FAO – Fisheries and Aquaculture Department (FI) (online). Rome. Updated 2016-08-24, http://www.fao.org/geonetwork/srv/en/main.home?uuid=fao-species-map-col; **(b)** modified from NordNordWest [CC BY-SA 3.0 de (https://creativecommons.org/licenses/by-sa/3.0/de/deed.en)]; **(c)** modified from Yoruno – Own work, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=2719768; **(d)** John Turnbull, MarineExplorer.org; **(e)** modified from Marco Busdraghi [CC BY-SA 3.0 (http://creativecommons.org/licenses/by-sa/3.0/)]; **(f)** John Turnbull, MarineExplorer.org.

Corallium rubrum

Stakeholder Engagement

Though stakeholders are identified (*C. rubrum* fisheries, divers, dive centers), there is little information on methods and efficacy of engagement, though when there is a second workshop on *Corallium* science, stakeholder participation has been identified as a priority (Bruckner and Roberts, 2009; Betti et al., 2019).

Ecosystem Baseline Inventory

We found that historic baseline data is available for *C. rubrum* from several location across the Mediterranean (Garcia-Rodriguez and Mass, 1986; Garcia-Rodriguez and Massó, 1986; Garrabou and Harmelin, 2002), and has previously been used to help quantify population damage (Bruckner, 2009). *C. rubrum* is threatened by commercial collection for jewelry. As a consequence large, sexually mature colonies in less than

TABLE 1 | Examples of ongoing octocoral restoration in the context of the Society for Ecological Restoration (SER) framework.

SER framework standard practice bullet point	*Corallium rubrum*	*Dendronephthya australis*
1. Planning and design		
1.1 Stakeholder engagement	Information available	No peer-reviewed published information found
1.2 External context assessment	No peer-reviewed published information found	No peer-reviewed published information found
1.3 Ecosystem baseline inventory	Information available	Information available
1.4 Reference ecosystem identification	Information available	Information available
1.5 Targets, goals, and objectives	No peer-reviewed published information found	No peer-reviewed published information found
1.6 Restoration treatment prescription	Information available	Information available
1.7 Assessing security of site tenure and post-treatment maintenance scheduling	Limited information available	Limited information available
1.8 Analysing logistics	No peer-reviewed published information found	No peer-reviewed published information found
1.9 Review process scheduling	No peer-reviewed published information found	No peer-reviewed published information found
2. Implementation		
As no full-scale reconstruction efforts have begun for either *C. rubrum* or *D. australis*, sections two, three, and four will focus on natural regeneration of *C. rubrum* within MPAs.		
2.1 No further or lasting damage is caused by the restoration works	Information available	No peer-reviewed published information found
2.2 Treatments are interpreted and carried out responsibly, effectively, and efficiently	Information available	No peer-reviewed published information found
2.3 All treatments are undertaken in a manner that is responsive to natural processes and fosters and protects potential for natural and assisted recovery	No manipulative treatments undertaken on large scale	No manipulative treatments undertaken on large scale
2.4 Corrective changes of direction to adapt to unexpected ecosystem responses	Information available	No peer-reviewed published information found
2.5 All projects exercise full compliance with work, health and safety legislation	No peer-reviewed published information found	No peer-reviewed published information found
2.6 All project operatives communicate regularly with key stakeholders	No peer-reviewed published information found	No peer-reviewed published information found
3. Monitoring, documentation, evaluation, and reporting		
3.1 Monitoring	Information available	No peer-reviewed published information found
3.2 Adequate records of treatments are maintained	Information available	No peer-reviewed published information found
3.3 Evaluation	Information available	No peer-reviewed published information found
3.4 Reporting	Information available	Information available
4. Post-implementation maintenance		
Because conservation and restoration efforts for both *C. rubrum* and *D. australis* are ongoing, post-implementation maintenance cannot be evaluated.		

For each category in the International Standards for the Practice of Ecological Restoration Section III: Standard Practices for Planning and Implementing Ecological Restoration Projects, whether information was found is presented for both Corallium rubrum and Dendronephthya australis. If information is available, it is expanded on in the text in the section "Examples of ongoing restoration."

50m of water have been largely wiped out (Bruckner, 2009), though populations up to 150 m depth are also being exploited (Santangelo and Bramanti, 2010). Age structure in these exploited populations is skewed toward small and young colonies, a sign of frequent disturbance (**Figures 4c,e**; Tsounis et al., 2006). Exploitation has caused severe enough declines that it is now considered endangered by the IUCN (2016).

In addition to collection, *C. rubrum* populations are threatened by colonization by boring sponges, which can affect up to 50% of colonies in a population and are a major cause of natural coral mortality (Corriero et al., 1997; Bramanti et al., 2007). In order to mitigate threats from overharvesting strict collection quotas, size limits, and rotational harvesting plans have been implemented or are in the process of being implemented (Caddy, 1993; Santangelo and Abbiati, 2001; Bruckner, 2016). Unfortunately, these regulations have so far been unsuccessful in creating a sustainable harvest because of the slow growth and late sexual maturation of colonies (Santangelo and Abbiati, 2001; Bruckner, 2009, 2016). Additionally, marine protected areas (MPAs) have been established within the range of *C. rubrum*, and coral size and age has increased in these areas, though even 20–30 years of protection have not proved sufficient for full population recovery (Tsounis et al., 2006; Bruckner, 2009).

Reference Ecosystem Identification

Though protected populations have not fully recovered, study of these areas give insight into the expected recovery potential of *C. rubrum* regeneration or reconstruction and work well as reference ecosystems.

Restoration Treatment Prescription

Threats to *C. rubrum* by humans have been mitigated through collection policies as described in section "Ecosystem Baseline Inventory," though this has not eliminated overharvesting. To mitigate natural damage by boring sponges, Bramanti et al. (2007) conducted settlement experiments using different settlement media. They concluded that using marble plates greatly reduced instances of boring sponges on colonies (Bramanti et al., 2007). This information can be used in restoration treatment prescriptions in two ways – as in-situ settlement material to reduce boring sponge mortality in assisted regeneration, or as a source of sexually derived propagules for transplantation in reconstruction efforts. This is particularly important to reconstruction as experiments with other gorgonian species in the Mediterranean show that transplanted small, attached colonies have higher survival rates than transplanted fragments (Weinberg, 1979).

In addition, A successful reconstruction pilot experiment using confiscated poached fragments of *C. rubrum* has shown that it is resilient to stress associated with reconstruction. Despite being harvested, kept out of water in poacher's nets, kept in aquaria, and then transplanted back into the natural environment in direct contact with putty, over 90% of fragments survived over 4 years post-transplant. When populations were re-sampled, researchers found that fertility rates were comparable to natural populations, while fecundity was higher in transplanted populations (Montero-Serra et al., 2018). Unfortunately, models predict that recovery of populations to natural, undisturbed size distributions using this method will take upwards of 30 years due to the slow growth rate and other life history traits of *C. rubrum* (Montero-Serra et al., 2018).

Assessing Security of Site Tenure and Post-treatment Maintenance Scheduling

Marine Protected Areas (MPAs) exist in the range of *C. rubrum,* improving security of site tenure. Unfortunately, no peer-reviewed published information on post-treatment maintenance was found.

No Further or Lasting Damage Is Caused by the Restoration Works

Banning of collection within MPAs has not caused further damage to *C. rubrum* ecosystems, but implementation of collection quotas, size limits, and rotational harvests have not been sufficient to mitigate impacts on this species (Caddy, 1993; Santangelo and Abbiati, 2001; Bruckner, 2016).

Treatments Are Interpreted and Carried Out Responsibly, Effectively, and Efficiently

Though implementation of MPAs has increased *C. rubrum* population density and mean colony size, poaching is still a problem and may require additional interventions (Tsounis, 2005; Tsounis et al., 2006; Bruckner, 2009; Montero-Serra et al., 2018).

Corrective Changes of Direction to Adapt to Unexpected Ecosystem Responses

As 20–30 years of protection within MPAs have not been sufficient to completely mitigate impacts, reconstruction of populations may be required and pilot studies have been undertaken (Tsounis et al., 2006; Bruckner, 2009; Montero-Serra et al., 2018).

Monitoring

Ongoing monitoring of *C. rubrum* within MPAs has shown that this species requires decades without disturbance for full population recovery (Tsounis et al., 2006; Bruckner, 2009). This has been possible because of collection of pre-protection baseline data, understanding of baseline healthy population size structures, and ongoing surveys of recovering populations (Bruckner, 2009).

Adequate Records of Treatments Are Maintained

Size and date of implementation of MPAs and changes to laws regarding *C. rubrum* are well-documented (Caddy, 1993; Santangelo and Abbiati, 2001; Bruckner, 2009). Because of the poached nature of fragments used in the pilot reconstruction study, exact GPS coordinates of the fragments used could not be obtained (Montero-Serra et al., 2018), but should be where possible.

Evaluation

Results from monitoring, studies of life history traits, and pilot transplantations suggest that reconstruction may be an appropriate way to improve population densities in areas where impacts have been successfully mitigated (Montero-Serra et al., 2018).

Reporting

Reports and journal articles have been published and a metanalysis performed on the results of implementing MPAs (e.g., Santangelo and Abbiati, 2001; Tsounis, 2005; Tsounis et al., 2006; Bruckner, 2009), though the metanalysis has been contentious (Bruckner, 2010; Santangelo and Bramanti, 2010).

Dendronephthya australis

Ecosystem Baseline Inventory

Dendronephthya australis pre-disturbance distribution, population densities, and functional and ecosystem roles have been intensively studied in the Port Stephens estuary in central NSW, Australia (Poulos et al., 2013, 2016; Corry et al., 2018). *D. australis* lives in soft substrates in association with sponge gardens, and gardens with *D. australis* are associated with higher fish diversity than nearby sand, seagrass, and sponge habitats without *D. australis* (**Figure 4f**; Poulos et al., 2013). *D. australis* is non-photosynthetic, instead relying on strong currents to feed on zooplankton and detritus (Poulos et al., 2016; Corry et al., 2018). Taking all of these factors into account, models have identified appropriate unoccupied *D. australis* habitat within the Port Stephens estuary (Poulos et al., 2016). Unfortunately, populations are under threat from fishing line entanglement, boat anchor damage, mooring chain scour, and shifting sands (Harasti, 2016; Poulos et al., 2016). In fact populations in Port Stephens, where densities are greatest, have been reduced by up to 95% due to a catastrophic sand-shifting event (Harasti, 2016). In addition, a misplaced boat mooring scoured over 1000 m^2 of *D. australis* and sponge garden habitat, reducing the area to bare sand (Harasti, 2016). Though this mooring block has since been moved, populations have not yet recovered in either location. Resulting population declines have been so severe that the New South Wales Fisheries Scientific Committee have recommend listing *D. australis* as endangered (NSW Fisheries Scientific Committee, 2019). Little is known about natural recruitment and growth rate of these corals, which makes estimates of natural recovery difficult.

Reference Ecosystem Identification

Though some populations of *D. australis* within the Port Stephen's estuary were heavily impacted, others remained unaffected and are ideal reference ecosystems (Harasti, 2016).

Restoration Treatment Prescription

Little can be done to mitigate damage by large-scale, natural events such as the sand-shifting that smothered populations in 2010 (Wainwright, 2011). On the other hand, careful planning and placement of mooring blocks, and insuring that any mooring blocks near colonies are benthic friendly can help protect remnant populations (Demers et al., 2013).

Despite the wealth of demographic knowledge on this species, there is a lack of general information on non-photosynthetic octocoral transplantation and aquaculture. Many restoration techniques that work on stony corals do not necessarily work with this species. Aquaculture has proved problematic, as coral nubbins do not reliably attach to media and require labor intensive feeding.

Assessing Security of Site Tenure and Post-treatment Maintenance Scheduling

MPAs exist in the ranges *D. australis,* improving security of site tenure, though not all populations fall within MPA borders (Poulos et al., 2016). No peer-reviewed published information on post-treatment maintenance for *D. australis.*

Reporting

Results from unsuccesful transplantation trials on *D. australis* have been reported in an Honors thesis, but have not been published in a peer-reviewed journal. As Dr. Poulos was working with the NSW Department of Primary Industry during this research, it is available to appropriate managerial bodies.

SUMMARY OF CASE STUDY ASSESSMENT

By reviewing restoration of *C. rubrum* and *D. australis* in the context of the SER framework we have clarified both the strengths and gaps in knowledge for both species and pinpointed areas for future research. Overall, we have found that restoration of both species has a high chance of success but understanding of restoration techniques and expected recovery times is much more advanced for *C. rubrum.* Though studies show that both sexually and asexually derived propagules can be used in reconstruction efforts for *C. rubrum*, more information is needed on the elimination/mitigation of threats, ecologically appropriate methods for triggering regeneration, choosing appropriate genetic stock for each reconstruction site, and strategies for addressing genetic stock issues (McDonald et al., 2016a). For *D. australis,* more information is needed on propagation, aquaculture techniques, and transplantation in addition to the knowledge gaps identified for *C. rubrum* (McDonald et al., 2016a). Conclusions drawn from the restoration effort of these two species can inform restoration of other octocorals and anemones. For example, creating sustainable harvesting schemes for slow-growing *C. rubrum* would significantly expand our knowledge of sustainable use of benthic cnidarians, such as has previously been found for the Hawai'ian black coral (Grigg, 2001). Increasing our knowledge base of sustainable harvest of benthic resources would allow for better management of other species, such as the heavily exploited anemone *Entacmaea quadricolor* (Frisch et al., 2019). Transplantation of *D. australis* has also proven to be a challenge, though not a unique one. Developing attachment techniques would greatly enhance the viability of restoration efforts for any species with soft attachment sites, including most species of anemone. Additionally, developing aquaculture techniques for the azooxanthellate octocoral *D. australis* would inform aquaculture of other azooxanthellate octocoral and anemone species, greatly increasing the efficacy of captive propagation. Addressing these knowledge gaps would greatly increase the chances of successful restoration of these and other species.

CONCLUSION AND CRITICAL STEPS FORWARD FOR EFFECTIVE OCTOCORAL AND ANEMONE RESTORATION

Although octocorals and anemones are often overlooked in ecological studies, our review highlights their vulnerability to climate change and other human threats, and some species may require restoration projects to maintain or rehabilitate their populations and/or ecosystem services. There are many challenges to octocoral restoration, not the least of which is the difficulty in setting restoration parameters. Octocorals and anemones don't leave skeletons or other signs after die-off events, therefore reference surveys are needed to understand historic density and community composition. Unfortunately, in tropical environments many papers that report coral loss and bleaching either do not specify between stony corals, octocorals, or anemones or do not include them at all, instead focusing solely on stony corals, while deep-water environments are often difficult to survey. In addition, there is the added challenge that many long term studies, such as long term monitoring programs, have only recently begun reporting octocoral cover (e.g., Australian Institute of Marine Science [AIMS], 2018), so we have little understanding of historic coral cover. Temperate octocorals and anemones are often, but not always, better documented (e.g., Bruckner, 2009; Poulos et al., 2016). There are also many technical challenges to restoration of octocorals and anemones, most notably in sourcing reproductive propagules and attaching clonally sourced fragments to the benthos. Despite the challenges posed by knowledge gaps, certain characteristics of octocorals and anemones suggest they will be increasingly important components of the modern reefs of the Anthropocene across climate zones. Hence, an urgent focus on their biology, ecology, and restoration methods is needed.

AUTHOR CONTRIBUTIONS

RS wrote the original manuscript. KD, TA, and EJ helped develop the project and helped shape the final article, including editing and directional advice. All authors contributed to the article and approved the submitted version.

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Large-Scale Sea Urchin Culling Drives the Reduction of Subtidal Barren Grounds in the Mediterranean Sea

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Increasing anthropogenic pressures are causing long-lasting regime shifts from high-diversity ecosystems to low-diversity ones. In the Mediterranean Sea, large expanses of rocky subtidal habitats characterized by high diversity have been completely degraded to the barren state due to the high grazing pressure exerted by sea urchins, which could persist for a long time. In several areas of the world, removal of sea urchins has been found to have a positive effect on the recovery of overexploited subtidal rocky habitats. This study assessed, for the first time in the Mediterranean Sea, the effects of extensive sea urchin culling on the recovery of subtidal reefs from the barren state. We tested this approach within a Marine Protected Area where a combination of oligotrophic conditions, general depletion of fish stocks, dramatically high sea urchin densities, and the large expanses of barren grounds caused by date mussel fishery have hampered the natural recovery of shallow rocky reefs. Culling intervention (through hammering) was carried out in spring 2015, covering an area of 1.2 hectares at about 5 m depth. The effects of sea urchin removal were monitored at regular intervals for a time span of 3 years and were compared with two control sites adjacent to the culling area. We documented a progressive reduction in the extent of barren grounds in the fully protected area after the intervention. Also, very low re-colonization of sea urchins was observed during the experiment, so that no additional extensive culling was necessary. Our findings suggested sea urchin culling as a promising practice, also considering the limited costs of the intervention. However, since the reduction in extent of barren grounds was largely driven by turf-forming algae, caution is needed in the interpretation of the outcomes in terms of restoration, and results are discussed considering the factors involved in the observed shift and the synergies to be carried out for a full recovery of the system.

Keywords: macrobenthic assemblages, patch dynamics, rocky reefs, sea urchin barrens, restoration

INTRODUCTION

Habitat degradation, fragmentation, and loss are among the most dramatic consequences of the escalating anthropogenic pressures on natural systems (Tittensor et al., 2014; Haddad et al., 2015; Steffen et al., 2015) and usually imply significant changes in biodiversity and ecosystem functioning (Pereira et al., 2010; Bartlett et al., 2016). Global analyses showed unprecedented rates of decline at all levels of biological diversity (Butchart et al., 2010). Exacerbated by multiple and synergistic effects of climate change (Bozec and Mumby, 2015), human impacts are increasingly compromising the capacity of marine ecosystems to absorb recurrent perturbations (Nystrom et al., 2000; Gundersen and Pritchard, 2002; Folke et al., 2004), thus limiting the potential for natural recovery (Scheffer et al., 2001; Lotze et al., 2011). The ultimate result of this process is a substantial transition of ecological systems into less productive or otherwise undesired states that are often difficult to reverse, called regime (or phase) shifts (Scheffer et al., 2001; deYoung et al., 2008; Rocha et al., 2015). A continuing increase in these phenomena has been observed in marine ecosystems worldwide (Levin and Möllmann, 2015).

On temperate rocky reefs, one of the most frequent and persistent regime shifts is the transition from macroalgal-dominated habitats to barren grounds as a result of sea urchin overgrazing (Silliman et al., 2013; Steneck and Johnson, 2013; Filbee-Dexter and Scheibling, 2014; Ling et al., 2015). Anthropogenic stressors may play a crucial role in triggering and maintaining this shift by eroding the resilience of macroalgal beds while increasing the persistence of sea urchin barrens (Ling et al., 2015). For instance, the depletion of populations of sea urchin predators caused by overfishing has been invoked as the main driver leading to kelp bed collapse in different regions of the world [e.g., Hagen and Mann, 1992 (Canada); McClanahan, 2000 (Africa); Shears and Babcock, 2003 (New Zealand); Ling et al., 2009 (Australia); Watson and Estes, 2011 (Alaska)].

In the Mediterranean Sea, *Paracentrotus lividus* (Lamarck) and *Arbacia lixula* (L.) are the most common sea urchins inhabiting shallow hard bottoms (Bulleri et al., 1999; Boudouresque and Verlaque, 2001) and are of paramount importance in ecological processes leading to the shift from habitats characterized by well-structured macroalgal canopies (e.g., dominated by *Cystoseira* species) to less complex barren grounds dominated by encrusting coralline algae (Bulleri et al., 2002; Bonaviri et al., 2011; Agnetta et al., 2015). Although many processes underlie the population dynamics of these two species (Hereu et al., 2012 and reference therein), reduced top-down control of their populations due to overfishing of their predators has been demonstrated to play a crucial role in determining the establishment of the degraded alternative state in sublittoral rocky reefs (Micheli et al., 2005; Guidetti and Sala, 2007; Hereu et al., 2008; Sala et al., 2012; Cardona et al., 2013). However, given the hysteretic behavior of subtidal macroalgal systems (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015), barren-state conditions may persist for years despite the establishment of mitigation strategies [e.g., Marine Protected Areas (MPAs)] aimed at the recovery of adult sea urchin predators (Pinnegar et al., 2000; Babcock et al., 2010; Galasso et al., 2015). Understanding whether alternative management actions could be implemented in marine coastal systems to face this widespread phenomenon should be a priority.

Based on evidence for the positive effects of reducing sea urchin density on the recovery of overexploited subtidal rocky habitats (reviewed by Ling et al., 2015), the practice of systematic sea urchin culling on "incipient barrens" (i.e., spatially discrete areas <10 m^2) has been applied in some areas of the world, specifically for kelp restoration (e.g., Bernstein and Welsford, 1982; Leinaas and Christie, 1996; Sanderson et al., 2015; Tracey et al., 2015). This action can also represent an opportunity for the development of a sustainable economy (e.g., https://www.urchinomics.com) since sea urchins are considered a consumable fishery resource worldwide (Andrew et al., 2002; Grisolía et al., 2012; Fernández-Boán et al., 2014; Bertocci et al., 2018).

The present study represents the first attempt in the Mediterranean Sea to perform systematic large-scale sea urchin culling on "extensive barrens" (*sensu* Ling et al., 2015), i.e., over a scale of thousands of square meters of continuous bare rock. The restoration activity, developed within the framework of the EU H2020 project "Marine Ecosystem Restoration in Changing European Seas,"[1] is the scale-up of a pilot study carried out in the same area (Guarnieri et al., 2014), where the role of sea urchin removal in triggering the process of recovery of persistent barren grounds was highlighted at small spatial scale (tens of meters). The aim of this study was to assess: (1) The effectiveness of a large-scale culling intervention in maintaining the reduction of herbivore pressure on disturbed benthic assemblages; (2) The direction and time frame of the recovery of assemblages in barren grounds.

MATERIALS AND METHODS

Study Area

The study was carried out in the South West of Apulia (Italy) within the MPA of Porto Cesareo (**Figure 1A**), one of the largest Italian marine reserves (16654 ha). The coast is almost entirely characterized by a gently sloping calcareous rocky plateau that drops onto a sandbank starting from the isobath of 10 m depth. Large expanses of subtidal rocky reefs in the MPA and beyond its boundaries have historically been depleted by illegal date mussel (i.e., *Lithophaga lithophaga*) fishery (Fanelli et al., 1994; Fraschetti et al., 2001; Guidetti et al., 2003), as occurred in other areas of the Mediterranean Sea (Devescovi et al., 2005; Bevilacqua et al., 2006; Guidetti and Dulčić, 2007; Parravicini et al., 2010; Giakoumi et al., 2012). This fishing practice has been demonstrated to have a crucial role in triggering the process leading to seascape desertification (Airoldi and Beck, 2007). Recent studies highlighted that the effects of this destructive fishery (forbidden since 1988) on the shallow rocky sublittoral are clearly evident for many kilometers along the coast and, in spite of the establishment of the MPA in 1997, no significant signs of recovery have yet been observed. Here, the main factor

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[1] www.merces-project.eu

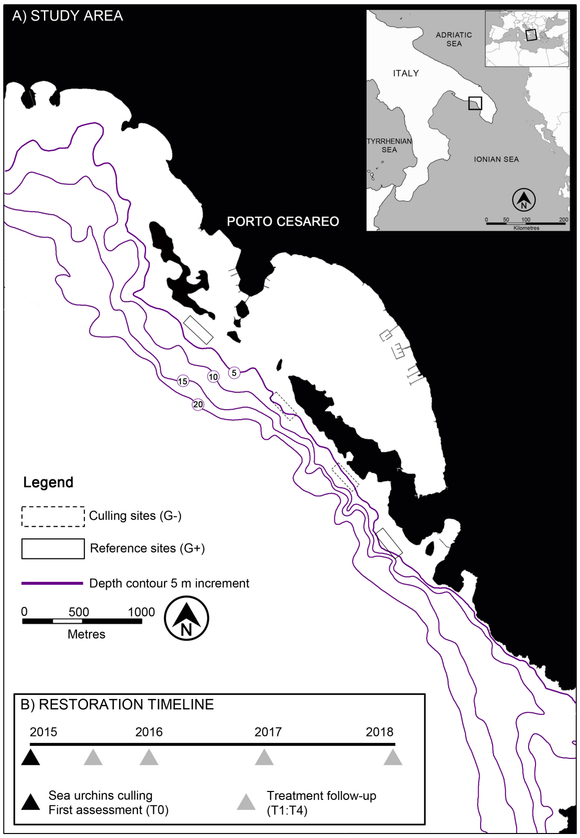

FIGURE 1 | (A) Study area and **(B)** timeline of the restoration intervention.

contributing to the inertia of the barren state is a combination of oligotrophic waters (Philippart et al., 2012), a general depletion of fish stocks (Guidetti et al., 2008; Giakoumi et al., 2017), and a dramatically high density (≈ 20 individuals m^{-2}) of sea urchins *A. lixula* and *P. lividus* (Guidetti et al., 2003), which are also prone to settle and/or recruit on reefs heavily impacted by date mussel fishery (Guidetti, 2011; Agnetta et al., 2013).

Based on preliminary surveys carried out along the 32 kilometers of rocky shore included in the MPA, we focused sea urchin culling within the no-take/no-access zone named "La Stream" (40°14′35″N – 17°54′07″E, **Figure 1A**) representing the area with the worst conditions in terms of desertification, with more than 60% of the plateau featuring barren grounds (Guarnieri et al., 2016). Our choice ensured, at the same time, the exclusion of any interference with the experiment due to human frequentation. Except for sparse patches colonized by the sponge *Chondrilla nucula* (covering just a few square meters) and some macroalgae (e.g., *Dictyota* spp., *Halimeda tuna*, *Amphiroa rigida*, and *Padina pavonica*), the barren grounds characterizing the study area were largely represented by bare rock dominated by encrusting coralline algae of the genera *Peyssonnelia* and *Lithophyllum* (Guidetti, 2011; Guarnieri et al., 2016).

A preliminary survey in the study area allowed the identification of two sites at 5–7 m depth (hereafter indicated as "G−") that were comparable in terms of extent (i.e., 6000 m^2 each), low substrate morphological complexity (i.e., absence of ridges and depressions), and inclination (<20%). Two control sites with similar conditions and extent (hereafter reported as "G+") were also included in the experiment (**Figure 1A**). This allowed the expected changes in the recovery rates caused by sea urchin removal to be separated from those potentially occurring during the time span of the intervention (i.e., 3 years) as a consequence of external long-term processes, such as natural fluctuations in grazer population demography and/or in patterns of distribution of benthic assemblages.

Culling and Monitoring Activities

The experimental intervention started in spring 2015. Sea urchins have a good dispersal distance (Paterno et al., 2017) and are thus able to colonize culled sites from adjacent areas. It was decided to perform culling before the typical reproductive periods in the study area (from spring to autumn) (Tenuzzo et al., 2012) to reduce larval supply from resident individuals. The systematic removal of sea urchins covered a total area of approximately 1.2 hectares. It was carried out in two sites with a linear extent of approximately 200 m, and it was achieved by means of a belt transect method in which transect lines (≈ 33 culling transects for each site) were laid perpendicular to the coast following the 210° course of a compass across the plateau (≈ 5 m depth) until its edge (transect length ≈ 30 m). Divers positioned themselves on one side of the line and advanced in parallel, creating a "cleaning front" so that approximately 3 m from both sides of the lead core rope along that path remained free of sea urchins. Divers worked in parallel during 8 days of activity until the entire experimental sites (G–) were cleaned. All visible individuals were culled using hammers; a knife was employed to remove them from crevices. The experiment was carried out in accordance with the European Committee Council Directive (86/609/EEC) and Italian animal welfare legislation (D.L. 116/92). Species manipulated in this study are not critically endangered species, and according to Italian (D.L.vo 26/2014) and EU (Directive 63/2010) legislation on the care and use of experimental animals, the activity does not require approval by an animal ethics committee if carried out on-site. Moreover, the Porto Cesareo MPA Authority issued all permits needed for performing the fieldwork.

For each diver engaged in the activity, the number of sea urchins removed and the time spent was also recorded in order to provide useful information about the feasibility of the intervention. A total amount of ≈ 92500 sea urchins were removed during the 8 days spent in the culling activities (**Supplementary Table S1A**) carried out at both sites. The number of divers per day who were engaged in the culling activity varied from a minimum of 5 up to 8 per day, each of them spending approximately 90 min underwater. A total of 84 h was devoted to the intervention, which corresponds to an average culling rate of 18.38 ± 0.41 urchins min^{-1} per diver. Regarding the sea urchins, *A. lixula* dominated on bare rocks, whereas both species co-occurred on sparse and small patches featuring the presence of *C. nucula* and macroalgae. The observed segregation was probably due to the high-energy hydrodynamic regime in the study area, which has been demonstrated to favor *A. lixula*, due to its higher resistance to dislodgment compared to *P. lividus*

(Bulleri et al., 1999; Guidetti and Mori, 2005; Agnetta et al., 2013). This pattern further supports the results of other studies stressing the ability of *A. lixula* to maintain the barren state in the Mediterranean Sea (Bulleri et al., 2002; Privitera et al., 2008; Bonaviri et al., 2011; Bulleri, 2013; Piazzi and Ceccherelli, 2017).

The effects of sea urchin removals were monitored at regular intervals (i.e., 6, 12, 24, and 36 months after culling, hereafter indicated as time [T] 1–4) by mean of video and photographic surveys, covering a time span of 3 years (i.e., until June 2018, **Figure 1B**). Before the culling treatment, all experimental sites were surveyed in order to provide the baseline information (T0) about the status of barren grounds in terms of average sea urchin density, % cover of bare rock, and structure of benthic assemblages.

Within each of the four sites (i.e., G– and G+), the average density of sea urchins was evaluated along three transects, each one covering a surface of 25 × 1 m and randomly located tens of meters apart from each other. Along each transect, continuous underwater video footage was taken by means of a digital video-camera (Nikon Coolpix W300) held orthogonally downward at a standard distance from the bottom. From each of the three video transects, 10 frames (covering a sampling surface of 1 m^2) were extracted at random to assess the% cover of barrens in the experimental sites. Since high image resolution was required for taxonomic identification of organisms, 10 randomly located surfaces of 16 × 25 cm were also photographed along each transect. At each site, 30 photographic samples were taken at each time of sampling, yielding a total of 600 observation units. For each photographic sample, the cover of sessile organisms was estimated under magnification by superimposing a grid of 24 sub-quadrats on the entire photographed surface, and final values were expressed as a percentage. Organisms that were not easily identifiable at species level were grouped into higher taxonomic groups or into morphological groups (see **Supplementary Table S2** for more details).

Statistical Analyses

A distance-based permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001; McArdle and Anderson, 2001) was employed to test for differences in the structure of sessile assemblages between culling and control sites (i.e., G– and G+, respectively) across time. The analysis was based on Bray–Curtis dissimilarities calculated on untransformed data, and each term was tested using 4999 random permutations. The experimental design consisted of four factors: Time (Ti, 5 levels, fixed), Treatment (Tr, 2 levels, G– and G+, fixed and orthogonal), Site (Si, 2 levels, random, and nested in Tr), and Transect (Ts, 3 levels, random, and nested in Si) with $n = 10$ replicates. Significant terms relevant to the hypothesis were investigated through *post hoc* pair-wise comparisons. Multivariate patterns of variation among the four different treatment combinations were visualized by non-metric multidimensional scaling (nMDS) of Ti × Si(Tr) centroids.

To identify taxa contributing most to temporal differences between culling and control sites, a canonical analysis of principal coordinates (CAP, Anderson and Willis, 2003) was also performed for the Ti × Tr interaction term, calculating the distance matrix among transects in culling and control sites in each time of sampling. Distinctness among Ti × Tr groups was assessed using leave-one-out allocation success (Anderson and Robinson, 2003). Individual taxa that might be responsible for any group differences seen in the CAP plot were investigated by calculating product–moment correlations of original variables (taxa) with canonical axes (e.g., Anderson and Willis, 2003). These correlations of individual variables with the two canonical axes (r^1 and r^2) were then represented as lines in the CAP plot. Taxa were included in the plot only if an arbitrarily chosen value of correlation was exceeded (i.e., $\sqrt{r_1^2 + r_2^2} \geq 0.3$). The same statistic was employed on a distance matrix based on Jaccard dissimilarities to investigate patterns of variation focusing on the assemblage composition.

ANOVA was employed to test for differences in the number of taxa and% cover of barren areas between culling and control sites. ANOVA was also used to test for differences due to sea urchin removal in the abundance of the algae and invertebrate components of sessile assemblages. The percentage cover of the different algal taxa was aggregated into two categories (see **Supplementary Table S2**) according to their morphology and size of thallus, i.e., <3 and >5 cm for turf-forming and erect algae, respectively (see Guarnieri et al., 2014 and reference therein). The same was done for invertebrates, which were grouped into a single category because of their limited coverage across experimental sites. Encrusting algae (e.g., *Lithophyllum* spp., *Peyssonnelia* spp.) were excluded from the univariate analyses since they represent a substrate suitable for the recruitment of a number of benthic organisms and can be considered equivalent to bare rock (Bulleri et al., 2012). For each response variable, univariate analyses were carried out following the same design as for multivariate analysis. Finally, ANOVA was employed to test for differences in sea urchin density by mean of a three-factor experimental design: Time (Ti, 5 levels, fixed), Treatment (Tr, 2 levels, fixed and orthogonal), and Site (Si, 2 levels, random, and nested in Tr) with $n = 3$ replicates. Prior to analyses, the homogeneity of variance was examined using Cochran's *C* test, and data were transformed if necessary. All univariate analyses were performed using GMAV version 5 software (University of Sydney, Australia), while multivariate analyses were carried out using the software PRIMER version 6, including the add-on package PERMANOVA+ (Anderson et al., 2008).

RESULTS

PERMANOVA on the assemblage structure based on Bray–Curtis dissimilarities revealed a significant Ti × Tr interaction (**Table 1**), indicating an effect of sea urchin culling on the recovery of the assemblage in barren grounds. As indicated by pair-wise comparisons, significant differences across time only occurred at sites where sea urchins were removed, with clear signs of recovery 1 year (T2) after the beginning of the experiment. By contrast, no temporal difference was detected in the structure of assemblages within control sites, indicating that bare conditions persisted during the whole experiment. Temporal variations among sites according to the different

TABLE 1 | Results of permutational multivariate analysis of variance (PERMANOVA) testing the effect of sea urchin culling on the structure of benthic assemblages.

Source of variation	df	MS	Pseudo-*F*	*P(perm)*
Time = Ti	4	39248	2.60	0.0068
Treatment = Tr	1	217990	9.75	0.0002
Site = Si(Tr)	2	22350	4.77	0.0190
Transect = Ts(Si(Tr))	8	4688	3.17	0.0002
Ti × Tr	4	31110	2.06	0.0338
Ti × Si(Tr)	8	15121	2.79	0.0002
Ti × Ts(Si(Tr))	32	5414	3.66	0.0002
Residuals	540	1481		
Total	599			
Pair-wise test for term Ti × Tr				
G+		G–		
T0 = T1 = T2 = T3 = T4		T0 = T1≠T2≠T3 = T4		
T0	T1	T2	T3	T4
G+ = G–	G+ = G–	G+ ≠ G–	G+ ≠ G–	G+ ≠ G–

Analyses were based on Bray–Curtis dissimilarities (untransformed data), and each test was performed using 4999 permutations of appropriate units. Results of pair-wise tests for the significant term Ti × Tr are reported below. G–, sea urchins culled; G+, reference conditions.

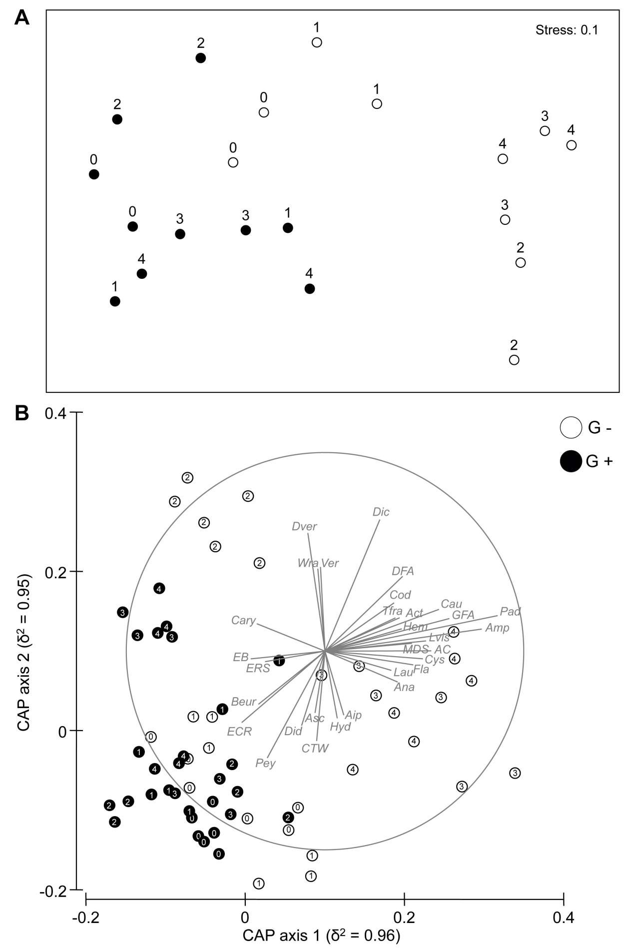

FIGURE 2 | (A) Non-metric multidimensional scaling (nMDS) ordination of Ti × Si(Tr) centroids on the basis of Bray–Curtis dissimilarities for the rocky bottom assemblages. **(B)** Canonical analysis of principal coordinates (CAP) for the factor Ti × Tr at the different sampling times (T0:T4). Individual taxa highly correlated with canonical axes are shown. Abbreviations for taxa used in CAP plots are given in **Supplementary Table S2**. Numbers (from 0 to 4) indicate the sampling times. G+, control sites; G–, culling sites.

treatments were portrayed in the nMDS plot (**Figure 2A**), which showed a progressive segregation between culling and control sites over time. CAP analysis showed that the observed changes in the structure of assemblages between G– and G+ were mostly driven by changes in the abundance of macroalgae components (**Figure 2B**), such as dark and green filamentous algae (DFA and GFA, respectively), articulated corallines (AC), *A. rigida* and *Liagora viscida* (belonging to the category of turf-forming algae), Dictyotales, *Laurencia* spp. *Cystoseira compressa*, *P. pavonica*, and *Wrangelia penicillata* (belonging to erect macroalgae). By contrast, invertebrates [encrusting bryozoans (EB) and red sponges (ERS), together with Didemnidae, the group of calcareous tube worms (CTW), and the anthozoa *Balanophyllia europaea*] and encrusting calcareous rhodophytes (i.e., ECR and *Peyssonnelia* spp.), which are typical of barren habitats, mostly contributed to differentiated assemblages within the sites where sea urchins were not removed. Assemblage composition did not differ over time for either control or culling sites (**Supplementary Table S3**). Also, no difference in taxon composition was detected between treatments at the beginning and at the end of the experiment, indicating a similar composition of assemblages at culling and control sites during the entire duration of the experiment (**Supplementary Figure S1** and **Supplementary Table S3**).

ANOVA on sea urchin density detected a significant ($F = 1120$, $P < 0.001$) effect of culling in reducing the sea urchin population at culling sites compared to control sites. This reduction was consistently maintained during the whole duration of the experiment (**Supplementary Table S1B**). At the end of the experiment, sea urchins at culling sites (G–) were approximately 75% less abundant than at the beginning (i.e., from 9.16 ± 1.02 to 2.30 ± 0.17 individuals m^{-2} at T0 and T4, respectively). A reduction in sea urchin density was observed at G+ during the experiment, although control sites showed consistently higher sea urchin densities than culling sites (**Figure 3**).

The results of ANOVA (**Table 2**) showed a progressive reduction of the extent of barren grounds at culling sites through time (**Figure 4A**), as indicated by the significant interaction term Ti × Tr. No difference was detected in terms of species richness (**Figure 4B**). Instead, ANOVA detected a significant increase in total cover for both turf-forming algae and erect macroalgae at culling sites during the experiment (**Figures 4C,D**). No differences between treatments were detected for invertebrates.

DISCUSSION

The understanding of mechanisms able to drive the recovery trajectories of barren grounds is critical for the development of widescale management strategies aimed at reverting the state of

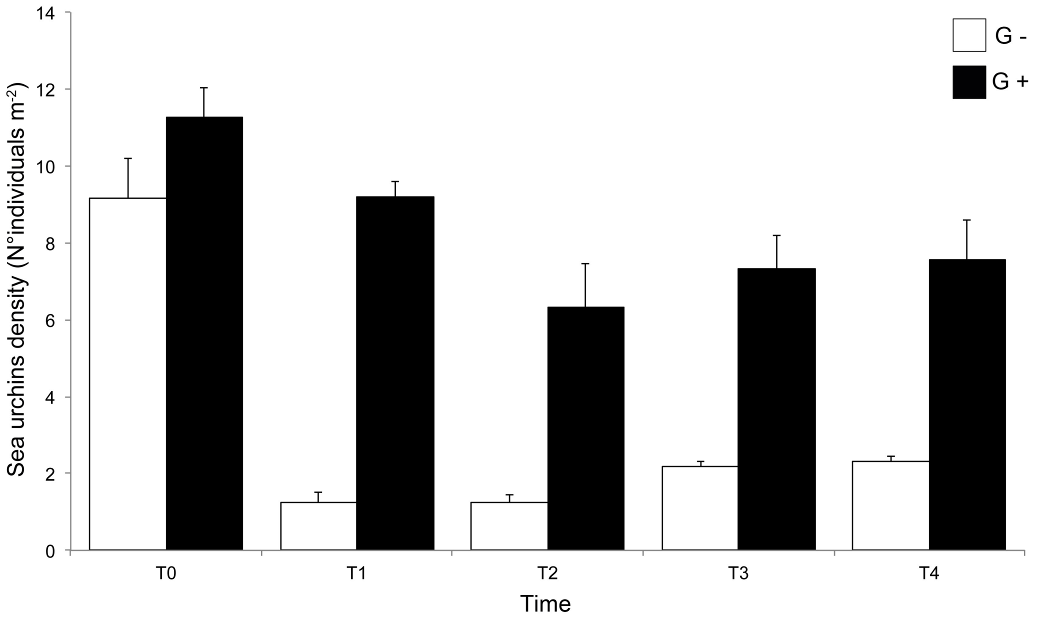

FIGURE 3 | Mean sea urchin density (±SE, *n* = 6) recorded at each time of sampling (T0:T4). G+, control sites; G–, culling sites.

TABLE 2 | Summary of ANOVA testing the effect of sea urchin culling on species richness (no. of taxa), percentage cover of bare rock, and the three main categories characterizing the surveyed assemblages (i.e., turf-forming algae, erect algae, and invertebrates) across time.

Source of variation	df	No. of taxa		Barren% cover		Turf-forming algae		Erect macroalgae		Invertebrates	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Ti	4	1.48		6.77		5.15		6.01		0.54	
Tr	1	2.14	NS	49	*	37.61	*	28.56	*	2.23	NS
Si(Tr)	2	9.67	**	4.01	NS	2.30	NS	5.89	*	1.62	NS
Ts(Si(Tr))	8	3.05		4.05		4.37		3.70		3.19	
Ti × Tr	4	0.46	NS	4.03	*	3.25	NS	2.59	NS	2.7	NS
Ti × Si(Tr)	8	10.35	***	3.02	*	2.23	*	2.57	*	1.24	NS
Ti × Ts(Si(Tr))	32	4.15		5.63		6.44		3.70		3.37	
Residuals	540										
Total	599										
Cochran's test (*C*)		0.0498 (NS)		0.0483 (NS)		0.0730 (NS)		0.0640 (NS)		0.0434 (NS)	
Transformation		None		None		None		None		Square root (x + 1)	

Only tests relevant to the hypotheses are reported. NS, not significant; for other abbreviations, see ***Table 1****. *P < 0.05, **P < 0.01, ***P < 0.001.*

these degraded habitats (Ling et al., 2015). In addition, there is a need to diversify restorative approaches, which could be carried out simultaneously or sequentially in disturbed areas (Possingham et al., 2015; McDonald et al., 2016). Assisted habitat regeneration (*sensu* Elliott et al., 2007) implies human-mediated interventions aimed at reducing the effects of specific stressors. When combined with other forms of passive restoration (e.g., conservation measures), it can be considered an effective strategy for rebuilding ecosystem resilience by enhancing the recovery of degraded ecosystems (Suding, 2011; Possingham et al., 2015; Geist and Hawkins, 2016).

Our study showed that, 36 months after sea urchin removal, significant changes had occurred in the structure of benthic assemblages as a consequence of the systematic removal activity carried out at the target sites (**Supplementary Figure S2**). A progressive contraction of barren extent was observed, with a reduction in bare substrate of 50% at T4 (2018) in favor of macroalgal stands. To our knowledge, this is the first large-scale experiment demonstrating that local recovery of discrete areas characterized by "extensive barrens" (i.e., thousands of m^2 of bare rock) within a relatively short time span can be feasible. At the end of the experiment, two wide areas of 6000 m^2 showed an overall increase in both erected and turf-forming algae. This result supports previous evidence on the potential of control measures aimed at reducing sea urchin abundance in an attempt to restore the vegetative component of overgrazed temperate rocky reefs (Ling et al., 2010; Bonaviri et al., 2011; Tracey et al., 2015; Piazzi and Ceccherelli, 2019).

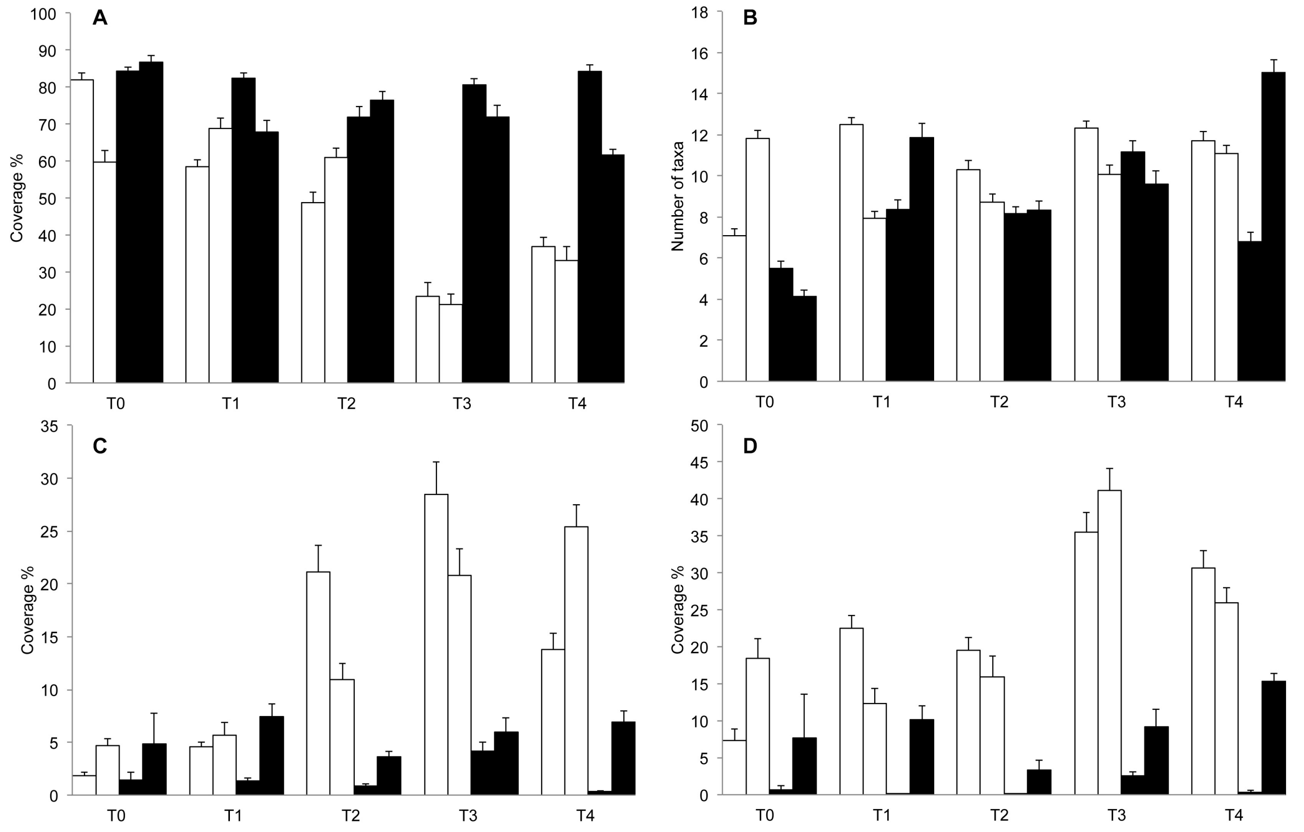

FIGURE 4 | Average (±SE, $n = 30$) **(A)** % barren surface, **(B)** species richness (i.e., no. of taxa), **(C)** turf-forming algae, and **(D)** erect macroalgae over time between experimental conditions. Black bars, reference conditions; white bars, manipulated conditions.

However, it is worth noting that the intervention was only conducive to a shift from one alternative state to another, without returning to the "healthy" conditions of the subtidal rocky reefs of the Mediterranean Sea (Sala et al., 2012; Thiriet et al., 2016). Actually, no difference was detected in the diversity and in the overall assemblage composition between culling and control sites, indicating that recovery trajectories did not reflect differences in the number of taxa nor in species composition between G– and G+. Differences were due, rather, to the increased relative abundance of macroalgal taxa, which were originally present in sparse, small, and isolated patches, generally in combination with the sponge *C. nucula* (Guarnieri et al., 2016). The observed increase in the algal component in culling areas was mostly driven by short (i.e., <10 cm) thallus species (e.g., Dictyotales, *Laurencia* spp., *W. penicillata*, and *P. pavonica*). These taxa are typical of shrubland-like habitats or turfs (Connell et al., 2014), representing the intermediate states of temperate reef along a gradient of structural and functional complexity ranging from canopy-forming habitats to barren grounds (Thiriet et al., 2016). The condition reached 1 year after the initial treatment did not evolve further, as suggested by the lack of differences between T3 and T4. This temporal pattern supports recent concerns about the pervasive trend of the alternative state characterized by the dominance of turfs persisting once established, thus preventing the recovery of highly structured macroalgal forests (Filbee-Dexter and Wernberg, 2018). Recruitment of habitat-forming species (i.e., *Cystoseria* and *Sargassum* species) was not observed in the culling sites within the timeframe of the study, and the contribution of the invertebrates to sessile assemblages, in terms of overall abundance, was still very limited and comparable to control sites at the end of the experiment. The observed re-colonization pattern was consistent with the outcomes of other studies, which stressed the importance of context in terms of habitat arrangement (e.g., Piazzi and Ceccherelli, 2017, 2019) and water trophic status (Boada et al., 2017) in driving the trajectories of recovery. When extensive barren areas and the absence of patches of canopy-forming algae combine with oligotrophic conditions, small, fast-growing, and opportunistic algae are able to take advantage of the high free space availability of barren grounds (Airoldi, 2000). Life history and physiological traits allow this algal guild to outcompete, also through vegetative regeneration, other important functional groups. The ultimate consequence is the local disappearance of species with complex life cycles and slow rates of growth and recruitment, such as the majority of sessile invertebrates (Watling and Norse, 1998; Bevilacqua et al., 2006) or the canopy-forming species of the genus *Cystoseira*, which are also characterized by a limited spreading potential (Thibaut et al., 2015; Piazzi and Ceccherelli, 2019).

