

Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation?

Loren D. Coen ^{a,*}, Mark W. Luckenbach ^b

^a South Carolina Department of Natural Resources, Marine Resources Research Institute, PO Box 12559, Charleston, SC 29422-2559, USA

^b Eastern Shore Laboratory, Virginia Institute of Marine Science, College of William and Mary, Wachapreague, VA 23480, USA

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Abstract

Habitat restoration encompasses a broad range of activities, emphasizing very different issues, goals, and approaches depending on the operational definition of ‘restoration’. This is particularly true for many shellfish (molluscan) dominated systems (e.g. oyster reefs, mussel beds, vermetid gastropod reefs). In contrast to other well-studied biogenic habitats, such as seagrasses, mangroves, or salt marshes, bivalves are directly consumed as a resource. Hence resource extraction has direct consequences for habitat health. Restoration objectives have typically included reduction of public health risks through improved water quality to increase harvest. Restoration or enhancement of populations of commercially exploited shellfish depressed by overharvesting and/or reduced environmental quality remains the principal motivation behind most shellfish ‘restoration’ efforts. Direct and indirect ecosystem services (e.g. filtering capacity, benthic–pelagic coupling, nutrient dynamics, sediment stabilization, provision of habitat, etc.) derived from oyster habitat have been largely ignored or underestimated. Only recently, the restoration of lost ecological function associated with shellfish communities has been included in our discussions and related research examining habitat development and function through a scientific approach. The former area has been reviewed extensively and will not be our focus here. In this review, we examine some of the restoration efforts made in the name of fisheries enhancement, address their effectiveness, and discuss some of the issues associated with realizing the broader goal of ecological restoration. We note the importance of linking success criteria to specific goals and make the case for a greater need in clarifying the ecological functions of shellfish and shellfish habitats. We recognize the limitations of existing datasets and summarize ongoing attempts to address oyster habitat restoration throughout the broad geographic distribution of the American oyster, *Crassostrea virginica* (Gmelin). In many ways this topic parallels the ongoing debate over ‘attraction versus production’ associated with artificial reef management. We consider how local conditions (e.g. tidal range, bottom topography, turbidity, salinity) and resulting habitat traits affect restoration strategies. We also discuss the underappreciated value of shellfish populations from those areas

* Corresponding author. Tel.: +1-843-7625033; fax: +1-843-7625110.

E-mail addresses: coenl@mrd.dnr.state.sc.us (L.D. Coen), luck@vims.edu (M.W. Luckenbach).

designated as closed to harvesting due to their intrinsic worth as habitat/larval reserves. The necessity of ecosystem (adaptive) management strategies emerges from this discussion. Finally, this overview supports our contention that shellfish habitat should be included in discussions of 'essential fish habitats' (or EFH). © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Restoration of shellfish habitat embodies several different issues and goals, including water quality indicators, fisheries enhancement, and restoration of ecological function. Until recently, the latter has received minimal attention from researchers and resource managers. For instance, a previous volume on the restoration of marine habitats (Thayer, 1992) did not include a section on shellfish habitat restoration nor does a recent review of the Eastern oyster (Kennedy et al., 1996) discuss the habitat value of this species or its ecological role. There is, however, a growing recognition that, in some coastal systems, assemblages of molluscan shellfish (e.g. oyster reefs, mussel beds, and clam beds) can have significant impact on communities and landscape-level processes. On some rocky shores, mussels can be *keystone species* (sensu Paine, 1966), interacting strongly with other species via trophic and habitat links. Numerous examples exist of filtration by dense bivalve populations controlling water column phytoplankton dynamics (e.g. clams in San Francisco Bay, Cloern, 1982; oysters in Chesapeake Bay, Newell, 1988; cockles and mussels in the Oosterchelde estuary, Smaal and Haas, 1997; zebra mussels in the Hudson River, Roditi et al., 1996; oysters in a South Carolina salt marsh, Dame et al., 1986; also see Dame, 1996 for a review of shellfish impacts on materials fluxes). After briefly considering other definitions of shellfish habitat restoration, we will focus this review on the small but growing body of knowledge related to restoration of ecological function in structured shellfish habitats, with a focus on the Eastern oyster, *Crassostrea virginica*, along the Atlantic and Gulf coasts of USA.

The most widespread activities under the umbrella of shellfish habitat restoration are those related to water quality improvements (see review in NOAA, 1997). State public health departments in the coastal United States maintain monitoring programs of potential shellfish-growing waters to evaluate public health risks (NOAA, 1997). These programs are cooperatively managed by state and federal agencies, including FDA, NOAA, and ISSC, to classify shellfish-growing waters and insure that shellfish for public consumption are from approved areas (NOAA, 1997). When high levels of bacterial indicator species (generally *Escherichia coli* or *Vibrio vulnificus*) or specific toxicants are observed, restrictions are placed on shellfish harvesting. Restoration in response to these situations seeks to reduce the input of point and nonpoint pollution into the receiving waters, thereby reducing restrictions on shellfish harvest. Although a goal of such restoration efforts is often fisheries enhancement, it is perhaps more frequently viewed as simply basic water quality improvement. Shellfish habitat restoration in this sense is not viewed as an end point, but rather as a surrogate for water quality enhancement. This type of restoration activity has been the subject of other reviews (e.g. Leonard, 1993) and will not be the focus of this review.

Frequently, shellfish restoration is considered to be synonymous with fisheries stock enhancement. Wild shellfish stocks in the United States support numerous valuable fisheries (e.g. Atlantic and Gulf coasts, MacKenzie et al., 1997a; Pacific coast, MacKenzie et al., 1997b), most of which are declining due to overfishing, habitat degradation, disease pressures, and interactions among these factors (e.g. Rothschild et al., 1994; Lenihan and Peterson, 1998; Lenihan et al., 1999). Efforts to sustain these fisheries by developing brood

stock sanctuaries, supplementing hard substrata on the bottom, relocating stocks, and occasionally supplementing natural populations with hatchery-reared stocks are underway in most coastal states in USA. Such efforts have generally not had the broader goal of habitat restoration, but merely fisheries enhancement (reviewed in MacKenzie, 1983, 1996a,b).

In this review we will focus on oyster (specifically *C. virginica*) reef habitat, and the current state of knowledge related to its restoration. We will review existing descriptive data on oyster reef habitat ecology and summarize some recent and ongoing experimental investigations that are relevant to understanding the structure and ecological function of oyster reefs. We will describe in greater detail two ongoing projects addressing oyster reef habitat restoration in Charleston, South Carolina, and Fisherman's Island, Virginia, USA, and summarize ongoing work by others (see also Coen et al., 1999b). Further, we will attempt to define specific success criteria for oyster reef habitat restoration and in doing so will be led to suggest needed areas for future research.

2. The Eastern oyster

The Eastern oyster's [*C. virginica* (Gmelin)] range extends from the St. Lawrence River in Canada to the Atlantic coast of Argentina (Carriker and Gaffney, 1996), with introductions into then northwest Pacific off USA. *C. virginica* is a reef-forming organism, but it varies throughout its range in habitat and growth form. Reefs may be intertidal or subtidal, fringing or patch reefs, and vary in size from 10 to 1000 m². Greatest abundance are found in areas where a partial predation refuge exists, either in low salinity (< 15 ppt) or in the intertidal zone.

C. virginica growth rates vary with temperature, throughout a wide range (6–32°C) with the highest rates generally observed around 25°C (Galtsoff, 1964). Harvest size restrictions vary between states, but a minimum size limit of 76 mm is required in most. Time to reach harvest size varies with latitude and local environmental conditions, but ranges from as much as 5 years in

the northern parts of its range to as little as 1 year in some southern locations. Though sexual maturity and spawning may occur in some individuals in the 0–1 year class, the species is a protandric hermaphrodite, with males generally preceding females; however, considerable variation in this pattern has been reported (summarized in Thompson et al., 1996). Loosanoff (1965) reports that oysters can live as long as 40 years and fecundity of females increases with size. Gametes are freely spawned into the water column and planktotrophic larvae usually develop over a 2–3 week period. Oyster larvae settle gregariously onto hard substrates (Cole and Knight-Jones, 1939) and there has been some debate about the source of attractant compounds involved in the process. Exudates from adult and juvenile oysters have been implicated (Crisp, 1967; Hidu, 1969; Hidu et al., 1978; Keck et al., 1971; Veitch and Hidu, 1971), as have microbial biofilms (Bonar et al., 1986, 1990; Fitt et al., 1989, 1990; Weiner et al., 1989). Zimmer-Faust and colleagues have demonstrated that extracts from both sources induce settlement behavior in oyster larvae in still water (Tamburri et al., 1992; Zimmer-Faust and Tamburri, 1994) and that whole oyster extract and the polypeptide glycl-glycyl-L-arginine enhance oyster settlement in turbulent boundary flows (Turner et al., 1994). A consequence of this gregarious settlement is that oyster reefs develop as multiple generations settling one upon another. Restoration efforts have generally depended upon the natural development of biofilms onto deployed shell to induce settlement of oyster larvae; the use of natural extracts or synthetic peptides for inducers in restoration projects has not been employed, but may hold promise for enhancing larval settlement.

3. The oyster fishery

At its peak between 1880 and 1910, this fishery landed 160 million pounds of meats per year (Brooks, 1891; Ruge, 1898; MacKenzie, 1996a). By 1995 landings in the US had declined to 40.4 million pounds (Anon, 1996; cf. MacKenzie, 1996a) and once highly productive fisheries in Chesapeake Bay, Delaware Bay, and North Caro-

lina (Frankenberg, 1995) have virtually collapsed. Though diseases are often blamed, overharvesting and the resultant habitat destruction are more likely to have caused the dramatic declines throughout much of the region (see Rothschild et al., 1994; Paynter, foreword in Brooks, 1996 rev. ed.; Hargis and Haven, 1999).

Two protozoan parasites, *Perkinsus marinus* and *Haplosporidium nelsoni*, are endemic in *C. virginica* throughout much of its range. *P. marinus*, the causative agent of Dermo disease, has been reported from Maine to Tabasco, Mexico; *H. nelsoni*, which results in MSX disease, is known to infect oysters from Maine to the Atlantic coast of Florida (Ewart and Ford, 1993; Ford and Tripp, 1996). Both diseases have been reported to cause significant mortality, especially in oysters greater than 2 years of age, but their importance as the primary cause of the collapse of the regional fishery has been questioned (Rothschild et al., 1994).

