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# The benefits of bivalve reef restoration: A global synthesis of underrepresented species

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## Abstract

1. Bivalve habitat restoration is growing in geographic extent and scale globally. While addressing the wide-scale loss of these biogenic habitats is still a key motivation behind restoration efforts, stakeholders and funders are increasingly drawn to shellfish restoration for the many ecosystem services these habitats provide.
2. There is clear evidence for the provision of ecosystem services from species targeted for restoration in the USA, in particular *Crassostrea virginica*. Ecosystem services, however, remain largely unquantified or even undescribed for the majority of other species targeted for restoration.
3. A structured review of the literature was undertaken and supplemented by expert knowledge to identify which ecosystem services are documented in the following other bivalve species targeted for restoration: *Ostrea edulis*, *Ostrea angasi*, *Crassostrea rhizophorae*, *Perna canaliculus*, *Modiolus modiolus*, *Mytilus edulis*, *Mytilus platensis*, *Crassostrea gigas*, *Ostrea denselamellosa*, *Crassostrea ariakensis*, and *Crassostrea sikamea*.
4. Key knowledge gaps in quantifying ecosystem services and the ecosystem engineering properties of habitat-building bivalves contributing to the provision of ecosystem services were identified. Ecosystem services with the potential to be widely applicable across bivalve habitat-building species were identified.
5. Though there is evidence that many of the ecosystem engineering properties that underpin the provision of ecosystem services are universal, the degree to which services are provided will vary between locations and species. Species-specific, *in situ*, studies are needed in order to avoid the inappropriate transfer of the ecosystem service delivery between locations, and to further build support and understanding for these emerging targets of restoration.

KEYWORDS
coastal, ecosystem services, invertebrates, reef, restoration

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## 1 | INTRODUCTION

Biogenic reef habitats are raised, hard, complex structures created by the activity of animals. Such structures typically persist for decades to millennia (Kasoar, zu Ermgassen, Carranza, Hancock, & Spalding, 2015; Lindenbaum et al., 2008), yet they have been facing unprecedented global loss due to human activity, in particular unsustainable extraction and physical impacts of bottom-towed fishing gear (Beck et al., 2011; Cook et al., 2013; Hall-Spencer, Kelly, & Maggs, 2010; Nehring, 1999). In temperate and subtropical climates, biogenic reef habitats include coralline growth (e.g. maerl beds, cold-water coral reefs), biogenic encrustations (e.g. *Sabellaria* spp. reefs), and bivalve reefs (e.g. mussel and oyster beds). Despite the widespread decline of these valued marine habitats and the increasing momentum to ecologically restore habitats (e.g. through the UN Decade on Ecosystem Restoration), restoration of these marine habitats remains restricted to bivalve reefs, and even here the practice is still in its infancy.

Bivalve reef restoration has become commonplace in coastal waters across the USA and is gaining momentum in other regions of the world. The restoration efforts are largely motivated by evidence of the widespread decline of these bivalve species (Beck et al., 2011; Fariñas-Franco et al., 2018; Pogoda et al., 2019), combined with evidence of the potential ecosystem services provided by these threatened habitats and the capacity of restored systems to enhance the delivery of services (Smaal, Ferreira, Grant, Petersen, & Strand, 2019). Yet globally, the vast majority of studies on bivalve-reef-related benefits (e.g. biodiversity, productivity, water filtration) are based on *Crassostrea virginica* in the USA. The purpose of this study is to examine the level of ecosystem services provision that could be expected from other species of restoration interest. The underlying drivers of ecosystem services provision were also examined, and the likely potential ecosystem services benefits from all species and the gaps in quantitative evidence were identified.

Within the scope of this review, a subset of marine bivalve species, primarily in the Mytilidae (mussel) and the Ostreidae (oyster) families, are known ecosystem engineers, forming biogenic habitat. These species, in particular oysters, typically display aggregating behaviour, whereby the pelagic juveniles preferentially settle out of the water column in the presence of conspecific individuals, thus forming these biogenic habitats (Rodriguez-Perez et al., 2019). Biogenic bivalve beds and reefs historically dominated many temperate estuaries and coasts (e.g. Blake & zu Ermgassen, 2015; Drake, 1875). They were historically vast in spatial extent in many locations (see examples in zu Ermgassen, Hancock, et al. (2016) and case studies in Supporting Information Table S1), and often provided substantial vertical relief (Brooks, 1884; Zhang, Xi, & Ge, 2004), forming unique, biodiverse, and productive habitats (Möbius, 1877). Their complex biogenic nature, however, also results in their being especially sensitive to physical impacts (Cook et al., 2013).

Habitat-building bivalve species are increasingly recognized as ecologically important features of temperate coasts and estuaries and are recognized in their own right in international and national policy and legislation through, for example, OSPAR, the EU Habitats Directive, and most recently by being adopted as a wetland habitat type by Ramsar (Kasoar et al., 2015). Bivalve habitats have been subject to significant declines worldwide, with an estimated 85% decline globally (Beck et al., 2011). As such, there is an imperative to restore these sensitive habitats, both to address the biodiversity loss resulting from declines in these species and the loss of the ecosystem services they provide.

Restoration efforts based on *C. virginica* in the USA have led the way in developing potential approaches to restoring bivalve reefs, as well as a scientific understanding of the ecosystem service benefits where restoration is undertaken (Coen et al., 2007). Though efforts to restore bivalve reefs are increasing in multiple locations around the world, there is currently no overview of the status of ecosystem service science for the diverse species being restored. Until now, stakeholders in diverse geographies have been reliant primarily on restoration examples and science from the USA to understand the potential for bivalve habitat restoration and the ecosystem service benefits it may yield (see zu Ermgassen, Hancock, et al. (2016) for a comprehensive review). This information is, to a degree, transferable and can therefore benefit and provide a useful guideline for initiatives (Gillies, Crawford, & Hancock, 2017), but benefit transfer across regions and between genera can also result in erroneous estimates of ecosystem services value (Mtwana Nordlund, Koch, Barbier, & Creed, 2016; Plummer, 2009). The results of a structured review and expert-derived evidence of the status of ecosystem science for each of the species of restoration interest are presented, including identified knowledge gaps. This summary is intended to support an understanding of when it is appropriate (or not) to assume delivery of ecosystem services across species.

