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DL Breitburg
LD Coen
MW Luckenbach
Virginia Institute of Marine Science
R Mann
Virginia Institute of Marine Science
M Posey

See next page for additional authors

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Authors
DL Breitburg, LD Coen, MW Luckenbach, R Mann, M Posey, and J. A. Wesson

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OYSTER REEF RESTORATION: CONVERGENCE OF HARVEST AND CONSERVATION STRATEGIES

DENISE L. BREITBURG,1 LOREN D. COEN,2 MARK W. LUCKENBACH,3 ROGER MANN,4 MARTIN POSEY,3 AND JAMES A. WESSON6
1The Academy of Natural Sciences
Estuarine Research Center
10545 Mackall Road
St. Leonard, Maryland 20685
2South Carolina Department of Natural Resources
Marine Resources Research Institute
P.O. Box 12559
Charleston, South Carolina 29422-2559
3Eastern Shore Laboratory
Virginia Institute of Marine Science
College of William and Mary
Wachapreague, Virginia 23480
4School of Marine Science
Virginia Institute of Marine Science
College of William and Mary
Gloucester Point, Virginia 23062
5Department of Biological Sciences
University of North Carolina at Wilmington
Wilmington, North Carolina 28403
6Virginia Marine Resource Commission
P.O. Box 756
Newport News, Virginia 23607

ABSTRACT Oyster reef restoration, protection, and construction are important to meeting harvest, water quality, and fish habitat goals. However, the strategies needed to achieve harvest and conservation goals have often been considered to be at odds. We argue that these goals are, in fact, compatible and that the same strategies will promote a sustainable harvest of the resource, increased filtration of estuarine waters, and increased provision of structured habitat for finfish, crabs, and other organisms that utilize oyster reefs or receive benefit indirectly from them. Creation or designations of unharvested sites (refuge sites) are key components of these strategies. Unharvested reefs have the potential to provide vertical relief, which is typically destroyed by harvest practices, to act as a source of larvae, which potentially increases the supply of harvestable oysters, and to protect those individuals most likely to have some resistance to disease. Furthermore, proper monitoring and design of refuge and restoration efforts are critical to providing information needed to improve the success of future restoration efforts, and will simultaneously enhance the basic information needed to understand the ecology of oysters and their role in estuarine and coastal systems.

KEY WORDS: oyster reef, restoration, water quality, harvest, fish habitat, Crassostrea virginica, sanctuaries

INTRODUCTION

Oyster reef restoration is a recognized need by resource agencies in most states along the Atlantic and Gulf of Mexico coasts of the United States. In general, the initial impetus for these programs has been declining harvests and standing stocks of oysters that are at an all time low (MacKenzie et al. 1997a, MacKenzie et al. 1997b, Luckenbach et al. 1999, Coen and Luckenbach 2000 and references therein). Although numerous factors have been implicated in these declines, a consistent factor has been the destruction of reef habitat during the harvesting process (Hargis and Haven 1999, Lenihan and Micheli 1999). Harvest programs have focused on improving oyster habitat as a means of enhancing the commercial fishery (Luckenbach et al. 1999, Coen and Luckenbach 2000). Harvest of oysters involves removal of the reef substrate and, therefore, a decrease in available settlement and growth habitat for subsequent recruits to the oyster population. In addition, most harvesting practices are destructive to the reef matrix, reducing the vertical relief and damaging structural integrity in excess of that caused by removal of the individual oysters actually marketed (Hargis and Haven 1999, Lenihan and Micheli 1999). Shell repletion programs attempt to mitigate this habitat removal and destruction by adding shell as substrate for settlement of oyster larvae. A consequence of these repletion efforts has been a shift toward put-and-take fisheries (Coen and Luckenbach 2000).

