19

OYSTER-GENERATED MARINE HABITATS

Their services, enhancement, restoration and monitoring

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Introduction

The focus of this chapter is on reef-forming native and non-native bivalves (oysters primarily), where restoration efforts for non-extractive services have been directed since the 1990s (Luckenbach *et al*. 1999). Coastal estuarine habitats are recognized as some of the most productive and important aquatic ecosystems worldwide, providing foraging, nursery, and spawning habitats for ecologically and economically important organisms. Simultaneously they are also some of the most heavily degraded ecosystems on the planet (Lotze *et al*. 2006).

In 2000, almost 53 per cent of the inhabitants of the USA resided in coastal areas (including Great Lakes) that make up just 17 per cent by area, with numbers expected to reach over 24 per cent by 2025 (UN 2012). Along with similar increases worldwide, and as a consequence of anthropogenic activities (e.g. eutrophication and related effects), stressors, both natural and human-related (food webs, introduction of non-native or exotic species) will continue to grow (Ruesink *et al*. 2005; Coen and Bishop 2015 and references therein) both near and offshore. This degradation requires that we increase our efforts to restore and enhance these key habitats, in part because of their ecosystem services (MEA 2005).

Bivalve harvesting for human consumption has a long history worldwide and it was not until perhaps the nineteenth century that closed harvesting seasons were truly implemented and enforced (Beck *et al*. 2011; zu Ermgassen *et al*. 2012 and citations therein). Oysters, like lobsters, were often not considered a high value resource, with harvesting not just for consumption, but also for their shell use (Luckenbach *et al*. 1999; Coen and Grizzle 2016). Today, there are very few remaining wild shellfish reefs that produce oysters for direct harvesting without fisheries enhancement (reviewed in Beck *et al*. 2011). Most USA oyster fisheries were primarily subtidal (Figure 19.1J) found in estuaries like the Chesapeake (Maryland and Virginia) and Delaware Bays (Delaware and New Jersey) and throughout the Gulf of Mexico (Florida to Texas) (Luckenbach *et al*. 1999; NRC 2004; zu Ermgassen *et al*. 2012). In contrast, in the western Atlantic intertidal oyster (*C. virginica*) reefs dominate, including the seaside of VA, parts of NC and FL, SC, GA, USA and portions of the other four Gulf of Mexico states (Figure 19.1C–F; ASMFC 2007). Presently as much as 85 per cent of historical intertidal and subtidal oyster

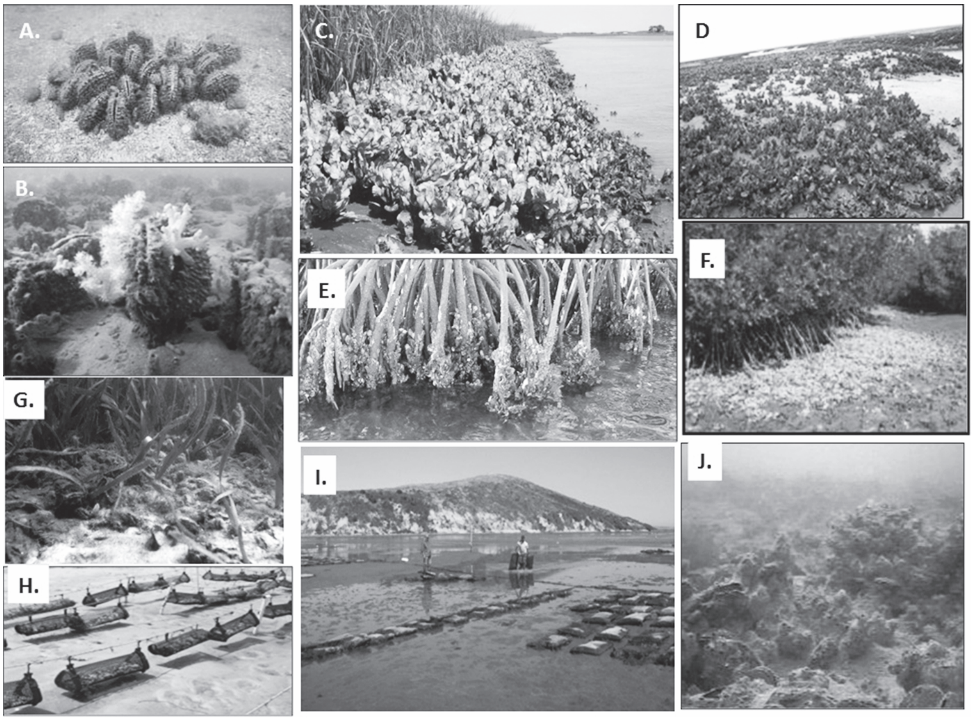

Figure 19.1 Composite figure of different intertidal and subtidal bivalve-generated habitats. (A) Dense pen shell aggregation in an intertidal seagrass bed in Dubai. (B) Subtidal pen shell aggregations of *Atrina zelandica*, in New Zealand. (C) *Crassostrea virginica* restored fringing intertidal oysters reefs adjacent to salt marsh, in South Carolina, USA. (D) Natural oyster (*C. virginica*) patch reefs in South Carolina, USA. (E) Natural oyster (*C. virginica*) recruitment onto red mangrove prop roots in Florida, USA. (F) Natural oyster (*C. virginica*) intertidal reef below mangroves in Florida, USA. (G) *Modiolus modiolus* subtidal mussels assemblages in St. Joe Bay, Florida, USA. (H) Suspended oyster culture in shrimp ponds near Charleston, South Carolina, USA. (I) Suspended and bottom planted racks and cages for bivalve oyster aquaculture, northwest coast of USA. (J) Subtidal restored *C. virginica* oyster reef

Sources: (A) R. Grizzle, UNH, Durham, NH, USA; (B) S. Thrush, University of Auckland, New Zealand; (C) J. Monck, SCDNR; (D–F) L. Coen; (G) B. Peterson, SUNY, Stony Brook, NY; (H) B. Cox, Island Fresh Seafood, South Carolina, USA; (I) A. Suhrbier, Pacific Shellfish Institute, Washington, USA; (J) R. Lipcius, VIMS, Gloucester Pt., VA, USA

reefs have been lost worldwide, suggesting that oysters in particular may be the most imperilled nearshore estuarine biogenic habitat (Beck *et al*. 2011). Oyster reefs are much like those formed by corals with only a veneer of living animals, and an extensive foundation composed of dead skeletons above and below the sediment surface. Thus, harvesting can easily remove millennia of reef growth in decades or centuries (Beck *et al*. 2011).

Ecosystem services and foundation species

Bivalve habitat types include aggregations, beds, and reefs generated by oysters, clams, and mussels (Figure 19.1). These filter-feeding species are vital components of coastal ecosystems providing ecosystem services including:

1 enhanced wildstock populations (consumptive uses);
2 improved water quality (clarity), nutrient sequestration/denitrification (potentially decreasing harmful algal blooms or HABs) and hypoxia;
3 habitat for associated organisms (finfish and invertebrates) and secondary production; and
4 enhancement of adjacent habitat/shoreline (often vegetated) by stabilization reducing erosion.

Shell mounds (middens) created by indigenous people are found in nearly all coastal areas worldwide (Alleway and Connell 2015), where most bivalves being important fisheries at one time (Kirby 2004). Cultural services must also include jewelery, trade, and aesthetic values (MEA 2005).