## 2 | METHODS

Bivalve reef restoration has only recently begun to gain traction outside of the USA. In order to identify species of restoration interest in emerging geographies in the absence of a global database of restoration efforts, existing bivalve habitat restoration programmes were identified via two approaches. First, the conference programmes of the International Conference on Shellfish Restoration from 2011 to 2014 were searched for oral or poster presentations detailing restoration work outside of the USA (i.e. excluding *C. virginica* and *Ostrea lurida*). Second, restoration efforts were identified by contacting The Global Oceans Team at The Nature Conservancy (B. Hancock, personal communication). The Nature Conservancy is a USA-based global conservation organization with a strong leadership role in bivalve habitat restoration globally.

At least one individual identified as working on each species represented within identified restoration efforts globally was contacted and asked to provide species- and region-specific details of the historical and ecological knowledge of the habitat-building species of interest, including information regarding the ecosystem service provision by the restored habitat. An emphasis was placed on these local experts utilizing grey literature and historical texts, both of which are not searchable through Web of Science. Experts were asked to provide historical ecological data available about the target species or its utilization, an assessment of the current status of the species in the case study area, and detail of the restoration activity undertaken.

In order to ensure that all scientific evidence for bivalve habitat ecosystem services was included for the species identified, a structured review was undertaken in Web of Science (https://webofknowledge.com/) for each bivalve species and potential ecosystem services (see Table 1 for full list of search terms). Potential ecosystem services were identified from summary literature on *C. virginica* (Coen et al., 2007; Grabowski et al., 2012). Searches were completed between March and December 2017. The title and abstracts of all journal articles identified through this process were read and assessed for possible relevance. Potentially relevant articles were then read in full, and any quantitative information regarding ecosystem services was compiled into a database. Where necessary, numeric data were extracted from graphs using WebPlotDigitizer (version 3.12). In order to ensure that ecosystem services at the local scale and services that are less well reported in the scientific literature were also captured, contributing experts were also requested to provide details of any ecosystem services they were aware of, related to the case study areas. Services were organized in accordance with the Common International Classification of Ecosystem Services (Haines-Young & Potschin, 2018). Though the status of biodiversity in and of itself within the ecosystem services framework is the source of much debate (Mace, Norris, & Fitter, 2012), biodiversity was included as a cultural value within this framework, as many restoration projects assign value to biodiversity gains.

Literature on bivalve feeding reports either filtration or clearance rates. Methods used were cross-referenced to include all

**TABLE 1** Search terms used in Web of Science

| | Ecosystem service search terms | | | | | |
|---|---|---|---|---|---|---|
| **Species** | **Filtration services** | **Production of associated species** | **Coastal protection** | **Sediment processes** | **Cultural value** | **Ecosystem service** |
| *Perna canaliculus*[a]<br>*Ostrea edulis*[a] | Filtration | Species richness | Coastal protection | Carbon sequestration | Cultural value | Ecosystem service |
| *Mytilus platensis*[a]<br>*Ostrea angasi*[a]<br>*Crassostrea gigas*[a]<br>*Modiolus modiolus* | Clearance rate<br>Water clarity | Fish production | Wave reduction<br>Shoreline protection | Sediment stabilization | Biodiversity<br>Community composition | |
| *Mytilus edulis*[a]<br>*Crassostrea rhizophorae*[a] | | Nursery habitat | | Benthopelagic coupling | Species diversity | |
| *Crassostrea sikamea*[a]<br>*Crassostrea ariakensis*[a]<br>*Ostrea denselamellosa*<br>*Saccostrea glomerata*[a] | | | Erosion reduction | Denitrification | | |

*Note:* Independent searches were undertaken for each species and group of ecosystem services.
[a]Species that are cultured.

measurements of bivalve clearance rates in one unified data set, including all studies using methods that measured the decrease in particles over time. The R package metagear (Lajeunesse, 2016) was used for bulk paper downloads in the R free software program (https://cran.r-project.org) version 3.4.3.

## 3 | RESULTS

### 3.1 | Summary of the historical and current status of case study bivalve populations

Eleven bivalve species were identified as the focus of active habitat restoration: six through International Conference on Shellfish Restoration abstracts and a further five through The Nature Conservancy's network. Four of these, *Crassostrea gigas*, *Crassostrea sikamea*, *Crassostrea ariakensis*, and *Ostrea denselamellosa*, were found in mixed beds dominated either by *C. gigas* (Dashentang, China), or *C. sikamea* (Xiaomiaohong, China). In summary, restoration efforts from nine regions, each representing a single species or mixed species reef, were identified (Figure 1).

Unsurprisingly, given that the species are all subject to restoration efforts, there was widespread evidence of declines in the habitat-building species across all sites. Overfishing is widely, but not exclusively, identified as the primary driver of decline, in many cases leading to collapse and closure of the bivalve fishery and the functional extinction of the habitat (Table 2). Furthermore, where overfishing is identified as the major driver, dredging is often identified as the primary and most damaging gear (six of nine). Even in the case of *Modiolus modiolus*, which is not directly targeted for extraction, towed gears are identified as a major driver of decline (Cook et al., 2013).

