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Oyster Reef Habitat Restoration : a synopsis and synthesis of approaches; proceedings from the symposium, Williamsburg, Virginia, April 1995

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Oyster Reef Habitat Restoration:
A Synopsis and Synthesis of Approaches

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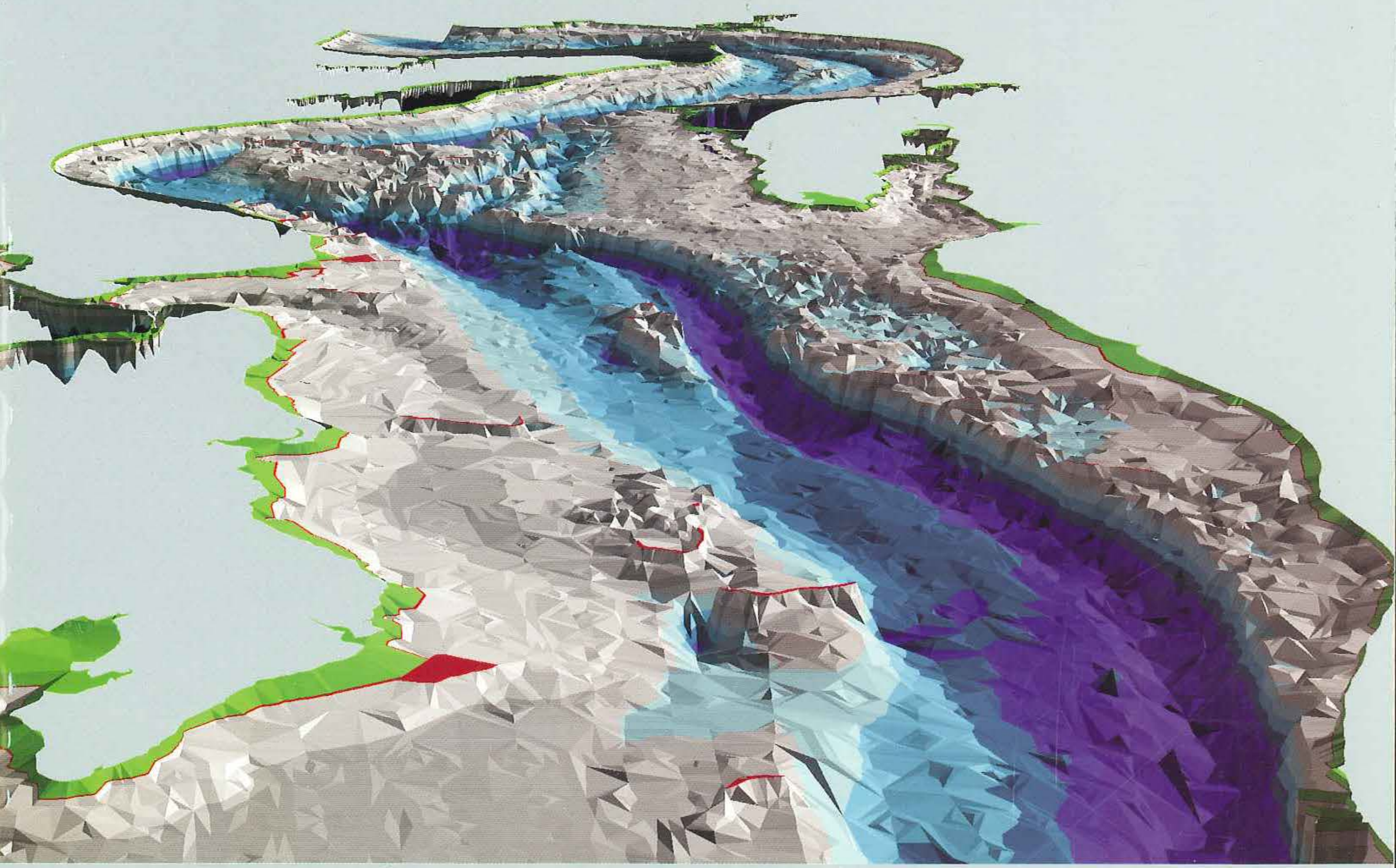

Proceedings from the Symposium • Williamsburg, Virginia • April 1995

Table of Contents

Introduction and Overview

The eastern oyster, Crassostrea virginica, *supported subsistence fishing by native American and early European colonists along the Atlantic and Gulf coasts of North America for centuries. Over the past 125 years it has also supported a major commercial fishery; however, that fishery is in decline throughout much of its range and in some areas, like the Chesapeake Bay, has collapsed. In response, most states from Connecticut to Texas along the U.S. Atlantic and Gulf coasts support some form of oyster enhancement effort. The rationale for these efforts has, until very recently, been entirely directed towards increasing or sustaining oyster harvest. A growing body of evidence indicates that oysters and the habitats that they generate provide important ecosystem services. The widely recognized potential for oyster filtration to affect water column processes (e.g., Newell 1988) and their potential as ecosystem engineers (sensu Jones et al. 1994) to provide habitat and support biodiversity qualify them as keystone species in many estuaries. Indeed, there is reason to believe oyster reefs should be characterized as Essential Fish Habitat under a recently adopted management approach in the U.S. (Coen et al. 1999).*

This volume has its origin in a symposium held in Williamsburg, VA in April 1995, though most of the chapters have been significantly revised in the interim. The primary purpose of the symposium was to bring together state fisheries managers involved in fisheries-directed oyster enhancement and research scientists to refine approaches for enhancing oyster populations and to better develop the rationale for restoring reef habitats. We could hardly have anticipated the degree to which this been successful. In the interim between the symposium and the publication of this volume the notion that oyster reefs are valuable habitats, both for oysters and for the other ecosystem services they provide, has been gaining wider acceptance.

This volume is divided into five sections. The first is comprised of three chapters which use historical data sets to reconstruct the distribution and morphology of natural oyster reefs. In Chapter 1, Hargis traces the development of oyster reefs in the Chesapeake Bay through the Holocene, summarizing the processes which led to their development and the fishing activity which contributed to their demise. Kennedy and Sandford continue this vein in Chapter 2, describing the morphology of unexploited oyster reefs and early attempts to restore them. In Chapter 3, Smith and colleagues compare historical surveys of oyster reefs with current distributions to estimate losses of oyster resources and reef habitat.

In part II, efforts to manage and enhance oyster fisheries in several states are reviewed. Leard and co-authors provide a very thorough overview, in Chapter 4, of the oyster management and restoration efforts by Gulf coast states over the past 30 - 50 years, while in Chapters 5 & 6 specific restoration efforts in Louisiana and Alabama, respectively, are examined in greater detail. Marshall and colleagues detail oyster restoration efforts in North Carolina throughout this century in Chapter 7, pointing out successes and failures and suggesting new directions which emphasize habitat functions. Virginia's program of reconstructing reefs and brood stock sanctuaries is described in Chapter 8. Collectively, these chapters provide a synopsis of approaches which have met with varying degrees of success in enhancing oyster production. However, they do not examine specific mechanisms and or address ecological benefits of oyster reefs.

Part III examines various aspects of oyster reef ecology—including factors which contribute to the development of populations of oysters and other organisms on reefs, and the ecological impacts of oyster reefs–across a range of spatial scales. In Chapter 9, Coen et al. describe a large-scale experiment in South Carolina which is documenting the development of oyster populations and other assemblages on constructed reefs. The importance of interstitial space and vertical relief on oyster recruitment are examined in Chapter 10 by Bartol and Mann. In the next chapter, Coon and Fitt describe a very novel approach for enhancing oyster settlement in the field using a settlement inducing chemical. Drawing on information from other systems, Osman and Whitlatch in Chapter 12 examine processes which control local and regional recruitment of sessile invertebrates from two different coastal habitats—a California kelp community and fouling communities in Connecticut—and draw parallels for restoration of oyster reef communities. The next two chapters examine the utility of viewing oysters as metapopulations and using spatially explicit models to guide management and restoration strategies. In Chapter 15, Posey et al. examine the role of predation refugia in establishing patterns of reef utilization by fish and decapods, while in the subsequent chapter Breitburg examines the structural aspects of reefs which affect resident fishes. Chapter 17 describes flume experiments which highlight some of the difficulties associated with measuring the effects of oyster filtration in the field, while Dame takes the bigger view in Chapter 18, summarizing data on the role of oysters in affecting materials flux in estuarine ecosystems.

Part IV contains three chapters which examine the use of alternative materials for creating oyster reef habitat. Chapters 19 and 21 review case studies using dredge material, while Chapter 20 evaluates the use of several alternatives to oyster shell as cultch material.

The final section addresses some management options for restoring oyster reefs and developing sustainable fisheries. In Chapter 22, Paynter gives an overview and commentary on a restoration strategy in Maryland which emphasizes zoning harvest and restoration activities based upon disease pressure. Next, Hargis and Haven discuss the importance of oyster reefs for supporting sustained oyster production and suggest an approach towards restoring those habitats. In the final chapter, Supan et al. provide a cost accounting of the use of hatchery-produced oysters to supplement natural recruitment and suggest that such techniques can be used prudently to sustain an oyster fishery.

An increasing recognition of the ecological role of healthy oyster reef habitat, both for sustaining oyster populations and supporting broader ecosystem functions, can be expected to fuel greater efforts in the future to protect and restore these habitats. While at times these efforts may seem at odds with the short-term interest of the oyster fishery, we are confident that in the long run they not only provide the most effective means for restoring sustainable harvests, but also for developing a larger constituency in support of restoration efforts.

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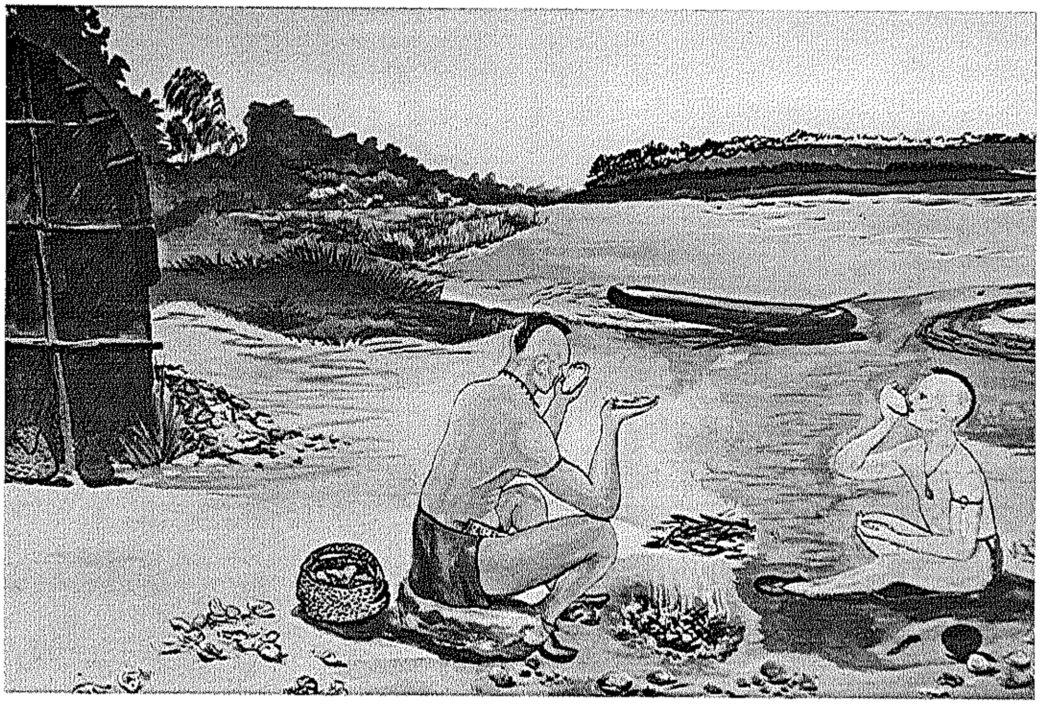
Part I
Historical Perspectives



The Evolution of the Chesapeake Oyster Reef System During the Holocene Epoch

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Abstract

The oyster industries of Virginia and Maryland were based upon adult and juvenile oysters, and their shells, produced naturally on the reefs of the Chesapeake oyster reef system. Without those reefs the billions of bushels of live oysters and shells taken by humans could neither have been produced naturally nor harvested and the valuable social and economic activities derived therefrom would never have occurred.