Increased foraging and sheltering habitat for vertebrate and invertebrate organisms, including finfish, birds (at exposure) and even mammals, is the most well studied service in natural and restored oyster habitats (Coen *et al.* 1999b, 2007; Baggett *et al.* 2014; Coen and Bishop 2015). Reef-associated organisms can rival seagrasses and other habitats (salt marshes or mangroves) for associated resident (present even during low tide), and transient (absent during reef exposure) organisms (Figure 19.1) and oyster reefs support much greater animal abundances than surrounding unstructured sand/mud habitats (Coen *et al.* 1999b, 2007, 2011; Coen and Grizzle 2016 and citations therein).

USA oyster habitats have been shown to support a diverse suite of resident and transient species. For example, >300 micro- to macroscopic species were found in the 1960s by H. W. Wells (1961) in NC. More recently, over 75 resident and 59 transient macroscopic species were collected on SC, intertidal reefs by Coen and colleagues (Coen *et al.* 1999a,b; Coen and Grizzle 2016 and citations therein), and over 100 species were on reefs in LA (Humphries and La Peyre 2015). Oyster aquaculture can also play many parallel roles (Dumbauld *et al.* 2009; Coen *et al.* 2011).

Of late, research has focused also on quantifying one or more ecosystem functions in economic terms (Peterson *et al.* 2003; Grabowski and Peterson 2007; Grabowski *et al.* 2012; Humphries and La Peyre 2015), with Grabowski *et al.* (2012) estimating oyster reefs services valued at >$99,000/hectare/year once restored. While it is difficult to capture one or all of the ecosystem services provided by bivalve habitats (Grabowski *et al.* 2012), it is clear that they are exceedingly important (Peterson *et al.* 2003; Baggett *et al.* 2014; Barbier *et al.* 2014; Powers and Boyer 2014).

In a meta-analysis of data from USA, zu Ermgassen and colleagues (2012, 2013) showed that losses of oyster habitat have resulted in lost filtration capacity by ~85 per cent having both direct and indirect consequences for estuarine health, through increased water residence times and lost estuarine processing of nutrient loads as filtration capacity scales with oyster population densities and size (Luckenbach *et al.* 1999; La Peyre *et al.* 2014). Filtration by bivalves can impact water quality and clarity by removing particulate matter (or seston) from overlying waters (Dame 1996; Luckenbach *et al.* 1999). Oysters ingest material and consume particles and then reject or ingest bound in mucus, then depositing them onto the sediment surface as faeces and pseudofaeces. This process can contribute to improved water quality (clarity) when oysters are sufficiently dense and the overlying water column is relatively shallow (Dame 1996; Newell 2004; and see Coen and Grizzle 2016 and papers cited within).

The role of reefs as nutrient sinks in estuaries has only recently been quantified and better understood, but results indicate it is significant when compared to other important habitats (Kellogg *et al.* 2014; Smyth *et al.* 2015). Oyster reefs can assimilate nutrients into tissues or shell, and augment subtidal denitrification along the sediment–water interface (reviewed in Kellogg *et al.* 2014), with net denitrification rates from 30–56 $g \cdot N \cdot m^{-2} \cdot y^{-1}$ and shell and tissue assimilation from 0.2 per cent and 9.3 per cent N g^{-1} dw, respectively (Kellogg *et al.* 2014). However, not all studies show significant differences between denitrification of intertidal oyster reefs and surrounding habitats (Smyth *et al.* 2015).

Bivalve reefs can function also as living breakwaters – often called 'living shorelines' (LS)[1] – or erosion reducers reducing waves and increasing sedimentation or decreasing sediment resuspenson around a LS structure (Figures 19.1C,F, 4F; Walles *et al.* 2015). In fact, oyster reefs facilitate sediment accretion by as much as 6.3 cm annually (Meyer *et al.* 1997). However, this is not the same as reducing erosion which is of particular importance when ameliorating loss of landward marsh habitat. Evidence that reefs buffer shorelines from waves (wind- or tidally generated) is equivocal (Piazza *et al.* 2005; Scyphers *et al.* 2011; La Peyre *et al.* 2014; Coen and Grizzle 2016), although the consensus is that effects are generally positive, but context-dependent (La Peyre *et al.* 2015). To be beneficial, habitat accretion must also exceed sea level rise (Rodriguez *et al.* 2014; Walles *et al.* 2015, 2016), and there may be a threshold where reefs cannot exist as larger storms exceed some upper ceiling (but see Walters *et al.* 2007).

Non-native foundation oyster species

Many oysters once supported significant commercial fisheries, but many are currently at <1–10 per cent of historical levels in various estuaries such as the Chesapeake Bay, USA (Beck *et al.* 2011). Worldwide, the Japanese or Pacific oyster (*Crassostrea gigas*) has been introduced by accident or design as an alternative species (Ruesink *et al.* 2005). In some areas its use as an engineer is being encouraged given its potential reef-building capacity and resistance to native diseases (Walles *et al.* 2015). Non-native species introductions, either through direct or accidental introductions, were first mentioned in Elton's 1958 seminal work on invasive species, and are having complex (positive, negative, or even neutral) impacts in many estuaries throughout the world where native species have declined (reviewed in NRC 2004; Ruesink *et al.* 2005; Coen and Bishop 2015). Introductions and expansion of Japanese or Pacific oyster, *Crassostrea gigas*, have had mixed results.

How non-native species contribute to novel ecosystems is something being hotly debated (see Coen and Bishop 2015 and citations therein). Introduced oyster species are transforming the landscape in many novel ways (Smaal *et al.* 2005). In the Wadden Sea for example, the invasion of the Pacific oyster *C. gigas* has caused major habitat shifts from the formerly dominant native bivalves such as blue mussel, *Mytilus edulis,* the native flat oyster, *Ostrea edulis*, and cockles, which formed dense beds to intertidal oyster reefs (Smaal *et al.* 2005; Coen and Grizzle 2016). The consequences for native benthic communities, mussel-eating invertebrates, and other higher food web vertebrate consumers (i.e. birds) have yet to be resolved. In contrast, in the Netherlands, these non-native ecosystem engineers are reducing erosion and adding novel intertidal habitat (Smaal *et al.* 2005; Walles *et al.* 2015). In Australia, no obvious negative consequences have been observed with *C. gigas* (Wilkie *et al.* 2012). Whether introduced biogenic-forming species will continue to thrive, given novel diseases and native and introduced predators, will be of interest to ecologists long into the future (Coen and Bishop 2015; Walles *et al.* 2015; Coen and Grizzle 2016).

Enhancement and restoration of oyster reef habitats

No matter what area or species, it is clear that bivalve restoration will need to be scaled up significantly from 1–10 hectares to hundreds soon (e.g. the Chesapeake Bay or Gulf of Mexico supported by Deep Water Horizon oil spill funding). Central to successful enhancement and restoration efforts is an understanding of how the target species interacts with its biophysical environment.

For example, oysters are found both intertidally and subtidally, in both nearshore and estuarine waters worldwide (Galtsoff 1964). Intertidal oysters form isolated reefs away from shorelines (patch reefs) or bordering vegetated (salt marsh or mangrove) shorelines in tidal creeks, rivers, sounds, and bays (fringing reefs) (ASMFC 2007; Coen and Grizzle 2016; Galtsoff 1964). Shallow (<10 m) reef-forming oysters create different individual and habitat morphologies in response to various environmental and biological forces (*ibid*.). To examine bivalve habitat-forming morphologies, the following categories have been suggested:

1 reef-forming (e.g. genus *Crassostrea*);
2 aggregation–forming (e.g. *Ostrea* spp.); and
3 shell-accumulating (many scallop and clam) species (Figure 19.1; ASMFC 2007; Coen and Grizzle 2016).