The vast majority (eight of nine) of restoration projects identified have taken place since 2010 (Table 2). It is notable that, despite the relative novelty of bivalve restoration outside of the USA (the exception being intertidal *Mytilus edulis* in the Netherlands), many of the reported projects are already restoring at large (hectare) scales (Table 2). Seven of the nine projects were undertaken in marine protected areas, although not all of the protected area designations confer protection to the restoration sites themselves (see Supporting Information Table S1 for further details). In all but one instance, however, the restoration sites themselves are afforded protection from harvest, with *Perna canaliculus* being the exception.

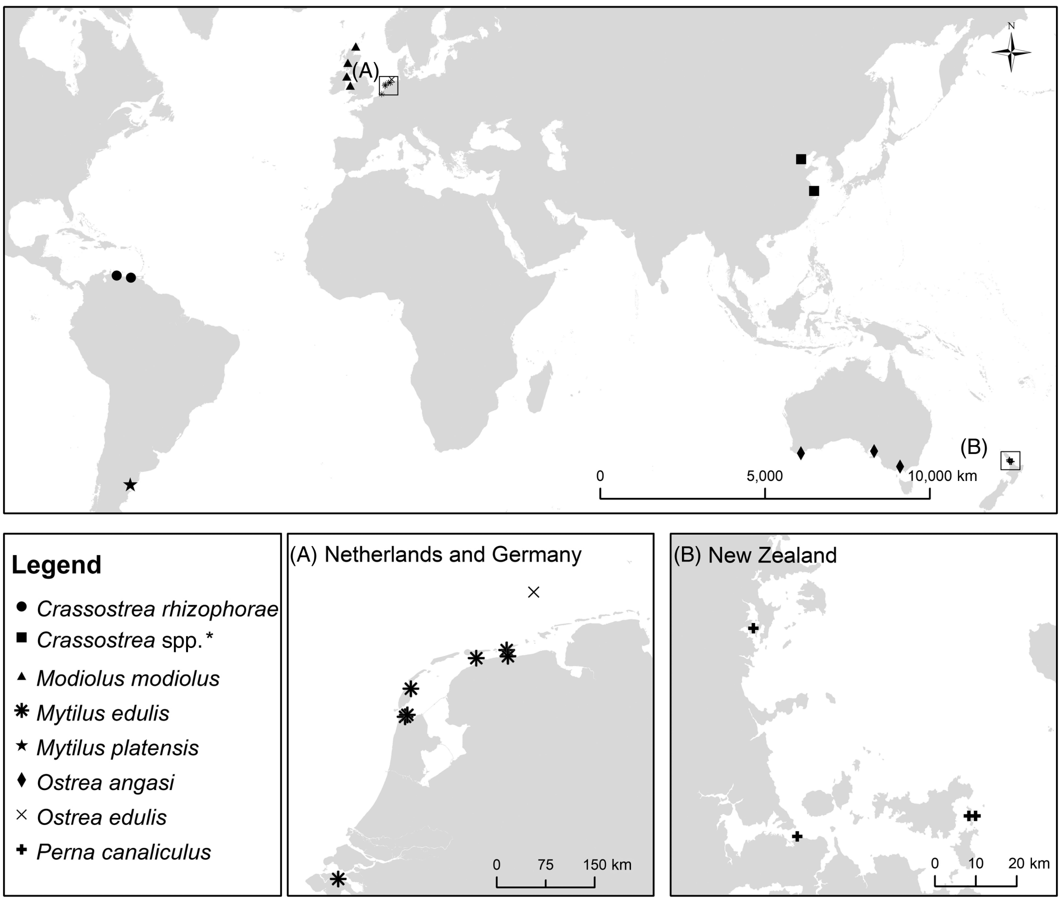


**FIGURE 1** Map of locations of restoration efforts by species. *Crassostrea* spp. include *C. gigas*, *C. sikemea*, and *C. ariakensis*, see text for further details. Basemap in ArcGIS Light Gray Canvas Map and Ocean Basemap. Credits: Esri, DeLorme, GEBCO, Geonames.org, HERE, MapMyIndia, National Geographic, NOAA NGDC, and other contributors

**TABLE 2** An example location for each identified shellfish species/community, listing the historical distribution, primary driver and approximate timing of decline, current status, and details of recent restoration efforts

| Species: country | Location (designation) | Historical distribution (year of observation) | Reported reason for decline | Current status of fishery/beds | Restoration method | Year | Area restored | References |
|---|---|---|---|---|---|---|---|---|
| *Ostrea edulis*: Germany | German Bight (Natura 2000 site and nature conservation area) | ~21,000 km$^2$ | Overfishing, commercial oyster fishing and use of dredge equipment | Collapse recorded in the 1920s. Habitat now extirpated | Replacement of lost hard substrate (mixed substrate: limestone, granite, sandstone structures and shell cultch) and reseeding (spat-on-shell) | 2019–2023 | tbd | Boos, Buchholz, Buchholz, & Gutow, 2004; Caspers, 1950; Gerken & Schmidt, 2014; Möbius, 1877; Pogoda, 2019 |
| *Ostrea angasi*: Australia | South Australia (proposed management; declared aquatic reserve under the Fisheries Management Act 2007) | Harvesting recorded at 67 locations across 1,500 km (19th century) | Commercial oyster fishing and use of dredge equipment | Today low levels of production occur through aquaculture. Oyster reef habitat functionally extinct. | Replacement of lost hard substrate (mixed substrate: limestone and concrete structures) and reseeding (spat and adults) | 2017–2019 | 20 ha | Alleway & Connell, 2015; Gillies et al., 2018 |
| *Crassostrea rhizophorae*: Venezuela | Mochima Bay (National Park Mochima) | Abundant spat settlement from wild stocks (ca. 1972). Extent of oyster habitat not recorded, but abundance in mangrove areas noted | Overfishing through manual collection, primarily cutting of mangrove roots | Oyster 'beds' considered 'dead' (2010) and no wild recruitment noted since ca. 1980 | Transplantation of oyster spat from nearby lagoon, Laguna de la Restinga | 2010 | Not reported | Carranza et al., 2011, C. Lodeiros, personal communication; Rodríguez & Rojas-Suárez, 2008; Vélez, 1972 |
| *Perna canaliculus*: New Zealand | Firth of Thames (not designated) | Fishermen described mussel beds occurring within an area of 530 km$^2$ within the Firth of Thames. (pre-1958) | Overfishing by commercial dredge fishery. Sedimentation may have been a minor driver in some locations | Landings peaked in 1961 and the fishery collapsed in 1966. Remnant beds still found in Whangapoua Harbour (Great Barrier Island), the western Firth of Thames, and Ohiwa Harbour | Transplantation of mussels from mussel aquaculture directly deployed onto subtidal soft sediments | 2013–2019 | Not reported | Greenway, 1969; McLeod, 2009; McLeod, Parsons, Morrison, Le Port, & Taylor, 2012; Paul, 2012; Wilcox, Kelly, & Jeffs, 2018 |