The manner in which this fishery is performed has been particularly destructive for reef habitat. Harvest methods (reviewed in MacKenzie, 1996a; MacKenzie et al., 1997a,b) have included hand- and hydraulically-operated tongs, dredges pulled by sailing and motor-powered vessels, and hand-harvesting on intertidal reefs. With the exception of the latter, these harvesting practices are analogous to strip mining, breaking off pieces of the reef and removing all size classes of oysters (see Brooks, 1891). Size restrictions placed by fisheries regulations and market demand may result in small oysters being culled from the catch and returned to the water, but these oysters are no longer attached to the reef and the damage to the reef is irreparable (see Dayton et al., 1995; Kaufman and Dayton, 1997). Therefore, most oyster restoration efforts operate as a 'put-and-take' fishery. Lenihan and Peterson (1998) and others (Lenihan and Micheli, 2000) have demonstrated by using experimental reefs that dredging dramatically alters the morphology of reefs, which in turn affects oyster growth rate and survival. Hargis and Haven (1995, 1999), Lenihan and Peterson (1998), Lenihan and Micheli (2000) all discuss the detrimental impacts that this indiscriminate harvesting have had on the integrity and ecological function of oyster reef habitat.

4. Ecology of oyster reefs

Few data are available on the ecology of oyster reefs. Several studies have reported community profiles for macroinvertebrates and fishes associated with intertidal and subtidal oyster reefs along the South Atlantic and Gulf coasts (e.g. Wells, 1961; Dame, 1979; Bahr and Lanier, 1981; Klemanowicz, 1985; Burrell, 1986; Stanley and Sellers, 1986; Zimmerman et al., 1989). These studies reveal that oyster reef communities are highly diverse and include numerous species rare or absent in adjacent sedimentary habitats. However, all these studies have been largely descriptive; long-term and systematic characterization of community development and ecosystem function of oyster reefs is generally lacking. Unequivocally relating the ecological functions of reefs (e.g. materials fluxes, provision of habitat, and trophic dynamics) to structural characteristics (e.g. oyster density, spatial extent, elevation, construction material) will require manipulative experiments using replicated reefs varying in structural characteristics.

A few recent studies have demonstrated the importance of physical factors related to reef construction in the settlement, growth and survival of oysters. Lenihan (1996), Lenihan and Peterson (1998), Lenihan et al. (1996) have created experimental subtidal reefs that vary in morphology, water depth, and location within the Neuse River estuary in North Carolina. They have demonstrated that subtidal oyster growth, survival (Lenihan and Peterson, 1998), and disease dynamics (Lenihan et al., 1999) vary with reef height, position and depth, in relation to flow velocity, sedimentation rate, and dissolved oxygen regime. Their work indicates that, particularly in stratified estuaries, materials for subtidal reef restoration should be placed with prior knowledge of local hydrographic conditions (e.g. current velocities, sedimentation rates, temperature and density stratification, and oxygen levels).

The importance of interstitial space within a reef for oyster recruitment and survival has been reported by Bartol and Mann (1999). On a large, constructed, unreplicated, intertidal reef in the Piankatank River, Virginia, with small tidal am-

plitude, they observed that survival of oysters was greater below the reef surface, in the interstices between shells, than on the reef surface itself. This difference was most pronounced in the high intertidal and subtidal regions of the reef. In the high intertidal zone, oysters below the reef surface were afforded some protection from desiccation in the summer and ice scour in the winter, while in the subtidal region of the reef, interstitial habitat for juvenile oysters was presumed to provide a refuge from predation. These findings have implications for the types of substrates and planting configurations needed to support the development of oyster populations and epifaunal assemblages on constructed reefs.

4.1. Habitat value

An understanding of the dynamic processes by which both mobile and resident species utilize oyster reef habitat is just beginning to emerge. Posey et al. (1999) conducted mesocosm experiments that demonstrated that grass shrimp *Palaeomonetes pugio* seek refuge in a simulated oyster reef when threatened by finfish predators. In mesocosms containing varying combinations of three presumed refuge habitats — shallow water, artificial seagrass, and oyster shell — grass shrimp preferentially moved into the oyster reef habitat when a predatory fish (mummichog, *Fundulus heteroclitus*) was present, but not when a non-predatory fish (white mullet, *Mugil ceramus*) or no fish were present. They suggest that some decapod and finfish species may be facultative reef residents, moving onto reefs in response to tidal stage and predator abundance.

Breitburg (1999) defined three groups of finfish associated with a subtidal oyster reef in Chesapeake Bay, (1) reef residents, which use the reef as their primary habitat; (2) facultative residents that are generally associated with structured habitats; and (3) transient species that may forage on or near the reef, but are wide-ranging. Large number of larvae of resident fish species (particularly those of the naked goby, *Gobiosoma bosc*) can be found in the down current side of oysters reefs in Chesapeake Bay, where presumably they are capable of maintaining their position until

metamorphosing and assuming a demersal lifestyle (Breitburg, 1999; Breitburg et al., 1995). Larval and juvenile naked gobies and other resident fishes have been shown to be very significant predators on zooplankton (Breitburg, 1999), including bivalve larvae (see also Harding, 1999). These resident fishes in turn are prey for larger transient fishes, including striped bass (*Morone saxatilis*), which had been observed in high density associated with oyster reefs by Breitburg (1999). From diver surveys over small structures (33 × 33 × 33 cm concrete cubes), Breitburg (1999) reported observing juvenile striped bass at a density of 15.4 individuals per m² of 'reef' surface; these fish were aggregating a few centimeters over the reef surface and actively feeding on naked goby larvae which were congregated on the down current side of the 'reefs'.

Many resident oyster reef fish species utilize specific microhabitats within the reef as nesting sites. Oyster toadfish attach eggs to the underside of oyster shells and gobies, and blennies and skillet fish lay eggs on the inside of recently dead oyster shells that are still articulated (Breitburg, 1999). Based on development of fishes of the Mid-Atlantic Bight (Breitburg, pers. com. taken from Hardy, 1978a,b; Johnson, 1978; Jones et al., 1978; Martin and Drewry, 1978) fishes potentially utilizing oyster habitat as sites for reproduction include, *G. bosc*, *G. ginsburgi*, *Microgobius thalassinus*, *Myoxocephalus octodecemspinosus*, *Chasmodes bosquianus*, *Hypsoblennius hentz*, *Gobiosox strumosus*, *Opsanus tau*, *Opsanus beta*, *Porichthys plectrodon*, and *Syngnathus fuscus*. Breitburg (1999), Coen et al. (1999b) suggest that in a well-developed oyster reef a steady supply of new nesting sites (i.e. large, clean, still-articulated oyster shells) should result from natural and low levels of oyster mortality in all size classes.

The importance of habitat scale in the maintenance of biodiversity has received much attention in terrestrial conservation biology, e.g. the issue of whether single large or several small (or SLOSS, see Boecklen, 1997) habitat patches support greater biodiversity. Likewise, this issue has been addressed in marine artificial reef programs (Attraction–Production Debate, reviewed in Lindberg, 1997, and accompanying papers in same

Fisheries issue). Little attention, however, has been paid to this topic for oyster reef communities (see also Coen et al., 1999b). Defining the specific habitat requirements for resident and transient species associated with oyster reefs and the scale dependence of these requirements remains an obvious gap to be filled in future research efforts.

4.2. Water column filtration

There is good evidence that dense populations of suspension-feeding shellfish can have a significant impact on basin-wide water quality and phytoplankton dynamics (Cloern, 1982; Cohen et al., 1984; Fréchette et al., 1989; Dame, 1996). Specifically, for intertidal oysters in South Carolina, Dame et al. (1984, 1992) demonstrated with models and field flumes (e.g. their 'BEST' tunnel) that changes in phytoplankton concentrations and energy flow rates change as water passes over an oyster bed (reviewed in Dame, 1996). Based on historical densities of *C. virginica*, Newell (1988) calculated that, prior to 1870, the Bay's oyster populations could filter the entire volume of the Chesapeake Bay in 3.3 days; but after nearly a century of harvesting, it would take the reduced oyster populations 325 days to perform the same activity. Using a model of carbon flux in the mesohaline reaches of the Chesapeake Bay developed by Baird and Ulanowicz (1989), Ulanowicz and Tuttle (1992) estimated that a decrease in the annual exploitation rate of the oyster by 23% would lead to a 150% increase in oyster standing stocks, a 29% increase in benthic diatom primary productivity, and a 12% decrease in planktonic primary productivity. They suggested that the combined effect of decreased planktonic primary productivity and increased benthic primary productivity might potentially reduce eutrophication in the Chesapeake Bay. Estimates built on laboratory filtration rates, particularly those from static systems (in Dame, 1996, see Table 19), provide only first-order estimates of ecosystem-level impacts of materials processing by oyster reefs (Dame, 1996). We still need to incorporate an understanding of how hydrodynamics, oyster reef size, shape, and species composition affect the dynamics of benthic–pelagic coupling, and how

this varies with the development of assemblages on the reef. Such an understanding will be essential to planning and evaluating specific restoration projects (see for example Lenihan, 1996).

As examples of reef restoration projects addressing some of these issues, we discuss below two ongoing long-term projects, directed by the authors, which differ in their settings (i.e. habitat characteristics, tidal regimes, hydrographics, scale) and approaches (i.e. reef construction materials and sampling methods) and are focusing on developing success criteria.

5. Charleston, South Carolina, experimental reefs

5.1. Background and project overview

In the southeastern USA (portions of South Carolina, North Carolina, Georgia, and Florida), oyster reefs are a conspicuous feature of the intertidal zone in most estuaries (Dame, 1979; Bahr and Lanier, 1981; Burrell, 1986). Dame and coworkers (Dame, 1996; Dame et al., 1984, 1992) have demonstrated that intertidal oyster reefs contribute both physically and biologically (e.g. nutrient recycling, particle flux and hydrodynamic flow) to ecosystem functioning. In South Carolina, most oyster reef habitat is intertidal (Burrell, 1986; Coen et al. 1999a; SCDNR-OFM data), often adjacent to emergent vegetation, in areas with tidal ranges of > 1–2 m, which contrasts sharply with oyster reefs in Chesapeake Bay and Gulf of Mexico, where tidal amplitudes are much smaller. By forming extensive biogenic intertidal reefs, oysters provide only three-dimensional structural relief in an otherwise unstructured soft-sediment bottom. Thus, intertidal oyster reefs may have a similar ecological function as SAV or emergent vegetation in other areas, by providing critical habitat for numerous other species (Coen et al. 1999b). At present, we have little understanding of the temporal sequence of reef community development, and we lack a thorough understanding of its contribution to the broader ecological functioning of tidal creek systems. A long-term experimental program was initiated near Charleston, South Carolina, in 1994, using a

replicated experimental design with reefs constructed of identical units to address habitat development, function and restoration questions (Wenner et al., 1996; Coen et al., 1999a).