The origin and development of the formerly massive, naturally self-renewing Chesapeake reef system were directly associated with the evolution of the Bay. Its destruction can be linked primarily to the increase of humans around the Bay and beyond and their demand for oysters and shells. Both phases, development and destruction, of reef history have occurred during the last three-quarters to two-thirds of the post-glacial Holocene period, around 7,000 years or less.

The current episode of global warming, begun about 18,000 years ago, sent melting ice cap waters seaward. Atlantic waters bearing ocean salts and oyster larvae rose erratically and, after a few significant retreats, advanced between the promontories now called the Virginia Capes into the developing Bay about 7,500 BP. By about 4,500 BP the Bay's head passed the latitude of Annapolis, reaching its present location about 2,500 BP. As larvae-bearing waters reached suitable sites, setting occurred on available cultch and reef formation began. Reef formation moved inland with advancing brackish waters until the reef system extended most of the length of the Chesapeake, about 160 nautical miles (296 km). On its sheltering reefs successive generations of colonial *Crassostrea virginica* struck, grew, reproduced and died leaving their progeny and shells behind and reefs and reef fields increased and expanded as did associated oyster populations.

When English colonists arrived in 1607 AD the reef system extended throughout the Bay and the estuarine portions of its tributaries and was self-maintaining. Nearly 200 years ago the Chesapeake oyster populations and their reef system began to shrink under pressures of increasing harvesting (and other man-affected factors such as increased sedimentation due to extensive deforestation and destructive agricultural practices). Today, destruction of the oyster's prime habitat in the Chesapeake, the natural, self-renewing upthrusting oyster reefs, is nearing completion. When they are gone it will have taken somewhat less than two centuries to destroy some 6,000 to 7,000 years of nature's works.

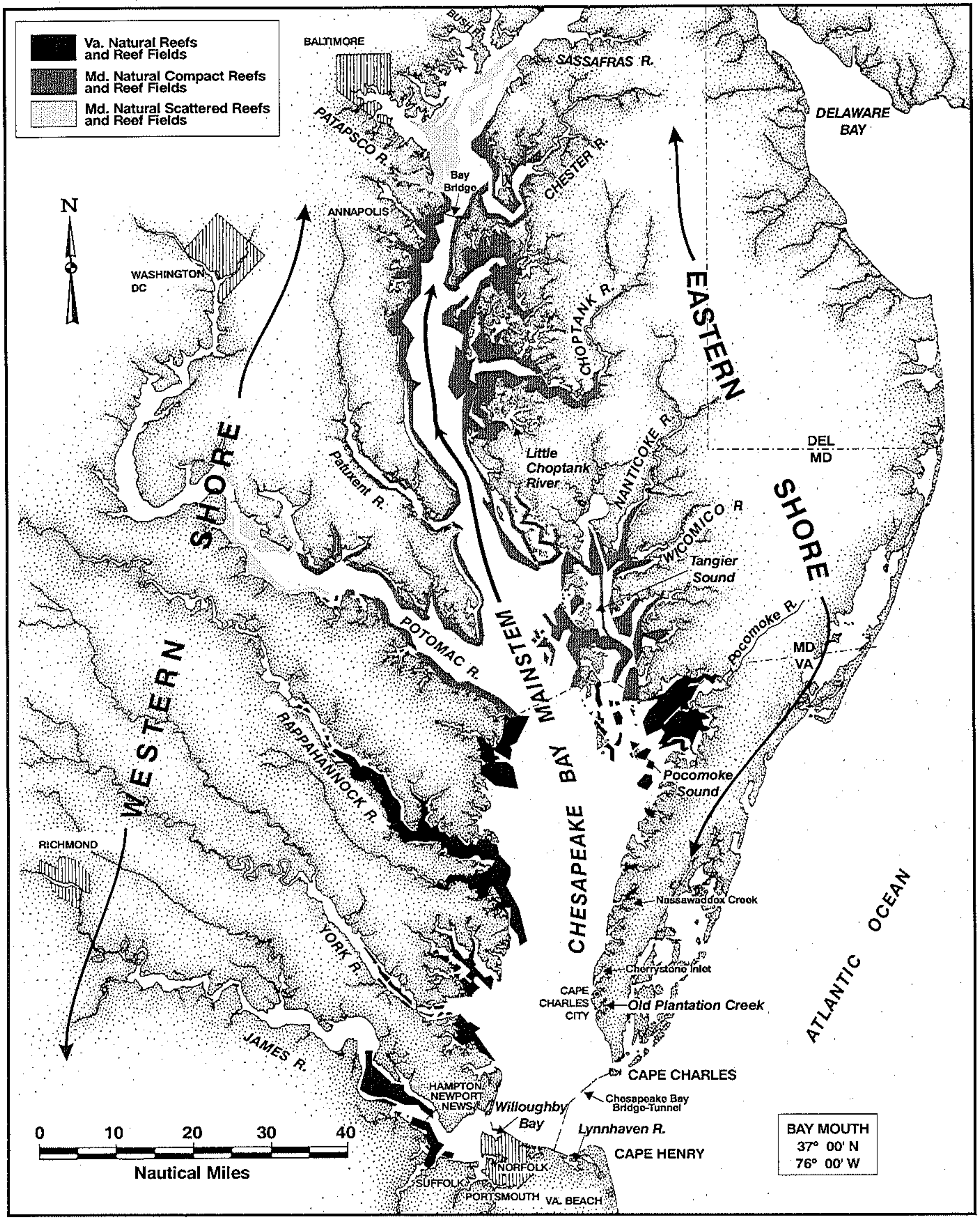


Figure 1. *The Chesapeake Oyster Reef System of the mainstem of the Bay and its tributary estuaries. A composite of the chart of Stevenson (1894), which depicted the reef system of Maryland (including the Potomac River and the mainstem of the upper Bay and its tributaries), and that of Baylor (1894) with later modifications, for Virginia's Chesapeake and tributary waters, this chart also identifies the principal tributaries of the Bay and the places mentioned in the text but not illustrated elsewhere.*

Introduction

Most oysters of the Chesapeake Bay have occurred in large colonial aggregations extending almost the entire lengths of its mainstem and of the estuarine portions of its tributaries (Figure 1). Chesapeake Bay oystermen have called these aggregations oyster beds, bars, banks, bottoms, shoals, and rocks. By these or any other names they are really reefs, as has long been recognized in waters of the South Atlantic states and those along the Gulf of Mexico (Chestnut 1974). Like those made by corals, oyster reefs were and their remnants still are important to the well-being and productivity of the colonial animals which established, formed, and maintained them.

In 1894, Stevenson, reporting on his study of the oyster industry of Maryland and the resources it depended upon, correctly identified the Chesapeake oyster rocks as reefs. He also established their importance to Bay oyster populations and charted their general extent and density in Maryland waters (upper portion of Figure 1). Further, he noted early warning signs of the decline of the reefs and their oysters and its bearing on the increasingly precarious future of the resource. J. W. Bailey, scientist at the Virginia Fisheries Laboratory (VFL), predecessor of the Virginia Institute of Marine Science (VIMS), referred to oyster rocks of the York River as reefs in 1940. Further, he reported a significant decline in the height of one York reef (Page's Rock) during the period between 1858 and the 1930s as indicated by comparisons of soundings reported on relevant charts of the U.S. Coast Survey (USCS) and its successor, U.S. Coast and Geodetic Survey (USCGS). This retrogression he attributed to harvesting (Bailey 1940). About 10 years later Nelson Marshall, second Director of the VFL, determined that the oyster bars of the James River seed area (Figures 1 and 2) had declined in height under pressures of harvesting and natural forces based upon comparison of soundings made in 1854-55 and 1871-73 by the USCS and in 1943-48 by its successor, the USCGS. He called the intertidal portions of these bars—oyster reefs (p 176, Marshall 1954). [Unfortunately, his restriction of the term reef to the intertidal parts of the oyster bars was too narrow. As with coral reefs the entire structure (biocoenose), submerged as well as intertidal, is "the oyster reef".] Recognition of the shrinkage of oyster reefs and their diminishing contribution to the welfare of oyster populations of the Chesapeake (and of the industry dependent thereon) prompted a review of their general histories during geological and recent times. The results of this study are reported herein.

I recognize two *basic* types of natural oyster reefs, *upthrusting reefs* (protruding upward from the bottom and *fringing reefs* extending outward from and usually attached to adjacent exposed coastal formations or shorelines.) The former usually occur in deeper estuarine and enclosed coastal waters such as the Chesapeake and Delaware bays, the mouth of the Hudson River, and Long Island Sound—especially "drowned" river valleys. The latter are usually found in

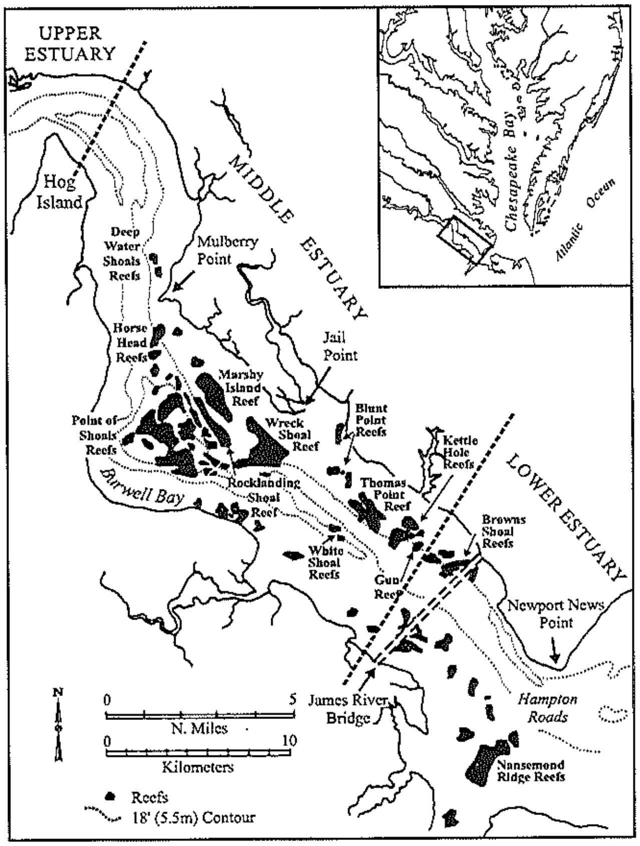


Figure 2. Reefs and Reef Fields of the James River Estuary exclusive of those in Hampton Roads, as of 1878 and 1879 and later. (Names of of some reefs excluded for simplicity.)

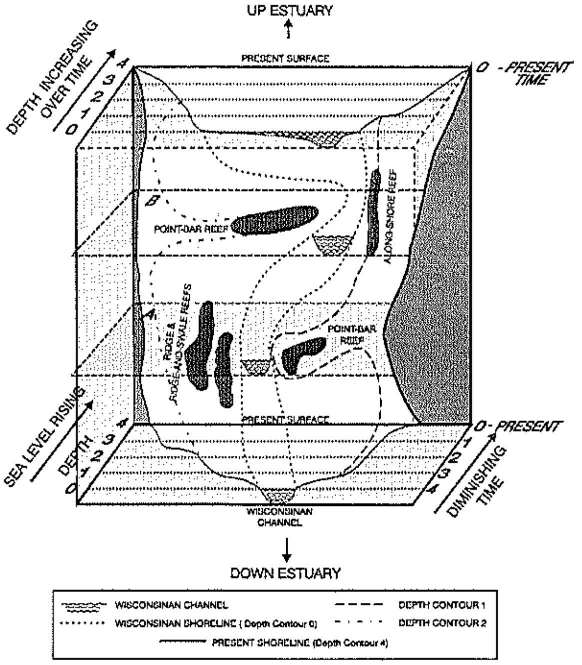
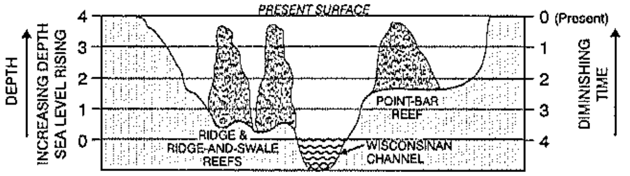
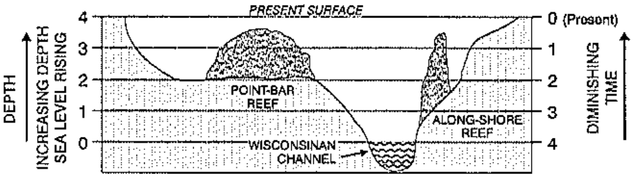


Figure 3a.