**TABLE 2** (Continued)

| Species: country | Location (designation) | Historical distribution (year of observation) | Reported reason for decline | Current status of fishery/beds | Restoration method | Year | Area restored | References |
|---|---|---|---|---|---|---|---|---|
| *Modiolus modiolus*: Northern Ireland | Strangford Lough (special area of conservation, with biogenic reefs as protected feature) | 1970s: Beds contained an average density of 134 $m^{-2}$; 1982: 12.6 $km^2$ | Destruction by scallop trawling | 2011: Beds contained an average density of 3.8 $m^{-2}$<br>From 1975 to 1995 *M. modiolus* distribution declined by >40%<br>By 2007 bed measured 5.7 $km^2$ | Elevated shell cultch, flat shell cultch, no shell, translocated *M. modiolus* clumps | 2010 | ≤25 $m^2$ | Fariñas-Franco & Roberts, 2014; Holt, Rees, Hawkins, & Seed, 1998; Service & Magorrian, 1997; Strong, Service, & Moore, 2016 |
| *Mytilus edulis*: Netherlands | Wadden Sea (Natura 2000 site; mussel beds not explicitly protected) | Minimum estimated extent 1955–1978: 6,000 ha | Overfishing by commercial dredge fishery | Around 1990 the majority of intertidal beds declined in the Dutch Wadden Sea (1.5 m kg harvested). Fishery ceased in 1994 | Numerous attempts at translocation of adults and seed were unsuccessful (see Supporting Information Table S2). Protection of some intertidal areas for cockle have resulted in recovery of intertidal mussel beds | 1995-present | Natural recovery of 4,250 ha by 2017 | Dankers et al., 2003; Van den Ende, Brummelhuis, Van Zweeden, Van Asch, & Troost, 2017; Ens, Smaal, & de Vlas, 2004 |
| *Mytilus platensis*: Argentina | San Matias Gulf (Bahía de San Antonio Protected Natural Area) | Mussels exploited by ancient settlers (6,000–450 BP). Extent not known but annual landings peaked at 2100 t $year^{-1}$ in 1989 | Overfishing and use of industrial dredge gears. | No successful recruitment 1992–2001 | Aquaculture practices, including experimentally deployed ropes to catch seed, combined with a dredge-free experimental area | 2011 | Not reported | Morsan & Zaidman, 2008; Narvarte, González, & Filippo, 2007; Steffan & Morsan, 2015 |
| *Crassostrea gigas; O. denselamellosa*: China | Dashentang (Dashentang Oyster Reef National Marine Special Reserve) | 1970s: 35 $km^2$ | Overfishing and use of industrial dredge gears, poor fishing practice (retaining of shell), land reclamation and pollution | 2006: 3 $km^2$<br>2013: 0.6 $km^2$<br>Active fishery from 1999 to 2006: about 12,500 t $year^{-1}$ | Placement of oyster shell bags as cultch | 2014 | 10 ha | Fan et al., 2010; Fang, Li, & Yu, 2007; Guo, 2003; Qiao & Chen, 2014; Sun, Wen, & Bai, 2014 |

(Continues)

**TABLE 2** (Continued)

| Species: country | Location (designation) | Historical distribution (year of observation) | Reported reason for decline | Current status of fishery/beds | Restoration method | Year | Area restored | References |
|---|---|---|---|---|---|---|---|---|
| | | | | Fishery is currently banned. | | | | |
| *C. gigas*; *C. ariakensis*; *C. sikamea*; *O. denselamellosa*: China | Xiaomiaohong Sea (Liyashan National Marine Park) | 1960s: 3.55 $km^2$ only known occurrence of natural, intertidal oyster reefs in China | Sedimentation caused by land reclamation and port construction. Pollution and overfishing by hand harvesting in the intertidal | 2002: about 0.9 $km^2$, average reefs height was 1–1.5 m. 2013: 0.2 $km^2$. Informal survey in 2016 few live oysters observed | Placement of oyster shell bags | 2013–2014 | 2,335 $m^2$ | Gu, Qi, Ge, Yu, & Zhang, 2005; Q. Liu, The Nature Conservancy,2019, personal communication; Quan et al., 2017; Zhang et al., 2004; Zhao, 2009 |

*Note*: This is not an exhaustive list of the historical or current extent of each species.
Abbreviation: tbd: to be determined.

## 3.2 | Summary of recorded ecosystem services provision by habitat-building bivalves

In total, the literature review by species and ecosystem service resulted in the identification of 1,609 articles. Of these, 176 contained data on ecosystem service provision. This was further augmented by expert knowledge, in particular for assessing whether the bivalves were subject to harvest or provided cultural services, as this is commonly underrepresented in peer-reviewed literature (Himes-Cornell, Grose, & Pendleton, 2018).

