Oyster Reef Habitat Restoration: Relationships Between Oyster Abundance and Community Development based on Two Studies in Virginia and South Carolina

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ABSTRACT

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Most Atlantic and Gulf coast U.S. states with an oyster fishery have operated some form of oyster reef enhancement program over the past 50 years. Although programs were initially only directed at oyster fisheries augmentation, recent emphasis has shifted to include the restoration of their ecological functions. Furthermore, many of these programs are managed by environmental organizations or state agencies not traditionally involved in fisheries management or research, but rather in ecological restoration, monitoring, and/or environmental education. A simple assessment of shellfish meetings over the past five years, including the inaugural Restore America's Estuaries meeting from which this paper is derived, revealed more than 300 presentations related to oyster restoration, with fewer than 25% focused solely on oyster fishery restoration. Unfortunately, many of those efforts lacked well-defined "success criteria," with progress often judged using fisheries-based metrics such as market-sized (generally 75 mm or 3") oysters. Here we discuss our findings as they relate to the value of alternative restoration metrics and associated success criteria using data from two very different systems and approaches: one conducted in Virginia's lower Chesapeake Bay (Rappahannock River), based on data from a two-year program utilizing subtidally constructed reefs of different reef "scale," and the other a long-term study in South Carolina focusing on intertidal reefs. For each system, we compared newly created reef structures, relating oyster abundance and size to resident species abundance and biodiversity over time. Our results revealed positive correlations between several community descriptors and the size and density of oysters on the reefs. Of the 15 significant (and 5 marginally insignificant) correlations observed out of a total of 78 examined across both studies, all but one were positive. The exception was for epifaunal invertebrate diversity vs. oyster biomass on the Rappahannock reefs. Despite these numerous positive correlations, none indicated that market-sized oysters are a prerequisite for supporting an abundant and diverse community. For example, intertidal oysters >75 mm in South Carolina typically make up <10% of all reef oysters, with a maximum of 18%. Finally, until we have a more thorough understanding of the interactions between individual species and the mechanisms linking oyster populations and reef community attributes, we propose that oyster abundance/size structure be used for assessments. Future studies need to develop and evaluate restoration progress using a combination of standardized criteria that can be applied to reef success over a wide geographical range and surrogate or indirect ecological measures (*e.g.*, filtering, habitat use).

ADDITIONAL INDEX WORDS: *Ecological restoration, habitat, oysters, metrics, success criteria, South Carolina, Virginia, intertidal, subtidal, reefs,* Crassostrea virginica.

INTRODUCTION

Recognition of the important ecological role of *Crassostrea virginica* (Eastern oyster) in many es-

tuaries along the U.S. Atlantic and Gulf of Mexico coasts (NEWELL, 1988; BREITBURG, 1999; LENIHAN, 1996, 1999; LENIHAN *et al.*, 1999; DAME, 1999; COEN *et al.*, 1999a; LUCKENBACH *et al.*, 1999; COEN and LUCKENBACH, 2000) has fueled increased efforts to

restore depressed oyster populations over the past decade since the workshop on oyster restoration in 1995 at the Virginia Institute of Marine Science (LUCKENBACH et al., 1999). There is now evidence that oysters can (or could at historical abundances) control phytoplankton abundance and alter estuarine food webs by enhancing benthic-pelagic coupling (DAME et al., 1984, 2001; DAME and LIBES, 1993; NEWELL, 1988; ULANOWICZ and TUTTLE, 1992; ROTHSCHILD et al., 1994). Indeed, there is an increasing recognition that top-down control of phytoplankton abundance via oysters should be an important part of overall strategies to improve water quality in eutrophic estuaries (NEWELL, 1988; KAUFMAN and DAYTON, 1997; PETERSON and LUBCHENCO, 1997; JACKSON et al., 2001). Moreover, oysters are quintessential "ecosystem engineers" (JONES et al., 1994; LENIHAN, 1999), constructing biogenic habitats that provide refuges, nesting sites, and foraging grounds for a variety of resident and transient species (LENIHAN and GRABOWSKI, 1998; BREITGURG, 1999; COEN et al., 1999b; EGGLESTON et al., 1999; HARDING and MANN, 1999; POSEY et al., 1999). Several studies have now demonstrated greater biodiversity associated with oyster reefs than with adjacent sedimentary habitats (POSEY et al., 1999; COEN and LUCKENBACH, 2000; O'BEIRN et al., 2000). In fact, for many estuaries along the Mid-Atlantic and Gulf coasts of the U.S., oyster reefs are the primary source of hard substrate, and as such they may support unique assemblages of organisms. Further, there is evidence that oyster reefs contribute significantly to enhanced production, not merely the concentration of finfish and decapod crustaceans (PETERSON et al., 2003).

Over the past decade, the number of oyster restoration projects along the U.S. Atlantic and Gulf of Mexico coasts has increased dramatically, largely in an effort to restore one or more of the potentially lost ecological services (see reviews above). Many of these projects are being conducted by state and federal agencies not typically involved in fisheries management, such as the Virginia Department of Environmental Quality, the South Carolina Department of Health and Environmental Control, the National Oceanic and Atmospheric Administration (NOAA) Restoration Center, the NOAA Coastal Services Center, and the U.S. Army Corps of Engineers. In addition, numerous nongovernmental organizations and community groups (e.g., NY/NJ Baykeepers, Chesapeake Bay Foundation, South Carolina's Oyster Restoration

and Enhancement Program (or SCORE) with South Carolina Coastal Conservation League and Coastal Conservation Association (CCA), North Carolina Coastal Federation, and Tampa Baywatch) are actively involved in oyster reef restoration for ecological motives. Funding sources for oyster restoration have also included agencies and organizations with environmental restoration agendas (e.g., NOAA's Community Restoration Program and FishAmerica). One indication of this enhanced level of restoration activity is the large number of papers presented by such groups on oyster restoration at recent meetings of the International Conference of Shellfish Restoration, the National Shellfisheries Association, and at the Marine Benthic Ecology meeting. A review of the published abstracts and program schedules for those meetings over the past five years and the inaugural meeting of Restore America's Estuaries reveals more than 300 presentations related to oyster restoration with fewer than 25% focused on oyster fishery restoration (LUCKENBACH, unpublished data).

Unfortunately, many of the projects referred to in the previous section have limited data, with few results published to date in the primary literature. In the absence of expressly stated success criteria (COEN and LUCKENBACH, 2000) and directed monitoring, the early success of oyster restoration projects, unfortunately, tends to be judged solely on either the abundance of market-sized (typically 75 mm or 3") oysters or fishery landings data, neither of which may be crucial to achieving more ecologically based restoration goals.