Cross-Section A.
Looking Up-Estuary, Ridge-and-Swale Reefs on Wisconsinan Terrace (between depth contours 0 and 1). Point-Bar Reef on 1st Terrace above Wisconsinan Terrace (between depth contours 1 and 2).



Cross-Section B.
Looking Up-Estuary, Along-Shore Reef on 1st Terrace above Wisconsinan Terrace (depth contour 1). Point-Bar Reef on 2nd Terrace above Wisconsinan Terrace (depth contour 2).

Figure 3b.

Figure 3.
Formation of Point-Bar, Along-Shore and Ridge-and-Swale Reefs Over Time with Rising Sea Level. Figure 3a is a 3-D presentation which is best viewed beginning from bottom of figure and moving eyes upward.

semi-protected shallow embayments, lagoons, creeks and in sheltered, shallow tributaries of larger estuaries. As with most such biological categories there are intergrades and many, probably most, Chesapeake upthrusting reefs began as fringing reefs attached to the shore (i.e. point-bar and along-shore reefs) or to some mid-stream, elongated prominence or "gut" (i.e. ridge or ridge-and-swale reefs, figures 3a and 3b). As sea level rose, the fringing reefs became surrounded and separated from the shore. Afterward, other hydrographically-significant factors, such as erosion of adjacent shores, intervened and isolation increased. Ridge and ridge-and-swale reefs were isolated early-on and their isolation increased further and further as sea level continued to rise. Reefs which were attached to or close to ancient high-energy promonitories, shorelines and spits, could have lost their landward connections because of inshore erosion, heavy sanding and/or siltation, wave and current induced bottom movements, lack of suitable cultch inshore of the developing reefs, and excessive predation by land animals. As human populations and their use of oysters increased, nearby (handy) inshore oyster populations would have been subjected to increasing harvesting pressure early on. Even sparse aboriginal human populations would have harvested readily accessible shallow water oyster populations first and most heavily. In some places, such as the Burwell Bay-Mulberry Island reach of the middle James estuary, ridge, ridge-and-swale, point-bar and along-shore reefs are close together, often superimposed (Figure2).

De Alteris (1988) described and illustrated the basic process of reef formation in his discussion of the evolution of the Wreck Shoal reef field of the middle James estuary of Virginia. My concept of the development of each type of upthrusting reef (i.e. point-bar and along-shore fringing reefs and ridge and ridge-and-swale reefs) is illustrated by Figures 3a and 3b.

Other papers of this volume will feature the comparatively low-profile shallow water reefs, fringing or isolated, so common in the shallow lagoons and embayments of the Eastern Shore of Virginia, Maryland and lower Delaware and similar waters elsewhere, especially along the South Atlantic and Gulf Coasts. The, generally, higher profile upthrusting reefs (Figure 4) of the deeper and more salinity-variable Chesapeake Bay (and similar estuaries) are the principal subjects of this paper. In all probability the same basic biogeological and hydrographic principles apply to all reef types.

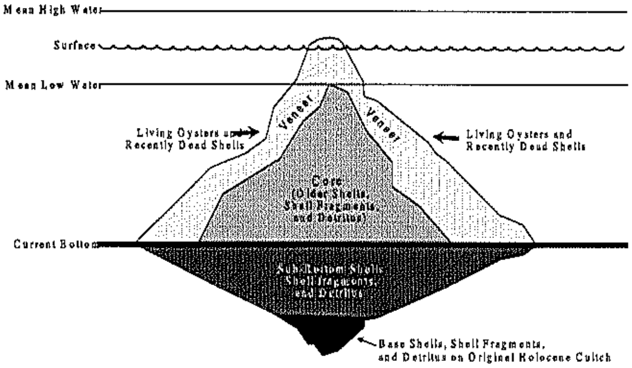


Figure 4. *Diagram of an "Upthrusting" Chesapeake Oyster Reef, the oyster's (a communal animal) "most-hospitable" habitat. (Details of the early post-Wisconsinan, "original Holocene cultch" Base are hypothetical. To my knowledge, no one has actually carefully dissected the sub-bottom portion of an upthrusting reef.)*

The shapes, location, and extent of oyster reefs were determined by the natural geomorphological characteristics of their sites and the hydrographic and biological features pertaining during their establishment and development. In recent times oyster harvesting and shell mining and, to a far lesser extent, the sediment-increasing activities of man have influenced these aspects (Hargis and Haven, Chapter 23, this volume).

In some ecologically favorable areas of the Chesapeake, such as the James estuary of Virginia, or Pocomoke and Tangier Sounds, shared by both states, and the mainstem and north shore of the Potomac River and the upper Bay region of Maryland (i.e., Little Choptank River to Chester River—and elsewhere), numerous upthrusting reefs developed close to each other, even merging in places (Figures 1 and 2). Such aggregations of reefs may be termed reef fields. The extensive natural (self-establishing, self-building, and self-sustaining—formerly) reefs and reef fields of the Bay and its tributary estuaries are here referred to as the Chesapeake Bay's Oyster Reef System (Figure 1).

The utility and economic value of most biological resources whose useful and sought-after individuals (edible and marketable units) are small and of relatively little value by themselves are largely based upon accessible and economically harvestable aggregations of numerous massed individuals. The reefs and reef fields of the Chesapeake reef system provided such aggregations. Without the reefs and reef fields of this great estuarine oyster reef system and their massive accumulations of easily exploited self-renewing populations the once extremely valuable public and private oyster industries of the Chesapeake could not have developed.

Though recognized only recently (unfortunately) the Bay's Oyster Reef System (biocoenose) was its most important, characteristic and productive community before its destruction.

Materials and Methods

Recorded observations (anecdotal, hydrographic or otherwise) of oyster reefs of the Chesapeake can be no older than about 400 years, the time when Europeans began to seriously explore and, later, colonize the area. Information of prior times must be gleaned from writings on historical geology, paleontology, and stratigraphy and written or verbal reports of current researches or reviews involving these and related disciplines.

This study is based partially upon certain historical anecdotal accounts of early explorers, navigators, colonists and later observers. An excellent review of many of them was provided by Wharton (1957) from which I have drawn.

Being primarily concerned with successful voyaging, early marine navigators and pilots recorded very little information pertaining directly to oyster reefs. Such hydrographic information as they left related mostly to location, recognition and avoidance of reefs as perils to navigation. However, in some instances it is possible to work backward from current or recent oyster ground surveys and hydrographic charts to charts or maps of earlier times, such as the 1607 AD chart of Robert Tindall (Figure 5), which illustrated shoals in the Burwell('s) Bay reach of the upper James estuary, calling them Tindall's Shoals (Morrison and Hansen 1990). A Dutch chart of Powhatan's River (another early name for the James River) made around 1638 from earlier ship's soundings, shows similar shoals in the Burwell('s) Bay reach of the estuary and below (Vingboons, ca. 1638). Such a comparison indicates that the shoals, almost certainly the prominent oyster reefs now known to have been present in that area from surviving reefs and reef traces (Haven et al. 1981) and from records and charts of earlier James River surveys (Winslow 1882, Baylor 1894, Moore 1910), were there when Tindall and the other navigators and chartmakers involved made their observations almost 400 years ago. It tells little else. The same is true of a few of the soundings and depictions of other early chart makers.

Though governmental entities, such as the British Navy, often surveyed and prepared relatively detailed charts of American coastal areas involved in naval actions or associated military activities, official, organized modern chart-making of North American waters did not begin until the British Admiralty established its hydrographic office in 1795. After that time the accuracy and utility of nautical charts improved. Prior to then most charts were based upon information obtained on an ad hoc basis and many were privately developed and maintained. Hydrographic surveying of those times was unsophisticated and early navigators, or their sponsors, often regarded soundings and sailing

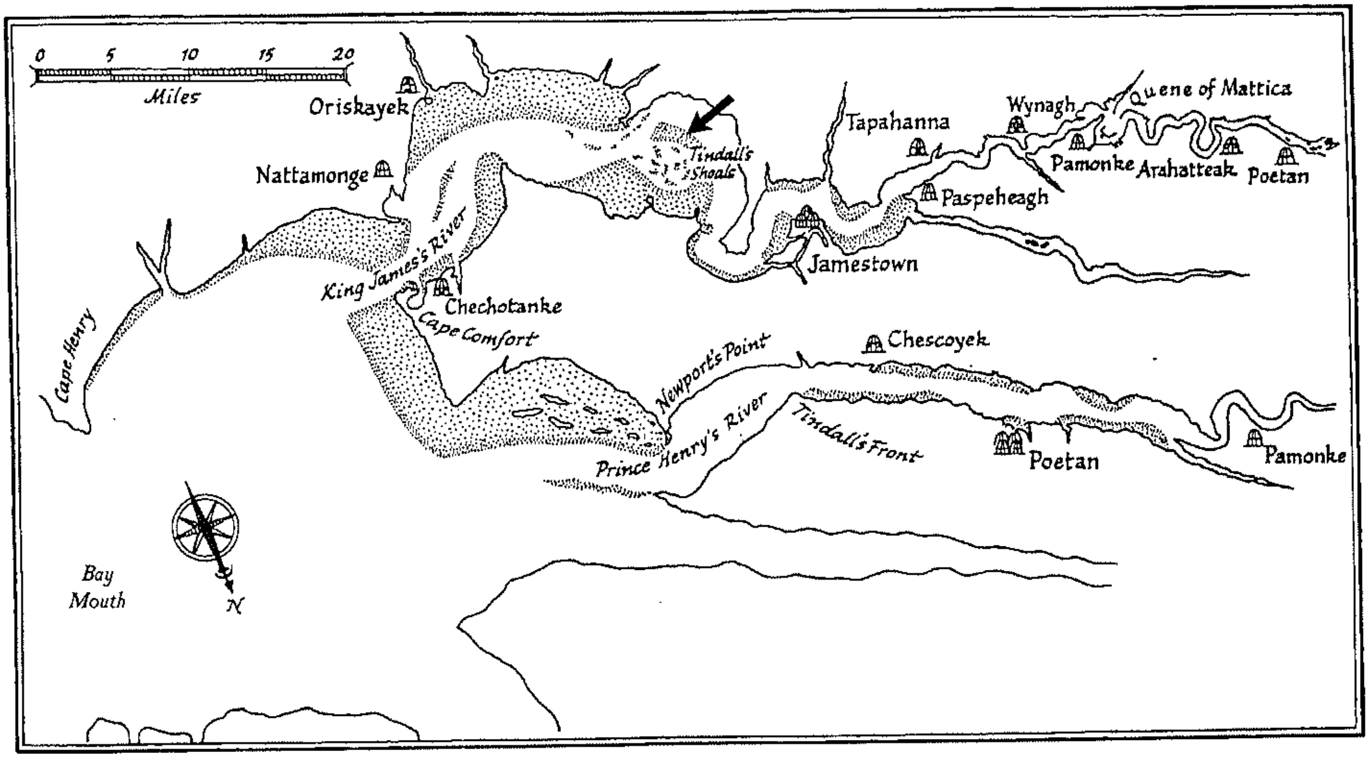


Figure 5. *The reconstruction of Robert Tindall's chart (1607) which appeared as Figure 1 in Morrison and Hanson (1990). The James River (King James' River) and York River (Prince Henry's River) are depicted with their northwesterly-directed long axes toward the right (i.e. lying on their "sides"), a common orientation of early American charts and maps. Tindall's Shoals (arrow) are in the area of the James Estuary now known as Burwell('s) Bay (see Figures 2, 6, 7 and 8). (Spellings of Indian town names are Tindall's. Shading, including that alongshore, obviously represents shoals, some of which undoubtedly were oyster reefs and reef fields.)*
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instructions as being proprietary and held them closely.

Once the U.S. Coast Survey (USCS), later the U.S. Coast and Geodetic Survey (USCGS) and now the Coast Survey of the National Ocean Service (NOS) of the National Oceanographic and Atmospheric Administration (NOAA), began its hydrographic charting work in 1833, coastal and estuarine soundings of waters around the United States became more accurate and intensive. Certain boat sheets and charts prepared by the Survey have been employed in this study. Of greatest utility thus far have been the two USCS charts with Registry Nos. 1179a and 1179b, approved for registry in 1872 and 1874, respectively. (These registry dates are employed herein as their publication dates, i.e. USCS 1872 and 1874. These two charts, covering most of the estuarine portion of the James, apparently were neither printed nor circulated widely.) Even though these U.S. Coast Survey charts of 1872 and 1874 are not included therein, the extensive review of the history of Chesapeake Bay charts by Morrison and Hansen (1990) provides a particularly valuable and detailed history of surveying and charting of the Chesapeake region and of the resultant charts.