Recognition of oyster reefs as valuable estuarine habitats that provide a range of ecosystem services is increasing (Coen and Luckenbach 2000, Coen et al. 1999b). The original goal of restoring and enhancing fishery stocks has been augmented, and in a few instances, succeeded, by two additional goals: (1) improving water quality (by removing a portion of the phytoplankton standing stock) and (2) providing a structured habitat that may increase
secondary production, including production of finfish and decapod crustaceans, such as crabs (Fig. 1) (Wenner et al. 1996, Coen et al. 1999a, Coen 1999b). Extrapolations from laboratory filtration rates (Newell 1988, Powell et al. 1992), direct field measurements (Dame 1996 and references therein), and ecosystem-level modeling (Ulanowicz and Tuttle 1992) have clearly demonstrated that oyster reefs can have significant impacts on material processing and energy flow in estuarine systems. The recognition of the importance of oysters' ability to reduce phytoplankton biomass as a result of their filtering capabilities coincides with an increased concern over eutrophication in coastal waters. Increased anthropogenic loadings of nutrients make the ecosystem-level role of suspension feeders (such as oysters) all the more critical at the same time that overharvest and disease have reduced populations through much of their range.

Furthermore, descriptive and experimental studies have pointed to the importance of oyster reefs as habitat for commercially and ecologically important finfish and decapod crustaceans (see Wells 1961, Bahr and Lanier 1981, Stanley and Sellers 1986, Breitburg 1992, Breitburg 1999, Wenner et al. 1996, Coen et al. 1999a, Coen 1999b, Harding and Mann 1999). Although few specifics are known about the relationships among oyster reef structure, oyster population structure, and the provision of these ecosystem services, it is likely they are related to the vertical relief of reefs, the size and numbers of reefs, the overall estuarine habitat landscape, habitat health, and the population density and age structure of oyster populations. Seemingly, this sets up a conflict between the goals of fisheries exploitation and those of ecological restoration and conservation. With recent revisions to the Magnuson–Stevens Fishery Conservation and Management Act (1996) this conflict might be expected to intensify (Coen et al. 1999b).

In this paper, we address the challenge of simultaneously achieving all three goals of oyster reef restoration (fisheries, water quality, and habitat), highlight ecological processes that may make the feasibility of meeting all three goals more or less difficult, and discuss the potential benefits of melding research and restoration activities. We emphasize our belief that these goals are generally compatible and the importance of keeping all three goals in mind to achieve sound habitat and resource management and restoration. Many of the ideas in this paper stem from discussions at the special session and workshop on oyster reef restoration organized by L. Coen and M. Luckenbach at the 2nd International Conference on Shellfish Restoration held in Hilton Head, South Carolina, in November 1998. Our intent is to summarize some of the major themes and explore the constraints associated with sustaining the goals of fisheries exploitation and habitat conservation, not to provide a comprehensive review of the workshop and presentations or to address all of the issues related to oyster restoration raised therein.

![Diagram](image)

**Requirements**

**Benefits of Reef Restoration**

- Sustainable harvest
- Improved water quality
- Habitat for finfish, decapods & benthic invertebrates
- Protection of other habitats

*Figure 1. Restoration of oyster reefs has three primary goals: increasing sustainable harvests of oysters, improving water quality through the removal of phytoplankton biomass, and increasing structured habitat utilized by finfish, crabs, benthic invertebrates, and (especially for intertidal reefs) birds. In addition, studies by Meyer and colleagues indicate the possibility that oyster reefs can play a significant role in reducing shoreline erosion and protecting salt marsh habitat (see Meyer et al. 1996, Meyer et al. 1997).*
Although many areas of uncertainty remain, we believe a pattern of convergence is emerging (see recent reviews by Lenihan and Peterson 1998, Coen et al. 1999b, Luckenbach et al. 1999, Coen and Luckenbach 2000).