Several feedback processes might have impaired the recovery of sea urchin populations at culling sites. For the entire duration of the experiment, a very low re-colonization of sea urchins was observed, with average sea urchin density ranging from 1.25 ± 0.28 to 2.30 ± 0.17 individuals m-2 at T1 and T4, respectively, so that no additional extensive removal of sea urchins was required during the time span covered by the study. The low rate of recruitment recorded after culling is a relevant and unexpected result. It highlights the importance of the spatial extent at which the sea urchin removal is conducted in reducing their population numbers. Moreover, it provides practical information about the feasibility of the intervention because it is conducive to a significant reduction of maintenance costs. On the other hand, this important outcome supports the results of recent global analyses (e.g., Filbee-Dexter and Scheibling, 2014; Ling et al., 2015) suggesting the existence of threshold levels in sea urchin density able to reverse the process of formation/maintenance of barren grounds (see Boada et al., 2017 for a special focus on the Mediterranean Sea).

A combination of system state-dependent stressors could have contributed to limiting the recovery potential of the sea urchin population and the observed long-lasting decrease in their density in manipulated sites (Ling et al., 2015). In particular, there is evidence that, for *A. lixula* (i.e., the sea urchin species dominating the study area), the availability of bare rock colonized by encrusting coralline algae represents an indispensable condition for settlement and the ensuing establishment of the high densities typical of barren grounds (Micheli et al., 2005; Guidetti and Dulčić, 2007; Privitera et al., 2011). Specific morpho-functional traits, proper to the species, make it particularly adapted to this type of habitat as compared to the co-occurring species (i.e., *P. lividus*) inhabiting Mediterranean shallow rocky reefs (Agnetta et al., 2013). Based on studies conducted in other areas of the Mediterranean Sea (e.g., Bulleri et al., 1999; Gianguzza et al., 2010; Privitera et al., 2011; Bonaviri et al., 2012), it is likely that the observed increase in algal coverage may have affected, both directly and indirectly, the processes occurring at the immediate post-settling stage, thus representing an important control of sea urchin populations in the manipulated areas: firstly, because of the development of unsuitable conditions for the settlement of sea urchins (Bulleri et al., 1999; Gianguzza et al., 2010; Privitera et al., 2011) and, also, by exposing settlers to higher predation rates as a result of a likely increase in mesofauna (e.g., decapod crustaceans) associated with macroalgal beds (Bonaviri et al., 2012). In addition, the intense hydrodynamism characterizing exposed rocky coasts further contributed to exacerbating the effects of the experimental treatment, given the high vulnerability of sea urchin juveniles to dislodgement (Guidetti and Mori, 2005). Finally, since adults can play a crucial role in reducing predation rates on juveniles through refuge provisioning (Zhang et al., 2011; Hereu et al., 2012; Clemente et al., 2013) or mesopredator consumption (Bonaviri et al., 2012), the survival of juveniles may also have been compromised by the extreme reduction of conspecific adults, as a direct consequence of the culling intervention.

Unfortunately, the lack of detailed information on potential variations in the background environmental conditions (e.g., thermal regime, spread of pathogens) during the experiment follow-up limits our understanding of the cause and effect relationships governing the population dynamics, at a local scale, beyond culling intervention. Since, in the control areas, a significant but slight reduction of sea urchin densities was also observed along the 3 years of the experiment, long-term investigations (at regional scale) in other areas historically characterized by the presence of barren grounds are necessary. Information on the size distribution of sea urchin populations should also be obtained to provide additional information about recruitment dynamics. This would allow the recovery intervention to be framed in a wider context, as well as taking into account a combination of acute or chronic environmental stressors, mostly related to climate change, such as intensified storms (Hereu et al., 2012; Medrano et al., 2019), and/or diseases (Privitera et al., 2012), which could play a crucial role in affecting the outcomes of culling interventions and associated costs.

There is wide consensus that coastal overgrazed habitats in shallow rocky reefs can represent an opportunity for the development and implementation of proactive restoration measures (Filbee-Dexter and Scheibling, 2014; Ling et al., 2015; Boada et al., 2017), even though the hysteresis effect governing the persistence of barren grounds might challenge the success of the interventions. This recognition stems from the general availability of baseline information related to causes (i.e., driving forces), tipping points, life history, and functional traits of species triggering the shift to and the maintenance of the degraded state typical of barren grounds. To date, the recovery of prey–predator interactions through the establishment of fishing restrictions (e.g., MPA) and/or the selective harvesting of sea urchins (Hill et al., 2003; Guidetti, 2006; Watanuki et al., 2010; Medrano et al., 2019) have been demonstrated to have the potential to revert the barrens into vegetated habitats. However, the effectiveness of these strategies could be compromised in sites where barren grounds are too extensive and/or environmental constraints (e.g., oligotrophic nutrient regimes, limited larval supply, high sea urchin recruitment rates) favor their persistence (e.g., Sanderson et al., 2015; Guarnieri et al., 2016). We demonstrated that sea urchin culling in the shallow subtidal zone represents a promising approach, thus supporting previous attempts in this direction in other geographic areas (i.e., Tracey et al., 2015). Our study also stressed that the success of restoration actions should be evaluated at adequate spatial scales to match the scale of disturbance leading to habitat degradation. This need is crucial also when considering shared targets aimed at halting or reversing widespread trends of biodiversity loss and habitat degradation (EU, 2011 [Target 2]; CBD, 2014 [Target 15]) through the restoration of at least the 15% of degraded ecosystems by 2020, and the recent commitments of the UN on ecosystem restoration in the next decade[2].

Taking into account that in the Mediterranean Sea the occurrence of barren grounds is expected to increase

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[2] https://undocs.org/pdf?symbol=en/A/RES/73/284

(Gianguzza et al., 2011), we anticipate that the results of the present study could represent a starting point for the implementation of long-term interventions carried out at large scale, to be adopted in areas affected by similar conditions. MPAs represent eligible sites where this type of intervention should be prioritized. However, complementary interventions, such as the transplantation of species with a critical ecological role, should be planned to enhance the restoration of shallow rocky reefs, considering the widely recognized importance of these habitats for the functioning of coastal ecosystems.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

SF conceived and supervised all steps of the study. GG, SB, NF, and SF established the restoration action. All authors were involved in collecting data during the monitoring period and contributed to the draft and gave final approval for publication. GG and LT analyzed the data. GG led the writing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00519/full#supplementary-material

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Beyond Reef Restoration: Next-Generation Techniques for Coral Gardening, Landscaping, and Outreach

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Anthropogenic disturbances have led to the degradation of coral reef systems globally, calling for proactive and progressive local strategies to manage individual ecosystems. Although restoration strategies such as assisted evolution have recently been proposed to enhance the performance of coral reef populations in response to current and future stressors, scalability of these concepts and implementation in habitat or ecosystem-wide management remains a major limitation for logistical and financial reasons. We propose to implement these restoration efforts into an ecotourism approach that embeds land-based coral gardening efforts as architectural landscape elements to enhance and beautify coastal development sites, providing additional value and rationale for ecotourism stakeholders to invest. Our approach extends and complements existing concepts integrating coral reef restoration in ecotourism projects by creating a participatory platform that can be experienced by the public, while effectively integrating numerous restoration techniques, and providing opportunities for long-term restoration and monitoring studies. In this context, we discuss options for pre-selection of corals and systematic, large-scale monitoring of coral genotype performance targeting higher resilience to future stressors. To reduce operating costs during out-planting, we suggest to create coral seeding hubs, clusters of closely transplanted conspecifics, to quickly and efficiently restore/enhance active reproduction. We discuss our land-based coral gardening approach in the context of positive impacts beyond reef restoration. By restoring and strengthening resilience of local populations, we believe this strategy will contribute to a net positive conservation impact, create a culture on restoration and enhance and secure blue economical investments that rely on healthy marine systems.

Keywords: coral restoration, blue economy, adaptive coral gardening, coral seeding hubs, ecotourism

INTRODUCTION

Coral reef systems have undergone severe global degradation and loss during the past decades (Wilkinson, 2004; De'ath et al., 2012; Hughes et al., 2017). They are predicted to experience a further loss of up to 99% of remaining reefs under moderate climate predictions (Bindoff et al., 2019). The development of new strategies for coral reef management have become a conservation imperative to secure the vital ecological and economical services they provide for the livelihoods of hundreds of millions of people (Moberg and Folke, 1999). The increasing frequency and severity of coral bleaching events (Hughes et al., 2003, 2017; Heron et al., 2016) has forced scientists to consider more radical interventions to mitigate the impacts of global warming and other cumulative anthropogenic stressors (van Oppen et al., 2015; Anthony et al., 2017; Damjanovic et al., 2017; van Oppen et al., 2017; National Academies of Sciences, Engineering, and Medicine, 2019). Although strategies such as assisted gene flow (Palumbi et al., 2014; Dixon et al., 2015) and selective breeding (van Oppen et al., 2015) target climate resilience, the biggest challenge of these efforts to date remains the identification of economically viable approaches to implement and scale-up restoration efforts to achieve a zero-net loss or, ideally, an increase in coral reef area (Duarte et al., 2020).

Coral reef restoration costs are amongst the highest for marine coastal habitat restoration efforts (Bayraktarov et al., 2016). Estimates based on scientific literature vary substantially with a median cost of 404,147 \$US ha^{-1} (at base year 2010; Bayraktarov et al., 2019). However, these estimates have limitations as little data exists on the costs of non-scientific programs. These high costs, resulting from high labor intensity associated with coral restoration, limit the scale at which it is conducted, with a current median size of only 100 m^2 (based on scientific literature; Bayraktarov et al., 2019) to 500 m^2 per project (including both scientific and gray literature; Boström-Einarsson et al., 2018). Additionally, current projects seem to lack proportionate cost savings when production is increased (Bayraktarov et al., 2016). One of the biggest criticisms of coral restoration is the lack of meaningful scalability. While the expense may be high, reported survival rates of restoration efforts are considerable (64.5%; Bayraktarov et al., 2019). However, limitations of these estimations are the short observational period of most studies (median duration of 12 months) and lack of sustained monitoring to evaluate long-term success (Boström-Einarsson et al., 2020). Further, these estimates may be biased as failure in restoration is often not reported (Hobbs, 2009).

Motivations for coral restoration are diverse, ranging from biodiversity enhancement, social outcomes, scientific projects, to projects restoring or maintaining ecosystem services for fisheries, tourism, coastal protection among others (Bayraktarov et al., 2020). While ecological outcomes are often reported, reports on economic and social outcomes are often neglected (Bayraktarov et al., 2019). Aside from the ecological impacts at local scales, most coral reef restoration operators emphasize education and public awareness as a main benefit (Young et al., 2012; Hein et al., 2019). Involvement of the public in restoration through citizen-science projects reduces costs and adds socio-economic benefits, such as creating employment and generating stewardship for local coral habitats (dela Cruz et al., 2014; Lirman and Schopmeyer, 2016; Hein et al., 2018).

We advocate for an approach that builds upon the outreach potential of coral restoration efforts and integrates coral gardens into ecotourism and coastal development as architectural and landscape features that are shared and open to public participation. We believe that the use of land based, *ex situ*, coral gardens as landscape elements will be a powerful tool to educate and raise awareness to a greater audience while contributing to the scalability of coral reef restoration projects. Implementing coral garden efforts as an economic driver to attract visitors via the creation of unique citizen and visitor experiences, will provide additional values and rationale for hotels and tourism businesses to invest in coral reef restoration. This, will generate economic revenues that can be utilized to scale-up and optimize efforts. Our idea aligns with the goals of the "UN Decade of Ecological Restoration" (UNEP, 2019) starting in 2021 calling to create a culture toward ecological restoration.

As increasing ocean warming and marine heatwaves threaten coral reefs at a global scale (Hughes et al., 2017, 2018, Leggat et al., 2019), long-term success of coral restoration efforts relies on the tolerance of local populations for future climate scenarios. Using landscape embedded coral gardens as a platform, we discuss a structured approach integrating a systematic assessment and monitoring to optimize coral gardening efforts and to build local populations with higher resilience. Restoring and strengthening resilience will contribute to secure ecological and blue economical assets, those associated to a sustainable use of ocean resources which target the improvement of livelihoods while preserving the health of marine ecosystems (Spalding, 2016).

CORAL GARDENING

The most common and effective approach to coral reef restoration is coral gardening (Young et al., 2012). Corals are grown in an intermediate nursery phase, before being transplanted for restoration (Rinkevich, 1995). In the initial phase of the coral gardening, corals are fragmented or recruited and grown in sheltered sites, before they are transplanted at reasonable size to natural habitats in the second phase. Mid-shelf nurseries have been shown to be very successful in growing a variety of species (Levy et al., 2010; Rinkevich, 2014).

Land-based coral gardening efforts are less explored and have been mostly used for sexual reproduction of corals (O'Neil, 2015) or asexual reproduction via micro-fragmentation (Forsman et al., 2015). The great advantage of *ex situ* coral gardening facilities is the ability to engineer the environment to enhance growth and survival (Leal et al., 2016), and reduce costs by avoiding SCUBA diving during the gardening stage. Land-based coral nurseries have also been suggested to serve as genetic repositories (Schopmeyer et al., 2012). Providing easy access to the cultured organisms, they allow detailed monitoring of abiotic conditions (light and temperature), organism performance, and quick intervention if problems arise. Additionally, land-based nurseries allow the co-culturing of beneficial biota that reduce competing algae (Craggs et al., 2019) and mimic co-existing partnerships found *in situ* (within their natural environment), increasing coral health. To date there is a vast knowledge base of successful *ex situ* coral culture practices, within the aquaria industry, which can be optimized and possibly scaled-up (Leal et al., 2016).

INTEGRATION OF ADAPTIVE MANAGEMENT

Adaptive management refers to strategies, whereby practices get iteratively better overtime by incorporating and maximizing opportunities to learn from systematic monitoring (Holling, 1978; Hicks et al., 2009). With respect to adaptive coral gardening, examining stress resilience of the donor colonies and growth, survival, reproductive activity, etc., of propagated individuals can provide a feedback loop to inform and guide better selection of stocks. This strengthens populations on a site by site basis (**Figure 1**). Applying adaptive management strategies may ultimately help to reduce costs in the long term and make restoration efforts economically more viable. Using this strategy, restoration projects may accumulate vast datasets over time that allow informed and optimized restoration efforts and guide the development of innovative new approaches and technologies. This approach allows unprecedented, large-scale experimentation to advance knowledge on the drivers of resilience.

Ideally, restoration projects should record and characterize the original habitat and genotype of each donor/paternal colony (Johnson et al., 2011). Baums et al. (2019) showed that modern sequencing techniques provide a vast array of genotyping technologies, allowing to examine a wide spectrum of genotypic characteristics that may improve restoration efforts, such as symbiont association or genetic traits associated with phenotypic performance. Considering hidden species diversity is often found in corals (Schmidt-Roach et al., 2012), these technologies can also provide taxonomical confirmation, guarantying fertilization compatibility during sexual propagation.

The creation of detailed records is vital to carefully track the performance of transplantation efforts (IUCN, 2002; Boström-Einarsson et al., 2018). Records for each individual coral ramet transplanted should be cataloged and examined. We suggest employing Radio-frequency identification (RFID) transponders that can be attached/cemented into the base of ramets/juveniles. RFID transponders have been shown to be functional underwater (Benelli et al., 2009) and could provide an innovative and cheap way to track individuals during gardening efforts and after transplantation. Furthermore, conventional plastic/metal tags are esthetically not very appealing, add pollution and can also be hard to recover.

Although an increasing number of projects include sexual propagation (Horoszowski-Fridman et al., 2011; Linden and Rinkevich, 2011; Guest et al., 2014; Omori and Iwao, 2014; dela Cruz and Harrison, 2017; Linden and Rinkevich, 2017; Calle-Trivino et al., 2018), most coral restoration projects still rely on asexual reproduction (fragmentation) due to a lack of feasibility and scalability (Young et al., 2012). Careful consideration is required when choosing genotypes for restoration efforts to maintain genotypic diversity and avoid genotypic depletion by inbreeding (Baums, 2008). In this context, finding strategies for reliable tagging is vital in order to identify individual genotypes.

ENHANCING STRESS RESILIENCE AND REPRODUCTIVE ACTIVITY

Selective reproduction/breeding has been suggested as a mechanism to build resilience toward climatic stressors (van Oppen et al., 2015; van Oppen et al., 2017). Selection of resilient genotypes could improve restoration efficiency, reduce costs and, ensure that restored populations do not meet the same fate as their predecessors. Although recommended in restoration guidelines (e.g., Baums et al., 2019; Coral Restoration Consortium, 2020), few projects report pre-selecting genotypes via an assessment of stress resilience before conducting nursery efforts (e.g., Morikawa and Palumbi, 2019; Fundemar and Iberostar case studies in Bayraktarov et al., 2020). Restoration efforts show genotypic driven phenotypic divergence in survivorship and response to thermal stress (Drury et al., 2017; Ladd et al., 2017), yet our understanding of which traits may assure resilience to future climate conditions remains rudimentary.

Strategies need to be identified that allow high-throughput and reliable phenotypic assessments to identify resilient genotypes. The spectrum of approaches used to identify suitable genotypes ranges from stress assessments (e.g., Morikawa and Palumbi, 2019), valuations of the genotypic performance based on habitat origin (Drury et al., 2017) or past bleaching/disease susceptibility, to genetic tools (Baums, 2008; **Figure 1**). Global warming is likely the most severe future stressor for coral populations (Hughes et al., 2017). A large amount of literature has focused on understanding the drivers of thermal tolerance (see Cziesielski et al., 2019). Thus, selection approaches should consider multi-stressor resilience, as bleaching responses may be coupled with other stressors (DeCarlo and Harrison, 2019).

Based on the current knowledge limitations, Baums et al. (2019) proposed to target the increase of genetic diversity in restoration efforts in order to maximize levels of standing genetic variation that may counteract future stressors. Incorporating sexual reproduction into restoration could have the biggest benefit, but is currently still limited due to feasibility at larger scales and high costs (Guest et al., 2014; Randall et al., 2020). New strategies have recently been proposed to enhance sexual propagation in restoration using seeding tiles that can be out planted with low efforts and cost (Chamberland et al., 2017). Although these techniques seem successful, they are limited to species that easily settle on artificial substrates. For coral species with larvae not easily settled *ex situ*, techniques such as direct seeding of depleted reefs with relocated larvae harvested *ex situ* (dela Cruz and Harrison, 2017) or wild-caught from coral larvae slicks (Doropoulos et al., 2019) may be applicable.

Most coral restorations approaches are very expensive as they try to recreate natural habitats often transplanting vast numbers of corals. In contrast to large scale transplantation, we suggest to revive/strengthen populations by restoring/enhancing reproductive activity using corals nurtured in land-based coral

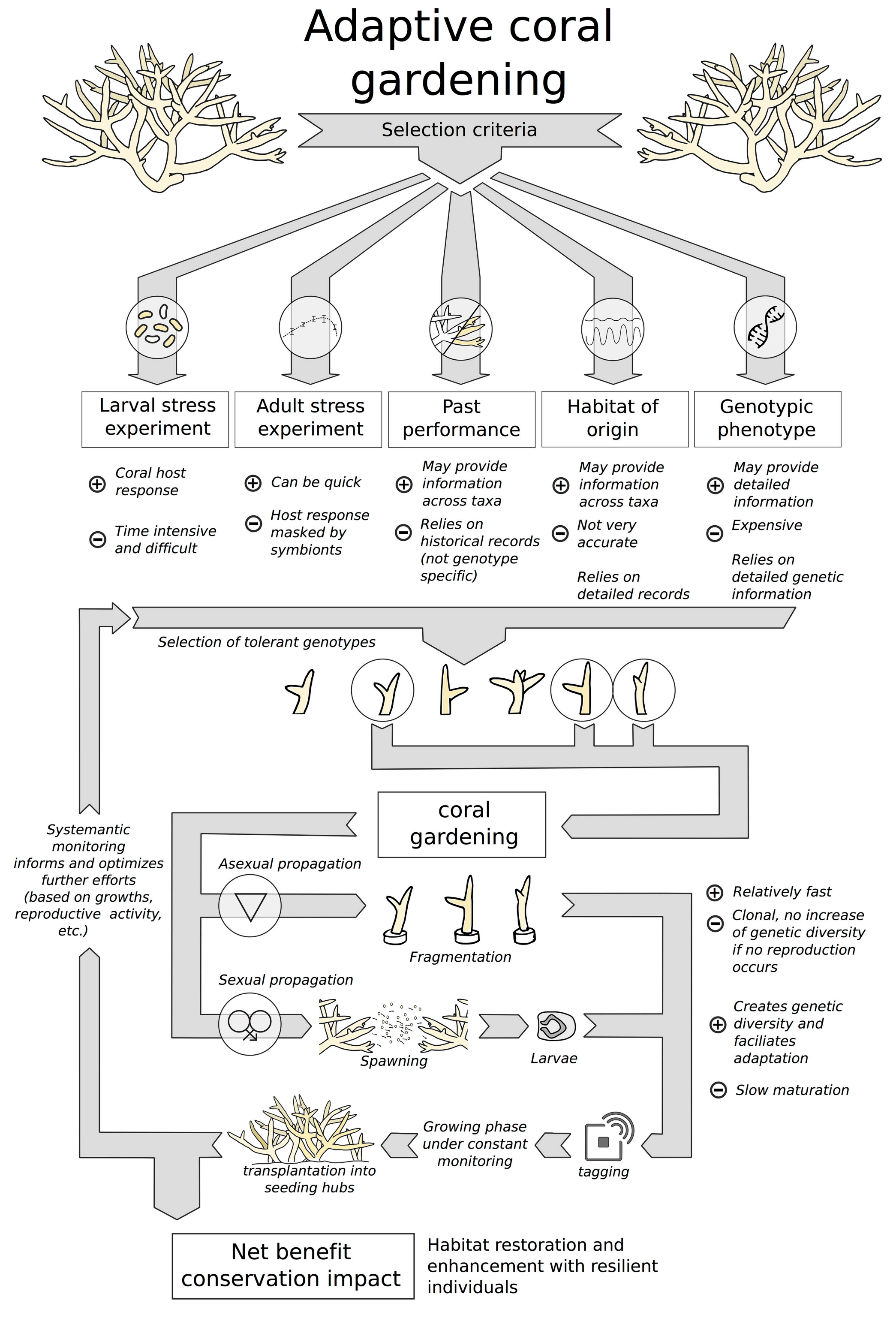

FIGURE 1 | Adaptive coral gardening with pre-selected genotypes to increase resilience.

gardens. Coral seeding hubs (CSH), aggregations of conspecific corals transplanted within proximate distances to one another, may be a cheap and effective measure for coral restoration. Sperm seems to be the limiting factor in the sea, with decreasing sperm concentration over distance due to dilution resulting in lower fertilization rates (Levitan, 1993; Levitan and Petersen, 1995). Consequently, the number of conspecifics in a reef may be insufficient to guarantee successful reproduction after catastrophic events. Concentrating the number of reproductive conspecifics within the CSH could dramatically increase fertilization rates and reproductive success.

Shearer et al. (2009) estimated that ten randomly selected donor colonies could be sufficient to retain 50% of the original allelic diversity, while 35 colonies could provide 90%. Thus, a few closely transplanted genotypes may be sufficient to recover relatively high genetic diversity and contribute to standing genetic diversity. Corals seem to predominantly recruit locally (Miller and Mundy, 2003; Miller and Ayre, 2008) and, transplantation has been shown to increase recruitment (Maya et al., 2016). CSHs may be a powerful and cost-effective strategy to recover the reproductive potential within populations. Strategic placement, considering local current regimes, may lead to self-sustaining populations which can be quickly applied across different taxa. CSHs can be established for a diversity of taxa, supplied by the land-based gardens and linked via citizen science programs.

Informed selection of genotypes placed in the CSHs may increase the standing genetic diversity of local populations ultimately building up resilience. The advantage of this strategy over conventional restoration via direct large-scale transplantation is that the likelihood of sexual propagation is maximized and allows for natural selection to act on the offspring generated in the CSHs. Consequently, the genotypic architecture of a reef may be less altered than by conventional strategies.

LAND-BASED CORAL GARDENS AS BLUE ECONOMICAL ASSETS

Ex situ based coral gardening efforts are predominantly concentrated within research or industrial settings in land-based facilities. Commercial efforts cater toward the aquarium industry (private and public), explore restoration as a business (e.g., CoralVita), or seek to engage guests in hotels (Hein et al., 2018). Although some operators facilitate partial public access, few systems are specifically built to cater to a greater audience including non-swimmers or non-divers. However, operators are starting to explore this avenue, as for example the Wave of Change project of the Iberostar Group in Bayahibe, Dominican Republic, which creates an *ex situ*, land-based, nursery that caters to both, research as well as educational purposes (Bayraktarov et al., 2020). Nevertheless, the outreach, entertainment and educative value to a greater public audience of coastal land-based coral gardens remains vastly unexplored. Arguably public aquaria

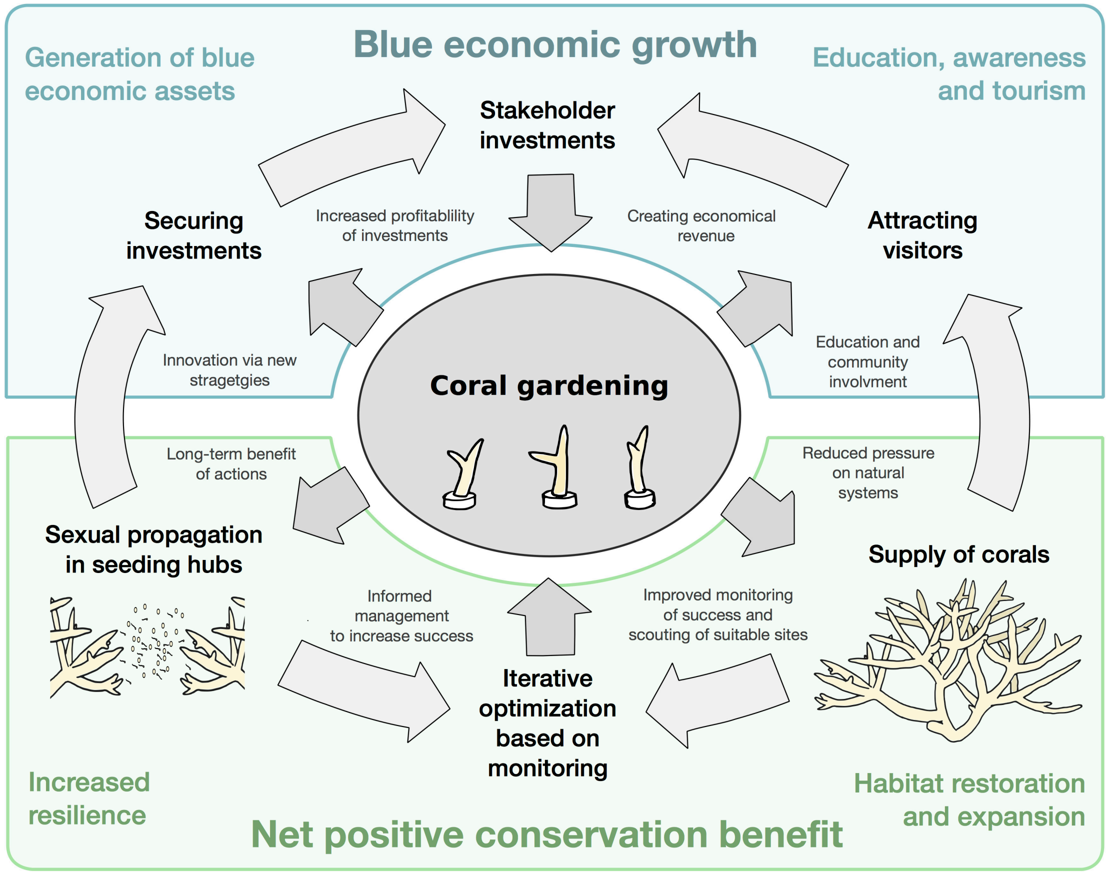

FIGURE 2 | Land-based coral nurseries as an entity to serve toward blue economic growths as well as conservation.

cater toward this purpose, but their main role in coral conservation besides education has been to serve as repositories (Petersen et al., 2008) rather than to participate in active restoration.

In preparation for the UN Decade on Ecosystem Restoration aiming at enhancing the role of restoration as a path to rebuild blue natural capital (Duarte et al., 2020; Waltham et al., 2020), we propose to embed coral gardening efforts within coastal ecotourism and developmental projects at large scale (**Figure 2**). Powered by renewable energies, we envisage extended land-based coral garden nurseries with flow through seawater cascading through public spaces, essentially replacing flowerbeds with the ornamental values of reef organisms. In addition to beautification, this will directly expose citizens and visitors to the marine environment, thereby serving as a tool to create stewardship and awareness. The global tourism revenue of coral reefs is estimated at approximately $36 billion annually (Spalding et al., 2016, 2017), reflecting a large public interest for these unique ecosystems and a great economic potential if a larger audience of non-swimmers and non-divers could be engaged. Creating land-based coral gardens as a participatory platforms that can be experienced by the public, may be a tool to further explore the economic potential of coral reefs and generate economic profits for these areas (e.g., hotels, resorts, golf courses, and public parks) that host these unique elements. Resulting economic revenues and profits may entice private and corporate stakeholders to invest in these concepts and by default assist to scale-up and advance restoration efforts to achieve meaningful ecological outcomes. Adding to blue urbanism, practices of creating a mutually sustainable relationship between coastal populations and the marine environment (Beatley, 2014), this approach may ultimately assist to counteract the degradation of and species loss in coral reefs often observed due to coastal urbanization (Poquita-Du et al., 2019).

In addition to socio-ecological benefits (Hein et al., 2018), restoring and maintaining healthy coral reef ecosystems will also contribute to preserving the services they provide for coastal protection and fisheries. Further, by enhancing awareness and changing the interactions between people and the ecosystem novel services can emerge (Woodhead et al., 2019). Creation of an interdisciplinary environment that reaches out to a variety of experts, from engineers to landscape architects, may ultimately drive innovation and foster the exploration of novel services. Consequently, generating coral garden landscaping as blue economic assets that support *in situ* restoration efforts may drive blue economic growth and help achieve net positive conservation benefits for coral reefs (**Figure 2**). Land-based coral nurseries have been suggested as ecological and economically viable solutions for scalable reef restoration (CoralVita, 2019). The novelty in our approach is the embedment of these efforts as landscape elements within ecotourism, developmental and urban landscapes, ultimately serving a triple mission: educate, restore, and enhance.

CONCLUSION

A global reduction of greenhouse gas (GHG) emissions would be the most effective and economically viable long-term strategy to mitigate climate change effects and protect vulnerable ecosystems such as coral reefs (Bindoff et al., 2019). Restoration efforts may have reduced effects in mitigating climate change impacts globally (Morrison et al., 2020). However, assuming the global community will comply with the GHG emission pathway, this will not suffice to either conserve coral reefs or restore their previous abundance. Hence, relying solely on decarbonization to counteract the degradation of tropical habitats is unrealistic (Gordon et al., 2020). Therefore, an action plan involving reduction of pressures, including climate change, pollution and overfishing, protection and active restoration provides the pathway to the best possible future for tropical coral reefs (Duarte et al., 2020).

Embedding coral gardening into architectural landscapes will integrate engineers, architects and urban developers, laying the foundation for an interdisciplinary community of practice that would be best able to deliver innovative solutions incorporating bio-printing, material science, architecture and design, as well as renewable energy and pathways to scalability of these solutions to coral reef restoration.

AUTHOR CONTRIBUTIONS

SS-R drafted the manuscript. All authors read and commented on the final version.

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frontiers in Marine Science

REVIEW
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Seagrass Restoration Is Possible: Insights and Lessons From Australia and New Zealand

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Seagrasses are important marine ecosystems situated throughout the world's coastlines. They are facing declines around the world due to global and local threats such as rising ocean temperatures, coastal development and pollution from sewage outfalls and agriculture. Efforts have been made to reduce seagrass loss through reducing local and regional stressors, and through active restoration. Seagrass restoration is a rapidly maturing discipline, but improved restoration practices are needed to enhance the success of future programs. Major gaps in knowledge remain, however, prior research efforts have provided valuable insights into factors influencing the outcomes of restoration and there are now several examples of successful large-scale restoration programs. A variety of tools and techniques have recently been developed that will improve the efficiency, cost effectiveness, and scalability of restoration programs. This review describes several restoration successes in Australia and New Zealand, with a focus on emerging techniques for restoration, key considerations for future programs, and highlights the benefits of increased collaboration, Traditional Owner (First Nation) and stakeholder engagement. Combined, these lessons and emerging approaches show that seagrass restoration is possible, and efforts should be directed at upscaling seagrass restoration into the future. This is critical for the future conservation of this important ecosystem and the ecological and coastal communities they support.

Keywords: seagrass ecosystems, coastal, climate change, marine plants, restoration

INTRODUCTION

Seagrasses are marine angiosperms that grow in the coastal waters of every continent except Antarctica (Cullen-Unsworth and Unsworth, 2016), providing a wide range of ecosystem services to coastal communities (Nordlund et al., 2018a). Some of the key ecosystem services provided by seagrasses include coastal protection (Ondiviela et al., 2014; Boudouresque et al., 2016), nutrient cycling (Hemminga and Duarte, 2000; McGlathery et al., 2007), pathogen reduction (Lamb et al., 2017), storage of sedimentary carbon (Macreadie et al., 2014; Serrano et al., 2019), and the provision of nursery grounds for many species that support fisheries (de la Torre-Castro et al., 2014; Tuya et al., 2014; Nordlund et al., 2018b). Yet, despite their environmental, socio-economic and cultural value, seagrasses globally are undergoing accelerated rates of decline due to a range of threats including rising sea surface temperatures, extreme temperature events, coastal development, coastal urban and agricultural runoffs, and untreated sewage and industrial waste outfalls (Freeman et al., 2008; Grech et al., 2012; Arias-Ortiz et al., 2018). Declines to date have amounted to an estimated loss of 29% of areal extent, or 3370 km^2, since records started in 1879 (Waycott et al., 2009). However, the true extent of seagrass loss remains uncertain due to estimates of seagrass areal extent globally being unknown, with many regions of Southeast Asia, the Caribbean, and the western Indian Ocean still largely understudied and/or undocumented (Gullström et al., 2002; Wabnitz et al., 2008; Fortes et al., 2018). Furthermore, seagrass losses are expected to continue, further exacerbated by climate change impacts. While increased temperatures and carbon dioxide concentrations associated with climate change could potentially increase growth rates in various species (Olsen et al., 2012; Koch et al., 2013), the increased frequency of extreme temperature and storm events is expected to increase mortality (Collier and Waycott, 2014; Rasheed et al., 2014).

The decline in seagrass habitats has clear and detrimental ecological and socio-economic consequences, and stemming this decline through facilitating recovery is urgently needed. Passive restoration efforts, or rehabilitation, have reduced anthropogenic stressors to facilitate natural regeneration, such as the improvement of water quality through removal of sewage outfalls and agricultural run-off to tackle eutrophication (Bryars and Neverauskas, 2004; Riemann et al., 2016). Despite the potential to curb the influence of anthropogenic stressors, rehabilitation efforts on a global scale have seen varying degrees of success. It is widely acknowledged that seagrass rehabilitation is a slow process, often taking years to decades for successful recolonization and meadow establishment (Leschen et al., 2010; Vaudrey et al., 2010; Greening et al., 2011). Rehabilitation failure has been attributed to a variety of factors including limited propagule supply (Orth et al., 1994; Kendrick et al., 2012), biotic and abiotic interactions e.g., predation or physical disturbance (Moksnes et al., 2008; Valdemarsen et al., 2010), shifts to unsuitable environmental conditions e.g., sediment type or sediment resuspension (Munkes, 2005; Carstensen et al., 2013), or failing to fully take into account the original cause of loss. Significant investment in seagrass restoration or the creation of new seagrass meadows where they were previously not found has been used to facilitate recovery of seagrass meadows in different parts of the world including Europe, North America, Australia, and New Zealand (e.g., Campbell, 2002; Bastyan and Cambridge, 2008; Orth and McGlathery, 2012; Matheson et al., 2017; Paulo et al., 2019). Unlike rehabilitation which ultimately relies on natural recolonization (Kirkman, 1989), restoration involves active intervention geared toward returning degraded habitats to a condition resembling their original condition (Paling et al., 2009), while habitat creation establishes new meadows in areas suitable for seagrass establishment but that were historically uninhabited by these plants (Morris et al., 2006). Habitat restoration and creation may include efforts such as the physical planting of seagrasses, distribution or planting of seagrass seeds, or coastal engineering to modify sediment and/or hydrodynamic regimes (Campbell, 2003; Weatherall et al., 2016). In this review, the term seagrass restoration is used to encompass rehabilitation, habitat restoration, and habitat creation.

Historically, marine restoration has trailed behind terrestrial and freshwater ecosystems, owing in part due to the scale of the marine environment and common ownership of resources (e.g., in international waters) which often leads to difficulties in management (Hawkins et al., 2002). Furthermore, marine environments are much more difficult to access and work in compared to terrestrial environments, and the impacts of degradation are not always clearly visible to society (Sinclair et al., 2013). Restoration of terrestrial systems (including forests, lakes, and grasslands) has a relatively long history, developing restoration techniques that are now sufficiently advanced for adequate returns on high levels of investment (Ruiz-Jaen and Aide, 2005). The successes currently experienced in terrestrial restoration have been built upon decades of knowledge and experience gained through numerous studies and experiments, many of which were not successful initially but were invaluable for understanding why early restoration attempts did not work, and allowed for improvements to restoration methods and techniques to be made (Nellemann and Corcoran, 2010). In contrast, restoration of marine coastal ecosystems (seagrasses, macroalgae, corals, saltmarshes, mangroves) is still a maturing area of science (Wood et al., 2019). Seagrass restoration is often deemed too expensive due to a multitude of reasons including but not limited to high labor costs, challenges of propagation, and the need for repeated planting efforts due to losses (Bayraktarov et al., 2016). These high costs have hindered efforts over the years. The median cost of seagrass restoration was estimated at USD 106,782 per hectare based on 64 published studies (Bayraktarov et al., 2016), and this can be 10–400 times higher than the costs documented for terrestrial ecosystem restoration (Jacob et al., 2018).

Seagrass practitioners, *indeed all marine restoration practitioners*, can benefit from restoration science and practice that has been developed over decades in terrestrial ecosystems and could be applied in marine environments. For instance, mine site rehabilitation practices considerably focus on the preparation, composition, form and microbial community of top soils before planting (Cooke and Johnson, 2002). These parameters are also likely to be important for seagrass colonization, and should be given equal consideration as the more well-known and studied parameters of light, depth and water quality. Yet sediment dynamics are relatively understudied (except see Campbell et al., 2018) and often neglected in seagrass site suitability assessments and preparation. Valuable lessons are still to be learned from the broader field of applied ecosystem restoration and continued exploration of methodologies will yield improved outcomes for some systems. Incorporating knowledge from the broader field of ecological restoration, and particularly seeking out ecosystems and methods that are less familiar to marine ecologists, is likely to yield many benefits and shortcuts for the young yet rapidly maturing field of seagrass restoration.

Initial seagrass restoration studies date back to 1939, with the majority of the work occurring in the United States, Europe or eastern Asia (China, Japan, and Korea). Efforts were largely focused on *Zostera marina* (van Katwijk et al., 2016). A successful example is the recovery of approximately 1700 ha of *Z. marina* in the Virginia Coast Reserve (Orth and McGlathery, 2012). These efforts resulted in epifauna invertebrate recovery in the 1990s (Lefcheck et al., 2017). Recent success has also occurred in Whangarei Harbor, New Zealand, with at least 600 ha of *Zostera muelleri* being rehabilitated due to management actions taken to improve water quality and subsequent restoration planting trials (Matheson et al., 2017). However, many other restoration efforts have seen lower rates of success (van Katwijk et al., 2016). Nonetheless, the knowledge and experience gained from these early studies have proved invaluable for developing the knowledge that has made large-scale seagrass restoration feasible today.

This review aims to highlight some of the recent seagrass losses in Australia and New Zealand, and emphasize the seagrass restoration successes we have experienced. We focus on some of the challenges that remain and need to be overcome to enable large-scale seagrass restoration and highlight emerging tools and techniques being developed that can help achieve restoration success. Lastly, we discuss the need for management strategies that address the threats of climate change and incorporate evolutionary potential for "climate-proofing" remnant and restored seagrass meadows. Heavier emphasis is given to Australian restoration work in this review, largely due to the fact that although there has been recent activity with regards to seagrass restoration in New Zealand, the New Zealand effort to date, lags far behind Australia and the world. With the exception of the research undertaken by Matheson, restoration efforts in New Zealand are typically focused upon shellfish (e.g., Marsden and Adkins, 2010; Hewitt and Cummings, 2013), which are important taonga for Māori (e.g., Paul-Burke et al., 2018). Seagrass research in New Zealand has focused on understanding fundamental community ecology and biology (e.g., Dos Santos et al., 2012; Kohlmeier et al., 2014; Morrison et al., 2014; Sørensen et al., 2018; Cussioli et al., 2019, 2020), macroinvertebrate and fish communities interactions (e.g., Mills and Berkenbusch, 2009; Lundquist et al., 2018) and impacts upon these communities (e.g., Bulmer et al., 2016; Cussioli et al., 2019; Li et al., 2019; Matheson et al., submitted). The fundamental research that is occurring in New Zealand is required to understand how New Zealand seagrass function and thereby formulate a comprehensive understanding of local seagrass dynamics to successfully implement site specific restoration practices (e.g., Matheson et al., 2017).

Seagrass Loss and Restoration: An Australian and New Zealand Perspective

Seagrass losses in Australia follow global patterns, with a reported loss of at least 291,783 ha, representing 5.5% of estimated areal extent, since the 1930s (Statton et al., 2018). These losses include several large-scale declines in Shark Bay, West Australia, Western Port, Victoria, and metropolitan Adelaide, which lost 154,800, 17,800, and 5,200 ha of seagrass habitat, respectively (Tanner et al., 2014; Arias-Ortiz et al., 2018; Statton et al., 2018). Losses have also been documented in New Zealand (Park, 1999, 2016; Inglis, 2003; Turner and Schwarz, 2006; Matheson et al., 2011), with one of the more significant examples being the disappearance of 14,100 ha of seagrass from Tauranga Harbor since 1959 (Park, 1999, 2016). These losses, and the associated losses in ecosystem goods and services, can have major ecological, socioeconomic, and political ramifications (Smale et al., 2019). For example, the recent estimated loss of 36% of seagrass meadows in Shark Bay followed extreme temperature events and resulted in declines of various herbivorous species such as green turtles and dugongs, seagrass-associated fish populations, and closure of scallop and blue swimmer crab fisheries (Nowicki et al., 2017; Kendrick et al., 2019). Similarly, carbon and nutrient cycling was disrupted (Smale et al., 2019). Declining seagrass habitats are recognized as a significant threat to fisheries production, with estimates that seagrasses contribute AUD $31.5 million per year to Australia's commercial fisheries (Jänes et al., 2019). In the tropics of Queensland, historically, seagrasses have shown a remarkable capacity to recover from large disturbance events without direct intervention (Rasheed et al., 2014; Coles et al., 2015). This is likely due to a combination of relatively well-connected seagrass populations (Grech et al., 2018) and life history strategies of tropical species allowing for rapid colonization and growth (Rasheed, 1999, 2004). However, in recent times this situation has changed, with the relative frequency of La Niña climate events and severe storms leading to sustained losses (McKenna et al., 2015) and cases where natural seagrass recovery is unlikely. These conditions are predicted to become more common with climate change (Rasheed and Unsworth, 2011), making knowledge of how to restore these tropical species increasingly important. Thus, seagrass losses represent a major financial cost that could escalate in the event of complete habitat destruction.

Restoration research in Australia and New Zealand has focused on small-scale experimental tests using a variety of techniques ranging from the planting of sprigs (seagrass fragments) or plugs (seagrass cores) to seed-based restoration (**Supplementary Table S1**; **Figure 1**). The majority of seagrass restoration trials to date have used shoot-based techniques, with at least 46 studies since 1986 (**Supplementary Table S1**). These have ranged from small-scale pilot studies (e.g., Irving et al., 2010) to large-scale transplantation trials (e.g., West et al., 1990; Bastyan and Cambridge, 2008), involving both manual and mechanical planting (e.g., Paling et al., 2001), and a wide range of anchoring methods [e.g., artificial seagrass (West et al., 1990; Campbell and Paling, 2003; Matheson et al., 2017), biodegradable pots (Kirkman, 1999), and hooks or pegs (Bastyan and Cambridge, 2008)]. Although survival of transplanted seagrass fragments or cores was low in many studies, promising results are increasingly reported, with transplant units surviving more than 2 years or showing shoot densities similar to naturally occurring meadows (e.g., Bastyan and Cambridge, 2008; Oceanica Consulting Pty Ltd., 2011, Matheson et al., 2017).

There are no published trials of restoration using seeds in Australia and New Zealand to date. However, scientists at the University of Western Australia are currently developing an approach to collect, process, and remotely deliver seeds of *Posidonia australis*, and have seen some early successes at the trial stages[1]. Scientists from Central Queensland University in the multicommodity Port of Gladstone (Great Barrier Reef World Heritage Area) have also assessed the practicality of seed collection, storage, and germination for *Z. muelleri* restoration (E. L. Jackson, Central Queensland University, personal communication). The use of seedlings in restoration is more well-established, especially in the use of hessian bags which act as a substrate for *Amphibolis* seedling recruitment. Long-term trials involving the use of hessian bags placed on the ocean floor to aid natural seedling recruitment started in 2004, with many showing long-term survival (Irving et al., 2010; Tanner, 2015). Studies on seed-based restoration for other species have been highly variable and less successful, highlighting the need for more in-depth research (Lord et al., 1999; Irving et al., 2010).

The restoration successes seen in Australia and New Zealand today largely come from studies on *Posidonia* and *Amphibolis*, as well as *Z. muelleri* in New Zealand (**Figure 1**). While these studies have contributed to the overall knowledge of restoration, more species- and habitat-specific studies are required to improve restoration success. Species-specific studies are required to establish clarity around seagrass resilience, especially local adaptive potential in the face of climate change. Successful restoration efforts will rely upon whether transplants or seeds are able to persist under future conditions. Success will require accurate forecasting, which requires rigorous species, site, habitat, and methodological data.

GOING FORWARD: WHAT ARE THE GAPS TO BE FILLED?

There are several well-established seagrass restoration frameworks published to date, including the five-step program by Campbell (2002), which consists of decision-making trees in the planning process for restoration. A review by van Katwijk et al. (2016) has highlighted considerations, such as the removal of the original cause of seagrass decline or site-specific planting techniques, that needs to occur before starting on any restoration activity. Yet, knowledge gaps still exist, which are discussed in the following sections. There are also lessons to be learned and applied from the terrestrial restoration community here, and that designing effective restoration efforts will require input from multiple disciplines (Miller et al., 2017).

Pre-restoration Considerations

Clear Accountability and Adequate Resourcing

It is essential to put enabling policies and legislation in place to facilitate broad-scale seagrass restoration efforts required to halt or reverse rates of seagrass decline. This includes clear delineation of roles and responsibilities between various agencies, and attachment of necessary resources to deliver meaningful programs. For example, the Catchment Management Framework in Victoria, Australia, set up under the *Catchment and Land Protection Act 1994* (CaLP Act), incorporates environmental, economic, and social considerations for the coordinated management of land, water, and biodiversity resources based on catchment areas (State Government of Victoria, 2020). Each catchment area has its own management authority, which works together with other agencies and groups such as Parks Victoria, Victorian Coastal Council, and local councils and Landcare groups (State Government of Victoria, 2016). This ensures legislative accountability for all involved parties, leading to resources being utilized efficiently, and reasons for failures identified. In New Zealand, seagrass (*Z. muelleri*) is listed as at risk – declining by the Department of Conservation (de Lange et al., 2017). The New Zealand Government's draft National Policy Statement for Freshwater Management (NPS-FM) issued by the Minister for the Environment in September 2019 requires councils to provide for and encourage the restoration of inland wetlands. However, there is as yet no similar requirement for coastal wetlands (which include seagrass meadows to 2 m below low water). Nevertheless, the proposed NPS-FM and proposed National Environmental Standard for Freshwater do provide increased protections for coastal wetlands from activities including disturbance of the bed and removal of indigenous vegetation. Whilst restoration policy is rapidly being embedded into international agreements (e.g., New Deal for Nature, Convention on Biological Diversity Conference of Parties 15 (COP), and climate change challenges for COP26

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[1] https://seagrassrestorationnetwork.com/seed-based-restoration-1

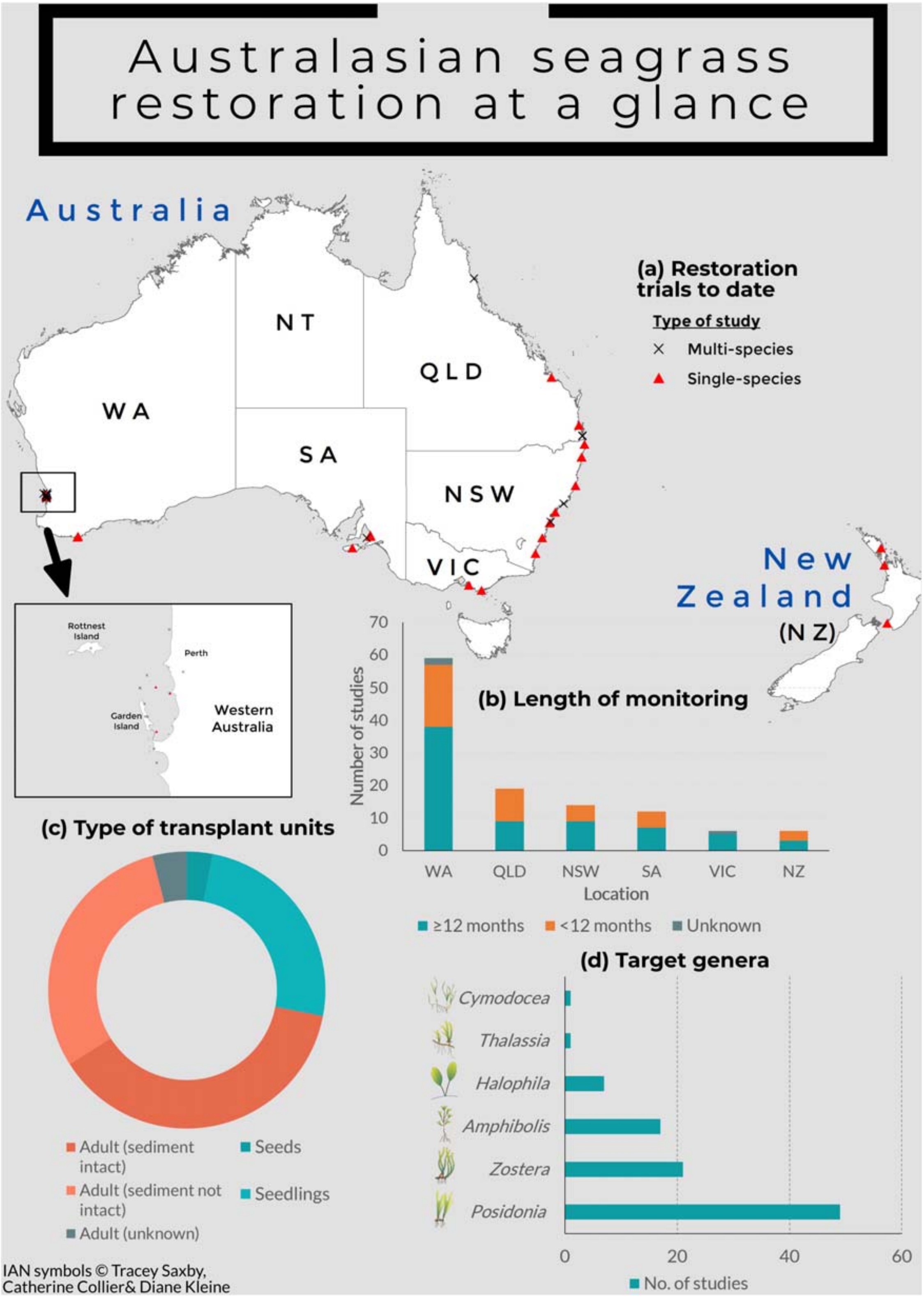

FIGURE 1 | Infographic showing **(a)** all seagrass restoration trials carried out to date in Australasia, with inset map showing the concentration of studies carried out in Cockburn Sound, Western Australia; **(b)** length of monitoring of seagrass restoration trials based on states, **(c)** the proportion of different types of transplant units used in restoration trials across Australasia; and **(d)** the target genera in restoration trials across Australasia.