## 3.3 | Provisioning services

Three key provisioning services derived from habitat-building bivalves were identified: bivalve harvest, enhancement of other fisheries species by the shellfish habitat, and shell mining (Table 3). Many of the bivalve species being restored in large part originally declined due to overharvest, and many still have fisheries associated with them at least somewhere in their range (Table 2). The use of shell as a product via shell mining, in contrast, was only listed for one of the species, *Ostrea angasi*, although the use of shell as a by-product of fishing was noted for *Ostrea edulis* and *C. gigas* (Supporting Information Table S1). Historically, such shells were returned to the seafloor in order to replenish the underlying habitat, but a market for crushed shells as soil conditioner has resulted in some shells going to market instead (Supporting Information Table S1). The failure to return shell material to the habitat from which it was extracted has been implicated many times in the history of overexploitation of oyster fisheries as a major driver of decline (e.g. Blake & zu Ermgassen, 2015).

Though there is substantial evidence that bivalve habitats often support a greater abundance of associated species than nearby unstructured habitats (Supporting Information Table S2), the contribution of this to the provision of other fisheries species was quantified in only one case study. *M. modiolus* beds were found to have three times higher densities of whelk, *Buccinum undatum*, 20 times higher densities of queen scallop, *Aequipecten opercularis*, and four times higher densities of spider crab, *Maja brachydactyla*, than on non-mussel sites (Kent et al., 2017; Kent, Gray, Last, & Sanderson, 2016). Five of the 11 species examined yielded no studies examining the associated communities (Table 2). Where changes in abundance of associated species were recorded, the bivalve habitats were widely found to support increased numbers of individuals relative to unstructured habitats (e.g. Cook et al., 2013; de Montaudouin, Audemard, & Labourg, 1999; Kristensen et al., 2015; Norling, Lindegarth, Lindegarth, & Strand, 2015; Supporting Information Table S2).

## 3.4 | Regulating services

Bivalve habitats provide a range of regulating services, predominantly through their allogenic ecosystem engineering properties (i.e. filter feeding), but also through their physical building of the habitat

**TABLE 3** Summary of available evidence for ecosystem service provision by shellfish species that are currently the subject of restoration efforts outside of the USA

| | | Mussels | | | | Oysters | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Ecosystem services** | *Perna canaliculus* | *Mytilus platensis* | *Modiolus modiolus* | *Mytilus edulis* | *Ostrea edulis* | *Ostrea angasi* | *Ostrea denselamellosa* | *Crassostrea gigas* | *Crassostrea rhizophorae* | *Crassostrea sikamea* | *Crassostrea ariakensis* | *Crassostrea virginica* |
| Provisioning | Fisheries production/ nursery function | – | – | ● | O | – | – | – | – | – | – | – | ● |
| | Shellfish harvest | ● | ● | O | ● | ● | ● | – | ● | ● | ● | ● | ● |
| | Shell extraction | – | – | – | – | – | O | – | – | – | – | – | ● |
| Regulating services | Clearance rate | ● | – | O | ● | ● | O[a] | – | ● | – | – | O | ● |
| | *In situ* evidence of improved water clarity | – | – | – | – | – | – | – | – | – | – | – | ● |
| | Coastal protection | – | – | – | – | – | – | – | O | – | – | – | ● |
| | Carbon sequestration | O | – | O | – | – | – | – | – | – | – | – | ● |
| | Sediment stabilization | – | – | O | O | ●[c] | – | – | O | – | – | – | ● |
| | Denitrification enhancement | O | – | – | O | – | – | – | ● | – | – | – | ● |
| Cultural value | Biodiversity | – | – | ● | ● | ● | O | – | ● | – | – | ● | ● |
| | Cultural harvest practices | O | – | – | – | ● | O[b] | – | – | O | – | – | ● |
| | Religious significance | – | – | – | – | O[b] | – | – | – | – | – | – | – |
| | Recreational | – | – | – | ● | – | – | – | – | – | – | – | ● |

*Note:* Evidence relating to *C. virginica* is presented only for comparison and for identifying data gaps. ●: strong evidence (multiple peer reviewed studies); O: some evidence (few studies/local knowledge); –: no data. See Supporting Information Table S2 for further details and references.

Abbreviation: NA, not applicable.

[a]Clearance rate assessed in larvae only.

[b]Historical.

[c]Not identified in the structured review, but reported in Lee, Davies, Baxter, Diele, & Sanderson (2020).

(autogenic ecosystem engineering; sensu Jones, Lawton, & Shachak, 1994). These regulating services include filtration services, enhancing sediment processes, and coastal protection.

Clearance rate was the best quantified proxy for an ecosystem service (96 scientific references). Available clearance rate estimates were largely confined to species of aquaculture interest, with the exception of *Modiolus modiolus* (Table 3), and for four of the 11 species there were no clearance rates in the literature. Clearance rates were highly variable both within and between species, ranging from 0 to 6–34 L $hr^{-1}$ $g^{-1}$ (Supporting Information Table S2). The reported measurements also covered a variety of conditions, including different temperatures, suspended sediment loads, and size classes of bivalves (Supporting Information Table S2). Given the range of conditions, it was not deemed appropriate to undertake a statistical comparison of the reported rates. Though there is strong evidence in the literature that species or family groups differ with regard to their clearance rate (Powell, Hofmann, Klinck, & Ray, 1992), high variability in rates is a defining feature (Cranford, Evans, & Shumway, 2011). The resulting summary of reported clearance rates by species of conservation interest nevertheless provides some insight into the potential clearance rates achieved by these species (Supporting Information Table S2).