**COMPATIBILITY OF HARVEST AND ECOLOGICAL GOALS OF OYSTER REEF RESTORATION**

Are sustainable harvest and ecological goals of oyster reef restoration compatible? The relationships between production and biomass, as well as between the fishery and ecological benefits of unharvested refuge areas, contribute to our belief that the answer is yes. Figure 2 illustrates the possible relationships between production and biomass. Maximum production of a resource is achieved at a biomass lower than the maximum potential biomass because of processes ranging from self-shading in phytoplankton, to age-dependent growth declines, to prey depletion that occurs at high population densities of consumers. In part, the degree to which harvest and ecological values of reefs coincide will depend on which of the family of curves depicted in Figure 2 best describes estuarine oyster populations. Maximum sustainable yield strategies in fisheries generally focus on keeping a population near its maximum rate of production but on the descending portion of the curve (i.e., biomass greater than that at maximum production), where overharvesting of the resource is less likely to occur than along the ascending portion of the curve (see Applegate et al. 1998, Restrepo et al. 1998 for a comprehensive discussion of these curves in a fishery management context). Because maximum filtration rates and maximum production are both related positively to per capita growth rates (Powell et al. 1992, Hoffman et al. 1995), population densities producing high levels of sustainable harvests should also be those that lead to a high (possibly maximal) ecological benefit of water filtration by oysters. Finally, although less well understood, we argue that "more is better" in terms of the habitat oysters provide for fish, crabs, and other benthic organisms, but, as with the other goals, there is a decreasing benefit portion of the curve. Something short of complete coverage by oysters is needed to produce a diversity of benthic habitats that includes soft bottom, submerged aquatic vegetation, salt marsh, oyster reefs, and clam beds, where these have naturally or historically co-occurred. As important, many fish and decapods orient toward the edges of reefs and do not simply utilize the large interior areas (Powell 1994, Breitburg 1999). It is critical to keep in mind that even if the optimal biomass for harvest and ecological goals do not coincide precisely, movement toward all three goals requires increasing oyster biomass in most estuarine systems.

The more the production versus biomass curves are skewed to the right (e.g., curve C rather than curve A in Fig. 2), the higher will be the optimum oyster standing stock for a sustainable fishery and the greater will be the coincidence between biomass levels optimizing the filtration capacity of the oyster population and the provision of habitat for other biota. Several features of oyster biology, as well as ecological interactions among oysters, the

**Figure 2. Relationship between production and biomass.** Theoretical considerations suggest that maximum production will often occur at one half the maximum biomass (Applegate et al. 1998). However, interference competition and resource depletion can skew the curve to the left (A), and increased efficiency or reproductive success at high densities can skew the curve to the right (C). We suggest that under most conditions, oyster populations will be described by curves B or C, making harvest, water quality, and habitat restoration goals compatible.
physical environment, and other biota suggest a high-biomass-high-productivity relationship, with greatest success for all three goals occurring with well-developed or "mature" high-relief reefs. High density within oyster beds is likely the optimal condition for the oysters themselves, because the preferred settlement substrate for oyster larvae is oyster shell (e.g., Hidu 1969, Luckenbach et al. 1997, Bartol and Mann 1999), the fertilization success of sessile animals is increased at high densities (Levitan 1991, Levitan et al. 1992), and the subtidal reefs will maintain greater vertical relief, reducing sedimentation effects and enhancing local flow rates (Lenihan and Peterson 1998). High aerial coverage by oysters should provide insurance against the strong spatiotemporal variability in physical and biotic factors that can influence both spat set and the health of adults (Lenihan and Peterson 1998). For systems with limited water exchange and/or small tidal creeks with relatively large tidal ranges (> 1–2 m), minimum reef area may be essential for maintenance of local populations. In more open systems, increased cover may provide a buffer against local disturbances and recruitment variability.