Glasgow), it is yet to filter down adequately into Australian and New Zealand state or federal government policies for seagrass restoration. For example, the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) is one of the key environmental protection legislations in Australia. While the EPBC Act does provide some provisions for restoration such as through species recovery plans, these are generally only for threatened ecosystems (of which seagrass is yet to become), and these plans are slow to develop. However, there are also a range of restoration policies in the context of other ecosystems (e.g., Victorian Waterway Health Management Strategy), and others that do aim to protect seagrasses (e.g., Ramsar management framework, NZ's NPS-FM). Australia and New Zealand could expand on these existing polices, and learn from other regions which have more proactive policies on marine restoration, such as Living Shorelines (National Oceanic and Atmospheric Administration [NOAA], 2015), or from terrestrial ecosystems [e.g., Working for Water South Africa (Department of Environmental Affairs, 2019) or the Atlantic Forest Restoration Pact (2016)].

Strategic Prioritization of Efforts

While sound polices and legislation may provide a firm foundation for upscaling seagrass restoration efforts, investment may be quickly undermined if resources are not carefully targeted to areas where threats to seagrass persistence have been removed or reduced, successful seagrass restoration is feasible, stakeholders are willing and able to invest, and the benefits to other environmental and social values are the greatest. Accordingly, for many natural resource management agencies that operate at a regional to National scale, we emphasize the importance of adopting strategic prioritization approaches to identify high priority areas to guide conservation and/or restoration efforts. While more complex models (e.g., Leathwick et al., 2008; Moilanen et al., 2011) may be desirable in the longer term, simple decision support tools for prioritizing seagrass restoration already exist that allow management agencies to maximize returns by targeting sites where intervention would be the most cost-effective (e.g., Grech et al., 2011; Tan et al., 2018). These decision support tools are easy to use, and easily adaptable to suit different conservation priorities. Furthermore, these support tools can also be coupled or sequenced with ecosystem risk assessments, such as the IUCN Red List of Ecosystems (Rodríguez et al., 2015), allowing for a complete understanding of the conservation status of seagrass ecosystems, their current and future threats and opportunities for restoration. Identification of sites for seagrass restoration should be carried out collaboratively (i.e., between managers, scientists and the community), to not only ensure that financial resources are spent efficiently and effectively (instead of opportunistically as it is largely being done currently), but also so there is a shared understanding and ownership of restoration priorities.

Once priority areas are identified, at a more local scale, a clear understanding of environmental conditions should be incorporated into site selection before investing effort into restoration (Campbell, 2002; van Katwijk et al., 2016). This includes consideration of the original stressors that resulted in seagrass loss, whether they have been mediated or removed, resulting in a return to a favorable state for seagrass restoration; or if the environment has been too drastically altered to sustain seagrass. Accurate information on historical changes is preferred (but not always available), such as persistence, loss, gain, or recovery of seagrass meadows, and environmental drivers affecting their past, present, and future potential distribution such as light, sediment, temperature, and nutrients. This information will inform decisions when tackling stressors or threats (van Katwijk et al., 2016), and when considering which restoration approach may be most appropriate at a site (Campbell, 2002). These data can then also be incorporated into habitat suitability models to identify receptive restoration sites, which are regularly used in other marine systems like shellfish (Theuerkauf and Lipcius, 2016). Whilst many types of habitat suitability models exist, the principle of spatial planning and suitability indexes can be expanded to include development of restoration suitability models which encompass not only the environmental and physical suitability for seagrasses, but cultural, logistical, and social data as well.

Species-Specific Studies: Reproductive Biology, Dispersal, and Provenance

Reproductive Biology

There is now a growing emphasis on seed-based restoration, largely due to the lower impact it has on existing meadows (i.e., removal of large numbers of fragments or cores in shoot-based restoration), and its potential for upscaling (Orth et al., 2006). To facilitate the growing area of seed-based restoration, more information is required on how flowering and seed production varies within and across species, and the environmental factors that trigger reproduction and germination (Cumming et al., 2017). Substantial inter-annual and small-scale spatial variability in sexual reproduction has been reported from studies in Western Australia, New South Wales, Victoria, and New Zealand, with results suggesting that the timing and intensity of flowering are influenced by processes occurring across a range of spatial scales (Dos Santos and Matheson, 2016; Smith et al., 2016; Sherman et al., 2018). This is important given the differences in the geographical range of some Australian and New Zealand species. For example, some species such as *Halophila ovalis*, can be found from the tropical waters of Southeast Asia to the temperate waters of Western Australia and New South Wales (Short et al., 2010). In contrast, some species have a more confined range such as *Posidonia sinuosa*, which is endemic to western and southern Australia (Short et al., 2010).

Effective seed-based restoration will require improved techniques for the collection, handling and storage of seeds to optimize germination and survival. The efficiency of *Z. marina* seed collection has been improved through mechanical harvesting in North America, with an estimated maximum mechanical collection rate of 132,000 seeds/labor-hour versus 62,000 seeds/labor-hour using manual collection, with minimal damage to the donor meadow (Marion and Orth, 2010). Seed collection rates could differ based on meadow productivity, therefore, studies into whether mechanical harvesting efficiencies in the United States can be replicated on Australian and New Zealand species are worthwhile. Besides collection methods, species-specific studies on seed storage could also enhance restoration opportunities, with seeds being collected and stored for planting during a later more optimal planting season (Marion and Orth, 2010). Such studies need to take into account the different characteristics of Australian and New Zealand seagrass seeds, which have varying lengths of dormancy and sensitivity to desiccation that will affect the efficacy of seed storage (Orth et al., 2000; Statton et al., 2012). For example, the seeds of *Zostera* spp. which possess a hard seed coat can be viable up to 12 months in storage (Orth et al., 2000), whereas the seeds of *Enhalus acoroides* were only able to survive a maximum of 11 days in storage (Ambo-Rappe and Yasir, 2015). Lastly, while seed collection is considered to have less of an impact on donor meadows than collection of shoots, it is still important to understand the impact seed collection might have, especially surrounding how much can be collected without impacting donor meadows and other connected meadows.

Genetic Diversity and Connectivity

Seagrasses have the potential to disperse over long distances via ocean currents during various life-history stages (Kendrick et al., 2012; McMahon et al., 2018). Population genetic studies in combination with hydrodynamic models have increased our understanding of the role/potential of connectivity in natural seagrass meadow recovery (e.g., Sinclair et al., 2016, 2018; Smith et al., 2018). Although there is a growing understanding of the movement ecology of seagrasses (McMahon et al., 2014; Smith et al., 2018), studies on propagule viability and survival, and establishment success are currently limited (but see Campbell, 2003; Weatherall et al., 2016). A combined understanding of the dispersal mechanisms and reproductive biology of seagrasses will add to the overall understanding of spatial and genetic connectivity.

Spatial patterns of genetic connectivity can inform decision-making and help to prioritize management actions (e.g., Sherman et al., 2016). For example, connectivity estimates can be used to identify areas that are more likely to recover naturally following decline (e.g., areas that have steady supply of propagules from non-local sources) and areas that have limited recovery potential due to recruitment limitations (e.g., isolated areas expected to receive minimal or no propagule recruitment from non-local sources). Habitat enhancement and ecological engineering to encourage settlement would become priority management actions for areas showing limited signs of recovery despite expected propagule supply. In contrast, translocations (e.g., physical planting) in combination with habitat restoration investments would be needed in areas with limited propagule supply to ensure population establishment.

The level of genetic diversity of source and recipient seagrass meadows is also an important factor to consider when augmenting remnant seagrass meadows or establishing new meadows. Seagrass meadows at the edge of their range may have lower genetic diversity and higher levels of clonality (e.g., Evans et al., 2014) or have reduced seed production as a result of pollen limitation (e.g., Sinclair et al., in press). Small isolated populations often have similar issues (Kendrick et al., 2012; Reynolds et al., 2013; McMahon et al., 2014). Overall genetic diversity is positively associated with population fitness (Connolly et al., 2018), and standing genetic variation within populations is closely tied to adaptive capacity and resilience to environmental change (Reed and Frankham, 2003; Leimu et al., 2006). Previous studies also indicate that genetic diversity is positively correlated with seagrass-related community species richness and productivity (Crutsinger et al., 2006; Whitlock, 2014). Consequently, selecting genetically diverse meadow(s) as a donor source is important for maximizing restoration success (Reynolds et al., 2012, 2013).

Provenance

Declines of many seagrass species have been attributed to thermal stress associated with rising sea surface temperatures and extreme temperature events (Marbà and Duarte, 2010; Thomson et al., 2015; Carlson et al., 2018; Babcock et al., 2019). Many seagrass species persist in low energy and shallow water environments such as coastal embayments, inlets and fjords. These environments are particularly susceptible to warming and extreme temperature fluctuations, compared with open coastal environments (Harley et al., 2006). Consequently, projections of rising sea surface temperatures and more frequent heatwave events pose a significant risk to both natural and restored seagrass populations (Smale et al., 2019). Populations inhabiting trailing (or warming) range edges are often less well connected through dispersal, but can exhibit a high degree of local adaptation and thus contain unique genotypes necessary for future survival. However, they are also often most threatened under climate change (Hampe and Petit, 2005; Zardi et al., 2015). Similarly, intertidal species show niche partitioning of rhizome depth based upon substrate temperature envelopes (Campbell et al., 2018), which has further implications when selecting plants from donor for receiving environs and transplantation depth. This reinforces the need for management strategies to address the risks of climate change and maximize adaptive potential.

Traditionally, restoration policy has advocated the use of local genetic material (known as local provenancing) when undertaking restoration activities (Jordan et al., 2019). However, evidence suggests that non-local sources of restoration material may outperform those from local provenance under future climates (Sgrò et al., 2011; Aitken and Whitlock, 2013; Miller et al., 2019a). Therefore, future restoration may require looking at alternative strategies, such as mixed provenancing (mixing of seed from multiple sources; Broadhurst et al., 2008). Such approaches can help to broaden the genetic basis of restored populations to overcome risks maladaptation by providing new genetic variants for selection to act on (Prober et al., 2015; Wood et al., 2019). Such approaches can also help to overcome fitness reductions is small, inbred and genetically depauperate populations (Broadhurst et al., 2008; Weeks et al., 2011).

Overcoming risks of maladaptation may be further assisted by identifying and introducing pre-adapted genotypes (Browne et al., 2019). This might be achieved by moving genotypes from warmer adapted populations to cooler locations to increase the probability of tolerance to rising ocean temperatures (Schueler et al., 2013; Bansal et al., 2015; Wood et al., 2019). This typically applies to widespread species with wide latitudinal ranges, many of which show genetically based clines in performance across thermal gradients (Staehr and Wernberg, 2009; Mohring et al., 2014; Bennett et al., 2015). Identifying pre-adapted or "climate-ready" seed sources for restoration requires an understanding of adaptive genetic differentiation among populations spanning thermal gradients. Typically, this can be determined empirically using quantitative (e.g., glass house or common garden experiments; Byars et al., 2007; Browne et al., 2019; Miller et al., 2019a) or correlative (e.g., genomic assessments for genotype x environment associations; Jordan et al., 2017; Miller et al., 2019b) genetic approaches. When genetic data is not available, climate matching (between restoration areas and others spanning the species climatic distribution) can help identify genotypes expected to be suited to future predicted climates at the restoration area (Winder et al., 2011; Benito-Garzón et al., 2013).

While opportunities may exist to bolster the genetic basis of seagrass populations, consideration needs to be given to species' climate niches under future climates. Species distribution models suggest that major shifts in suitable habitat will occur under climate change. In some cases, it has been suggested that there will be no (or minimal) overlap between current and future predicted climatic niches (Rehfeldt and Jaquish, 2010; Ledig et al., 2012; Wang et al., 2016). In such cases conservation of remnant populations persisting in areas more likely to support the species under climate change becomes a priority, and interventions, such as assisted range expansion, to facilitate species movement to climatically suitable areas may need to be considered (Hoegh-Guldberg et al., 2008; Cole et al., 2011; Winder et al., 2011; Wadgymar et al., 2015). Numerous cautions have been raised when considering assisted migration, particularly in aquatic systems (Ricciardi and Simberloff, 2009, but see Schlaepfer et al., 2009): potential for the species to become invasive (Hoegh-Guldberg et al., 2008; Mueller and Hellman, 2008, Aitken and Whitlock, 2013; Hancock and Gallagher, 2014) and transfer of pests and pathogens from source locations (Simler et al., 2019). Clearly no assisted migration is risk free, but appropriate precautions including rigorous risk assessment and biosecurity protocols will act to minimize some concerns (Hancock and Gallagher, 2014; Simler et al., 2019).

Knowledge of Tropical Species

One of the major gaps in knowledge remains our understanding of how to restore tropical species in Australia. Most of the specific knowledge and current restoration paradigms have been developed from temperate or subtropical experience. There have been small process studies in the tropics (Rasheed, 1999, 2004) but to date no larger scale restoration attempts. What we do know from observations of natural recovery processes in tropical Australia (Rasheed et al., 2014; McKenna et al., 2015) is that the life history and reproductive strategies of many tropical species could be well-suited to restoration as they have the capacity for rapid clonal growth once established. As to whether a modified or different set of considerations are required for successful tropical restoration requires an increased research focus on understanding the basics.

Ecological Engineering

Ecological engineering was first formally defined as "the design of sustainable ecosystems that integrate human society with its natural environment for the benefit of both" (Mitsch, 2012). Since its inception, ecological engineering has come to encompass approaches such as replacing traditional built infrastructure with newly created or restored coastal ecosystems such as mangroves or salt marshes (Temmerman et al., 2013), or designing new or altering old infrastructure to add structural complexity to promote settlement of marine organisms (Martins et al., 2010; Loke et al., 2017) and reduce settlement of non-indigenous species (e.g., Dafforn, 2017). These same principles could be applied to seagrass restoration, following studies to elucidate conditions where settlement and/or colonization can be promoted. The suitable conditions for seagrass growth are generally well established, including light availability (Duarte, 1991; Ralph et al., 2007), hydrodynamic environment (Fonseca and Kenworthy, 1987; Schanz and Asmus, 2003), substratum type (Erftemeijer and Middelburg, 1993; van Katwijk and Wijgergangs, 2004), or nutrient availability (Udy and Dennison, 1997; Touchette and Burkholder, 2000). This knowledge combined with site-specific studies can be used to inform future development and restoration plans in terms of ecological engineering. In this instance, ecological engineering is a form of "passive" restoration, where the conditions to encourage settlement and establishment are included in development design. Unintended recruitment has already been reported, for example, in Singapore, where a small seagrass meadow formed on a reclaimed shoreline behind a breakwater (Yaakub et al., 2014; Lai et al., 2018). In certain situations, coastal development will proceed, and loss of seagrass habitat is inevitable. However, there are opportunities through the coastal development design phases to incorporate ecological engineering, such as building breakwaters to mimic shallow embayments to enhance the settlement of seagrass seeds, propagules or fragments. To be most effective, these designs need to be combined with other studies, such as modeling of seagrass seed or fragment dispersal and meadow connectivity.

Upscaling Restoration Trials

There have been many small-scale restoration trials that have shown success. However, the challenge remains to translate small-scale success into large-scale restoration programs (van Katwijk et al., 2016). To upscale restoration programs, the involvement and commitment of industry partners, local communities, non-governmental organizations (NGOs), and state and federal government agencies are required to establish multi-year to decadal funded restoration projects. Programs need to be holistic and focus on the landscapes and associated benefits, rather than just a single species. Collaborative designing of restoration programs between researchers, managers, and the various community stakeholders would likely increase restoration success, as each of these groups bring their own unique (though sometimes overlapping) skills and experiences.

While grassroots restoration efforts are important for upscaling restoration efforts, there needs to be effective communication of the science underpinning restoration to regional managers and community volunteers to improve the likelihood of success. In turn, scientists can also gain valuable insights into local environmental and socio-economic conditions from regional managers who have on-the-ground experience and knowledge, which could prove to be extremely beneficial to restoration programs. For example, coordinated efforts by governmental bodies and restoration scientists to restore *Amphibolis* meadows in South Australia has shown promising results, with trials using hessian bags in seedling recruitment showing survival for at least 5 years and greater stem lengths compared to natural meadows (Tanner, 2015; **Supplementary Table S1**).

Increased Knowledge Sharing

Various academic research groups and management bodies around the globe work on seagrass restoration, and while their research outputs are published in international journals and gray literature, it is well-established that a publication bias toward successful restoration outcomes exists (Zedler, 2007). There is much that can be learned from unsuccessful restoration attempts, or unexpected outcomes that largely go unpublished, and a platform for knowledge sharing would greatly aid in disseminating information and generating greater discussion between seagrass scientists, managers and practitioners. Scientists clearly provide an important role during research and development, and ongoing monitoring and providing information for adaptive management. However, as restoration projects scale up, they need to be managed like any other large infrastructure development projects, and most researchers rarely have the skill sets, experience or capacity to manage such projects. There is therefore a need to facilitate knowledge sharing not only between researchers, but also with industries that have the expertise and knowledge that allows upscaling of seagrass restoration efforts. Knowledge sharing can be facilitated through a variety of platforms including formal partnerships and agreements between industry and research institutions to collaborate on delivering restoration projects, workshops that facilitate a broad range of stakeholder engagement and through the development of network communities. One example of this is the Seagrass Restoration Network[2], which was established in 2015 to link researchers, managers and practitioners worldwide and facilitate the sharing of knowledge and tools for seagrass conservation and restoration. The Network currently has more than 50 members from around the globe.

More Long-Term Monitoring of Meadows

Lastly, more long-term and regular monitoring of seagrass meadows is needed to understand rates and patterns of seagrass loss, the likely drivers of these losses, identify potential restoration sites, and effectively determine the success of intervention (Duffy et al., 2019). In Australia, estimates of seagrass coverage are still incomplete, with many regions currently lacking this basic knowledge (York et al., 2017). In New Zealand, a national scale inventory of seagrass has recently been collated by the Department of Conservation's SeaSketch project. The NZ SeaSketch project is acknowledged as incomplete, lacking data for the many unmapped locations, especially those with smaller areas of seagrass (Anderson et al., 2019). Further monitoring is required to make informed decisions on where seagrass has been lost, and where it could potentially be restored. Importantly such monitoring needs to incorporate larger spatial scale assessments and mapping to be effective. Long-term monitoring is also needed for restoration projects, with approximately 61% of Australian and New Zealand studies monitoring beyond a year, although the longest running *Posidonia* restoration site has been monitored in excess of 20 years (**Supplementary Table S1**; **Figure 1**). This is a problem not unique to Australian and New Zealand studies (van Katwijk et al., 2016). Among the studies with long-term monitoring, many lack regular monitoring, with a few studies only monitoring at the start and end of the restoration trial (e.g., Connolly et al., 2016). Without long-term information, the effectiveness of the restoration methods cannot be assessed accurately, and improvements to the method cannot be made. Monitoring could incorporate the use of appropriately trained volunteers, which will help drive research costs down, raise awareness and encourage local communities to have a sense of ownership in restoration programs. The use of novel and potentially more efficient monitoring techniques should also be expanded upon, such as the use of remote sensing or drones (Duffy et al., 2018; Nahirnick et al., 2019; Phinn et al., 2018).

Future restoration programs should dedicate funding for monitoring programs to ensure that appropriate monitoring durations are captured. It is important to note that seagrass restoration is at the stage where effective methods are still in development, and while we are going through this phase, many failures are to be expected. As a result, monitoring results from restoration programs may be discouraging to managers or community groups who may feel pressure for successful outcomes due to substantial investment of time and/or money. This may in turn make it harder to secure funding for future restoration works if the outcomes are uncertain, or even long-term monitoring programs which may be more expensive than the restoration itself. However, it is essential to recognize that results are not immediate, and that resources need to be invested to work toward effective restoration programs.

EMERGING TOOLS, TECHNIQUES AND APPROACHES

There are a variety of new restoration tools and techniques that have been developed and trialed internationally that show relatively high degrees of success. However, there is no "one solution fits all" approach to suit the life history traits of all species across all conditions. The emerging tools now make seagrass restoration feasible for many species and at the large spatial scales needed to restore seagrass meadows and associated ecosystem services. Emerging approaches focusing on holistic and collaborative restoration practices have also

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[2] https://seagrassrestorationnetwork.com

recently been highlighted, aimed at creating a "global restorative culture" in order to improve human, and ecosystem health (Aronson et al., 2020). The success of these tools, techniques, and approaches are underpinned from previous lessons learned, including many restoration "failures."

Emerging Techniques in Seed-Based Restoration

Buoy-Deployed Seeding (BuDS)

The BuDS technique involves the collection of mature reproductive shoots which are placed in mesh nets attached to buoys, suspended above plots to be restored with the aim that negatively buoyant seeds when released, will settle over the desired restoration plot (Pickerell et al., 2005; **Figure 2**). The collection of reproductive shoots can be relatively easy and rapid (depending on the target species), and BuDS can be deployed over relatively large spatial scales. Recruitment based on this technique is currently low, at approximately 1 (Marion and Orth, 2010) to 6.9% of seeds deployed (Pickerell et al., 2005). The use of BuDS ensures high genetic diversity, which is positively correlated to rates of sexual reproduction, vegetative propagation, and overall shoot density (Williams, 2001; Reynolds et al., 2012). However, BuDS are unlikely to be suitable for all conditions and species, having only been tested on *Z. marina* thus far (Pickerell et al., 2005; Busch et al., 2010; Marion and Orth, 2010). BuDS deployed in areas with strong hydrodynamics might be less effective as seeds can be washed away at high rates. Marion and Orth (2010) also found that many of the buoys deployed were coated in drifting macroalgae, and were potentially grazed upon by large numbers of amphipods and juvenile crabs, reducing the number of seeds available. Thus, the overall effectiveness of the method might be limited.

Dispenser Injection Seeding

One of the most recently developed techniques in seagrass restoration comes from the Dutch Wadden Sea, where seeds are mixed with local sediment to create a sediment-seed mixture that is then injected into the substrate using modified sealant guns (**Figure 2**). A predetermined amount of seeds is mixed with sieved fine-grained sediment (median grain size $<100\ \mu\text{m}$), loaded into sealant tubes, and injected into the sediment using calibrated sealant guns up to a depth of 1–4 cm, depending on the depth that the seeds of the target species naturally recruit from. Sediment is collected close to the restoration sites so as not to introduce foreign substrate, and is fine-grained as this allows a cohesive substrate to be formed which in turn keeps the seeds together for injection into the sediment and keeps injections standardized. Inorganic clay can also be added to the natural sediment to improve cohesiveness of the seed-sediment mixture. This method was trialed in the intertidal Dutch Wadden Sea, using *Z. marina* seeds in 2017 and 2018 (Govers, 2018). Resulting plant densities exceeded target densities of 10 plants m^{-2} (**Figure 2**).

This method is promising, especially for sites with strong tidal currents, such as the intertidal zone, where hand-casting and BuDS have not been very successful. However, direct injecting of seeds has yet to be trialed for other seagrass species and is likely more labor intensive compared to other seeding techniques such as hand-casting. The technique is also currently suitable for seeds between 0.5 and 4 mm in size, however, the equipment needed can be adjusted accordingly for different seed sizes. Additionally,

FIGURE 2 | Emerging tools and techniques developed within the international seagrass restoration community. First row left to right: buoy-deployed seeding (© Jannes Heusinkveld), Dispenser Injection Seeding (© Laura Govers). Second row left to right: seagrass nurseries (© Gary Kendrick and John Statton); anchoring shoots using iron nails (© Troels Lange). Third row left to right: artificial in-water structures (© Peter Macreadie), and collection and use of alternative sources of transplantation (© Harriet Spark).

if the restoration site is predominantly coarse-grained sediment, the use of mud (fine-grained sediment) required by this technique might not be ideal. Nonetheless, it is a valuable technique and is still less labor-intensive than attempting restoration via planting vegetative fragments. An adapted version of this method is currently being trialed for underwater seeding.

Nurseries

The use of aquaculture systems in seagrass restoration is relatively new, and the few published studies to date have shown promising results. Under controlled conditions, Tanner and Parham (2010) were able to germinate and grow *Z. marina* plants to a size that was large enough for transplanting within 70–100 days. Furthermore, the nursery reared plants had a higher survival rate and better growth than plants transplanted from natural beds (Tanner et al., 2010). In Australia, seedling culture has also been carried out on *Prunus angustifolia* (Irving et al., 2010) and *P. australis* (Statton et al., 2013). While the survival of cultured *P. angustifolia* seedlings and subsequent outplanting survival was low (Irving et al., 2010), *P. australis* fared much better, with 100% cultured seedling survival after 7 months (Statton et al., 2013). Furthermore, Statton et al. (2013) were able to produce larger *P. australis* seedlings by modifying the sediment composition used (**Figure 2**). These studies demonstrate that aquaculture of seagrass seedlings is a viable source of planting units in restoration. In combination with more species-specific studies on seed germination and optimum storage conditions, the use of nurseries is an effective addition in seagrass restoration, especially for areas or species where seed production is high.

Anchoring of Shoots With Iron Nails

The use of shoots has been widely used in restoration. These are often planted directly into the substrate (e.g., Matheson et al., 2017), however, several anchoring techniques have been used to varying degrees of success. One of the most successful examples of the use of anchored shoots for seagrass restoration has been in Denmark (Lange et al., in review). Danish waters are typically characterized with periods of severe wave action, and it has not been possible to transplant *Z. marina* as unanchored shoots which tend to be uprooted within short periods. Instead, the transplanted shoots which had 5–10 cm rhizome were attached to iron nails of 8 × 0.3 cm by winding a thin iron wire of 0.5 mm thickness around the rhizome and the nail (**Figure 2**). The nails were uncoated pure iron (not corrosion treated) and corroded within the first year without leaving heavy metals in the sediment. During transplanting, the rhizome and nail are gently pushed about 1 cm down into the sediment, ensuring that the base of the shoots is sitting at the sediment-water interface. This technique provides sufficient weight to keep the transplanted shoots in place and has led to the successful restoration of about 1.5 ha of seagrass in three estuaries (Lange et al., in review). Altogether, more than 40,000 shoots were transplanted in the three systems. The transplantations were laid out in a chess board pattern, mixing bare bottom and transplanted areas. The shoot density increased from 19 to 900 m^{-2} within the first 2 years, with vegetative propagations also partly covering the bare bottom areas. The return of ecosystem services was also measurable as increased accumulation of C, N, and P in the sediment, increased infauna and epifauna biodiversity and species densities compared to the bare bottom. The success of this technique could be due to the addition of iron into the sediment when the nail corrodes. Iron addition into a well-oxidized seagrass rhizosphere increases the absorption capacity for phosphorus and reduces sulfide toxicity, in turn increasing seagrass productivity (Holmer et al., 2005; Ruiz-Halpern et al., 2008). As such, the benefits of iron addition in combination with this anchoring technique should also be considered as a mechanism for increasing restoration success.

Artificial In-Water Structures

The use of artificial in-water structures to protect restoration trials is not new, and some have been shown to improve survival of both transplanted shoots and seedlings (Campbell and Paling, 2003; Tuya et al., 2017). For example, artificial seagrass units (**Figure 2**) which mimic the physical properties of seagrass have been shown to enhance aspects of the habitat, such as stabilizing sediment grain size (Campbell and Paling, 2003), preventing herbivory (Tuya et al., 2017). However, artificial seagrass is often made of plastic, and given the growing awareness of marine plastic pollution (Haward, 2018), its use in restoration is generally undesirable. To counter the use of plastic, researchers are developing artificial seagrass made entirely out of fully biodegradable materials to help facilitate restoration without the plastic footprint (The SeaArt Project, 2020).

Artificial in-water structures can also be used as anchoring devices to increase the chance of transplant unit survival. These include tying seagrass shoots to metal frames which are lowered to the seafloor (e.g., Transplanting Eelgrass Remotely with Frame Systems (TERFS), Calumpong and Fonseca, 2001; Wendländer et al., 2020), or to oyster shells (Lee and Park, 2008). These methods increase restoration success through ensuring adequate anchoring and tend to be more cost-effective as they do not require the planting of individual shoots one at a time.

Biodegradable materials, such as hessian and jute, have also been trialed with great success. These materials can promote the establishment of naturally dispersing seedlings (Tanner, 2015), protect seeds from predation (Orth et al., 2006), enhance survival of restored shoots (Ferretto et al., 2019), and exclude bioturbating animals, thus increasing survival rates (Wendländer et al., 2020). The use of these biodegradable products should continue to be explored to improve seagrass restoration outcomes through the challenging establishment phase, although their utility will likely vary with location.

Alternative Sources of Transplant Units and Use of Seagrass Wrack

Seagrass propagules are often limited and highly seasonal, and the collection of transplantation material could potentially put greater risks on donor meadows. Thus, alternative sources of transplant units are required to minimize the overall negative impact of sourcing restoration material. A potentially viable source of transplant units is seagrass wrack, detached biomass transported by wind and tides and accumulated on beaches globally (Macreadie et al., 2017). Seagrass wrack has many important ecological functions (Kirkman and Kendrick, 1997; Ince et al., 2007; Del Vecchio et al., 2017), but can also pose problems for coastal managers as its over-accumulation is often viewed as a nuisance by the public and high costs are incurred in their removal (Macreadie et al., 2017). Efforts are already being made to make use of this valuable resource, such as during the aquaculture of *P. australis* seedlings where it was recommended as a low cost and readily available nutritional supplement in restoration (Statton et al., 2013). Beyond its use as a nutritional supplement, seagrass wrack can also be a valuable source of transplant material. Terrados et al. (2013) used *Posidonia oceanica* seedlings from beach-cast fruits for seagrass plantings and obtained relatively high success, with 44% survival for 3 years. The use of wrack-collected seedlings in culturing and outplanting was also trialed in Australia, albeit to lower success. Wrack-collected *P. angustifolia* seedlings showed survival of 6–9% after 11 months in aquaculture, and survival upon outplanting was also low (Irving et al., 2010). Storm-generated rhizome fragments of *Posidonia* found within the wrack have also been used successfully for restoration in the Mediterranean (Balestri et al., 2011) and are currently being used successfully to restore *P. australis* in Australia (Ferretto et al., 2019; **Figure 2**).

Promoting Positive Biological Interactions

Harnessing positive biological interactions can increase restoration success (Halpern et al., 2007; Silliman et al., 2015; Gagnon et al., 2020). Biological interactions in seagrasses include plant-substrate, plant-microbial communities, plant-plant (both intra- and interspecific), and between seagrass and other marine organisms/species such as shellfish, mangroves, and coral reefs. Many of these interactions are currently well-understood, and should be considered and included during restoration.

Plant-bivalve interactions have been shown to be largely positive, with a review which included all marine angiosperms (i.e., seagrass, salt marshes, mangroves, and freshwater submerged aquatic vegetation) showing that 70% of studies with a restoration focus showed positive interactions compared to 5% for negative interactions (Gagnon et al., 2020). For example, oyster reefs have been shown to facilitate seagrass productivity through a variety of mechanisms. Oyster reefs enhance conditions for seagrass growth through provision of physical protection from wave action (Piazza et al., 2005), improve water clarity through filtering particulate organic matter (Plutchak et al., 2010), and increase sedimentation and nutrient inputs through addition of feces (Newell and Koch, 2004). Like seagrasses, shellfish reefs are also some of the most degraded marine ecosystems globally (Beck et al., 2011), and a cross-ecosystem restoration approach could benefit both oyster reefs and seagrasses. For example, restored oyster reefs in the Northern Gulf of Mexico resulted in an increase in seagrass cover which was not observed in nearby areas (Sharma et al., 2016). New Zealand provides an ideal location to incorporate seagrass restoration with existing shellfish restoration efforts that are a major focus of Māori coastal research (e.g., Mullard, 2018). Similarly, several shellfish restoration projects have also been initiated in Australia (Gillies et al., 2018). The linkages between healthy shellfish and seagrass are a stepping stone to increase focus on seagrass restoration in a holistic manner.

Similarly, plant-soil feedbacks are emerging as an important area in terrestrial restoration projects, where interactions between plants, soil and soil microorganisms can have positive impacts on ecosystem functions. As marine angiosperms with root and rhizome systems anchored in sediments, seagrasses exist in a unique ecological niche in the marine system as organisms that create underwater rhizospheres. The composition of the microbiome on seagrass roots or within rhizospheres is an important indicator of seagrass health, and is already being applied for seagrass monitoring purposes (Trevathan-Tackett et al., 2019; Martin et al., 2020a). As an extension, understanding seagrass-microbial interactions could allow us to manipulate the seagrass microbiome in order to increase restoration success, given the strong effect the microbiome can have on sediment biogeochemical processes. For example, the bacterium *Ca.* Thiodiazotropha oxidizes sulfides in sediments, which can prevent sulfide intrusion, a driver that is known to hinder seagrass recolonization (Fraser and Kendrick, 2017). These bacteria are present in lucinid clam gills (van der Heide et al., 2012) but have also been found growing directly on the roots of numerous different seagrass species and may alleviate sulfide stress (Martin et al., 2020b). Fundamental research is required to further understand the nature of similar seagrass-microbe interactions in a natural context, before potentially beneficial bacteria (like *Ca.* Thiodiazotropha) are identified and incorporated into restoration plans.

Lastly, the current consensus in seagrass restoration is to arrange transplanted seeds, fragments or cores spaced apart to reduce competition, allowing for increased growth and survival (Halpern et al., 2007). However, this negates the benefits of self-facilitation (van der Heide et al., 2007). Saltmarsh restoration experiments carried out in the Western and Eastern Atlantic found that planting saltmarsh propagules in close proximity increased yields by 107% on average compared to dispersed planting (Silliman et al., 2015). Facilitation can also occur between seagrass species. Compressed succession was used in a restoration project in the Florida Keys National Marine Sanctuary, whereby *Halodule wrightii*, a fast-growing, opportunistic species was used to facilitate the recovery of *Thalassia testudinum*, a slow-growing, climax species by promoting more suitable conditions and reducing additional erosion (Fonseca et al., 2000; Kenworthy et al., 2018). While long-term monitoring in this study has shown that *T. testudinum* recolonization was still incomplete at 7 years (Furman et al., 2019), Tanner and Theil (2019) have found both *Zostera* and *Posidonia* seagrasses naturally recruiting within patches of restored *Amphibolis*.

These positive interactions could be especially important for species that are not abundant seed producers, and should be carefully considered to not only increase restoration success, but also potentially reduce donor meadow impact through making the best use of the plants harvested.

Community Involvement

A longstanding limitation in seagrass restoration is the high labor costs associated with collection of restoration material and deployment of transplant units. This cost can be greatly reduced by engaging "citizen scientists" or volunteers. Community involvement in seagrass conservation is not new, with long term community-based monitoring programs in Queensland (McKenzie et al., 2000) and Western Australia (McKenzie et al., 2017). Well-established volunteer-based programs are often associated with assigning simple, realistic, achievable and locally appropriate tasks (Danielsen et al., 2005), while keeping volunteers and the wider community up to date on the progress or results of the program (Sharpe and Conrad, 2006). These same principles can be applied to seagrass restoration.

A few restoration trials in Australia and New Zealand have utilized community volunteers, such as the collection of *Posidonia* shoots detached after storms for transplantation[3], community planting days on Kangaroo Island (Tanner et al., 2014), engaging recreational fishers in broadcasting seagrass seeds (Seeds for Snapper)[4], collection of *Z. muelleri* spathes for seed-based restoration in partnership with Indigenous sea rangers (Gidarjil Development Corporation) in the Port of Gladstone (Central Queensland University, 2020), and participation in seagrass transplantation trials in Whangarei and Porirua Harbors, New Zealand (F.E. Matheson, NIWA, pers. comm.). These were done in consultation with restoration ecologists to ensure appropriate methods were deployed. Involving community members in restoration and subsequent monitoring of restoration success not only raises awareness but creates a sense of ownership and encourages volunteers to return and donate more of their time (Tanner et al., 2014). Volunteers are a valuable resource for seagrass restoration, and there is an opportunity to engage with growing public awareness surrounding marine conservation and willingness to participate in citizen science to supplement current restoration efforts (Martin et al., 2016).

Working in Partnership With Traditional Owners

Indigenous cultures have been keen observers and active managers of their natural environment for thousands of years, and have long-held cultural and traditional responsibilities to protect and manage their land and sea country. They can provide valuable insights, observations, and interpretations relating to the state of the biological, physical, and spiritual environments (Ens et al., 2015). The Aboriginal and Torres Strait Islander peoples in Australia are important landowners and managers of coastal land and sea Country through native title bodies, cultural and natural resource management organizations, and other corporations (McLeod et al., 2018). In New Zealand, the Treaty of Waitangi (Te Tiriti O Waitangi) underpins the Crown-Māori relationship and Treaty settlements are enabling Māori to be increasingly involved in resource management as owners, managers or co-managers of strategic environmental assets.

Integration of western science and Traditional Ecological Knowledge (TEK) through collaborations is likely to provide improved outcomes for restoration activities, as well as improved custodianship of the environment by all stakeholders into the future (Aronson et al., 2020). In Australia, national guidelines for engagement of Traditional Owners in research exist (see AIATSIS, 2012) and workshops at the Australian Marine Science Association annual conferences have been key to establishing protocols for collaborations on sea country (e.g., Hedge and Bessen, 2019), and protocols/strategies are being developed to establish collaborative and respectful partnerships for sea country research, conservation, restoration, and monitoring. In New Zealand, it is recommended that restoration initiatives be grounded in tikanga Māori and Māori values and perspectives, and be co-designed with Māori to ensure benefit and utility to Māori (Williams et al., 2018).

TEK is useful in countering perceptions around "shifting baselines," especially in "pristine" conservation areas (Jardine, 2019), and observations and whole system approaches to ecosystem health and climate change (e.g., Mantyka-Pringle et al., 2017; Nursey-Bray et al., 2019). However, the needs and aspirations of Traditional Owners should be kept at the forefront. It is important to consider how Traditional Owners and the local community are likely to benefit from a collaborative project. Facilitating time on Country and aligning research questions with the land and sea management aspirations of the local Indigenous community can be developed through employment and training opportunities. This requires extensive pre-planning and sufficient time to consult with Traditional Owners prior to a project commencing. An Australian example from Western Australia's Dampier Peninsula includes a collaboration between Western Scientists and the Bardi Jawi Indigenous rangers who have joint objectives to incorporate indigenous knowledge into the management of over 250 km of Kimberley coastline (Depczynski et al., 2019).

A new program for assisting seagrass recovery in Shark Bay is also a collaborative effort between western scientists and newly trained Malgana Indigenous rangers. Such collaborations with Indigenous sea ranger programs provide a great model to facilitate restoration and assist the existing traditional custodianship of Sea Country into the future. New Zealand Māori have been important initiators, partners and/or supporters of seagrass restoration projects in Whangarei Harbor (i.e., Whangarei Harbor kaitiaki roopu, Reed et al., 2004), Bay of Islands (i.e., Ngāti Kuta-Patukeha, Matheson et al., 2010), and Porirua Harbor (i.e., Ngāti Toa, Matheson and Wadhwa, 2012).

CONCLUSION

There is a growing number of seagrass restoration success stories and an increasing number of researchers and practitioners in seagrass restoration in Australia and New Zealand. However, there are still many knowledge gaps that need to be filled, especially surrounding species-specific studies and the lack of knowledge for tropical Australian species to avoid generalization of restoration techniques. This is further exacerbated by a lack of funding, as restoration is often perceived as too expensive and wrought with failures. We have now reached a point where ecologically meaningful large-scale seagrass restoration is possible given enough scientific, community, and political

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[3] https://www.operationposidonia.com/

[4] https://ozfish.org.au/seeds-for-snapper/

support. Restoration success rates are improving globally, and while future failures cannot be ruled out, they will offer guidance for improving subsequent attempts. Seagrass meadows continue to be threatened by anthropogenic impacts, so it is imperative that we attempt to stem the decline and work toward restoring degraded habitats. A lot of the hard work has now occurred, and we should now build upon our collective knowledge, engage with emerging tools, technology, and techniques, and maintain and build our research effort into seagrass restoration in Australia and New Zealand.

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All authors contributed to the writing of the manuscript and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00617/full#supplementary-material

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Facilitating Better Outcomes: How Positive Species Interactions Can Improve Oyster Reef Restoration

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Over 85% of the world's oyster reefs have been lost in the past two centuries, triggering a global effort to restore shellfish reef ecosystems and the ecosystem services they provide. While there has been considerable success in re-establishing oyster reefs, many challenges remain. These include: high incidence of failed restoration, high cost of restoration per unit area, and increasing stress from climate change. In order to leverage our past successes and progress the field, we must increase restoration efficiencies that not only reduce cost per unit area, but also increase the resilience of restored ecosystems. To help address this need, we qualitatively review the literature associated with the structure and function of oyster reef ecosystems to identify key positive species interactions (i.e., those species interactions where at least one partner benefits and no partners are harmed). We classified positive inter- and intraspecific interactions between oysters and organisms associated with oyster ecosystems into the following seven functional categories: (1) physical reef creation, (2) positive density dependence, (3) refugia from physical stress, (4) refugia from biological stress, (5) biodiversity enhancement, (6) settlement improvement, and (7) long-distance facilitation. We discuss each category of positive interaction and how restoration practitioners can use knowledge of such processes to enhance restoration success. We propose that systematic incorporation of positive species interactions into restoration practice will both enhance ecological services provided by restored reefs and increase restoration success.

Keywords: mutualism, facilitation, restoration, oyster reef, ecosystem services, systematic review, positive interactions

INTRODUCTION

Ecologists have long emphasized the importance of negative interactions (i.e., competition, predation, parasitism), physical disturbances, and physiological stress in driving species diversity and shaping ecological communities (Darwin, 1859; Connell, 1956; Paine, 1965). However, over the past three decades, research has shown that positive interactions (i.e., those where neither species is harmed and at least one species benefits) are equally important in shaping population and community-level structure (Bertness and Leonard, 1997; Stachowicz, 2001; Bruno et al., 2003; Silliman et al., 2011). Positive interactions occur when one organism makes the local environment more favorable for another organism. This can happen directly, such as when canopy-forming macroalgae shade the intertidal zone and reduce desiccation stress for other organisms (Thomsen et al., 2018). Alternatively it can happen indirectly, such as when predators consume grazers, indirectly facilitating plants by reducing stress from herbivory (Stachowicz, 2001; Bruno et al., 2003).

Research on positive interactions has established a theoretical framework that predicts the relative importance of positive interactions in space and time (Bertness and Callaway, 1994). The Stress Gradient Hypothesis (SGH) predicts that facilitation among neighboring individuals is more likely under high physical or biological stress. Contrastingly, according to the SGH, negative interactions such as competition or predation prevail under low stress conditions (Bertness and Callaway, 1994; Bertness and Leonard, 1997; Bruno et al., 2003; He et al., 2013). This idea has been tested over 1,000 times across marine, terrestrial and aquatic systems both qualitatively and quantitatively (He et al., 2013). The SGH is now considered a foundational theory in ecology that generally predicts when and where positive species interactions will drive species diversity patterns and ranges (Stachowicz, 2001; Silliman et al., 2013; Silliman and He, 2018). In addition to its contribution to ecological theory, the SGH offers an important theoretical framework when considering how to restore species or ecosystems and their functions (Halpern et al., 2007).

In the field of ecological restoration, practitioners aim to reassemble a species, population, community, or ecosystem and to re-establish the ecological interactions that occurred preceding degradation (Jordan et al., 1987). Since degraded systems in need of repair are often under high stress, the SGH suggests positive species interactions should be important in helping them recover, and thus harnessing these interactions could improve restoration outcomes. However, the foundational paradigm in coastal and marine restoration has been that competition limits an organism's regrowth. Accordingly, restoration projects have focused on minimizing negative interactions, while largely ignoring potential positive ones (Silliman et al., 2015; Renzi et al., 2019; Valdez et al., 2020). However, this "foundational" principle stating that negative interactions are paramount in restoration came directly from forestry science without first testing it in marine systems (Halpern et al., 2007). In contrast to forest restoration, recent work in salt marshes testing this paradigm in a restoration context found that the lack of positive species interactions incorporated into planting designs dramatically limited restoration success. Researchers found that outplants positioned next to, rather than further apart from other outplants—as called for by the current paradigm—increased restoration success by >100% with no extra cost (Silliman et al., 2015). Planting marsh grasses close to each other encouraged intraspecific facilitation whereby grass clumps were better able to resist wave erosion and low oxygen stress than individual outplants. Restoring other naturally occurring positive interactions may bring restored ecosystem functional processes closer to those of the target ecosystem, but for many coastal systems this has yet to be tested.

Several recent reviews have stressed the importance of incorporating positive species interactions into restoration because of their potential to increase project success. These reviews cover aquatic systems in general (Halpern et al., 2007) as well as mangrove (Gedan and Silliman, 2009; Renzi et al., 2019), coral (Shaver and Silliman, 2017), tidal marsh (Derksen-Hooijberg et al., 2018; Renzi et al., 2019), seagrass (Valdez et al., 2020), and terrestrial (Gómez-Aparicio et al., 2004; Gómez-Aparicio, 2009) systems. However, similar syntheses for oyster reef ecosystems are lacking.

Oyster reefs were once ubiquitous in many shallow water marine environments, replacing corals as the dominant reef forming ecosystem in higher latitude environments. However, over the past two centuries, more than 85% of oyster reefs around the world have been lost (Beck et al., 2011). In response, there has been a worldwide effort to restore shellfish reef ecosystems and the ecosystem services they provide, including water filtration, nutrient cycling, fish production, and shoreline protection (Fitzsimons et al., 2019; McLeod et al., 2019; Pogoda et al., 2019). Historically, restoration has focused on oyster population enhancement as a means to restore oyster reefs (Brumbaugh and Coen, 2009; Schulte et al., 2009), likely because oyster reefs were traditionally managed as a fishery rather than as an ecosystem (Coen and Luckenbach, 2000; Luckenbach et al., 2005). The field of oyster restoration primarily developed in the United States over the past 20 years (Luckenbach et al., 1999; Schrack et al., 2012) but has recently grown to encompass non-North American oyster species [e.g., *Saccostrea glomerata*, *Ostrea edulis*, *Ostrea angasi*, *Magallana (Crassostrea) sikamea*, *Magallana (Crassostrea) hongkongensis*], mussel species (e.g., *Mytilus galloprovincialis* and *Perna canaliculus*), and new geographic regions such as Australia, New Zealand, Europe, and Asia (Fitzsimons et al., 2019, 2020).

In this study, we systematically reviewed the scientific literature associated with the structure and function of oyster reef ecosystems to define and identify studies on positive species interactions that support key ecological processes. To do this, we took a whole system approach and examined both the benefits provided by other species to oysters and the benefits provided by oysters to other species, given that oyster reef restoration is not only undertaken to rejuvenate oyster populations themselves, but also for associated species that depend on oyster reefs. The ability of oysters to support other organisms is increasingly a primary reason why oyster reefs are restored, as oyster and associated species support ecosystem functions such as water filtration, fish production, and hard reef structure (Coen et al., 2007; Grabowski and Peterson, 2007; Grabowski et al., 2012; Kellogg et al., 2014; Zu Ermgassen et al., 2016). We define oyster ecosystems to include both structural forms of the ecosystem (i.e., largely two-dimensional oyster beds and higher profile reefs) and include all ecosystem-forming species described in the literature. The aim of this study was to synthesize any positive species interactions that have previously been identified in the oyster restoration literature to provide an overview of relevant positive interactions

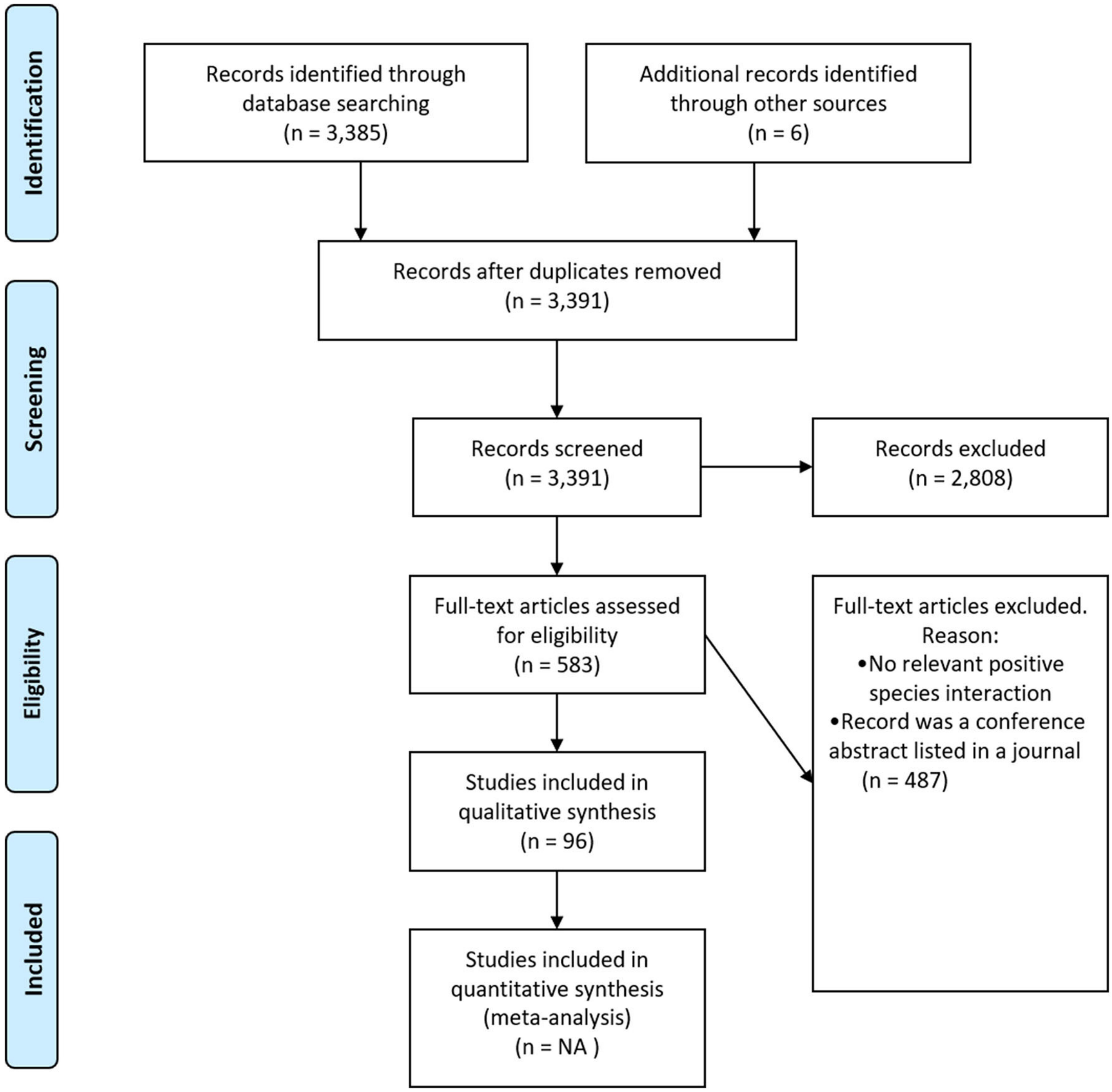

FIGURE 1 | Systematic review flow diagram. The PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) flow diagram for the systematic review detailing the database searches, the number of abstracts screened, and the full texts retrieved.

that could be useful to restoration practitioners. However, we do not rank the importance of these interactions, as each restoration project will have situational drivers that could result in different positive interactions being more or less important. We hope this systematic review will advance understanding of positive interactions and serve as a tool to improve ecosystem function outcomes of restoration projects and the management of wild oyster ecosystems.