As most measurements of clearance rates take place in controlled laboratory conditions, often with a standardized algal mixture and a single bivalve individual, there has been some discussion of the relevance of these studies to the field of bivalve habitat restoration, where mixed-species reefs, changeable water currents, and natural seston may result in laboratory clearance rates translating poorly into in-situ effects of bivalve filtration (Grizzle, Greene, & Coen, 2008; Wheat & Ruesink, 2013). There have been recent efforts to quantify clearance rates of *M. edulis* and *C. gigas* in the field (Lüskow & Riisgård, 2018; Smaal & Zurburg, 1997; Vismann et al., 2016; Wheat & Ruesink, 2013). Only two of these studies take measurements outside of sealed enclosures, and therefore account for the critical variability in currents (Smaal & Zurburg, 1997; Wheat & Ruesink, 2013), and only one of these studies (Wheat & Ruesink, 2013), accounts for the three-dimensional structure of the reef as well as the associated community beyond the reef-building bivalve, in a reduction in chlorophyll *a* in an open system. The remaining efforts are still notable in attempting to remove some of the biases that may arise from laboratory studies being translated into the field, and in quantifying clearance rates in situ; however, it is noted that the impact of bivalve habitats on water clarity extends beyond clearance rates alone (Grizzle et al., 2008; Wheat & Ruesink, 2013). Methods to measure *in situ* changes in water clarity (including changes in turbidity, and not chlorophyll *a* alone) have been developed for *C. virginica* in the USA (Grizzle, Rasmussen, Martignette, Ward, & Coen, 2018).

Habitat-building bivalve molluscs have been observed to increase the rate of sedimentation, and hence the drawdown of material, including carbon, to the benthos (Haven & Morales-Alamo, 1966). This is a product both of the physical structure of the reefs altering small-scale hydrodynamics and of the feeding action of the bivalves (Kent, Mair, et al., 2017). The structured review identified quantifications of enhanced sedimentation only in *P. canaliculus* (Giles, Pilditch, & Bell, 2006), *M. modiolus* (Kent, Last, Harries, & Sanderson, 2017), and *O. angasi* (McLeod et al., 2019)—but see also Lee et al. (2020) for more recent quantification of *O. edulis*. In each case, deposition was increased substantially, with twice as much deposition occurring around live *M. modiolus* relative to nearby unstructured habitat (Kent, Last, et al., 2017). This enhanced sedimentation contributed to increased sediment stabilization and bentho-pelagic coupling.

A further effect of enhanced biodeposition around bivalve habitats is carbon and nitrogen loading of the sediments. This, in turn, may increase microbial activity in the sediments, including those of denitrifying bacteria (Newell, Cornwell, & Owens, 2002). Enhanced rates of denitrification have been measured in sediments surrounding habitat built by *P. canaliculus* and *C. gigas* (Caffrey, Hollibaugh, & Mortazavi, 2016; Ning et al., 2016; Zeldis, 2005), but this remains unquantified in the other species examined.

Coastal protection was the final regulating service identified. *C. gigas* was the only species in the present study for which coastal protection had been assessed in the literature. Walles, Salvador de Paiva, van Prooijen, Ysebaert, and Smaal (2015) found that the presence of *C. gigas* reefs resulted in elevated areas of sediment on the leeward side of reefs in the Oosterschelde estuary, the Netherlands. It should be noted that this was within the non-native range of this species.

## 3.5 | Cultural services

Cultural services were the most poorly represented in the peer-reviewed literature, with no published examples identified in the structured review. Experts, however, identified cultural values in a handful of species, predominantly linked to harvesting traditions (Table 3; see Supporting Information Table S2 for further details). For example, *P. canaliculus* plays an important role in present-day cultural harvesting practices in New Zealand (B. Hughes, Environmental Manager Ngati Awa, personal communication), and *O. edulis* historically had religious significance in parts of its range (zu Ermgassen, Spalding, & Allison, 2013). A cultural relationship with native shellfish species lies at the heart of a current interest in 'conservation aquaculture', in which the aquaculture of native species for food can be tied inextricably to the species' restoration (Froehlich, Gentry, & Halpern, 2017). Finally, intertidal *M. edulis* reefs provide critical habitat to important bird populations, in particular the oystercatcher (*Haematopus ostralegus*) in the Wadden Sea (Smit, Dankers, Ens, & Meijboom, 1998). These bird populations have both biodiversity and recreational value.

Though the cultural value of biodiversity was not explicitly stated in peer-reviewed publications, it was clear from engaging with restoration practitioners that increases in biodiversity associated with restoration were valued. The relative species richness associated with bivalve habitats has been quantified in only seven of 11 species (Table 3; Supporting Information Table S2). Where it has been quantified, bivalve habitats were generally found to have higher species richness and diversity than nearby unstructured habitats (e.g. McLeod, Parsons, Morrison, Van Dijken, & Taylor, 2014; Norling et al., 2015; Supporting Information Table S2), and the highest species richness across all the sampled habitats in a sea area in one case (Robinson et al., 2012). There are, however, examples of bivalve habitats supporting lower species diversity where the bivalve reached high densities and dominated the community (Dürr & Wahl, 2004; Enderlein & Wahl, 2004).

## 4 | DISCUSSION

### 4.1 | Historical ecology and motivation to restore

Given that the species in this study were selected on the basis of active restoration efforts, it is unsurprising that there is universal evidence for historical declines in the abundance and extent of all of the species. The primary driver in most cases has been the direct extraction of the habitat-building bivalve species by dredging (Table 2). Other forms of harvesting, pollution, coastal development, and impacts of mobile gear also played a role in some cases. The historical evidence gathered supports the widely understood impact of industrial fishing and coastal modification in causing catastrophic declines in otherwise widespread and often culturally important species. Numerous case studies outline a decline from expansive areas (many square kilometres) with a high density of bivalves, often supporting large and productive fisheries, to effective extirpation of the habitat (Supporting Information Table S1).