Heavy reliance regarding the late glacial and postglacial history of the Chesapeake region has been given to the writings and/or advice of modern geological scientists specializing in the Chesapeake estuary and/or similar coastal waters. Among them are: R. J. Byrne, C. H. Hobbs, III, J. D. Milliman, M. M. Nichols, and L. D. Wright of the Virginia Institute of Marine Science; G. H. Johnson of the Geology Department of the College of William and Mary; L. W. Ward of the Virginia Museum of Natural History; and J. R. Schubel formerly of Johns Hopkins University and, more recently, of the New England Aquarium, Boston, MA. Information provided by them and/or their relevant publications is included in the text below. Other references from which background material was gleaned are presented in the Literature Cited section.

While a number of geologists and geological references were consulted, establishment of really "tight" estimates of the times at which the events described below proved difficult. Time estimates provided by the various individuals and references differed somewhat. On the one hand, there is genuine disagreement on integration and interpretation of the various types of available data and of their details; on the other, the scarcity of detailed data for certain time periods or geochronically important phenomena prevents precision. Also, the accuracy of some dating techniques allows only approximations of time periods. Nonetheless, available data and consensus permits confidence that the estimated times presented below are reasonably consistent with the evidence and geological opinions at hand.

Results

The earliest available English descriptions of Chesapeake oysters and oyster reefs, called beds, banks, and shoals in at least one Colonial report, were those of certain Jamestown colonists whose writings began shortly following their landing at the place called Cape Henry (Figures 1 and 5) after their ships first entered the Bay (Wharton 1957, Hargis and Haven 1995). Though, with certain exceptions, most notably the 1607 chart of colonist Robert Tindall and the ca. 1638 Dutch chart mentioned above, they did not provide pertinent charts or survey data, colonial observers and later travellers clearly described large shoals of oysters, the crests of which protruded above the water's surface at low tide, and from which live oysters could be harvested directly.

As noted above, log books, boat sheets, and finished charts of the old U.S. Coast Survey and its successors are useful in establishing the geographic locations and rough outlines of some of the Bay's reefs and reef systems. Some were of sufficient detail to allow reconstruction of the elevations and contours of certain oyster reefs in the James River. Figures 6, 7, and 8 were traced directly from charts based upon data acquired during hydrographic surveys made in Virginia's

James estuary by that organization during 1871, 1872 and 1873 (USCS Charts, Registry Nos. 1179 a and b, Registry dates, 1872 and 1874, here cited as USCS 1872 and 1874). These presentations confirm graphically that the intertidal crests of many of the oyster reefs, mentioned in earlier anecdotal accounts, such as those included in Wharton (1957), had persisted for nearly 100 years after the Colonial period ended with the Revolutionary War, or some 264 years after first permanent settlement.

Sustained federal and state interest in the fishery resources and socioeconomic aspects of the fisheries based upon them began soon after the Revolution but did not gain strength until after the massive social, economic, and military disturbances of the Civil War, some 80 years after the Republic was established. The study by Ingersoll (1881), done in conjunction with the 1880 census, incorporated the results of the first extensive examination of the nation's oyster industries . It contains much useful information about the early years of the Chesapeake Bay oyster fishery.

Specific field surveys directed at discovering the location, extent and productivity of oyster reefs of the Chesapeake apparently did not begin until 1878 when Lt. Francis Winslow of the U.S. Navy, then on duty with the U.S. Coast and Geodetic Survey, began his Chesapeake Bay work in the James River estuary of Virginia and then quickly moved his survey team to Pocomoke and Tangier Sounds, shared by Virginia and Maryland (Winslow 1882). These field examinations were followed by the more extensive but less detailed ones of Baylor who surveyed all of the then-recognized public "grounds" of Virginia in 1892 and 1893 and charted them in simple outline form (Baylor 1894). In 1909 H. F. Moore, of the U.S. Bureau of Fisheries, studied the oyster reefs of the James River (VA) in greater detail than either Winslow or Baylor had and provided geographical and density information in the resultant text and charts describing his work (Moore 1910). During the years 1906 to 1912 C. C. Yates, of the U.S. Coast and Geodetic Survey, surveyed

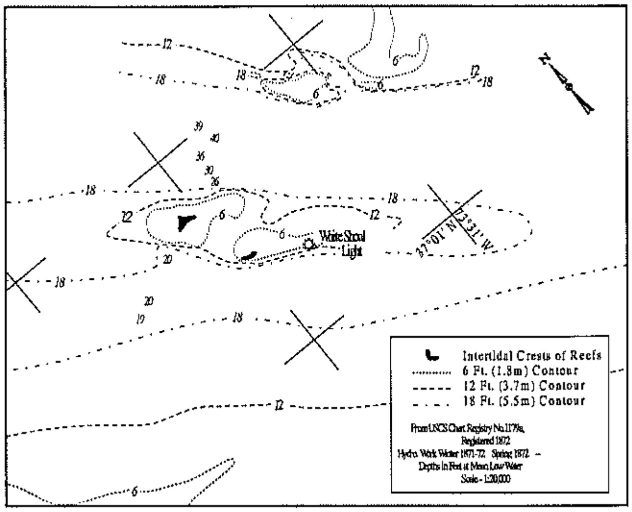

Figure 6. White Shoal Reef Field, Lower Portion of Middle James Estuary

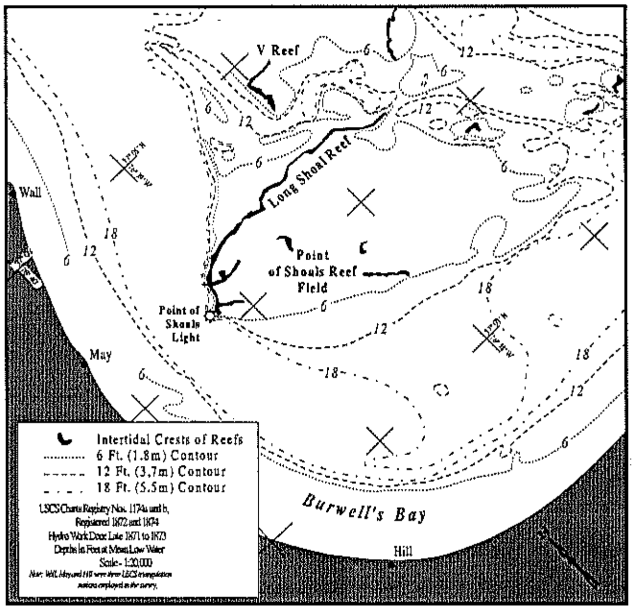

Figure 7. Point of Shoals Reef Field, Middle James Estuary,including dominant Long Shoal Reef and other prominent reefs in the Burwell's Bay complex reef field.

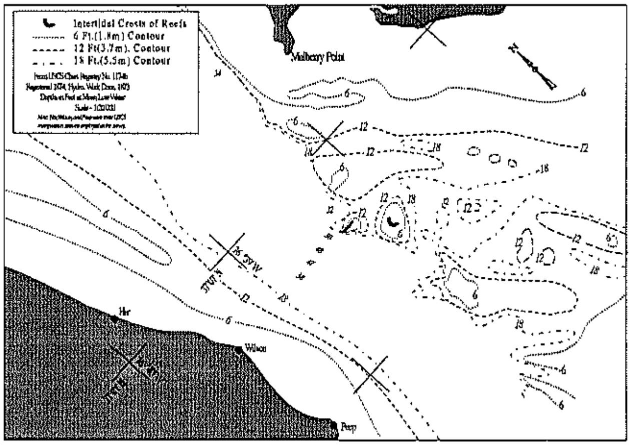

Figure 8. Horse Head Reef Field, Middle James Estuary

the oyster reefs of each Maryland tidewater county bordering waters of appropriate salinity. A series of publications described his results in considerable detail county by county with relevant charts: The entire six-year work is summarized in Yates (1913). Unfortunately, by the time of these efforts, reef destruction had progressed at ever-increasing rates for 100 years or more, resulting in the reduction of most, probably nearly all, of the regularly emergent (intertidal) Chesapeake oyster reefs to the point that their crests no longer surfaced at mean low water (MLW) or any usual stage of the tide. However, the crests of some reefs in the James estuary, and elsewhere, continued to be close to the surface at MLW. When Moore (1910) surveyed these same James estuary reefs in 1909, he reported crest depths as shallow as 2.5 feet (0.76m) and 3.0 feet (0.9m) at MLW, respectively. Assuming reasonable comparability of sounding techniques, sounding stations and of the resulting depth data, it would seem that between 1873 and 1909 the heights or crests of the oyster reefs of the James had declined measurably. Apparently the crest of only one—the upper reef of the White Shoal reef field, still breaks the surface [see National Ocean Service (NOAA) Chart No. 12248] even though it is mostly, or entirely, bereft of living oysters. J. D. Andrews, well-known oyster scientist of VIMS, reports (personal communication) that he was able to stand on and hand-pick numbers of small rounded oysters from the exposed crest of White Shoal Reef as late as 1955. This is possible no more.

As mentioned above, N. Marshall (1954), comparing soundings along selected transects made by the USCS in 1854-55 and 1871-73 with those of the USCGS in 1943, described a loss of 6 inches (15.2 cm) due to harvesting. Though his estimate of crest loss is probably far too small, Marshall's report of a definite reduction in the heights of several James River seed and market area reefs that he had examined was the first quantitative effort published.

By 1981 an extensive survey showed almost no intertidal reefs in Virginia's Chesapeake Bay (Haven et al. 1981) Fathometer traces in typical locations showed tops of hard reef areas in the following depth zones: James River, 5 to 15 ft. (ca 1.5 to 4.6m); Pocomoke Sound, 15 to 20 ft (ca 4.6 to 6.1m); and the Rappahannock River, 10 to 18 ft (ca 3.1 to 5.5m) (Haven and Whitcomb 1983, Whitcomb and Haven 1987, Whitcomb and Haven 1989).

The Chesapeake reef system extended throughout the Bay. Encompassing numerous reefs and reef fields on the Southern Shores of the Bay, it reached from the Lynnhaven River and Willoughby Bay into the James estuary. On the Western Shore, reefs were found in all of the rivers and creeks with appropriate salinities in both Virginia and Maryland, where they extended into waters around and within the mouth of the Patapsco River and northward to slightly above the mouth of the Bush River. On Bayside of the Eastern Shore of Virginia and Maryland they extended up the mainstem of the Chesapeake and were in all of its tributary creeks, rivers and sounds from Nassawadox Creek (or perhaps other creeks below) in Virginia to the mouth of the Sassafras River in Maryland (Figure 1).

Many of these reef fields incorporated more than two reefs. Some individual reefs and reef fields, such as those in the middle estuarine portion of the James River above Blunt Point, known since at least 1909 as the oyster seed area (Moore 1910), were very large (Figure 2). As the oyster industry based upon the Bay's reefs grew and harvesting increased, most reefs or reef fields received individual names. In Virginia there were over 390 individual named reefs at the time of Baylor's survey in 1892 (Baylor 1894). Yates (1913) identified over 700 in Maryland waters. There had been more in each state.

Evolution of the Chesapeake Reef System

Earth's climate has varied considerably through geological time. During the Pleistocene Epoch (from about 2.4 million years BP to about

10,000 BP) wide fluctuations in global atmospheric temperatures resulted in numerous ice ages and warming periods. The paleontological record indicates more than a dozen such periods during the last two million years (Chorlton et al 1983). The cooling phases of the cycle, during which huge glacial ice caps developed around or over Earth's polar regions—extending into lower latitudes in each hemisphere—generally lasted from 100,000 to 125,000 years (Chorlton et al. 1983, Schubel 1981).

During these prolonged periods of intense cold, polar, montane and continental glaciers covered much of the Northern Hemisphere, land and sea, as well (Bailey et al 1982). In the most recent Ice Age, termed the Wisconsinan in North America, the massive Laurentide glacier, covering the northern parts of mid-western and north-eastern North America, extended southwestward from Greenland, Labrador and Hudson Bay reaching as far south as Sunbury in Pennsylvania, which is well below the present city of Wilkes-Barre on the North Branch of the Susquehanna River (Figure 9). Thus, it covered the entire North Branch. It also covered part of the West Branch of the Susquehanna from Sunbury to Williamsport and beyond (Flint 1957, King et al 1974, Mehringer 1988, Redfern 1983). During the depths of the cooling periods great quantities of Earth's freshwater were bound in the snow and ice of glaciers, which averaged a mile or more in thickness, and little reached the oceans. During the Wisconsinan Ice Age the surface of the North Atlantic was as much as 120 m (394 ft) below its current level and the continental shelf of today was mostly above water. At the peak of the Wisconsinan cold period, ice in the ancient "Atlantic" apparently extended as far south as the latitude of current Cape Hatteras with "pack ice" slightly below the latitude of today's Long Island and "drift ice" extending the rest of the way southward.