Previously, we (COEN and LUCKENBACH, 2000) stressed the importance of developing metrics for evaluating the specific goals of ecological restoration. It is clear from that earlier work that a viable oyster population is a critical component of a successful oyster reef restoration effort. However, it is not clear if harvestable quantities of market-sized (75 mm shell height (SH)) oysters are a critical requisite for restoration success. In states where minimum harvest sizes are regulated (e.g., 75 mm SH in Virginia and elsewhere) oysters may be reproductively capable and populations sustainable, with relatively low abundances of market-sized animals. Studies have now begun to demonstrate that not all of the "ecological services" of oyster communities come only after the oyster populations are well established. In several recent reviews (COEN et al., 1999a, 1999b, 2000; COEN and LUCKENBACH, 2000; BREITBURG et al., 2000) we sug-

gested that oysters, although the key to a fully functioning oyster reef, are not necessary to provide many of the ecosystem services that, for example, artificial reefs provide, such as structure and refugia (BREITBURG, 1999; EGGLESTON *et al.*, 1999; LEHNERT and ALLEN, 2002; GLANCY, 2003). Biogeochemical coupling benefits as measured in the "CREEK" Project in South Carolina (DAME *et al.*, 2000, 2001) showed that nekton feeding coupled nutrients around structured sites without live oysters. Hence, oysters may not be critical, initially, in judging success and should not be used to imply failure early in the life of a restoration program.

Alternatively, as suggested by COEN *et al.* (1999a) and BREITBURG *et al.* (2000), large oysters and "mature" reefs may be critical to achieving both fisheries enhancement and restoration goals. In discussing many of the challenges faced in attempting to meet fisheries rehabilitation and ecological restoration goals for oyster reefs, COEN and LUCKENBACH (2000) further stressed the importance of developing meaningful success measures and implementing rigorous monitoring programs to track progress towards those goals. Thus, to better evaluate the success of ecological restoration efforts, we need to develop a better understanding of the relationship between oyster population structure and abundance and any potential "ecological services" that we are seeking to restore.

In response to this need, we present the results from two studies conducted in different estuaries on the U.S. Atlantic coast. One study in the Rappahannock River, a mesohaline sub-estuary of the Chesapeake Bay, is still ongoing and is addressing the role of spatial scale (ranging from a few meters to several kilometers) on the development of oyster populations and associated fauna. The other study, conducted along the central coast of South Carolina, compared the development of oyster populations and associated assemblages on constructed reefs to adjacent natural intertidal reefs over a six-year period between 1995 and 2001. Both studies afford the opportunity to relate the reef-associated assemblages of organisms to oyster densities and population size structure over time. Our objective in examining these relationships is to provide a basis for beginning to formulate metrics for restoration success that reflect the biodiversity and habitat goals of many projects and to make recommendations for future work.
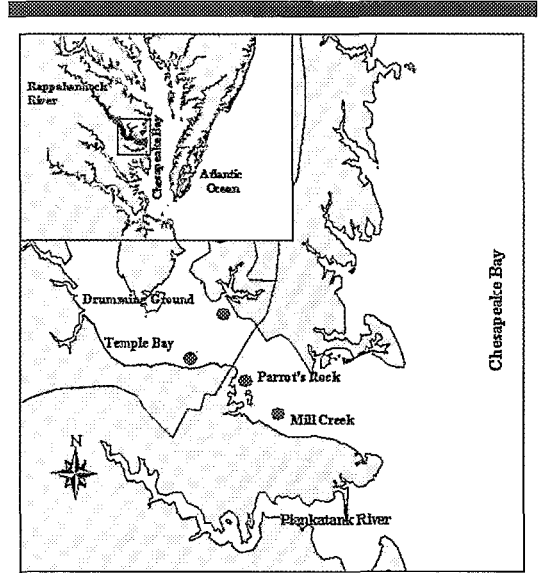

Figure 1. Experimental reef restoration sites in the Rappahannock River, Chesapeake Bay, Virginia.

METHODS

Rappahannock River, Virginia

Study Site and Reef Construction

This study was conducted at four sites in the lower portion of the Rappahannock River, Virginia, USA, which is a tributary of the Chesapeake Bay (upriver-most site, Drumming Ground: N 37° 39.248', W 76° 27.648' downriver-most site: Mill Creek N 37° 35.157', W 76° 24.024', see Figure 1). Historically, this region of the Rappahannock was a highly productive oyster harvesting area, with extensive natural reefs (HARGIS, 1999). The specific sites chosen for the construction of reefs in this study formerly supported viable oyster reefs that through a combination of over-fishing, disease, and habitat degradation had all but disappeared. Reef bases were constructed in August 2000 by placing shell piles in arrays as shown in Figure 2. Core material for individual mounds was comprised of surf clam (*Spisula solidissima*) shell that was capped off with a veneer (generally 10–20 cm) of clean oyster shell. Materials were barged to the four reef sites and deployed via a crane and bucket rig, creating "upside-down egg carton" shaped subtidal reefs elevated approximately 3 m above seabed and 1–2 m below the water surface at mean low water (Figure 2). Reefs ranged in area, from
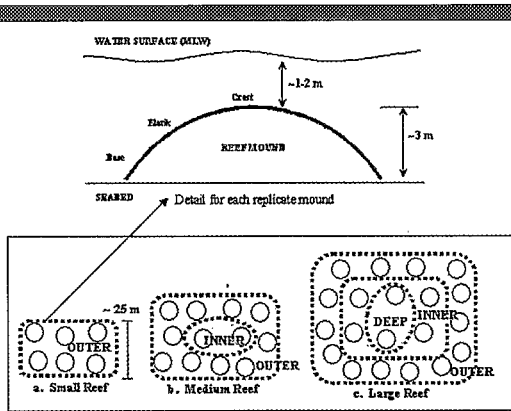
Figure 2. Generalized aerial footprint of reefs denoting intra-reef locations. Each circle represents a mound approximately 10 m diameter. Generalized side view of an individual shell mound shown for each replicate reef mound at arrow.

Figure 3. Inlet Creek study site in Charleston Harbor, South Carolina. See COEN et al., 1999b, and COEN and LUCKENBACH, 2000, for additional details.

approximately 400 m² to 8,000 m². Intra-reef locations were designated in relation to distance from reef edge along longitudinal axes (Figure 2). A subsequent manuscript will address the development of oyster populations and associated communities in relation to scale. Here we present our findings relating the density and population structure of oysters to the development of reef-associated community assemblages. For more detail, see LUCKENBACH and ROSS (2003).