The restoration efforts presented here all focused on restoration of the habitat; therefore, though a fishery is often implicated in the decline, relatively few of the case studies cited reinstatement of the commercial fishery as a major motivator of restoration efforts. There are occasions when restoration efforts seek to yield improved reef habitat alongside a sustainable fishery, such as in the case of *Crassostrea rhizophorae* in Venezuela and *Mytilus platensis* in Argentina. In all cases, the primary motivation to restore was to improve the condition of a threatened and often protected habitat. Though biodiversity commitments are the sole driver in some cases (e.g. *O. edulis* restoration in Germany), ecosystem service gains have been important in stakeholder engagement and in motivating efforts in other regions. For example, some restoration activity of *P. canaliculus* has been undertaken with the stated objective of improving water quality in the affected waterbody (http://www.reviveourgulf.org.nz), whereas the potential non-oyster fisheries benefits of oyster habitats have been a key motivator in Australian and New Zealand restoration projects (Gillies, Creighton, & McLeod, 2015; van Kampen, 2017). It is noteworthy that, in some contexts (e.g. in the case of Australian oyster reef restoration efforts), the link between bivalve reefs and enhanced production of finfish and associated species has been pivotal in securing support for scaling up restoration efforts (Gillies, Creighton, & McLeod, 2015). This is likely to be the case in a growing number of locations, as fisheries managers move towards ecosystem-based fisheries management, in part through recognition and protection of essential fish habitats.

### 4.2 | Restoration efforts

Restoration efforts for habitat-building bivalves outside of the USA are still a relatively new venture, with almost all projects identified taking place since 2010, the exception being intertidal *M. edulis* in the Netherlands. Though the examples given here represent only a selection of restoration efforts being undertaken globally, it is notable that several of these projects are already large in spatial extent (Table 2). The short lag time (relative to the US experience in the 1990s) between project conception and scaling up is something that is widely attributed both to restoration techniques having being trialled in the USA and to the engagement of stakeholders and funders with ecosystem service delivery from bivalve habitats (Gillies, Fitzsimons, et al., 2015).

Restoration techniques primarily involve reseeding areas with transplanted or hatchery-reared individuals. In the case of oysters, this is frequently accompanied by the addition of hard substrate to enhance settlement potential to the area and prevent re-laid stock from becoming buried. Mussel restoration may also involve the addition of hard substrate, but this is less commonly the case. Where larval supply is deemed sufficient, such as in Dashenteng Oyster Reefs National Marine Special Reserve and Xiaomiaohong, the addition of hard substrate alone could promote the recovery of oyster habitat.

All restoration efforts require the cessation of the cause of decline in order to ensure success. In the case of intertidal *M. edulis* beds in the Dutch Wadden Sea, it appears that protection of habitats suitable for settlement of *M. edulis* is sufficient on its own to promote the recovery of this species. In this case, restoration efforts involving the re-laying of mussels appear to have had limited success relative to protecting areas with good natural recruitment (Dankers & Fey-Hofstede, 2015; van der Meer et al., 2019; Supporting Information Table S1).

It should be noted that the list of restoration sites provided does not represent a complete inventory of existing projects, but rather a limited number of case studies. It is not appropriate, therefore, to seek to identify universal trends, but it is possible to identify a number of unifying factors between species and geographies.

### 4.3 | Bivalve habitat ecosystem service delivery

Many of the identified ecosystem services provided are the result of ecosystem engineering properties of these habitat-building bivalves. A review of ecosystem engineering properties by Berke (2010) identified four broad functional classes of ecosystem engineer: structural engineers, light engineers, chemical engineers, and bioturbators. Habitat-building bivalves are widely recognized as structural, light, and chemical engineers (Smaal et al., 2019). The mussels and oysters that build the bivalve habitats are sessile and do not themselves bioturbate the sediments. Though studies are limited, there is evidence that the presence of bivalves does not enhance, and may reduce, the abundance of macro-infauna (Ragnarsson & Raffaelli, 1999), which are largely responsible for bioturbation in soft sediments. Ecological engineering properties of habitat-building bivalves were therefore determined to be best defined by the first three classes (Table 4).

In more detail, through building a physical reef or bed, the bivalves create structure, and this, in turn, increases the availability and complexity of hard substrate. This, in turn, is critical in underpinning their role as a habitat supporting associated species (Norling et al., 2015) and, under certain conditions, the potential to reduce coastal erosion (Walles et al., 2015). Through the universal filter feeding action of habitat-building bivalves, these species have the potential to act as light engineers, which in turn may increase the amenity value of surrounding areas by increasing water clarity and even seagrass abundance (Wall, Peterson, & Gobler, 2008). Finally, the habitat-building bivalves can also act as chemical engineers, enhancing the drawdown of carbon and nitrogen to the sediments, as well as physically creating a large surface area for microbial action (Heisterkamp et al., 2013; Kellogg, Cornwell, Owens, & Paynter, 2013). Though these ecosystem effects are largely universal (Table 4), evidence from the well-studied *C. virginica* illustrates that the delivery of ecosystem services will be highly spatially variable, depending both on the hydrodynamic setting of the habitat and the accessibility of the site to human beneficiaries (La Peyre, Humphries, Casas, & La Peyre, 2014; Theuerkauf, Eggleston, & Puckett, 2019). As such, though their universal ecosystem engineering properties mean habitat-building bivalves have the potential to provide a suite of similar ecosystem services across their global distribution, the degree to which these services are provided will depend on both the location and the species in question. Identifying species-specific knowledge gaps is therefore key to making the case for shellfish restoration moving forward.