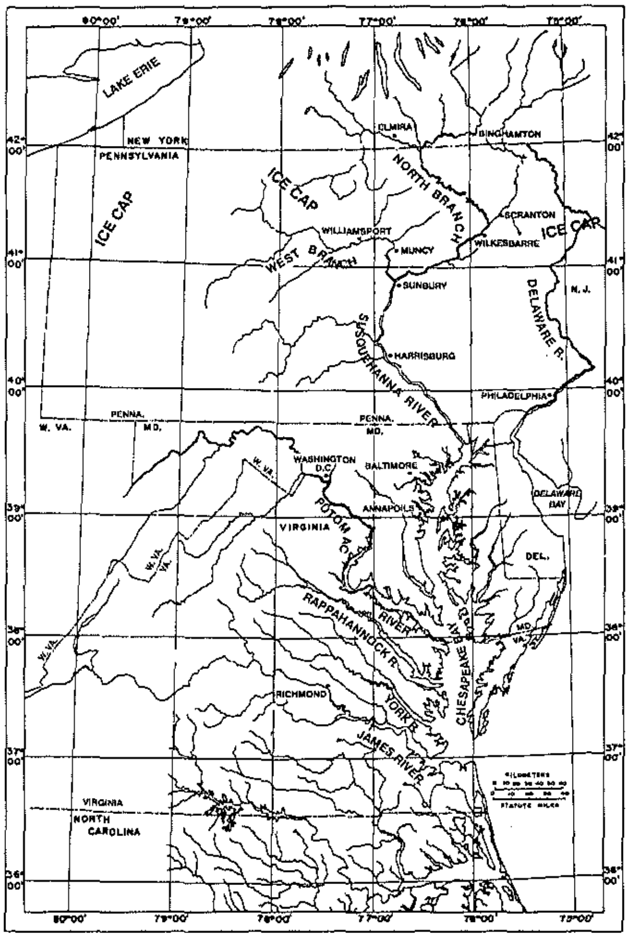

FIGURE 9. Southernmost Extension of Wisconsinan Ice Cap Into Future Chesapeake Bay Drainage Basin.

Alternating with ice ages were periods of warming in the Northern hemisphere -- probably globally. During prolonged warming periods glaciers melted and meltwaters coursed seaward. In the ocean, floating glaciers calved and melted contributing ice floes and melt water as the sea warmed. Sea and pack ice floes melted farther as warming continued. Meltwaters from all stages of glacier, sea ice, and pack ice disintegration and dissolution contributed to rising sea level and transgression. Fluvial and oceanic water on and from the edge of the melting and retreating land and sea ice cap (glaciers and icebergs, etc.) would have been very cold early on. Oceanic waters in the offing of the current Mid-Atlantic would have been much colder than now due to melting of sea ice and icebergs. The physical and biological impacts of this cold water would have been significant. The "North Atlantic" basin filled and, when rising ocean waters reached the ancient coastal river valleys of the "Susquehanna" and "James," intruded into and "drowned" them and created new estuaries. Eventually, "Atlantic" waters reached levels high enough to spill over onto, encroach upon and inundate the previously dry "continental shelves." The warming periods (interglacials) have been much shorter than the cooling ones (glacials), generally lasting about 10,000 years (Chorlton et al. 1983, Schubel 1981). Consequently, the coastal estuaries resulting from associated interglacial oceanic transgressions have been relatively short-lived, persisting around 10,000 years (Schubel 1981).

Estuaries may be defined as more-or-less open (or semi-enclosed) coastal waters where freshwater from the land meets, mixes with and dilutes the higher salinity water from the ocean. Brackish estuarine waters are decreasingly salty in the upstream direction and vice versa. The Chesapeake Bay is both a drowned river valley and an estuary. Actually the Chesapeake estuary consists of the drowned valleys of the lower reaches of the Wisconsinan "Susquehanna" and "James" river systems—at least in its southernmost part. The future Susquehanna (which apparently received all or most of the tributaries north of the James) and James Rivers flowed separately to the sea during Wisconsinan glacial and early post-glacial times (Schubel 1981).

Geologists are in general agreement with the sequence of events described above and below but some disagree over details of timing. Their differences apparently lie in the specifics of the elevation of sea level and associated transgressions through time. Schubel (1981) and others have written that the most recent Ice Age (the Wisconsinan glacial period) ended and the current post-glacial (or the most recent interglacial, should another ice age follow as many believe will occur based upon the sequential occurrence of many glacial-interglacial cycles in the last several million years) began around 20,000 BP to 18,000 BP. Some geologists consider that the Holocene Epoch (see just below) began with this early changeover. Current geological evidence indicates and consensus accepts that, indeed, eustatic (global or general) sea level began to rise because of general climate-warming and resultant glacial melting, in the Northern Hemisphere at least, about 18,000 BP, but that warming halted and eustatic sea-level retreated during at least two periods in which atmospheric temperatures cooled markedly.

The most significant of these pre-Holocene cooling episodes is known as the Younger Dryas event (Fairbanks 1989). The general warming trend resumed at the end of the Younger Dryas cooling event around 11,500-10,000 BP and, with reversals of varying lengths and intensity, has continued since. The current interglacial period, known as the Holocene Epoch, is said by most geologists I have contacted or read for this study, to have begun around 10,000 BP. Some say it began more recently, about 9,000 BP: (Personal Communications; C. H. Hobbs, III, G. H. Johnson, M. N. Nichols, L. W. Ward, J. D. Milliman, L. D. Wright and the books and/or articles by Bailey et al 1982, Chorlton et al. 1983, Colman et al 1990, Colman et al 1992 , Emery and Aubrey 1991, Halka et al 1989, Levin 1983, Fairbanks 1989, Flint 1957, Wright 1995; and, Redfern 1983). For purposes of this paper I have accepted the apparent consensus among these communicants and authors and chosen 10,000 BP as the beginning of the Holocene Epoch.

The timing of the several geological events involved in the development of the Chesapeake Bay, itself, is important to this study which attempts to determine as closely as possible the length of time required for the reefs and reef fields of the Chesapeake oyster reef system to have become established and evolved to their 1600 AD status. *C. virginica* cannot live for long in freshwater. The processes of reproduction, survival and reef formation by this oyster can occur only in waters with appropriate salinity levels. Hence, Chesapeake oyster reefs could not have developed where they have been found in the Bay and its tributary subestuaries until waters of appropriate salinity, bearing setting-stage oyster larvae reached those locations and those larvae settled successfully, survived, matured and reproduced.

Current geological consensus indicates that the Chesapeake we know did not exist 18,000 years ago when the Wisconsinan ice cap began to recede. Instead, the great valleys of the ancient Wisconsinan Susquehanna and James Rivers wound separately (Schubel 1981) seaward through channels which were much deeper than those of today (Halka et al 1989, Colman et al 1990). The two erosive river systems coursed down their respective valleys across the broad, gently-sloping coastal plain of glacial times, now known as the continental shelf, reaching the ancient Atlantic Ocean via canyons on the edge of that great shallow expanse some 240+ km (150+ statute miles) eastward of the current bay mouth and continental shoreline.

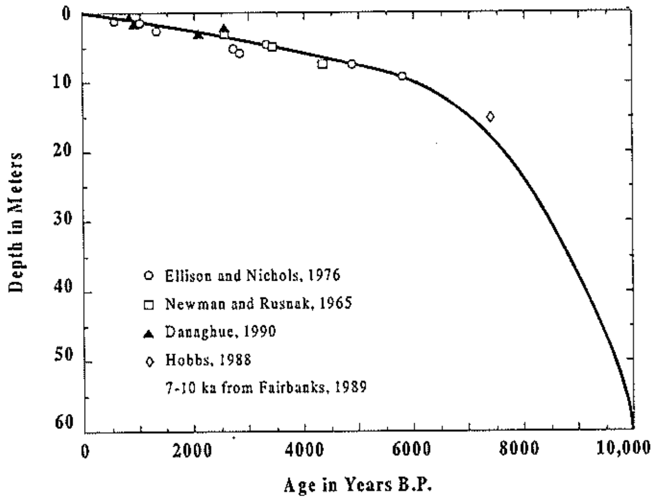

Figure 10. Chesapeake Holocene Sea Level Curve. From Coleman, et.al, 1992. The curve is smoothed and does not reflect the perturbations which actually occurred as atmospheric tempertatues rose and fell (see text below). Reprinted with permission from the Society for Sedimentary Geology.

With global atmospheric warming, North Atlantic waters began to rise as freshwater from the melting North American Wisconsinan Ice Cap flowed into the ocean. (Geologists term the landward movement of rising ocean waters up the ancient river valleys, over the shelves and onto the low-lying portions seaward of today's highlands, transgression). Eustatic (general) sea level rise and the associated transgression was relatively rapid at first with temporary periods of reversal of the warming trend, as described below, and then slowed around 6,000 BP (Emery and Aubrey 1991). (Some place the time of slowing at 5,000 BP.) [Though not critical to this particular discussion of the origin and evolution of the Chesapeake oyster reefs during the Holocene Epoch, it is interesting to note that even after 6,000 BP several cooling periods occurred. Probably those periods, such as the "mini-ice age", which extended some 500 years from about AD 1300 (700 BP) to AD 1800 (200 BP) (Emery and Aubrey 1991), caused minor fluctuations in glaciation and sea-level movements (Chorlton et al. 1983). Such extended temperature fluctuations undoubtedly affected the fortunes of biological populations of the geographical areas involved, including submerged ones such as oysters and their reefs even though water absorbs and releases heat more slowly than air or land. This aspect should be examined.]

Employing the Holocene sea level rise model of Colman et al. (1992) (Figure 10) and considering that the Holocene Epoch began about 10,000 BP, it would appear that rising Atlantic waters flowed up the separate Wisconsinan river valleys of the ancient Susquehanna and James River systems and reached the approximate location of the promontories now called Capes Henry and Charles around 7,500± BP and the formation of today's Bay may be said to have actually begun. Though the curve in the model depicted in Figure 10 is presented as a smooth line, the actual rise of sea level was erratic, slowing as hemispheric or global air temperatures decreased and accelerating as they increased. As Atlantic waters rose, the portions of the Wisconsinan valleys of the two probably separate rivers near the "Capes" were filled and covered; and the waters above them coalesced, forming the lower Bay which today receives water from both the Wisconsinan Susquehanna and James River systems. They also flooded the drowning valleys of the Susquehanna and James rivers (and their tributaries) and moved onto and eventually transgressed and covered the nearby Bay and river shelves and shallows (terraces), as they had the continental shelf earlier.

Rising waters of appropriate salinity brought oyster larvae from "estuarine" and coastal waters of the late Wisconsinan "Atlantic" into the lower Chesapeake and the developing James estuary around 6,000 BP - 4,000 BP. As they did, setting-stage larvae "struck" on such suitable, firm substrates as then existed, clumps and colonies of adult oysters became established and reefs began to form. This process, described in more detail above, continued as estuarine waters of suitable salinity and temperature bearing viable larvae invaded new setting sites. Figures 3a and 3b above, represents an attempt to illustrate the process diagrammatically. New reefs developed upstream and landward on the shoulders and shallows of nearby terraces successively as rising waters of appropriate salinity bearing larvae reached suitable setting sites. Most such larvae-bearing waters by this stage would have come from mature oysters farther, and/or deeper down the developing "Chesapeake" estuary instead of directly from the Atlantic as formerly. Reef initiation and subsequent formation would have occurred in more-or-less continuous fashion as larvae-bearing waters flowed up the Wisconsinan channels of the Susquehanna and James and especially as they rose laterally over adjacent Bay and river shallows and flood plains.

By about 4,000 ± BP saline waters in the mainstem of the Bay reached the latitude of present-day Annapolis. Around 1,500 years later (2,500 ± BP) the Chesapeake reached its approximate present configuration (Figure 1). Its general boundaries and major landmarks would then have been identifiable by today's boatmen, watermen and navigators. (Though its relative rate had slowed and, at times, even reversed, sea level continued its rise as it apparently does today.)