Sampling Methods

Standing stocks of oysters were estimated from diver-collected samples taken at all reefs. Fifty-one replicate 0.25 m × 0.25 m quadrates were haphazardly placed onto randomly-selected mounds within ten reefs (number of samples partitioned by reef size, i.e., 5 of the 6, 7 of the 12 and 8 of the 20 mounds for small, medium, and large "reefs," respectively; see Figure 2 and LUCKENBACH and ROSS, 2003, for details). One sample was collected from each mound, as mounds were treated as replicates within a reef treatment, such that multiple replicate samples were taken at the time of sampling (see Figure 2). All reef material was excavated to a depth of 10 cm by divers and transported to the surface in fine mesh bags. All live oysters in each sample were counted and SH (longest lip to hinge linear distance, the standard measure for oyster) measured. Samples were collected in July 2001, October 2001, and July 2002.
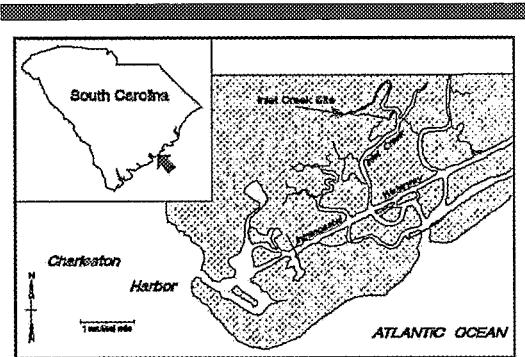
A sub-sample of 132 oysters covering the range of oyster SH encountered was measured for dry tissue biomass from the October 2001 sample. The shear number of oysters encountered prohibited ashing all oysters throughout the study, justifying the use of a regression equation to estimate biomass. Biomass values for oysters were computed from a regression of ash-free dry weight on shell height [biomass (mg) = 0.007 × shell height (in mm)$^{2.8614}$, R^2 = 0.8988, n = 132]. All sessile epifauna on the reef substrate or on the oysters in quadrat samples were identified to the lowest practical taxon and reported as either densities (e.g., for barnacles and tunicates) or percent cover (e.g., for bryozoans and sponges).

Small resident mobile fishes and crustaceans were sampled using substrate baskets embedded in the reef. Thirty-centimeter diameter PVC pipe was cut into 15-cm lengths and one end covered with 1-mm plastic mesh. Three 5-cm diameter holes were cut along the midline of the PCV ring and covered with 1-mm mesh. Baskets were then filled with clean oyster shells similar to those used in the reef construction and buried flush with the reef surface by divers. The mesh bottom and holes in the sides permitted the exchange of interstitial pore water with the surrounding reef, while the basket allowed the retrieval of intact samples which retained the more mobile reef residents such as blennies, gobies, and mud crabs. During April 2001, a total of 189 baskets were deployed at haphazardly located positions on a subset of the reef crests (1 per randomly selected replicate mound; see above replicate allocation for the quadrats) due to logistics and time constraints, versus

the alternative of randomly picking the exact spot on each subtidal reef, as we had no reason to think the micro-location of a basket on a small mound would yield any bias. Divers retrieved the above replicate baskets in July 2001 (n = 62), October 2001 (n = 60), and July 2002 (n = 24) from all combinations of reef locations. The small number of samples retrieved during the last sampling period reflects loss of gear due to the erosive forces during the 15 months that the final baskets were in the field. In the laboratory, all motile organisms in the baskets were thoroughly rinsed over a 1-mm sieve mesh to remove all motile organisms, which were fixed in isotonic Normalin® and then transferred to 70% ethanol. All organisms were later identified to the lowest practical taxon, enumerated, and, where appropriate, measured (decapod crustaceans, carapace width, and finfish, total length). Taxa such as amphipods and polychaetes were not measured.

Transient fishes associated with the reefs were sampled using gill nets. Although nets were set during 2001, only data collected during two sampling efforts in May and June 2002 were used for analysis. As previously mentioned, we also used oyster population data from this period for analyses. Nets were 9 m long by 3 m high and rigged to fish from the seabed up (i.e. sinking rigged net). Nets utilizing 6.3 cm and 7.5 cm stretch mesh were used during 2002 and were randomly allocated throughout sampling periods. Anchored monofilament gill nets were deployed for 3 h on all reef sizes at both inner and outer reef locations when applicable. Sets were repeated so that all locations were sampled with both mesh sizes during both flood and ebb tidal cycles within sampling periods. Although the majority of gill net sampling occurred between dawn and dusk, one sample effort that included all scale treatments was undertaken during the night. Nets were randomly allocated to specific locations within each region of the reefs. This resulted in over 200 individual sets (see LUCKENBACH and ROSS, 2003 for more details). After 3 hr, nets were retrieved and fish were identified, enumerated, measured, and released a short distance from the reefs. In some cases, due to high catches, processing of samples had to be undertaken after all nets were harvested and taken to a remote location.

Statistical Analyses

Temporal patterns in oyster abundance and biomass, along with abundances of selected species and community metrics, are presented graphically for all sites combined. One-way ANOVAs were used to test the effect of reef site on oyster abundance and biomass for July 2002 samples only (n = 4). Tukey's Multiple Comparisons were subsequently utilized to elucidate reef site differences (SOKAL and ROHLF, 1981). Furthermore, for data from this sample period, we tested for differences between individual reefs (n = 10) independent of geographic location. Both analyses were meant to provide some background regarding the general oyster populations prior to subsequent correlation analyses that are undertaken at the individual reef level. Oyster reefs were constructed in 2000, which resulted in missing oyster settlement for that year, so no measured settlement was quantified until Fall 2001. We chose to use the 2002 sampling only because it represented 2001 recruitment and mortality, along with recruitment and mortality through July 2002, therefore painting a more appropriate picture of existing oyster populations. This is important because these were new reefs just developing oyster populations during the course of this study. Size frequency data for oysters from this same sampling date are presented graphically by site.