5.2. Approach

Two study sites were chosen, one in a ‘developed’ area, the other in a more pristine ‘reference’ area, to evaluate experimentally how oyster reefs develop and function within respective ecosystems and how observed habitat quality parameters may affect reef function. The ‘developed’ site was at Toler’s Cove Marina, a moderate-sized marina (approximately 138 boat slips) located within a small tidal creek (depths to 3 m). The marina is bordered by an extensive salt marsh habitat (primarily *Spartina alterniflora*). Oysters are numerous, but harvesting is currently prohibited. Some prior contaminant and oyster growth data were available from this site, supporting its selection as our developed site (Van Dolah et al., 1992; Wendt and Levisen, unpublished data). The second site, Inlet Creek, is a tidal creek, that is relatively pristine (i.e. reference site) and our specific research site is within its upper reaches. It has extensive oyster habitat, a large marsh buffer (primarily *S. alterniflora*), and relatively little adjacent development. The two sites are approximately 3.2 km apart (Wenner et al., 1996). Both sites are located off the Atlantic Intracoastal Waterway (AIW) and are dominated by fine sediments that are often > 75% silt/clay with little or no sand (Coen et al., 1997 and unpublished data). Reef construction (see Coen et al., 1999a) was initiated, so that constructed reefs were sufficiently large to include an experimental reef and an equivalent natural reef area populated with oysters. These two reefs were spatially separated, so that sampling of one would not significantly disturb the other. Sites were prepared for experimental reef fabrication by removing all oysters/shell from within an area equivalent to reef size ($\sim 8.2 \times 2.9$ m). Paired 24 m² natural areas were staked and marked with signs to minimize future disturbance. Three replicate experimental reefs (24 m²) were constructed at each site in October 1994. This size reef and its 156 constituent subunits (i.e.

trays or quadrats) allowed for adequate sampling, without resampling, over the long-term period of this study (> 5 years). Overall, our reef design used over 8.66 tons of material (shell and trays) and 936 perforated plastic trays filled with oyster shell. Trays provided initial support to the reef and were used in numbers sufficient to avoid repeated sampling and disturbance of areas sampled previously. Utilizing standardized quadrates to construct each reef allows replicate sampling of resident fauna over time from a balanced experimental reef design. Thus, sampling over extended periods (years) does not disturb an excessive portion of established total reef area (additional details may be found in Wenner et al., 1996; Coen et al., 1999a). Oyster recruitment began sometime in late spring 1995 with seasonal spatfall (Coen et al., unpublished data).

Briefly, we are gathering extensive physical/biological data at both sites including, (1) logging D.O., intertidal/subtidal temperatures, salinity, pH, water depth with Hydrolab™ Datasonde 3s and Onset temperature dataloggers; (2) quantifying chlorophyll *a* concentrations as an indirect measure of relative food quantity for filter-feeders; (3) quantifying sedimentation rates on reefs using sediment traps; (4) sediment toxicity bioassays (Microtox® solid-phase and pore-water tests on natural sediments) and quantifying selected metals and polycyclic or nuclear aromatic hydrocarbons (PAHs) using standard EPA methods; (5) monitoring (spatfall, diseases, oyster population development) and experiments (growth, mortality, disease epidemiology) examining native and subtidally and intertidally deployed hatchery-reared specific-pathogen-free (SPF) oysters (Hadley et al., 1996; Giotta and Coen, 1999; Giotta, 1999); and (6) sampling macrofaunal communities associated with both constructed and natural reefs.

In the past, most efforts to evaluate intertidal reef communities have focused on the faunal component remaining in the reef shell matrix during low tide exposure (e.g. Wells, 1961; Dame, 1979; Klemanowicz, 1985; Burrell et al., 1991). Exclusive examination of this portion of the reef fauna (henceforth referred to as ‘residents’), however, does not quantify organisms utilizing the reef

while submerged. Rather than ignoring this larger mobile assemblage (i.e. fishes and decapod crustaceans) that makes transitory use of reefs and often feeds on residents during high tide (henceforth termed ‘transients’), we employed two different sampling methods, which allowed us to adequately quantify these two different faunal components (Wenner et al., 1996; Coen et al., 1999a,b). Our sampling design and associated methodologies allow us to evaluate quantitatively habitat utilization by important fisheries species during reef development. This will aid us in assigning functional importance to these critical ‘fish’ habitats (or EFHs) (see also Coen et al., 1999b).

Since 1995, we have sampled reef residents from randomly selected quadrats collected from each of the experimental reefs. Tray samples are sorted on a 0.5-mm mesh sieve and enumerated. After rinsing, trays with original shell are replaced in their original position within the reef to maintain overall reef size, oyster populations, and integrity for transients. Concurrent samples are also collected from adjacent natural reefs allowing us to compute sample variance estimates among and within sites and sampling intervals, using appropriate statistics (see Coen et al., 1999a, for details). We can then test for significance in abundance and diversity of faunal associates on developed versus reference (undeveloped) reefs. The design also facilitates an evaluation of the convergence (or divergence) of the natural and experimental reefs over time.

To quantitatively sample transient fishes and decapod crustaceans, we developed a sampling regime using a modification of a flume-weir (see Wenner et al., 1996; Coen et al., 1999a) described by Kneib (1991). The flume-lift net system uses a mesh block net 2.44 m high (supported by posts), attached at the base to a fixed buried cable completely enclosing either an experimental or adjacent natural oyster reef. Nets are placed around each reef area at low tide and can be raised in less than 5 s from a remote boat (30–35 m away) at slack high tide. At low tide, nets are carefully censused and all organisms removed (Wenner et al., 1996; Coen et al., 1999a).

5.3. Results/discussion

To date we have been sampling the two sites, monitoring recruitment, growth, and survival of both subtidal and intertidal oysters (Giotta, 1999; Giotta and Coen, 1999), sampling transient and resident faunas associated with natural and developing oyster reef habitat, generating a long-term environmental data set in conjunction with oyster disease (Bobo et al., 1997 and unpublished data for MSX and Dermo), epidemiology and conducting experiments evaluating factors structuring subtidal and intertidal oyster communities. It is our expectation that intertidal and subtidal oyster habitats, especially where tidal ranges exceed 1 m, will vary in some quite significant ways (e.g. oyster population and disease dynamics, habitat quality for other species, predation, etc.). Using an experimental approach to understanding the link between habitat and fishery value of intertidal reef habitat, we have developed new methods to sample this intertidal oyster habitat (Wenner et al., 1996; Coen et al., 1999a,b) and developed the ability to produce SPF oysters for this related research (Hadley et al., 1996).

One of the most revealing measures of successful habitat development has been the abundance of recruited oysters quantified in each of our constructed reefs. Oyster populations from these reefs are compared with adjacent natural reef areas in January 1997 and 1998 surveys in Fig. 1. Nearly 3 years of post-construction, cumulative oyster abundance and size frequencies are still very different (Fig. 1). For example, based on our most recent January 1998 surveys, oyster densities (per unit area) on experimental reefs at our developed site still have only 17% of the oysters found on adjacent natural reefs (averaged across replicate reefs); the experimental reef populations at the reference site have reached only 23% of the adjacent natural areas. Similarly, maximum observed oyster shell heights (SH) (Toler’s and Inlet combined) range from 70 to 98 mm SH on experimental reefs to 103–136 mm on natural reefs. In contrast, mean overall oyster sizes across sites and reef types are for the most part quite similar, ranging from 30 to 47 mm shell height.

In early preliminary (March 1995–January 1996) resident faunal analysis, we have collected over 74 species (see Fig. 2, Coen et al., 1997, unpublished data) and a total of 45 000 macrofauna (over 800 animals per 0.14 m² area). Despite the low oyster populations on experimental reefs, species richness at the two sites was not different when natural and experimental areas were compared (Fig. 2). Preliminarily, several mussel species

(*Geukensia demissa* and *Brachidontes exustus*) were an important community component (> 90% biomass, Coen et al., 1997, unpublished data). Though these bivalve filter-feeders are quite common and have received much attention in salt marsh habitats, they have been rarely mentioned in relation to oyster habitats (e.g. Stiven and Kuenzler, 1979; Jordan and Valiela, 1982; Bertness and Grosholz, 1985; Franz 1996, 1997).

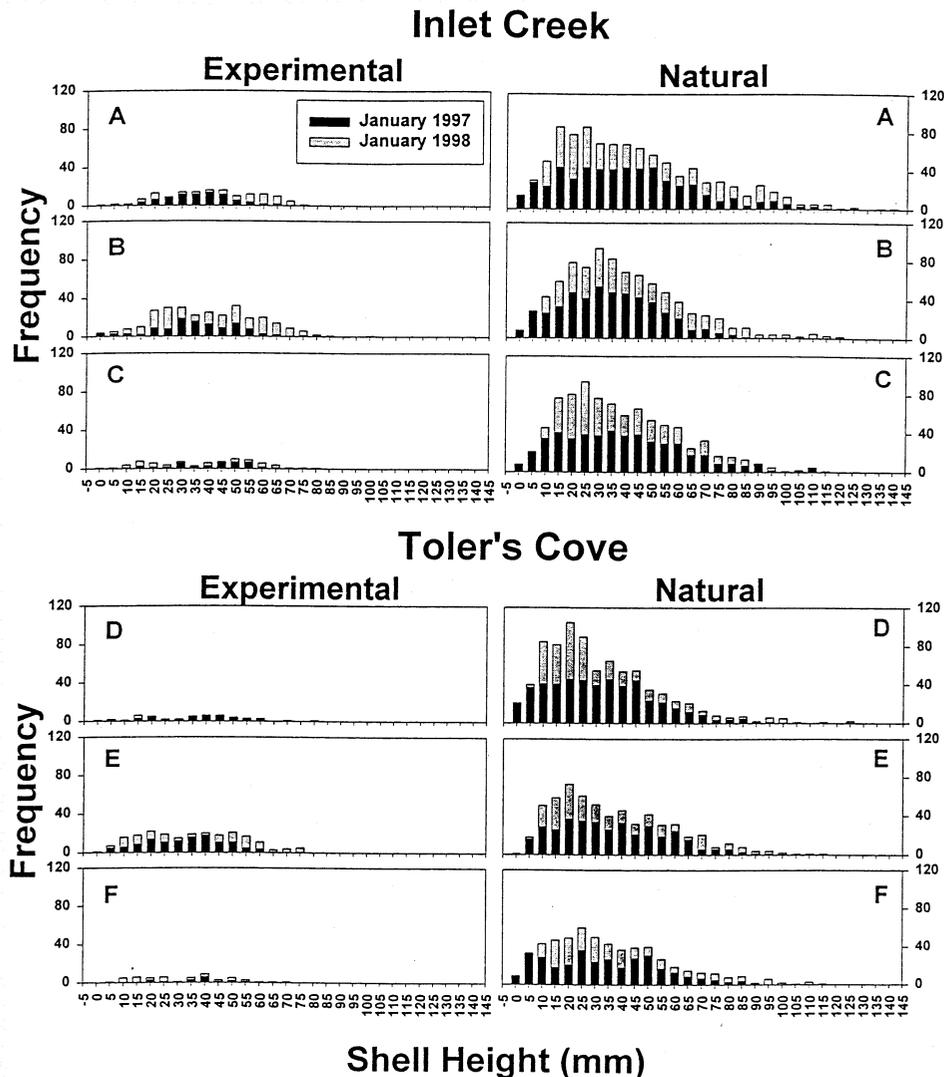


Fig. 1. Size frequency distribution of oyster populations censused in January 1997 and 1998 on natural and experimental oyster reefs at our two study sites. Summed area sampled at each of the six reefs (A–F), 0.42 m².