At about the same times the foundations of most Bay oyster reefs and reef fields had been formed around the clumps and colonies of oysters, which had struck on suitable cultch along the old Wisconsinan river bottoms, on the point-bars and along the shorelines and on and in ridges-and-swales of the ancient flood plains (Figures 3a and b). They grew and expanded over time. As eustatic (general) and isostatic (local) sea level rose so did the heights, or crests, of the prospering reefs. Over the next 3 or 4 millennia the self-sustaining oyster reefs expanded basally, vertically and volumetrically, keeping pace with sea level rise, local subsidence and/or emergence (post-glacial rebound, etc.) and sedimentation. Their surface areas increased, as did the numbers of living oysters in the veneer and on its surface and dead shells, shell fragments and detritus (which constitute some of the deeper-lying layers of the veneers and cores of the reefs) (Figure 4). More larvae were produced: More larvae set and survived, and the self-renewing and self-perpetuating reef structures rose. The process was limited only by prevailing general and local geomorphological, hydrographic, and ecological constraints.

As the reefs and reef fields grew and expanded they intruded ever more significantly into the surrounding water column, eventually developing into significant barriers, serving as "dams", wiers and baffles, which interacted with and affected the macro-, meso- and microcurrents and other hydraulic characteristics of their immediate and near-field localities. For example, the USCS Charts (USCS 1872 and 1874) show that, in the Burwell Bay reach of the upper James estuary (the "seed oyster area" of Moore 1910), they extended almost solidly southwesterly to northeasterly from shore to shore about 4.4 miles (7.0 km.) and up and down river for about 9.4 miles (13.5 km), leaving only a few relatively deep but narrow channels open (Figures 2,6,7 and 8), [In the "market oyster area" portion of the James Estuary below Wreck Shoal Reef (Moore 1910), the reefs and reef fields were mostly on the flanks of the natural channel and the shallows (or terraces) alongside, except White Shoal Reefs which were on a ridge or shoal (which, alternatively, might have been a long, centrally-located point-bar) in the middle of the river (Figures 2 and 6).] Erosion and sedimentation patterns in the vicinities of the reefs and reef fields were altered by them as well. Additionally, larval distribution and other biological features were modified, as were setting and survival patterns. Thus, the burgeoning oyster populations established and transformed their own general, meso- and microhabitats throughout the long and close interaction with their immediate environments. The three-dimensional reefs and reef fields served as nature's off-bottom oyster culture structures.

Normal and abnormal seasonal climatic processes and catastrophic natural events involving episodic freshets, severe wind-related water turbulence, icing and heavy sedimentation, as well as diseases, predators and temporary food shortages have undoubtedly always been present in the brackish water areas occupied by coastal oyster populations of the North Atlantic. Before extensive harvesting developed *Crassotrea virginica* continued to increase in numbers and to build and expand its reefs in number and geographical extent, height and volume in the Chesapeake despite these adverse factors. Indeed, the reefs afforded plentiful setting surfaces and kept most of their inhabitants well above the less-hospitable bottom and undoubtedly contributed directly to the survival and success of the Bay's oysters (Hargis and Haven, Chapter 23, this volume). Because of survival advantages offered by the higher portions of the reefs and the suitable setting surfaces of the living and dead shells in and on the veneer, the reef's upward growth towards and even into the "lower" intertidal continued as sea level increased.

And Then Came Humans

Most paleontologists and anthropologists currently agree that the earliest successful human explorers and colonizers (actually hunter/gatherers) reached the North American continent from notheastern Asia by crossing the land-bridge across the Bering Sea (called Beringia by some) resulting from lowered sea level during the last Wisconsinan Ice Age, some 20,000 years ago. Indeed, artifacts such as Clovis spear points found at certain North American sites indicate possible earlier dates for this occurrence, perhaps as early as 30,000 years BP (Garrett 1988, Mehringer 1988).

After crossing Beringia and traveling down one or more ice free corridors between the Cordilleran Ice Sheet on the West and the Laurentide Ice Sheet on the East or along the beaches, tundra, and permafrost of the Pacific littoral, the travelers of Asian origin and or their descendants reached the northwestern portion of the area now known as the United States (Mehringer 1988). Descendants of these wandering hunter-gatherers apparently reached the ancient Susquehanna and James basins about 15,000 years ago. Charts in the publication of Barber (1979) show that campsites of ancient Paleo-Indians existed before 10,000 BP along what are now tidal waters but then were unidirectional flowing rivers or creeks of the ancient James and Potomac drainage basins. These peoples undoubtedly ranged widely in the "Chesapeake" region. Recent geological and archeological research at Jamestown Island on the upper James estuary (upper reaches of the normal estuarine zone just above the uppermost oyster reefs around present-day Deep Water Shoals, Figures 1 and 2) unearthed artifacts the dating of which established persistent human occupation at that site beginning about 12,000 BP (Blanton and Kandle 1995, Johnson et al. 1995). It now appears possible that some Paleo-Indians were on the upper Nottoway River nearby as early as 16,000 BP (H. A. McCord, personal communication). Some disagree, placing this occupation at around 14,000 BP. Whichever finally is generally accepted, these early Paleo-Indians and many of their successor generations undoubtedly observed the flooding of the ancient Wisconsinan James river valley nearby as sea level rose. They and their confreres to the north also witnessed the rising of the water into the Susquehanna portion of the developing "Bay" and its tributaries.

Extensive middens from several pre-historic Indian periods reveal widespread use of oysters (*C. virginica*), hard clams (*Mercenaria mercenaria*) and bay scallops (*Argopectan irradians*), among other estuarine and marine molluscs, as food and for other uses, such as tools, jewelry and currency. Because these early people were relatively few in number compared with later Chesapeake region populations and their harvesting technologies limited, oyster populations, except perhaps those closest to shore and most accessible by wading, continued to thrive and the self-renewing reefs continued and probably even expanded throughout most of the Paleo-, Archaic and Woodland Indian periods and early and mid-Colonial times.

European settlers arrived in AD 1607 (ca 391 BP) and spread along the James and nearby rivers and creeks (Figure 5). After a prolonged, faltering beginning, this and other colonization efforts along the Atlantic coast succeeded and numbers of colonists and later immigrants grew and spread throughout the coastal plain and piedmont regions and into the western territories and demands for oysters and shell increased. For almost 200 years after 1607 AD Chesapeake oyster reef populations were able to meet the slowly-growing human demand and yet maintain the reefs upon which they depended and grew well (Hargis and Haven, Chapter 23, this volume).

Around 200 years ago demand for and subsequent harvesting of live oysters (old and young) and of shell increased to proportions which, magnified by improving harvesting technologies, began to outstrip the natural abilities of the oysters to replace themselves and to provide shell for reef maintenance and growth. Oyster populations and oyster reefs began to stop growing, stabilized and then dwindled. A synergistic cycle developed involving ever-smaller self-renewing oyster populations, slower natural reef replenishment and vice-versa. The rate of reef and population decline was not steady, varying with the more-or-less favorable or adverse years of setting, growth and survival and natural replacement and with harvesting pressure, but, over the long term, the trends of natural oyster production, population trends and reef replacement were downward. As noted above, Stevenson (1894) was probably the first to formally and clearly note this cycle of reef destruction and ever-decreasing oyster populations in the Chesapeake and comment on its possible socioeconomic consequences over a century ago. Winslow (1882) had commented obliquely on it as early as 1878 through he apparently did not recognize the oyster "beds" as being true reefs.

Excessive harvesting and associated reef (microhabitat) destruction were the major but not the only human-affected factor that Chesapeake oysters and oyster reefs faced. Land clearing and agricultural practices of colonists and their numerically-increasing successors were extremely destructive of ground-cover and soil. Amounts of sediment reaching oyster reefs grew to damaging proportions. Many were made "poorer." Some were smothered. Additionally, extensive logging over the entire Chesapeake watershed destroyed ground cover and caused further sedimentation. Widespread logging in the northern and western branches of the Susquehanna drainage basin continued into the early 1900s as did contamination of the Susquehanna-influenced waters of the upper Bay by logging-caused sedimentation (Stranahan 1993). Certainly, resultant highland and shoreline erosion and excessive sediment action impacted many susceptible reefs and reef fields, especially those in the shallow waters of the upper estuarine zones of the Bay and of its tributaries. However, had natural oyster reef growth not been impacted by increasingly destructive harvesting and shell-mining, the deleterious effects of increased sedimentation on Chesapeake oyster populations would have been lessened everywhere.

By the time the first formal Chesapeake oyster reef surveys of Winslow in 1878 and later (Winslow 1882), and those of Baylor in 1892 and 1893 (Baylor 1894), Moore in 1909 (Moore 1910), and Yates in 1906 to 1912 (Yates 1913) were undertaken, self-renewing oyster populations, as evidenced by reported public market oyster harvests from the publicly-owned natural reefs of Maryland and Virginia, were in general decline all over the Chesapeake (Hargis and Haven 1995). Though the charts of Moore

(1910) show some water depths of from 0.33 feet (0.10m) to 3.0 feet (0.91m) over some James estuary reefs at MLW, none of the charts and maps prepared from the special oyster surveys examined thus far show prominent broaching or emergent reefs. Modern soundings of Virginia's Baylor grounds made by Haven and his colleagues at VIMS in the 1980s (and by earlier 20th century workers) have clearly shown that most reefs in Virginia's waters had shrunk vertically (and a number in basal extent) by the time their extremely comprehensive and careful survey was conducted. Many are mere flattened "footprints" on the bottom. A significant number are now buried by sedimentary overburden (Hargis and Haven, Chapter 23, this volume). A much smaller number have been destroyed by channel dredging or buried by dredging-associated spoil disposal. A few (probably more than a few) have been "finished off" by directed shell mining (dredging) activities. The general trend of reef shrinkage has continued in Maryland as well. Thus, with (perhaps) a very few local exceptions, reefs and reef fields have diminished Bay-wide and the Chesapeake reef system continues its general, widespread decline.

Summary and Conclusions

The Chesapeake oyster reef system developed as the Bay, itself, evolved during the last 7,000 to 6,000 years of the Holocene Epoch. As sea level rose, colonial *C. virginica* populations developed and thrived, building the oyster reefs (their own special macrohabitats or biocenoses) and reef fields, which came to constitute the reef system encountered by Indians and early colonists. The process continued as the Bay expanded with the rise in eustatic (global or general) sea level and changes in other geological factors affecting the relationship between land and water. The balance between general (eustatic) and local (isostatic) sea level rise, associated hydrography and geomorphology and reef growth apparently continued until about 200 years ago.

Until the growing harvests of Indians and colonists and the eventually overwhelming food- and seed-oyster harvests and shell-mining activities of their successors intervened, the heights of most Chesapeake oyster reefs would have risen along with sea level—and their sides and bases would have expanded except where erosion, deposition and lack of suitable cultch and stable firm bottoms and overwhelming currents prevented expansion. Of course, it was not necessary that the crests of all reefs actually broke the water's surface for Chesapeake oyster populations and their reefs to continue. Indeed, in all probability, a number did not. It was only necessary that the survival advantages afforded by reef-living (nature's off-bottom oyster culture arrangement) be maintained by upward (and outward) growth of the reef keeping pace with rising sea-level and local basin changes due to subsidence, emergence or tectonic forces and increasing sedimentation so common in coastal plain estuaries. But many would have continued to break the surface at mean low water. (Undoubtedly, sedimentation damaged some, even burying a number in the shallow turbid upper reaches of the estuarine zones of the mainstem of the upper Bay and some of its tributary subestuaries or along high energy, eroding shorelines. But, by-and large, the upwardly-growing reefs provided a certain protection from the effects of sedimentation). Instead, the oyster reefs began to dwindle under man's destructive extractive processes. The overall decline of the natural Chesapeake reef system, (erroneously denied by many harvesters and a few state managers), continues, as does that of the naturally self-renewing populations of Chesapeake oysters.

Evolution of the Bay's reef system to pre-Colonial dimensions required about 6,000 to 7,000 years: Its reduction to present low levels has taken only somewhat less than 200 years. In terms of the once extensive and valuable populations of oysters and oyster reefs and the Chesapeake reef system, humans and human socioeconomic and technological advances and the resource management efforts of state (VA and MD) and local (MD) governments have not been favorable but destructive. The need for and possible reversal of this unfortunate situation by bringing about, enabling and/or encouraging recovery of the once naturally self-renewing oyster reefs of the Chesapeake Bay and the public fisheries dependent upon them are discussed by Hargis and Haven, Chapter 23, this volume.