Spearman product-moment correlation coefficients related total oyster abundance, abundance of age-class-two oysters, and biomass to the abundances and biomass of dominant reef-associated species to selected community descriptors. Comparisons included abundance and biomass (for ribbed mussels (*Guekinsia demissa*) only) of dominant (based on measured abundance in this study), reef-associated species in logical groups, as well as total abundance, species richness, and diversity (Shannon-Weiner Diversity Index) of broader taxonomic groupings. Broad functional groupings were (1) epifaunal invertebrates, (2) resident finfish, and (3) transient finfish. Dominant species/group specific analyses were (1) for attached epifauna, barnacles (*Balanus* spp.), (2) for decapod crustaceans, mud crabs (*Xanthidae*), (3) for bivalves, ribbed mussels, (4) for resident finfish, skilletfish (*Gobiesox strumosus*), and (5) for transient finfish, white perch (*Morone americanus*). For transient species, in addition to the dominant species, striped bass (*Morone saxatilis*) data were included because of their management importance along the Atlantic seaboard. We deemed these functional groups to be the most logical assemblage that we were able to quantitatively sample in this study.

Spearman correlations were computed using means for individual reefs across intra-reef locations for a given sampling period. For epifaunal and transient finfish assemblages, we analyzed data from the Summer 2002 sampling period. For the resident finfish and crustaceans, we used data from the Fall 2001 sampling period because some of the later samples were lost during processing. We tested the null hypothesis that these correlation coefficients did not differ from zero using t-tests (SOKAL and ROHLF, 1981). All data sets were tested for normality using the Kolmogorov-Smirnov test (SAS Institute Inc., 1990) and homoscedasticity using Hartley's F_{max} Test (SOKAL and ROHLF, 1981). Many data sets did not meet these assumptions, especially for equal variances. Therefore, Spearman's rank correlations were utilized for comparisons. All data analyses were carried out using SAS, except Hartley's F-Max tests which were computed manually according to SOKAL and ROHLF (1981). A report (LUCKENBACH and ROSS, 2003) and a subsequent manuscript have or will address variations in relation to reef size and location within the reef.

Inlet Creek, South Carolina

Study Site and Background

The South Carolina studies were conducted in Inlet Creek, a tributary adjacent to Charleston Harbor, as part of a larger study examining the development of intertidal oyster reefs in relation to reef age and season at sites with differing adjacent development (COEN et al., 1999b). We also compared these intensively studied sites to numerous sampling sites from across the state. For the purpose of this overview, we focus only on the three experimental reefs constructed in Inlet Creek (N 32° 47.93', W 79° 49.73') and the three adjacent, natural reef areas (see Figure 3). The design and construction of these reefs, as well as preliminary physical descriptions of the site, have been reported in detail in WENNER et al., 1996; COEN et al., 1999b; COEN and LUCKENBACH, 2000, so we present only a brief overview here. In October 1994, three replicate 24-m² experimental reefs were constructed on an intertidal oyster flat within Inlet Creek. Each experimental reef was comprised of 156 plastic trays (0.46 m × 0.31 m × 0.11 m) filled with clean oyster shell and arranged in a 6 × 26 array, with each reef paired with an adjacent natural reef of similar size (see Figure 2 in COEN et al., 1999b). Here we discuss the results

for Inlet Creek only, the more undeveloped of the two sites at the time of study. Oyster sampling began on experimental reefs after initial recruitment in the late spring to early summer 1995, whereas resident sampling began earlier in March 1995 (COEN et al., 1999a, 1999b; COEN and LUCKENBACH, 2000). Natural oyster sampling in Inlet Creek started in 1997. Additional work included transients, disease, and environmental sampling during the overall study from 1995–2001 (see COEN et al., 1999a, 1999b). However for this paper, only a portion of the overall dataset was used.

Sampling Methods

Resident fauna (defined here as those organisms remaining within the shell matrix when exposed at low tide) on the experimental reefs were sampled by removing three randomly selected "quadrats" (= trays) sampled only once from each of the three experimental reefs. We rinsed the material on a 0.5-mm sieve and retained all organisms caught on the sieve. All oyster shell was thoroughly sorted and all live oysters counted and measured. For the natural oyster residents, we sampled using quadrates randomly placed on adjacent oyster reefs outside of the paired natural reef to minimize disturbance of other sampling. All organisms, including oysters, were excavated to a depth of 11 cm and removed. Macrofauna were enumerated to the lowest practical taxon for the first four years. Thereafter, only decapod crabs and mussels were identified and counted due to logistical constraints. Macrofaunal biomass was quantified using wet weights (see COEN et al., 1999b) for specific taxonomic groupings (i.e. "Decapod Crabs" and "Shrimp," "Amphipods," "Isopods," "Polychaetes," and "Mussels") throughout the entire project duration. Sampling for reef residents began in March 1995, five months after the experimental reefs were constructed and prior to any recruiting oysters, with the reefs sampled bimonthly during the first year and quarterly during the second year. The more frequent sampling allowed for better initial resolution as reefs began to receive both oyster and resident recruits. Over the next three years, 1997–1999, sampling was reduced to summer and winter samples, collected from the experimental and natural reefs as described above. For 2000–2001, resident samples were collected only during the winter due to logistical (primarily funding and manpower) constraints over time (see above also).
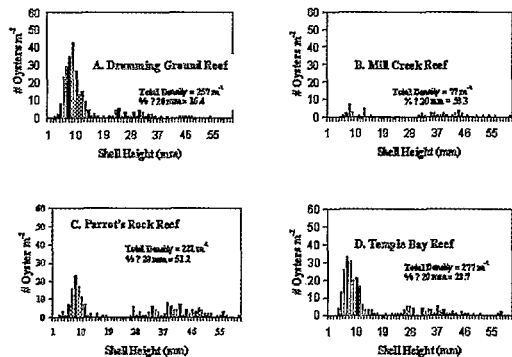
Figure 4. Oyster abundance and size distribution at the four reef sites in the Rappahannock River, Chesapeake Bay. Data are from samples taken during summer 2002 and are pooled across all reefs (sizes and intra-reef locations) within a site. For total abundance, Drumming Ground = Temple Bay = Parrot's Rock > Mill Creek (Tukey's Studentized Range Test, P ≤ 0.05).

Statistical Analyses

Two-way ANOVAs (PCSAS 8.2) were used to test for the effects of time (categorical depending on particular sampling frequency) and reef type on oyster abundance and mean shell height. All assumptions were tested prior to statistical analyses. Mean abundances and oyster size frequencies from the experimental and natural reefs are presented graphically for the January sampling period only for 1997 through 2001 for simplicity here. Although we sampled and measured oysters from experimental reefs from 1995, we did not begin to measure adjacent natural oyster populations until 1997, whereas resident sampling began soon after the reefs were constructed in March 1995. Since we are using both for comparison, we show the 1997–2001 data only. We computed Pearson product-moment correlation coefficients (SigmaStat 2.0) relating mean oyster abundance and mean shell height to the abundances and biomass of dominant reef-associated species and to various "community descriptors" for the experimental and natural reefs. Data from January 1998 were selected for this analysis because that represented the latest time period for which complete data on epifaunal abundance and diversity were available for the study.