**IMPORTANCE OF HARVEST REFUGES**

Unharvested (refuge) areas are critical to achieving both harvest and ecological roles of oyster reefs. Refuge areas protect brood stock and, as a result, can enhance oyster populations in surrounding harvested areas that are many times the size of the refuge itself (Wesson 1998). Moreover, in areas affected by oyster diseases, refuges provide protection for individuals that may have some resistance to disease. In harvested areas, the largest oysters, which are the individuals that have survived in the presence of disease pressure and have the highest fecundity, are the ones culled from the population (Rothschild et al. 1994, Coen et al. 1999b). Protecting some reefs from harvest should, therefore, serve to enhance the vigor of stocks.

In addition, harvest-free sanctuaries allow reefs to develop and retain vertical relief and structural complexity that are important to both oysters and associated fauna. Vertical relief can provide oysters with the means to avoid near-bottom oxygen depletion and high sedimentation rates, and to take advantage of increased flow velocity and enhanced growth rates (Lenihan et al. 1996, Lenihan and Peterson 1998, Lenihan et al. 1999). In addition to reef elevation, vertical complexity of the reef itself (i.e., the presence of high culms interspersed with low areas) enhances fish and decapod utilization (e.g., Breitburg et al. 1995, Breitburg 1999, Coen et al. 1999b, Harding and Mann 1999, Posey et al. 1999, Coen and Luckenbach 2000) and may protect oyster spat from predation (Wesson 1998, unpubl. data, Giotta and Coen 1999). Because harvesting reduces vertical complexity, these habitat functions may benefit from creation of unharvested (refuge) areas (Coen et al. 1999b, Lenihan and Micheli 1999). However, there is also a view that some thinning may enhance intertidal oyster populations (Lenihan and Micheli 1999, W. Anderson, South Carolina Department of Natural Resources, pers. comm.).

Refuges also provide a tool at the landscape level that allows reefs to be placed in areas that are protected or closed to harvest and that will maximize desired functions (reviewed in Lenihan and Peterson 1998, Coen et al. 1999b, Luckenbach et al. 1999, Coen and Luckenbach 2000). For example, low-salinity refuge areas in the Maryland portion of the Chesapeake Bay are designated to protect oyster brood stock in areas generally unaffected by either Perkinsus (Dermo) or Haplosporidium (MSX) (Bushek and Allen 1996a,b, Paynter 1999, Coen and Luckenbach 2000). Similarly, designated areas closed to direct harvesting for health reasons may act as refugia as an indirect result of their value as habitat and brood stock reserves (Coen and Luckenbach 1999).

**SPATIAL CONSIDERATIONS**

There is still much to be learned about the importance of the location of restored oyster reefs within an estuarine landscape (Posey et al. 1998, Coen et al. 1999b). Whitlach and Osman (1999) have developed a metapopulation demographic model of oyster populations that illustrates the importance of dispersal between spatially distinct subpopulations to the persistence of oyster reefs. The foregoing discussion about brood stock sanctuaries and the dispersal of larvae from them to nearby reefs clearly illustrates the importance of reef position within a landscape to the development of reefs and potential fisheries production. Further, the location of reefs will affect the ecosystem services that they provide (see Lenihan and Peterson 1998, Coen et al. 1999b, Coen and Luckenbach 2000). For instance, restoring or constructing reefs in locations key to intercepting waters with high nutrient loadings and the associated high phytoplankton biomass should be possible. Similarly, the proximity to other structured habitat may be important to the function of oyster reefs (Micheli 1997, Coen et al. 1999b). Reefs could be sited in areas with little or no other structured habitat so that they could function as important "stepping stones" or migration corridors along the landscape. Alternatively, if data indicate the advisability of doing so, reefs could be sited in close proximity to other structured habitat to maximize interactions and connections between, for example, submerged aquatic vegetation or salt marsh grass and oyster reef assemblages.

A particularly intriguing ecosystem service provided by constructed oyster reefs adjacent to salt marshes has been discussed by Meyer et al. (1996, Meyer et al. 1997). In addition to providing structured habitat for fauna, these reefs stabilize the creek banks and reduce erosion of adjacent marshes (Meyer et al. 1996, Meyer et al. 1997, Meyer and Townsend 2000). As more information is gathered, the role of oyster reefs in erosion control may be determined to be as important as their other ecological services. Reefs with substantial vertical relief that reach the surface of the water may dissipate much of the energy generated where fetch on open bodies of water allows substantial energy to accumulate.