Oyster biology as it relates to restoration

Regardless of form, most bivalves are filter-feeders, with the exception of some specialists (Coen and Bishop 2015; Coen and Grizzle 2016), such that a sufficient supply of seston (or suspended food and sediment) is needed to support viable populations (Dame 1996). Interestingly, several studies have suggested, based on remote imagery, that intertidal oyster reef organization is not random, but rather potentially self-organizing, paralleling observations of European mussels (van de Koppel *et al.* 2008). For subtidal oysters in the Gulf of Mexico, habitat suitability index (HSI) models have incorporated biotic and abiotic factors to help assist with the site selection for restoration efforts, as well as how oyster populations thrive under different biological and physical scenarios (Pollack *et al.* 2012; Soniat *et al.* 2013; La Peyre *et al.* 2015).

The life cycle of oysters consists of a larval (either a crawling or planktonic) phase prior to settlement and a sedentary, or sessile, adult phase. Once having settled (cemented) on the required hard substrate, adults cannot relocate. Chemical clues are also involved in reef aggregation (Kennedy *et al.* 1996). Successful recruitment of oyster larvae and post-larvae over successive years (multiple age classes) is fundamental to reef persistence and expansion (Coen and Luckenbach 2000; Luckenbach *et al.* 2005).

Healthy populations require the renewal of hard substrate, as both harvesting and natural mortality, burial and shell degradation (i.e. taphonomic processes) remove reef substrate. In the past, buried shell was dredged from estuary bottoms, but this has been discontinued in many areas. When shell is unavailable, then alternative materials such as fossil shell, limestone, granite or recycled manmade materials (concrete) can provide the necessary substrate for reef construction. Presently and into the future, increasing restoration efforts (hundreds hectares) will require much more shell (i.e. alternative materials) than is currently available.

The quantity and quality of food can be directly correlated with water quality (e.g. nutrients, salinity, temperature, and hydrology; Pollack *et al.* 2012), with oysters thriving in highly turbid waters. Many intertidal *C. virginica* reefs (western Atlantic and Gulf of Mexico) (Figure 19.1C–F) can thrive where salinities are higher than subtidal ranges (15–30 ppt vs. 10–15 ppt), and sediments are quite fine (Galtsoff 1964; Bahr and Lanier 1981).

Today, aquaculture has taken over as the primary method for producing oysters for consumption (Figure 19.1H–I; Shumway 2011). Worldwide, many use a hybrid approach where oyster larvae are set onto deployed substrates and then harvested or relayed to better areas or seed beds for grow-out (e.g. LA, USA). Elsewhere, including the Pacific coast of the USA, several non-native oysters (especially the Pacific oyster, *C. gigas*) have been introduced, requiring intensive labour and capital (e.g. land-based hatcheries) (Shumway 2011 and citations therein).

Need for restoration

Whether enhancing or restoring (creating) these important bivalve biogenic habitats it should be noted that the approach is quite different from those employed in the recovery of other non-foundation (and mobile) species such as finfish or crustaceans (Coen and Luckenbach 2000; Coen *et al.* 2011). Past oyster restoration efforts generally focused only on recovering lost or impaired oyster fisheries (extractive services). The causes for the decline of many bivalves are manifest and include more than one reason (e.g. over-harvesting, pollution and related impacts, habitat destruction, and native and non-native oyster diseases; Lenihan *et al.* 1999; Coen and Luckenbach 2000; Kirby 2004; NRC 2004).

As mentioned earlier in this chapter, early European settlers into the Americas were able to harvest abundant shellfish in relatively shallow estuarine waters. However, by the late nineteenth and early twentieth centuries, most of these populations were significantly depleted or driven to near local extinction (Kirby 2004; Beck *et al.* 2011). Elsewhere (Europe, Asia) and even earlier, many native oyster populations were extirpated (Beck *et al.* 2011; Alleway and Connell 2015).

Today, native and non-native species are receiving attention either through enhancement or restoration, especially in the USA for the non-extractive ecosystem services of two native species, the Eastern oyster (*Crassostrea virginica*, Atlantic and Gulf of Mexico), and the greatly depleted Olympia oyster (*Ostrea lurida,* Pacific coast of North America). Similarly, but lagging those USA and Canadian efforts are plans to restore the native flat oyster (*Ostrea edulis*) in Europe and the UK. However, diseases and depleted local populations may make their return difficult (Coen and Bishop 2015).

Because of the numerous ecosystem services mentioned previously, bivalves are being increasingly protected, enhanced, or restored in greater numbers. A major requirement before enhancement or restoration occurs is to assess their current status and to eventually conduct triage assessments determining where to focus limited resources (NRC 2017). This typically requires that one map, assess, and quantify the extent and health of oyster reefs, and then input the data into a GIS geodatabase for long-term use in assessing status and change.[2]

Also critical to any restoration assessment are: (1) the inclusion of explicit goals and objectives; (2) consistent approaches, related metrics, and success criteria; (3) rigorous designs for monitoring natural (including replicated constructed, reference, and/or control areas) and restored habitats; and (4) monitored over a sufficiently appropriate time period (Coen *et al.* 2004; SER 2004; Baggett *et al.* 2014; NRC 2017). These should be developed a priori and be appropriate to the proposed effort, including the distinction as to whether one is restoring intertidal, shallow subtidal, or deeper (>5 m MLW) habitats. The importance of population connectivity (metapopulations) also needs to be considered as part of the effort.

Aquaculture is also having an increasing role for bivalve sustainability, not just for seafood (Dumbauld *et al.* 2009; Shumway 2011 and chapters within; Coen and Bishop 2015). A recent survey (Shinn *et al.* 2015) of the top 69 aquatic (brackish to marine waters) cultured species found that molluscan aquaculture leads animal production by tonnage (31.7 per cent overall). Of special concern, molluscan aquaculture, as compared to finfish, is always concentrated relatively close to the coastal zone (including estuaries), an area concurrently being heavily impacted by human populations and related development (Coen *et al*. 2011; Coen and Bishop 2015 and papers cited therein). While we know a great deal about shellfish populations in North America and Europe, the status and potential trends in data-poor areas such as Africa, South America, and southeastern Asia are even less clear.

Although bivalve restoration for other services has seen a recent surge outside of North America, such as in Europe and the Pacific from China to New Zealand, we still know relatively little about their successes or failures, in part due to a lack of published reports or extended duration (>10 years). For instance, over 120 km of intertidal oyster reef has been created in the Yangtze River estuary, China – an extremely large-scale effort by most accounts, but only a limited portion of the results have been reported to date (Quan *et al*. 2013 and citations therein). Japan has a long history of enhancing shellfish populations for consumption using aquaculture and Australia and New Zealand have only recently begun to recognize the need for restoration of native oyster habitat (e.g. Alleway and Connell 2015; Gillies *et al.* 2015). Elsewhere, sea level rise is making living shoreline efforts with oysters a potentially important approach for the shorter-term impacts in places like Bangladesh (Bilkovic *et al*. 2017).

As mentioned earlier many bivalve species (e.g. clams, scallops, mussels) can relocate as conditions become unfavourable (low dissolved oxygen, sedimentation), reef-forming species cannot (Kennedy *et al*. 1996). This sedentary life makes oysters susceptible to any environmental stressors (oiling and burial from dredging, hurricanes; Coen and Bishop 2015), and must be considered when planning restoration projects as part of site selection (Coen and Grizzle 2016).