RESULTS

Rappahannock River, Virginia

Two years after construction, reefs at the four sites in the lower Rappahannock River differed
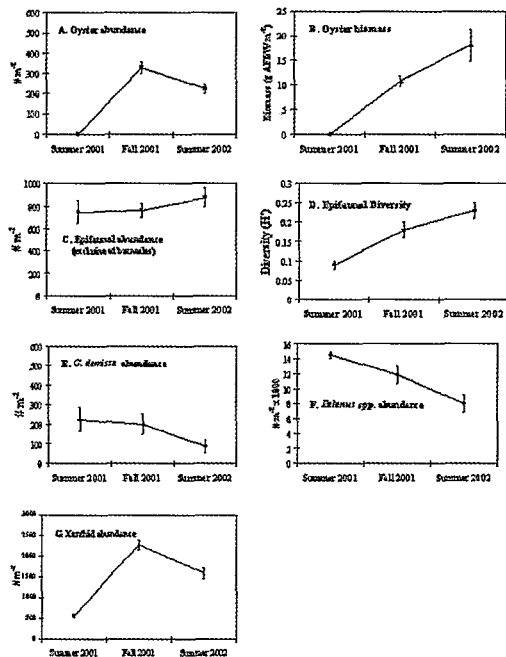

Figure 5. Temporal patterns of (A) oyster abundance, (B) oyster biomass, (C) epifaunal abundance, (D) epifaunal diversity, (E) *Geukensia demissa* abundance, (F) *Balanus* spp. abundance, and (G) xanthid crab abundance on the reefs in the Rappahannock River, Chesapeake Bay, Virginia. Values are means ± SE by reef site.

both in abundance and size structure of oyster populations (Figure 4). Total oyster density varied significantly between sites (F = 5.82, df = 3, P = 0.0018), with Parrot's Rock, Drumming Ground, and Temple Bay reefs all having greater mean densities than Mill Creek reef (see Figure 4). However, no significant differences were observed between individual reefs independent of geographic "location" (F = 1.94, df = 9, P = 0.0731). Reefs also differed in densities of 1–2 year class oysters (i.e. those with SH ≥ 20 mm), which are shown in the size distribution plots in Figure 4. Prior to recruitment in the summer of 2001, oyster abundances at all of the reef sites were zero (Figure 5A). Mean oyster abundances peaked in fall 2001 at approximately 350 oyster/m² following recruitment during summer 2001 and fell slightly by summer 2002. Biomass of oysters on the reefs increased throughout this period (Figure 5B), as would be expected with newly recruiting oyster populations on these reefs.

Epifaunal abundances were dominated by bar-

nacles in the genus *Balanus,* especially during the first summer when densities exceeded 14,000/m² (Figure 5F). Exclusive of barnacles, epifaunal abundances changed little over the course of the study (Figure 5C). Overall diversity of epifauna increased throughout the time period (Figure 5D), both as a result of an increase in species richness and a decline in barnacle densities (Figure 5F). Prominent members of the epifaunal assemblage, in addition to barnacles, included bivalves (*Macoma balthica, Mulinia lateralis, Mya arenaria, Geukensia demissa* (Figure 5E), *Mytilus edulis,* and *Petricola pholadiformis*), solitary and colonial tunicates, an ectoproct (*Membranipora tenuis*), a serpulid polychaete (*Hydroides dianthus*), and xanthid crabs (Figure 5G). In addition, the reefs supported seasonally abundant and diverse assemblages of macroalgae.

Within a single season, correlation coefficients between oysters (mean total abundance, mean abundance of year class 2 oysters, and biomass across reef sites) and various community descriptors and dominant species varied considerably (Table 1). The only significant correlation we found with total oyster abundance was with the abundance of skillet fish, which showed a very strong positive correlation, and the total abundance of resident finfish, which showed a positive correlation. Similar significant positive correlations were observed with the abundance of year class 2 oysters. In addition to these two parameters, barnacle abundance, ribbed mussel biomass, and epifaunal diversity were also significantly correlated with oyster biomass, with total epifaunal abundance only marginally insignificant (P = 0.054, see Table 1). Interestingly, the only negative correlation observed was between oyster biomass and epifaunal diversity. It is important to note here that while a large number of samples and individual organisms were part of these analyses, the correlations were conducted using means for each individual reef and thus the tests for significance, with only 8 degrees of freedom, had relatively low power (HOENIG and HEISEY, 2001).

Inlet Creek, South Carolina

Overall during the study, we collected over 87 resident and 60 transient species associated with our reefs (COEN *et al.,* 1999a). Oyster abundance on the experimental reefs at Inlet Creek increased during the period from January 1997 through January 2001, but means (±SE) remained well below

Table 1. *Correlations between oysters (abundance and biomass), dominant taxa, and community metrics for reefs in the Rappahannock River, Virginia. Epifaunal invertebrate and transient finfish analyses are from Summer 2002; resident finfish analyses are from Fall 2001. S = Species Richness, H' = Shannon-Weiner Diversity Index, r = Spearman coefficients, p = Probability of r = 0. Sample size, n = 10 overall for each value below.*

| Oyster C. virginica	Epifaunal Invertebrates						Resident Finfish				Transient Finfish			
	Barnacle Abun.	Xanthid Abun.	G. demissa Biomass	Total Abun.[1]	S	H'	G. strumosu Abun.	Total Abun.	S	H'	M. saxatilis Abun.	M. americanus Abun.	Total Abun.	S
Total Abundance														
r	−0.188	−0.255	−0.119	−0.195	0.018	0.188	0.909	0.685	−0.261	−0.509	0.176	0.067	−0.390	0.214
p	0.602	0.477	0.743	0.590	0.960	0.602	<0.001	0.029	0.467	0.133	0.626	0.854	0.265	0.553
Abundance Year Class 2														
r	0.584	0.182	0.593	0.413	0.383	−0.505	0.750	0.782	−0.018	−0.399	−0.316	0.448	0.381	0.089
p	0.077	0.614	0.071	0.235	0.275	0.137	0.013	0.008	0.960	0.254	0.374	0.194	0.277	0.808
Biomass														
r	0.745	0.200	0.632	0.624	0.455	−0.697	0.744	0.915	0.164	−0.166	−0.455	0.505	0.608	0.146
p	0.013	0.580	0.050	0.054	0.187	0.025	0.014	<0.001	0.652	0.647	0.187	0.137	0.062	0.687