METHODS

We reviewed the scientific literature, following guidelines for preferred reporting items for systematic reviews and meta-analyses (PRISMA; **Figure 1**), by searching Web of Science and SCOPUS using the search string: TOPIC = [(oyster* OR "oyster reef*" "OR" "oyster bed*") AND (restor* OR creat* OR rehabilit* OR reconstruct* OR recover* OR benefit* OR construct* OR "ecosystem service*" "OR" "ecosystem function*" OR facilitat*)]. Timespan: All Years (1945–2019); Indexes: SCI-EXPANDED, SSCI, A&HCI, ESCI, which returned 3,385 unique articles. We reviewed these articles at the title-, keyword-, and abstract-level to determine whether the article might involve a species interaction involving oysters. We only included studies that were field-, lab-, or modeling-based; reviews and meta-analyses were excluded (**Figure 1**—PRISMA flow diagram).

Following the initial review, 583 articles remained, and these articles were screened at the full-text level (**Figure 1**—PRISMA flow diagram). Articles were included in the final database if:

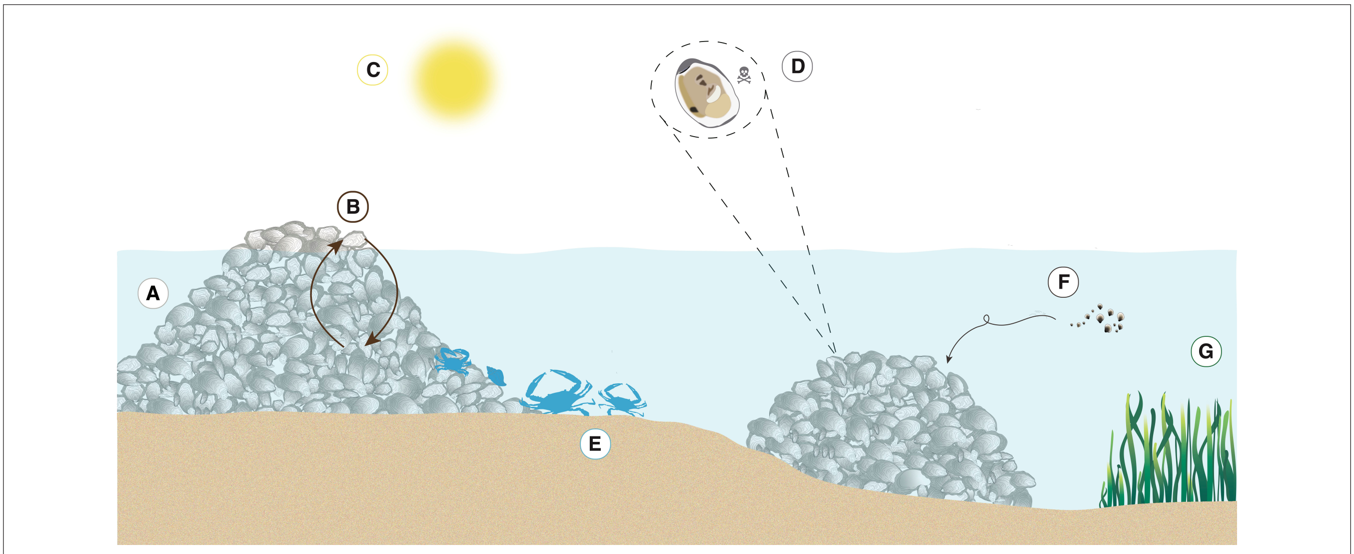

FIGURE 2 | Schematic depiction of the seven categories of positive interactions on oyster reefs: **(A)** physical reef creation, **(B)** positive density dependence, **(C)** refugia from abiotic stress, **(D)** refugia from biotic stress, **(E)** biodiversity enhancement, **(F)** settlement improvement, and **(G)** long-distance facilitation.

they examined a positive species interaction where oysters were involved directly or indirectly [e.g., oysters acting as refugia for other species (direct)/fish facilitate oysters by consuming shell crushing crabs (indirect)]. From each of those articles, we extracted: (1) the species of oyster involved; (2) where the study was conducted; (3) whether the research was a lab, field, or modeling study; (4) whether the study was intertidal or subtidal; (5) the life stages of the species involved; (6) whether the species involved were native or non-native; (7) what metric was used to assess species' benefit; (8) whether the interaction was mutually beneficial; (9) whether the authors found the relationship to be context-dependent (i.e., a positive relationship in some contexts and not in others); and (10) a short description of the interaction. An article could have multiple observations of positive interactions, if for example a positive interaction was studied in multiple experimental systems (i.e., a laboratory and field study) or if there were multiple positive interactions within a study. Each article was screened by at least two different authors for consistency.

After creating the database, we qualitatively screened the observations into seven categories of positive interactions (**Figure 2**, **Table 1**: Interaction category): (1) physical reef creation, (2) positive density dependence, (3) refugia from physical stress, (4) refugia from biological stress, (5) biodiversity enhancement, (6) settlement improvement, and (7) long-distance facilitation. For three of the categories (settlement improvement, refugia from physical stress, and refugia from biological stress), we also sub-categorized the positive interaction mechanism to capture additional information (**Table 1**: Interaction sub-category). "Settlement improvement" was broken down into two further sub-categories: substrate type and settlement cues. "Refugia from physical stress" was sub-categorized into five specific types of physical stress: thermal, flow, sediment, water chemistry, and water stress; and "refugia from biological stress" was broken down to trophic, competition, disease and nutrient stress. We also identified ten benefit outcomes from the partnerships (**Table 1**): (i) enhanced survival, (ii) enhanced growth, (iii) enhanced abundance of a single species or of many species (i.e., biodiversity), (iv) increased settlement, (v) improved filtration, (vi) reduced stress response, (vii) enhanced reproduction, (viii) reduced disease prevalence, (ix) improved reef structural integrity and (x) enhanced foraging. For a small number of studies, it was difficult to define a single positive interaction mechanism. For example, Aquino-Thomas and Proffitt (2014) found that red mangrove prop roots provided a good settlement surface for oysters, as prop roots provided a refuge from sedimentation and wave exposure during storms, improving survival of oysters. From this study three mechanisms were identified underlying two positive interactions: (1) "settlement improvement" by mangrove prop roots resulting in enhanced settlement; and (2) "refugia from physical stress" due to (a) refugia from sedimentation and (b) refugia from water flow both resulting in enhanced survival. As a result, the number of observations of positive interactions and mechanisms underlying these positive interactions may be greater than the total number of studies included in our review.

RESULTS AND DISCUSSION

Out of the 3,391 studies initially identified, we found 96 studies that reported positive interactions associated with oyster reef ecosystems, a result that is consistent with many similar syntheses on positive interactions from marsh, mangrove, kelp, and coral reef systems showing that positive interactions are relatively understudied (Halpern et al., 2007; Gedan and Silliman, 2009; Shaver and Silliman, 2017; Renzi et al., 2019; Valdez et al., 2020). Through these studies, we identified 199 observations of positive intra- and interspecific interactions between pairs

TABLE 1 | Descriptions of positive interaction mechanisms with outcomes and examples.

Interaction category	#	Interaction sub-category	#	Description	Enhanced survival	Enhanced growth	Enhanced abundance/ biodiversity	Enhanced settlement	Improved filtration	Reduced stress response	Enhanced reproduction	Reduced disease prevalence	Improved structural integrity	Enhanced foraging	Example	References
Refugia from physical stress	52	Refugia from thermal stress	8	A species is positively impacted by the provision of refugia from heat stress by another species	2		2			4					Vertically oriented oysters provided microclimates that facilitated cooler invertebrate body temperatures; associated organisms were less stressed when cool (heart rate and osmology)	McAfee et al., 2018
		Refugia from sediment stress	14	A species is positively impacted by the provision of refugia from sediment stress by another species	5	3	3	3							Increased foraging movement of mud crabs reduces sedimentation	Kimbro et al., 2014
		Refugia from hydrodynamic stress	13	A species is positively impacted by the provision of refugia from hydrodynamic stress (water flow and wave energy) by another species	4	2	3	4							Increased oyster shell reef height increased water flow over reefs and decreased sedimentation; growth of oysters increased with reef height; mechanism is that flow increases feeding efficiency and food availability	Lenihan, 1999
		Refugia from water chemistry stress	10	A species is positively impacted by the provision of refugia from water chemistry related stress (ocean pH and anoxia) by another species	2	6			2						Presence of ulva algae increased growth in juvenile oysters, particularly under elevated ocean acidification scenarios	Young and Gobler, 2018
		Refugia from water stress	7	A species is positively impacted by the provision of refugia from water stress (desiccation or too much water) by another species	2	3		1		1					Vertically oriented oysters provided microclimates that reduced desiccation stress	McAfee et al., 2018
Refugia from biotic stressors	52	Refugia from trophic stress	38	A species is positively impacted through the feeding activities of another species	29	4	1	2						2	Mud crab predators (Oyster toadfish and Blue crabs) limited mud crab predation on oyster recruits due to non-consumptive effects i.e., fear of being predated on resulting, in improved settlement and survival of eastern oysters	Kimbro et al., 2014

(Continued)

TABLE 1 | Continued

Interaction category	#	Interaction sub-category	#	Description	Enhanced survival	Enhanced growth	Enhanced abundance/ biodiversity	Enhanced settlement	Improved filtration	Reduced stress response	Enhanced reproduction	Reduced disease prevalence	Improved structural integrity	Enhanced foraging	Example	References
		Refugia from competitive stress	10	A species is positively impacted through the activity of another species that reduces competition on the initial species	5	3	1	1							The kelp *Ecklonia radiata* on artificial reefs increased oyster density ∼3-fold. Appeared to facilitate oysters through its capacity to reduce benthic light and thus suppress competition from turfing algae	Shelamoff et al., 2019
		Refugia from disease	2	A species is positively impacted through the activity of another species that reduces disease acting on the initial species								2			Presence of oyster in co-culture with seagrass resulted in reduced infection by the pathogen that causes eelgrass wasting disease (EWD); mechanism is that oysters filter the pathogen out of the water column reducing the abundance of the pathogen	Groner et al., 2018
		Refugia from nutrient stress	2	A species is positively impacted through the activity of another species that alters nutrient supply to the initial species		1	1								Medium (75 m^2) and low (15 m^2) *C. virginica* densities promoted higher seagrass growth, however this was context specific as high (150 m^2) densities did not promote growth. Increased growth likely due to positive relationship found between oyster density and porewater NH_4 and PO_4	Booth and Heck, 2009
Settlement	41	Provision of settlement cues	4	A species is positively influenced by the provision of a settlement cue by intra/interspecific taxa	1			3							Found subtidal oyster reef soundscapes facilitated the recruitment of oyster larvae	Lillis et al., 2015
		Provision of settlement substrate	37	A species is positively influenced by the provision or improvement of a settlement substrate by intra/interspecific taxa	5		2	29							Density of settling oyster larvae increased with age of biofilm on substrate with greatest larval set when biofilm had developed for 4 weeks and had the greatest biomass	Campbell et al., 2011

(Continued)

TABLE 1 | Continued

Interaction category	#	Interaction sub-category	#	Description	Enhanced survival	Enhanced growth	Enhanced abundance/ biodiversity	Enhanced settlement	Improved filtration	Reduced stress response	Enhanced reproduction	Reduced disease prevalence	Improved structural integrity	Enhanced foraging	Example	References
Physical reef creation	30	-	30	Increase species abundance and diversity by increasing the numbers and types of habitats available for colonization	1	2	25						2		Macrofaunal abundance was 20 times higher on reef than in bare mud; abundance increased by a factor of 5 compared to rock; reefs on rocks had 3× higher macrofaunal abundance than reefs on mud. For 1 m^2 of colonized substrate, the reef added 3.87 m^2 ($SD = 0.94$) of surface available for epibenthic species on soft sediment and 3.97 m^2 ($SD = 1.89$) on rock.	Lejart and Hily, 2011
Long-distance facilitation	13	-	13	A species is positively influenced by a species that is beyond the direct neighborhood of the original species i.e., spatially separated by 10's to 1,000's of meters			13								Seagrass in close proximity to oyster reefs facilitated greater abundance of Yellowfin bream and Moses perch in comparison to oyster reefs without seagrass in close proximity	Gilby et al., 2019
Positive density dependence	6	-	6	A species is positively affected by the increased density of the same species	1	1		2			2				Abundance of brooded larvae were significantly higher in oysters which were <1.5 m away from their nearest neighboring oyster	Guy et al., 2019
Biodiversity	5	-	5	A species is positively influenced by altered species, genetic, functional, or ecological diversity	1	1			3						Greater allelic diversity resulted in greater survival, perhaps as a result of greater trait diversity this was however context dependent as survival not so evident under high predation	Hughes et al., 2019

The number of interaction observations for each category/sub-category are shown in each cell and additionally color coded with a blue to black color ramp to show low (cooler colors i.e., blues and greens) through to high (warmer colors i.e., oranges, reds and black) numbers of identified interactions.

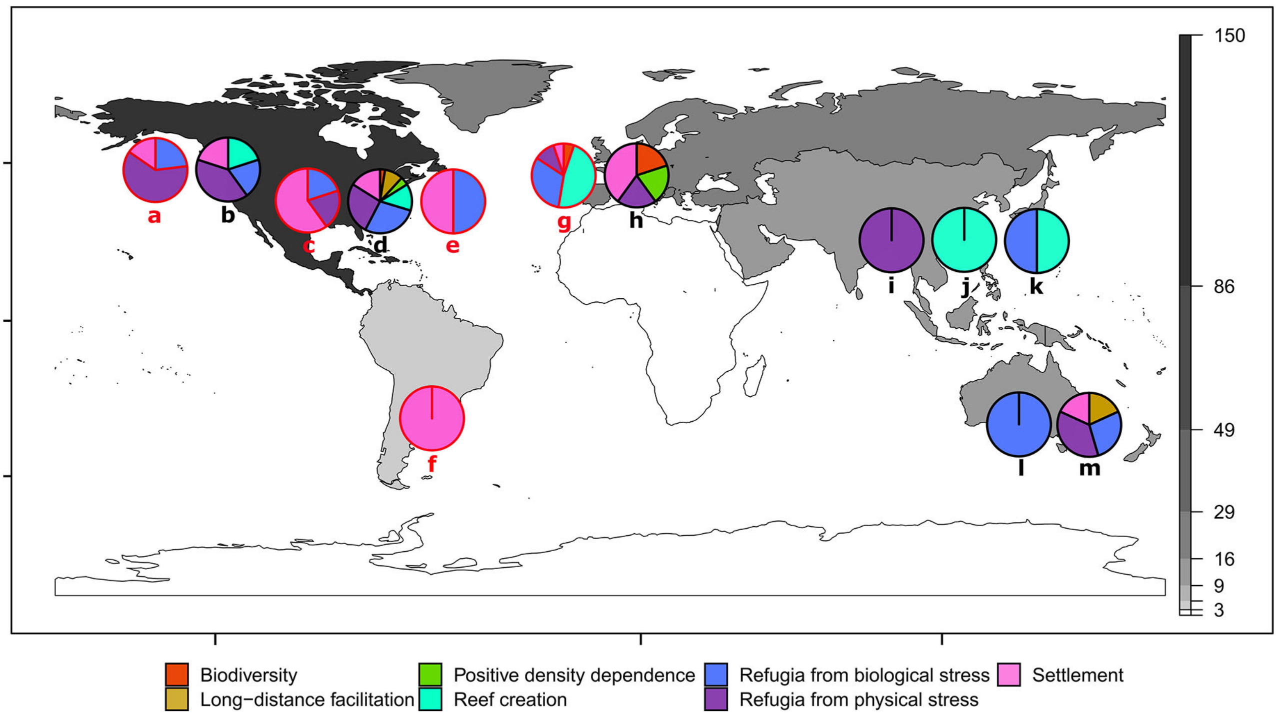

FIGURE 3 | Positive interactions for shellfish restoration summarized for 10 ecosystem-forming oyster species. Continents are color coded by the number of positive species interactions synthesized from the review (e.g., black = 86–150 observations; and white = zero observations). Lower case letters indicate oyster species. Pie charts and letters in red (a, c, e, f, g) show non-native oyster taxa for that region. West coast of North America: **(a)** *Crassostrea (Magallana) gigas*, Pacific oyster–non-native (13 obs.); **(b)** *O. lurida*, Olympia oyster—native (10 obs.). East coast of North America: **(c)** *Crassostrea (Magallana) ariakensis*, Suminoe oyster–non-native (5 obs.); **(d)** *Crassostrea virginica*, Eastern oyster–native (118 obs.); **(e)** *C. gigas*, Pacific oyster–non-native (4 obs.). South America: **(f)** *C. gigas*, Pacific oyster–non-native (3 obs.). Europe: **(g)** *C. gigas*, Pacific oyster–non-native (19 obs.); **(h)** *Ostrea edulis*, European flat oyster (5 obs.). Asia: **(i)** *Saccostrea culccullata*, Natal oyster–native (6 obs.), **(j)** *Crassostrea (Magallana) angulata*, Portugeuse oyster–native (2 obs.); **(k)** *C. gigas*, Pacific oyster–native (2 obs.). Australasia and Oceania: **(l)** *O. angasi,* Australian flat oyster–native (1 obs.); **(m)** *Saccostrea glomerata*, Sydney rock oyster–native (11 obs.).

of organisms. The effects of these positive species interactions included: enhanced survival and growth of species, increased abundance of species, promotion of settlement, improved water filtration, reduced stress to organisms, enhanced reproduction, reduced disease prevalence, improved reef structural integrity, and enhanced foraging.

Positive interactions were reported for oyster ecosystems in most geographic regions, with the notable exception of Africa, which had no relevant studies (**Figure 3**). There was a geographic concentration in the dataset, with the largest number of observations from North America (72%) and the fewest from South America (1%), excluding Africa (0%). Even when split into sub-regions (North Atlantic, Atlantic Bight, Chesapeake, Gulf of Mexico and West Coast), four of the five North American sub-regions still had more observations than any other continent. The Atlantic Bight region of the east coast of North America had the most observations (44 obs. from North Carolina, South Carolina, Georgia and Atlantic coast of Florida) followed by the Chesapeake Bay (32 obs. from Virginia and Maryland). This geographic bias may be in part because much of the research comes from "developed economies" with greater amounts of government funding available for conservation/restoration research and practice, in comparison to low/lower-middle income economies with fewer resources (James, 1999; Waldron et al., 2013). The geographic distribution of our results may also be skewed because we only used English language articles, which may underrepresent studies from non-English speaking regions that are published in native languages. Given the predominance of non-English languages in the regions outside of North America and Australia (i.e., South America, Europe, Asia, and Africa), and the bias of online databases to English language articles (Gates, 2002), the potential likelihood of missing articles is high. Encompassing non-English language studies, consulting with experts from all regions and including information on oyster restoration from the gray literature (e.g., monitoring and technical reports) would likely further improve our understanding of species interactions globally.

Broad Patterns in Positive Interactions for Oyster Reef Restoration

The oyster species with the greatest number of positive interactions reported was *Crassostrea virginica* (**Figure 3d**), which is likely due to the proportionally greater research effort for this species (56% of studies in the review). Comparatively, the species with the next greatest diversity of positive interactions and research effort was *Magallena (Crossostrea) gigas*–the Pacific oyster, which accounted for 25% of studies (**Figures 3a,e–g**). Most positive interactions observed for *M. gigas* were outside of its native range (e.g., North America and Europe). Our review shows that *M. gigas,* like other invasive foundation species (Ramus et al., 2017), can generate positive interactions outside of its native range, such as providing native bivalves in Europe (e.g., *O. edulis* and *Mytilus edulis)* with settlement substrate (Christianen et al., 2018) and refuge from predation (Markert et al., 2009). Positive interactions occur in oyster ecosystems globally and are evident for many reef-building oyster species, irrespective of whether the oyster is native or introduced (**Figure 3**).

Seventy-two percent (69 studies) of studies were undertaken directly in the field, as opposed to in the laboratory or modeled (**Figure 4A**). Out of the studies where tidal zonation was defined, 70% of observations were from intertidal studies (**Figure 4B**). This could support the ecological theory that positive interactions should be more prevalent under stressful physical conditions, such as in the intertidal where there are extreme daily temperature, light, and water level fluctuations (i.e., the stress gradient hypothesis SGH) (Bertness and Callaway, 1994; Stachowicz, 2001). Alternatively, it may simply be that intertidal shellfish systems are more accessible and more easily manipulated than subtidal systems, resulting in a greater number of intertidal studies. However, if positive interactions are indeed more important in the intertidal, which is supported by theory, incorporating positive interactions in the intertidal may be more important when restoring intertidal shellfish reefs than in the subtidal.

While many of the studies did not define the life-stage of the organism being facilitated, a large proportion of the observations that did identify the life-stage were sub-adults (i.e., larvae or recruits; **Figure 4C**). This could reflect a study bias toward early life stages, however it may also be that species early in their ontogeny will benefit more from positive interactions, as the benefits to early life stages are thought to diminish as juveniles become more hardy and resistant to physical stress, competition, or predation (Callaway and Walker, 1997; Stachowicz, 2001). Given that restoration projects try to promote target species settlement, an improved understanding of how positive species interactions affect early ontogenetic stages to promote the settlement of both the primary ecosystem engineers (i.e., oysters), and associated species will likely enhance the overall success of reef development.

Our review only found 35 studies that identified mutualistic relationships in oyster reef ecosystems (+,+; **Figure 4D**), which is likely because the majority of the studies reviewed only defined the effect of an interaction on one species. However, our review demonstrates that oysters facilitate many taxonomic groups, and in return are also facilitated by these groups (**Figure 5**). This under-identification of mutualisms could result from studies often focusing on understanding a single target species as opposed to understanding a two-way interaction between species. Alternatively, this finding could result from varied interaction outcomes at different life-stages, which can be difficult to observe in a single study. Further, if facilitations occur over spatial or temporal scales outside the range of an individual study, these mutualistic relationships could be missed and may only become apparent through synthesizing findings across multiple studies, as done here. Our results suggest that mutualistic relationships may be more prevalent in oyster ecosystems than previously accounted for and future research may uncover a greater diversity of mechanisms underpinning these mutualisms. Below we discuss in detail the importance of positive species interactions in oyster reef restoration using the seven categories defined in our study.

Intraspecific Facilitation: Oysters Helping Oysters

Our review found strong evidence that oysters facilitate the presence of other oysters (**Figure 5**), primarily through providing settlement cues (Tamburri et al., 2007, 2008), providing settlement substrate (Tamburri et al., 2008; Whitman and Reidenbach, 2012), and other positive density-dependent effects (Guy et al., 2019). Oysters, like other marine benthic invertebrates, are gregarious settlers. By preferentially settling onto aggregations of adult conspecifics, individuals increase their likelihood of successful fertilization and increase the likelihood that they settle in an area with favorable environmental conditions. Dense aggregations of oysters also perform better: they experience reduced predation pressure and exhibit higher filter-feeding efficiency. These fitness benefits of gregarious living can outweigh the negative effects of competition for limited resources (i.e., light, food, or space). Below we identify examples where positive intraspecific interactions led to improved fecundity and amelioration of external stressors, resulting in enhanced reproductive output, recruitment and survival of oysters (**Figure 6**).

Settlement Substrate

Restoration of degraded oyster reef habitat generally begins with the addition of substrate that serves as a reef base and site for oyster spat attachment. Years of oyster restoration practice has shown that selecting the right substrate is important for oyster recruitment and retention. Practitioners often use conspecific oyster or other bivalve shells as settlement substrate, as they emit chemical cues to attract and induce settlement of oysters and provide high surface complexity that is critical for survival of oyster larvae (Tamburri et al., 2008; Barnes et al., 2010; George et al., 2015). Our review identified 19 studies with 33 observations of positive interactions relating to substrate choice. In the majority of cases, the use of oyster shell material as a restoration substrate resulted in greater oyster settlement (Tamburri et al., 2008; White et al., 2009; Whitman and Reidenbach, 2012), and in fewer cases, enhanced survival of spat (Ruesink, 2007; Barnes et al., 2010) (**Figure 6D**).

Settlement Cues

Gregarious settlement in oysters is induced by settlement cues that enable pelagic larvae to recognize reef habitat and conspecifics, by sight, sound, or smell. Our review identified six studies with 11 observations of positive outcomes from provision of settlement cues (**Figure 6D**). Five of these studies identified positive interactions from conspecific olfactory cues, which

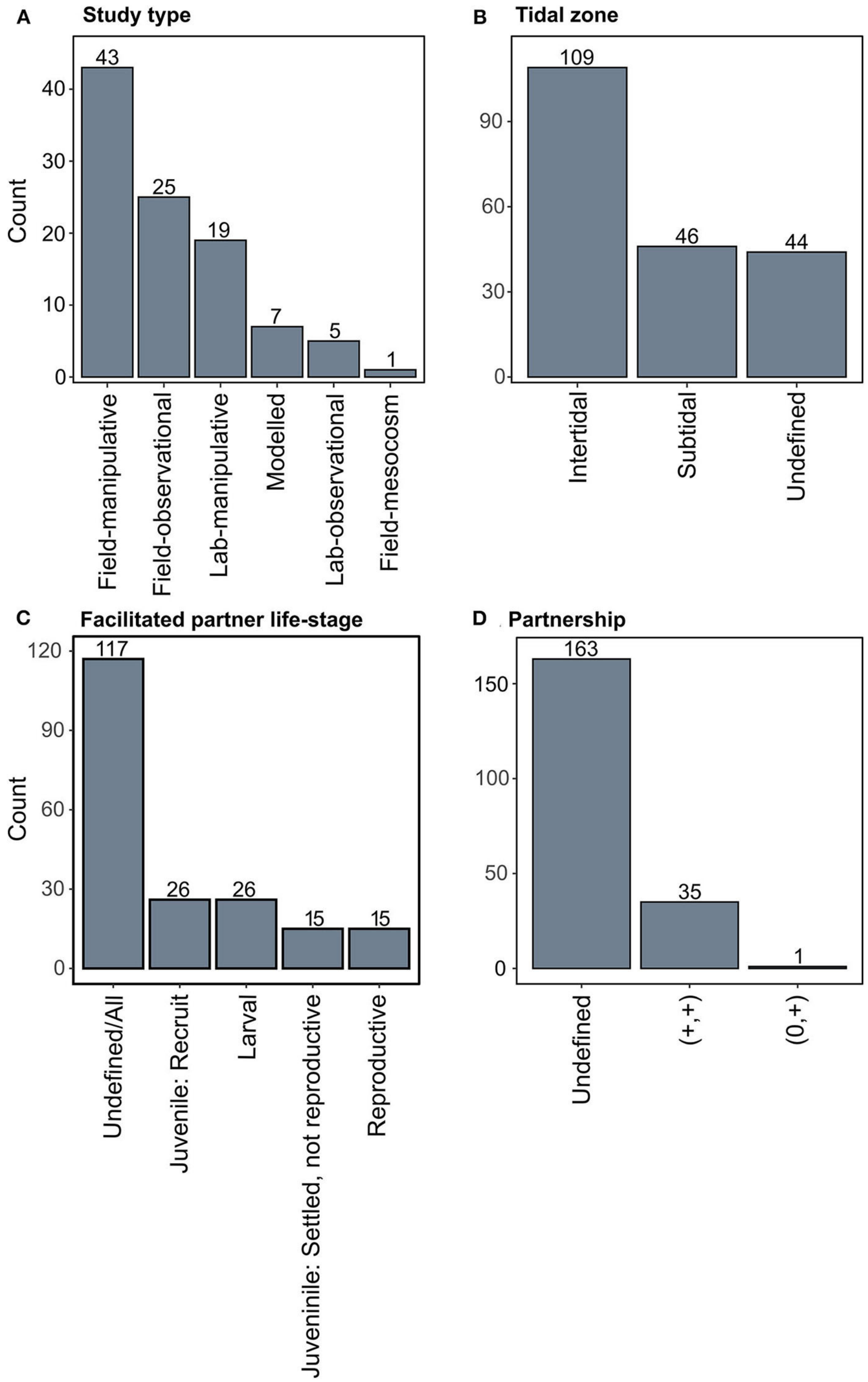

FIGURE 4 | Summary of key parameters for positive interactions from oyster beds and reefs. **(A)** Studies that identified positive interactions summarized by study type, **(B)** the tidal zone where the positive species interaction occurred, **(C)** the life-stage of the facilitated partner, and **(D)** the type of partnership for each species interaction.

enhanced settlement of oyster larvae. For example, Tamburri et al. (2007) showed that oyster larvae were attracted to the scent of conspecific adults. In still-water trials, larvae moved downward and settled after contacting a waterborne, adult chemical cue. For benthic filter feeders, this may seem to be a perilous choice given the potential risk of being cannibalized by adult conspecifics.

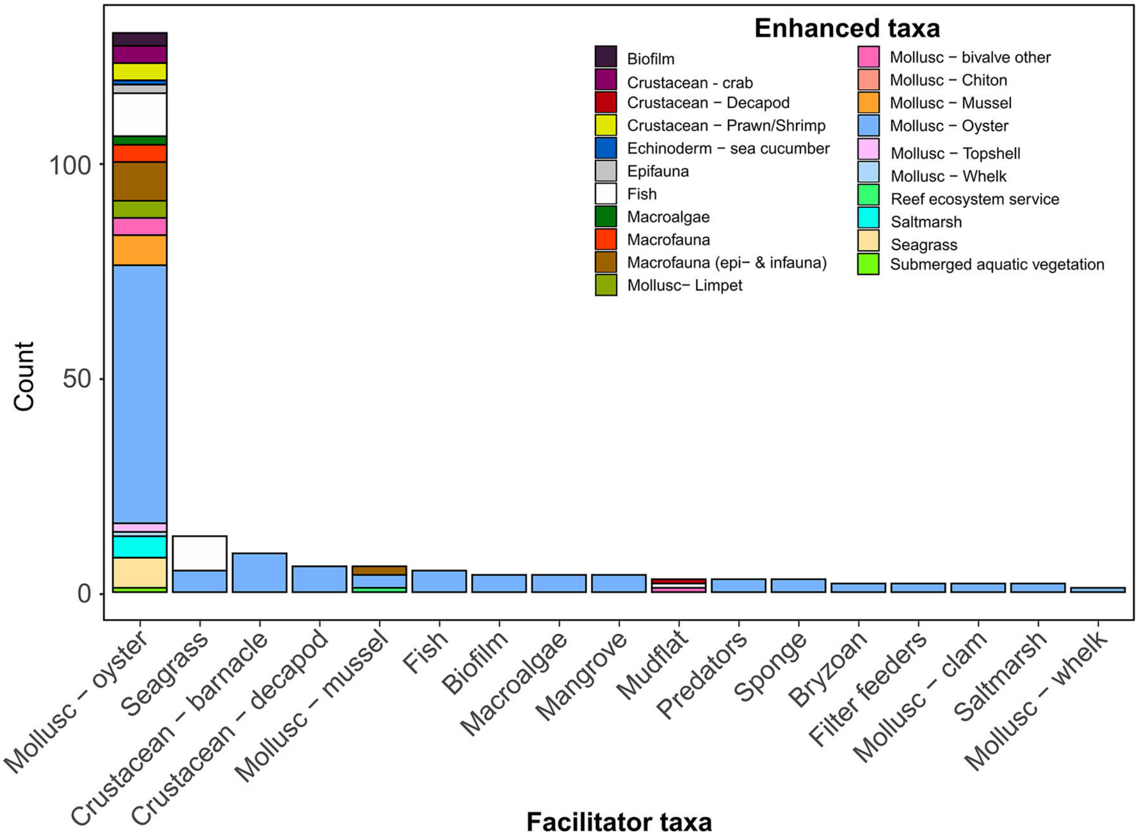

FIGURE 5 | Positive species interactions on oyster reef ecosystems. Taxa on the x-axis facilitate and enhance other taxa identified by the colored fill of the stacked bars (Enhanced taxa), with the number of observations for each facilitator-enhanced taxa pairing (species interaction) on the y-axis. For example, the Mollusc-whelk and Mollusc-Oyster pairing (far right bar) shows one observation where this interaction was reported.

However, for Pacific oysters, ciliary feeding currents were too weak to entrain conspecific larvae and larvae were only ingested when they landed directly on the gape region of a feeding oyster. This gape area only represents a small proportion of the total surface area of a reef, and thus the end result was that larvae responding to adult chemical cues were more likely to settle within hospitable habitat on the reef then be at risk of conspecific predation (Tamburri et al., 2007).

Our review also identified one study that examined the importance of auditory cues, (i.e., oyster reef soundscapes) for oyster settlement (Lillis et al., 2015). Many marine vertebrates (Simpson et al., 2005; Montgomery et al., 2006; Huijbers et al., 2012; Parmentier et al., 2015) and invertebrates (Vermeij et al., 2010; Lillis et al., 2015; Stanley et al., 2015) use sound as a directional cue to navigate toward settlement habitats or away from undesired habitats. Because of this reliance on auditory cues by many marine organisms, degraded soundscapes could hamper the recovery of ecosystems by directly attracting a lower number of propagules from critical foundation species (Rossi et al., 2017), such as coral and oyster larvae (Vermeij et al., 2010; Lillis et al., 2015). However, soundscapes can also play a role in restoring ecosystem function and recovering degraded systems. Lillis et al. (2015) demonstrated the utility of using recordings of oyster reef soundscapes (intermixed conspecific and heterospecific sounds) to attract larvae, induce settlement, and enhance recruitment of *C. virginica*.

Both olfactory and auditory cues from conspecifics are likely important for orientation and habitat selection by oyster larvae at different temporal and spatial scales. For this reason, restoration projects may benefit from manipulating both types of cues at restoration sites. For example, playback of healthy oyster soundscapes at restoration sites may enhance natural settlement of oysters and other reef organisms and facilitate recovery. Additionally, using oyster shell as substrate and seeding the target reef with a small number of adult oysters prior to spatfall, may ensure the presence of chemical conspecific cues important for attracting oyster larvae. Identifying the relative importance of substrate complexity, olfactory cues, and auditory cues for promoting settlement may further optimize restoration success, but more research is needed to determine the relative importance of these factors, as they may not generalize across oyster species.

Positive Density-Dependence

Seeding restoration sites with sufficient densities of adult oysters could improve restoration success in more ways than one. In many of the studies reviewed, we found the presence of

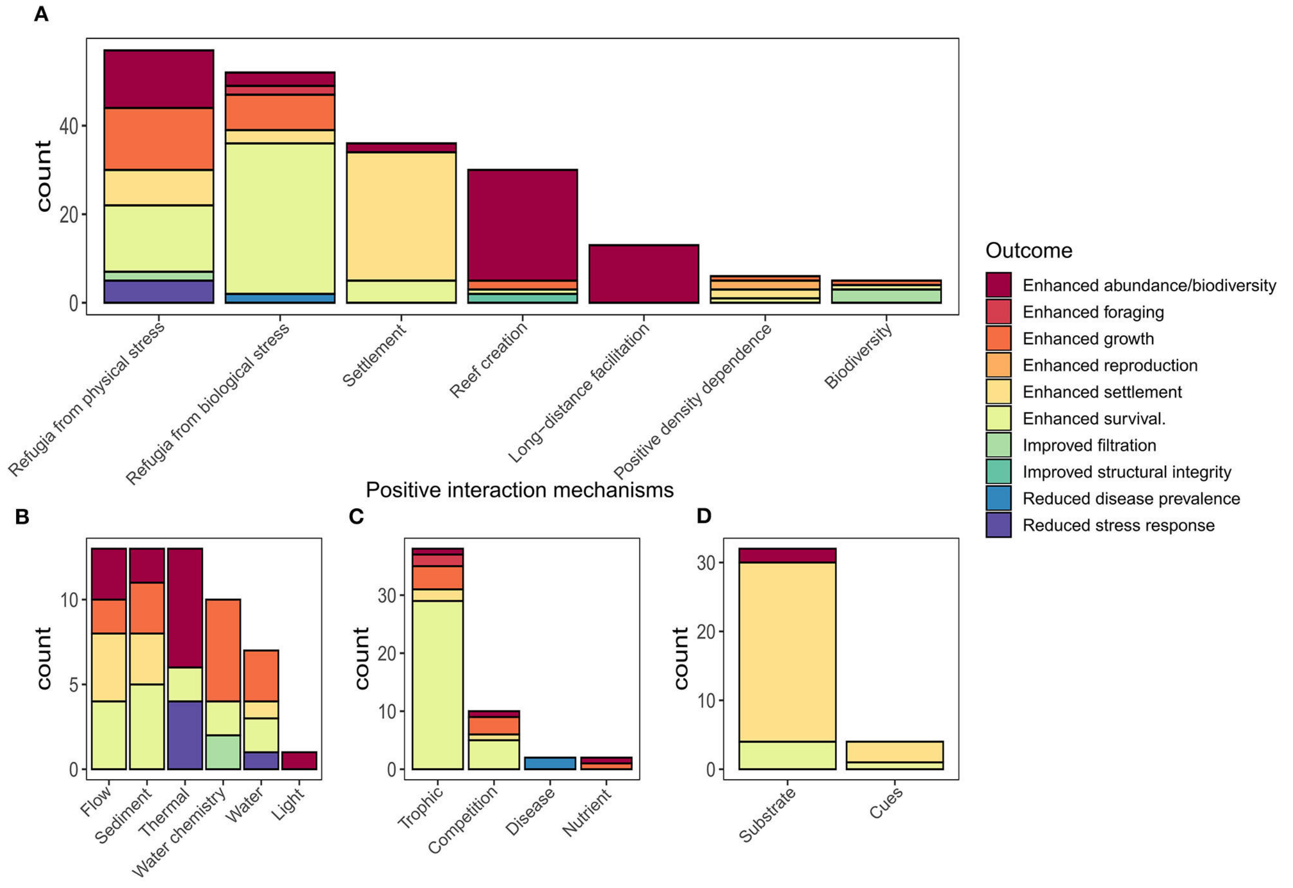

FIGURE 6 | Outcomes of positive species interactions summarized by interaction mechanisms: **(A)** overview of positive interaction mechanisms by category, **(B–D)** display sub-categories for **(B)** refugia from physical stress; **(C)** refugia from biological stress; and **(D)** settlement categories individually summarized for sub-categories of positive species interactions. Note y-axis scales differ between plots.

adult oysters and the density of conspecifics facilitated oyster production, recruitment, and survival (**Figure 6**). Our review identified six examples of these positive density-dependent effects for oysters, where a positive relationship existed between the density of oysters on an established reef and the outcome measured (**Figure 6**). For example, for *Ostrea edulis*, Guy et al. (2019) identified a maximum distance to nearest conspecific neighbors of <1.5 m that resulted in greater production of brooded larvae compared to nearest neighbors >1.5 m. Considering the benefit of increased production on oyster restoration outcomes, this suggests a minimum stocking density should be applied for restoration of *O. edulis,* which may also be applicable for other brooding oyster species (e.g., *O. angasi* and *O. chilensis*). Given the importance of positive density dependence, where available, oyster restoration efforts should look to mix live oysters with dead shell instead of using dead shell alone.

Oysters Facilitate Biodiversity and Reef Communities Through Reef Creation

Positive interactions have the potential to cascade throughout the community, changing the presence and abundance of important species (e.g., increases in important fish species or decreases in oyster predators) (Stachowicz, 2001). Our study found that oysters are important for facilitating ecological assemblages through several processes defined below. While it is clear oysters increase diversity, it is less clear whether this diversity feeds back to facilitate oysters.

Creating Structure

Our review identified 21 studies with 37 observations (**Figure 6**) of positive interactions associated with the creation of reef structure. Two out of the 21 studies showed the importance of an inorganic-organic adhesive produced by live oysters that binds oyster shells to substrate, which is fundamental for creating a resilient and persistent reef structure (Burkett et al., 2010; Alberts et al., 2015). The remaining 19 studies demonstrated that using oyster shells as substrate enhanced resident invertebrates and fishes in reference to mudflats, tidal marshes, and seagrasses (Grabowski et al., 2005). For example, Lejart and Hily (2011) found that shell reefs added 3.97 and 3.87 m^2 of additional surface area for rock and mudflats respectively, increasing habitat area for colonization by epifauna as compared to habitats without shell reefs.

Refuge From Physical Stress

The physical structure created by the oyster shell/live oyster matrix influences local environmental conditions, facilitating a suite of species by providing refugia from abiotic (i.e., thermal, flow, sediments, and water chemistry; **Figure 6B**) and biotic (i.e., competition, predation, and disease; **Figure 6C**) stressors. Our review identified 16 studies encompassing 57 interactions demonstrating facilitation of oysters and other taxa by the provision of refugia from abiotic stressors, including hydrodynamic, heat, sediment, salinity, oxygen, pH, light, and water stress (**Figure 6D**). The majority of these studies considered how altering the physical structure (orientation to flow, height, rugosity, and shape) of oyster shell reefs influenced these stressors and altered outcomes such as spat settlement density, oyster growth, and survival, as well as physiological stress and survival of associated invertebrates.

For instance, Lenihan (1999) examined how the height of shell reefs influenced water movement around reefs and oyster performance. This study found that flow speed increased, and sedimentation decreased, with elevation on a reef. Oyster recruitment was greatest at the front of reefs where flow was lowest, whilst growth, condition and survival of oysters increased with flow and elevation on a reef. Similarly, Colden et al. (2016) manipulated the orientation of oyster shell reefs to flow and found that reefs perpendicular to current flow produced conditions that were more favorable for reef persistence. Both Lenihan (1999) and Colden et al. (2016) stressed the importance of crests and vertical relief on reefs, suggesting that heterogeneous reefs will create favorable hydrodynamic conditions. They note that structure is critical for increasing flow, resuspending sediments, contributing to reef growth and ultimately determines whether reefs persist or degrade (Lenihan and Peterson, 1998; Lipcius et al., 2015; Colden et al., 2017). These studies show that intraspecific interactions between oysters (i.e., oyster density/height, reef shape) are important for oyster growth and should be considered in restoration designs.

Substrate orientation at the scale of individuals is also important for providing physical refugia. A number of studies identified the importance of shading by oysters, which influences the thermal conditions experienced by oysters and associated invertebrates (Padilla, 2010; McAfee et al., 2016, 2017, 2018; McAfee and Bishop, 2019). For instance, vertically oriented oysters provide greater shading than horizontally oriented oysters, which reduces heat and desiccation stress for other organisms (McAfee et al., 2018; McAfee and Bishop, 2019). These small-scale substrate orientation factors may be increasingly important in intertidal restoration settings where heat and desiccation stress will be highest.

Knowledge of how these positive interactions vary along an environmental gradient can help inform restoration practice. For example, across a 900 km latitudinal gradient, McAfee and Bishop (2019) identified that in warmer estuaries, shading by intertidal oysters had a larger effect on biodiversity, whereas in cooler estuaries, the provision of a predation refuge by oysters played a more important role. This demonstrates that context plays an important role in restoration planning and a project may benefit more or less from consideration of positive interactions depending on the type and amount of stress encountered in a system (e.g., an intertidal oyster restoration project in a hot arid climate vs. one in a cool temperate climate).

Interspecific Facilitation

Settlement

We found evidence that several species facilitate the presence of oysters and that the sequence of species colonization on reefs affects reef communities. For instance, Shelamoff et al. (2019) demonstrated that kelps can control turfing algae by abrading algae and reducing light levels, freeing space on the substrate and enhancing settlement density of *Ostrea angasi*. A number of other studies also reported that barnacles (Barnes et al., 2010), mangrove prop roots (Aquino-Thomas and Proffitt, 2014), kelps (Shelamoff et al., 2019), biofilms (Campbell et al., 2011), mobile invertebrates (Kimbro et al., 2014) and fishes can facilitate other species by enhancing surfaces for larval settlement (**Table 1**).

Refuge From Biological Stress

The stress gradient hypothesis predicts that refugia from biological stress—such as competition, predation, and disease—may be more important in more physically benign systems such as sub-tidal oyster reefs. Our review identified 29 studies encompassing 52 observations of organisms providing other organisms with refugia from biological stress (**Figure 6**). Of these observations 73% (38 obs.) involved trophic facilitations, 17% (10 obs.) involved refugia from competition, 3% (2 obs.) involved disease reduction, and 3% (2 obs.) involved the bio-availability of nutrients [i.e., oysters enriching nutrients in benthic sediments; Booth and Heck (2009)]. These positive interactions resulted in a diverse array of outcomes. Enhanced survival was most common 61% (28 obs.), followed by enhanced abundance/biodiversity 13% (6 obs.), enhanced growth (11%; 5 obs.), enhanced water quality 7% (3 obs.), enhanced settlement 4% (2 obs.), and reduced disease prevalence 4% (2 obs.) (**Figure 6D**).

Trophic facilitation is a form of indirect positive interaction, where one species is positively impacted through the feeding activities of another species. Many of the examples in our review were examples of trophic cascades where predators suppressed densities of primary consumers, resulting in increased densities of basal prey species. For example, oyster toadfish (*Opsanus tau*) enhance juvenile oyster survival by reducing mud crab (*Panopeus herbstii*) predation via non-consumptive (i.e., predation threat) and consumptive (i.e., predation) pathways. In this example the oyster toadfish indirectly increased oyster survivorship through reducing the number of oysters consumed by mud crabs (Grabowski, 2004; Grabowski et al., 2008; Kimbro et al., 2014, 2017). Similarly, native rock crabs control oyster drill populations, limiting oyster drill predation on *Ostrea lurida* and resulting in enhanced survival of *O. lurida* (Cheng and Grosholz, 2016). In addition to fishes and crabs, nudibranchs and sea urchins that eat boring sponges [e.g., the lemon drop nudibranch (*Doriopsilla pharpa*), and sea urchins (*Arbucia punctulata* and *Lytechinus variegatus*) (Lamarck), sea urchin *Lytechinus variegatus* (Lamarck)] can indirectly facilitate oysters by reducing boring sponge pressure on reefs (Guida, 1976).

Long-Distance Facilitation

Positive interactions can also occur at much larger spatial scales and involve species that are not in direct contact with oyster reefs. These long-distance positive interactions are often generated by the amelioration of physical and/or biological stress across landscapes (Van De Koppel et al., 2015). At the reef scale, oysters can have a significant impact on water quality by filter feeding, which in turn enriches surrounding benthic habitats with the deposition of organic rich bio-deposits such as feces and pseudofeces. For this reason, the potential of oyster reefs to enhance water quality has been the subject of extensive research and a motivating force for large-scale oyster restorations (Grizzle et al., 2008; Zu Ermgassen et al., 2013). Two studies in our review identified the capacity of oysters to filter pathogens out of the water column, reducing the impact of disease on oysters (Ben-Horin et al., 2018) and seagrasses (Groner et al., 2018). Benthic-pelagic coupling by oysters also enables the removal of nutrients from the water column and subsequent enrichment of sediments, which increases seagrass growth (Booth and Heck, 2009). Furthermore, our review also found examples of long distance interspecific facilitation enhancing the abundance of fish and invertebrate fauna on shellfish reefs when constructed in close proximity to seagrass, tidal marsh, and mudflat systems (Grabowski et al., 2005; Gilby et al., 2019), suggesting that a seascape view of habitat restoration could be beneficial for maximizing restoration success and outcomes for any particular ecosystem.

Modeling and field studies have demonstrated that oysters reduce suspended sediment concentrations dramatically, increasing water clarity and enhancing seagrass growth (Newell and Koch, 2004; Sharma et al., 2016). However, most restoration permitting frameworks have yet to recognize this potential interaction and restrict shellfish restoration in areas with seagrass. For example, development approval for shellfish restoration in many Australian states requires deployment of reef base to avoid areas of seagrass (i.e., >40% cover of *Posidonia* spp.) to limit potentially negative impacts to these vulnerable ecosystems. However, this results in restoration sites being sited in areas away from existing structured habitat (e.g., seagrass beds, rocky reefs), reducing the likelihood of long distance facilitation (e.g., water filtration and wave attenuation). Future research should focus on determining the value of co-restoring neighboring structured habitats and quantifying the value of long-distance facilitation between habitats. This research will build a knowledge base that can support restoration permitting frameworks to allow co-locating habitats and promote a seascape view of habitat restoration (i.e., restoration of multiple types of habitat patches across a seascape).

Biodiversity and Enhanced Ecosystem Function

Biodiversity encompasses the species, genetic, functional, and ecological diversity of living things (Shaver and Silliman, 2017). Recent evidence suggests that biodiversity often enhances ecosystem function, ecosystem service provisioning and ecosystem resilience (Van Wesenbeeck et al., 2013; Angelini et al., 2015). Ecologists refer to this as the portfolio effect, analogous to the portfolio concept in finance. In finance, the portfolio effect notes that diversified financial investment portfolios tend to produce more stable returns than simple portfolios. Similarly, in ecology the portfolio effect states that diversified ecosystems tend to produce higher functioning, more resilient ecosystems (Tilman et al., 1998; Schindler et al., 2015). This is partially because as diversity increases in an ecosystem, the functional redundancy (i.e., multiple species performing the same ecological function) often increases as well, which can lead to higher ecosystem resilience if one or a few species are lost (the insurance hypothesis: Yachi and Loreau, 1999).