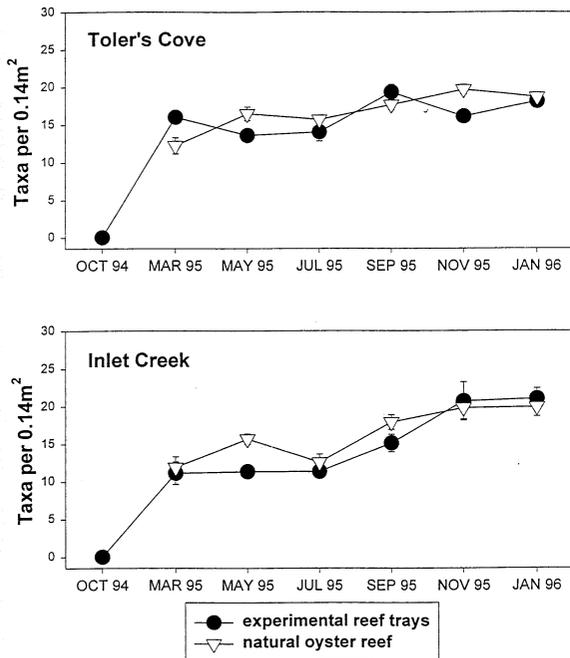


Fig. 2. Mean number of resident taxa (± 1 S.E.) per quadrat ($n = 3$ per reef, three reefs per site) sampled since March 1995 associated with both experimental and natural oyster reef habitats at the reference and developed study sites (Note, two mussel species were excluded from March 1995 plots).

In terms of the transient (mobile) faunal component collected in association with reef habitats, we have collected 42 species (see Wenner et al., 1996; Coen et al., 1997) for a total of 68 000 individuals. *Palaemonetes* spp. (grass shrimp) were the most abundant macrofaunal component, with numbers often exceeding 5600 individuals (or over 230 individuals per m^2) per reef (Wenner et al., 1996; Coen et al., 1999b). Large numbers of adult and juvenile recreationally and commercially important fish, shrimp, and crab species were also collected (see Wenner et al., 1996; Coen et al., 1999b). For example, over 200 brown shrimp, *Penaeus aztecus*, were captured on reefs during some seasons. Finally, large numbers of transient animals (often exceeding numbers collected at our Inlet Creek reference site, Coen et al., 1997, 1999b) and similar taxonomic numbers (Fig. 3) were collected at our developed site closed to shellfish harvesting. This supports our con-

tention that areas closed to shellfish harvesting still have significant value and that oyster habitats in the southeast should be included as EFHs (see Coen et al., 1999b).

6. Fisherman's Island, Virginia, experimental reefs

6.1. Project overview

Both oyster fishery enhancement and ecological restoration generally include the placement of various substrata on the bottom to enhance oyster recruitment. The most commonly used substrata are fresh and fossil oyster shells, but shortages of these shells in some regions have led to the use of other materials, including surf clam, *Spisula solidissima*, shells in Virginia (Wesson et al., 1999), limestone marl in Louisiana (Haywood et al., 1999), and stabilized coal combustion by-products (coal ash pellets) in Virginia (Andrews et al., 1997) and Texas (A. Landry, unpublished data).

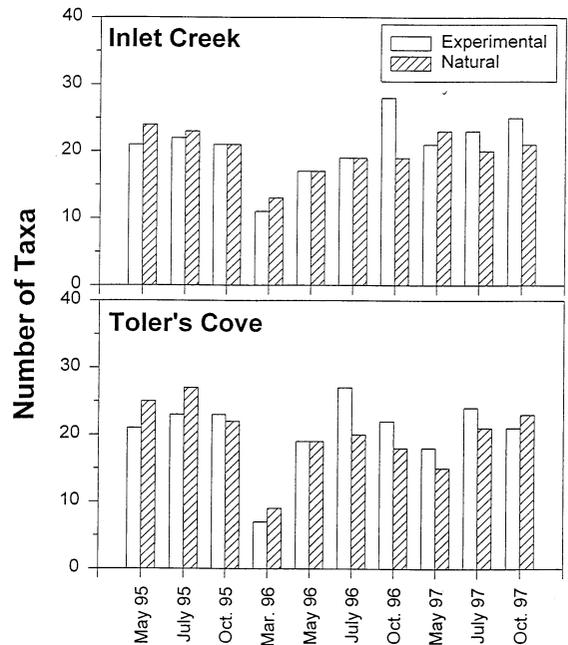


Fig. 3. Total number of species collected in seasonal transient sampling ($n = 3$ per site) over experimental and natural oyster reef habitats (each $24 m^2$) since May 1995 at the reference and developed study sites.

Table 1

Substrate types and plan view areas for reefs used to characterize the development of resident assemblages at Fisherman's Island, Virginia (see Luckenbach et al., 1997 for more details)

Substrate type	Plan view area (m ²)
<i>Oyster shell</i>	
Reef 1	202.4
Reef 2	161.9
<i>Clam shell</i>	
Reef 1	202.4
Reef 2	323.8
<i>Coal ash</i>	
Reef 1	283.3
Reef 2	323.8

Increasingly, ecological restoration has been used as part of the justification for this activity. Unfortunately, natural, non-degraded oyster reef habitats no longer exist in this region; thus, reference sites for establishing natural ecosystem structure and function are not available. Moreover, large-scale replicate experiments characterizing community development on artificial, 'restored' reefs have not been conducted previously. Towards that end, one of us (MWL) is conducting a long-term research project at Fisherman's Island, Virginia, in the vicinity of the Chesapeake Bay mouth, to investigate the temporal patterns of species colonization, abundance, and growth in reef habitats constructed of various materials. Assemblages on restored reefs are being compared with adjacent unmanipulated habitats. Results from the first year of the study are reported in Luckenbach et al. (1997), O'Beirn et al. (2000) and are briefly summarized below.

6.2. Approach

The study site is in a polyhaline salt marsh habitat with a tidal amplitude of 1.25 m. In the summer of 1996, 11 reef bases (henceforth referred to as reefs) were constructed from either oyster shells, surf clam shells, or coal pellets. Substrates were deployed from barges using a backhoe onto barren sediment in a region where a shallow subtidal mudflat (water depth ~ 0.5 m below mean low water [MLW]) sloped towards a

channel (water depth ~ 2 m below MLW); average depth for the bases of the reefs was ~ 1.0 m below MLW and average height of the reefs ~ 1.5 m above MLW. Varying availability of the substrates resulted in an unbalanced design with five reefs constructed with surf clam shells, two with oyster shells, and four with coal ash pellets. The physical characteristics of the latter material are given in Andrews et al. (1997) and shown to provide an environmentally suitable substrate for oyster settlement and growth (Alden et al., 1996). Limited availability of oyster shells resulted in the smaller number of reefs constructed with that material. These reefs made from each of the above materials range in size from 81 to 930 m² and extend from the shallow subtidal into the intertidal zone. We selected two reefs of each type with similar areas and tidal exposures for characterization of resident fauna (Table 1). Temporal patterns of species composition and abundance associated with these reefs and adjacent unmanipulated mudflat and channel habitats were characterized for the following species groups, (1) attached macroalgae; (2) epifaunal macrobenthos; (3) infaunal macrobenthos; (4) resident fishes; (5) transient fishes and macroinvertebrates; and (6) shorebirds. Detailed methods and findings for the first five groups are described in O'Beirn et al. (2000) and Nestlerode et al. (unpublished). Briefly, epibenthic macroalgae and macroinvertebrates were identified from three replicate 0.062 m² quadrats haphazardly located with three tidal height strata — high (10–25 cm above MLW), middle (\sim MLW), and low (10–25 cm below MLW) — on each of two replicates of each reef type (oyster shell, clam shell, and coal ash). All shell and/or coal ash with attached materials were removed to a depth of 15 cm and all organisms were identified to the lowest practical taxonomic level and appropriate abundance measures for each taxon recorded (e.g. counts for solitary organisms, percent cover for encrusting colonial forms, and biomass for macroalgae).

Resident reef fishes and small decapods were collected with plastic-coated wire mesh baskets (40 \times 40 \times 8 cm) containing comparable substrate to the reef. These baskets were embedded subtidally on the reef flush with the surface. During the

fall of 1996, six baskets were placed, onto each of two replicates of each reef type for retrieval without replacement on approximately monthly schedules. The additional two baskets were added to one replicate of each reef type; these were retrieved at each sampling period and replaced by a new basket of clean substrate. Upon retrieval, all samples were placed on ice and transported to the lab, where all macrofauna were removed, identified, and enumerated.

Three different gear types were used to quantify transient finfish assemblages in the vicinity of the reefs, (1) a 10 m seine (mesh size = 3/8 in.); (2) a 3 m otter trawl; and (3) gill nets (30 and 100 m lengths) with panels ranging from 1 to 4 in. mesh size. Given the small sizes of the reefs, we are unable to evaluate the use of individual reefs by large fishes. Rather, we have been able to compare fishes captured in the vicinity of the reefs with those 100 m or greater from the reefs by using the otter trawl and gill nets.