[1] Exclusive of barnacles.
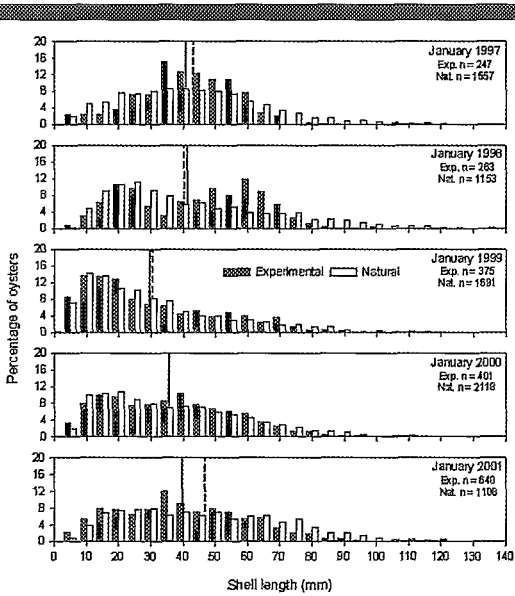
Figure 6. Oyster size (abundance)-frequency distributions for natural and experimental population samples collected from Inlet Creek, Charleston Harbor, South Carolina, resident samples (n = 9 for each date × reef type). The vertical lines of each plot represent overall mean size for each reef type; solid is for oysters on the experimental reefs, dashed represents oysters on natural reefs. (Note: Values overlap for January 2000.)
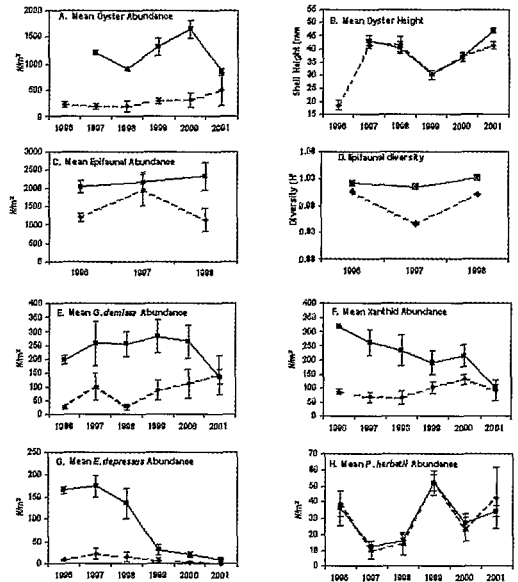

Figure 7. Temporal patterns for (A) mean oyster abundance, (B) mean oyster height, (C) mean epifaunal abundance, (D) epifaunal diversity, (E) mean *Geukensia demissa* abundance, (F) mean xanthid crab abundance, (G) mean *Eurypanopeus depressus* abundance, and (H) *Panopeus herbstii* abundance for experimental (dashed lines) and natural (solid lines) reefs in Inlet Creek, Charleston Harbor, South Carolina. All values are means ± SE by reef type (experimental vs. natural) except for D, epifaunal diversity.

(*e.g.,* January 2001, mean no. 497 ± 282) densities found on adjacent natural reefs at Inlet (January 2000 and 2001, means from 861–1646/m²) or any of the other sites we have sampled across the state (Figures 6 and 7A). For comparison, mean densities across South Carolina ranged from a low of 500/m² (±88) to over 6,436/m² (±500), for samples collected by us from 1997 to 2002. A two-way ANOVA revealed significant effects for reef type (F = 201.80, P < 0.0001), time of sampling (F = 3.68, P = 0.0022), and the interaction term (F = 3.37, P = 0.0043) for oyster abundance. Oyster size frequency distributions were similar on the experimental and natural reefs, with natural reefs at Inlet having more oysters above 75 mm SH (Figures 6 and 7B), resulting in marginally insignificant differences (P = 0.0581) in mean SH of oysters between the reef types.

South Carolina has no harvest size limit, so these differences are not relevant for the resource. Prominent members of the resident faunal assemblage (numerically) included polychaetes (*Nereis succinea* and *Streblospio benedicti*), several mus-

sels (*Brachidontes exustus* and *Geukensia demissa*), a gastropod (*Creedonia succinea*), mites, and a peracarid (*Gammarus palustris*). In addition to the above taxa, natural reefs also had large numbers of the gastropod ectoparasite *Boonea impressa* and the xanthid crab *Eurypanopeus depressus*. Epifaunal abundance and diversity measures are only available for this site for the years 1996–1998; during January 1997, total epifaunal abundance on the experimental reefs was similar to that on the natural reefs because of high abundances of gastropods (primarily *C. succinea*), mussels (*B. exustus* and *G. demissa*), and acarinids (mites), but diversity was lower (Figures 7C and D).

Ribbed mussel and xanthid crab (total of 14 spp.) abundances showed similar patterns, although densities on the natural reefs exceeded those on the experimental reefs until 2001 (Figures 7E and F). Initially high abundances of the xanthid crab *Eurypanopeus depressus* on the natural reefs declined between 1998 and 1999; abundances remained comparatively low during the

Table 2. *Correlations between oysters (abundance and height), dominant taxa, and community metrics for reefs in Inlet Creek, South Carolina, January 1998. S = Species Richness, H' = Shannon-Weiner Diversity Index, r = Pearson product moment coefficients, p = Probability of r = 0. Sample size, n = 9 per site for each in A and B.*

Oyster C. virginica	Mean # species	S	H'	Epifaunal Invertebrates					Xanthid sp.	
				Total Abun.	Total Biomass	Xanthid Abun.	G. demissa Abun.	G. demissa Biomass	E. depressus Abun.	P. herbstii Abun.
A. Experimental Reefs										
Abundance										
r		0.103	0.513	0.055	−0.118	0.761	0.775	−0.218	0.706	0.605
p	17.67	0.791	0.158	0.888	0.762	0.017	0.014	0.574	0.034	0.085
Mean Height										
r		0.636	0.070	0.832	0.599	0.374	0.285	0.542	−0.046	0.722
p		0.065	0.858	0.005	0.089	0.321	0.457	0.132	0.906	0.028
B. Adjacent Natural Reefs										
Abundance										
r		−0.036	0.225	0.661	0.105	0.495	0.745	0.092	0.475	−0.183
p	18.78	0.927	0.560	0.053	0.788	0.175	0.021	0.814	0.196	0.637
Mean Height										
r		0.203	−0.169	−0.084	−0.285	0.218	−0.144	−0.309	−0.021	0.608
p		0.600	0.664	0.829	0.457	0.572	0.712	0.418	0.958	0.083

study on the experimental reefs (Figure 7G). In contrast, the xanthid crab *Panopeus herbstii* abundances varied in a similar manner on both reef types throughout the study (Figure 7H).