While a number of key studies have documented both the loss of oyster reefs (Beck et al., 2011) and their value in terms of ecosystem services (Coen et al., 2007; Grabowski and Peterson, 2007; Grabowski et al., 2012; Zu Ermgassen et al., 2013, 2016), few have considered the role of multiple foundation species in supporting those ecosystem services. If multiple foundation species increase ecosystem services and/or biodiversity, accounting for their effects could alter the projected approach and benefits of restoration (Gedan et al., 2014). Several studies have shown positive relationships between hooked mussels (*Ischadium recurvum*) and eastern oysters (*C. virginica*) (Gedan et al., 2014; Lipcius and Burke, 2018). In terms of filtration, the hooked mussel shows some niche overlap with oysters, particularly for larger size classes of phytoplankton, but the hooked mussel can filter picoplankton more efficiently than the eastern oyster (Fulford et al., 2007; Gedan et al., 2014). Thus, while they may compete at times or in places where phytoplankton resources are limiting, both species can contribute significantly to the improvement of water quality by oyster reef restoration (Gedan et al., 2014). Multiple foundation species also produce habitat on oyster reefs, as associated sessile marine taxa (i.e., sponges, barnacles and algae) aid in binding the reef together and in supplementing the reef matrix, facilitating oyster settlement and enhancing the diversity of reef associated species (Manley et al., 2010).

Ecological restoration often focuses on a single ecosystem engineering species, with many restoration projects using a single species to form an entire ecological community. Oyster restoration traditionally focuses on the restoration of a single species of oyster to create an entire reef and deliver a suite of ecosystem services. However, our review suggests that considering multiple native foundation species will help support a self-sustaining oyster population, control oyster competitors, and boost filtration. The resulting increases in diversity should also support resilient ecosystem functioning and enhance the delivery of ecosystem services.

Future research should examine the role of multiple foundation species in accelerating the rate or trajectory of restoration projects [i.e., Williams et al. (2017) for tropical seagrass] and the importance of multiple taxa in delivering ecosystem services. However, care has to be taken in the selection of the multiple foundations species, as the aim is not to create a novel ecosystem by creating communities of foundation species that do not naturally co-exist, but to restore an ecosystem that occurred in the past. Achieving this outcome is aided by the use of a model system for the local native ecosystem being restored (McDonald et al., 2016; Gillies et al., 2017).

CONCLUSION

Our review intentionally focused on positive interactions and therefore did not report neutral or negative interactions. We acknowledge that in order to understand functioning of ecosystems both positive and negative interactions should be considered collectively. Yet in order to do so, further research on positive interactions is needed to provide a more complete picture of species interactions and complement existing research on negative interactions. While we make several recommendations for improving restoration practice in this review, we acknowledge further research may be needed to justify their wide-spread use (**Table 1**; e.g., playback of healthy oyster soundscapes at restoration sites to enhance natural settlement of oysters). In all instances, relevance to the particular restoration context should be considered and tested by appropriate experimental designs (i.e., Before After Control Impact—BACI) before scaling such novel enhancement methods. Further, future work might benefit from understanding the magnitude and effect size of positive interactions as this may aid outcomes of restoration projects by enabling prioritization of practical interventions that apply positive interactions.

Reef building oysters are autogenic ecosystem engineers that create their own habitat. Reef-building oysters make the environment less stressful for themselves, but also for many other species, creating a diverse ecological community that collectively produces important ecosystem services like coastal protection, water filtration, and fish production. To keep oyster predators, competitors and abiotic stressors low, in turn, the oysters depend on the reef inhabitants that they shelter. This review emphasizes the importance of positive interactions for not only oyster populations, but also for the biodiversity and resultant ecosystem functions and services that oysters engineer. By exploring nearly 200 examples of positive species interactions from 96 scientific studies, our review and database (available at the Knowledge Network for Biocomplexity. doi: 10.5063/F1125R1W) provides a tool for oyster reef restoration practitioners and scientists to explore the importance of positive interactions for creating and maintaining oyster ecosystems. These results can be used to improve our understanding of how these interactions can be applied to enhance outcomes of restoration projects and the management of wild oyster ecosystems.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: The dataset generated for this study can be found in the Knowledge Network for Biocomplexity "doi: 10.5063/F1125R1W".

AUTHOR CONTRIBUTIONS

SR, JR, CG, BH, and BS conceptualized the manuscript. SR, JR, and EF undertook the review. SR analysed the database and produced **Figures 1**, **3–6**. JR produced **Figure 2**. SR, JR, EF, and CG wrote the initial draft and all authors edited and reviewed the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00656/full#supplementary-material

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REVIEW
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Blue Restoration – Building Confidence and Overcoming Barriers

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Marine coastal (or "blue") ecosystems provide valuable services to humanity and the environment, but global loss and degradation of blue ecosystems necessitates ecological restoration. However, blue restoration is an emerging field and is still relatively experimental and small-scale. Identification of the key barriers to scaling-up blue restoration will enable targeted problem solving and increase the likelihood of success. Here we describe the environmental, technical, social, economic, and political barriers to restoration of blue ecosystems, including saltmarsh, mangroves, seagrass, shellfish reefs, coral reefs, and kelp forests. We provide managers, practitioners, and decision-makers with solutions to construct barrier-informed blue restoration plans and illustrate these solutions through the use of case studies where barriers were overcome. We offer a way forward to build confidence in blue restoration for society, government, and restoration practitioners at larger and more ambitious scales.

Keywords: marine coastal restoration, mangroves, seagrasses, saltmarsh, corals, kelp, shellfish, ecosystem services

IN A NUTSHELL

- Marine and coastal, or "blue" restoration is increasing in relevance and need due to degradation and loss of habitat, combined with increasing need for ecosystem-based climate change mitigation and adaptation.
- Restoration of blue ecosystems can be challenging due to environmental, technical, social, economic, and political barriers.
- Case studies provide insights of how to overcome barriers to restoration.
- Identifying barriers and evaluating potential pathways to achieve success is essential to enable blue restoration to play a major role in biodiversity conservation, and climate change mitigation and adaptation.

INTRODUCTION

Marine and coastal, or "blue" ecosystems, such as saltmarsh, mangroves, seagrass, shellfish reefs, coral reefs, tidal flats, and kelp forests and other seaweed beds, provide significant ecosystem services that have intrinsic value to environmental, social, and economic sustainability (MEA, 2005). These ecosystem services include regulating and maintenance services (e.g., coastal protection, climate regulation), provisioning (e.g., food, nutrient cycling, water quality), and cultural benefits (e.g., recreation, tourism) (Barbier et al., 2011). However, blue ecosystems are also some of the most heavily modified systems on Earth. Large scale global losses in habitat have been reported for mangroves and saltmarshes (Valiela et al., 2001; Gedan et al., 2009), kelp forests (Krumhansl et al., 2016), coral reefs (Hughes et al., 2017), shellfish reefs (Beck et al., 2011), seagrass (Waycott et al., 2009; Arias-Ortiz et al., 2018), and tidal flats (Murray et al., 2019). Drivers of loss vary and include pollution, invasive or pest species, disease, overexploitation or destructive fishing methods, land conversion, and the threats associated with climate change and associated extreme weather events (Valiela et al., 2001; Waycott et al., 2009; Beck et al., 2011). Ecological restoration is a priority where the natural recovery of degraded habitat(s) is slow, absent, or hindered by physical or biological factors (Perrow and Davy, 2002; SER, 2004).

Restoration describes interventions to assist in the recovery of an ecosystem, while "blue restoration" refers to interventions focused on the recovery of marine and coastal ecosystems. The importance of restoration of natural systems is recognized by numerous global accords and conventions, all aimed at accelerating ecological restoration. These include the Millennium Ecosystem Assessment (MEA, 2005), the Convention on Biological Diversity (CBD, 2010), Bonn Challenge (restoration of 350 million hectares by 2030), the United Nations Sustainable Development Goals (SDGs) in particular SDG14 "Life Below Water," and the recent United Nations (UN) declarations for "Decade for Ecosystem Restoration 2021–2030" (Salvador, 2018; Waltham et al., 2020) and "Decade of Ocean Science for Sustainable Development 2021–2030" (UN, 2019).

Until recently, the focus of restoration has been largely terrestrial; with blue restoration still mostly small-scale, costly, and with limited long-term success (Bayraktarov et al., 2016). Meeting the ambitious global targets will require successful implementation of blue restoration at scales not yet seen. Successful blue restoration must overcome environmental, technical, social, economic, and political barriers to implementation. The identification and assessment of common barriers will allow managers to target, prioritize, and potentially eliminate barriers during the planning phase, increasing the likelihood of project success. Here we describe common barriers to blue restoration projects, evaluate the level of threat they pose to success for each ecosystem type, detail the relationship between barriers and restoration success, and provide real-world examples where barriers have been overcome. Now is the time to build confidence in society, government, and amongst restoration practitioners through resolving how to overcome multiple barriers to enable scaling-up blue restoration to ecologically-relevant scales.

BARRIERS TO BLUE RESTORATION

A series of workshop discussions among the authors drew on our knowledge of the restoration literature to identify common barriers to successful blue restoration at the scale required to meet future targets (MEA, 2005; CBD, 2010; Salvador, 2018; GMA, 2019). We categorized these into five broad classes: environmental, technical, social, economic, and political (**Figure 1**). To supplement the knowledge of the authors, we conducted a targeted search of the Web of Science databases and Google Scholar. The resulting literature (Web**Table 1**) was used to (1) describe how environmental, technical, social, economic, and political barriers can hinder success of blue restoration projects, and (2) give solutions to these barriers based on our literature search (**Table 1**). We further illustrate these solutions utilizing case studies including:

- Coral reef restoration in Sulawesi, Indonesia, where technical barriers were overcome using new, relatively inexpensive technology (**Box 1**);
- Mangrove restoration in Sulawesi, Indonesia, where environmental (hydrological) barriers were overcome using creative solutions that were based on sound technical knowledge (**Box 2**);
- Seagrass restoration in Chesapeake Bay, United States, where technical knowledge was used to increase restoration capacity by implementing seed propagation technology (**Box 3**); and
- Shellfish restoration in Chesapeake Bay, United States, to illustrate where political barriers were overcome by fostering collaboration between stakeholders (**Box 4**).

The case studies presented here are examples of success in overcoming barriers and are not intended to be portrayed as representative of the norm in the blue restoration industry. For example, seed propagation is not always as successful in large-scale seagrass restoration as it was in Chesapeake Bay (e.g., only 12% survival on Kangaroo Island in Australia: Tanner et al., 2014). This is due to the relatively young nature of the blue restoration industry, where solution to some barriers have not yet been widely implemented. We expect that more solutions will emerge as the blue restoration industry matures.

Environmental Barriers

Environmental barriers are physical, chemical, biological, or hydrological characteristics that decrease the likelihood of restoration success (Perrow and Davy, 2002). These barriers include land conversion, hydrological modification, poor water quality, pest species, overexploitation, climate change, and extreme weather events (**Figure 1**).

Land Conversion

Land conversion has been one of the key causes of loss of approximately one third of the world's saltmarsh, seagrass, and

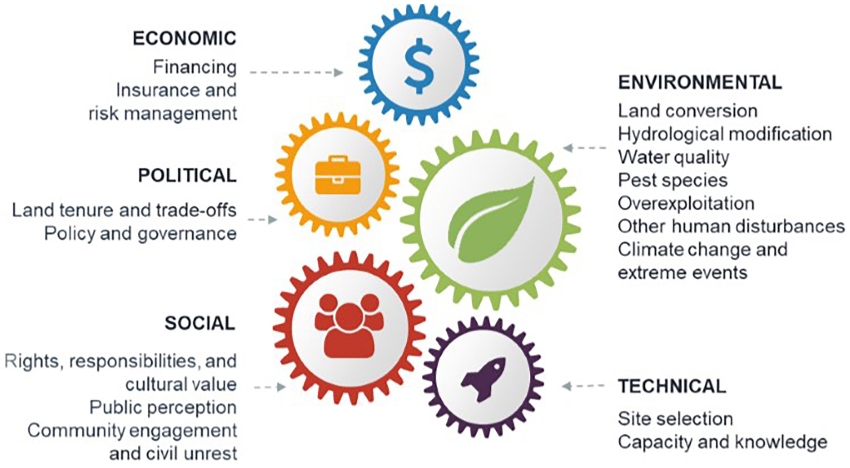

FIGURE 1 | Common barriers to successful blue restoration. Barriers are shown for the restoration of saltmarsh, mangroves, seagrass, shellfish reefs, coral reefs, and kelp.

mangroves (Valiela et al., 2001; Gedan et al., 2009; Waycott et al., 2009). Environmental barriers associated with changes in land-use include changes in the structure (compaction) and biogeochemistry of soils (nutrients and other pollutants), which may be difficult to reverse, particularly in the cases of blue ecosystems where the original ecosystem is lost through land reclamation. In cases that do not include land reclamation, solutions that have been identified include adding sediment in saltmarshes where soils and their elevations are inappropriate for plant growth (Berkowitz et al., 2017). The negative impacts of mobilizing pollutants can be minimized through staged reflooding and liming (treating with lime) in acid sulfate soils (Portnoy and Giblin, 1997).

Payments for ecosystem services (including carbon sequestration) have been successfully used to motivate and finance the restoration of converted agricultural landscapes in terrestrial systems, as in China's Grain-to-Green Program (Chen et al., 2009) and Madagascar's Ankeniheny-Mantadia-Zahamena Biodiversity Conservation and Restoration Project (Wendland et al., 2010). Carbon finance is applicable to blue ecosystems (Wylie et al., 2016), and methodologies are available for a range of restoration activities for mangroves, saltmarshes, and seagrass (e.g., rewetting landscapes to restore coastal wetlands (Emmer et al., 2015; Needelman et al., 2018). A wide range of projects are emerging to restore mangroves and saltmarshes on converted agricultural and aquaculture landscapes, both for carbon payments, for example Conservation International's project in Cispatá, Colombia (Bernal et al., 2017), and restoration of saltmarsh in Canada (Wollenberg et al., 2018), and also for supporting biodiversity and other co-benefits, including nutrient cycling (e.g., Land Restoration Fund projects in Queensland, Australia; Queensland Government, 2020).

Hydrological Modification

Degradation of coastal wetlands is often the result of changes in hydrology to support aquaculture and agriculture; for example, drainage, impoundment with seawalls, or excavation (Lewis et al., 2016). Changes to hydrology can cause major alterations to the suitability for plants and animals of blue ecosystems. Mangrove ecosystems can be difficult to restore where aquaculture ponds and channels excavated for shrimp aquaculture result in hydrological modifications of the landscape (Brown et al., 2015). Re-establishing hydrological regimes that are suitable for plant communities has been achieved in a range of saltmarsh settings (Glamore, 2012; Esteves and Williams, 2017), although success has been variable (Wolters et al., 2005). There remain technical barriers to predicting outcomes of hydrological change (e.g., because of difficulties in predicting tidal attenuation in complex environments; Rodríguez et al., 2017) and development of accessible hydrological models is key, although often not possible due to limitations in resources, data, or capacity (Boumans et al., 2002).

Water Quality

Water quality has large effects on how blue ecosystems function and persist, and often preclude successful blue restoration (van Katwijk et al., 2016). Eutrophication (excess nutrient loads resulting in significant reductions in dissolved oxygen) is one of the most prominent cause of seagrass loss (Waycott et al., 2009), and has also contributed to loss of oyster reefs (Beck et al., 2011). Seagrass restoration in the Wadden Sea was more feasible with a higher likelihood of success at sites where water quality issues such as eutrophication and turbidity had been improved in the late 1980s, after extensive seagrass losses had occurred (van Katwijk et al., 2009).

Pest Species

Pest species have caused widespread damage to blue ecosystems, often threatening the success of restoration projects. Pest species can reduce the survival and persistence of restored blue ecosystems. For example, Crown-of-Thorns starfish (*Acanthaster planci*) and Indo-Pacific lionfish (*Pterois volitans*) have threatened reef restoration projects in Australia and the

TABLE 1 | Examples of solutions to the common barriers to blue restoration.

Challenge	Solution	References
Environmental		
Land conversion	Sediment addition, staged reflooding, liming, and payments for ecosystem services.	Portnoy and Giblin, 1997; Chen et al., 2009; Wendland et al., 2010; Konnerup et al., 2014; Emmer et al., 2015; Berkowitz et al., 2017; Bernal et al., 2017; Needelman et al., 2018; Wollenberg et al., 2018
Hydrological modification	Re-establishing hydrological regimes, development of hydrological models.	Boumans et al., 2002; Wolters et al., 2005; Glamore, 2012; Esteves and Williams, 2017
Water quality	Water quality management, site selection.	van Katwijk et al., 2009
Pest species	Site selection, manual removal, increase biodiversity, and native species.	Johnson et al., 1990; Davis et al., 1998; Steneck et al., 2002
Overexploitation	Harvesting bans/limits, complementary planting, provision of alternative livelihoods, and community engagement.	Winterwerp et al., 2016; Wylie et al., 2016; Chan and Hodgson, 2017; Owuor et al., 2019
Other human disturbances	Eco-mooring, zoning for low-impact areas, policy changes, and site selection.	Stowers et al., 2000; Precht et al., 2001; Cullen-Unsworth and Unsworth, 2016
Climate change and Extreme events	Site selection, risk management, niche modeling, benefit-cost analysis, and adaptive management.	Alleman and Hester, 2011; Perry et al., 2015; Adams et al., 2016; Beyer et al., 2018; Runting et al., 2018
Technical		
Site selection	Guidance documents, trait matching for site conditions, avoiding sites with climate-induced extremes.	Lewis, 2005; Precht, 2006; Srivastava, 2017; Ladd et al., 2018; The Nature Conservancy, 2018; Fitzsimons et al., 2019
Capacity and knowledge	Investment into research and development, increased communication of restoration outside of the global north.	RRAP, 2018; Zhang et al., 2018
Social		
Rights, responsibilities, and cultural value	Allow cultural harvest, valuation and investment in cultural ecosystem services, inclusion of indigenous peoples.	Allan et al., 2015; Poe et al., 2016; Brown, 2017; Wehi and Lord, 2017
Public perception	Actively address concerns of public.	Rey et al., 2012.
Community engagement and civil unrest	Create co-benefits and increase livelihoods. Increase community engagement through job creation, and encouraging cultural practices. Use citizen science.	Dickinson et al., 2012; Kittinger et al., 2013; Huddart et al., 2016; Disney et al., 2017; Hesley et al., 2017; Livelihoods funds, 2019
Economic		
Financing	Use financial models (e.g., REDD +, debt-for-nature-swaps, green taxes, biodiversity offsets etc.). Use a range of investors (e.g., private, public, donors etc.). Government policy.	Iftekhar et al., 2017; Srivastava, 2017; Herr et al., 2019
Insurance and risk management	Charge private stakeholders for ecosystem services, catastrophe bonds, and parametric insurance.	Bell and Lovelock, 2013; Colgan et al., 2017; Lab, 2017
Political		
Land tenure and trade-offs	Payment for ecosystem services, sustainable harvesting.	Beck et al., 2011; Lovelock and Brown, 2019
Policy and governance	Consider cultural context, incorporate social science, knowledge sharing, and consider barriers to restoration.	Ferrol-Schulte et al., 2015; Bell-James, 2016; France, 2016

Caribbean, respectively (Omori, 2010), green crabs (*Carcinus maenas*) have reduced survival of restored seagrass (Davis et al., 1998), sea urchins have damaged kelp restoration projects (Watanuki et al., 2010), and the common reed (*Phragmites australis)* has reduced success of saltmarsh restoration in North American (Silliman and Bertness, 2004). In some cases, the only solution to reducing the impact of pest species on restoration projects is by avoidance through careful site selection (e.g., green crabs in seagrass; Davis et al., 1998). In other cases, manual removal is necessary (e.g. Crown-of-Thorns starfish, Great Barrier Reef, Australia), although this can increase the cost of restoration projects (Johnson et al., 1990). Restoring the biodiversity of blue ecosystems may help resist invasion of pest species, such as in kelp forests (Steneck et al., 2002), while reduced biodiversity is associated with invasions in saltmarsh (e.g., in New England; Silliman and Bertness, 2004). This demonstrates a positive feedback loop between restoration of biodiversity and reduced incidence of pest species.

Overexploitation

In many nations, overharvesting has led to degradation of mangroves and reduction in important ecosystem services, such as coastal protection and stabilization. Restoration is unlikely to

BOX 1 | Sulawesi, Indonesia – coral reef restoration.
Ecosystem: Coral reef.
Background: The site (Pulau Badi, South Sulawesi, Indonesia) was damaged by storms, blast-fishing, coral mining, and the construction of a boat channel, resulting in a coral rubble field (Williams et al., 2019). Restoration success was measured against a reference site which was a nearby, undisturbed reef.

Photo: 'Spiders' used to stabilize rubble for coral transplantation.
Barrier 1: Technical – low levels of substrate availability for coral recruits.
Context and solution: The project deployed small, modular, open structures ('spiders') to stabilize rubble and to support transplanted coral fragments over 2 years. The structures allowed unrestricted water flow, trapped broken coral fragments and rubble, and stabilized the substratum to support coral recruitment, growth, and diversity. Live coral cover on the structures increased from less than 10% to greater than 60%, although this varied depending on depth, deployment date, location, and disturbances.

be successful unless harvesting of timber from restoration sites is prevented, either through regulation with enforcement or the provision of local people with alternatives resources. Provision of alternative livelihoods has proven a valuable tool to reduce over-exploitation of mangroves, for example in the Mikoko Pamoja mangrove restoration project in Kenya, complementary planting of terrestrial species for timber production reduces pressure on the restored forest (Wylie et al., 2016; Owuor et al., 2019).

Other Human Disturbances

Direct physical damage by human activities can reduce success of restoration projects through increased costs or decreased survival. Physical damage, such as that done by boat propellers and chain moorings, can have a large impact on the success of restoration by reducing the density of seagrass – in some areas to zero (Demers et al., 2013). Eco-mooring systems that prevent damage or designating certain sensitive areas as "low-impact" (i.e., no high-impact moorings), may provide a solution to damage of restoration sites (Cullen-Unsworth and Unsworth, 2016). Implementation of policy that protects seagrass from damage has been successful in Tampa Bay, where areas of restored seagrass were closed to boats with combustion engines, perhaps providing a model for other restoration projects (Stowers et al., 2000).

Larger-scale damage, such as damage to corals by ship groundings, can in some cases be managed with appropriate site selection for restoration (e.g., in the Florida Keys). In this example, areas of high relief did not recover on their own and required restoration, while low-relief, hardground coral sites recovered without the need for assisted restoration. Restoration with appropriate site selection (i.e., that focuses on damaged high-relief habitat) can reduce the cost and increase the feasibility of restoration in cases of ship groundings (Precht et al., 2001).

Climate Change and Extreme Events

Climate change can have a direct impact on blue ecosystems through gradual increased ocean temperatures, sea level rise, and ocean acidification, as well as increasing intensity and frequency of extreme weather events. Restoration projects can be vulnerable to extreme weather events if sites are not chosen carefully to include areas that are less vulnerable (see "Site Selection;" van Katwijk et al., 2016). The projected impacts of climate change should be incorporated into restoration planning, with consideration given to species' ability to adapt

BOX 2 | Sulawesi, Indonesia – mangrove restoration.
Ecosystem: Mangrove.
Background: Mangrove restoration in two locations – Tiwoho Village, North Sulawesi (site referenced in Brown and Djamaluddin, 2017); and in Tanakeke Island, South Sulawesi (site referenced in Brown et al., 2014). While these sites have a similar history of clearing and land-use conversion, they represent very different conditions for mangrove restoration. Tiwoho is a high productivity mangrove system where the soil is silty and deep, whereas Tanakeke is a low productivity mangrove system on shallow coral sands (Cameron et al., 2019).

Photo: By Rignolda Djamaluddin of hydrological restoration of mangroves (Brown and Djamaluddin, 2017).
Barrier: Environmental – hydrodynamics.
Context and solutions: Collaboration among scientists at Blue Forests (Yayasan Hutan Biru), Charles Darwin University, and the National University of Singapore, focused on mangrove restoration by implementing Ecological Mangrove Restoration (EMR) (Lewis, 2005). This methodology involves hydrological modifications following an assessment of the current conditions and site-specific needs. Restoration of hydrology included strategic pond wall breaching, creating hand-dug drainage and tidal channels, and creating mounds of substrate to facilitate mangrove colonization in deeper areas of ponds. These techniques simulated the natural conditions to allow mangrove propagules to naturally recruit to the restoration sites. These projects are successful examples of overcoming complicated hydrological challenges with creative solutions.

or range shift. Blue ecosystems are diverse and will suffer diverse impacts of climate change and, as such, appropriate restoration techniques and management will depend upon the specific stressors to that system (Erwin, 2008). For example, corals will be impacted by increased temperatures, seagrass and kelps are sensitive to marine heatwaves, while wetland ecosystems may be sensitive to salt water intrusion and sea-level rise [including the impacts of "coastal squeeze" (Mills et al., 2016)].

Modern portfolio theory, which seeks to maximize return and minimize risk, has been applied to selected sites to minimize risks for establishing mangroves under projected climate change scenarios (Runting et al., 2018). A similar approach was used to assess priorities with lowest climatic risks (i.e., risk management) for global investment in conservation of coral reefs (Beyer et al., 2018), but other approaches include species niche modeling with assessment of benefits and costs (Johnston et al., 2002; Adams et al., 2016). Restoration practitioners must consider not only which restoration techniques should be used, but also how effective these are under multiple potential future climate projections, while leaving room in projects for adaptive management of restoration projects (Perry et al., 2015). More knowledge is needed in all blue ecosystems on how restoration practices should change and be adapted to incorporate the effects of climate change (Harris et al., 2006).

Technical Barriers

Technical barriers to blue restoration threaten project success most often when there is poor site selection or

BOX 3 | Chesapeake Bay, United States – seagrass restoration.

Ecosystems: Seagrass

Background: Chesapeake Bay ecosystems have been overexploited and degraded since European settlement over 400 years ago (Cameron et al., 2019). The seagrass, *Zostera marina,* was lost from 50% of its distribution, followed by 30% decline in the 1990's (Orth et al., 2012). In response to bay-wide environmental degradation, the Chesapeake Bay Program Partnership was formed in 1983. The Chesapeake Bay Foundation estimated the economic benefits of cleaning up the bay watershed would total US$130 billion annually.

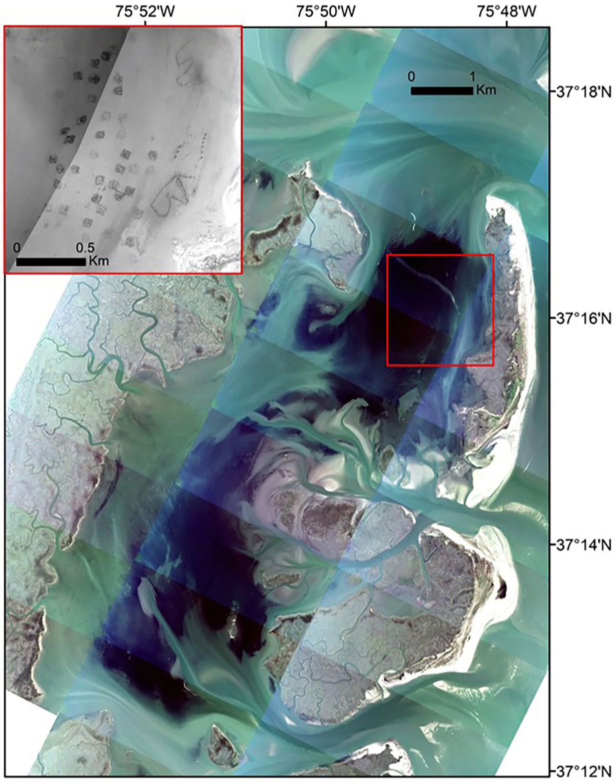

Photo: *Zostera marina* restoration in South bay, Chesapeake Bay, United States.

Barrier: Technical – seagrass recruitment

Context and solution: Natural recovery of seagrass was slow, despite improvements to water quality. This prompted interventions to assist seagrass recovery. Seed-based restoration provides a greater abundance of genetically diverse propagules. Large-scale restoration using seeds collected from areas adjacent to Chesapeake Bay was initiated in the late 1990s (Orth et al., 2012). This enhanced recruitment above natural levels. Currently, 72 million seeds have been added between 1999 and 2015, to plots ranging in size from 0.01 to 2 ha, totaling 200 ha across four coastal bays. Expansion from these initial plots to approximately 2500 ha of seafloor is attributable to seed dispersal and reproduction from the original plots (Orth and Reeves, 2018, pers. comm.).

BOX 4 | Chesapeake Bay, United States – shellfish.

Ecosystems: Shellfish

Background: In Chesapeake Bay, the eastern oyster *(Crassostrea virginica)* provides valuable services to commercial fisheries, water filtration, and habitat. Over-harvesting, disease, and habitat loss has led to oyster populations <1% of their historic levels (Wilberg et al., 2011). Oyster restoration in the Chesapeake Bay started in 1914 and has led to restoration of 100s of hectares (Wilberg et al., 2011).

Photo: By Will Parson/Chesapeake Bay Program of clump of oysters from Harris Creek (Chesapeake Bay Program, 2019).

Barrier 1: Political.

Context and solution: Oyster restoration/management in the Chesapeake has been a collaborative and coordinated approach across political jurisdictions. This was driven by a 2009 US Executive Order (no. 13508), which was implemented by the Chesapeake Bay Watershed Agreement (2014), Chesapeake Bay Program (2019). Within this, the Oyster Outcome is to Continually increase finfish and shellfish habitat and water quality benefits from restored oyster populations, restore native oyster habitat and populations in 10 tributaries by 2025 and ensure their protection' this has catalyzed oyster restoration at scale: by 2018, 289 and 194 hectares had been restored in Maryland and Virginia, respectively. The outcomes of this restoration has been quantified and in Maryland alone, US$51 milion has been invested in oyster restoration, with a fisheries output benefit valued at US$22.3 milion per year, an additional 313 jobs per year, and between US$3-18 million in nitrogen removal value (Chesapeake Bay Program, 2019).

limited capacity and knowledge to support restoration projects (**Figure 1**).

Site Selection

Site selection has been responsible for many failed mangrove restoration projects in low and middle income countries (Lee et al., 2019), where the average survival of restored mangrove seedlings is only 11% (Bayraktarov et al., 2016). However, appropriate site selection is not necessarily an easily solved problem. For example, many failed mangrove plantings were on sites selected to avoid conflicts with private land use (see "Land tenure and trade-offs;" Lewis, 2005; Lovelock and Brown, 2019). Mangrove restoration success has been increased by development of technical guidance including initiatives such as Ecological Mangrove Restoration (EMR; Lewis, 2005) and the UN-led Restoration Opportunities Assessment Methodology (ROAM; Srivastava, 2017). Similar tools are available for shellfish reefs, such as the Ocean Resilience application (The Nature Conservancy, 2018) and the Restoration Guidelines for Shellfish Reefs (Fitzsimons et al., 2019). In coral reefs, matching of coral phenotypic traits with site conditions may lead to increased survival and overall success of restoration projects (Ladd et al., 2018). For example, sites affected by high water temperatures due to climate change could require outplanting of coral genotypes with high thermal tolerance. Further successes may be achieved by strategic placement of coral reef restoration in areas where water currents minimize bleaching of restored corals (Precht, 2006).

Capacity and Knowledge

Limited knowledge of restoration processes and skills can hinder restoration success and implementation.

A solution to a lack of knowledge is increased investment into research and development of blue restoration methods, and training of project personnel. For example, AUD$100 million has been allocated to coral reef restoration research and development on the Great Barrier Reef, which has been focused on technological solutions for climate change impacts, such as the restoration of bleached areas using assisted translocation of coral larvae (RRAP, 2018). This example also underscores an information and investment bias toward blue restoration in nations with high-income economies. For example, Bayraktarov et al. (2016) found that investment is greater in countries with high income economies compared to low/lower middle economy nations for coral (median 282,719 US$ ha^{-1} cf. 162,455 US$ ha^{-1}) and mangrove restoration (52,006 US$ ha^{-1} cf. 1,771 US$ ha^{-1}), while in seagrass, saltmarsh, and oyster reef restoration there was no published evidence of investment in low/lower middle income nations. There is limited information on blue restoration from Africa, Asia, and South America. There needs to be increased communication of restoration outside of the developed world (Zhang et al., 2018). Many locally run projects have limited access to communication with restoration experts, and so may waste valuable time and resources developing restoration techniques that work, or the project may suffer from reduced success as a result. Information-sharing and publicly available best-practice guidelines may reduce this limitation.

Social Barriers

Social approval and participation in blue restoration is often overlooked but can be central to successful implementation of large-scale blue restoration (**Figure 1**).

Rights, Responsibilities, and Cultural Value

Restoration has the potential to greatly impact the human populations living in proximity to restoration projects and those who are dependent on the habitats being restored. As such, consideration of the rights and responsibilities of coastal peoples, and inclusion of all the relevant stakeholders, is crucial to blue restoration success (Lundquist and Granek, 2005).

The cultural value placed on blue ecosystems has the potential to cause conflict with restoration project objectives, particularly where indigenous communities have rights to resource use (e.g., burning mangrove wood for fuel; Torpey-Saboe et al., 2015). For example, the use of mangrove tree resources was criminalized in Para state, northern Brazil (Glaser et al., 2003). The ban was aimed at commercial users; however, it also restricted access to local communities who required wood for their subsistence. The ban created social conflict, resource and economic insecurity, and threatened the local use and restoration of the mangrove habitat (Glaser et al., 2003). Similar concerns have been raised by REDD + (Reduced Emissions from Deforestation and Degradation) projects for mangrove conservation, noting that restoration may compromise access to land and livelihoods by limiting indigenous and local people from traditional use of mangrove land (Griffiths and Martone, 2008). Cultural harvest (i.e., resource use by local or traditional communities) is one of the key cultural values of restored habitats (Wehi and Lord, 2017). Inclusion of sustainable harvest within restored habitats may increase the cultural value of restoration projects and thereby increase community support for restoration projects (Wehi and Lord, 2017). In Puget Sound, in the United States, people's "sense of place" was an important motivation for resident support of restoration and sustainable harvesting of shellfish (Poe et al., 2016). In North America's Laurentian Great Lakes, cultural ecosystem services from restoration have guided investment of more than US$1.5 billion into restoration, which increased uptake and success of restoration projects (Allan et al., 2015).

Research into the cultural ecosystem services provided by blue ecosystems is biased toward examples from nations with developed economies and thus does not often include cultural use and value placed on blue ecosystems beyond western values (Rodrigues et al., 2017). The inclusion of local peoples in the planning and implementation of restoration projects has enhanced the success of mangrove restoration projects in Indonesia (Brown, 2017).

Public Perception

Public perception of the impacts of restoring ecosystems has large implications for restoration of blue ecosystems. In Florida, mosquitoes associated with saltmarsh and mangrove forests can become abundant, which has negative impacts on human health and well-being (Rey et al., 2012). Due to negative public perception of saltmarshes and mangroves, because of their association with mosquitoes and other biting insects, much of the historic areas of coastal saltmarsh were drained and mangroves impounded to reduce mosquito numbers. Restoration of coastal wetlands therefore had to overcome the concerns of the public, and thus as a solution, restoration of these marsh areas was paired with mosquito control (Rey et al., 2012).

Public perceptions of the benefits of blue ecosystems are likely to differ from those quantified by ecosystem service valuation (Costanza et al., 1997), where the public values recreation and access to food/fuel over services such as increasing water quality. In order to bring differing perspectives together, it is important to engage a variety of stakeholders (e.g., indigenous and community groups) when planning and implementing blue restoration projects (Lundquist and Granek, 2005).

Community Engagement and Civil Unrest

Civil unrest and conflict can prevent restoration efforts due to weak governance, corruption, and disputes over land tenure (Herr et al., 2019). For example, upstream dam construction and prolonged drought in Senegal has stimulated estuarine mangrove restoration, which has led to a range of social conflicts (Manikowski and Strapasson, 2016; Cormier-Salem, 2017). Non-government organizations have initiated large scale restoration of mangroves, which has had co-benefits of restoring rice and seafood sources for local livelihoods (Livelihoods funds, 2019), although social conflict remains over the carbon financing used for the project (Cormier-Salem, 2017).

Active community engagement in blue restoration projects can combat the negative influence of social conflict and be mutually beneficial to both restoration practitioners and other stakeholders in the community. For example, the effectiveness of strong community engagement for successful restoration was demonstrated in Hawaiian coral restoration, where coral reef restoration benefited the local community by creating jobs, reviving cultural practices, harvest and use of coral-associated algae, increased awareness of the marine environment, and overall increased adaptive capacity for global change (Kittinger et al., 2013).

Other strategies to increase community engagement, such as citizen science, use volunteers to support river restoration activities (Huddart et al., 2016), seagrass (Disney et al., 2017), and coral reef restoration (Hesley et al., 2017). The use of citizen science programs that engage with volunteers can reduce levels of investment needed for monitoring of restoration projects. While there may be a trade-off in data quality and consistency when data collection is done by many volunteers, citizen science can contribute to project success by improving cost effectiveness as well as increasing public engagement and support (Dickinson et al., 2012).

Economic Barriers

Financing and risk management of blue restoration are major barriers to implementation of projects at a meaningful scale (**Figure 1**). Financing the costs of all components of projects (including capital and operating costs) depends on funding availability, financial benefit, risk management (e.g., through feasibility estimates or insurance), and a stable political climate (Vanderklift et al., 2019).

Financing

Lack of long-term funding for restoration has been identified as one of the major barriers to restoration success (Iftekhar et al., 2017). Most restoration projects are limited to short-term funding (i.e., less than 3 years) and, as a result of this short duration, successful establishment, maintenance, and ongoing monitoring is significantly restricted. This lack of long-term funding has potentially contributed to the relatively low rates of success in blue restoration (Bayraktarov et al., 2016). Financing for blue restoration has historically been acquired through a multitude of ways, including valuation of ecosystem services, carbon financing (e.g., REDD +), debt-for-nature-swaps, green taxes, biodiversity offsets, payment for ecosystem services, impact investments, green bonds, and parametric insurance (Herr et al., 2019). Organizations that have provided finance include: (1) private for-profit, (2) private non-profit, (3) public sector expenditure, and (4) multilateral and bilateral donors (Srivastava, 2017). In some cases, government policy is developed to support financing of blue restoration. For example, in Kenya, a Climate Compatible Development policy was applied to mangrove forests in the Kwale District, which uses valuation of mangroves and estimated mangrove loss to predict the future benefits of sustainable mangrove management, including restoration (Herr et al., 2019).

Insurance and Risk Management

Investment in blue restoration depends on reducing and managing the risk of failure, since investors are generally risk-averse and restoration success (quantified as survival of restored organisms) varies widely from 0 to 65% (Bayraktarov et al., 2016). Reduction of risks can be achieved through insurance in situations where it is possible to charge private stakeholders for ecosystem services (Colgan et al., 2017). The insurance industry is developing tools for managing environmental risks, such as catastrophe bonds, that could be used to manage risks associated with large-scale restoration projects (Colgan et al., 2017). Insurance of mangroves, based on the coastal protection they provide, has been found to be technically feasible in Australia, but thus far has not been implemented (Bell and Lovelock, 2013). Risk management for valuable coral reef habitat occurred in Quintana Roo, Mexico, through parametric insurance where the coral reef was insured for restoration by a private-public partnership (Lab, 2017). The insured party (i.e., the hotel owners) benefit from the tourism income provided by a healthy reef, while the benefit for blue restoration is that if the coral reef is damaged (for example by storms), then restoration programs will be paid out (Lab, 2017). Thus, insuring blue ecosystems for restoration offers a solution to management of risk, and could improve restoration success through increases in the funding available for restoration projects including post-establishment maintenance and ongoing monitoring.

Political Barriers

Political barriers to implementation of blue restoration interventions, such as trade-offs between conflicting objectives, and issues with political delay of approvals and permits, can be significant barriers (**Figure 1**).

Land Tenure and Trade-Offs

Land conversion to agriculture, aquaculture, and urbanization often results from a change in land ownership from public or indigenously managed land to private land (Esteves and Williams, 2017). In mangroves converted to aquaculture, private landowners do not necessarily live locally and thus may not directly benefit from ecosystem services arising from mangrove restoration, while the local community may feel disempowered by land-use regimes that do not consider community involvement (Lovelock and Brown, 2019). Restoration of blue ecosystems on common land reduces the social barriers, but can result in over-exploitation (Crooks et al., 2011). Land-tenure bottlenecks can result in plantings in inappropriate, low intertidal areas, leading to high failure rates (Lee et al., 2019). One of the solutions to land tenure barriers is payment for ecosystem services of restored habitat to multiple stakeholders, which may include separating carbon and fisheries rights from land rights (Bell-James and Lovelock, 2019).

Conflicting objectives for usage of restored ecosystems (e.g., recreation, fisheries, carbon or conservation) can also lead to project failure. In the Chesapeake Bay, native oysters have been restored but trade-offs occur where fisheries want to harvest the restored oyster stocks, directly inhibiting restoration efforts, and ultimately leading to restoration failure (Beck et al., 2011). A solution to this is early stakeholder engagement and consultation, resulting in agreeable compromise, where oyster stocks (for example) are harvested sustainably, allowing for increases in the cultural value of the restoration project, while still achieving the environmental goals (see **Box 4**).

Policy and Governance

Political issues that may delay or prevent approvals and permits can delay or prevent blue restoration projects. For example, governments can alter national or regional planning strategies thereby reducing priority for restoration, reducing available funds, or relaxing regulations protecting restored sites (Vanderklift et al., 2019). Despite promotion of blue restoration through national policies (e.g., REDD +), they can be ineffective when not consistently applied across landscapes, or due to a lack of political will (Vanderklift et al., 2019). In Vietnam and Madagascar (Markets and Mangroves project) the planning, time and resources required to implement a REDD + project was so extensive that the REDD + model was discarded (Wylie et al., 2016). Failure of the REDD + scheme in Vietnam was due to the length of time it took to fulfill the requirements of the scheme, whereas in Madagascar government policy, which does not classify mangroves as forests, was the cause (Wylie et al., 2016).

The governance of blue restoration has rarely been explored in literature, but lessons from terrestrial restoration indicate that blue restoration would benefit from considering the cultural context of the restoration, incorporating social science into restoration planning, collaborating with interdisciplinary stakeholders, and combining knowledge from scientific and local experts (France, 2016). However, governance of blue restoration differs from terrestrial restoration in some key ways. For example, land tenure rights are more complicated in blue ecosystems, since restoration sites may not be privately owned, leaving responsibility for restoration projects in the hands of communities and governments. Threats and impacts on blue ecosystems are different to those in the terrestrial environment, and feasibility of blue restoration is reduced by higher costs and risk of failure than in terrestrial restoration. Finally, blue ecosystems may take longer to recover than terrestrial ecosystems, leading to a slower rate of returns and ultimately reduced investment (Bell-James, 2016). Governments and non-government organizations could encourage blue restoration through subsidies, partnerships, or payment for ecosystems services schemes to overcome these barriers (e.g., for blue carbon; Bell-James, 2016).

CONCLUSION

Blue restoration can make an important contribution to meeting global environmental targets. Blue restoration is a less established field than terrestrial restoration, which has moved on from simple interventions at local scales and based on a static environment, to more advanced interventions acknowledging and planning for changing environments. It is a field that has been relatively under-funded, and predominantly limited to smaller-scale and somewhat experimentally localized projects. Conversely, terrestrial restoration is trending toward large-scale restoration aiming to fulfill multiple goals (e.g., conservation, ecosystem function, climate change mitigation and adaptation), with an increased sensitivity to the societal context of restoration (Perring et al., 2015). The success of blue restoration depends upon progressing quickly along this trajectory, while acknowledging unique characteristics of blue ecosystems (Bell-James, 2016). Understanding which restoration interventions will be most successful and where, is a crucial priority for the field (Perring et al., 2015). For example, the ecological, technical, and financial feasibility of a project is redundant if socio-political contexts make projects unworkable (Lovelock and Brown, 2019). Numerous barriers are regularly encountered during blue restoration projects and are not confined to a single ecosystem type. Understanding these barriers, as well as utilizing the knowledge gained from projects that have approached innovative and multi-faceted solutions to overcoming those barriers, is key to improving the future success of blue restoration, as well as the ability for restoration projects to be scaled up. Successful scaling-up of blue restoration requires an inter-disciplinary approach that addresses the barriers outlined in this paper and doing so is the only solution to meeting global restoration goals. Demonstrations of blue restoration projects where solutions to common barriers have been discovered can inspire, generate innovative solutions, and provide guidance to the global blue restoration community.

AUTHOR CONTRIBUTIONS

PS-S conceived of and initiated the workshop that all authors contributed to and attended. The bulk of the writing and figure creation was done by PS-S. All authors contributed to the development and writing of the manuscript for their area of expertise. The case studies were researched and written by groups within the author list, and then the overall manuscript was edited by all authors.

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SUPPLEMENTARY MATERIAL

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PERSPECTIVE
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Financial and Institutional Support Are Important for Large-Scale Kelp Forest Restoration

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Kelps form extensive underwater forests that underpin valuable ecosystem goods and services in temperate and polar rocky coastlines globally. Stressors, such as ocean warming and pollution are causing regional declines of kelp forests and their associated services worldwide. Kelp forest restoration is becoming a prominent management intervention, but we have little understanding of what drives restoration success at appropriate spatial scales. Though most restoration guidelines stress the importance of planning, stressor mitigation and ecological knowledge, other factors, such as lack of resources or institutional support are rarely discussed despite being potentially critical to achieving desired restoration outcomes. In this paper, we work to understand the importance of finances and institutions in the context of four of the world's largest kelp restoration projects. These projects span four countries, six kelp genera and were initiated in response to different causes of decline. We argue that to restore kelp at desired scales, adequate financing, and institutional support are critical to overcome ecological and environmental limitations. Acknowledging limitations, we outline ways to mobilize resources and encourage institutions to support kelp restoration.

Keywords: kelp, restoration, success, large scale, transplants, coastal management, urchins

INTRODUCTION

Kelp forest restoration (Orders Laminariales and Fucales) aims to reverse the loss of these ecologically and economically important coastal ecosystems (Dayton, 1985; Wernberg et al., 2019). To be successful, restoration projects must first mitigate or remove the cause of decline, which can include ocean warming, overgrazing, habitat destruction, pollution, and overfishing (Steneck et al., 2002; Vergés et al., 2014; Wernberg et al., 2019). If there is sufficient propagule supply, removing grazers (North, 1978; Fujita, 2010; Tracey et al., 2015), adding hard substrate (Carlisle et al., 1964), remediating water quality (Driskell et al., 2001), or a combination of each, may be enough to restore populations (Reed et al., 2004; Foster and Schiel, 2010). Additional actions are required when local propagule supply is insufficient or recruitment is limited (North, 1978; Campbell et al., 2014). Methods to overcome these barriers include introducing reproductive material or donor plants into degraded areas via seeding or transplanting (Carney et al., 2005; Verdura et al., 2018). Notwithstanding these advances in the field, most kelp restoration projects to date have been small scale (<100 m^2), short in duration (<2 years), and academically motivated (Eger et al., 2020; Morris et al., 2020). As a result, questions remain about how the field of kelp restoration can meet its goal of restoring populations at scales that match those of degradation or loss.

General ecosystem restoration principles are well-established and can help guide kelp restoration (**Figure 1**). These steps are extensively discussed elsewhere (Hobbs and Harris, 2001; Gann et al., 2019), but briefly involve: (1) defining clear goals and criteria to evaluate success, which then allows for (2) designing and (3) implementing the project, followed by (4) evaluating programs to determine if the performance criteria are met. If criteria are not met, these previous steps allow for (5) identifying reasons for failure and (6) using adaptive management to remediate the project to meet its goals (**Figure 1**). While the ecological barriers and methodological steps to restoration are often well-defined, the social, governance, and financial barriers to restoration typically receive less attention and are the focus of this perspective.

Past research has demonstrated how substantial financial resources are needed to support restoration activity and how institutions can provide the logistical, legal, and social framework to initiate and sustain restoration activity. Ecosystem restoration is cost and labor intensive, with median costs of 10s of thousands USD (2010) per hectare in terrestrial systems (De Groot et al., 2013) and 100s of thousands of USD in marine ecosystems (Bayraktarov et al., 2016). Indeed, many marine restoration projects have been flagged as too expensive to implement (Yeemin et al., 2006; Bellwood et al., 2019). Each step involved in restoration projects requires funding (**Figure 1**) and failure to finance any step is likely to compromise further steps and undermine the success of the whole project. Therefore, large-scale marine restoration projects require considerable financial inputs. Furthermore, failing to engage with the local stakeholders who interact with the ecosystem is likely to negatively influence the success of projects. Hence, restoration projects must consider social aspects to achieve long term success (Abelson et al., 2016; Budiharta et al., 2016). Such aspects are particularly complex in marine ecosystems as these have multiple resource users and restoration sites are often in the public domain (Ruddle et al., 1992; Ounanian et al., 2018).

Strong institutional support (national, regional, or local) can help remove socio-economic barriers. First, trusted institutions, such as NGOs, private industry, and community groups have significant social influence and can increase community support for projects (Voyer and van Leeuwen, 2019) while making sure the projects meet the needs of the community. Second, government institutions often have considerable resources to fund projects (Meyers et al., 2020). They also have the legal authority to mandate restoration, work within maritime laws, and incentivize restoration projects (Clewell and Aronson, 2006).

Here, we take a case study approach to examine the role of financial and institutional support in four of the largest kelp restoration projects documented to date. We identified projects with the largest area resorted (110–21,000 ha) by querying the results of a kelp restoration database which contains multi-language published and unpublished records of kelp restoration projects from 1957 to 2020 (Eger et al., 2020). The selected projects are in California (United States), Norway, Korea, and Japan, and span six genera of macroalgae. Kelp loss in these areas was due to water pollution, herbivore grazing and urban development, and restoration was done through the use of transplants, seeding, and herbivore removal, as well as deployment of artificial reefs (**Figure 2**).

LARGE-SCALE RESTORATION PROJECTS

Wheeler North Reef, Southern California, United States

Discharge of cooling water from the San Onofre Nuclear Generating Station (SONGS) in southern California caused the loss of 73 ha of giant kelp *Macrocystis pyrifera*. To offset this damage, the State of California mandated the utility company that owned SONGS to: (1) construct an artificial reef that was large enough to replace the kelp forest destroyed by SONGS' operations, and (2) provide funding for independent monitoring to ensure that the artificial reef maintains similar ecological levels of kelp and fauna as adjacent natural reefs while also meeting absolute targets to offset the losses of the initial reef (Songs Experimental Reef Permit E-97-10 Adopted Findings, 1999). Practitioners built the SONGS artificial reef, named "Wheeler North Reef," in three phases. The first phase started in 1999, and spent 5-years testing the efficacy of different reef designs to restore kelp (Reed et al., 2004, 2006). The monitoring results from this first phase were used to inform the design of the second phase: an additional 62 ha of reef. Ten years of additional monitoring showed that while the reef had similar kelp density and biota composition to nearby natural reefs, it did not meet the absolute standing stock standards for giant kelp and reef fish because the reef was deemed to be too small (Schroeter et al., 2018). In response, the state of California required the owners of SONGS to construct a third phase of the project (2019–2020) that added 85 ha of quarry rock reef. The resulting 156 ha reef extends along 7 km of coast and is one of the world's largest man-made rocky reefs. Cost estimates of the construction and monitoring of Phases 1 and 2 is tens of millions of USD, with monitoring costing ∼\$1 million USD/year while the estimated construction costs for Phase 3 are between \$17.62–\$27.89 million (USD, 2010; Southern California Edison, 2017).