Critical steps for restoration-related efforts

For the purposes of our discussion below, we define restoration as: 'the process of establishing or reestablishing a habitat that in time can come to closely resemble a natural condition in terms of structure and function' (Coen and Luckenbach 2000; Peterson *et al*. 2003; Grabowski and Peterson 2007).

Site selection concepts, historical information, and related concepts

Site selection may be the single-most important set of factors for determining the success of an enhancement or restoration project. Derived from a workshop of restoration practitioners in 2004, site selection parameters were assessed and then ranked (Table 19.1) (Coen and Luckenbach 2000; Coen *et al*. 2004; ASMFC 2007; Brumbaugh and Coen 2009; Baggett *et al.* 2014). Responses were by reef type (intertidal or subtidal) for *C. virginica*. Some recommended establishing restored reefs only in areas (reef footprints) where oyster populations existed historically. These can typically be determined from navigation charts, past historical surveys, state mapping efforts, or published fishing records[3] (Baggett *et al.* 2014), while others recommended using habitat suitability index (HSI) models to determine optimal site conditions, potentially ensuring longer-term sustainability (Pollack *et al*. 2012; La Peyre *et al*. 2015 and references therein; but see Coen and Bishop 2015; NRC 2017).

Briefly here we describe the most important site selection criteria for intertidal and subtidal restoration focusing on physical and biological site traits. Highest ranked parameters (Table 19.1) are by reef type. These parameters and monitoring logistics are crucial to a project's success and associated costs. Later adaptive management (including as a means of tweaking a project or understanding why a particular effort worked or failed) need to be based on sufficient project monitoring whose aim is to ensure a long-lasting, positive result (Coen and Luckenbach 2000; Coen *et al*. 2004; Baggett *et al*. 2014; NRC 2017).

Table 19.1 A summary of ranked site selection parameters for intertidal and subtidal oyster reef restoration modified from Coen *et al.* (2004) based on responses to a questionnaire circulated among attendees, other active restoration practitioners, and oyster fisheries managers working with *Crassostrea virginica* in the USA

Subtidal	*Ranking*	*Intertidal*
Physical parameters		
Reef depth	1	Primary underlying substrate
Primary substrate for planting	2	Mean salinity
Substrate firmness for planting	3	Substrate firmness for planting
Water quality	4	Siltation/sedimentation
Mean salinity	5	Potential reef height relative to MLW
Elevation off bottom	6	Water quality
Siltation/sedimentation	7	Runoff from adjacent land
Current flow rate	8	Current flow rate
Reef orientation	9	Bank slope to be planted
Channel depth (lowest tide) logistics for construction	10	Width of intertidal zone for planting
Runoff from adjacent land	11	Erosion potential
Erosion potential if shallow	12	Fetch (wind wave exposure)
Fetch (wind wave exposure)	13	Channel width and depth for (lowest tide) logistics for construction
	14	Reef orientation
Biological parameters		
Disease (MSX, Dermo)	1	Recruitment of oysters (larval supply)
Recruitment of oysters (larval supply	2	Disease (MSX, Dermo)
Predation	3	Fouling communities
Proximity to extant oyster populations	4	Food quantity and quality
Food quantity and quality	5	Predation
Fouling communities	6	Proximity to extant oyster populations

Also critical for a given project's success are:

1 scale of restoration footprint (Figures 19.2–19.4; hundreds of metres to hundreds of hectares);
2 reef type (intertidal or subtidal) and nearby sources of larvae;
3 relevant permitting details (e.g. adjacent habitats, species of concern, materials, direct and indirect effects, attractive nuisance effects, signage, etc.); and
4 pertinent site staging logistics (e.g. proximity to boat ramps, staging of personnel for volunteer labour, access by boat or barge, etc.).

Project goals and related objectives significantly affect *all* of the above-mentioned concepts. A given project's scale (Figures 19.2–19.4) also influences sampling design, metrics, replication, duration, etc. and should not be given short shrift in the 'costing-out' of a given restoration project (Coen *et al.* 1999a, 2004; Kennedy *et al.* 2011; Baggett *et al.* 2014; NRC 2017). We cannot emphasize enough one's attention to the details discussed here and are not able to describe most in any great detail here.[4] The above-mentioned designs and sampling must be considered upfront prior to the initiation of any given restoration effort or else their later inclusion will be of limited value.

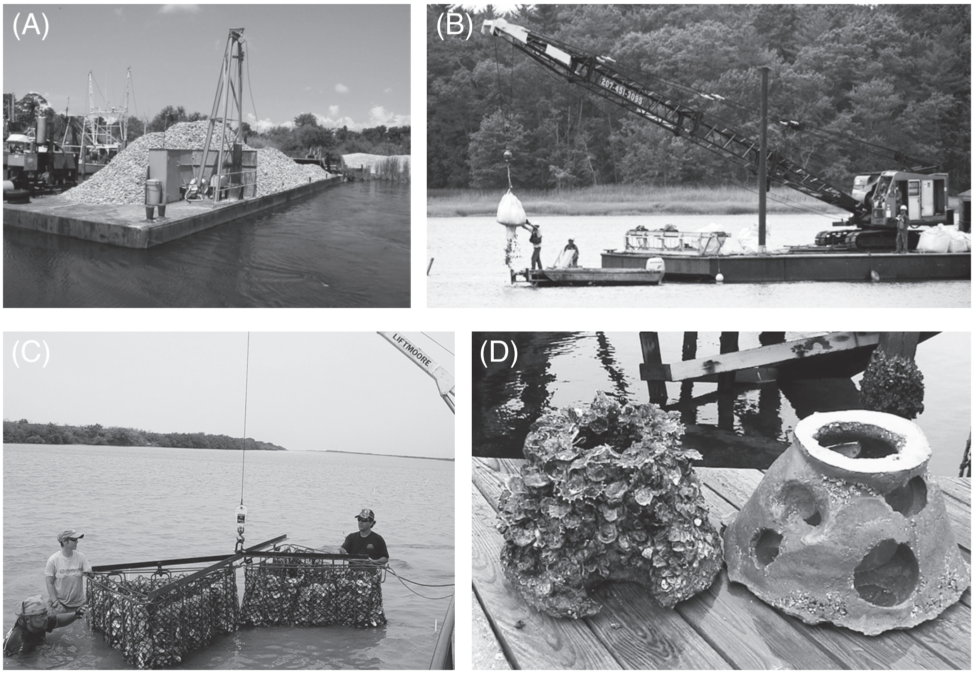

Figure 19.2 (A & B) Examples of different oyster reef restoration techniques using loose unaggregated shell; (A) Barge with shell; (B) Barge deploying shell using One Ton Bags™; (C) Trianglular metal rebar structures filled with shell contained within, Mad Island, TX., USA. (Reefblk™); and (D) Reef balls made from composite cement substrate before and after deployment with recruited oysters in Tampa, FL, USA.

Sources: (A) M. Berrigan, Department of Agriculture and Consumer Services; (B) see www.onetonbag.com/. R. Konisky, NH TNC, USA; (C) TNC; (D) Tampa Bay Watch

Site selection attributes

Subtidal/intertidal reef type, height, and depth

Constructing subtidal reefs with sufficient vertical relief (height above the sediment's surface, cm to 0.5 m or more in some cases) can reduce the negative effects of sedimentation and dissolved oxygen, while enhancing local flow (Lenihan 1999; Schulte *et al*. 2009), including the use of taller vertical areas of material (cultch), interspersed with lower relief areas. On a smaller spatial scale this is often termed rugosity which can also enhance flow and reef complexity with recruitment, and thus reef use by associated organisms (Coen *et al*. 1999b; Coen and Luckenbach 2000; Baggett *et al*. 2014).