Correlation coefficients between oysters (mean abundance and shell height) and community metrics and dominant species revealed several significant positive relationships on the experimental and natural reefs (Table 2). For the experimental reefs, the abundance of the ribbed mussel *Geukensia demissa* and the xanthid crab *Eurypanopeus depressus* varied positively with total oyster abundance, while total numbers of epifaunal invertebrates and the abundance of the xanthid crab *Panopeus herbstii* were positively correlated with oyster height (Table 2A). On the adjacent natural oyster reefs (of unknown age), the only significant correlations were between overall oyster abundance versus total epifaunal densities or overall mussel abundance (Table 2B). No significant negative correlations were observed between either oyster abundance or size and any of the other variables.

DISCUSSION

Understanding the relationship between the development of oyster populations and other reef-associated organisms is a key element in evaluating the ecological success of oyster reef restoration efforts. The two studies outlined here were each de-

signed with different specific goals in mind; nevertheless, they provide an opportunity to examine several aspects of community development in relation to oyster populations on reefs from very different systems. The Rappahannock reefs are relatively large, subtidal mounds extending several meters above the seabed. In contrast, the South Carolina reefs, both natural and experimental, are relatively small by comparison, located entirely within the intertidal zone, and generally extend 10–30 cm above the upper sediment surface; although oysters extend 1–3 m or more from the low intertidal to upper intertidal as reefs. The reefs in the two systems are also at very different stages of development, with less than two years since construction for the Rappahannock River reefs compared to from six to seven years for the South Carolina intertidal reefs. Differences in reef morphology, experimental design, and sampling techniques make direct statistical comparisons of data from the two systems inappropriate. However, consideration of patterns within each system should make the general conclusions informative within a region or reef type (i.e. subtidal or intertidal).

Central to our objective here is to ask whether or not successful ecological restoration of oyster reefs is dependent upon various oyster population attributes such as "abundance" or "size" (as measured here by shell height or indirectly as bio-

mass). The reefs at the Rappahannock River site were still too young to assess patterns in relation to market-sized oysters, but they do allow us to examine the relationship between the early development of oyster populations and reef-associated organisms. The reef bases in the Rappahannock River were constructed in August 2000 after natural oyster recruitment had occurred. Samples taken during the early summer of 2001, prior to the peak of oyster recruitment in the region, found no oysters on the reef substrate. By the summer 2002, two age classes of oysters were evident on all of the reefs at densities ranging from 77 to 277 oysters/m². Even at the highest of these densities, oysters do not monopolize the space on the original substrate material and are considerably less abundant than on natural and other restored reefs from the Chesapeake Bay (O'BEIRN *et al.,* 2000). Numerous epifauna, especially barnacles, recruited in large numbers to all of the reefs prior to any oyster recruitment occurring in 2001 (Figure 5). Epifaunal abundances (exclusive of barnacles) increased only slightly over time, as oyster abundance and biomass increased, while barnacle abundances declined with time and presumably reef development.

Though not presented in the Results section, the abundances of transient finfish averaged across all of the reefs over time revealed a strong seasonal pattern, but no clear inter-annual pattern that could be related to oyster abundance or biomass. This study did not include any natural "control" reefs for comparison, so we are unable to relate the various descriptors of the reef assemblages to "natural reefs" and must rely on comparisons with oyster abundance and "size" (most common measurement is shell height or calculated biomass) across experimental reefs. This is in large part due to the fact that there are few or no healthy reefs for comparison as there are in the South Carolina study.

In contrast to the observation for Virginia that larval supply may play a significant role in restoration success without the significant addition of "seed" oysters to jump start reef oyster populations, South Carolina restoration success appears to be simply the result of the addition of the limiting substrate, oyster shell. The experimental reefs in Inlet Creek, South Carolina, did have extensive natural reefs for comparison, and over the time period from 1995 to 2000 they failed to converge with the natural reefs, as measured by either total oyster density or abundance of market-sized >75 mm oysters observed on the natural

reefs. Using our historical statewide South Carolina data, oysters >75 mm typically make up less than 10% of all reef oysters, with a maximum of 18% at only two of the sites to date. Also, although the filtering capacity of a mature oyster reef may not have been reached due to low oyster initial densities, mussels recruited to reefs in large numbers (as high as 1,500/m²), potentially providing previously unrealized benefits, not noted for oyster reefs before (COEN *et al.,* 1999). Nesting sites for resident fish are also critical, as is a complex three-dimensional structure for the associated decapod crabs (GRANT and MCDONALD, 1979; BREITBURG, 1999; COEN *et al.,* 1999; MEYER and TOWNSEND, 2000; GRABOWKSI, 2002; GLANCY *et al.,* 2003). Although oysters are not necessary to establish some of these ecological benefits, sustainability over time and augmentation of these benefits (*e.g.,* increased habitat) does require establishment of oyster populations.

Total epifaunal abundance and epifaunal diversity (available only for the period from 1996–1998) did not show temporal patterns (with increasing age) related to either oyster abundance (= density) or "size" (shell height or biomass) over the same time period, but epifaunal abundance on the experimental reefs did approach that found on the natural reefs in January 1997, largely as a result of gastropods (2 spp.) and mussels (2 spp.) recruiting in large numbers to the experimental reefs. Temporal patterns of abundance were similar for some species on the experimental and natural reefs (*e.g., Panopeus herbstii*) and different for others (*e.g., Geukensia demissa*), though the latter did have similar abundances during 2001 when oyster abundances on the two reef types began to converge.