Urchin Culling, Northern Norway

During the 1970s, population expansions of sea urchins (*Strongylocentrotus droebachiensis*) formed grazing fronts

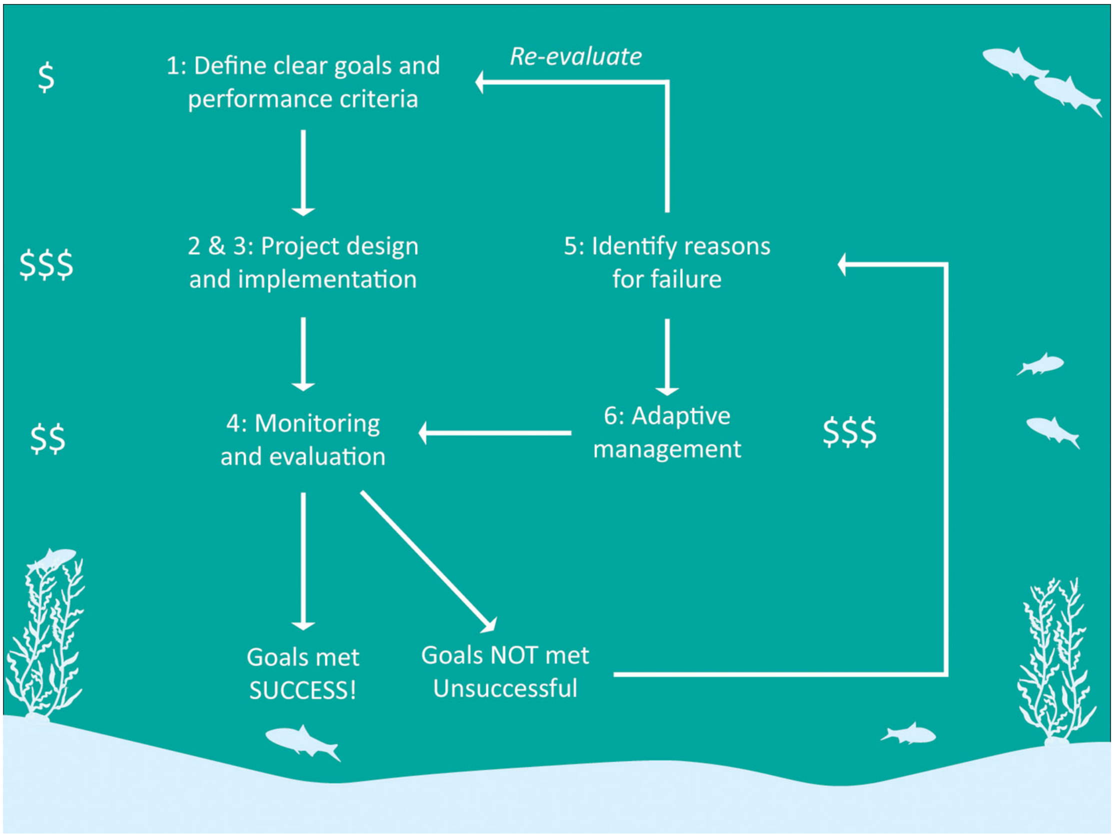

FIGURE 1 | Flow chart of best-practice steps involved in restoration projects. Dollar signs indicate the relative costs of each step.

that transformed approximately 900,000 ha of kelp forest along the northern coast of Norway into persistent urchin barrens (Norderhaug and Christie, 2009). In 2011, a pilot project involving local authorities, research institutions, and industry tested whether the use of quicklime (CaO), which dissolves urchin tests on contact, had any unintended environmental impacts in Porsanger Fjord. After 1 year, cover of macroalgae and kelp increased, and the method was then scaled up in Porsanger in year 2 (~30 ha) and replicated in nearby Hammerfest over an area of ~80 ha in 2017 (Strand et al., 2020). These efforts resulted in the return of the kelps *Saccharina latissima* and *Alaria esculenta* and increases in faunal biodiversity. The estimated cost of applying quicklime over 100 ha was $130,000 (USD, 2010), but the Norwegian Research Council provided substantial additional funds for pilot projects, monitoring, and research between 2011 and 2017.

Marine Restoration Program, Korea

Kelp declines along the east coast of Korea have been mostly caused by sea urchin grazing, resulting in the loss of *Sargassum* spp., *Undaria pinnatifida*, and *Saccharina* spp. On the south coast and off the island of Jeju, urchins are absent and declines of *Ecklonia* spp., *Sargassum* spp., and *U. pinnatifida* are mainly due to coastal development and habitat loss. These deforested areas increased rapidly in the 1990s and individual restoration efforts first began in 2002 (Choi et al., 2003).

In 2009, the government sought to upscale initial restoration efforts and established a national research fund for kelp restoration. The project has been managed by two government bodies, first the National Institute of Fisheries Science (NIFS) and later by the Korea Fisheries Resource Agency (FIRA). The project also partnered with Sungkyunkwan University and Pukyong National University to evaluate the status of kelp beds and urchin barrens, and to develop new restoration techniques. This initiative aims to restore 54,000 ha of kelp forests (Park et al., 2019) by the year 2030 and to enhance fisheries in Korea.

The project focuses on deploying concrete artificial reefs in areas with low urchin density (Jeon et al., 2015) in combination with juvenile kelp transplants, seeding (spore bags), and/or urchin removal, and subsequent monitoring. As of 2019, reefs and transplants were deployed over an area of approximately 21,489 ha (Park et al., 2019; Hwang et al., 2020) with a survival rate of ~50% (Jeon, 2019, personal communication). Artificial reefs were originally used because the agency believed that transplanting kelp onto rock covered by crustose coralline algae would limit success, but new methods are being developed to deploy transplants onto natural rocky reefs. The final goal involves restoration at 260 locations across the coast and a budget of $267 million (USD, 2010) for the years 2015–2030.

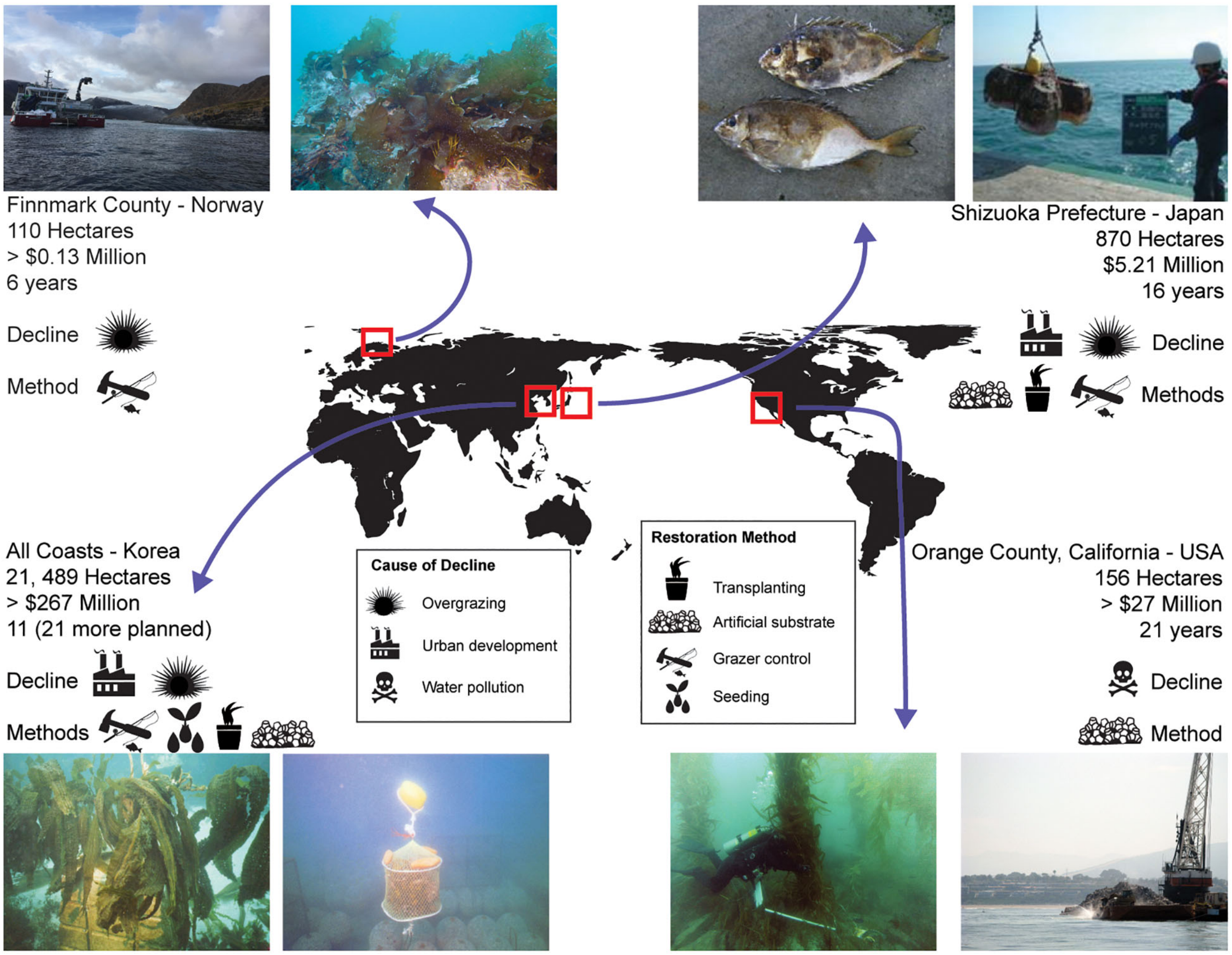

FIGURE 2 | Location, methods, cause of decline, size, and costs of the four large scale kelp restoration case studies. All costs are reported in USD for the year 2010.

Transplants, Shizuoka Prefecture, Japan

Increased turbidity and browsing by herbivores contributed to the decline of 8,000 ha of *Ecklonia cava* and *Eisenia nipponica* beds in Hainan, Japan between 1985 and 2000 (Hasegawa, 2010). As a result, the wild *Eisenia* and abalone fisheries closed and interest in renewing these resources soon followed (Unnno et al., 2010). In 1999, the Shizuoka Prefectural Government started initial restoration efforts by transplanting small concrete blocks into nearby *Ecklonia* beds to accumulate sporophytes, which were then relocated to the target site in the Hainan area. Initially, this work was successful, but within three years, herbivorous fish (e.g., *Siganus fuscescens*) grazed the transplants. A second, larger attempt then followed. Instead of seeding blocks in the field, *Ecklonia* sporophytes were mass cultured using a deep-sea water circulation system and attached to 2,162 concrete blocks, which were then placed onto natural rocky reefs. Placing the transplants on the blocks elevated the plants off benthos, a place where they are vulnerable to increased turbidity. In addition, the governing bodies paid local fishermen to remove herbivorous fish. This attempt was supported by local fishery cooperative, the municipal, prefectural, and national governments, which each provided logistical support and financial resources. The project ran between 2002 and 2010, with a budget of $5.21 million (USD, 2010). Following continued efforts, monitoring shows the project has restored approximately 870 ha of kelp habitat as of 2018 and fisheries cooperatives are now considering the re-opening of the abalone fishery.

PROJECT COMMONALITIES

Subtidal coastal restoration is a complex and expensive enterprise that is estimated to cost thousands to millions of dollars (USD, 2010) per hectare (Bayraktarov et al., 2016). Restoring kelp forests is no exception and actions, such as urchin culling, kelp cultivation, outplanting, and reef building are both time and resource intensive. Projects described here had budgets from $5 to $267 million USD (2010), which also allowed them to run for extended periods of time (>6 years). In addition, all four projects were managed by multipartite partnerships from universities, industry, and government agencies. We believe that strong financial and institutional support, typically by government, enabled these projects to conduct kelp restoration on such large scales.

Supporting Best Practices in Restoration

Though high levels of investment do not guarantee success (Bayraktarov et al., 2016), they enable projects to follow best practices for restoration. In all the described projects, funding over an extended period allowed managers to develop and test methodologies, assess initial results and alter the approach taken based on evidence. For example, the urchin culling efforts in Norway repeatedly tested the potential impacts and efficacy of the quicklime approach before investing further resources and upscaling the project. Although the planning stages of a project (**Figure 1-1**) represent a small part of the overall budget, they are important to ensure an effective framework for restoration (**Figure 1**). Because populations take several years to establish and even longer for a full ecosystem to return (Carter et al., 1985; Tegner et al., 1997) monitoring is required over an extended period of time. In the Wheeler North Reef project, extensive monitoring revealed that although kelp recruited on the reef within 9 months, the kelp biomass failed to offset the original estimated losses of kelp and fish biomass, even 12 years after restoration. Moreover, adaptive management is only feasible if active monitoring occurs. Adaptive management can be vital to the success of a project and may often be the most expensive step because it requires effective monitoring and quick mobilization of resources to address the detected problems (**Figure 1-6**).

Having multiple groups from different sectors involved in the restoration process can help reduce individual costs per group and draw on different areas of expertise (Gann et al., 2019). All four projects were the result of multiple collaborations between different stakeholders from academia to government to industry, with government participation being the one common partner group across the four projects. This commonality suggests that working with relevant government agencies can help achieve restoration at meaningful scales. This may be because government bodies lend legitimacy to the project (Van Tatenhove, 2011), provide legal backing (Lausche and Burhenne-Guilmin, 2011) and secure sustained funding (Waldron et al., 2013). Involvement from academia can help develop methodologies while locally based groups can ensure that the project has the support and is meeting the needs of the community.

Just as financial and institutional support can enable project success, their absence can lead to failure. Early efforts (1959–1976) in Southern California were initially successful in restoring patches of *Macrocystis*, but insecure funding resulted in sporadic maintenance of the sites and, eventually, project termination. Where restoration projects were not completed, sites often returned to their unrestored condition (Wilson and North, 1983). Indeed, many projects often run by volunteers and funded with donations have had to cease operations as funding depleted (Eger et al., 2020). Regulations meant to protect ocean resources can also hinder projects. For example, working to install kelp transplants or seeding is subject to stringent environmental reviews in most locations around the world and this poses as a barrier to entry for many groups (Pace and Morgan, 2016). Nevertheless, working within such regulations will help ensure that restoration activities are conducted in a safe and ethical manner but factors, such as an expedited review process for urgent environmental decisions and modifications to regulations to facilitate a future of increasing restoration must be considered.

Mobilizing Financial and Institutional Support for Large Scale Restoration

Developing strategies to enhance financial and institutional support for kelp forest restoration is critical for the success of large-scale restoration projects. Financial support often flows from institutional support, i.e., once institutions are motivated, they will fund restoration, not *vice versa*. There are many levers that can be pulled to increase this support. First, most institutions will only invest in an enterprise if it is understood to benefit them. Currently, the benefits of kelp forest ecosystems are poorly understood, and institutions are therefore reticent to invest in their restoration (De Groot et al., 2013). Therefore, a key first step in increasing support for restoration is quantifying and promoting the value of ecosystem services in kelp forests (see early work in Vásquez et al., 2014; Blamey and Bolton, 2018) and then integrating those values into government decision making processes. This connection is well-demonstrated in Korea and Japan where both countries have strong socio-economic ties to the ocean and have invested millions of dollars into restoration (Bestor and Bestor, 2014).

International frameworks and agreements can also be used to mobilize resources. For instance, the Global Oceans Accounts Partnership (GOAP)[1] provides an initial framework for quantifying ecosystem services and using the economic values in decision making. GOAP has support from the UN-ESCAP, Fisheries and Oceans Canada, the World Bank, and is being piloted in 11 countries (Global Ocean Accounts Partnership, 2019). Other multi-national organizations and agreements can also be used to further restoration. The UN Decade on Ecosystem Restoration and the UN Decade of Ocean Science for Sustainable Development were agreed to by all 193 UN member states and provide paired international imperatives to set binding targets for kelp forest restoration. These international targets should motivate national restoration projects.

Creating and reinforcing environmental protection laws and mandating development projects to mitigate and offset damages to marine habitat will help institutionalize restoration that may otherwise not occur (Akhtar-Khavari and Richardson, 2019). The benefits of these requirements were well-demonstrated in Wheeler North Reef restoration project. The utility company was legally required to offset habitat losses from the operation of their commercial activities. Many countries currently have offsetting laws (Niner et al., 2017) but few kelp restoration projects have been completed in response to development projects that destroyed habitat (Eger et al., 2020). This gap suggests that kelp maybe an overlooked habitat with regard to offsetting.

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[1] www.oceanaccounts.org

Financing for future kelp restoration projects will likely come from a mix of for-profit (e.g., industry) and non-profit (e.g., governments, universities, NGOs, philanthropies) funds and initiatives. Investments from non-profit sources are likely to be motivated by the provision of publicly available ecosystem services, such as fisheries and cultural values. Whereas profit driven funding will require private financial returns. Mechanisms like payments for ecosystem services and blue bonds (Salzman et al., 2018) can be used to attract for-profit funding to restoration projects (Thiele and Gerber, 2017). In other instances, businesses may invest in ventures that generate a commodity, such as sea urchin roe or the kelp itself but still work to restore wild populations (Gentry et al., 2020). Some of these ventures will be purely private whereas others will be mixture of private and public funds (i.e., blended finance, Rode et al., 2019).

CONCLUSION

Financial and institutional support of kelp restoration projects appear to be critical to enable kelp restoration at relevant scales. These supports are in addition to, not replacement of, good planning and ecological understanding of the system and are crucial at most, if not all, steps of the restoration process (**Figure 1**). Encouragingly, we show that with the appropriate financial and institutional support, successful kelp restoration is achievable at large scales. Fortunately, there are several ways to gain such support, including clearly demonstrating the ecological and socio-economic values of the services provided by ecosystems. Financial and institutional support will become more important in the future as ocean ecosystems change and new solutions to sustain them are required (Coleman and Goold, 2019).

DATA AVAILABILITY STATEMENT

All datasets analyzed for this study are included in the article/supplementary material.

AUTHOR CONTRIBUTIONS

AE, AV, DR, PS, MM-P, and EM conceived the idea for the manuscript. AE and EM led the writing. CF and HC wrote the Norway section. MH and DF wrote the Japan section. JK and CC wrote the Korea section. DR wrote the California section. AE, AV, MC, MM-P, PS, and EM wrote the first draft. All authors provided comments, edited, and approved the full manuscript for submission.

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REVIEW
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Challenges for Restoration of Coastal Marine Ecosystems in the Anthropocene

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Coastal marine ecosystems provide critical goods and services to humanity but many are experiencing rapid degradation. The need for effective restoration tools capable of promoting large-scale recovery of coastal ecosystems in the face of intensifying climatic stress has never been greater. We identify four major challenges for more effective implementation of coastal marine ecosystem restoration (MER): (1) development of effective, scalable restoration methods, (2) incorporation of innovative tools that promote climate adaptation, (3) integration of social and ecological restoration priorities, and (4) promotion of the perception and use of coastal MER as a scientifically credible management approach. Tackling these challenges should improve restoration success rates, heighten their recognition, and accelerate investment in and promotion of coastal MER. To reverse the accelerating decline of marine ecosystems, we discuss potential directions for meeting these challenges by applying coastal MER tools that are science-based and actionable. For coastal restoration to have a global impact, it must incorporate social science, technological and conceptual advances, and plan for future climate scenarios.

Keywords: coastal marine ecosystems, social-ecological restoration, coral reefs, seagrass, mangrove, oyster reefs, kelp, saltmarshes

BACKGROUND

Humanity is facing serious environmental challenges at the onset of the Anthropocene (Crutzen, 2002; Kareiva et al., 2011; He and Silliman, 2019). The swift decay of natural ecosystems, their biodiversity, and services to humans presents a global challenge (Dobson et al., 2006; Dirzo et al., 2014; Hautier et al., 2015). Coastal marine ecosystems are immensely important for human well-being (Barbier, 2012; Duarte et al., 2013), and they are among those facing the most rapid ecological degradation (Lotze et al., 2006; Duke et al., 2007; Waycott et al., 2009; Beck et al., 2011; Burke et al., 2011; Bugnot et al., 2020), resulting in declines in the goods and services that they provide to society (Cesar, 2000; Barbier, 2012; Costanza et al., 2014).

The decline of many coastal ecosystems and current lack of effective solutions for reversing this trend have triggered growing interest in developing tools for the restoration of degraded marine environments (Edwards, 1999; Elliott et al., 2007; Borja, 2014; Possingham et al., 2015; Kienker et al., 2018; Airoldi et al., 2020). For example, recovering ecosystem structure and function through restoration has recently been identified as one of eight "grand challenges" in marine ecosystems ecology (Borja, 2014). Although significant progress has been made in some coastal systems, notably mangroves, kelp forests, wetlands, seagrass meadows, oyster reefs, and to some extent, coral reefs (Hashim et al., 2010; Beck et al., 2011; Roman and Burdick, 2012; Campbell et al., 2014; van Katwijk et al., 2016; Boström-Einarsson et al., 2020; Eger et al., 2020), restoration science of coastal marine ecosystems lags behind terrestrial and freshwater counterparts (Craig, 2002; Suding, 2011).

Restoration has been defined in multiple ways (Elliott et al., 2007). Here, we use the common definition, "the process of assisting the recovery of damaged, degraded, or destroyed ecosystems" (Hobbs et al., 2004; SER, 2004), which views restoration as a broad term that spans from preventative management aimed at stress relief to full habitat reconstruction. We consider restoration to be an integral part of conservation management (Abelson et al., 2015; Possingham et al., 2015), but the full recognition of ecological restoration as an essential element of coastal marine management (Murcia et al., 2014) will require well-defined and achievable objectives, and reliable cost-effective restoration tools (Bayraktarov et al., 2016). While we acknowledge that progress has been made in developing novel tools for marine ecosystem restoration (MER; e.g., eco-engineering or nature-based solutions; Morris et al., 2019), the increasing rate of degradation of coastal environments emphasizes the need for rapid development of integrative approaches to science-based restoration of marine ecosystems (e.g., Elliott et al., 2007; Abelson et al., 2015; Possingham et al., 2015; Airoldi et al., 2020). An important first step in this process is to identify major scientific, societal and operational gaps in coastal MER, which should help to accelerate the development of more effective, scalable tools and practical approaches for coastal MER. Overall, our goal is to build an effective framework for enhancing the multidisciplinary science of coastal MER via the following objectives: (1) development of cost-effective, scalable restoration tools, (2) use of these tools to promote adaptation of coastal marine ecosystems to cope with climate change and global stressors, (3) integration of social and ecological restoration priorities, and (4) fostering the acceptance and routine consideration of coastal MER as a scientifically credible management tool (**Figure 1**).

DEVELOPMENT OF EFFECTIVE, SCALABLE RESTORATION TOOLS

Many current coastal MER tools (techniques and methodologies) have been criticized for high costs that exceed perceived benefits, often with superficial treatment of symptoms rather than the causes of degradation (Elliott et al., 2007; Mumby and Steneck, 2008; van Katwijk et al., 2016; but see Lefcheck et al., 2018; Reguero et al., 2018). Four common and potentially interrelated methodological problems that can result in coastal MER failure are: (1) lack of clear criteria for success, (2) challenging site selection, (3) inadequate or inappropriate tool selection/availability including scalability commensurate with the scale of degraded habitats, and (4) poorly designed assessment protocols (Suding, 2011; Abelson et al., 2015; Bayraktarov et al., 2016).

Lack of Clear Criteria for Success

The implementation of clear, measurable restoration goals requires quantifiable benchmarks for determining whether or not the stated restoration goals are achieved (SER, 2004; Suding, 2011). Specific criteria used to measure success (such as resilience indicators; Maynard et al., 2015) will by necessity vary depending on project goals and stakeholder interests, and should be specified at the outset. The inclusion of key stakeholders and the institutions they represent is crucial in the framing of restoration strategies and related expectations of the outcomes of the MER effort. Projects are likely to gain wider acceptance if their goals are broadened to include ecosystem services such as coastal protection and job creation (Temmerman et al., 2013; Kittinger et al., 2016; World Bank, 2016) that benefit a variety of aware and connected stakeholders (Coen and Luckenbach, 2000; Abelson et al., 2015; Strain et al., 2019).

Site Selection Issues

Appropriate site selection, especially complicated in increasingly urbanized and fragmented systems, is a major determinant of restoration success (Suding, 2011; Bayraktarov et al., 2016). The selection of sites to be restored should be done carefully with consideration of both ecological (e.g., connectivity among populations) and social (e.g., business plan for long-term stewardship) objectives that can reduce the risk of restoration failures (Abelson et al., 2015; Bayraktarov et al., 2016). Also, restoration should be prioritized in areas where the local stressors responsible for the initial degradation of the site are known and can be reduced to levels compatible with the long-term sustainability of the intervention. In cases of non-manageable stressors, e.g., climate-change effects or heavy boat traffic, a different restoration approach should be applied, which promotes adaptation to cope with climate-change conditions (see section "Promoted adaptation"), or eco-engineering techniques, such as living breakwaters, to insulate against stressors (see New tools, approaches, and conceptual framework, below). If multiple candidate sites are available, then these should be compared by relating past, present and predicted future community states using information on environmental conditions, ambient stressors, risks, biodiversity values, and ecosystem services (e.g., Game et al., 2008; Abelson et al., 2015, 2016a).

Assessment of Achievements

Inadequate funding for well-designed monitoring aimed at evaluating the success of a project in meeting its objectives is

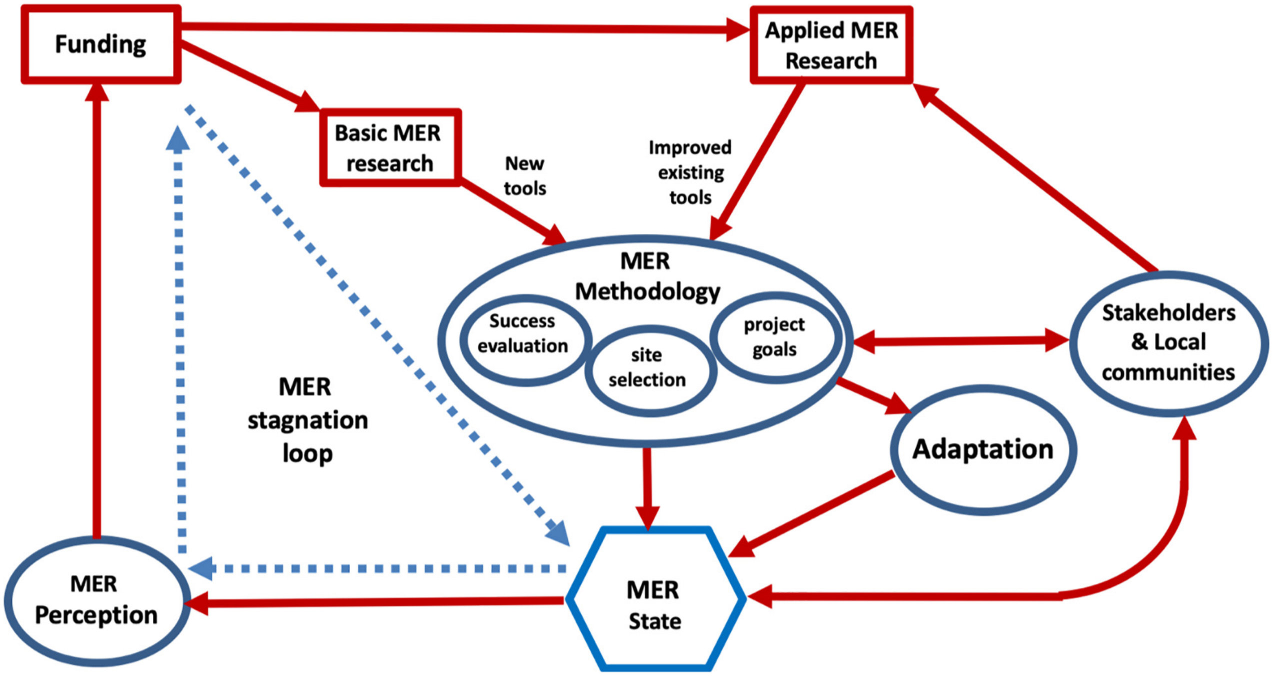

FIGURE 1 | Conceptual framework of the four major coastal Marine Ecosystem Restoration (MER) challenges (i.e., development of tools, adaptation to global stressors, social-ecological integration, and promotion of MER perception; blue circles), and their governing and interacting factors (red rectangles), all of which influence the state of coastal MER (i.e., the success and progress of MER projects; hexagon). Solid arrows indicate flow of knowledge, labor and other monetary values. Broken arrows indicate interactions among the coastal MER positive-feedback loop ("stagnation loop").

another major drawback of restoration efforts in general (Palmer and Filoso, 2009; Suding, 2011), and in coastal marine ecosystems in particular (Bayraktarov et al., 2016). Even in cases where monitoring and evaluation is planned, it is often funded for a short period of time, not allowing for proper assessment of the outcome of the project over time (Statton et al., 2012, 2018). In other cases, monitoring is overlooked and considered to be an unnecessary additional cost of restoration (Bayraktarov et al., 2016). However, information gained from monitoring (ecological and social parameters) is not only necessary for determining whether the restoration goals are being met, but is essential in determining the reasons for failures, which are critically important for informing future restoration and conservation efforts. Such information is also essential for evaluating the long-term resilience of MER interventions in the face of changing climatic and societal pressures such as land use that results in continued degradation of water quality and habitat destruction (Bouma et al., 2014). The length of monitoring will depend on the stated restoration goals and performance criteria, and on the ecology of the system being restored, which influences rates of recovery. Additionally, the timescales of recovery periods may be related to the life-history characteristics of the key species targeted for restoration (e.g., ecosystem engineer species, Montero-Serra et al., 2018). Therefore, the design of monitoring programs should include relevant ecological (e.g., demographic knowledge) and social performance metrics and governance indicators (e.g., fish functional diversity, fish catch yields, coastal erosion rates, level of conflict among stakeholders), with the cost of developing and implementing a monitoring plan included as a prerequisite for all restoration projects.

New Tools, Approaches, and Conceptual Frameworks

Advancements in restoration tools and approaches that optimize success and cost-effectiveness of coastal MER may take several directions. First, indirect restoration tools can revitalize damaged ecosystems by alleviating physical stressors or improving local conditions (also termed passive restoration; Perrow and Davy, 2002). For example, improving the quality of coastal waters by restoring terrestrial ecosystems within the relevant watershed area (e.g., by re-forestation, retention ponds and constructed wetlands; Bartley et al., 2014; Abelson et al., 2016a; Roque et al., 2016; Lefcheck et al., 2018). The restoration of the hydrological conditions in mangrove rehabilitation areas provides another example, including dismantling weirs and removing dikes and dams to reduce the duration of inundation with polluted water. This in turn may enhance the dispersal and successful colonization of propagules, and promote the chances of natural regeneration (Van Loon et al., 2016). The implementation of indirect tools that have the potential to accelerate recovery and enhance resilience of restored systems should be considered in combination with direct approaches (e.g., planting and seeding) to achieve restoration goals (e.g., Lefcheck et al., 2018).

Second, technological advances can lead to efficiencies of scale and drastic reductions in cost. For instance, restoring corals through large-scale capture and release of coral larvae on decayed reefs is predicted to be much cheaper than restoring the same amount of area with garden-grown adult corals (Doropoulos et al., 2019). Likewise, restoring marsh grasses and seagrasses is sometimes more successful when they are outplanted with biodegradable structures that protect them from wave action and sediment erosion (Temmink et al., 2020, but see Orth et al., 1999; Statton et al., 2018). Another potential direction for optimizing restoration success is the development of relatively low-cost restoration tools that can be effectively scaled to different sized projects (Spurgeon, 1999; Spurgeon and Lindahl, 2000; Bayraktarov et al., 2016). An example of one such restoration approach involves restocking of key consumers (also termed "biomanipulation;" Lindegren et al., 2010). For instance, depleted herbivorous fish populations on degraded coral reefs can lead to undesirable algal-dominated phase shifts following natural disturbance events (e.g., Bellwood et al., 2006). However, in many cases the recovery of fish populations under strict fishery management and fishing bans may take many years (up to several decades; e.g., MacNeil et al., 2015). Therefore, restocking of herbivorous fish populations (accepting the prerequisite of protection in the restored site) may prevent the excessive proliferation of macroalgae, or accelerate their eradication and aid in the recovery of degraded reefs that have undergone a phase shift to an undesirable macroalgal-dominated state (Abelson et al., 2016b; Obolski et al., 2016). Under certain circumstances, eradication or culling of, for example, herbivores may be included in the restoration, mainly in temperate ecosystems (Piazzi and Ceccherelli, 2019; Guarnieri et al., 2020; Medrano et al., 2020).

Third, to improve outplanting yields, the paradigm in restoration ecology can be expanded from one frameworks that systematically identifies and reduces physical stressors, to one that also systematically harnesses positive species interactions at all levels of biological organization. This paradigm change was first proposed by Halpern et al. (2007) and Gedan and Silliman (2009) and received the first experimental support by Silliman et al. (2015), who found that planting marsh plants in clumps rather than in dispersed patterns as the paradigm called for resulted in a 100–200% increase in plant yields at no extra cost. Importantly, this study did not add extra resources to the restoration project; instead a simple design change in planting arrangement allowed for naturally occurring positive interactions to occur, as plants in clumps interacted to resist erosion and oxygen stress in the soil (Silliman et al., 2015).

Recent conceptual papers highlight that inserting positive species interactions into restoration of corals, seagrasses and mangroves, as well as into eco-engineered structures, can have beneficial outcomes and need not be limited to just intraspecific facilitation (Shaver and Silliman, 2017; Bulleri et al., 2018; Renzi et al., 2019; Smith et al., 2020; Valdez et al., 2020). Interspecific facilitation and mutualism could be equally or more important. For example, manipulation of the bacterial community is likely to enhance settlement and establishment of foundation species (e.g., corals, seaweeds and mangroves; Holguin et al., 2001; Kelly et al., 2014; Qiu et al., 2019); waterborne chemicals from various species could be mimicked at scale to induce coral settlement and fish grazing behavior (Dixson and Hay, 2012; Dixson et al., 2014); key autogenic ecosystem engineer species can enhance stress tolerance for associated organisms (i.e., "human-assisted evolution;" *sensu* Palumbi et al., 2014; van Oppen et al., 2015; see: section "Promoted adaptation"); predators can facilitate regrowth of seagrass systems and increase their tolerance to nutrient stress by promoting populations of algal grazing sea slugs (Hughes, 2014); and positive landscape-scale interactions involving fluxes of energy, materials and organisms among ecosystems can facilitate the establishment and persistence of foundation species (Gillis et al., 2014; van de Koppel et al., 2015). While incorporating positive species interactions into restoration designs holds great promise, a recent review unfortunately found that only 3% of over 600 studies investigating coastal restoration actually tested for the effects of inserting facilitation by design (Zhang et al., 2018).

Finally, management concepts should be implemented that combine restoration efforts with protection. Currently, protection and restoration are rarely integrated into management programs. Protection from anthropogenic stressors is generally not a prerequisite for MER projects, and restoration is often disregarded as a tool in MPA (marine protected area) management plans (Abelson et al., 2016a). We believe that including protection (MPAs) and stress relief in restoration projects as part of ecosystem-based management may be highly effective in conservation and the recovery of coastal marine ecosystems, and therefore, should be a normative baseline.

PROMOTED ADAPTATION

At present, coastal MER tools rarely enhance ecosystem resistance to climate-change related stressors such as ocean warming, sea-level rise and acidification (but see Shaver et al., 2018; He and Silliman, 2019). However, restoration of coastal vegetation-based ecosystems, which are major carbon sinks (i.e., saltmarshes, mangrove forests and seagrass meadows) can help mitigate climate change over large scales (Gattuso et al., 2018). When combined with other local-management actions, they can also help buffer global climatic impacts and compensate for critical ecosystem services that are impaired (Duarte et al., 2013; Possingham et al., 2015; Abelson et al., 2016a; Anthony et al., 2017; Darling and Côté, 2018; He and Silliman, 2019). Nevertheless, as climate-change mitigation (reduction of greenhouse gases emission) can take at least decades to affect the Earth's climate (Solomon et al., 2009), there is a growing recognition of the need to identify practical tools to promote adaptation to climate change, so that coastal marine ecosystems can continue to function and provide ecosystem services under a range of future environmental conditions (Webster et al., 2017; Darling and Côté, 2018; Abelson, 2020). We suggest that beyond fostering the services and ecosystem health of degraded coastal marine ecosystems, restoration tools be used to promote adaptation management to cope with future climate-change conditions. We further argue that under the reality of climate-change conditions, practices that promote adaptation should be included in coastal MER projects to improve their long-term success.

Promoted adaptation can be implemented via two potential directions: "Predict-and-Prescribe" approaches (e.g., "assisted evolution" and "designer reefs;" Mascarelli, 2014; Webster et al., 2017; Darling and Côté, 2018), which attempt to foresee future conditions; and the "Portfolio" approach, which considers the range of uncertainty of future conditions (Schindler et al., 2015; Webster et al., 2017; **Figure 2**). Although the two strategies are distinct, they may serve as complementary tools. That is, even though their applications depend on specific circumstances, both strategies can be simultaneously applied to increase the likelihood of recovery as well as helping to cope with future unpredictable conditions.

Predict-and-Prescribe

Predict and prescribe approaches are based on the notion that future environmental conditions can be predicted to some extent. Promoting adaptation of coastal marine ecosystems to predicted plausible climate change scenarios can be achieved by increasing either the intrinsic or extrinsic resistance of a system (Darling and Côté, 2018). Adaptation, in the context of "intrinsic resistance," often involves manipulating species or genotypes of ecosystem engineers (e.g., coral, mangrove, and seagrass species) to make the system better equipped to contend with changing conditions (e.g., elevated temperature and acidification), and to better resist climate change and other global stressors. Restoration employing "intrinsic resistance" approaches involves identifying or developing resistant genotypes or species, stockpiling them in sufficient quantity (e.g., via culture), and transplanting, re-introducing, or restocking them in areas most influenced by changing conditions – a process termed "assisted colonization" or "assisted migration" (Hoegh-Guldberg et al., 2008; Palumbi et al., 2014; van Oppen et al., 2015; Darling and Côté, 2018; Coleman and Goold, 2019).

Restoration employing "extrinsic resistance" approaches involves identifying and ensuring spatial refuge sites (i.e., "Resistance and Refuge;" Darling and Côté, 2018). Existing "no-take" MPAs tend to support high fish biomass, but typically provide little resistance to large-scale disturbances (Bates et al., 2019; but see Bates et al., 2014), which suggests a need for management to identify and protect regional refugia (Graham et al., 2008). Suitable refugia may include locations that are less vulnerable to climate disturbances (e.g., cool currents and deeper sites; Darling and Côté, 2018), or stressful or frequently disturbed habitats (e.g., high sedimentation, elevated temperature, acidified waters) whose constituent species are locally adapted to tolerate exposure to chronic stressors (Fabricius, 2005; Palumbi et al., 2014; Shamberger et al., 2014; Webster et al., 2017). Such habitats could serve as potential refugia due to their future resistance potential (e.g., Palumbi et al., 2014). Local refugia have the potential to drive cascading processes of large-scale recovery ("robust source sites;" Hock et al., 2017) by possessing high connectivity with the wider ecosystem network, and a low risk of exposure or sensitivity to disturbances. They serve as a source of replenishment when other sites are depleted, and promote the recovery of desirable species (Hock et al., 2017). Sites identified as potential local refugia need to be protected and the recovery of degraded sites of potentially high extrinsic resistance ("potential refugia") should be promoted by relevant restoration interventions. That is, sites can play a role as potential refugia thanks to favorable environmental conditions dictated by their location. However, if these sites are in a degraded state due to local anthropogenic stressors, they cannot serve as effective refugia, unless those local stressors have been eliminated or reduced and these systems have recovered. Also, for effective restoration and the selection of potential refugia, empirical genetic information is required to assess diversity and the potential adaptive capacity to cope with future conditions (Coleman et al., 2020). This is particularly pertinent for species that exhibit limited dispersal and are therefore susceptible to reduced gene flow (e.g., Buonomo et al., 2017).

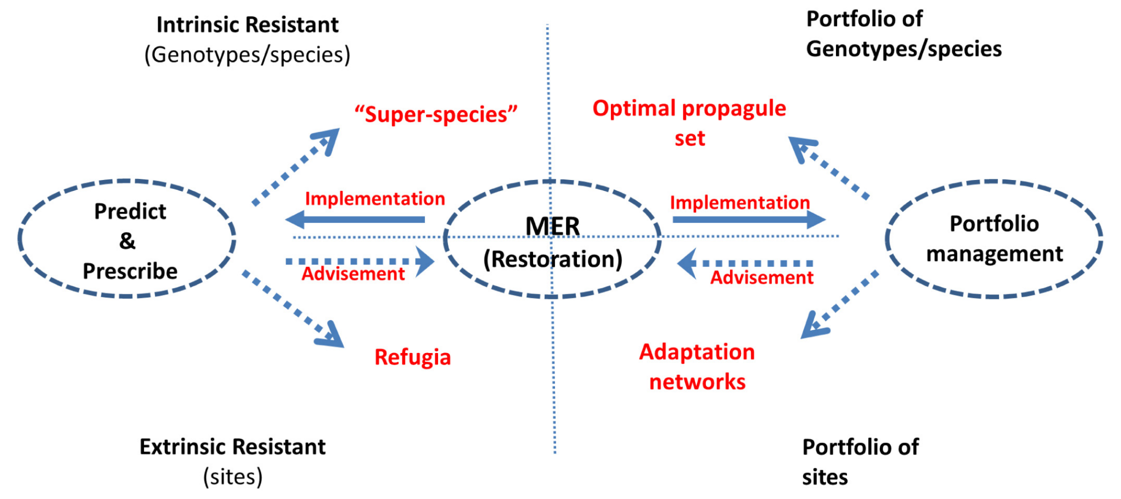

FIGURE 2 | Applying coastal Marine Ecosystem Restoration (MER) to build adaptation via two directions: "Predict and Prescribe" and "Portfolio management" approaches. Restoration tools can serve as implementation vectors of promoted adaptation. Alternatively, adaptation concepts can serve as considerations in planning sound restoration interventions.

The "Portfolio Management" Approach

The "Portfolio" approach is a risk management tool adopted from financial portfolio theory, which exploits information about spatial covariances in future ecological conditions and applies that tool to spatial targeting of conservation and restoration investments (Schindler et al., 2015; Webster et al., 2017). Recent research in fisheries and terrestrial ecosystems suggests that the portfolio theory can be applied as a potential approach to promote adaptation, while taking into account our inability to fully understand or predict the impacts of large-scale stressors (Crowe and Parker, 2008; Ando and Mallory, 2012; Schindler et al., 2015; Webster et al., 2017). The portfolio approach can be applied in coastal marine ecosystem management via two operational routes: portfolio of sites (adaptation networks of management units; Webster et al., 2017), and portfolio of genotypes and species (optimal sets of propagules; Crowe and Parker, 2008).

Portfolio of Sites

This approach is applied via adaptation networks, which are regional systems of managed areas (i.e., "management units") with attributes that promote adaptation (i.e., managed areas of high diversity, connectivity, and spatial risk mitigation; Webster et al., 2017). The management units should comprise sites of different states, depths and locations, and under diverse environmental conditions, but which are connected physically (horizontally and/or vertically) or demographically (via passive dispersal or active movement) to form networks. To maximize the ecological outcomes of each "management unit," adequate investment in protection features (planning and maintenance), notably staff capacity, fishery governance, effective enforcement, and MPA area size, has to be ensured (Edgar et al., 2014; Cinner et al., 2016; Gill et al., 2017). However, as most coastal marine ecosystems experience some extent of degradation, protection alone is insufficient and should therefore be integrated with restoration (Possingham et al., 2015; Abelson et al., 2016a). This requires investment in the exploration, examination, and development of restoration tools (e.g., Rogers et al., 2015; Abelson et al., 2016a; Anthony et al., 2017), the aim of which is to improve the recovery of each management unit.

Even if a minimum viable fraction of a given ecosystem can be protected, isolated sites may substantially weaken connectivity among the management units within the potential adaptation network (Green et al., 2015), which may in turn compromise ecosystem functioning and neutralize the effectiveness of the network (Gaines et al., 2010; Berglund et al., 2012; Green et al., 2015). Thus, the restoration of degraded coastal marine ecosystems can promote the recovery of otherwise low-quality management units and subsequently improve the connectivity (e.g., Abelson et al., 2016a; Bayraktarov et al., 2016) and the effectiveness of the "adaptation networks."

Portfolio of Genotypes and Species

Another application of portfolio theory is to select an optimal set of propagule sources ("propagule portfolio;" i.e., larvae, seeds, seedlings, and fragments) to be used to restore sites in environments of multiple plausible future climates, based on the results of a climate change impact model (e.g., Crowe and Parker, 2008). This approach combines the "intrinsic resistance" and the portfolio approaches, by applying the restoration tools required for the former with the concept of the portfolio of genotypes and species, which expands the set of propagules by a wide range of source sites under diverse environmental conditions.

To apply the "propagule portfolio," consideration should be given to selecting and culturing propagules comprising an optimal set of genotypes (i.e., a set that minimizes risk of maladaptation across a variety of future plausible climates, while meeting targets on mean adaptive suitability; Crowe and Parker, 2008), collected from populations that experience different environmental conditions, to use in the restoration of a target site via transplantation or restocking. This approach requires two data sources: (1) provenance trial data derived from multiple common culture trials of multiple propagule sources collected from populations located at various environmental conditions ("geographic points") within a region (e.g., genotypes adapted to pollution; Whitehead et al., 2017); and (2) environmental data for those geographic points (Crowe and Parker, 2008).

The portfolio approach is still largely theoretical with regard to the marine realm (but see Beyer et al., 2018). However, there is a growing array of models and proposed implementation methods that support its high potential as a management approach to cope with climate change and other unpredictable effects (e.g., Aplet and McKinley, 2017; Holsman et al., 2019; Walsworth et al., 2019). Moreover, some studies, from terrestrial and aquatic ecosystems, provide encouraging support for its applicability (e.g., Crowe and Parker, 2008; Penaluna et al., 2018; Eaton et al., 2019).

INTEGRATED SOCIAL-ECOLOGICAL RESTORATION

A major question related to ecosystem restoration in the Anthropocene is whether we can devise and implement restoration practices that service both the needs of society and promote sustained ecological functions and values (i.e., social-ecological restoration). The concept of "social-ecological restoration" extends beyond the usual scientific scope of "ecological restoration," to include reciprocal relationships between ecosystems and humans (Geist and Galatowitsch, 1999). We give this concept particular attention as restoration is a fundamentally human endeavor and social processes have been historically understudied (Wortley et al., 2013), despite the fact that they can be integral to project success (Bernhardt et al., 2007; Druschke and Hychka, 2015). Social-ecological restoration is not meant to replace ecological restoration and the consideration of natural heritage or biodiversity values, but rather to complement, as they are both nested subsets within the overall definition of restoration. Here, we highlight a few key ways that MER may benefit from the inclusion of social priorities as restoration goals and via the broadened participation of society.

The adoption of a social-ecological approach to restoration can help delineate clearer goals and aid in evaluating project achievements through performance criteria that go beyond just habitat creation (e.g., Palmer and Filoso, 2009) and contribute to the "blue economy" (World Bank United Nations Department of Economic and Social Affairs, 2017). Practically, this can be implemented by prioritizing targeted ecological and social restoration goals (e.g., conservation value, job creation, flood risk reduction; Abelson et al., 2015) that are valued by relevant stakeholders. For example, Stone et al. (2008) found that different resource user-groups were willing to contribute time and money to mangrove restoration in India, but the motivations and level of support were not consistent across groups and related to different perceived ecosystem services (i.e., fisherman supported restoration because they believed mangroves were good fish nurseries whereas rice farmers believed mangroves would control erosion). Accordingly, understanding local motivations for restoration and using that information to set and communicate clear and relevant restoration goals may enhance community buy-in and ongoing support for restoration initiatives. Furthermore, increasing societal understanding of and connection to restoration projects may facilitate more widespread support of ecological restoration as an effective management tool (Challenge 3; e.g., Edwards et al., 2013; NOAA SAB, 2014; World Bank, 2016; Strain et al., 2019).

With emerging threats from climate change and coastal urbanization, we can expect heightened conflict between MER, the propagation of new development and infrastructure, and shifting ecosystems that may impede MER efforts (e.g., mussel restocking in the wake of ocean acidification). Rising to this challenge, the field of eco-engineering has emerged with the goal of restoring ecosystems in a way that maximizes services that are desired by humans (e.g., coastal protection, waste-water treatment), rather than restoring to a previous state. These "designer ecosystems" are unlikely to deliver on all restoration goals (e.g., maximizing the restoration of biodiversity), but they are nevertheless likely to become a vital component of future coastal conservation plans for several reasons (Airoldi et al., 2020). First, eco-engineering projects that combine habitat restoration with infrastructure may be applicable in highly urbanized marine environments where large-scale restoration projects are infeasible or undesirable (Sutton-Grier et al., 2015; Morris et al., 2019). Recent research suggests that perceptions about what is desirable and acceptable in the marine environment seem to be normalizing toward degraded and artificial states (Strain et al., 2019); in these cases, eco-engineering projects can act as demonstration sites exhibiting some of the benefits of restoration within communities that are otherwise disconnected from nature. Second, eco-engineering projects may be able to provide a direct substitute for gray infrastructure that individuals and municipalities are already accustomed to paying for, and thus we may be able to redirect funding that has typically been spent to build and repair expensive gray infrastructure toward restoration (McCreless and Beck, 2016; Sutton-Grier et al., 2018; Airoldi et al., 2020). Finally, by diversifying the goals and motivations behind coastal MER projects, away from purely ecological priorities, it is likely that a larger sector of society will be engaged, restoration will be possible in a greater variety of environments, and highly urbanized areas will be able to contribute toward global restoration goals (e.g., The Bonn Challenge).

Societal involvement in the planning, implementation, and monitoring of restoration projects can play an important role in restoration success. Past experience suggests that integrated coastal MER projects that include consensus among different stakeholder groups are likely to be the most successful and cost-effective, especially in developing countries (Bayraktarov et al., 2016). Moreover, awareness of and connectedness to the marine environment can strongly predict social support for projects aimed at coastal rehabilitation (Strain et al., 2019). Therefore, the early and continuous engagement of key stakeholders (on multiple levels) should be integrated into restoration plans (**Figure 1**; Abelson et al., 2015; Zhang et al., 2018; Gann et al., 2019). Potential applications for such integration include "Marine Spatial Planning" (MSP; Tallis et al., 2012), marine protected area planning (Giakoumi et al., 2018) and other quantitative frameworks (Samhouri et al., 2012; Tallis et al., 2012). Furthermore, it has become increasingly popular to involve volunteers and citizen scientists in restoration practice and monitoring (Huddart et al., 2016), which can lower project costs (Bayraktarov et al., 2016), confer benefits to the participants including greater life satisfaction (Miles et al., 1998), and foster a stronger environmental ethos (Leigh, 2005). This in turn could help to raise support for other restoration initiatives that volunteers are not directly involved with, and potentially increase the social acceptability of projects. This mirrors the common notion that local communities are responsible for granting (or withholding) social license for a restoration effort, as these will be felt locally. Yet in practice, the dynamics of social acceptance frequently extend beyond local regions and can include stakeholders that are based far from the site in question. As Moffat et al. (2016) argue, restricting social license to local communities "neglects the organizational reality in a modern globalized world"; social license cannot therefore be restricted to "the exclusive domain of fence-line community members and operational managers." Nevertheless, volunteer efforts may not be feasible or cost-effective in certain contexts or at large scales, in which case it may be more efficient to employ local professionals.