A suggested minimum value or range for subtidal reefs encountering low DO is ~0.5–1 m (Lenihan 1999; Gregalis *et al*. 2009). However, increasing the vertical reef height beyond >15 cm post-construction yields a concomitant increase in material and cost that many projects cannot afford. For intertidal reefs, a minimum has yet to be established, but 7–15 cm should be a minimum post-construction height after settling and cultch dispersal, especially where boat wakes, soft sediments, and sloping shorelines (often with high fetches and waves) affect pre-aggregation (i.e. cementing by oysters, etc.), reef longevity, and ultimately success (but see Rodriguez *et al*. 2014 and Byers *et al*. 2015 related to sea level rise and tidal range).

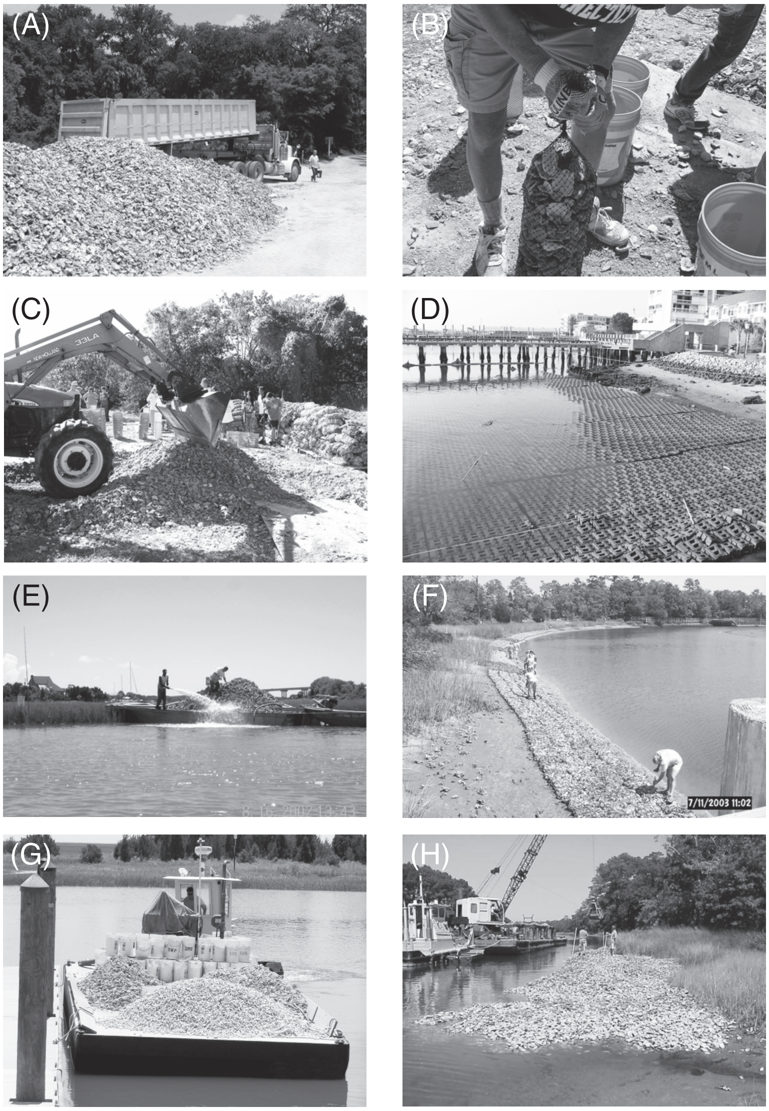

Figure 19.3 Scale of restoration and enhancement efforts. These include: (A) fossil shell delivery (15.3 m^3 or 20 yd^3) for community restoration project on Sanibel, FL, USA; (B) small- to medium-scale shell bagging (1000s) using polypropylene mesh with community volunteers; (C) community restoration effort bagging (mesh) shell or alternative materials for intertidal reef constructionn; (D) use of articulated concrete blocks (SHOREBLOCK™ SD Series, see www.shoretec.com/shoreblock-sd.php) for capping of sediments using geotextile material and blocks as hard substrate at the SC Aquarium and Ft. Sumter U.S. Park Service facility; (E) larger scale intertidal planting of loose oyster shell on reefs fringing salt marsh using barge and high pressure cannon at high tide in South Carolina, USA; (F) shell (mesh) bags deployed at a relatively large reef construction site near Charleston, South Carolina, USA; (G) moving shell and other materials for intertidal restoration experiments using barge and buckets at Cape Romain, NWR, South Carolina, USA; (H) planted shell exposed at low tide for intertidal habitat enhancement using barge and crane for TNC project in Lynnhaven River, Virginia, USA

Sources: (A–C) L. Coen; (D) T. Effinger, SCANA; (E–G) L. Coen; (H) E. Moleen

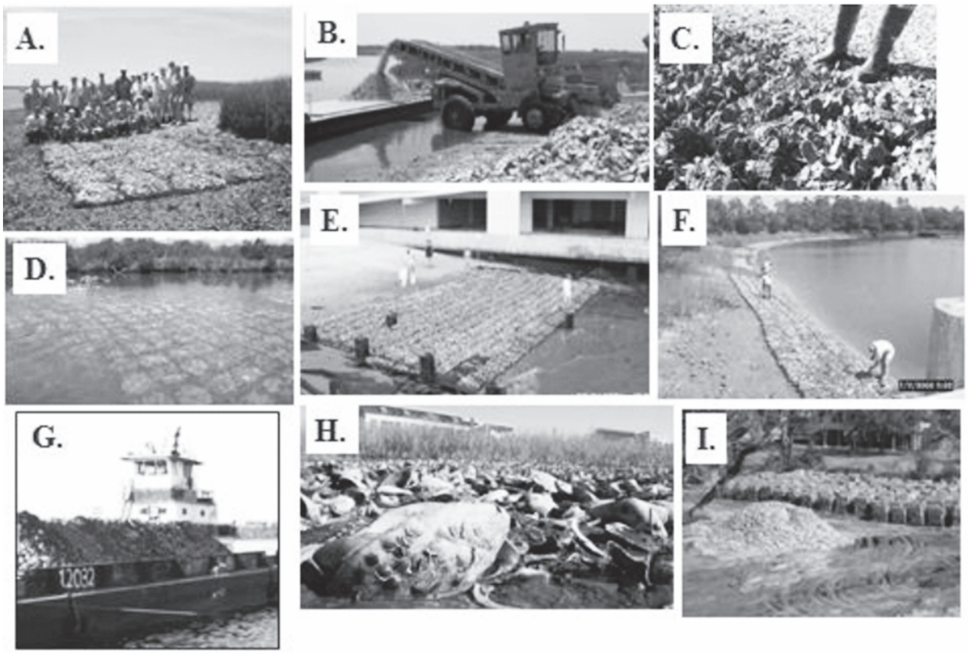

Figure 19.4 Restoration of oyster reef habitats. (A) Post-construction view of one of three replicate 10 m^2 intertidal oyster shell bag (100 total) reefs in Murrells Inlet, South Carolina, USA; (B) Loading of loose oyster shell onto barge with front end loader for intertidal reef planting, Bowens Island, South Carolina, USA; (C) Close-up of recruited intertidal oysters (*C. virginica*) onto loose stabilized (mesh) shell in ACE Basin NERR, South Carolina, USA; (D) Intertidal to shallow subtidal oyster shell 'mats' submerged in Indian River Lagoon, Florida, USA. Mats composed of ~36 shells, attached to a small mesh mat with zipties. The mats are later attached to each other in the water, forming a large quilt-like structure; (E) Large intertidal shell bag reef (~124 m^2) adjacent to the South Carolina Aquarium, Charleston, South Carolina, USA; (F) Large shell bag reefs (total ~340 m, acreage, ~0.22 ha) at Coffee Island, Alabama; (G) Large-scale shell barge planting in Apalachicola, Florida, USA; (H) Aerial image of replicate subtidal reefs and living shorelines, Pelican Point, Alabama, USA; and (I) Tens of thousands of oyster shell bags filled using automated bagging machine in coastal Alabama, USA