6.3. Results/discussion

The various substrates produce notably different reef bases for oyster attachment. *S. solidissima* shells fracture readily during the handling involved in transport and deployment, resulting in small, thin pieces of shell that compact when placed on the seafloor, leaving little critical interstitial space. Similarly, during fabrication of the coal ash pellets and their subsequent transport and deployment, fine material (< 1 cm diameter) was produced that filled much of the interstices between the larger pellets. In contrast, oyster shells generally remained intact throughout this process and provided a reef base with more inter-

stitial space available for the initial colonization and survival of oysters.

Details of oyster settlement, survival, and growth by tidal height on each reef type are reported in Luckenbach et al. (1997), O'Beirn et al. (2000). The pattern supports the finding by Bartol and Mann (1999) that interstitial space is important, significantly with greater numbers of oysters recruiting to and surviving on the oyster shell reefs, compared with the other reef construction materials (Table 2). Species composition and abundance patterns of macroinvertebrates, attached macroalgae, and resident crustaceans and finfish also varied across reef type (Luckenbach et al., 1997; Nestlerode et al., unpublished data). For the purposes of this review and our objective of establishing success criteria, it is instructive to examine different metrics of this community development. The choice of the metrics affects our picture of community development over time and across reef types (Fig. 4). For the epifaunal assemblages, mean number of species per unit area was always greater on the oyster shell reef than on either the clam shell or ash reefs (Fig. 4A), as was the cumulative number of species over time (Fig. 4B). However, the total number of species collected per reef (Fig. 4C) and the Shannon–Weiner diversity index (Fig. 4D) both show greater variability over time, with the ash reefs having the greatest values to date in the fall 1997. Though the reefs differed slightly in area (Table 1), the observed differences in species richness (Fig. 4) did not reflect a species-area relationship. As with the South Carolina study, Fisherman's Island study is ongoing and will continue to characterize the development of resident and transient assemblages associated with each reef type. Concurrently, gut analysis of reef fishes is clarifying trophic links to provide a better understanding of ecological functions within these habitats.

Table 2
Mean oyster densities per m² (\pm 1 S.D.) at Fisherman's Island, Virginia, reefs, censused on November 11, 1997

	Tidal height		
	High	Mid	Low
Clam	245 (163)	325 (198)	304 (172)
Oyster	1701 (432)	1704 (247)	384 (199)
Ash	528 (185)	197 (170)	123 (115)

7. Developing success criteria

Restoration of oyster reef habitat invariably involves the addition of substrate and occasionally wild or hatchery-reared seed oysters to the shallow seafloor (e.g. MacKenzie, 1983, 1996b;

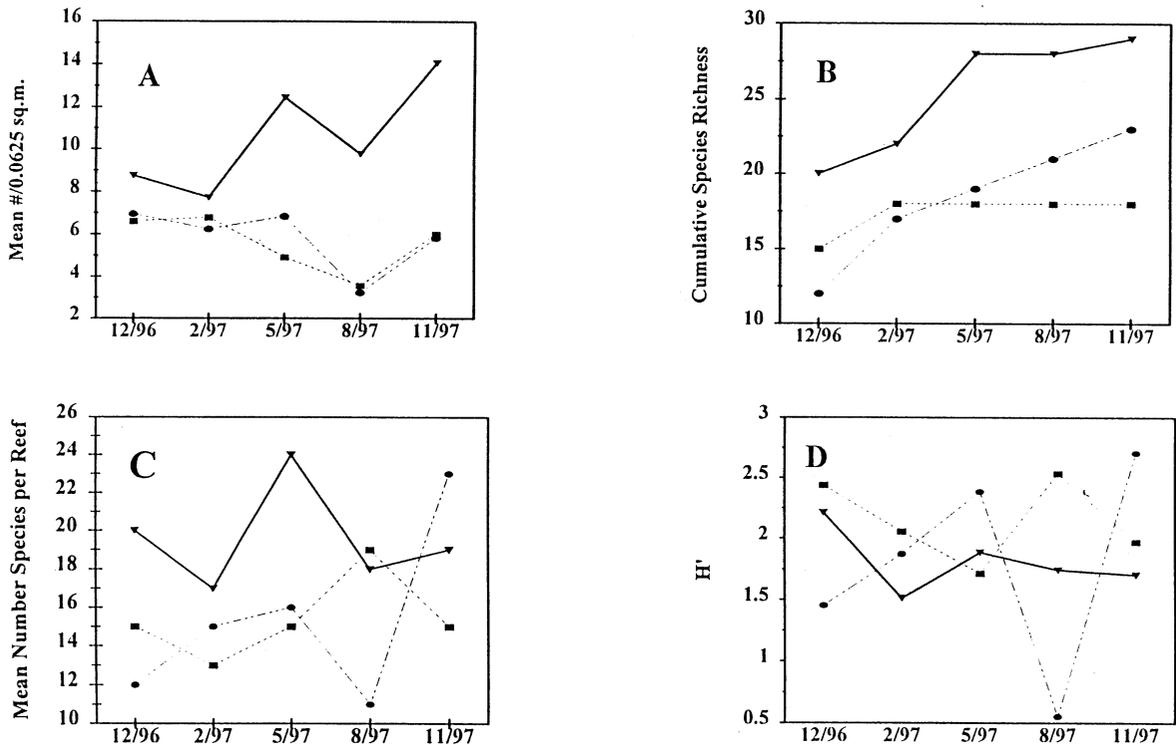


Fig. 4. Diversity of epifaunal species on each reef type (▼ oyster, ■ clam, ● coal ash) over time, computed as, (A) mean number of species per quadrat; (B) cumulative number of species throughout the study; (C) total number of species per reef type at each sampling time; (D) Shannon–Weiner diversity index over time.

Burrell et al., 1991). When the primary motivation is to increase the harvest of oysters, evaluating success is straightforward — economic returns for increased landings together with the social benefits of supporting fishermen should exceed the cost of planting substrate and/or oysters. The available data are equivocal (reviewed in Luckenbach et al., 1999). For example, in Virginia, which supports a significant shell-planting program, current returns (total harvest value, not just increased production) equal to between 0.25 and 1 × of the cost of the restoration program (J. Wesson, VA, Marine Resources Commission, pers. commun.); for North Carolina, the dollars expended restoring oyster reefs are roughly 3 × of the return (Frankenberg, 1995); clearly this practice is not uniformly cost-effective. A more limited program in Louisiana, using hatchery production of oyster juveniles to supplement wild recruitment in poor years, has been shown to be cost-effective (Supan et al., 1999).

We expect that ecologically motivated restoration of oyster reef habitat will be a growing practice in the United States for at least four reasons (in no order of importance):

1. resource-based economics alone do not always justify the practice;
2. increasing aquaculture production of native oysters will continue to ease some of the fishing pressure on wild oyster stocks (and may offer the only alternative where native oyster populations have been reduced to very low levels; e.g. see Frankenberg, 1995);
3. there is a growing recognition of the ecological importance (i.e. ecological services) of oyster reefs in estuarine and near-shore environments; and
4. some public agencies have begun to require mitigation for disturbance to shallow water habitats, and oyster reefs are a viable option for enhancement/restoration.

The challenge is to identify the realistic ecological milestones for oyster reef restoration and to develop approaches to achieve those goals. In the broadest sense, the goals of such restoration are obvious — maintenance of biodiversity, increased finfish and shellfish production, and improved ecosystem services (reviewed in Dame, 1996; Peterson and Lubchenco, 1997; Lenihan and Peterson, 1998; Luckenbach et al., 1999). Setting specific targets and quantifying success is, however, more problematic. Although clearly valuable as habitat, there is no definitive species list, due in part to the broad geographic range of *C. virginica*, with which to characterize a successfully restored, fully functioning oyster reef. Should there be specific targets for species richness or diversity? Are there specific functional groups or guilds critical to a fully restored reef? What type of food web structure is necessary for supporting increased production of desired species? As Palmer et al. (1998) point out, the answers to these questions are generally poorly understood for aquatic ecosystems. Answering these and other specific questions requires additional experimentation and numerous long-term reef studies throughout the oyster's extensive range.

Despite the documented filtration capabilities of oysters and their presumed system-level consequences (Ulanowicz and Tuttle, 1992; Dame, 1996), details of materials processing by oyster reefs and specific restoration targets have been poorly documented. For only one habitat, intertidal oyster reefs in South Carolina, are materials flux rates known over natural reefs (reviewed in Dame, 1996; also see Dame et al., 1984; Dame and Libes, 1993). What should be the specific targets for materials fluxes between the water column and oyster reefs (e.g. gram carbon or nitrogen per m² per day)? How does the community composition affect the size range of particles filtered, or for that matter overall benthic–pelagic coupling? For example, how do the added filtering/habitat effects of large numbers of mussels on South Carolina reefs compare with those of oysters? What is the temporal pattern of materials processing in a developing reef? Resolving these issues will require large-scale manipulative field studies and mesocosm experiments.

Likewise, the value of oyster reefs as habitat for numerous species is being elucidated, but many questions remain regarding success criteria. What are the specific habitat features of importance to target species? Can we specify target goals for biodiversity and/or productivity associated with a fully restored reef? If so, how do these change with latitude and with successional stage? Are there specific design criteria (beyond those important to oysters) which are important to the restoration of ecological functions of oyster reefs? It is apparent that answering many of these questions will require manipulative field experiments and large-scale monitoring programs carried out in conjunction with restoration projects.

In advance of a resolution of these specific issues, one aspect of oyster reef restoration is evident. Viable oyster populations must be sustained on the reef for successful restoration to occur. While many other species are integral to the community, the presence of a healthy oyster population is essential to the development and maintenance of the habitat. It is doubtful that any other species within the oyster reef assemblage, including epifaunal mussels (primarily *Mytilus edulis* and *G. demissa*), is capable of providing sufficient structural relief to overcome sediment deposition rates and near–bottom hypoxia characteristic of many estuarine habitats and to serve the crucial role as habitat for other organisms (see Lenihan and Peterson, 1998).

Several factors necessary for the restoration of local oyster populations are evident. First, site selection is crucial. Perhaps the most critical aspect of site selection is the availability of oyster recruits to an area. In some habitats, in which circulation patterns facilitate larval retention and recruitment onto their reefs of origin, stocking programs (using relocated wild stocks or hatchery-produced stocks) may prove effective in establishing self-sustaining oyster populations; however, the utility of this method for the majority of sites would appear to be doubtful. Because recruitment variability can be quite high (e.g. Kenny et al., 1990; Ortega and Sutherland, 1992; O'Beirn, 1996), reef restoration should be preceded by one or more years of oyster recruitment monitoring where possible.