Currently, in many conservation and restoration projects, high paying jobs and management positions go to outside professional experts and significant benefits do not reach local communities (e.g., Blue economy; World Bank United Nations Department of Economic and Social Affairs, 2017). Training and incorporating community-based professionals (e.g., Australia's Vocational Education Training programs in "Natural Area Restoration" and "Marine Habitats Conservation and Restoration") as active participants in all project stages will increase societal benefits as well as reduce potential tensions.

The value of implementing a social-ecological restoration approach in management frameworks is gaining traction. This is partly due to the ongoing degradation of coastal marine ecosystem services and the failure of traditional management practices to halt this decline (Possingham et al., 2015; Golden et al., 2016). Incorporating a social-ecological restoration component that focuses on ecosystem service outcomes, rather than exclusively relying on outcomes like biodiversity, may help compensate for decreasing ecosystem services, which now lie well below historical levels in many regions due to misuse, over-exploitation and the emerging threats of climate change (e.g., Golden et al., 2016 and citations therein). Expanding coastal MER to an integrated social-ecological system will increase the scope and complexity of restoration science and governance, and therefore demands expanded investments in development, implementation and maintenance.

PROMOTING THE PERCEPTION OF MER AS A SCIENTIFICALLY CREDIBLE MANAGEMENT APPROACH

The end of the 20th and early years of the 21st century yielded several key studies that raised the scientific background and awareness of ecological restoration, including coastal MER (e.g., Dobson et al., 1997; Edwards, 1999; Jaap, 2000; Young, 2000; Palmer et al., 2004).

In a literature search (Google Scholar) of the terms (restor* or rehabilitat*) and (marine ecosystem*, coral, mangrove, oyster, saltmarsh, kelp, or seagrass) in the title, we found relatively few restoration papers published prior to 2000 (**Figure 3**). The trend changed significantly circa 2000 with an order of magnitude increase in the number of restoration studies in six major coastal ecosystems (**Figure 3**). However, the total number of coastal MER studies remains negligible relative to restoration studies in terrestrial (e.g., forests) and freshwater (e.g., rivers and lakes) ecosystems. We recognize that our figures may be underestimates of the actual numbers of restoration studies. However, figures obtained by our search should provide a reasonable indication of the general trend of restoration ecology as a field of science, and the relative fraction of each sub-field for different ecosystems.

If the number of peer-reviewed publications serves as a proxy of investment in science (Ebadi and Schiffauerova, 2016), then it can be argued that, despite the growing research in coastal MER, investment is still relatively low, lagging behind restoration research of non-marine environments. A possible reason for this lagging behind of restoration of marine ecosystems is that their restoration projects are still undervalued (Gordon et al., 2020), mainly due to criticism about their limited spatial scale and high costs, which are too expensive to combat the extent of anthropogenic threats driving habitat loss (Gordon et al., 2020). The consequence is that major gaps remain in the applicability (e.g., cost-effectiveness) and relevance (i.e., goals detached from the definition of ecological restoration) of many coastal MER projects and practices, which may explain the current poor perception of coastal MER among many marine scientists (e.g., Adger et al., 2005; Mumby and Steneck, 2008: Bayraktarov et al., 2020). Although large-scale successful and relatively low-cost projects exist (notably large-scale mangrove forest, oyster reef and salt-marsh restoration projects; e.g., Beck et al., 2011; Bayraktarov et al., 2016; Friess et al., 2016; Duarte et al., 2020) many restoration projects are costly, conducted at small scales, and with narrow goals that do not benefit a diverse stakeholder group (including the majority of coral reef restoration projects; Bayraktarov et al., 2016). At present, a widespread goal of coastal MER projects is to achieve "item-based success" (i.e., survival of planted transplants, seedlings, or spat; *sensu* Bayraktarov et al., 2016), which in part reflects a common expectation for quick, measurable results, and a general assumption that associated ecosystem services will follow. The consequence is that basic science and "non-simplistic" applied research projects are missing,

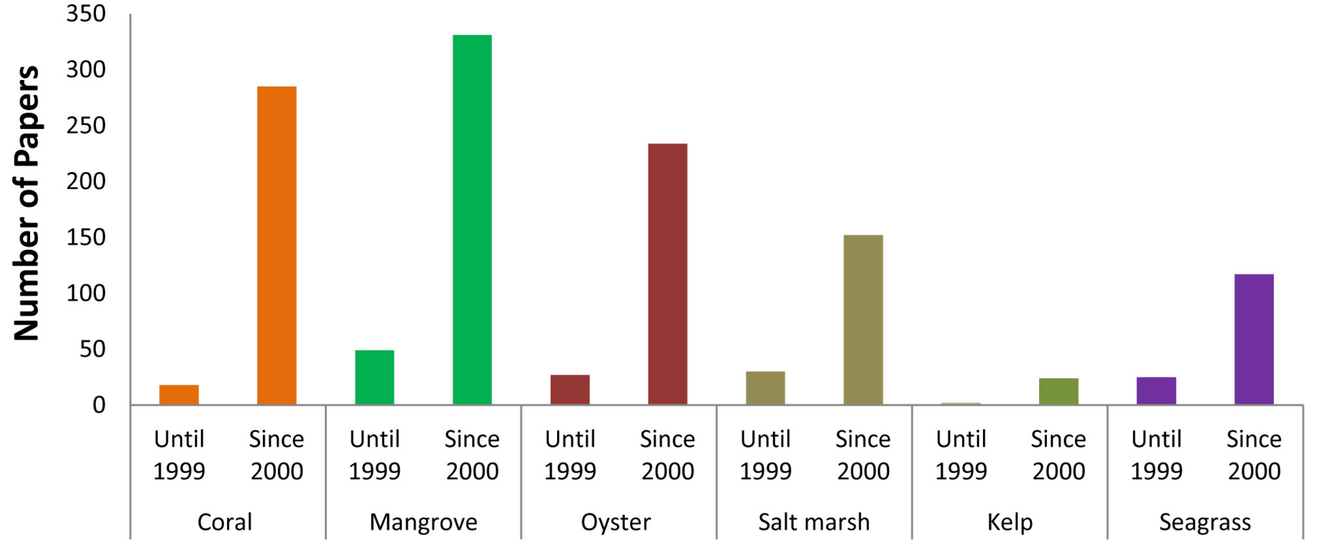

FIGURE 3 | The number of coastal Marine Ecosystem Restoration (MER) papers: the general term "marine ecosystems" and each of the six major coastal ecosystems: coral reefs, mangrove forests, oyster reefs, salt marshes, kelp forests and seagrass meadows, pre- and post-2000.

but are needed to promote tools, practices and scaling up of coastal MER (Bayraktarov et al., 2020). Moreover, MER is seen as a "risky choice" for resource managers and science policy-makers. Basic science is an important source of new ideas that figure prominently into developing solutions for many of society's needs (Remedios, 2000). Therefore, support for basic long-term research is crucial for the development and implementation of coastal MER. However, at present the development and implementation of most coastal MER sectors suffer from the effects of a "performance-perception-funding" cycle ("stagnation loop;" **Figure 1**), in which poorly performing restoration projects lead to poor images of coastal MER, and therefore hinder adequate investment in development of coastal MER science and practice despite general recognition of ecosystem decline. Breaking out of this "stagnation loop" requires major achievements by restoration projects in the relevant ecosystems.

Potential advantages of coastal MER compared with conservation-based management approaches reliant on area protection are best highlighted by successful restoration projects involving mangrove, oyster reefs (Beck et al., 2011; Bayraktarov et al., 2016; Friess et al., 2016) and seagrass meadows (Orth et al., 2012). However, although the list of successful large-scale MER projects continues to increase over time, modeling studies that compare the expected ecological and socio-economic benefits of different management approaches through time should be encouraged to demonstrate the economic benefits of restoration. Results from such studies done to date suggest that restoration-based conservation programs in coral reefs and large-scale efforts in seagrass-based restoration, despite the costly investment, may prove to be worthwhile due to the faster recovery and enhanced ecosystem services (Obolski et al., 2016; van Katwijk et al., 2016).

Targeted restoration projects with realistic ecological and socio-economic goals should help identify important knowledge gaps in coastal MER (i.e., SER, 2004 definition). Such goals include ecosystem-level parameters (e.g., fish species diversity and biomass) and upgraded ecosystem services, rather than "item-based success" indicators (e.g., survival of planted ecosystem engineer species). Likewise, coastal MER projects should be scaled up, beyond the usual but limited experimental scales, provided that the stressors that led to the degradation have been eliminated or minimized, or new tools, which help overcome the still existing stressors, are applied. The current proliferation of small-scale, item-based, trial projects, with no stakeholder involvement (Bayraktarov et al., 2016), is unlikely to fill the gaps and needs of realistic coastal MER. Hence, a shift toward realistic coastal MER interventions (i.e., feasible interventions of ecological and socio-economic benefits) is critically needed for coastal MER to gain wider acceptance. We believe that combining coastal MER and coastal ecosystem conservation into a single social-ecological framework (Possingham et al., 2015) has great potential to provide significant socially relevant gains in conserving and restoring highly valued coastal ecosystems. Such integration may further help to increase the traction of coastal MER and improve its perception and acceptance as an effective management strategy.

RECOMMENDATIONS

In view of the ongoing degradation of coastal marine ecosystems, restoration is an inevitable component of conservation management. Successful coastal MER offers great promise for accelerating the recovery of collapsed populations (including globally threatened species), destroyed habitats, and impaired ecosystem services, which may otherwise take much longer to recover (years to decades), if at all. To this end, effective implementation of coastal MER will benefit from incorporation of socio-economic elements, a wider portfolio of methodological tools, more focused post-restoration assessment, climate-change considerations, and wider stakeholder acceptance and engagement. We note that policy and legislation to enable this approach is critical, and notable efforts are being made, including, for example, the United Nations Decade of Ocean Science for Sustainable Development (2021–2030), the United Nations Decade of Ecosystem Restoration (2021–2030), and the European Green Deal, which makes restoration one of the key objectives. We encourage the development of specific recommendations in this field to further support restoration as a fundamental strategy in the race to reverse the decline of coastal marine ecosystems.

We Conclude

- Indirect tools that remove or modulate stressors, accelerate recovery and enhance the resilience of restored systems should be used in combination with direct approaches (e.g., planting and seeding) to achieve restoration goals. Basic scientific research will contribute to identification of such indirect tools.
- The growing need for large-scale restoration interventions, notably projects that combine remediation of degraded ecosystems due to past impacts and adaptation to cope with future threats, requires refinement of existing methods scaled to address the extent of degraded habitat, and support for multidisciplinary research that explores and identifies new tools and approaches. Such research requires adequate funding and a substantial breadth of skills; however, inadequacies in both have hampered the advancement of coastal MER. Therefore, concept promotion and education by ecological restoration proponents is essential for fundamental breakthroughs and coastal MER progress.
- Improved identification and understanding of social processes, drivers and priorities is needed to ensure broad public support and the long-term success of restoration efforts. Ideally, restoration and conservation approaches should be integrated with marine and coastal management. Under this umbrella, engaging local communities in the planning and monitoring of MER projects and designing projects with them to deliver specific socio-economic benefits will greatly enhance the long-term success of both conservation and restoration activities.
- Beyond fostering the ecosystem health and services of degraded coastal marine ecosystems, restoration tools can be used to promote adaptation to cope with

climate-change. Promoted adaptation can be implemented via two potential directions: the "Predict-and-Prescribe" approaches (e.g., "assisted evolution" and "designer reefs"), which attempt to foresee future conditions; and the "Portfolio" approach, which considers the range in uncertainty of future conditions. We argue that MER-based practices that can promote adaptation should be included in coastal zone management plans to improve their long-term success.

AUTHOR CONTRIBUTIONS

All authors have conceived the study. AA led the writing of the manuscript and project coordination. All co-authors contributed to the draft and gave final approval for publication.

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frontiers in Marine Science

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Optimal Planting Distance in a Simple Model of Habitat Restoration With an Allee Effect

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Ecological restoration is emerging as an important strategy to improve the recovery of degraded lands and to combat habitat and biodiversity loss worldwide. One central unresolved question revolves around the optimal spatial design for outplanted propagules that maximizes restoration success. Essentially, two contrasting paradigms exist: the first aims to plant propagules in dispersed arrangements to minimize competitive interactions. In contrast, ecological theory and recent field experiments emphasize the importance of positive species interactions, suggesting instead clumped planting configurations. However, planting too many propagules too closely is likely to waste restoration resources as larger clumps have less edges and have relatively lower spread rates. Thus, given the constraint of limited restoration efforts, there should be an optimal planting distance that both is able to harness positive species interactions but at the same time maximizes spread in the treated area. To explore these ideas, here we propose a simple mathematical model that tests the influence of positive species interactions on the optimal design of restoration efforts. We model the growth and spatial spread of a population starting from different initial conditions that represent either clumped or dispersed configurations of planted habitat patches in bare substrate. We measure the spatio-temporal development of the population, its relative and absolute growth rates as well as the time-discounted population size and its dependence on the presence of an Allee effect. Finally, we assess whether clumped or dispersed configurations perform better in our models and qualitatively compare the simulation outcomes with a recent wetland restoration experiment in a coastal wetland. Our study shows that intermediate clumping is likely to maximize plant spread under medium and high stress conditions (high occurrence of positive interactions) while dispersed designs maximize growth under low stress conditions where competitive interactions dominate. These results highlight the value of mathematical modeling for optimizing the efficiency of restoration efforts and call for integration of this theory into practice.

Keywords: restoration, restoration design, optimality, Allee effect, diffusion, mathematical modeling, coastal wetlands

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1. INTRODUCTION

Over the past century, many ecosystems worldwide and the valuable services they provide have been lost and degraded as a result of anthropogenic stressors, such has habitat loss, over-exploitation, and climate-change (Leemans and De Groot, 2003). Coastal habitats are especially threatened natural systems and have drastically declined in coverage and condition across the globe (Worm et al., 2006; Halpern et al., 2008). The magnitude of ecosystem degradation and the associated loss of biodiversity and ecosystem functions, such as the protection of shorelines from flooding and storm events in coastal systems (Barbier et al., 2011), generated a pressing need for conservation strategies that actively combat this decline. Ecological restoration is one conservation intervention used to combat habitat loss. It aims to repair or otherwise enhance the structure and function of an ecosystem that has been impacted by disturbance or environmental change. In recent years, restoration has emerged as an important conservation tool for improving the recovery of degraded lands and to counteract habitat and biodiversity loss (Jordan et al., 1990; Dobson et al., 1997; Young, 2000; Young et al., 2005; Suding, 2011). As restoration resources are economically limited, it is of utmost importance to guarantee the efficiency of ecological restoration (Aronson et al., 2006; Suding, 2011; Zhang et al., 2018).

One central aspect influencing the efficiency and success of restoration projects is the spatial design of the outplanted propagules. The long-held paradigm in restoration projects has been to plant propagules in dispersed arrangements to minimize competitive interactions. In contrast, ecological theory emphasizes the importance of positive species interactions, such as facilitation, for ecosystem stability, expansion, and recovery from disturbance. According to the stress-gradient hypothesis (Bertness and Callaway, 1994; Stachowicz, 2001; He et al., 2013; Silliman and He, 2018), positive interactions are particularly important and are measurably more influential in situations of high physical stress, such as the recolonization of bare substrate. In the case of high physical stress, positive interactions help lessen abiotic stress by making the local habitat more suitable. For example, salt marshes plants with neighbors do better in high flow and oxygen stressed areas, as neighbor plants help ameliorate wave stress and low oxygen in soils (Silliman et al., 2015). These ideas would suggest using clumped restoration designs that maximize positive interactions, in particular in situations of high physical stress (Halpern et al., 2007; Gedan and Silliman, 2009; Renzi et al., 2019).

These ideas were confirmed in recent field experiments which showed that the restoration success can be significantly enhanced in planting configurations that place propagules next to, rather than at a distance from, each other. For salt marshes, for example, an experiment by Silliman et al. (2015) found that in coastal wetland restoration clumped configurations are more favorable than dispersed configurations. Planting seedlings in tight rather than loose clusters while keeping the initial number of propagules constant led to higher survival rates and densities, more biomass and increased expansion rates. Similar results were found in mangrove restoration where a clumped design resulted in significantly lower mortality when compared with a uniform design (Bakrin Sofawi et al., 2017). Further, incorporating positive interactions enhances the plant growth in seagrass restoration (Valdez et al., 2020). Clumped planting arrangements are also beneficial for the restoration of woodland, for example planting designs for eucalypts where conspecifics are close to each other improved seed production (McCallum et al., 2019). These experimental studies confirmed that small adjustments in restoration design that harness positive species interactions result in significantly enhanced restoration success with no added cost.

On the other hand, planting propagules in too large clumps may waste restoration resources because restoration efforts are concentrated in smaller spatial localities. At some point the benefits of having larger and larger clumps should be outweighed by the slower and slower spread of those clumps at their edges, as the growth rate of clumps is directly related to their edge to area ratio. Thus, given the constraint of limited restoration efforts there should be an optimal planting distance that both is able to harness positive species interactions but at the same time is maximally spreading out the treated area. In this study, we propose to apply mathematical modeling to explore these questions quantitatively.

Mathematical models have proven to be useful tools to assess the impact of restoration efforts on the ecosystem state and biodiversity (Dobson et al., 1997). To date, modeling of ecological restoration has mostly focused on quantitative models and on matching the behavior of a selected species or ecosystems, for example using agent-based models (e.g., Sleeman et al., 2005 for coral reef restoration) or data-driven forecasting models (e.g., Benjamin et al., 2017 also for corals). However, a simple conceptual modeling study that explores the joint effect of different initial planting configurations and growth functions is still missing.

Here, we develop a simple mathematical model in the form of a reaction-diffusion system to investigate the optimal design in spatial habitat restoration. We model the growth and spatial spread of a single population starting from different initial conditions that represent clumped and dispersed planting configurations and consist of one or more patches of maximal population density, surrounded by bare substrate. We study the spatial coverage of the recovering ecosystem from the different initial conditions and investigate how it is influenced by positive species interactions, which are incorporated into the model in form of a weak or strong Allee effect (Courchamp et al., 1999). Using the developed model, we assess whether clumped or dispersed configurations perform better in our models and qualitatively compare the simulation outcomes with the experimental results in a coastal wetland from Silliman et al. (2015).

Our main finding is that restoration efficiency crucially depends on the assumed time horizon, that is, on whether or not traveling fronts starting from initial plantings have already merged. When competition was the only interaction in our model, that is when using logistic growth, dispersed configurations always performed better for short time horizons. In contrast, when the model included an Allee effect (i.e., positive species interactions) we observed that intermediate density is optimal for planting configurations. This supports the experimental results that dispersed configurations are not favorable when interactions other than competition are present. Our study provides new avenues for improving the efficiency of restoration campaigns and highlights the value of mathematical modeling for optimizing the configuration of habitat restoration.

2. METHODS

2.1. Diffusive Single-Species Model

We model the growth and spatial spread of a population of organisms planted at the start of the restoration process in a one-dimensional habitat. The dynamics are captured in form of a basic reaction-diffusion model (Murray, 1993; Ryabov and Blasius, 2008)

$$\dot{u} = \underbrace{f(u)}_{\text{reaction}} + \underbrace{D\Delta u}_{\text{diffusion}}\,, \tag{1}$$

where $u = u(t, x)$ is the population density at time t and location x, the "reaction" $f(u)$ describes the population growth at a specific location and the "diffusion" $\Delta u = \partial_x^2 u(t, x)$ models the dispersal from and to this location with diffusion strength D.

We compare two conceptual growth functions: logistic growth, capturing the effect of intraspecific competition among planted individuals,

$$f_{\mathrm{L}}(u) = ru(1-u), \tag{2}$$

as well as a growth function including an Allee effect, which we consider as a proxy for additionally positive species interactions (Courchamp et al., 1999),

$$f_{\mathrm{A}}(u) = ru(u-a)(1-u). \tag{3}$$

Implicitly, the carrying capacity of the population density was set to $K = 1$, meaning that u is expressed in fractions of the carrying capacity. Further, the intrinsic growth rate r as well as the diffusion constant D are set to 1, non-dimensionalizing the equation and justifying the omission of units. The parameter a is the Allee threshold; population densities below the threshold have negative growth rates (**Supplementary Figure 1**). Setting $a = 0$ gives a weak Allee effect and $a > 0$ results in a strong Allee effect. We chose $a = 0.1$ in the latter case. Note that several growth function definitions exist to model a weak and strong Allee effect (Courchamp et al., 1999). We merely chose a simple function that exhibits small values close to $u = 1$ and small (even negative in the case of the strong Allee effect) values close to $u = 0$. We expect that similar results will be obtained for qualitatively similar growth functions.

Since u is a density, the total population size P_t at time t is computed by integrating over the whole area. We used a one-dimensional area, $-L \le x \le L$, representing for example the coastline in a marine restoration project. Consequently, the total population size is

$$P_t = \int_{-L}^{L} u(t, x)\mathrm{d}x.$$

At the border of the simulated area we use Neumann (no-flux) boundary conditions

$$\partial_x u = 0 \quad \text{for } x = \pm L.$$

However, the precise boundary conditions are not of great importance since the habitat size was always chosen large enough so that the population did not reach the boundaries within the simulated time frame. The models were numerically solved with the Matlab `pdepe` solver.

2.2. Initial Conditions

To represent the initial plantings, we used step functions that at each location x take either the value $u(x) = 0$ (bare substrate) or $u(x) = 1$ (carrying capacity of the population density), as shown in **Figure 1**.

2.2.1. Single-Patch Set-Up

We started by examining the behavior of a single patch of propagules planted at the center of the habitat. Formally, this is the initial condition

$$u_0(x) = u(0, x) = \begin{cases} 1, & -\frac{S}{2} \le x \le \frac{S}{2} \\ 0, & \text{elsewhere} \end{cases}, \tag{4}$$

where S is the initial width of the patch. Thus, the initial total population size equals $P_0 = S$. For the simulations of a single patch system we varied the patch widths in the range $0.05 \le S \le 10$ and we used the habitat size of $L = 50$ throughout.

To evaluate the influence of the initial width S on the development of the patches, we defined the absolute and relative growth rate. The absolute growth rate until time t is

$$g_{\mathrm{abs}}(S, t) = \frac{P_t - S}{t}\,. \tag{5}$$

If the absolute growth rate is positive, it describes how much larger the total population has become from the start until time t. If it is negative, it describes how much the population has shrunk until time t. We deliberately chose the slightly cumbersome term "absolute growth rate" to distinguish it from more common notions of growth rate and especially the relative growth rate.

The relative growth rate accounts for the fact that resources are limited in restoration projects due to the initial effort. It divides the absolute growth rate by the initial width (corresponding to the initial population size), that is

$$g_{\mathrm{rel}}(S, t) = \frac{P_t - S}{tS}. \tag{6}$$

For example, if two patches increased by the same amount within a given time frame, the patch with the smaller initial population size (and therefore fewer used resources) would have a higher relative growth rate.

2.2.2. Multi-Patch Set-Up

Next, we generalized our model to a configuration with multiple patches of initial plantings (**Figure 1**). We designed the planting

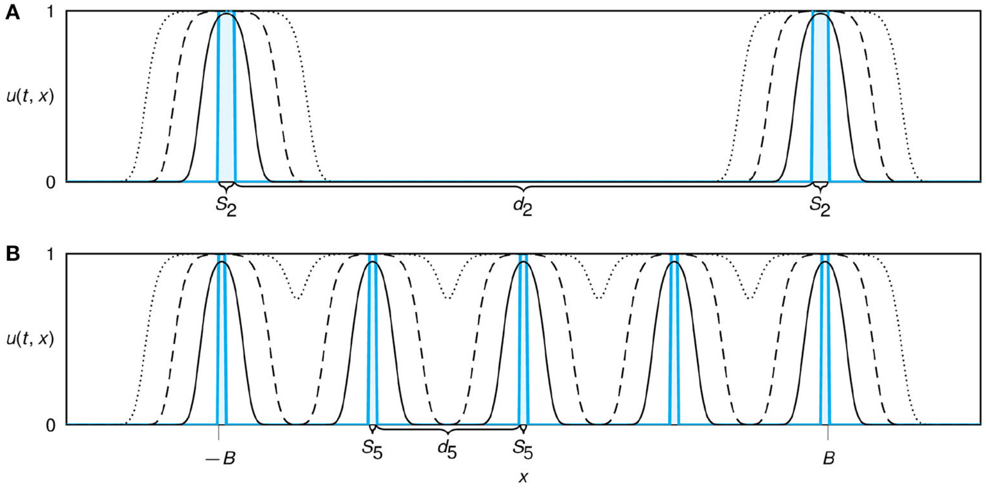

FIGURE 1 | Sketch of the modeled restoration design for a multi-patch set up of $n = 2$ **(A)** and $n = 5$ **(B)** patches. Initial conditions of planted propagules are shown in cyan. Patches are distributed equidistantly with inter-patch distance d_n. With increasing number of patches we reduce both the patch width S_n, keeping the initial total population size nS_n constant, and the distances between the patches d_n, ensuring that edges of the outer patches remain at the same locations $\pm B$ for all configurations. The solid, dashed, and dotted lines show simulated spatial profiles of the growing and expanding population at subsequent time points.

configuration in such a way that the invested restoration resources (the total initial population size P_0) were fixed and divided equally into n equidistant initial planting patches of width $S_n = P_0/n$. As a second constraint, in the multi-patch setting we kept the outer borders of the initial restoration region $(-B, B)$ fixed. Single patches (the case $n = 1$) were placed at the center of the domain as described before. For $n \geq 2$, the patches were placed such that the outer edges of the patches furthest left and right were at position $x = -B$ and $x = B$. Hence, the distance between two patches is always given as $d_n = \frac{2 \cdot B - P_0}{n-1}$ and thus, both the initial patch width S_n and the inter-patch distance d_n are decreasing functions of n. This set-up allows to mimic the clumped and dispersed configuration as described in the field experiment by Silliman et al. (2015).

Comparing different numbers of patches n, we denoted the total population size at time t by $P_t(n)$ to emphasize the dependence on the different initial configurations. As parameter values in the multi-patch set-up we used an initial total population size of $P_0 = 10$ and an initial restoration region of $B = 100$ throughout, varied the number of patches from $n = 1$ to $n = 15$ and increased the total habitat size to $L = 250$ so that edge effects did not play any role.

Note that the total population size $P_t(n)$, and thus the simulated planting success, always depends on the chosen time horizon t. In order to measure the efficiency of the restoration efforts in a time-independent fashion, we also computed the discounted total population size. Discounting is often used in economics and describes that yields in the future are less valuable than present yields. It is computed in the form of a population-size weighted time integral

$$P_\rho(n) = \int_0^\infty e^{-\rho t} P_t(n) \mathrm{d}t.$$

Here, ρ is the discounting factor which can be understood as a "negative interest rate". The larger ρ, the more the population size in the beginning is weighted and the less the population size in the end influences $P_\rho(n)$. The discounted population size only depends on the number n of patches in the initial conditions and thus indirectly on the initial planting distance. We chose $\rho = 0.1$ and $\rho = 0.5$. To make the results for the different discounting factors comparable we used the discounted sizes relative to the configuration with one patch, i.e., $P_\rho(n)/P_\rho(1)$.

3. RESULTS

3.1. Single-Patch Set-Up

The spatio-temporal development of a single, newly planted patch is illustrated in **Figure 2** for different growth functions and patch widths. In general, we can distinguish three characteristic growth phases: 1. "flattening," 2. "regrowth," and 3. "traveling fronts." In the first (flattening) phase, the diffusion term dominates, outweighing the local growth term $f(u)$ due to the sharp spatial gradient between the patch (representing the initial planting) and the surrounding area (representing the bare substrate). As a consequence, the population density decreases within the patch and increases in the area close to it. In this stage, the population either goes extinct (Ryabov and Blasius, 2008) or it may survive the initial decline. If the planted population does not go extinct it can enter the second and third growth phase. In the second phase (regrowth), the spatial variations equalize and the effect of diffusion is less intense. Consequently, the influence of the local growth function becomes more important, yielding a rising population density. Once the full population density $u = 1$ is reached again in the center of the patch, a traveling front is established on each side of the patch and the third growth phase is initiated. In this phase, the population

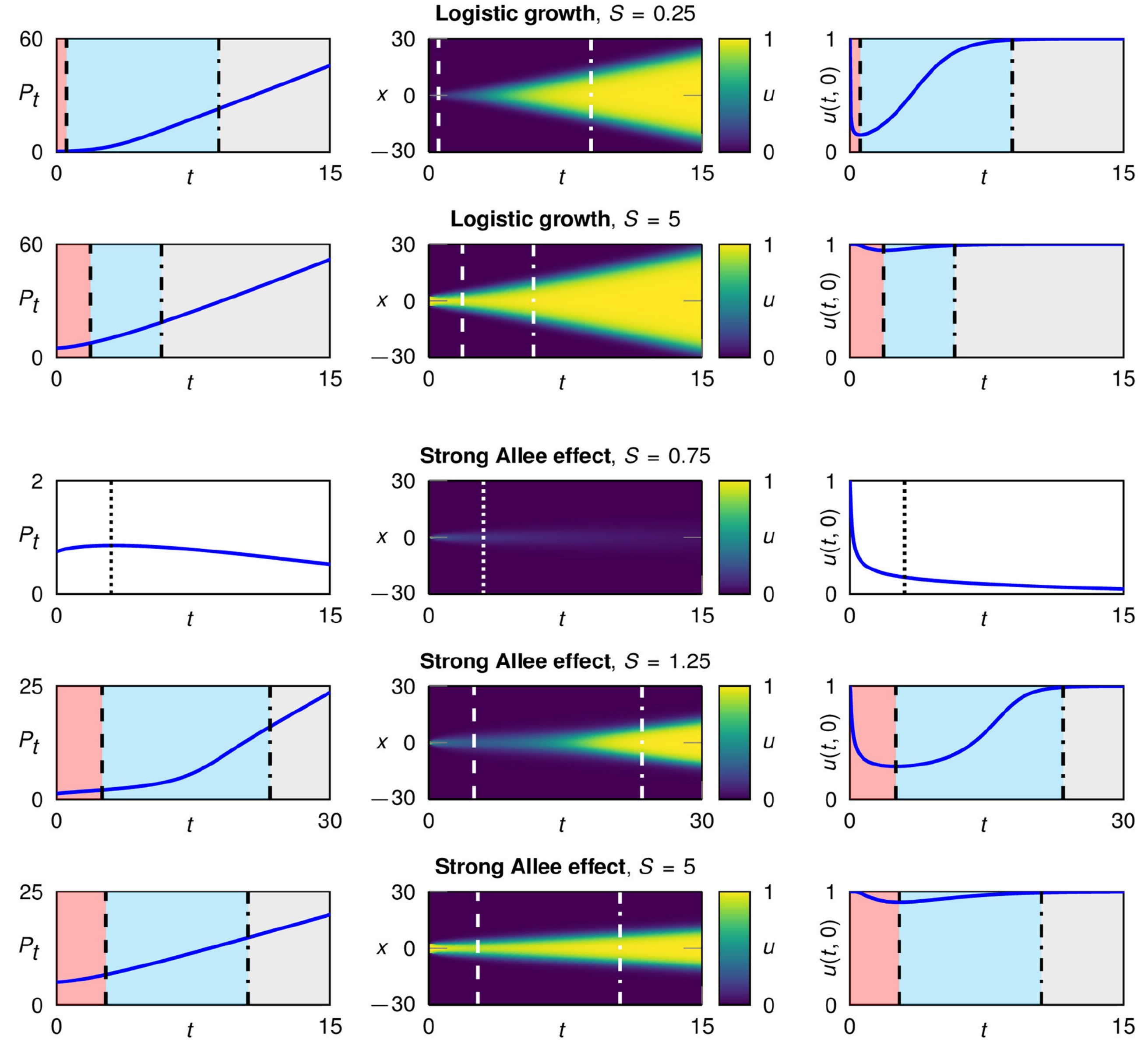

FIGURE 2 | Typical development of a population starting from single patch initial conditions with different widths, for logistic growth $f_L(u)$ **(rows 1 and 2)** and the strong Allee effect $f_A(u)$ with $a = 0.1$ **(rows 3–5)**. Plotted are the total population size over time **(left)**, the spatio-temporal development in color coding (middle column) and the population density in the center of the patch **(right)**. In the case of logistic growth the population survives for all patch widths; for the strong Allee effect, populations with a very narrow initial patch go extinct. A surviving population undergoes three characteristic growth phases: 1. flattening (red), 2. regrowth (blue), and 3. traveling fronts (gray).

spatially expands with nearly constant velocity. This spreading velocity can be analytically described as the asymptotic speed c of a traveling front for each of the three growth functions, yielding $c = \sqrt{2rD}$ for purely logistic growth and $c = \sqrt{2rD}(1/2 - a)$ in the presence of an Allee effect (Lewis and Kareiva, 1993; Murray, 1993; Ryabov and Blasius, 2008). Thus, the spatial spreading velocity of the planted population is highest for a population with logistic growth and lowest in the presence of a strong Allee effect.

The initial patch width S plays a central role for the growth dynamics. In particular, the duration of the first and the second growth phase crucially depends on S. The narrower the patch, the stronger is the influence of diffusion on both sides in relation to the whole patch. Consequently, for smaller initial patches the flattening happens faster and the first phase is shorter. Further, the population density in the center of the patch decreases more, leading to a prolonged second phase. This is illustrated in **Figure 2**, first and second row.

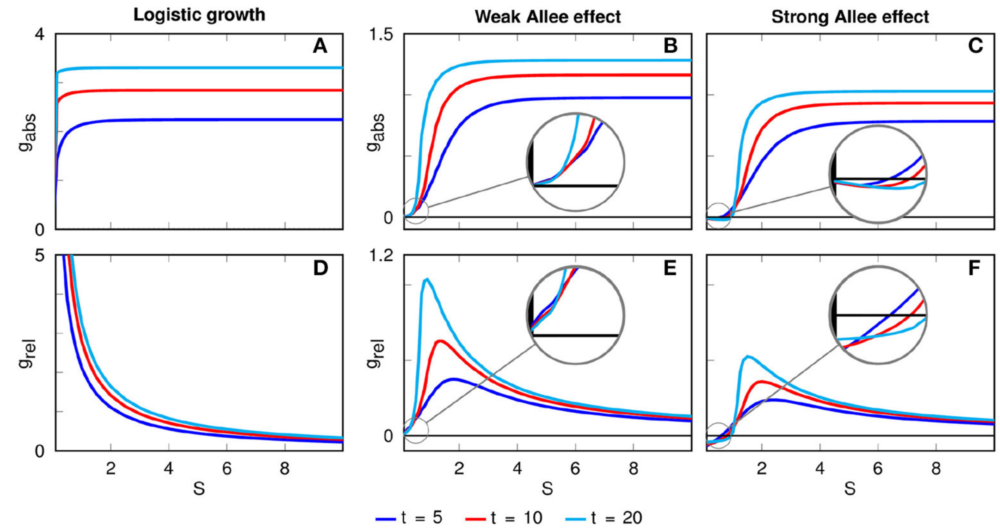

FIGURE 3 | Absolute **(A–C)** and relative **(D–F)** growth rates as functions of the patch width *S* for different time horizons. For logistic growth, the relative growth rate decreases with the initial patch width. In the presence of an Allee effect, there is an optimal patch width of maximal relative growth which depends on the considered time horizon. In the case of a strong Allee effect, the absolute and relative growth rates become negative for very narrow patches, leading to the extinction of the population on those patches.

For logistic growth and the weak Allee effect ($a = 0$) all populations survive the flattening growth phase irrespective of the initial patch width. In contrast, in the case of a strong Allee effect, a minimal initial patch width is needed for survival, while populations on narrow initial patches go extinct (**Figure 2**, third row). The patches that survive go through the three growth phases (**Figure 2**, fourth and fifth row). When logistic growth is used or a weak Allee effect is present, the local growth term $f(u)$ is positive as long as the population density u is positive (and smaller than the capacity). Therefore, the strong decrease of the population density in very narrow patches is not critical. If, in contrast, the local growth term includes a strong Allee effect, the growth rate $f(u)$ becomes negative for small population densities. For very narrow patches the population density can then fall below the Allee threshold and consequently the population goes extinct.

In **Figure 3**, we summarize the simulated population growth rates as a function of the initial patch width S for the three characteristic growth functions. To this end, we computed the absolute and relative growth rates, Equations (5, 6), for a fixed time horizon and analyzed the influence of the initial patch width. For logistic growth, the absolute growth rate g_{abs} is always positive and approximately equal for all patch widths (**Figure 3A**). For short time spans, e.g., $t = 1$, wider patches have higher absolute growth rates than narrower ones but this effect vanishes for longer time horizons. For $t = 20$, for example, all patches wider than $S \approx 1$ have almost equal values of g_{abs}. Since there is little variation of the absolute growth rates with the patch width, narrower patches have higher relative growth rates (**Figure 3D**). In terms of restoration efforts, narrow patches thus give a better "return on investment" when logistic growth is assumed.

In the presence of a weak Allee effect, the absolute growth rate is also always positive, but the differences between narrow and wide initial patches are more pronounced than in the case of logistic growth (**Figure 3B**). Particularly, there is an offset at very small widths before the absolute growth rate rises for intermediate widths and becomes constant for larger widths (**Figure 3B**). The offset is caused by the shape of the weak Allee effect's growth function (**Supplementary Figure 1B**): The stronger flattening of very narrow patches leads to small population densities u which have comparatively lower values in the local growth term $f(u)$. Very similar forms of the absolute growth rate are obtained for the case of a strong Allee effect. The main difference is that now g_{abs} can be negative for small S (**Figure 3C**), leading to the extinction of populations on very narrow initial patches.

The second row in **Figure 3** depicts the dependence of the relative growth rate g_{rel} on the initial patch width S. While for logistic growth g_{rel} is always decaying with S, in the case of a weak and strong Allee effect we obtain pronounced peaks of g_{rel} at intermediate values of S, indicating optimal patch widths. This optimal patch width S_{opt} depends on the considered time horizon. For example, for the time points $t = 5$, $t = 10$ and $t = 20$ in the case of a weak Allee effect we find $S_{\mathrm{opt}}(t = 5) = 1.8$, $S_{\mathrm{opt}}(t = 10) = 1.3$, and $S_{\mathrm{opt}}(t = 20) = 0.9$, while for a strong Allee effect we obtain $S_{\mathrm{opt}}(t = 5) = 2.3$, $S_{\mathrm{opt}}(t = 10) = 2.0$, and $S_{\mathrm{opt}}(t = 20) = 1.5$. Notice that the optimal width decreases with the time horizon for both weak and strong Allee effect, i.e., when longer time spans are considered narrow patches are recovering and the lower initial effort (that is, the initial patch width) is paying off.

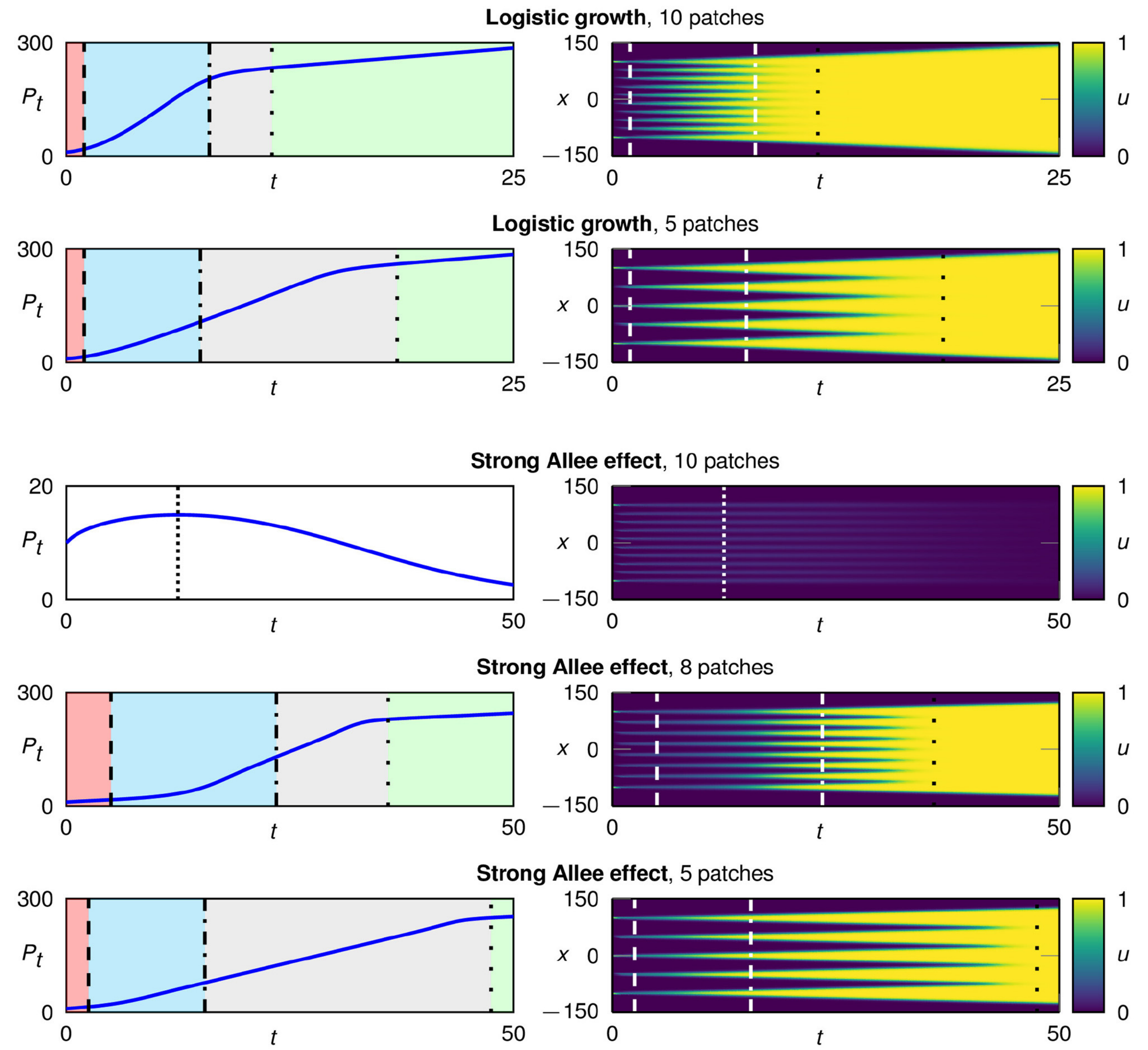

FIGURE 4 | Typical development in configurations starting with multiple initial patches for logistic growth $f_L(u)$ **(rows 1 and 2)** and the strong Allee effect $f_A(u)$ with $a = 0.1$ **(rows 3–5)**. We plot the total population size over time **(left)** and the spatio-temporal development in color coding **(right)**. In the case of logistic growth, the population survives for all spatial configurations. In contrast, for a strong Allee effect, populations starting from a configuration with many and therefore very narrow patches go extinct. A surviving population undergoes four characteristic growth phases: 1. flattening of each patch (red), 2. regrowth of each patch (blue), 3. traveling fronts for each patch (gray), and 4. expansion of the merged patch (green).

3.2. Multi-Patch Set-Up

The spatio-temporal development of a multi-patch set-up is illustrated in **Figure 4** for different growth functions and patch numbers. As in the case of a single-patch set-up, also for a configuration with multiple initial patches the planted population can always survive in a system with logistic growth or weak Allee effect, but may go extinct in the case of a strong Allee effect. This is explained by the fact that the initial width of each patch decays as $S_n = P_0/n$ with the number of patches. We already found in the single-patch set-up that populations do not survive on narrow initial patches when a strong Allee effect is present. This translates into the extinction in configurations with many, and therefore narrow, patches. A main point to keep in mind is that the total initial population size P_0 is fixed. The extinction of configurations with many patches is thus primarily caused by the patch widths S_n being too narrow and is only indirectly linked to the number of patches n.

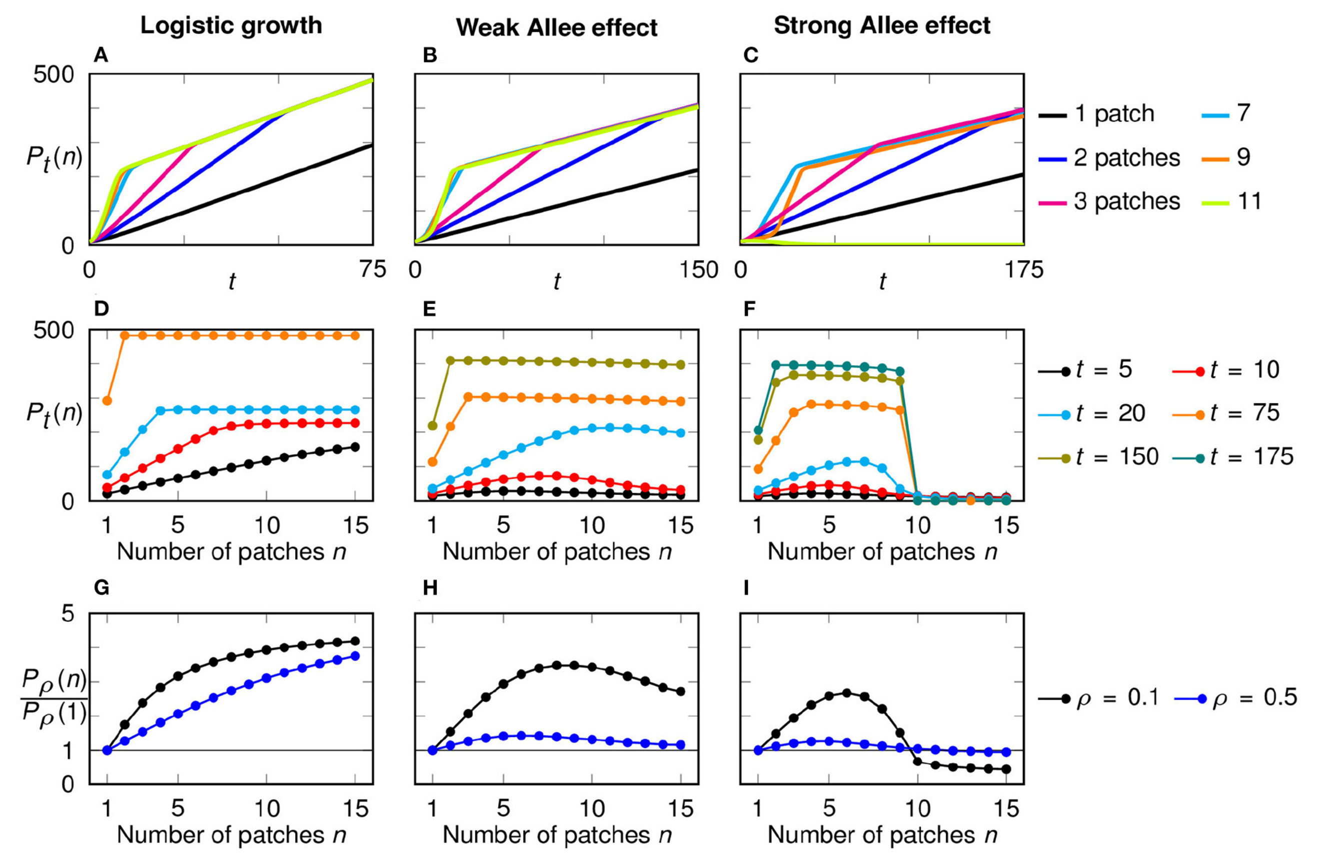

FIGURE 5 | Time dependence and growth dynamics in a configuration with multiple initial patches for logistic growth (left), weak Allee effect (middle), and strong Allee effect (right). **(A–C)** Temporal development of the total population size for different numbers n of initial patches, with a fixed total initial population size $P_0 = 10$. A kink in the growth curves indicates the point of merging. **(D–F)** Total population size after a fixed time horizon in dependence of the number of initial patches. For each model, only time horizons up to the merging of the configuration with two patches are selected. **(G–I)** Discounted population size relative to the discounted population size for one initial patch in dependence of the number of patches, shown for two discounting rates.

As shown in **Figure 4**, surviving populations go through four growth phases. At the start, the n patches develop separately from each other and we re-encounter the three growth phases 1. “flattening,” 2. “regrowth,” and 3. “traveling fronts” for each patch. In the third growth phase, the system now consists of $2n$ traveling fronts, which continue to spread until they eventually merge into one big patch with only two fronts remaining. This starts the fourth growth phase “expansion of the merged patch.” Due to the reduction from $2n$ traveling fronts to only two traveling fronts, after the transition to the fourth growth phase the speed of the population growth, i.e., the changing rate of the total population size $P_t(n)$, is strongly reduced (left column of **Figure 4**).

Figures 5A–C shows the time dependence of the total population size $P_t(n)$ for several configurations. While all configurations begin with the same initial population size P_0, the total population size as well as the speed of growth start to differ quickly. However, once the patches have merged, the further growth of the total population size P_t is independent of the number of initial patches n. This holds for all three growth functions. For each configuration, the transition into the fourth growth phase is clearly visible as a kink (a sudden change of the graph’s slope) in the respective growth curve. Note that due to the different asymptotic propagation speeds of traveling fronts, the time span needed to reach the fourth growth phase differs between the growth functions $f(u)$. For logistic growth, the fronts asymptotically travel faster, hence the merging occurs earlier than for the weak and strong Allee effect.

In **Figures 5D–F**, we plot the total population size $P_t(n)$ as a function of the number of initial patches n at selected time points. Thereby, it becomes transparent that for each growth function $f(u)$ we considered, there are two stages in the growth dynamics: before the merging (short-term behavior) and after the merging (long-term behavior).

We first study the short-term behavior. In the first three growth phases, before the occurrence of any mergings, we can assume that the patches develop separately from each other. Since they all have the same width S_n, they grow with the same speed. Hence the growth of the total population size until time t is n times the absolute growth rate of each patch, that is $n \cdot g_{\text{abs}}(S_n, t)$, with g_{abs} being the absolute growth rate of a single initial patch (Equation 5). Using the relations $g_{\text{rel}}(S_n, t) = g_{\text{abs}}(S_n, t)/S_n$ and

$S_n = P_0/n$ this can be rewritten as $P_0 \cdot g_{\mathrm{rel}}(S_n, t)$. That is, before the merging of the traveling fronts the absolute growth of the multi-patch configuration is proportional to the relative growth rate, Equation (6), of a single patch system.

Assume now that the population follows logistic growth. In the previous section we showed that in a single-patch configuration with logistic growth narrow patches always perform better and have higher relative growth rates, while the absolute growth rate is more or less independent of S (**Figures 3A,D**). From this we can deduce that multi-patch configurations with a larger number of smaller patches grow faster and initially can achieve higher total population sizes. That is, in a system with logistic growth the total population size $P_t(n)$ should scale with the number of initial patches n for short time horizons (**Figure 5D**).

This is quite different from the initial growth behavior in the presence of an Allee effect. In this case we found that a single-patch configuration exhibits a pronounced peak of g_{rel} for intermediate values of S (**Figures 3E,F**). Thus, for short time spans also a multi-patch system should exhibit highest growth rates for intermediate initial patch sizes and thus intermediate number of patches. This theory is confirmed in the numerical simulations which reveal a unimodal dependency of the total population size $P_n(t)$ as a function of n for time instances before the merger of traveling fronts (**Figures 5E,F**). The optimal number of patches that maximizes growth rates depends on the time horizon and by comparison with **Figures 3E,F** indeed is directly related to the optimal patch width derived in the single-patch set-up.