Sources: (A–C) L. Coen; (D) A. Birch, TNC; (E) L. Coen; (F) B. Maynor Young, TNC; (G) M. Berrigan, FDACS; (H) S. St. John; and (I) J. DeQuattro, TNC

Sediment dynamics (reef siltation/sedimentation)

In areas receiving high suspended sediment loads, deployed reef base substrates can typically experience poor recruitment success through fouled or covered substrates and high post-settlement mortality through burial (Coen and Grizzle 2016). Subsidence, flow, and sedimentary processes also decrease the post-construction overall reef footprint through time (Coen *et al.* 2004; Baggett *et al.* 2014; Coen and Grizzle 2016). Sedimentation is often greater at a reef's base where water currents are often slowest and finer particles tend to settle out (Lenihan 1999; Coen *et al.* 2004). As mentioned before, local conditions also influence sediment characteristics (grain size, depth, and load). Construction using heavier (denser) materials such as granite, fossil shell or recycled cement increase sinking rates, especially where sediments are finer (softer) requiring additional material to attain a acceptable final vertical reef height and avoidance of later costly adaptive management (Brumbaugh and Coen 2009).

Reef height relative to mean low water/width of intertidal zone

Oyster reef aerial exposure can greatly influence oyster reproduction, disease susceptibility, and responses to other anthropogenic stressors (Kennedy *et al*. 1996; Coen and Bishop 2015; Walles *et al*. 2015). Intertidal placement of reef base material relative to MLW (mean low water) determines the duration of exposure and likelihood of survival, especially in warm temperate to subtropical areas. In the western Atlantic, intertidal oysters in the USA typically occur from below MLW to about 1 m above MLW (Bahr and Lanier 1981), but this varies by site (latitude, shade from adjacent habitats, predominant solar orientation), tidal range, and type (diurnal vs. semi-diurnal) and other variables (fetch, waves, wind driven or boat wakes, 'rewetting' oysters during exposure (Walles *et al.* 2016; D. Bushek and L. Coen, personal observation).

Underlying substrate type and deployment

Existing substrate(s) type for reefs to be constructed requires sandy to muddy sand to mud (intertidal often) as a foundation for placing hard substrate or 'cultch'. Often larger projects use coarser natural or recycled material (granite or limestone or recycled cement) capped with oyster or fossil shell if in short supply (Luckenbach *et al*. 1999; Coen and Luckenbach 2000; ASMFC 2007; Powers and Boyer 2014). This is especially true as shell is limiting across the USA with increasing number and size of reef projects (>1–10 to hundreds hectares). One method using plastic mesh bags filled with material (Figures 19.3B–D, 4A,E,F,I; Baggett *et al.* 2014) or an under- or overlayments of geomeshes are used to reduce sinking or to retain shelly (or alternative) material in shallow areas where waves, wakes, and significant erosion occur. They are also easier to transport to and from the field (for assessment) when community volunteer restoration efforts are employed (Brumbaugh and Coen 2009).

Sediments consisting of high silt/clay percentages should be avoided wherever possible as sedimentation, siltation, and burial (subsidence) can be quite problematic for restoration efforts, requiring more material to attain an equivalent final reef height versus areas with coarser sediments. This can be assessed initially as the first part of site selection process to minimize failure. Reef footprints (area and vertical height above the surrounding sediment) through time need to be assessed as part of a longer-term monitoring and adaptive management programme (Table 19.1; Coen *et al*. 2004; Baggett *et al*. 2014; NRC 2017).

Dissolved oxygen and temperature

Reduced levels of dissolved oxygen (<2 mg L^{-1}), especially for extended durations of days to weeks, can cause significant oyster and associated species mortality (Lenihan and Peterson 1998; Lenihan 1999; ASMFC 2007). Hypoxia (<4 mg L^{-1}) often results in mobile species relocating from these areas to those with higher DO. Subtidal oyster reefs commonly can occur <5–10 m (MLW) of water below the surface. Historically they occurred deeper, perhaps given fewer hypoxic events. Natural subtidal reefs were often shallow (~1–5 m) and sufficiently elevated off the bottom so that oysters experienced fewer low oxygen (hypoxic to anoxic) conditions. DO varies with tide, and time of day, although in tidal creeks, low levels often occur nocturnally.

Intertidally, oysters encounter a suite of unique physiological challenges as they are exposed often to very high summer temperatures (e.g. in the southeastern USA, these can exceed 44°C internally; L. Coen and P. Lara, personal observation; Bahr and Lanier 1981; Walles *et al.* 2016) or very low winter freezing temperatures (e.g. north of VA; Coen *et al.* 2007; Coen and Bishop 2015). DO is less of a problem for intertidal reefs and associated mobile organisms as they must either move as tides fall or remain on exposed reefs 1–2 times per day (Coen *et al.* 1999a). Regardless, sessile intertidal organisms are aerially exposed daily and many (bivalves) can respire so that low DOs are less of a problem if they occur for <6–12 h d^{-1}.

Salinity

Prolonged exposure to low salinities (< 5 ppt or psu) can reduce feeding, growth, and reproduction, while also reducing observed negative effects of disease and predation (Figure 19.2; Coen and Bishop 2015). The oyster protozoan pathogens, *Perkinsus marinus* (Dermo disease), and *Haplosporidium nelsoni* (or MSX) are generally intolerant of salinities <10 ppt (summarized in Coen and Bishop 2015). For subtidal populations especially, higher temperatures and salinities (> 15–34 ppt) tend to cause increased disease levels and even epizootics (Coen and Bishop 2015 and references therein). Restoration located in close proximity to highly fluctuating or longer duration freshwater inflows can be affected significantly. Subtidal predators often greatly increase with higher (>15 ppt) salinities. Smaller species (flatworms) may feed on earlier post-settlement oyster stages (spat) and larger predators (gastropods, finfish, crabs; Figure 19.2) (Kennedy *et al.* 1996; Newell *et al.* 2000; Luckenbach *et al.* 1999; ASMFC 2007). The possible benefits of sites near freshwater inflows may be counter-balanced by increased oyster mortality either directly via osmotic stress or indirectly from sedimentation (Coen *et al.* 1999a, 2004; La Peyre *et al.* 2009) ultimately reducing the habitat value of both natural and restored reefs (Coen *et al.* 2004; ASMFC 2007).