## 4.4 | Knowledge gaps

Substantial knowledge gaps regarding ecosystem service provision remain for all species of restoration interest, aside from *C. virginica* (Table 3). The two best understood attributes across species are clearance rate and biodiversity enhancement, though even in these cases basic and consistent measures remain missing for a number of high-interest species (e.g. *O. angasi*; see Supporting Information Table S2). It should be noted that clearance rate is not in itself a service; rather, it is the process by which water quality benefits can be achieved. The associated in-situ measurements to determine the scale of water clarity improvements are lacking. As the impact of clearance rate on the water column is site specific, depending on numerous factors, including dissolved oxygen levels, flow rate, residence time, and suspended solid concentration (Gray & Langdon, 2018; Theuerkauf et al., 2019), field studies are critically important for understanding to what degree clearance by each species may be providing an ecosystem service.

Biodiversity enhancement is the second ecosystem service for which there is some evidence for multiple bivalve species. It should be noted, however, that whether the biodiversity in and of itself is considered an ecosystem service is itself culturally determined (Mace et al., 2012). As such, the existence of biodiversity enhancement on its own does not translate into a service 'value'. As with clearance rates, however, the potential cultural value, as well as other related services, such as enhanced associated species production and ecosystem stability and resilience, is implied. Field studies that examine the relationship between the enhanced biodiversity and the enhancement of harvestable associated species, the cultural value, and the role of biodiversity in other ecosystem service resilience and stability are required before the ecosystem service value related to biodiversity benefits can be quantified.

The remaining ecosystem services identified, including coastal protection, denitrification, cultural values, and field verification of the potential nursery function of bivalve habitats, are woefully absent from the literature on the species of restoration interest. These gaps

**TABLE 4** Role of universal ecosystem engineering properties of habitat-building bivalves in providing ecosystem services

| Class of engineer | Ecosystem effect | Universality of ecosystem effect | Ecosystem service |
|---|---|---|---|
| Structural engineer | Create living space/alter diversity | Universal | Fish production |
| | | | Enhance biodiversity and species richness (relative to unstructured habitats) |
| | Alter hydrodynamics | Dependent on spatial scale of habitat. Ecosystem effect more likely with species building high-relief reefs | Stabilization of adjacent habitat and shoreline |
| | Alter sedimentation | Universal | Carbon sequestration |
| Light engineer | Alter turbidity | Universal | Enhancement of adjacent submerged aquatic vegetation habitat |
| | | | Enhances amenity value |
| Chemical engineer | Create biogeochemical gradient | Universal | Enhances denitrification and improves water quality |

*Note:* Class of engineer and ecosystem effects are as listed by Berke (2010). Universality is determined on the basis of author expert opinion. Universality relates to ecosystem effect only. In all cases, spatial variability in ecosystem services is likely; for example, in relation to water depth and flow.

can only be tackled through a combination of social, laboratory, and field studies to identify the degree to which these services are provided. Given the potential importance of a more complete understanding of ecosystem service benefits, such as fish nursery habitat value, in building the case for ecosystem restoration and the scaling up of restoration efforts, this knowledge gap is particularly worthy of note.

Though many services can be inferred (i.e. implied by benefit transfer) from our understanding of the universal ecosystem engineering properties of bivalve habitats (Table 4), their relative and absolute value in different geographies is a critical missing piece in understanding the value of bivalve reef restoration around the world. Even within species, there can be substantial differences in ecosystem service delivery between geographies, as evidenced by the regional differences in fish and mobile invertebrate production from *C. virginica* reefs in the Gulf of Mexico relative to the South and Mid-Atlantic USA (zu Ermgassen, Grabowski, Gair, & Powers, 2016). The environmental setting can also play a critical role in the degree of service delivery; for example, oysters are unlikely to have played as important a role in water quality on the Pacific coast of the USA relative to the Atlantic coast, not only because the native species of oyster, *O. lurida*, has slower clearance rates, but also because Pacific coast estuaries tend to have lower residence times (zu Ermgassen, Gray, Langdon, Spalding, & Brumbaugh, 2013). As such, there is a strong case for building a greater quantitative knowledge for each species, despite having confidence that certain ecosystem services are likely to arise from universal ecosystem engineering properties.

Our review identifies a strong need for *in situ* studies of the potential benefits of habitat-building bivalves. Though ecosystem processes that result in ecosystem services are well understood theoretically, quantitative evidence of the delivery of these services in the field is a prominent knowledge gap. For some species, where the habitat is considered extinct (Beck et al., 2011), the first challenge is to restore sufficient habitat to allow for quantification of associated ecosystem services. For other species, such locations can be identified, in which case field methods for determining *in situ* delivery of coastal protection, improved water quality (both from decreased turbidity and from enhanced denitrification), and fisheries production from associated species are well established for *C. virginica* habitat in the USA (Baggett et al., 2015), and many methods could be transferred to other species and locations.

This study focused on the habitat-building bivalve species that are currently the focus of ecological restoration efforts. The knowledge gaps identified here are, however, likely to apply more widely to many understudied, threatened biogenic reef habitats. Although many biogenic reef habitats (such as *Sabellaria* spp. reefs) are not currently the focus of restoration efforts, quantifying their potential to provide ecosystem services can play an important role in their protection. For example, evidence that reefs are valuable nursery habitats for fish (Hall-Spencer, Grall, Moore, & Atkinson, 2003; Rabaut, Van de Moortel, Vincx, & Degraer, 2010) can contribute to decisions regarding marine protection (Department of Food and Rural Affairs, 2011). Understanding the ecosystem services provided can also be an important factor in stakeholder engagement, which can in turn also be a deciding factor in the success of marine protected areas (Giakoumi et al., 2018). It is therefore important that identified gaps in understanding and quantification of ecosystem services associated with biogenic reefs more widely also be similarly considered.

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## CONFLICT OF INTEREST

The authors confirm that they have no conflicts of interest to declare in relation to this submission.

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## SUPPORTING INFORMATION

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

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