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Characteristics of Relatively Unexploited Beds of the Eastern Oyster, *Crassostrea virginica*, and Early Restoration Programs

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> *Like the polyps of the Indian Ocean,*
> *this mollusk, if left to itself,*
> *would change the hydrography of coasts.*
> -de Broca 1865

Abstract

We examined historical reports about the eastern oyster *Crassostrea virginica* and its early fishery in North America to obtain information useful to managers seeking to rehabilitate oyster grounds. These reports revealed that the morphology of relatively unexploited oyster beds differed within the species' range, and even within a water body. Nevertheless, three categories of bed morphology can be designated: (1) string reefs, which extended at right angles to the shore and to tidal currents; (2) fringe reefs, which were also near shore, but ran in the direction of tidal currents along the shoulders of an axial channel; and (3) patch reefs, which formed away from the shore and had an irregular, compact form. Some large reefs were mixtures of the first two categories. Substrate, salinity, sediment, water circulation, aerial exposure, predation, and larval supply seem to have had roles in influencing reef morphologies. The local influences of these factors, as well as the presence of hypoxia, need to be considered during rehabilitation efforts. We also examined historical recommendations for placement of cultch and seed. The recommendations, which led to greatly improved oyster harvests in the past, varied with geographic region but included distributing either cultch as a settlement substrate or seed oysters for growth on suitable bottom, "hardening" the estuarine bottom with coarse sand or shell if necessary before distributing cultch or seed oysters, and adding adult oysters on top of the cultch.

Introduction

Oyster populations worldwide have suffered major declines (e.g., Mobius 1877; Ingersoll 1881; Gross and Smyth 1946; Haven et al. 1978; Chew 1983; Heral 1990) caused by a number of factors including overfishing, habitat destruction, pollution, and disease. Such declines have stimulated efforts to restore habitat and fisheries (e.g., de Broca 1865; Ingersoll 1881; Heral 1990), including throughout the North American range of the eastern oyster *Crassostrea virginica*. Because pre-Colonial assemblages of eastern oysters were the end product of eons of natural "experimentation", we believe that restoration measures can benefit from knowledge of the morphology and physical oceanography of oyster beds before or shortly after they began to be heavily exploited at the turn of the 20th Century. Restoration efforts also can benefit from insights gained by early attempts to restore oyster habitat.

We have examined historical accounts of factors influencing eastern oyster communities in North America, and begin by describing past abundances and the subsequent depletion of the resource that led to the need for rehabilitation. We then consider general characteristics of oyster beds and follow with historical descriptions of relatively unexploited beds along the eastern and Gulf coasts of North America. Subsequently, we present early and modern explanations of oyster bed location and morphology in relation to a variety of environmental factors. We conclude by reviewing early efforts at restoring habitat and oyster fisheries and by presenting our own general recommendations.

We recognize that the historical accounts are more anecdotal than quantitative, but many were derived from years of careful and thoughtful observations by experienced scientists and oyster "farmers" and we believe they can be useful today. Indeed, the findings of some early observers (e.g., Oemler [1894] on the relation between oyster bed height and silt deposition) are being supported quantitatively a century later (e.g., Lenihan, in press).

A variety of terms (bank, bar, bed, bottom, ground, reef, rock) have been used to categorize accumulations of eastern oysters. Moore (1899) stated:

> *"... a natural oyster reef, bar, or bed is an area of not less than 500 square yards [420 m^2] of the bottom of any body of water upon which oysters are found or have been found within a term of five years -- in quantities which would warrant taking them for profit by means of tongs."*

Bahr and Lanier (1981) defined reefs in Georgia as:

> *"the natural structures found between the tide lines that are composed of oyster shell, live oysters, and other organisms and that are discrete, contiguous, and clearly distinguishable (during ebb tide) from scattered oysters in marshes and mud flats, and from wave-formed shell windrows."*

DeAlteris (1988) used the term "oyster reef" to include oysters in abundances varying from very concentrated (1000 m^{-2}) to sparse and scattered (10 m^{-2}). We use the terms "bed" or "reef" and focus on the association of eastern oysters (and other animals) in distinguishable groups without specifying areal extent of the bed, its history of commercial use, its relation to tide lines, or oyster abundances thereon.

Past Abundances and Sizes of Eastern Oysters

Pre-Colonial abundances of eastern oysters were high, but destined to decline as human populations and industrialization expanded in the New World. European colonists were astonished not only by the abundance but also by the size of eastern oysters. Ingersoll (1881) and Wharton (1957) cited 17th and 18th Century reports about the need to divide oysters harvested from waters of the Gulf of Maine, Massachusetts, and Chesapeake Bay into two or three portions before they could be eaten. de Broca (1865) wrote that such large oysters were occasionally available in his time, and that a bushel of Chesapeake Bay oysters contained 200 to 250 oysters; this compares with 350 in a Maryland bushel today (Krantz 1983). In Maine and Florida (Ingersoll 1881) and South Carolina (Lunz 1938), Indians built extensive oyster-shell middens. Many midden shells in Maine were over 30 cm long (Ingersoll 1881), corroborating the early reports about the size of the soft tissue. Midden shells in South Carolina and Florida also were larger than living shells on nearby beds (Ingersoll 1881; Gunter 1938; Lunz 1938).

Colonial sailors in New England, Chesapeake Bay, and Florida found that oyster reefs could be navigation hazards (Ingersoll 1881; Wharton 1957). de Broca (1865) expressed an early understanding of the effects of commercial fishing on natural structures and processes when he wrote that oysters in certain localities would form reefs, modify currents, and obstruct channels if it were not for their constant removal by harvesting. Unfortunately, such harvesting subsequently depleted oyster populations and disrupted their beds greatly.

Commercial harvests in the eastern oyster's northern range began to decline in the early 19th Century as human populations increased. Ingersoll (1881) blamed overfishing, pollution, and decreased temperatures (in northern New England) for the downswing, which continued into the 20th Century as overfishing, pollution, and subsequent habitat degradation persisted (Sweet 1941; Matthiessen 1970; Chew 1983), and as disease affected some localities (e.g., Needler 1931). In the mid-Atlantic region, commercial harvesting began in the early 1800s in Delaware Bay (Jeffries et al. 1983) and Chesapeake Bay (Kennedy 1989), with peak harvests occurring in the late 1800s, declining thereafter because of overfishing, habitat destruction, and disease (Kennedy and Breisch 1981; Kennedy 1989). Landings in the South Atlantic region were much lower than in Chesapeake Bay and the period of peak landings occurred later (Burrell 1983), but harvesting activities were often as deleterious to the resource (e.g., Oemler [1894], who commented on increased siltation on depleted oyster beds and on loss of settlement substrate by removal of shell from beds). In the Gulf of Mexico, oysters were fished all along Florida's west coast in the late 1800s (Swift 1898), but urbanization and pollution eventually depleted the resource except in Apalachicola Bay (Ingle 1983). Populations elsewhere in the Gulf also declined, but to a lesser extent than on the east coast (Butler 1954).

General Characteristics of Eastern Oyster Beds

An understanding of how unexploited beds developed, then changed as mechanical harvesting techniques were implemented, and how rehabilitation might be accomplished requires an understanding of the biological structure of eastern oyster beds. Such structure is influenced by the form, growth patterns, and orientation of oysters on natural beds, which can vary significantly in response to changes in local conditions (e.g., Bahr and Lanier 1981).

Oyster beds are built by the cementing together of oyster shells, with additional hard substrate provided by associates such as other bivalves, barnacles, and calcareous tube builders like serpulid polychaetes. Larvae of these invertebrates settle seasonally on this substrate. Oyster growth raises the available settlement surfaces on the beds towards the water surface over time. Substrate detaching and falling from the bed's edges provides for a slow lateral expansion of the bed, depending on the firmness of the surrounding sediment. Churchill (1920) noted that natural oyster beds were like islands in a sea of soft sediments, where shell debris had "hardened" the bottom.

Bahr and Lanier (1981) proposed a model of the life of an intertidal bed. As on subtidal beds, larvae initially colonize hard surfaces, primarily oyster shell, and survivors grow and provide substrate that supports additional settlement. Gradually a mound forms and grows vertically and laterally as oysters accumulate and as shell is scattered in the bed's vicinity. Eventually the mound attains the form of a flat platform with steeply-sloping sides (Fig. 1). As the platform

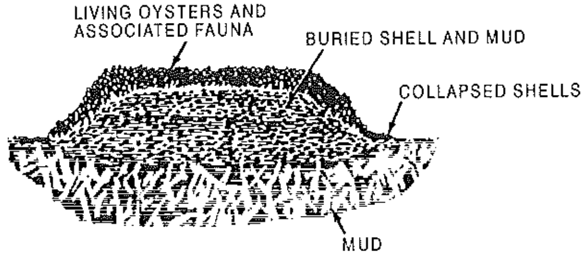

Figure 1. *Diagram of a section through an eastern oyster bed (adapted from Bahr and Lanier 1981).*

begins to break the water surface, wave action may lead to an accumulation of sediment and fine shell grit in the center of the platform, smothering oysters. Constant abrasion by the shell grit may hinder spat settlement (Gunter 1979). Continued wave action tosses shell fragments, sand, and mud intertidally and above high water, sometimes raising the crest of the bed above high water (Churchill 1920). On beds that are no longer growing vertically, the aerially-exposed central region (the hogback; Gunter 1979) may develop into marsh surrounded by intertidal oysters (Grave 1905; Churchill 1920).

In cross-section, the subtidal or intertidal bed comprises a relatively thin layer of living oysters on a base of buried substrate and sediment (Fig. 1), which can vary between and within beds. For example, DeAlteris (1989) found that Wreck Shoal bed (James River, VA) included both "hard-rock" habitat (relatively thick shell layer, coarse interstitial sediment, slight sediment overlay, relatively abundant oysters) and "mud-shell" habitat (thin shell layer, fine interstitial sediment, greater sediment overlay, fewer oysters).

SHELL SHAPE, SMALL-SCALE DISTRIBUTION, AND ORIENTATION OF EASTERN OYSTERS

The structure of oyster beds influences and is influenced by oyster shell shape, which is highly variable (Galtsoff 1964). Commercially desirable oysters have a rounded, cupped shape, with shells that do not break easily during shucking. Crowded oysters develop the characteristic and commercially undesirable shape of "raccoon"[1] oysters, with elongate, thin, sharp-edged shells and watery, flaccid, transparent body tissue, perhaps the result of intraspecific competition for food in these crowded conditions (Winslow 1881; Dean 1892). Glaser (1905) performed a series of experiments that showed that the ratio of width to length for raccoon oysters that were separated from their cluster and held in cages in a strong tidal current increased within 48 days. The ability to attain the more commercially desirable shape decreased with increasing oyster size.

Crowding may not be the only cause of elongated shape. Galtsoff and Luce (1930) reported that individual oysters placed on their side on mud would be found living vertically within 3 or 4 weeks, with their heavier, narrow hinge end buried in the mud and their bill end protruding above the mud surface. The effort to keep pace with silt deposition in this environment may lead to the elongate shape.

Raccoon oysters may form vertical arrays of long, narrow individuals attached to the upper edge of a dead ancestor's shell, which in turn is attached similarly to its ancestor below, and so on down to the base of the bed on the estuary floor (Dean 1892; see Fig. 19 in Galtsoff 1964). In South Carolina, Dean (1892) found that a tall cluster of raccoon oysters within an intertidal area of 1 ft^2 (0.09 m^2) contained 186 vertically-oriented individuals.

Even if such crowding results in competition for food particles and subsequent poor tissue condition, there may be a physiological advantage to crowding in intertidal habitats in hot environments. Vertical orientation exposes less shell surface to the sun and crowding results in mutual shading. In Georgia, the internal body temperature of vertically oriented oysters was lower (34° C) than that of horizontally oriented oysters (>38° C; Bahr and Lanier 1981).