Regardless of other spatial considerations for oyster reef restoration and creation, several aspects of the placement of reefs within the landscape will influence their success both in terms of reef longevity and their measurable, short-term impact on the surrounding habitat. Successful siting of reefs generally depends upon locating substrate capable of supporting the added shell (without rapid burial), and therefore, generally favors their construction on footprints of historical oysters reefs. In addition, placement of brood stock sanctuaries should consider local circulation to maximize retention and recruitment of resultant larvae. This philosophy has dictated the placement of constructed reef sanctuaries in the Virginia portion of the Chesapeake predominantly in small subestuaries with limited watersheds, small tidal excursions, and basin topographies that encourage gyre-like circulation near the river mouths (Haven et al. 1981, Southworth and Mann 2000, Wesson unpubl. data).

**STRATEGIES FOR RESTORATION**

The harvest and ecological goals of oyster restoration are most likely to be compatible where management efforts focus on the ultimate goals, and the harvest is managed as a sustainable rather
than a "put-and-take" fishery. For example, targets for the amount of acreage for oyster restoration and protection could be set by determining the volume of water to be filtered within a given time or by determining the ratio of unharvested to harvested area required to sustain a target harvest quantity. We argue that such goal-oriented target setting is more likely to achieve the desired result than setting targets based upon historical oyster populations. Moreover, it is important to consider that restoration efforts proceed one step (i.e., one or a few reefs) at a time and that metrics to gauge the success of these efforts need to reflect both the value of the individual projects and their contribution toward the ultimate goal. For instance, the harvest potential of an individual reef expressed in terms of the biomass that may be harvested sustainably per unit area (rather than as the number of bushels of market-sized oysters in the standing stock) embodies both the productivity of the reef and the total area necessary to achieve the desired harvest levels. Similarly, the fishery value of a protected (unharvested) reef area based on its potential contribution to harvest in other areas after allowing for a number of years of reef development is a more reasonable assessment of the value of a refuge than would be a simple calculation of the number of acres taken out of the active fishery. Likewise, measures of the ability of a unit area of reef to filter a specified volume of water or to support a specified biomass of finfish, decapods, shorebirds, or other target species will be more useful metrics than attempts to define the contribution of a single reef to the percent of the entire water mass filtered each day or to the biomass of a particular fish within an entire estuary.

LEARNING FROM RESTORATION EFFORTS

Restoration efforts, when properly designed and monitored, present an unparalleled opportunity to improve our understanding of both the optimal design for future restoration efforts and the ecological role of oyster reefs in coastal systems (Table 1). There are two key elements required to maximize the information from restoration efforts. The first is careful planning in the design and siting of reefs to match the restoration efforts with the information desired. For example, in areas such as the northern portion of the Chesapeake Bay and Delaware Bay where subtidal reefs were likely the historical norm, there may be concern that reefs not visible from but near the surface of the water may present navigation hazards. However, constructing reefs in deep water (thus, creating no navigation hazard) can expose oysters and associated biota to low dissolved oxygen concentrations during summer. By constructing and monitoring replicated reefs similar in size and relief (and thus cost) at shallow and deep sites, the optimal depth for reef placement in future restoration efforts could be determined. Simultaneously, important basic information could be gathered on the similarities and differences in the oyster populations and the ecological functioning of deep and shallow oyster reefs. More generally, by designing restoration efforts to allow comparisons between reasonable alternatives, becomes possible to answer many important restoration questions. These include such questions as: (1) Does the benefit (i.e., growth, recruitment, or survival of oysters) derived from the construction of high vertical relief beds outweigh the costs of constructing such reefs? (2) Do oyster reefs placed near other structured habitats (such as SAV beds or tidal marsh areas) have higher or lower habitat value for finfish? (3) Is the extended "footprint" (i.e., area of increased oyster recruitment surrounding restored reefs) greater near harvested or unharvested restoration sites? (4) Does the addition of juvenile or adult brood stock oysters (either wild or hatchery-reared) increase long-term productivity of a reef sufficiently to justify the costs? (5) Does the benefit of oysters' water filtration...