We used correlation rather than regression in analyzing relationships between oysters and various components of the reef assemblage, because we were lacking specific information regarding cause and effect relationships among the assemblage entities and the observed oyster populations. We can hypothesize that positive relationships might be associated with: (1) increased habitat heterogeneity, (2) the provision of refuges, (3) availability of nesting sites for resident fishes (BREITBURG, 1999), and (4) enhanced benthic-pelagic coupling. Conversely, competitive interactions for (1) space and (2) food, as well as (3) exclusion of some species from refuges, could result in negative relationships between oysters and other species. Alternatively, there may be no direct

causal relationship, and the parameters may co-vary in relation to some other factor (*e.g.*, local water quality, larval supply, or food availability). It is informative that of the 15 significant (and 5 marginally insignificant) correlations out of a total of 78 examined (or 19% significant) that we observed between oysters and the evaluated community descriptors or dominant species across both studies and various reef types, *all* but one were positive, the exception being epifaunal invertebrate diversity in relation to oyster biomass on the Rappahannock reefs. For the Virginia subtidal reefs, the most consistent pattern observed was a positive relationship between resident finfish (total abundance and *G. strumosus*) and all measures of oyster density (total abundance, year class 2 abundance, and biomass). For the South Carolina study, three of the seven (or 43%) significant invertebrate correlations (Table 2A) observed for the experimental reefs were with total oyster density, while only one of the seven was significant for natural reefs (Table 2B). For mean height, only two of the seven and none of the seven were significant for the experimental and natural reefs, respectively (Table 2). For the experimental reefs where oyster density is gradually increasing, key community metrics such as total xanthid crabs and the mean abundance of either the mussel *G. demissa* or the xanthid crab *E. depressus* are potentially valuable indicators of reef progress.

Abundances for some species varied differently with oyster abundance or size/biomass depending on whether they were viewed over temporal or spatial scales. For instance, on the reefs in the Rappahannock, the abundance of *Balanus* spp. declines sharply between the summers of 2001 and 2002, during which time mean oyster biomass increases from 0 to ~18 g/m² (Figures 5B and F); however, when we examine the relationship between oyster biomass and barnacle abundance during that last sampling period, we observe a significant positive relationship (Table 1). Similarly, on both the experimental and natural reefs in South Carolina, the abundance of *Panopeus herbstii* is strongly inversely related to mean oyster size (as directly measured here) between 1996 and 2001 (compare Figures 7B and H). Yet, when we examine the relationship between oyster shell height and *P. herbstii* abundance at a single sampling period (January 1998), we find a significant positive correlation on the experimental reefs (Table 2A) and a similar, though marginally insignificant, pattern on the natural reefs (Table 2B). Po-

tential explanations for these discrepancies between temporal and spatial patterns include: (1) that in either one or both cases that the organisms in question and oysters co-vary in response to some other factor(s), and (2) that the magnitude of temporal variations in oyster abundance or "size" (shell height or biomass) over the course of these studies exceeds those observed at any one time across treatment replicates and thus represents a more robust test of the effects of oysters.

A correlational approach alone will not suffice to truly evaluate the relationships between oyster populations and the ecological functions of restored oyster reefs. We still need to develop a better understanding of specific interactions between species. For instance, we did not observe a consistent relationship between either the temporal or spatial patterns of oysters and xanthid crabs at either study site, despite the fact that xanthid crabs are an important predator on small oysters, while also providing a refugia for the same crabs and other resident finfish (COEN *et al.*, 1999a; GRABOWSKI, 2002, *in press*). Direct and indirect effects of predator-prey interactions among reef-associated organisms along with their relationship to oyster population structure, need to be clarified. Further, the consequences of the competing roles that oysters play in facilitating the establishment of some species by providing hard substrate, and in competing with many of those same species for space and food, are not well understood. Many resident fish require large, clean, and dead articulated shells for complex life histories (BREITBURG, 1999; COEN *et al.*, 1999a). Additionally, we suspect that there are numerous aspects of reef morphology, location within respect to tidal range, and position in the landscape affecting the development of reef communities that have yet to be clarified (GRABOWSKI, 2002, *in press*).

As PALMER *et al.* (1997) point out, choosing restoration endpoints is a crucial and often difficult task in ecological restoration. Habitat restoration success should not be dependent solely on the growth/survival of the restored species (CRAFT *et al.*, 1999). A focus only on the resource (*e.g.*, harvestable oysters, fishing mortality) will miss possibly critically important measures of reef restoration success (*e.g.*, benthic pelagic coupling, hydrodynamic effects). In a similar vein, we need to better understand how feedbacks work in healthy and degraded systems and whether their restoration results in alternative states not predicted

from past observations and recent work (SUDING, 2003).

Declines in *Crassostrea virginica* abundances throughout much of the U.S. Atlantic coast have had important fisheries and ecological implications (NEWELL, 1988; KAUFMAN and DAYTON, 1997; PETERSON and LUBCHENCO, 1997; COEN *et al.,* 1999a; JACKSON *et al.,* 2001; PETERSON *et al.,* 2003). Fisheries restoration is, undoubtedly, a desirable restoration endpoint and the explicit goal of numerous restoration efforts. However, it is restoration of lost ecological functions provided by oyster reefs that has been the focus of most recent efforts. While our results reveal positive correlations between the diversity and abundance of reef-associated species and the abundance and direct or indirect measure of oyster "size" (shell height or biomass), they do not indicate that market-sized oysters are requisite for supporting an abundant and diverse community. Although South Carolina experimental reefs have not converged with the natural reefs, even after six years, using numbers of oysters or some measure of vertical complexity of oyster clusters versus the natural reefs, they are persisting with slowly increasing oyster populations, and they support a diverse assemblage of resident organisms. Similarly, the Rappahannock reefs, at the time of final sampling, were only two years old and did not yet support any market-sized oysters. However, they did support resident and transient community assemblages, many of which were positively correlated with the abundance and size (shell height or biomass) of oysters on the reefs. Until we develop a more thorough understanding of the individual species interactions and mechanisms linking oyster population structure to the composition and diversity of reef communities, we suggest that oyster abundance and some measure of "size" (age) structure provides a quantitative measure of restoration success, but harvestable quantities of market-sized oysters are not required for achieving some level of ecological restoration.

In the future, we need to develop and evaluate restoration progress by using standard criteria that can be applied to projects or programs being conducted over a wide geographic range. In some cases, it may be easier and more cost effective to measure surrogate or indirect benefits (*e.g.,* filtering, habitat use) than to focus on the oyster populations alone. For example, seston uptake might be able to estimate the total effect of the oyster reef (constructed or natural) community on water quality by quantifying the amount of the water column that is cleared of seston (GRIZZLE and LUTZ, 1989). This is one of the major "ecosystem services" often touted in the oyster restoration literature, but rarely quantified.

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