Another consideration in the placement of material for reef restoration is disease risk. Although *P. marinus* has been observed to persist in oysters in salinities below 5 ppt (Ewart and Ford, 1993), it generally exhibits poor tolerance to salinity below 8–9 ppt and epizootics are observed at salinities of 12 ppt and greater (Ford and Tripp, 1996; but see Bobo et al., 1997). *H. nelsoni* does not tolerate salinities below 10 ppt and generally requires 15 ppt or greater to cause significant mortality (see Bobo et al., 1997 for discussion for South Carolina). The persistence of some oyster reefs in low salinity areas of estuaries otherwise hard hit by disease (e.g. upper Delaware Bay and the James River subestuary in the Chesapeake Bay) suggests that restoring reefs to oligohaline regions of estuaries may be possible (see Powell et al., 1997). However, such areas are also subject to freshets that can devastate oyster populations. Alternatively, restoration of reefs in moderate to high salinity areas would seem to provide the only mechanism for developing and sustaining disease tolerant wild strains of oysters. Bushek and Allen (1996) have reported that *C. virginica* and *P. marinus* exhibit spatial variation in disease tolerance and virulence, respectively, and that disease dynamics vary over their range with differing degrees of pathogenicity observed between populations. For instance, *P. marinus* is prevalent in South Carolina oyster populations, but it does not appear to cause widespread mortality (Bobo et al., 1997). Evidence from areas where oyster harvesting is minimal or restricted suggests that in the absence of harvesting, disease tolerant oysters persist though the heritability of such tolerance has not been quantified. It is evident that the materials employed and the configuration (i.e. size, shape, relief, interstitial spacing, etc.) of constructed reefs affects the development of oyster populations on reefs. We have indicated previously that interstitial space affects oyster recruitment, growth and survival, yet we do not have a full understanding of how the quantity or size of the interstitial matrix of a reef affect oysters survival and growth. Other factors which will affect the successful establishment of oysters on restored reefs include water quality issues such as those addressed by Lenihan and colleagues in North

Carolina (Lenihan, 1996; Lenihan and Peterson, 1998; Lenihan et al., 1999) and Coen and colleagues in South Carolina (described above).

Ultimately, the success of an oyster reef restoration effort will be judged by the ability of the habitat to support a self-sustaining oyster population. Although some factors necessary to achieve this remain to be clarified, others are apparent. Specifically, it is necessary (1) that sufficient quantities of substrate providing three-dimensional relief above the seabed and interstitial space available to oysters be placed (2) in sites with sufficient recruitment rates and (3) adequate water quality to support growth and development of oysters. Additionally, management of the sites must include (4) restrictions on harvesting practices that are destructive to the habitat and (5) over exploit the resource. This latter point may be especially critical in disease endemic areas where (6) protection of older oysters may be necessary to promote the development of disease tolerant strains.

Integral to evaluating the success of any reef habitat restoration project will be support of an integrated long-term monitoring program to establish the viability of the resident oyster population and the development of the reef community. Too often, this aspect has been largely ignored or underfunded (both in duration and extent) by funding agencies. For instance, in depositional environments, vertical growth of the reef must minimally exceed sedimentation rates for reefs to persist. Because, recruitment and survival patterns for oysters vary spatially and temporally, monitoring is required to pursue effective adaptive management strategies (sensu Walters, 1986; Christensen et al., 1996; Peterson and Lubchenco, 1997; Lenihan and Peterson, 1998), such as the placement of additional substrate or direct planting of oysters, to meet this goal. As specific success criteria are developed for oyster production, species diversity, trophic complexity, and materials fluxes, well-designed monitoring programs will be fundamental to evaluating success.

Perhaps most critical to establishing meaningful success criteria will be achieving a proper balance of socio-political constraints and ecological objectives. Fisheries interests have considerable politi-

cal support in some regions (e.g. Chesapeake Bay) and are, in most cases, the principal basis for funding oyster reef restoration efforts. Balancing short-term exploitation with the need to establish sustainable, ecologically functional reefs poses a formidable challenge. Generally, we expect that establishing reef sanctuaries that may, among other benefits, serve as sources of oyster larvae for surrounding exploited areas will be a tractable approach. Ultimately, we will have to weigh the habitat's ecosystem services with the resource's economic value (Costanza et al., 1997; Daily, 1997; Kaufman and Dayton, 1997).

8. Future needs

Successful restoration of oyster reef habitat, including the establishment and verification of success criteria, will require further research in several areas. The following account of some of these research needs is far from complete, but represents what we believe to be some of the most urgent needs.

Further clarification of host–pathogen–environment relations for the two major pathogens *P. marinus* and *H. nelsoni* is needed to guide the placement of reefs and use of oyster stocks. This research avenue is currently beginning in South Carolina (Bushek et al., 1999) where host–parasite interactions are currently being explored in replicated field experiments in creeks with and without oysters. This study will be particularly critical to evaluating the efficacy of using transplanted wild stock and/or hatchery-produced improved stocks in reef restoration.

Knowledge of how larval supply and post-settlement survival interact to determine oyster recruitment success on a site-specific basis will be likely required to understand regional population sources and sinks (Whitlatch and Osman, 1999). However, the development and testing of generic metapopulation models with oysters should serve to establish some guidelines for restoration, particularly for the approach of establishing sanctuaries surrounded by areas open to harvesting.

Results from our work in South Carolina and

Virginia make it clear that considerable work remains to be done to establish appropriate metrics for gauging success of restoration projects. This will require further research on natural reefs to clarify ecological functions, critical species and functional groups, and trophic structure interactions. It will also require continued characterization of the development of 'restored' reefs to establish successional trajectories and appropriate time scales. A focal point of this effort needs to be the identification of critical habitat components for other target species (e.g. nesting sites and refuge and foraging sites for resident finfish). Currently we have very little data for natural systems (Coen et al., 1999b).

We also need to begin to evaluate landscape issues relative to oyster habitat and other EFHs such as seagrasses and salt marsh habitat (Coen et al., 1999b). For example, recent work by Meyer and Townsend (2000), Meyer et al. (1997) in North Carolina has used oyster reef construction, in conjunction with salt marsh restoration. In the southeast, oyster and marsh habitats are often interspersed at creek margins. In their case, they are using the stabilizing effect of the oyster shell and recruited oysters to enhance/buffer marsh restoration efforts.

Within the United States, the National Marine Fisheries Service and Regional Fisheries Councils, through the 1996 Magnuson–Stevens Fishery Conservation and Management Act (Public Law 104-208), designed to improve commercial fisheries, are one recent example of governmental action to evaluate and protect Essential Fish Habitat (EFH) in nearshore coastal regions (see Benaka, 1999; Coen et al., 1999b). It is important, therefore, to define those habitat aspects that are crucial for maintaining/enhancing fisheries production. Detailed analyses of trophic links to transient finfish species are currently underway in several studies (reviewed in Coen et al., 1999b) and should provide critical information on the value of these habitats to commercially exploited finfish (e.g. Lenihan and Grabowski, 1998).

Achieving a working balance between restoring ecological functions and enhancing/restoring

fisheries exploitation of oysters from reefs will require the development and testing of alternative harvest practices which permit extraction of oysters after some developmental period, while maintaining habitat services as discussed above (Lenihan and Micheli, 2000). Currently, we do not know whether extraction and habitat function are compatible (Kaufman and Dayton, 1997; Lenihan and Micheli, 2000). Implicit in this situation is the need for adaptive management approaches that incorporate good monitoring and research-based information into restoration efforts and management decisions (Grumbine, 1994; Christensen et al., 1996; ESA, 1998; Lenihan and Peterson, 1998).

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References

- Alden, R., Luckenbach, M., Dombrowski, A., Harlow, V., Abby, A., Ramirez, L., Weber, I., 1996. An evaluation of the feasibility and environmental acceptability of using pellitized coal fly ash as a substrate for oyster reef development. AMRL Technical Report No. 3013, Old Dominion University, Norfolk, VA.
- Andrews, R.S., Alden III, R.W., Luckenbach, M.W., Wesson, J.A., 1997. The use of coal combustion by-product as substrate for oyster reef development. In: Sakkestad, B.A. (Ed.), Proceedings of the 22nd International Technical Conference on Coal Utilization and Fuel Systems. Coal and Slurry Technology Association of America, Washington, DC, pp. 363–375.
- Bahr, L.M., Lanier, W.P., 1981. The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. US Fish Wildlife Service Program FWS/OBS/-81/15, 105 pp.
- Baird, D., Ulanowicz, R.E., 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecol. Monogr.* 59, 329–364.
- Bartol, I., Mann, R., 1999. Small-scale patterns of recruitment on a constructed intertidal reef: the role of spatial refugia. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 159–170.
- Benaka, L.R. (Ed.), 1999. *Fish Habitat: Essential Fish Habitat and Rehabilitation*. American Fisheries Society, Symposium 22, Bethesda, MD, 459 pp.
- Bertness, M.D., Grosholz, E., 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* 2, 192–204.
- Bobo, M.Y., Richardson, D.L., Coen, L.D., Burrell, V.G., 1997. A report on the protozoan pathogens *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX) in South Carolina shellfish populations, with an overview of these shellfish pathogens. SCDNR-MRD-MRRI Technical Report 86, Charleston, SC, 50 pp.
- Boecklen, W.J., 1997. Nestedness, biogeographic theory, and the design of nature reserves. *Oecologia* 112, 123–142.
- Bonar, D.B., Weiner, R.M., Colwell, R.R., 1986. Microbial-invertebrate interactions and potential for biotechnology. *Microb. Ecol.* 12, 101–110.
- Bonar, D.B., Coon, S.L., Walch, M., Weiner, R.M., Fitt, W., 1990. Control of oyster settlement and metamorphosis by endogenous and exogenous chemical cues. *Bull. Mar. Sci.* 46, 484–498.
- Breitburg, D.C., 1999. Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 239–250.