Predators and competitors

Predators can have significant effects on both oysters (spat to adults), as well as on other reef-associated species. Predators range from smaller species such as flatworms (genus *Stylochus* spp. can feed on small, early post-settlement spat recruits; Newell *et al.* 2000), to larger invertebrate species such as other molluscs (gastropods), echinoderms (starfish), crabs, and vertebrates (finfish) (White and Wilson 1996). Many stenohaline predators only live in higher salinity environments (e.g. gastropod drills, echinoderms, rays), but are greatly diminished when salinities are relatively low (< 10–15 ppt). At most *C. virginica* sites, decapod crabs such as xanthids (e.g. *Panopeus* spp., *Eurypanopeus* spp., *Menippe* spp.) or portunids (genus *Callinectes* spp.) can cause significant oyster mortality, as well as other reef-associated species (White and Wilson 1996; Baggett *et al.* 2014). Oyster predators also include vertebrates spanning the gambit from finfish (including rays) when submerged, to raccoons and birds who feed on intertidal reef habitats when exposed.

Competitors such as fouling organisms (barnacles, tunicates, sponges, and even other bivalve mussels) may attach to oyster shell and limit free-space available for settlement of oyster larvae (Luckenbach *et al.* 2005; Brumbaugh *et al.* 2006; Brumbaugh and Coen 2009; Baggett *et al.* 2014). These can include both native, as well as non-native species (Kennedy *et al.* 1996; Luckenbach *et al.* 1999; NRC 2004; ASMFC 2007; Coen and Bishop 2015).

Hydrology and food

Sites with greater water (current) flows are often associated with greater oyster survival and faster growth (Lenihan 1999). Oyster shape, unlike many other molluscs, is quite plastic, with flow, sediments, and exposure affecting overall size, shell shape, and thickness (Galtsoff 1964). Flows ranging from 156–260 cm sec^{-1} are often associated with enhanced growth (Lenihan 1999; Coen *et al.* 2004). Oysters filter seston (phytoplankton, resuspended benthos, and other organic particles) from the water column (Kennedy *et al.* 1996) so an adequate food concentration is necessary for growth and survival. Currents not only deliver seston, but also carry away silt, oyster pseudofaeces, and faeces from reefs (Dame 1996). Water column chlorophyll *a* levels can be used as a proxy for food quantity. The quality of food and the potential filtering effects of developing reefs is more difficult to quantify, but it can be done (zu Ermgassen *et al.* 2013). Circulation patterns should be examined (along with appropriate modelling, see Kim *et al.* 2013) during peak spawning when larvae are recruiting (Southworth and Mann 1998).

Based on limited efforts, we know that lab-reared oysters with reduced (<4 cm sec^{-1}) flows have slower growth and greater mortality versus those reared under higher flow rates (7–20 cm sec^{-1}). Cholorophyll *a* concentrations greater than 30 mg m^{-3} result in rapid oyster growth.

Oyster recruitment potential (larval supply)

The availability of adequate bivalve (oyster spat) larval supply is critical for successful reef restoration. Otherwise as mentioned elsewhere the cost of the effort will be greatly increased. As part of site selection for any restoration effort, one or more oyster recruitment seasons (years) should be assessed prior to construction to ensure the availability of oyster recruits is sufficient (Coen and Luckenbach 2000; Baggett *et al.* 2014; NRC 2017).

One way to assess where one's sites might reside on the continuum between recruit- to substrate-limited sites is through the assessment of post-settlement recruitment and survival. The deployment of settlement plates, shell strings, vertical cylinders, and containers filled with various materials can be used to assess larval supply, growth, and ultimately juvenile to adult densities (reported in m^{-2}; Coen *et al.* 1999a; Baggett *et al.* 2014).

One easy, low-cost method to assess recruitment potential (larval supply) for shallow subtidal and intertidal projects is to deploy large mesh-covered replicate plastic trays filled with appropriate material at sites under consideration prior to the recruitment season (generally May to October). These can be placed on subtidal or intertidal reefs or bottoms and shorelines without hard substrates or for uniformity (age, timing, and material) to assess colonization of substrates before and even during ongoing restoration projects (Coen *et al.* 1999a, 2004; Luckenbach *et al.* 1999; Brumbaugh *et al.* 2006; Brumbaugh and Coen 2009; Baggett *et al.* 2014). They can be collected and assessed sometime in the fall to winter or even the spring of the following year. By assessing live (and dead) oysters and their relative sizes (and frequencies and densities·m^{-2}), one can gain a lot of information prior to investing significant resources, especially for large-scale restoration projects (Baggett *et al.* 2014).

However, in some areas (e.g. New York Hudson River estuary), larval supply and associated recruitment is so low that costly alternatives such as: (1) deploying spat-on-shell (spat set on shell or other substrate in hatchery and grown-out in a field nursery); (2) alternatively, though more costly, small single juvenile oysters (< 10–15 mm shell height, SH), can be added to reefs to jump start restoration efforts (Baggett *et al.* 2014; Lodge *et al.*, unpublished data).[5]

Proximity to natural (extant) oyster reefs

Larval supply is critical for the survival and development of restored reefs (Brumbaugh and Coen 2009). It is also invaluable for cost-effective restoration efforts, especially at larger scales. As broadcast spawners, members of the genus *Crassostrea* are sequential protandric hermaphrodites, with external fertilization. Larvae are then carried by local currents for up to two weeks until they are ready (competent) to settle on an appropriate hard substrate. For the genus *Crassotrea*, recruitment can occur into areas without any nearby (many km) reefs given that the requisite hard substrate is present first and relatively clean as many sites may be substrate- vs. recruit-limited (Brumbaugh and Coen 2009). Other genera (*Ostrea* spp., west coast of North America, Europe, IWP-Asia) are brooders undergoing internal fertilization and releasing juveniles rather than gametes for external fertilization. By placing material into areas without prior substrate, novel reefs can arise where did not occur formerly. Settlement behaviour is also mediated chemically (Kennedy *et al*. 1996 and references therein) such that newly settling oysters settle gregariously onto existing reefs with live oysters. Under certain conditions, natural recirculation patterns (retention estuaries) may enable existing reefs to resupply native or constructed reefs with new recruits (Southworth and Mann 1998).

Disease

Oyster diseases worldwide are diverse (Coen and Bishop 2015), but *C. virginica* usually refers to the presence of either Dermo (occurs from the Gulf of Mexico to Maine), whereas MSX has been observed from Florida to Canada (Kennedy *et al*. 1996 and references therein).[6] Infection by these two pathogens causes reduced growth rates, and ultimately death in areas with appropriate salinities where disease prevalence is high; these subtidal areas should be avoided where possible as potential restoration sites (Coen and Bishop 2015).

Explicit goals and related objectives for restoration

As mentioned previously any oyster restoration effort should be well-planned with clear goals that represent desired outputs and ecosystem services specified *a priori* (Coen and Luckenbach 2000; Kennedy *et al*. 2011; Baggett *et al*. 2014). Given limited space here, we refer the reader to recent reviews such as Coen *et al*. (2004), Kennedy *et al*. (2011), Baggett *et al*. (2014, 2015), La Peyre *et al*. (2014), and Powers and Boyer (2014). An NRC (2017) review addresses pre-construction and post-construction monitoring and related issues. All of the above discuss explicit goals which represent specific ecosystem services, individual objectives and related metrics, and associated success criteria to be sampled to achieve these.

However, because these ecosystems are quite complex, *measuring all variables is not feasible*. Hence, selection of which variables provide the most value for a given cost for assessing oyster reef restoration progress requires a clear understanding of appropriate protocols, and a clear knowledge of suitable sampling techniques. However, the selection of a limited suite of either general, basic, or as some have referred to them 'universal metrics and variables', should be required for *all* projects using comparable methods to assess performance (maximize success or understand failure), and later, if required, apply appropriate adaptive management to get back on track restoration project positive trajectories (reviewed in Coen and Luckenbach 2000; Kennedy *et al*. 2011; Baggett *et al*. 2014; NRC 2017).