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Restoration efforts can be designed in ways that will provide information critical for improving future restoration work. In addition, they provide the opportunity for large-scale ecosystem manipulations that may greatly improve the understanding of the structure and functioning of coastal systems. The examples of these opportunities in the table are intended to be illustrative, not exhaustive.
capabilities vary with location, depth, habitat type, shape, etc.? (6) How do the shape and vertical complexity of reefs affect habitat function? (7) How do the answers to these and other related questions differ among sites and systems (e.g., intertidal versus subtidal oyster reef habitats, areas with significantly different tidal ranges, etc.)?

The second element required to maximize information from restoration efforts is the necessity for adequate monitoring to evaluate their success (see discussion in Coen and Luckenbach 2000). The specific type and intensity of monitoring will be determined by the goals of any particular restoration effort, the comparisons being made (as above), the target levels being set for improved harvest and ecological benefits, and ultimately the available funding. In addition, evaluation of both the biological impact of reef restoration (both harvest and ecological benefit goals) and the economic considerations may often be important. Experiences from the past several decades with restoration of other marine and coastal habitats consistently point to the need for well-designed monitoring studies to evaluate the success of restoration efforts (see Thayer 1992). As pointed out by Zedler (1992), monitoring to assess success and research that can help clarify how to meet restoration goals, are often not supported adequately by the entities that fund the actual restoration projects (discussed also in Coen and Luckenbach 2000). A significant challenge for oyster reef restoration efforts will be developing potential funding sources to support both large-scale habitat manipulations and long-term monitoring and assessment activities.

By combining carefully planned and targeted restoration efforts with adequate monitoring of the results, it will be possible to obtain information on topics about which little is known. Some of these topics (see also Table 1) are: (1) the characteristics of oyster reefs that are important for transient fish and crab populations; (2) the area beyond the boundaries of the actual restoration effort in which both oysters and associated biota are affected under a range of hydrographic conditions; (3) the importance of the spatial arrangement of reefs within an estuarine landscape; and (4) the potential for oyster reefs to play a role in reducing shoreline erosion. These are not simply topics of academic interest but relate to the core goal of restoring oyster reefs as a sustainable fishery and minimizing anthropogenic effects to our coastal systems. In addition, among the most critical issues for future restoration efforts may be the questions: Where can sufficient reef substrate be obtained? And what oyster strains should be used to restore areas where oysters have long been in decline? Alternative substrates take on an increasingly significant role, as does the potential problem of introducing nonindigenous species or new disease strains with the importation of oyster shell from other regions (Bushek and Allen 1999a, Busheck and Allen 1999b, Buscheck 1997, Coen et al. unpublished, G. Ruiz pers. comm.).

FUTURE STEPS

Despite uncertainties surrounding many aspects of reef restoration, it is important to move forward with restoration efforts; it is clear that reef restoration has the potential to provide strong benefits to both the harvest and ecological functions of oyster reefs in coastal systems. Most important, restoration efforts should target all three functions of natural reefs: harvest, the provision of structured habitat, and the potential for improved water quality. Rather than an adversarial relationship between fisheries and conservation interests in this regard, we suggest there are enough similarities of interests and approaches—especially the desire to optimize the amount and location of settlement substrate—that compatible strategies may be achieved. A critical feature of achieving this compatibility will be clearly expressing the benefits of reef restoration (depicted in Fig. 1), and relating each benefit in a quantifiable way to reef and oyster production.

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