- Breitburg, D.L., Palmer, M.A., Loher, T., 1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. *Mar. Ecol. Prog. Ser.* 125, 45–60.
- Brooks, W.K., 1891. The oyster, re-issued, 1996 edition with a foreword by Paynter, K.T. Jr., Johns Hopkins University Press, Baltimore, MD, 230 pp.
- Burrell, V.G. Jr., 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) — American oyster. US Fish Wildlife Service Biological Report 82 (11.57), US Army Corps of Engineers TR EL-82-4, 17 pp.
- Burrell, V.G. Jr., Manzi, J.J., O'Rourke, C.B., 1991. Assessment of mechanical transplanting as a means of rehabilitating intertidal oyster beds. *Proceedings of the Gulf and Caribbean Fisheries Institute* 40, pp. 228–240.
- Bushek, D., Allen, S.K. Jr, 1996. Host–parasite interactions among broadly distributed populations of the eastern oyster *Crassostrea virginica* and the protozoan *Perkinsus marinus*. *Mar. Ecol. Prog. Ser.* 139, 127–141.
- Bushek, D., Erskine, A.E., Dame, R., Coen, L., Hadley, N., 1999. Transmission of *Perkinsus marinus* to intertidal oysters. *J. Shellfish Res.* 18, 317–318.
- Carriker, M.R., Gaffney, P.M., 1996. A catalogue of selected species of living oysters (Ostreacea) of the world. In: Kennedy, V.S., Newell, R.I.E., Eble A.F. (Eds.), *The Eastern Oyster, Crassostrea virginica*. Maryland Sea Grant College, University of Maryland, College Park, MD, pp. 1–18.
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., Woodmansee, R.G., 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. *Ecol. Applic.* 6, 665–691.
- Cloern, J.E., 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay? *Mar. Ecol. Prog. Ser.* 9, 191–202.
- Coen, L.D., Knott, D.M., Wenner, E.L., Hadley, N.H., Bobo, M.Y., 1997. Functional role of oyster reefs as 'critical' estuarine habitats. Annual Report to SC Sea Grant Consortium, 1996–1997.
- Coen, L.D., Knott, D.M., Wenner, E.L., Hadley, N.H., Ringwood, A.H., 1999a. Intertidal oyster reef studies in South Carolina: design, sampling and experimental focus for evaluating habitat value and function. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, pp. 133–158.
- Coen, L.D., Luckenbach, M.W., Breitburg, D.L., 1999b. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. In: Benaka, L.R. (Ed.), *Fish Habitat: Essential Fish Habitat and Rehabilitation*. American Fisheries Society, Symposium 22, Bethesda, MD, pp. 438–454.
- Cohen, R.R.H., Dresler, P.V., Phillips, E.J.P., Cory, R.L., 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnol. Oceanogr.* 29, 170–180.
- Cole, H.A., Knight-Jones, E.W., 1939. Some observations and experiments in the setting behavior of larvae of *Ostrea edulis*. *J. Cons. Perm. Int. Explor. Mer.* 14, 86–105.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neil, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387, 253–260.
- Crisp, D.J., 1967. Chemical factors inducing settlement in *Crassostrea virginica* (Gmelin). *J. Anim. Ecol.* 36, 329–335.
- Daily, G.C. (Ed.), 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC, 392 pp.
- Dame, R.F., 1979. The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. *Proc. Natl. Shellfish Assoc.* 68, 6–10.
- Dame, R.F., 1996. *Ecology of Bivalves: An Ecosystem Approach*. CRC Press, Boca Raton, FL, 254 pp.
- Dame, R., Libes, S., 1993. Oyster reefs and nutrient retention in tidal creeks. *J. Exp. Mar. Biol. Ecol.* 171, 251–258.
- Dame, R.F., Zingmark, R.G., Haskin, E., 1984. Oyster reefs as processors of estuarine materials. *J. Exp. Mar. Biol. Ecol.* 83, 239–247.
- Dame, R.F., Chrzanowski, T., Bildstein, K., Kjerfve, B., McKeller, H., Nelson, D., Spurrier, J., Stevenson, S., Vernberg, J., Zingmark, R., 1986. The outwelling hypothesis and North Inlet, South Carolina. *Mar. Ecol. Prog. Ser.* 33, 217–229.
- Dame, R.F., Spurrier, J.D., Zingmark, R.G., 1992. In situ metabolism of an oyster reef. *J. Exp. Mar. Biol. Ecol.* 164, 147–159.
- Dayton, P.K., Thrush, S.F., Agardy, M.T., Hoffman, R.J., 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5, 205–232.
- Ecological Society of America, 1998. Sustainable marine fisheries. *Ecol. Applic.* 8, S1–S174.
- Ewart, J.W., Ford, S.E., 1993. History and impact of MSX and Dermo diseases on oyster stocks in the northeastern region. NRAC Fact Sheet 200, Northeastern Regional Aquaculture Center, University of Mass., Dartmouth, MA.
- Fitt, W.K., Labare, M.P., Fuqua, W.C., Walch, M., Coon, S.T., Bonar, D.B., Colwell, R.R., Weiner, R.M., 1989. Factors influencing bacterial production of inducers of settlement behavior of larvae of the oyster *Crassostrea gigas*. *Microb. Ecol.* 17, 287–298.
- Fitt, W.K., Coon, S.L., Walch, M., Weiner, R.M., Colwell, R.R., Bonar, D.B., 1990. Settlement behavior and metamorphosis of oyster larvae (*Crassostrea gigas*) in response to bacterial supernatants. *Mar. Biol.* 106, 389–394.
- Ford, S.E., Tripp, M.R., 1996. Diseases and defense mechanisms. In: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), *The Eastern Oyster, Crassostrea virginica*, Maryland Sea Grant College, University of Maryland, College Park, MD, pp. 585–660.

- Frankenberg, D., 1995. North Carolina Blue Ribbon Advisory Council on Oysters: Final Report on Studies and Recommendations, 42 pp.
- Franz, D.R., 1996. Size and age at first reproduction of the ribbed mussel *Geukensia demissa* (Dillwyn) in relation to shore level in New York salt marsh. *J. Exp. Mar. Biol. Ecol.* 205, 1–13.
- Franz, D.R., 1997. Resource allocation in the intertidal salt-marsh mussel *Geukensia demissa* in relation to shore level. *Estuaries* 20, 134–148.
- Fréchette, M., Butman, C.A., Geyer, W.R., 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder. *Limnol. Oceanogr.* 34, 19–36.
- Galtsoff, P.S., 1964. The American oyster *Crassostrea virginica* Gmelin. *US Fish Wildl. Serv. Fish. Bull.* 64, 1–480.
- Giotta, R.E., 1999. Distribution of American oysters (*Crassostrea virginica*) in South Carolina: interacting effects of predation, sedimentation and water flow at varying tidal elevations. MSc Thesis, University of Charleston, SC, 97 pp.
- Giotta, R.E., Coen, L.D., 1999. Where are the subtidal oysters? An experimental evaluation of predation, tidal elevation, and siltation on oyster (*Crassostrea virginica*) distribution in South Carolina. *J. Shellfish Res.* 17, 1301.
- Grumbine, R.E., 1994. What is ecosystem management? *Conserv. Biol.* 8, 27–38.
- Hadley, N.H., Bobo, M.Y., Richardson, D., Coen, L.D., Bushek, D., 1996. Use of specific-pathogen-free (SPF) oysters to measure growth, mortality and onset of MSX and Dermo disease in South Carolina. *J. Shellfish Res.* 15, 496.
- Harding, J.M., 1999. Selective feeding behavior of larval naked gobies (*Gobiosoma bosc*), and blennies (*Chasmodes bosquianus* and *Hypsoblennius hentzi*): preferences for bivalve veligers. *Mar. Ecol. Prog. Ser.* 179, 145–153.
- Hardy, J.D. Jr., 1978a. Development of fishes of the mid-Atlantic Bight. Vol. II. Fish and Wildlife Service, US Department of the Interior, Washington, DC, USA.
- Hardy, J.D. Jr., 1978b. Development of fishes of the mid-Atlantic Bight. Vol. III. Fish and Wildlife Service, US Department of the Interior, Washington, DC, USA.
- Hargis, W.J. Jr., Haven, D.S., 1995. The precarious state of the Chesapeake public oyster resource. In: Hill, P.L., Nelson, S. (Eds.), *Toward a Sustainable Coastal Watershed: The Chesapeake Experiment*. Chesapeake Research Consortium Publication No. 149, Solomons, MD, pp. 559–558.
- Hargis, W.J. Jr., Haven, D.S., 1999. Chesapeake oyster reefs, their importance, destruction and guidelines for restoring them. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, 329–358.
- Haywood, E.L. III, Soniat, T.M., Broadhurst, R.C. III, 1999. Alternative to clam and oyster shell as cultch for eastern oysters. In: Luckenbach, M., Mann, R., Wesson, J. (Eds.), *Oyster Reef Habitat Restoration: A Synopsis of Approaches*. VIMS Press, Williamsburg, VA, 295–304.
- Hidu, H., 1969. Gregarious setting in the American oyster, *Crassostrea virginica* Gmelin. *Chesapeake Sci.* 10, 85–92.
- Hidu, H., Valleau, W.G., Veitch, F.P., 1978. Gregarious setting in the European and American oysters—response to surface chemistry vs. waterborne pheromones. *Proc. Natl. Shellfish Assoc.* 68, 11–16.
- Johnson, G.D., 1978. Development of fishes of the mid-Atlantic Bight. Vol. IV. Fish and Wildlife Service, US Department of the Interior, Washington, DC, USA.
- Jones, P.W., Martin, F.D., Hardy, J.D. Jr., 1978. Development of fishes of the mid-Atlantic Bight. Vol. I. Fish and Wildlife Service, US Department of the Interior, Washington, DC, USA.
- Jordan, J., Valiela, I., 1982. A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance to nitrogen flow in a New England salt marsh. *Limnol. Oceanogr.* 27, 75–90.
- Kaufman, L., Dayton, P.K., 1997. Impacts of marine resource extraction on ecosystem services and sustainability. In: Daily, G.C. (Ed.), *Nature Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC, pp. 275–293.
- Keck, R., Mauer, D., Kauer, J.C., Sheppard, W.A., 1971. Chemical stimulants affecting larval settlement in the American oyster. *Proc. Natl. Shellfish Assoc.* 61, 24–28.
- Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), 1996. *The Eastern Oyster: Crassostrea virginica*. Maryland Sea Grant, College Park, MD, 734 pp.
- Kenny, P.D., Michener, W.K., Allen, D.M., 1990. Spatial and temporal patterns of oyster settlement in a high salinity estuary. *J. Shellfish Res.* 9, 329–339.
- Klemanowicz, K.J., 1985. Effects of a mechanical oyster harvester on macrofaunal community structure. M.S. Thesis, The College of Charleston, South Carolina, 102 pp.
- Kneib, R.T., 1991. Flume weir for quantitative collection of nekton from vegetated intertidal habitats. *Mar. Ecol. Prog. Ser.* 75, 29–38.
- Lenihan, H.S., 1996. Physical–biological coupling on oyster reefs: hydrodynamics, sedimentation, and the production of oysters. Ph.D. Dissertation, University of North Carolina, Chapel Hill, 171 pp.
- Lenihan, H.S., Grabowski, J.H., 1998. Recruitment to and utilization of oyster reef habitat by fishes, shrimps, and blue crabs: an experiment with economic analyses. *Fisheries Resource Grant Report*, June 1998, North Carolina Division of Marine Fisheries, Morehead City, NC.
- Lenihan, H.S., Peterson, C.H., 1998. How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecol. Applic.* 8, 128–140.
- Lenihan, H.S., Peterson, C.H., Allen, J.M., 1996. Does flow speed also have a direct effect on growth of active suspension feeders: an experimental test on oysters, *Crassostrea virginica* (Gmelin). *Limnol. Oceanogr.* 41, 1359–1366.
- Lenihan, H.S., Micheli, F., 2000. Biological effects of shellfish harvesting on oyster reefs: resolving a fishery conflict using ecological experimentation. *Fish. Bull.* 98, 86–95.