Next we consider the growth behavior for larger time horizons, in the time after the merging of initial patches. In this regime the whole initial restoration region between $-B$ and B is fully populated. Thus, the further growth is only dependent on how far the two outer initial patches have spread. This is measured by the absolute growth rate $g_{\mathrm{abs}}(S, t)$. That is, after the merging of the traveling fronts the absolute growth of the multi-patch configuration is proportional to the absolute growth rate, Equation (5), of a single patch system.

Again, we first assume that the populations follow logistic growth. In **Figure 3A**, we showed that the absolute growth rate of single patch systems is almost independent of the patch width when t is large. Therefore, the differences between the configurations, that were present for shorter time spans, vanish; all configurations, except the single patch, reach the same total population size (**Figure 5D**). The lower values for the case $n = 1$ are explained by the structural disadvantage of a single patch in the center of the simulated area in our chosen initial conditions regarding the long-term behavior: All other configurations start their outwards growth from two sides at $x = \pm B$ while the single patch begins at the center.

For the weak and strong Allee effect, the configuration with two patches performs best in the long run (**Figures 5E,F**) since the absolute growth rate in a single patch system decreases with smaller widths (**Figures 3B,C**). The decrease of $P_t(n)$ with increasing n for a fixed but large enough time point t is less pronounced for the weak Allee effect than for the strong Allee effect. This is a reflection of the less distinct change in the absolute growth rate for small widths.

Regarding the discounted population size, the most dispersed configuration performs best when using logistic growth while an intermediate number of patches is optimal when an Allee effect is present (**Figures 5G–I**). These results are in line with the short-term behavior. This is natural since discounting puts more weight on the beginning. While the exact time point t was relevant in the comparison of the total population sizes $P_t(n)$, now the discounting factor ρ determines which configuration is optimal.

4. DISCUSSION

In this study we proposed a simple mathematical model that predicts the success of a plant restoration based on the planting configuration. We consider a standard logistic growth model that inherently includes competitive interactions among individuals and compare this to models that include positive interactions among individuals in which the growth of neighbors promotes the growth and survival of conspecifics. This is integrated into the models in the form of an Allee effect which describes an inverse, density dependence where population growth is positively correlated with density, at least at low population sizes like those found in the beginning of a restoration effort. We found that the optimal planting strategy depends on the type of interactions that take place among individuals, which in turn are related to environmental stress. Thereby, intermediate clumping is likely to maximize plant spread under medium and high stress conditions (high occurrence of Allee effects) while dispersed designs maximize growth under low stress conditions where competitive interactions dominate.

Our results coincide with the findings of a salt-marsh restoration experiment by Silliman et al. (2015). In this experiment only two planting arrangements were compared: the clumped and the dispersed configuration, where the first performed better. In our simulation, the configurations ranged from one wide patch (very clumped) to 15 narrow patches (very dispersed), aiming for a conceptual exploration rather than an exact replication of the experimental results. Our analysis of a model with logistic growth showed that the most dispersed configuration performed best in the short run in contrast to the experimental results. This suggests that positive species interactions, as expressed in our model by an Allee effect, are a crucial component to explain the findings by Silliman et al. (2015). Using simulations that included a weak or strong Allee effect, we found that population growth was optimized for an intermediate number of patches. Further increases in the number of patches, representing more dispersed configurations, only reduced the population growth. This simulation result is in line with the experimental finding that the restoration success was smaller in the dispersed than in the clumped configuration. In our simulations, the most clumped configuration yields the highest population density for short time spans when an Allee effect is present if the initial population size is chosen appropriately (**Supplementary Figure 2**). Our observation of reduced growth for over-clumped configurations (which was not investigated in the field experiment) can be explained by the fact that spreading of planted patches is only possible from the edges of the patch. Planting designs that were too clumped reduced the number of patches, and thus, the spreading potential.

These results are in line with other studies from the literature, which identified the Allee effect as an important factor for the invasion of plants. For example, Davis et al. (2004) suggested that an Allee effect limits the invasive spread of a salt marsh species and a model by Murphy and Johnson (2015) associated a reduced Allee effect with invasion success. The presence of an Allee effect also drastically changes spreading characteristics of invading species (Gastner et al., 2011). Finally, our results are largely confirmed in a recent field experiment by Duggan-Edwards et al. (2020) who investigated optimal configurations for a salt marsh restoration.

Our findings highlight the importance of positive species interactions for allowing establishment and maximizing population growth from a large number of small initial plantings—a typical configuration in restoration campaigns. The Allee effect expresses the fact that per capita population growth rates are reduced for small population densities. This means that positive interactions from conspecifics are needed to improve survival and reproductive success of an individual or population (Courchamp et al., 1999). This state of a small initial population density and a negative growth rate in the absence of other positive interactions (i.e., high physical stress) is exactly the situation that one should expect for freshly planted populations after restoration. In contrast, competitive interactions should become important only after successful establishment, that is, after the restoration effort already has succeeded. There are many examples for such facilitative mechanisms. In saltmarsh systems, for example, there are positive interactions between vegetation and the surrounding sediments. Plants dissipate wave energy which helps to mitigate wave-induced erosion stress and to shelter from destruction by storm events (Barbier et al., 2011). The reduction of hydrological energy stimulates sediment deposition, enhancing plant survival at higher elevations (Bouma et al., 2009; Silliman et al., 2015; Duggan-Edwards et al., 2020). Further positive interactions between neighboring plants can occur due to alleviation of physical stress due to anoxia. Here the positive feedback is provided in the form or oxygen diffusing from shallow roots into sediments which then becomes available to neighboring plants (Howes et al., 1986).

The Stress Gradient Hypothesis predicts that neighbors are more likely to cooperate with each other as biotic or abiotic stress increases in a system. This theory has been tested in numerous field studies and there is strong support for it as general rule in ecology (He et al., 2013). Although our model did not include stress, we did vary the contribution of positive species interactions by varying the strength of the Allee effect (none, weak, and strong). Given the stress gradient hypothesis, this can be considered as a proxy for environmental stress in the system, with a strong Allee effect signifying high stress and a low Allee effect low stress. With this correlation, we can then make predictions about what type of interactions restoration managers could expect among outplants across a stress gradient and accordingly how to design their planting arrangements to maximize growth rates (**Figure 6**). Our conceptual study shows that under low stress managers should use fully dispersed planting configurations while under intermediate or high stress, i.e., when when positive interactions likely play a significant role, managers should plant in medium sized clumps. This conclusion is supported by field data for salt-marshes from Silliman et al. (2015) which showed that in the high intertidal, where oxygen is plentiful, plants did better in dispersed than in clumped configurations. However, in the low intertidal, where flooding impedes oxygen diffusing into soil, clumped plants grew 200% more and expanded at greater rates since plants benefited from neighbors oxygenating the soils via translocation of air to their roots. Note that the nature of interactions shifts not only across the stress gradient but also with time. That is, even under conditions of high environmental stress, once a few years have passed, clumps grow into large areas and the foundation species reduces stress—the clones are likely to start to compete more than cooperate. Key then is a new step in restoration planning where managers map out and model stress and intraspecific interactions in their system across the planting zone to determine the optimal mixed method planting design for their area.

While we modeled an Allee effect with the specific growth function, $f(u) = u(u - a)(1 - u)$ with $a = 0$ and $a = 0.1$, we assume that our results generally also hold for other specifications of the weak and strong Allee effect. We were able to explain the behavior for the multi-patch set-up in terms of the dynamics of a single-patch system. Hence, we assume that very narrow patches go extinct for growth functions with negative values for small population densities, i.e., a strong Allee effect. Further, we suggest that there is an optimal patch width, resulting in an optimal number of patches, for all growth functions with smaller per capita growth rates at smaller population densities, i.e., growth functions with an Allee effect, instead of narrower patches always performing better as it is the case for logistic growth.

We investigated a planting configuration where a fixed amount of invested restoration resources is divided equally among the initial planting patches. That is, our simulation design implements an important trade-off where planting in a clumped design will necessarily reduce the spatial extent of the restoration as compared to planting with a dispersed design. The potential costs of doing this must be borne by the growth and spatial spread of the population. On the other hand, cost may be borne primarily in the extent to which ecosystem services are created by the restoration, e.g., if the restored habitat enhances faunal survival or biodiversity. This relates to the more general question of how restoration success is quantified. While our study measures restoration success as the total restored population size, in general, restoration success could be based on the relative magnitude and scale of ecosystem services. This is further complicated by the fact that restoration success also depends on time. Our analysis shows that the total population size reached after restoration varies with the investigated time horizon, depending on the characteristic growth phases shown in **Figures 2**, **4**. In particular, growth dynamics in a multi-patch configuration crucially depend on whether or not the traveling fronts starting from individual patches have already merged (as shown in **Figure 5**). Thus, also our estimation of the restoration

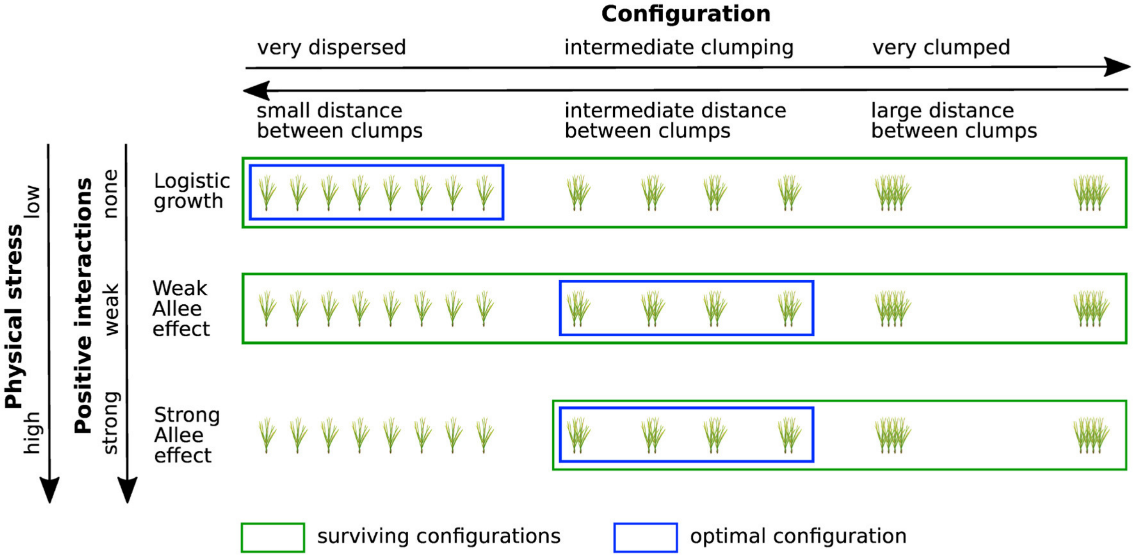

FIGURE 6 | Conceptual visualization of the performance of clumped and dispersed restoration designs in relation to the strength of positive interactions. Green boxes indicate surviving configurations, blue boxes indicate the most efficient method of planting for each growth function. If population dynamics follow logistic growth (no positive interactions) optimal restoration is achieved for a dispersed planting configuration with small distances between clumps. In the presence of an Allee effect optimal performance is obtained for intermediate clumping, while too clumped configurations yield bad restoration performance for all growth functions. According to the Stress Gradient Hypothesis positive interactions (e.g., facilitation) become more significant with increasing physical stress. Thus, although it is not explicitly included into our model, the strength of the Allee effect (none, weak, strong) can be considered as a proxy for physical stress, allowing us to draw conclusions on expected restoration success in different stress regimes.

success will depend on the considered time horizon. This raises the question how to equate restoration benefits and ecosystem services that come in the distant future to their value in the present. Here we follow the key paradigm in economics and cost-benefit analysis that future goods should be counted for less than present goods. That is, we discounted future population sizes to present population sizes through the use of a discounting rate, which expresses the intuitive notion that "a dollar today is worth more than a dollar tomorrow." These ideas from ecological economics are sometimes considered as being in conflict to our desire to have restorations that are sustainable and that persist for more than just the short term. This is a subtle and sometimes controversially discussed issue and we refer the reader to the excellent treatment by Broome (1994).

A diffusive single-species model is of course not a perfect description of the environmental and ecological situations in the restoration of ecosystems. It assumes a homogeneous environment, neglects stochastic events and does not feature interactions with other species, such as grazers or ecosystem engineers (e.g., Lewis and Kareiva, 1993). Additionally, there are many other factors that potentially contribute to restoration success. This includes community level processes, interspecies interactions, environmental change and disturbances, but also possible trade-offs between planting configuration and the potential effects of other species, or the rapidity with which restored habitat is colonized by higher organisms. Planting in a dispersed configuration, for example, can be seen as a form of bet hedging under the expectation of patchy disturbances by (e.g.,) physical disturbances, bioturbation, or herbivory. Consideration of such processes, all of which might be relevant for a real-world restoration scenario, is beyond the scope of this study which applies a simple single-population model for addressing the consequences of different initial plantings.

Considering the above mentioned processes, our study provides interesting new avenues for future model studies, for example, by extending our findings to a community level. Another interesting model extension would be to investigate the effects of non-local species interactions. In our model we assumed that the Allee effect acts only locally, i.e., the growth at point x depends only on the population density at this point. An important next step could be to include a term that measures the population density around each point, for example by using a convolution with a kernel. While most single species models that use a kernel focus on density dependent competition (e.g., Britton, 1989; Han et al., 2016), an interesting extension could be to use such a term to model facilitation and to explore its effect on the behavior of clumped and dispersed initial conditions.

Recently there has been a renewed interest in the application of optimal control theory for spatial ecology and the design of marine reserves (Neubert, 2003; Upmann et al., 2021). Our findings suggest that mathematical modeling and theoretical investigations of optimality might play a similar important role in helping to design optimal configurations and enhance the efficiency of spatial restoration efforts. Even though we used a simple conceptual model, our approach could easily be applied to specific systems and calls for integration of this theory into practice.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

BB and BS conceived the study. BB and LH designed the model. LH performed the numerical simulations. All authors contributed to the writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.610412/full#supplementary-material

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frontiers in Marine Science

ORIGINAL RESEARCH
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Inclusion of Intra- and Interspecific Facilitation Expands the Theoretical Framework for Seagrass Restoration

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Restoration is increasingly utilized as a strategy to stymie the loss of coastal habitats. Coastal habitat restoration has predominantly emphasized designs that minimize physical stress and competition. As evidence of the pervasiveness of this approach, we conducted a global survey of seagrass restorationers and found a strong affinity for stress-avoidant designs with adult shoots in dispersed rather than aggregated configurations. To test the alternative hypothesis that including positive interactions can enhance restoration success, we experimentally incorporated: (i) interspecific facilitation (clam additions) into seed sowing, and (ii) both intra- and interspecific facilitation (planting a single-large versus multiple-small patches and adding clams) into shoot planting. Clam additions to seeds significantly enhanced plant biomass and patch size; and nutrient analysis suggested the causative mechanism was clam enhancement of available nitrogen. In contrast, adult outplant growth was enhanced by intra- but not inter-specific facilitation. Dispersed configurations consistently declined, whereas large-intact patches, which had the same initial biomass as dispersed plots, increased in patch area and doubled in shoot density. These results demonstrate that expanding restoration strategies to include positive interactions with respect to seagrass ontogeny has the capability to switch the trajectory of restoration from failure to success.

Keywords: conservation, facilitation, positive interactions, restoration, seagrass

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INTRODUCTION

Climate change, pollution, habitat destruction, overharvest of predators, among others, have contributed to the global loss or conversion of roughly 29% of seagrasses (Waycott et al., 2009), 85% of oyster reefs (Beck et al., 2011), and 42% of North American salt marshes (Gedan and Silliman, 2009a). Countries subsequently invest millions of dollars annually toward coastal conservation efforts in order to stem the loss ecosystem services necessary for human well-being (Edwards et al., 2013; BenDor et al., 2015; Saunders et al., 2020). Restoration has recently been promoted as a primary strategy by nations, corporations, and non-profit organizations to bolster shoreline ecosystems and communities, combat habitat losses, compensate for urban development, and create jobs (CWA, 1972; ERA, 2000; RESTORE Act, 2012; Edwards et al., 2013; Sutton-Grier et al., 2015, 2018). To meet this increasing demand, marine restoration approaches must quickly become more affordable and effective, as the failure rate and costs of marine ecosystem restoration are often high (Bayraktarov et al., 2016; Saunders et al., 2020). Implementing ecological theories, such as the increasingly important role of positive species interactions in high stress environments (He et al., 2013; He and Bertness, 2014), in restoration methodologies will be critical for meeting this challenge.

The current theoretical framework in coastal restoration and planting designs is derived from forestry science (Gedan and Silliman, 2009b; Silliman et al., 2015; Shaver and Silliman, 2017), which places an emphasis on maximizing outplant yields by reducing physical stressors and planting propagules in designs aimed at minimizing competitive interactions (Halpern et al., 2007; Gedan and Silliman, 2009b). In contrast, many ecological studies in marine ecosystems have found that coastal plants experience increased growth when grown in clumps adjacent to neighbors of the same species, especially when recovering from disturbance (Van Keulen et al., 2003; Bos and Van Katwijk, 2007; Angelini et al., 2011; Silliman et al., 2015; Gittman et al., 2018). Key to determining if inclusion of positive species interactions can maximize restoration productivity and resilience across diverse ecosystems are tests that examine the utility of incorporating multiple types of facilitation in different marine habitats and at multiple stages of outplant maturity (e.g., seeds vs. adults) during restoration.

In response to accelerated declines in seagrasses across the globe, efforts to restore seagrass beds have increased dramatically over the last two decades (Zhang et al., 2018). While successful restoration efforts have occurred, outcomes are highly variable with an almost two-thirds failure rate (Reise and Kohlus, 2008; Orth et al., 2012; van Katwijk et al., 2016; Lefcheck et al., 2018). Hence, improving the success of small-scale designs is necessary to increase the feasibility of seagrass restoration. One potential way to harness facilitation in seagrass restoration is to plant aggregated or large-intact patches rather than dispersed designs, as large patches self-facilitate to resist and reduce hydrodynamic stress (Van Keulen et al., 2003; Bos and Van Katwijk, 2007). Moreover, clonal organisms such as seagrasses that can internally translocate nutrients may more readily resist abiotic stressors such low oxygen in sediments (de Kroon, 1993). Another promising approach to harness facilitation by design is to incorporate secondary foundation species into seagrass plantings. For example, bivalves in seagrass beds have the capability to enhance benthic-pelagic coupling and benefit seagrass growth (Wall et al., 2008), and some entangled seaweeds can enhance local biodiversity, particularly in low nutrient scenarios (Thomsen et al., 2018).

The high degree of variability in seagrass restoration outcomes necessitates an expansion of the current theoretical framework to include methods, such as harnessing positive interactions, that have been experimentally demonstrated to enhance restoration success. We utilized a multi-disciplinary approach to determine: (i) the extent to which facilitation has been utilized in seagrass restoration schemes and (ii) when and how inter- and intraspecific facilitation affects seagrass growth. Specifically, we conducted a global survey of practitioners to gain a broad understanding of the current and previous methodologies employed for planting and restoring seagrasses. We further conducted two separate field experiments to test our hypothesis that interspecific facilitation by bivalves could enhance the growth of *Zostera marina* from seed, and that both interspecific facilitation by bivalves and intraspecific facilitation among outplants could increase the growth, expansion, and persistence of mixed eelgrass and shoalgrass (*Zostera marina* and *Halodule wrightii*) patches in a restoration setting.

MATERIALS AND METHODS

To examine the effects of intra- and inter-specific facilitation on seagrass restoration, we took a multi-disciplinary approach. First, we conducted a global survey of restoration practitioners across a wide array of affiliations to determine the extent that positive species interactions were utilized in seagrass restoration projects. Second, we conducted two separate field experiments in the southern Outer Banks of North Carolina, United States to determine the direct effects of (1) infaunal clams on the success of outplanted seeds, and (2) the relative effects of clams and planting configuration on shoot restoration success.

Practitioner Survey

In order to gain a better understanding of previous seagrass restoration efforts and methodologies, we conducted a global survey of practitioners to assess typical project size, location, and the use of various planting techniques. The survey data presented here is a subset of a 20-question survey instrument that was developed and tested by an interdisciplinary team of academic researchers. We used Qualtrics survey software and Google Cloud Computing to solicit and distribute our survey to over 750 restoration individuals and organizations including academics, researchers, consulting companies, government agencies, and non-profit organizations. The list of potential respondents was compiled from known seagrass restoration practitioners and researchers (e.g., members of the Seagrass Restoration Network, scientists who publish on seagrass restoration topics, etc.), state agencies tasked with coastal environmental conservation and management, and organizations or companies frequently contracted for coastal environmental remediation and mitigation. Thus, our solicitation was aimed toward capturing a wide and representative swath of practitioners. Survey participants were recruited via an initial direct solicitation email on 18 February 2020 and a follow-up reminder email was sent 2 weeks after the initial solicitation on 3 March 2020 (**Supplementary A**). Each respondent was issued an individualized survey link that would allow only one response per link. Survey responses were recorded from 18 February-20 March 2020. Participants were asked various questions regarding

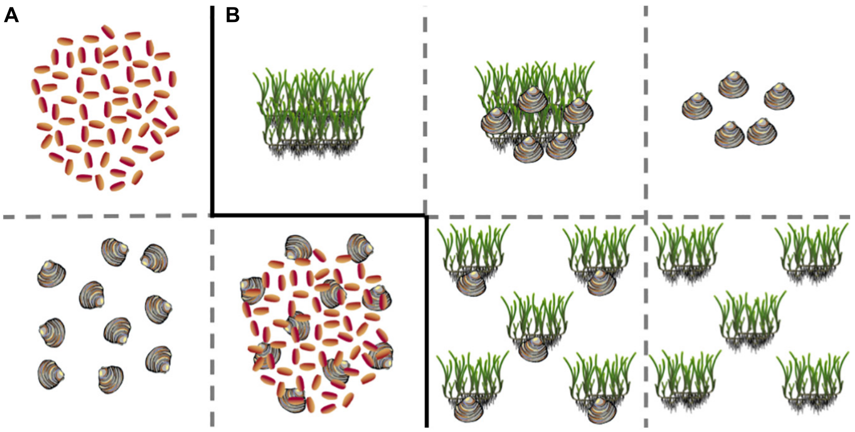

FIGURE 1 | Planting schematic of **(A)** seed and **(B)** adult shoot experiments. Solid black lines indicate different experiments. Each experiment also included a control bare plot not depicted here. Graphics courtesy of Abigail Poray, and Catherine Collier, Integration and Application Network, University of Maryland Center for Environmental Science.

location, planting methodologies, monitoring efforts, priorities, and restoration budget (**Supplementary A**).

Seed Planting Experiment

Reproductive eelgrass shoots were collected by hand in April and May 2017 from a donor seagrass bed near Harker's Island, NC, United States. Reproductive shoots were stored within an indoor, flow-through seawater system at the Duke Marine Lab in Beaufort, NC, United States with a thin layer of fine sediment. Aquaria were housed in an indoor facility with a 12-h light timer and air bubblers. Tanks were stirred on a daily basis to ensure that shoots did not desiccate and to encourage seeds to drop. After 3 weeks, excess plant material was removed by hand from the tanks, examined for any seeds that had not dropped, and disposed. Seeds were not moved, filtered from sediment, or transferred from initial holding tanks to minimize handling. Seeds were maintained in flow-through tanks until December 2017 (Marion and Orth, 2010). Prior to planting, 50 seeds were tested for viability using tetrazolium staining (Conacher et al., 1994). We found that our seed stock had an average viability of 80%, however, direct tests of germination (e.g., in petri dishes) likely would have revealed lower, more accurate rates of germination.

Seeds were planted in early December 2017 at Oscar Shoal, in Back Sound, NC to coincide with observed natural germination periods in NC when water temperatures consistently reached 15°C or below—the optimal temperature for germination of *Zostera marina* seeds (Marsh et al., 1986; Moore et al., 1993). We tested four treatments: bare, seed addition only, clam addition only, and clams and seagrass addition ($n = 5$ per treatment, **Figure 1A**). We used the quahog, *Mercenaria mercenaria*, in our experiment, as it is one of the most abundant bivalves in North Carolina and is the subject of extensive aquaculture such that large quantities are readily available at low cost from local hatcheries. Because large adult clams could adversely bioturbate seagrass seeds, juvenile clams (<1 cm width) were purchased from a local aquaculture farm, Morris Family Shellfish Farms, located in Sealevel, NC. Juvenile clams were stored in the same facility as seagrass seeds for 24 h prior to deployment. For clam treatments, 10 seed clams (<1 cm width) were added within the plot. Studies have found that phytoplankton in North Carolina waters is sufficient to maintain adult clams at densities of 60–80 m^2 with little effect on growth or survival (Peterson and Beal, 1989; Irlandi and Mehlich, 1996); thus, while our initial densities were high, it is not likely that juvenile clams were competing for resources with each other or with seeds. Previous studies of seed density in our area found an average seed density of 336 seeds per 0.5×0.5 m^2 plot (~1,350 seeds m^{-2}) in large, unfragmented seagrass beds (Livernois et al., 2017). Following these estimates, we manually planted 65 seeds within a 20×20 cm plot (~1,300 viable seeds m^{-2}). Both seeds and clams were covered with a thin layer of sediment (<2 cm) after planting. Plots were spaced 1 m apart to ensure that lateral growth could be attributed to growth from the initial quadrat. Prior to planting, cores ($n = 5$, 12.5 cm diameter) were taken from the planting site to determine natural seed abundances. No seeds were recovered in any of the pre-planting cores.

Plots were monitored monthly from December through March, and biweekly in April, and May for, patch dimensions, shoot density and grass growth rate. Seagrass growth was measured by marking 10 separate shoots approximately 1 cm below the sheath. After 2 weeks, marked shoots were collected and brought to the lab for processing. At the end of May, plots were entirely excavated and processed in lab to determine above and belowground biomass, shoot density, average shoot length, and reproductive effort. No growth was observed in either control (bare) or clam-only patches; thus, these treatments were dropped from the analysis, and only seed vs. seed-and-clam treatments were compared. Analyses were conducted with Student's t-tests ($\alpha = 0.05$) if data met test assumptions.

Because bivalves can increase seagrass growth by increasing nitrogen availability in the sediment through biodeposition, we further measured the carbon content (%C), nitrogen content (%N) and carbon to nitrogen ratio (C:N) in seagrass tissue by

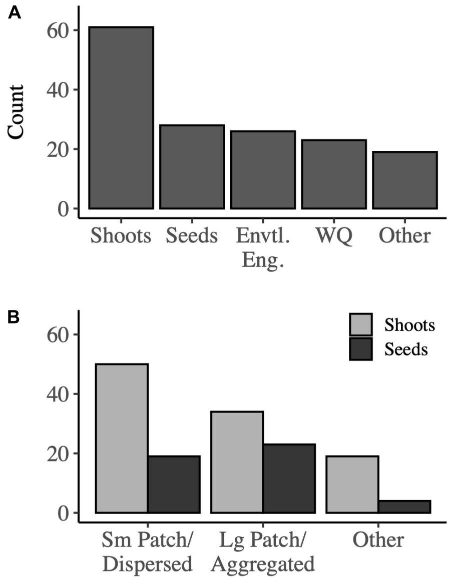

FIGURE 2 | Approaches to **(A)** seagrass restoration broadly, and **(B)** specific methodologies regarding planting configuration. Envtl. Eng. = Environmental engineering, and WQ = water quality. Other approaches included sediment filling and remediation, building breakwaters or living shorelines, and alteration of hydrodynamics.

clipping, drying, grinding, and acidifying (to remove inorganic nitrogen) samples of above and belowground biomass. CHN analyses were run by the Duke Environmental Stable Isotope Laboratory on a CE FlashEA 1112 (Thermo Fisher Scientific, Waltham, Massachusetts, United States). Total above- and belowground nitrogen was estimated by multiplying the above C:N ratio by plot biomass. Statistical differences in nitrogen content of patches between seed and seed-and-clam treatments were determined using a Student's *t*-test ($\alpha = 0.05$).

Adult Transplant Experiment

To directly test for potential differences between intra- and inter-specific facilitation on the growth of adult shoot transplants of both *Zostera marina* and *Halodule wrightii* (eelgrass and shoalgrass, respectively), we conducted a fully factorial experiment crossing planting arrangement with clam additions such that we had six treatments: large-intact patch only, several-dispersed patches only, large-intact patch + clams, several-dispersed patch + clams, clam-only patch, and a bare patch with seven replicates per treatment (**Figure 1B**). An intact turf of seagrass (25 × 25 cm), including rhizomes and sediment, was manually dug from a nearby seagrass bed and transplanted into an adjacent sandflat (<400 m away) that was determined from historical maps to have supported seagrass beds within the last 15 years at south Core Banks, NC. Transplant patches were sown such that all rhizomes were covered with at least 2–3 cm of sediment. Outplant patches were composed of both eelgrass and shoalgrass at an average of 23 eelgrass shoots and 84 shoalgrass (average total of 107) shoots per patch, with no significant differences between initial shoot densities. Several-dispersed treatments were composed of 5 separated, small patches planted within a 0.5 × 0.5 m monitoring plot for a combined initial seagrass area of 625 cm^2 (**Figure 1B**); whereas, large-intact outplants consisted of a singular, undivided patch measuring 25 × 25 cm (625 cm^2). Harvest-sized clams (2.89 cm mean umbo height) were purchased from local fishers and stored in flow-through seawater facilities for 24 h prior to deployment. To each clam addition treatment, five clams were added per plot and allowed to self-bury. Experiments were conducted from June through September 2018 and monitored monthly for seagrass density and patch dimensions as well as clam mortality. We maintained clam density at five per plot when obvious signs of mortality (shell fragments) were observed. To test for a statistical effect of patch configuration (large-intact versus several-dispersed) and clam addition on the above metrics of productivity, we checked to ensure data met test assumptions and used analysis of variance (ANOVA, $\alpha = 0.05$) and Tukey Honest Significant Differences (Tukey HSD) tests were to determine differences in main effects shown from ANOVA tests. We were unable to obtain samples for Carbon: Nitrogen analyses as experiments were abruptly concluded in September 2018 as a result of Hurricane Florence. Sites were surveyed immediately post-storm and in the 2019 growing season to determine if patches weathered the storm or would return the following year. We did not observe any indications of patch [re]growth post-storm.

RESULTS

Our survey was distributed globally to 750 seagrass restoration practitioners representative of multiple sectors including academic, governmental, non-profit, and private organizations (**Supplementary A**). From this, 152 respondents completed the survey; 103 indicated that they currently or had previously restored seagrasses, and 80 specifically responded to questions regarding positive interactions in restoration methodologies and approaches (**Supplementary B** and **Supplementary Figure S1**). Respondent affiliations were fairly heterogeneous with 24 non-profit, 26 academia, 30 governmental agencies, and 12 private companies (1 respondent indicated multiple) listed. However, respondents were located primarily in the United States, with no respondents from/in either the African continent or the Mediterranean region. Practitioners utilized various methods for restoring grasses including planting shoots, planting seeds, engineering and regrading sites, water quality amendments, among others (68, 32, 27 and, 24 responses, respectively, **Figure 2A**). More specifically, most respondents planted in dispersed arrangements (86% of respondents, **Figure 2B**). When planting shoots in particular, seagrasses were more frequently arranged in a dispersed configuration than in an aggregated or single large patch (48% dispersed, 33% aggregated). The reported average distance between shoot outplants was 0.75 ± 0.78 m (*N* = 56); whereas, the average distance between seed patches was 1.17 ± 1.13 m (*N* = 19). Respondents who had attempted or conducted co-restoration of seagrasses with other habitats or organisms rarely incorporated within-habitat facilitations such as planting with infaunal bivalves (**Supplementary B** and **Supplementary Table S1**), and notably, only one respondent attempted to restore multiple seagrass species in a single project.

Our from-seed restoration experiment found that clam addition was positively associated with multiple metrics seagrass productivity including significantly greater shoot length (p = 0.013) as well as patch expansion, and belowground biomass (**Figures 3A,B** and **Supplementary Table S2**). Seed patches with clams expanded on average 500% from initial area measurements; whereas, patches without clams did not change significantly in size (p = 0.010, $\bar{x}_S$ -10.63% and $\bar{x}_{SC}$ 513.62%, **Figure 3C**). Belowground biomass was also significantly greater in the presence of clams, with almost 10 times more belowground biomass in plots with clams (p = 0.010, $\bar{x}_S$ 0.37 g and $\bar{x}_{SC}$ 3.12 g, **Figure 3D**). However, aboveground biomass at experiment end was not significantly different, despite being, on average, nine times greater (p = 0.083, $\bar{x}_S$ 0.78 g and $\bar{x}_{SC}$ 6.80 g). We did not find an effect of clams on the number of seedlings that initially emerged (p = 0.6083), but reproductive effort, measured as both the number of seeds and the total biomass of reproductive grasses was on average 5—6 times greater in patches with clams, but the difference was not significant (p = 0.119, $\bar{x}_S$ 61.2 and $\bar{x}_{SC}$ 316.2 seeds/patch, and p = 0.163, $\bar{x}_S$ 0.35 g and $\bar{x}_{SC}$ 2.04 g, respectively). Carbon: Nitrogen analysis indicated that seagrass in plots with clams had a significantly lower C:N ratio in both the leaves (p = 0.005) and rhizomes (p = 0.005). Total aboveground nitrogen in seagrasses was over 10 times higher in plots with clams ($p < 0.001$, $\bar{x}_S$ 21.06 mg and $\bar{x}_{SC}$ 131.83 mg, **Figure 3E**), and total belowground nitrogen was over five times greater in the presence of clams ($p < 0.001$, $\bar{x}_S$ 5.12 mg and $\bar{x}_{SC}$ 27.57 g, **Figure 3E**). Conversely, we did not find a statistically significant difference in clam survivorship between clam and clams+seagrass treatments (P = 0.095).

When outplanting mixed-species seagrass sods, we did not find a significant effect of clam addition or an interactive effect of clams and planting arrangement on patch productivity. However, *post hoc* tests revealed siginificant variation between large-intact and several-dispersed configurations (**Supplementary B** and **Supplementary Table S3**). Patches transplanted as a single large-intact unit gained shoots in both August and September (2 and 3 months post-planting, intact vs. dispersed $p < 0.001$, **Figures 4A–C**); whereas, those divided into a several-dispersed arrangement consistently lost 2–21% of shoots throughout the experiment duration. Furthermore, despite all treatments having an initial total grass area of 625 cm^2 and no significant difference in initial eelgrass or shoalgrass density, large-intact patches on average increased in area, and several-dispersed patches decreased (p = 0.002, **Figure 4D**). Similarly, large-intact patches were nearly twice as large in area as several-dispersed patches at experiment end ($p < 0.001$).

DISCUSSION

Facilitations and mutualisms are powerful species interactions that play important roles in the organization, stability, and especially the recovery of coastal ecosystems (He et al., 2013; He and Bertness, 2014; Thomsen et al., 2018). Because restoration frequently takes place in heavily degraded areas that have lost many of the positive feedbacks crucial for maintaining ecosystem structure and stability, it is necessary for methodologies to consider and include approaches that harness beneficial species interactions. Here, we demonstrate that while including positive interactions in seagrass restoration approaches is an uncommon approach, for two different seagrass life stages, it can greatly increase restoration outcomes. For seeds, clam additions reversed restoration outplant trajectory from failure to success, while intraspecific facilitation greatly increased expansion rates of adult outplants. Combined, our survey results and experimental findings suggest a need to expand the theoretical framework of seagrass restoration to consider and incorporate all positive interactions possible, including facilitation cascades, intra- and interspecific facilitations within habitats, mutualisms, biodiversity enhancement, and long-distance facilitations.

Global Survey Reveals Stress-Avoidance Paradigm

In the next decade, efforts to conserve and restore coastal habitats and biodiversity will increase dramatically in frequency. Despite studies demonstrating the many benefits conferred by harnessing positive interactions in restoration (Halpern et al., 2007; Brooker et al., 2008), our practioner survey revealed that previous efforts have steered toward planting methodologies that minimize potential competitive or stressful interactions rather than capitalizing on intra- or interspecific facilitations. Although our survey was completed by respondents located across 23 different countries, it is still limited in geographic representation and is only a subset of all seagrass restorationers. In addition to stress-avoidance, multiple other factors may underlie our observed trends, including a lack of funding to restore multiple species, and/or a perception that multi-species restoration would be too costly and yield limited success compared to a single-species approach likely underlie the distinct lack of respondents who had attempted co-restoration of seagrasses with other habitats or organisms. Determining whether these prevailing approaches in seagrass restoration should be changed to systematically incorporate co-restoration and positive species interactions requires empirical tests that investigate how including facilitation can affect the success of seagrass plantings.

Clams Enhance Seed Establishment and Growth

Our restoration from seed experiment demonstrated that clam addition was associated with greater patch productivity and expansion. From subsequent CN analyses, we hypothesize that the mechanism for enhanced growth in our seed experiment was greater nitrogen uptake and concentration in newly germinated seagrass seeds and/or seedlings. The higher nitrogen content in both the leaves and rhizomes of seagrasses grown with clams suggests that organic matter deposited as pseudofeces from bivalves may elevate early seagrass growth (Peterson and Heck, 2001b). While our treatment of 10 juvenile seed clams (<1 cm umbo height) per 20 x 20 cm quadrat was initially high compared

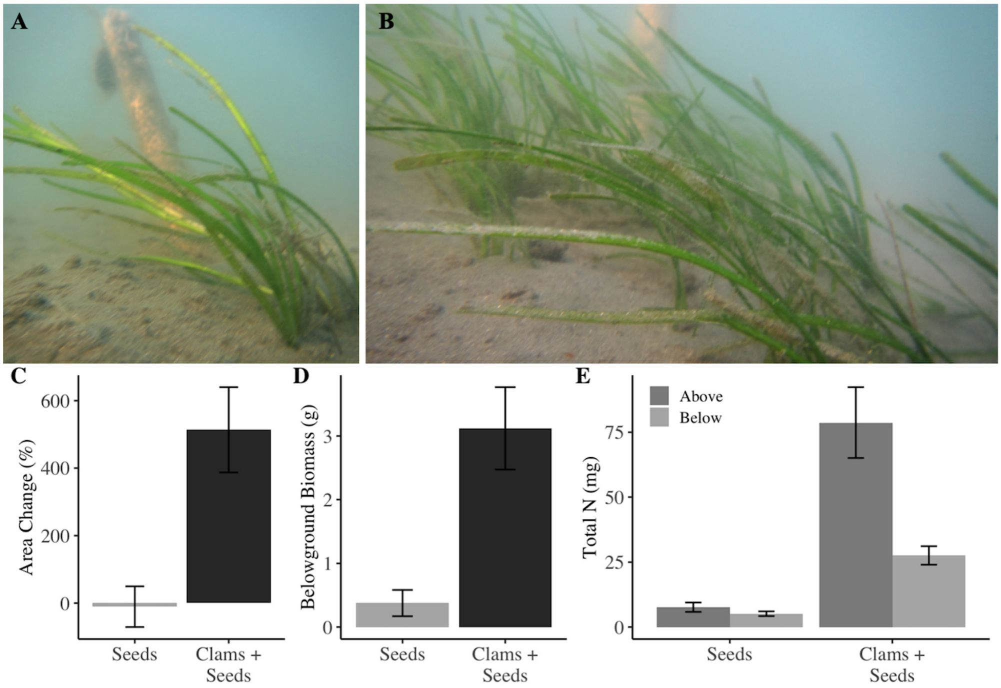

FIGURE 3 | Demonstrative **(A)** seed only and **(B)** seeds and clams plots in May 2018 at experiment end. Seagrass seeds sown with infaunal clams exhibited **(C)** over 500% increase in in patch area relative to initial patch size ($p = 0.023$), and **(D)** seven times more belowground biomass, $p = 0.04$, and significantly greater **(E)** total nitrogen above- and belowground ($p < 0.001$, $p < 0.001$). Error bars represent one standard error.

to observed natural adult clam densities in local seagrass beds (up to 6 m^{-2}, *pers. obs.*), our findings suggest that post-mortality, clam densities per plot (~2–3 $patch^{-1}$) leveled out to those of naturally-occurring densities. Decomposition of clam tissues could also have been a significant source of nitrogen in addition to pseudofeces deposits. Regardless, our experimental findings suggest that the addition of nutrients from clams may play a particularly vital role in the early stages of eelgrass development and expansion from seed. In addition, because eelgrasses in North Carolina are annuals, increases in sexual reproductive effort, as observed in our seed-and-clam treatments, may potentially enhance seed bank densities and the likelihood of patches returning in subsequent years.

Previous studies have found that fertilization of outplants in nutrient-poor sediments can increase restoration success (van Katwijk et al., 2016), and bivalves within a habitat may provide a similar function without adding commercial fertilizers (Reusch et al., 1994; Gagnon et al., 2020). Because infaunal clams deposit pseudofeces on sediment rather than into the water column, nutrients provided in pseudofeces are more readily available for seagrasses to utilize (Peterson and Heck, 2001b). To capitalize on this facilitative mechanism, approaches must consider site sediment characteristics, as fertilization in already high-nutrient sediment may inhibit seagrass growth by increasing sediment sulfide concentrations (Vinther et al., 2008). In addition to nutrient dynamics, the abundance and density of bivalves needed will be influenced by predation regimes and predicted rates of natural mortality. Seed predation by fish, marine mammals, and benthic invertebrates can be a major factor in seed loss across multiple localities (Fishman and Orth, 1996; Holbrook et al., 2000; Nakaoka, 2002; Robert et al., 2002), and predators foraging for infauna may bioturbate seagrasses. However, infaunal bivalves could further facilitate seagrasses by aiding in seed burial thus enhancing the likelihood of germination and seedling establishment (Li et al., 2017). While we did not directly measure germination in our experiment and our estimates of viable seeds are not directly interchangeable with germination rates, initial counts of aboveground shoots did not indicate a significant difference between treatments with respect to seedling establishment.

Intra- but Not Interspecific Facilitation Enhances Adult Seagrass Planting Success

In contrast to seeds, we did not find evidence to support an effect of clam addition on the success of transplanted mixed *Zostera marina* and *Halodule wrightii* (eelgrass and shoalgrass, respectively) patches. Rather, intra-specific facilitations and planting a single large-intact rather that several-small dispersed patches, was associated with patch growth. Given our context-dependent finding of positive clam effects, more studies are needed to specifically identify when and where clams provide positive or neutral effects on seagrass growth. Considering differences in seagrass ontogeny as well as site characteristics and bivalve type will be key to determining the role of

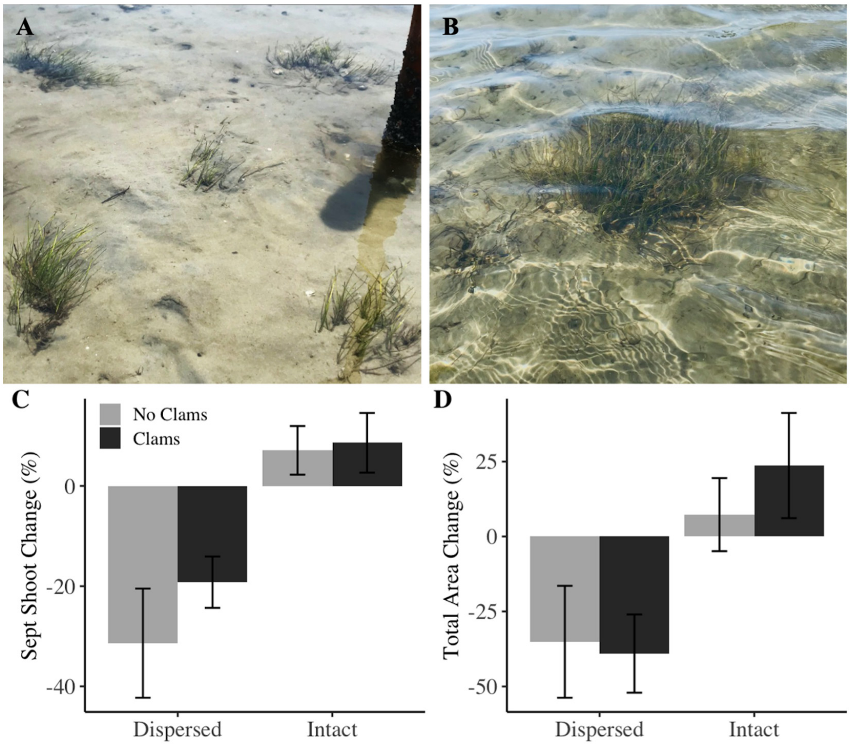

FIGURE 4 | Configurations of **(A)** dispersed and **(B)** single-intact plots. Photos taken approximately 1 month after planting in July 2018. Interactive and separate effects of adult planting configuration and clam addition from ANOVA tests indicated that clams did not alter productivity; rather, intact patches had significantly greater **(C)** proportional change in shoot density from August to September, and **(D)** total change in patch area over the entire experimental duration from June to September than several-dispersed configurations. Error bars represent one standard error.

positive interactions and expanding the theoretical framework for restoration. In addition to nitrogen deposition, bivalves may facilitate seagrasses by reducing sulfide concentrations in the sediment (van der Heide et al., 2012; de Fouw et al., 2016; Chin, 2020; Van Der Geest et al., 2020) or by consuming and reducing epiphyte loads that could otherwise hinder seagrass photosynthesis (Peterson and Heck, 2001a,b). Although we did not test for the effect of bivalves on epiphytes in our experiments, we suspect that this mechanism would have had a stronger effect on the adult transplant experiment where clams were significantly larger than seed clams (<1 cm umbo width). Moreover, because adult out plant patches were a mix of eel- and shoalgrass, epiphyte effects may also have been minimized by the more abundant and narrower blades of shoalgrass.

Myriad studies have shown that intraspecific facilitation via positive density dependence is critical for seagrass success under a range of stressful physical and biological conditions (summarized in van Katwijk et al., 2016). Our findings, while challenging restoration paradigms, align thoroughly with what has been found in ecological studies. Seagrasses grown in large-intact patches may facilitate one another by reducing erosion- and flow-related stress, conferring resistance to soil anoxia, and by sharing resources between ramets (Van Keulen et al., 2003; van Katwijk et al., 2016). Because all plots had the same initial area and shoot density, our experiment further demonstrated that intact patches only 25 × 25 cm in dimension were large enough to promote positive intraspecific feedbacks. These advantages are likely to positively scale with patch size but may decrease as patches become extremely large. As patch size increases and positive feedbacks ameliorate stressful environmental conditions, transplants may start to compete (Maestre et al., 2009). Although we were not able to collect measurements that would give inference on mechanisms because of Hurricane Florence in September 2019, we hypothesize that larger clumps increased patch growth via positive effects conferred by intact root systems that facilitate anchoring, erosion reduction, and nutrient acquisition and allocation, given past findings. Future studies should elucidate whether a size-dependent inflection point exists where additional increases in intact patch size does not confer additional benefits, and the extent to which facilitation can increase resilience to large natural disturbances.

When examining changes by seagrass species, we found that shoalgrass drove the overall observed trends in patch shoot density in all treatments (**Supplementary Figure S2**), as eelgrass continually declined in density and was completely absent from all plots by September. This pattern of growth and dieback matches the natural history of our system, as shoalgrass is a tropical seagrass that is more productive in the summer months and persists through the early fall when the experiment was conducted; whereas, eelgrass is a temperate species growing at the southern limit of its range and is most productive in the spring and dies back mid-summer. Facilitation may not effectively combat heat stress when a species is already at a thermal limit. Instead, our findings suggest that planting multiple species rather than a seagrass monoculture, where appropriate, may infer longer-term resilience of restoration patches similar to the act of successively sowing seeds.

CONCLUSION

Our results point out that when, where, and what type of positive interaction that is incorporated into restoration designs can depend on the life stage and history strategy of the foundation species being restored. The utility of facilitations can also vary by species, site, and habitat and lead to differential benefits and results (He et al., 2013; Gagnon et al., 2020; Valdez et al., 2020). Our study adds to the growing amount of literature that calls for a new coastal restoration paradigm that systematically includes positive interactions and facilitation theory into designs (van der Heide et al., 2007; Silliman et al., 2015; Maxwell et al., 2017; Shaver and Silliman, 2017; Zhang et al., 2018; Renzi et al., 2019; Valdez et al., 2020). Although our practitioner survey revealed that many restoration methodologies do not incorporate intra or inter-specific facilitations, we empirically demonstrate that small changes in methodology to harness positive species interactions can significantly enhance restoration efficiency at little to no extra cost. Additional advances in restoration efficacy could be achieved by applying temporary (e.g., biodegradable) structures that mimic the facilitation-generating traits of the clumped restoration designs used in this study. Such hybrid ecology- and engineering-based approaches may be particularly useful in situations where the amount of available donor material is limited (Temmink et al., 2020). As restoration moves toward an ecosystem- rather than single-species approach (Palmer et al., 1997), expansion of restoration paradigms and approaches that incorporate systematic harnessing of all types of positive interactions, such as trophic and non-trophic facilitations, microbial mutualisms, intra- and interspecific facilitation within a habitat as well as long-distance facilitations that underscore multi-habitat restoration, is needed to advance and enhance the scale and success of restoration efforts as a whole (Halpern et al., 2007; Shaver and Silliman, 2017; Thomsen et al., 2018; Valdez et al., 2020).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Duke University Campus IRB. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

YZ, RG, and BS designed the experiments. YZ, RG, and SD conducted the field experiments. YZ, RG, BS, SD, and ST designed and conducted the practitioner survey. YZ analyzed the data. All authors wrote and revised the manuscript and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.645673/full#supplementary-material

Data Sheet 1/Supplementary A | Practitioner survey solicitations and questionnaire.

Data Sheet 2/Supplementary B | Additional survey responses and experiment statistical analyses.

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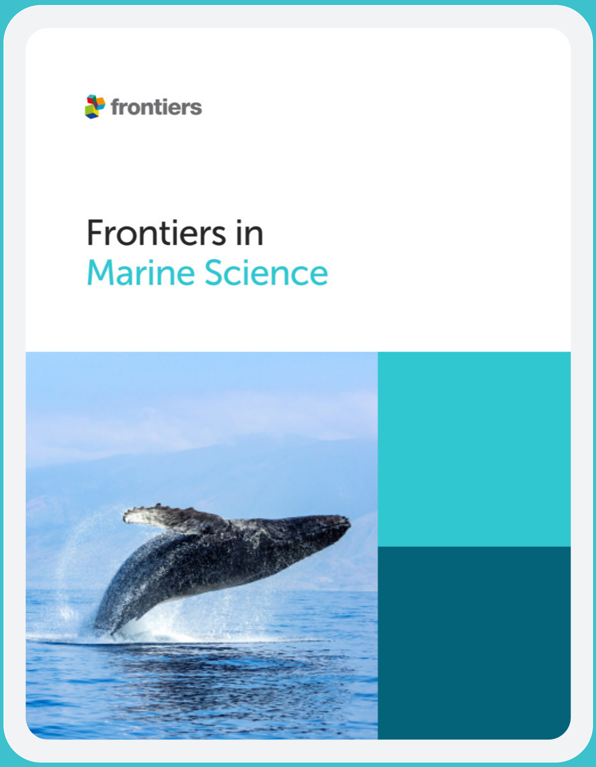

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