Suffice it to say that these universal metrics and universal environmental variables and Restoration Goal-Based Metrics have been put forth in Baggett *et al*. (2014) and are being used more and more by practitioners across the USA for *Crassostrea* spp. and *Ostrea* spp.[7] Below we discuss very briefly some goals and objectives that provide support for documenting specific ecosystem services as part of potential oyster restoration goals and related success.

Summary and future considerations

Future oyster restoration/enhancement projects need to consider the lessons learned from previous attempts, whether viewed as successes or failures, and then these need to be applied *a priori* or within an adaptive management framework (NRC 2017). Below we consider a few of the lessons learned and what future efforts could be implemented to increase the probability of a given project's success.

One of the key differences between a successful and non-successful restoration effort is adequate (post-construction reef footprint and vertical relief) hard substrate for settlement of oyster spat. Note simulation modelling is getting better at predicting some of the critical processes as they relate to successful restoration (e.g. Kim *et al.* 2013).

Another fundamental result of early subtidal restoration efforts is that where dissolved oxygen is a potential challenge, the use of higher relief reefs, mimicking historical natural ones, has proven to be more successful than low or very low relief reefs (Lenihan and Peterson 1998; Lenihan 1999; Woods *et al.* 2005; Breitburg *et al.* 2009; Coen and Luckenbach 2000). This has been shown in the Gulf of Mexico (Gregalis *et al.* 2009), the southeastern USA (Lenihan 1999), as well as the mid-Atlantic USA (Luckenbach *et al.* 1999; Schulte *et al.* 2009).

Shell budgets for subtidal oyster reefs in the northeastern USA have been calculated and used to assess reef shell trajectories and the likelihood of longer-term restoration success (Powell *et al.* 2006, 2011; Waldbusser and Salisbury 2014; Casas *et al.* 2015; Ekstrom *et al.* 2015). Also concurrent multiple habitat restoration can maximize the overall success if the association of adjacent habitats is potentially positive (Milbrandt *et al.* 2015).

In areas where larval supply is limited (e.g. Hudson River Estuary), shell with small already set oysters, either from hatcheries or from redeployed field sets, can be one approach to increase success (Coen and Luckenbach 2000; Coen *et al.* 2004; Brumbaugh *et al.* 2006; Baggett *et al.* 2014). Once the oysters reach a refuge size (often 2–4 cm SH) or shell thickness, effectively reducing predation losses, they can be added onto reefs loosely with the deployed shell and seeded directly onto newly constructed reefs. However, with larger deployed oyster's size, comes an obvious trade-off as hatchery/nursery costs also increases significantly with this increasing size.

Intertidal evaluations of natural oyster reef changes and restoration success can be more easily assessed using a number of approaches (Coen *et al.* 1999a; Luckenbach *et al.* 2005; ASMFC 2007; Powers *et al.* 2009; Baggett *et al.* 2014 and references therein). For a large number of restoration footprints over a range of post-construction ages, Powers *et al.* (2009) reassessed NC reefs and determined that intertidal success was much greater than for subtidal reefs. However, this finding may be confounded by a number of potential methodological problems by time and parameter selection.

A lot more work needs to be done with regard to the success of reef restoration beyond the normal funding cycle of 1–3 years perhaps (Brumbaugh and Coen 2009; Kennedy *et al.* 2011; Baggett *et al.* 2014; NRC 2017). The large-scale 2009 American Recovery and Reinvestment Act (NOAA ARRA) oyster reef-related projects across the Gulf of Mexico and eastern USA may provide some of these answers, but initial funding was limited for 12–18 months, a period too short to assess success.

Knowing the status and condition (for trend analyses) of relevant habitats to be restored are critical for placement and extent of construction.[8] In many areas, major efforts have taken place with new imagery and related mapping (ASMFC 2007; SCDNR 2008)[9] or are under way (e.g. RESTORE funding for the Gulf of Mexico post DWH spill) to assess natural reefs for triaging recovery efforts (e.g. Harris Creek Oyster Restoration Tributary Plan, MD, USA).[10]

There are many parallels in the services rendered by farmed and natural reef restoration approaches (Dumbauld *et al.* 2009; Coen *et al.* 2011). It should be noted that worldwide, aquaculture is playing an ever increasing role in the supply of bivalve molluscs (Dumbauld *et al.* 2009; Shumway 2011; Shinn *et al.* 2015). Of late it has value as a potential tool for documenting also other non-consumptive ecosystem services for coastal habitats worldwide (Coen *et al.* 2007, 2011; Grabowski and Peterson 2007; Brumbaugh and Coen 2009; Beck *et al.* 2011; Powers and Boyer 2014). Some have gone on to even suggest that mussel and potentially other bivalve (e.g. oyster) aquaculture may provide a mechanism for reducing eutrophication (Shumway 2011). However, not all of the aquaculture impacts are positive (Dumbauld *et al.* 2009; Coen *et al.* 2011; Coen and Bishop 2015).

Despite the loss or dramatic decline of many habitat-generating bivalve species worldwide (Beck *et al.* 2011), these species face even greater obstacles to their recovery, let alone continued existence. Current and future alteration of 'typical' conditions by: (1) climate change and associated sea level rise; (2) ocean and nearshore acidification and related changes in pH; (3) rising temperatures impacting diseases and species ranges; (4) rainfall and salinity shifts; (5) increasing hypoxic areal extent and duration for subtidal populations; (6) continued coastal development and related vegetated habitat losses; (7) introduction of non-native competitors, predators, diseases; and (8) changes in native diseases will create natural habitat winners and losers, while impacting restoration outcomes (discussed in Coen and Bishop 2015; NRC 2017).

Recently oyster reefs were included as one of nine potentially important nearshore habitats that can potentially protect coastal communities and infrastructure (Arkema *et al.* 2013). Because bivalve habitats are potentially one of the most important nearshore habitats that have the ability to feed populations, as well as helping to protect coastal communities and infrastructure (*ibid.*), it is critical that we increase the scale of our restoration efforts. Not only do we need to increase local capacity to perform such habitat restoration, but also figure out how to extend monitoring while effectively scaling-up restoration efforts.

Enhancing or restoring of bivalve populations for direct harvesting or delivery of their numerous ecosystem services will require a great deal more research on questions related to diseases, genetics, and scaling-up related to practical construction relevant to management decisions (Lotze *et al.* 2006; Powers and Boyer 2014; Coen and Bishop 2015). Novel environmental perturbations, along with declining wildstocks (Lotze *et al.* 2006) will be especially challenging as local, state, and federal budgets continue to shrink, along with many agencies being forced to ignore the effects of climate change and sea level rise, especially in the USA, and more recently in other countries such as Australia and Canada (Coen and Bishop 2015).

Notes

1 See www.oyster-restoration.org/living-shorelines.
2 Cf. www.dnr.sc.gov/GIS/descoysterbed.html.
3 E.g. for SCDNR 2008 see www.oyster-restoration.org/oyster-restoration-research-reports.
4 But see www.oyster-restoration.org.
5 See www.hudsonriver.org/?x=orrp.
6 See also www.dfo-mpo.gc.ca/science/aah-saa/diseases-maladies/index-eng.html as updated.
7 Handbook available at www.oyster-restoration.org (see 'Restoration Practices' dropdown).
8 See www.dnr.sc.gov/GIS/descoysterbed.html.

9 See www.oyster-restoration.org/oyster-restoration-research-reports.
10 See www.oyster-restoration.org.

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