- Lenihan, H.S., Micheli, F., Shelton, S.W., Peterson, C.H., 1999. The influence of multiple environmental stressors on susceptibility to parasites: an experimental determination with oysters. *Limnol. Oceanogr.* 44, 210–224.
- Leonard, D.L., 1993. Turning the tides on water quality on declining shellfish resources. *World Aquaculture* 24, 56–64.
- Lindberg, W.J., 1997. Can science resolve the attraction–production issue? *Fisheries* 22, 10–13.
- Loosanoff, V.L., 1965. The American or eastern oyster. *US Fish Wildl. Serv. Circ.* 205, 36.
- Luckenbach, M., Nestlerode, J., Hurlock, T., Coates, G., 1997. Characterization of resident and transient assemblages associated with constructed oyster reef habitats: beginning to relate structure and function. Final Report, Year 1, Aquatic Reef Habitat Program, Chesapeake Bay Program, 56 pp.
- Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), 1999. Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA, 366 pp.
- MacKenzie, C.L. Jr., 1983. To increase oyster production in the northeastern United States. *Mar. Fish. Rev.* 45, 1–22.
- MacKenzie, C.L. Jr., 1996a. History of oystering in the United States and Canada, featuring the eight greatest oyster estuaries. *Mar. Fish. Rev.* 58, 1–87.
- MacKenzie, C.L. Jr., 1996b. Management of natural populations. In: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), *The Eastern Oyster: Crassostrea virginica*. Maryland Sea Grant, College Park, MD, pp. 707–721.
- MacKenzie, C.L. Jr., Burrell, V.G. Jr., Rosenfield, A., Hobart, W.L. (Eds.), 1997a. The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe. Vol. 1, Atlantic and Gulf Coasts. US Department of Commerce, NOAA Technical Report NMFS 127, September 1997, Seattle, WA, 234 pp.
- MacKenzie, C.L. Jr., Burrell, V.G. Jr., Rosenfield, A., Hobart, W.L. (Eds.), 1997b. The History, Present Condition, and Future of the Molluscan Fisheries of North and Central America and Europe. Vol. 2, Pacific Coast and Supplemental Topics. US Department of Commerce, NOAA Technical Report NMFS 128, December 1997, Seattle, WA, 217 pp.
- Martin, F.D., Drewry, G.E., 1978. Development of fishes of the mid-Atlantic Bight. Vol. V. Fish and Wildlife Service, US Department of the Interior, Washington, DC, USA.
- Meyer, D.L., Townsend, E.C., 2000. Faunal utilization of created intertidal eastern Oyster (*Crassostrea virginica*) reefs in the southeastern United States. *Estuaries* 23, 34–45.
- Meyer, D.L., Townsend, E.C., Thayer, G.W., 1997. Stabilization and erosion control value of oyster cultch for intertidal marsh. *Restor. Ecol.* 5, 93–99.
- Newell, R.I.E., 1988. Ecological changes in Chesapeake Bay: are they the result of overharvesting the American oyster, *Crassostrea virginica*? In: Lynch, M.P., Krome, E.C. (Eds.), *Understanding the Estuary: Advances in Chesapeake Bay Research*. Chesapeake Research Consortium, Publication 129 CBP/TRS 24/88, Gloucester Point, VA, pp. 536–546.
- NOAA, 1997. The 1995 National Shellfish Register of Classified Growing Waters. Silver Spring, MD: Office of Ocean Resources Conservation and Assessment, SEAD, 398 pp.
- O’Beirn, F.X., 1996. Recruitment of the eastern oyster in coastal Georgia: patterns and recommendations. *North Am. J. Fish. Manage.* 16, 413–426.
- O’Beirn, F.X., Luckenbach, M.W., Nestlerode, J.A., Coates, G.M., 2000. Towards design criteria in constructed oyster reefs: oyster recruitment as a function of substrate type and tidal height. *J. Shellfish Res.* (in press).
- Ortega, S., Sutherland, J.P., 1992. Recruitment and growth of the eastern oyster, *Crassostrea virginica* in North Carolina. *Estuaries* 15, 158–170.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65–75.
- Palmer, M.A., Ambrose, R.F., Poff, N.L., 1998. Ecological theory and community restoration ecology. *Restor. Ecol.* 5, 291–300.
- Peterson, C.H., Lubchenco, J., 1997. Marine ecosystem services. In: Daily, G.C. (Ed.), *Nature Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC, pp. 177–194.
- Posey, M.H., Alphin, T.D., Powell, C.M., Townsend, E., 1999. Oyster reefs as habitat for fish and decapods. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*. Virginia Institute of Marine Science Press, Gloucester Point, VA, 229–237.
- Powell, E.N., Klinck, J.M., Hoffman, E.E., Ford, S., 1997. Varying the timing of oyster transplant: implications for management from simulation studies. *Fish. Oceanogr.* 6, 213–237.
- Roditi, H., Caraco, N.F., Cole, J.J., Strayer, D.L., 1996. Filtration of Hudson River water by the zebra mussel (*Dreissena polymorpha*). *Estuaries* 19, 824–832.
- Rothschild, B.J., Ault, J.S., Gouletquer, P., Héral, M., 1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. *Mar. Ecol. Prog. Ser.* 111, 29–39.
- Ruge, J.G., 1898. The oyster and oyster beds of Florida. *Bull. US Fish. Commun.* 17, 289–296.
- Smaal, A.C., Haas, H.A., 1997. Seston dynamics and food availability on mussel and cockle beds. *Estuarine Coastal Shelf. Sci.* 45, 247–259.
- Stanley, D.W., Sellers, M.A., 1986. Species profile: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico) — American oyster. *US Fish Wildlife Service Biological Report* 82(11.64) US Army Corps of Engineers, TR EL-82-4, 25 pp.
- Stiven, A.E., Kuenzler, E.J., 1979. The response of two salt marsh molluscs, *Littorina irrorata* and *Geukensia demissa*, to field manipulations of density and *Spartina* litter. *Ecol. Monogr.* 49, 151–171.

- Supan, J.A., Wilson, C.A., Roberts, K.J., 1999. Economics of augmentation of natural production using hatchery techniques. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA, 359–366.
- Tamburri, M.N., Zimmer-Faust, R.K., Tamplin, M.L., 1992. Natural sources and properties of chemical inducers mediating settlement of oyster larvae: a re-examination. Biol. Bull. 183, 327–338.
- Thayer, G.W. (Ed.), 1992. Restoring the Nation's Marine Environment. Maryland Sea Grant College, College Park, MD, 716 pp.
- Thompson, R.J., Newell, R.I.E., Kennedy, V.S., Mann, R., 1996. Reproductive processes and early development. In: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant College, University of Maryland, College Park, MD, pp. 335–370.
- Turner, E.J., Zimmer-Faust, R.K., Palmer, M.A., Luckenbach, M., Pentcheff, N.D., 1994. Settlement of oyster (*Crassostrea virginica*) larvae: effects of water flow and a water-soluble chemical cue. Limnol. Oceanogr. 39, 1579–1593.
- Ulanowicz, R.E., Tuttle, J.H., 1992. The trophic consequences of oyster stock rehabilitation in Chesapeake Bay. Estuaries 15, 298–306.
- Van Dolah, R.F., Bobo, M.Y., Levisen, M.V., Wendt, P.H., Manzi, J.J., 1992. Effects of marina proximity on the physiological condition, reproduction, and settlement of oyster populations. J. Shellfish Res. 11, 41–48.
- Veitch, F.P., Hidu, H., 1971. Gregarious setting in the American oyster *Crassostrea virginica* Gmelin: I. Properties of a partially purified setting factor. Chesapeake Sci. 12, 173–178.
- Walters, C., 1986. Adaptive Management of Renewable Resources. Macmillan, New York, 374 pp.
- Weiner, R.M., Walch, M., Labare, M.P., Bonar, D.B., Colwell, R.R., 1989. Effects of biofilms of the marine bacterium *Aeromonas collweliana* (LST) on the set of the oyster *Crassostrea gigas* (Gmelin, 1791). J. Shellfish Res. 8, 117–123.
- Wells, H.W., 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31, 266–329.
- Wenner, E., Beatty, H.R., Coen, L.D., 1996. Method for quantitatively sampling nekton on intertidal oyster reefs. J. Shellfish Res. 115, 769–775.
- Wesson, J.A., Mann, R., Luckenbach, M.W., 1999. Oyster reef restoration efforts in Virginia. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA, 117–129.
- Whitlatch, R.B., Osman, R.W., 1999. Oyster reefs as metapopulations: approaches for restoring and managing spatially fragmented habitats. In: Luckenbach, M.W., Mann, R., Wesson, J.A. (Eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Virginia Institute of Marine Science Press, Gloucester Point, VA, 199–211.
- Zimmer-Faust, R.K., Tamburri, M.N., 1994. Chemical identity and ecological implications of a waterborne, larval settlement cue. Limnol. Oceanogr. 39, 1075–1087.
- Zimmerman, R., Minello, T.J., Baumer, T., Castiglione, M., 1989. Oyster reef as habitat for estuarine macrofauna. NOAA Technical Memorandum NMFS-SEFC-249.