The structure of an oyster bed also is influenced by the spatial distribution of oysters of

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[1] "Raccoon" or "coon" oysters received their name because their elongated shell shape resembles a raccoon's paw (Dean 1892). Such oysters are also called "cat's-tongue" oysters.

different sizes and by the orientation of individuals to currents. The small-scale spatial distribution of eastern oysters on their beds has been rarely studied. Frey (1946) found for 17 exploited beds in the Potomac River, MD that market-size and small oysters (sizes not defined) were not distributed uniformly on a bed. Most were concentrated on a small portion of each bed: 60% of small oysters were on 17% of the area surveyed and 8% of market oysters were on 2.5% of the area. Both size groups generally overlapped in their distribution on a bed, but on a few beds the site of the greatest abundance of small oysters differed from the site where market oysters were most abundant. On one bed, small and market oysters were more common in deep and shallow water, respectively, but there was no correlation between water depth and oyster abundance on any other bed. It is not clear how the distributions noted by Frey (1946) had been affected by harvesting. However, it has long been known that spat settlement can be highly variable; one section of an oyster bed can be heavily encrusted by spat and another section can be spat-free (e.g., Moore 1897). Such variability in spatial distribution may persist as the survivors age.

The orientation of oysters on their beds also has received limited study. Lawrence (1971) examined the position of the shells of recent (*Crassostrea virginica*) and fossil (*C. gigantissima*) oysters on beds in South and North Carolina, respectively. The planes of commissure (where the two shells meet) of clustered oysters of both species were aligned parallel to the current, an orientation that may facilitate filtering behavior. Oysters displayed a similar alignment at a Georgia site with strong bi-directional currents (Bahr and Lanier 1981). We know of no report of oyster orientation on subtidal beds.

EFFECTS OF HARVEST PRACTICES

The characteristics of unexploited beds of eastern oysters, formed by natural processes over centuries, were much different from those of harvested beds. This was demonstrated by Winslow (1881) in Maryland's Chesapeake Bay. Unexploited beds harbored oysters that were clumped in groups of 3 to 15 individuals, compared with single animals or groups of two or three on harvested beds. Oysters on unexploited beds were generally clean and white, with worm-free shells (it is not clear if Winslow was referring to shell-boring or free-living worms), whereas those on harvested beds were covered with mud or sand and worms, with their shells invaded by pholad clams. Mature oysters from unexploited beds were of the raccoon type; oysters from harvested beds were less elongated and had thicker shell margins.

Unexploited beds were structurally solid (Ingersoll 1881), requiring more effort to detach oysters than on harvested beds, and they had less mud and shell debris (debris comprised 30% of dredged material, compared with up to 97% on harvested beds; Winslow 1881). On unexploited beds, 60% of over 20,000 oysters measured were young (this term was not defined) compared with 33% of 100,000 oysters taken from exploited beds. The number of oysters per unit area was greater on unexploited beds than on harvested beds. Winslow (1881) attributed the disparities in age, in the presence of debris, and in area-related abundance to deterioration caused by harvesting activity.

Descriptions of Relatively Unexploited Oyster Beds

Characteristics of oysters and oyster beds are influenced by factors that vary from region to region within the oyster's range. These include physical factors such as salinity, tidal height and flow, bottom morphology, and sediment type; chemical factors such as hypoxic or anoxic water conditions; and biological factors such as predation and disease. Changes in environmental factors over long periods of time also can affect oysters, even within a geographic region (e.g., for reasons that are unclear, fossil oysters in South Carolina were rounded and cupped in contrast to the raccoon oysters of the 19th Century; Dean 1892).

In this section, we first present descriptions from the late 19th and early 20th Centuries of regional differences in distributions of oysters with respect to tidal height and salinity. We then describe the morphologies of relatively unexploited beds. In the next section, we present and discuss the factors thought to be responsible for these distributions and morphologies.

DISTRIBUTIONS OF OYSTERS WITH RESPECT TO TIDAL HEIGHT AND SALINITY

Northern region — Oyster beds in their northern range were (and are) subtidal, presumably the result of the negative effects of winter air temperatures and ice scour on oysters that settled intertidally. Oyster beds were common at tidal river mouths, but also extended up-estuary (Ingersoll 1881).

Mid-Atlantic region — Oyster beds in the mid-Atlantic were (and are) predominantly subtidal. Although oysters occurred up to and above low tide level in limited areas (e.g., Marshall 1954b; DeAlteris 1988), winter temperatures could be lethal, especially when storms exposed shallow flats for several days. Strong wave action on exposed sandy beaches inhibited formation of nearshore oyster beds except in sheltered coves (Beaven 1952). Thus, although water depth over mid-Atlantic beds ranged from 0 m (intertidal) to over 30 m, most oysters occurred at depths of 2 to 10 m.

Unexploited oysters in Chesapeake Bay formed separate beds of crowded raccoon oysters, with few oysters found on the bottom between beds (Brooks 1891). The muddy channels of Chesapeake Bay and its tributaries harbored no oysters, in contrast to the firmer substrate of the shelf from the channel edge to the shore (the shelf's width varied from a few meters to several kilometers — Brooks 1891; Stevenson 1894). Oyster densities were often greater at the mouths of rivers and creeks, and along the shelf edge where there were steep increases in depth (Fig. 2; Winslow 1882).

South Atlantic region — In the estuaries of the South Atlantic Bight, firm channel shelf sediments suitable for oyster bottom were limited to shallow depths, which often meant that much of this habitat was exposed at low tide (Brooks 1891). Oysters occupied this shelf to the high tide mark, but the largest and most abundant oysters were found in well-defined beds at the channel's edge. Subtidal beds did grow up to 2 m above the bottom in riverine systems like the Neuse, New and Newport Rivers in North Carolina (Winslow 1889). Many subtidal beds in Pamlico Sound, NC differed from those in Chesapeake Bay and northward in that they occurred on sand surfaces and were composed of relatively thin layers of shell, thought to be the result of disturbance by waves that shifted the shells and prevented their accumulation in reefs (Grave 1905; in general, however, a shifting sandy bottom coupled with strong wave activity is the least favorable habitat for development of oyster beds in shallow waters [Bahr and Lanier 1981]).

In parts of North Carolina (Grave 1905), and in South Carolina (Dean 1892; Galtsoff and Prytherch 1927) and Georgia (Galtsoff and Luce 1930), raccoon oysters formed fringing intertidal beds, with few oysters found below the low-water mark. Intertidal beds crowded close to the salt-marsh shore and extended into muddy tidal creeks, conditions that prevail to this day (Dame 1979; Bahr and Lanier 1981). Intertidal oysters in this region apparently gained a respite from aquatic predators when the tide was out, in contrast to the situation on subtidal beds. Those oysters that lived subtidally in moderate salinities had rounded heavy shells and more marketable meat (Dean 1892). Bahr and Lanier (1981) reported that reef distribution along the Georgia coast had changed little between 1889 and 1972, but that the area containing living oysters had decreased by about 80%.

Intertidal oysters originally occurred along the Atlantic coast of Florida (Ruge 1898), but such populations are uncommon today (Ingle 1983). Populations in shallow, polyhaline Mosquito Lagoon, FL have been described by Grizzle (1990).

Gulf of Mexico — On Florida's west coast there were productive intertidal beds of raccoon

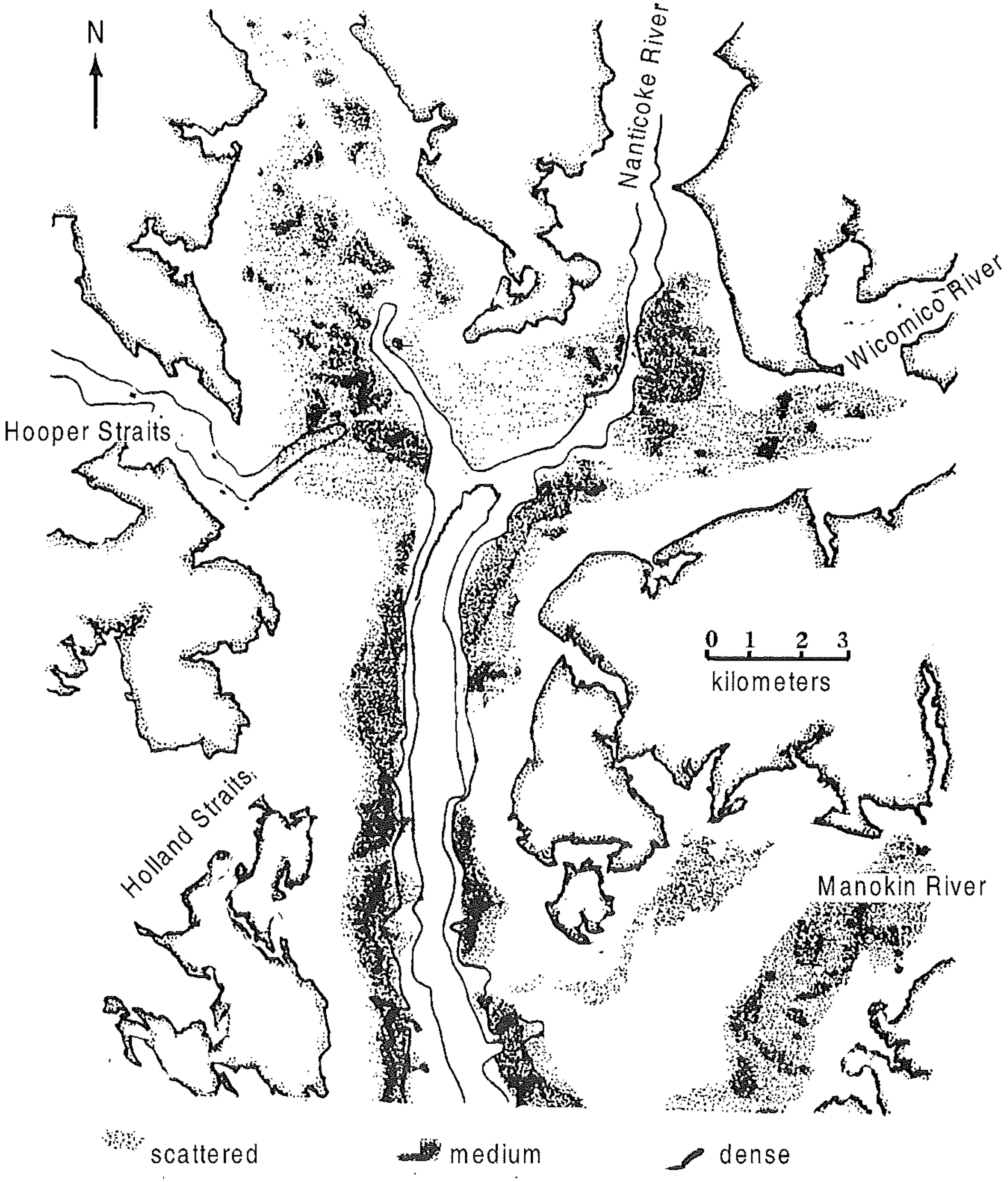

Figure 2. *Distribution of eastern oysters along the channel edge and on the shallow shelf regions of Tangier Sound MD (redrawn after Stenzel 1971 from data in Winslow 1882).*

oysters as well as subtidal beds to depths of 3 m (Swift 1898). Oyster grounds in Matagorda Bay, TX were subtidal, and generally occurred on level bottom in depths of 5 m or less (Moore 1907). The largest, oldest reefs in this bay usually had their crest awash at low tide, and in some parts of the bay there were shoreline beds with an elevated fringe of oysters that were exposed in winter. Oysters in Mississippi Sound grew mainly in shallow water (about 1 m deep;

Moore 1913a, b). Kilgen and Dugas (1989) report that oyster beds presently extant in the northern Gulf of Mexico are usually subtidal.

Butler (1954) summarized the situation for Gulf oysters in his day, which probably also held pre-historically for the region. Oysters were found from just above mean low water to depths of at least 10 m. Most were on sticky mud, but small clusters could be found on sand in sheltered areas. Butler (1954) described four categories of beds. Type 1 beds occurring near the head of an estuary (0-15 ppt; mean, 10 ppt) harbored small rounded oysters (often used as seed) that were free of fouling organisms and that had few predators or parasites. Spat settlement was meager on these beds and excessive freshwater flooding caused high mortality. Type 2 beds occurred between 10 and 20 ppt (mean, 15 ppt). Here, plentiful cultch, limited predators, and high fecundity resulted in an abundance of individuals that grew well, but crowding produced the raccoon shape. Oysters on Type 3 beds nearer the estuary mouth (10-30 ppt; mean, 25 ppt) were highly fecund and grew well, but predators and parasites limited their abundances by imposing a high mortality in the oyster's first year. Finally, oysters on Type 4 beds in marine regions of the Gulf grew slowly, mortality from predators was high, and cultch was limited, so oyster abundances were low. These salinity-influenced categories probably pertain throughout the present range of the eastern oyster.

MORPHOLOGY OF OYSTER BEDS

Of the various accounts of the morphology of relatively unexploited beds of eastern oysters, the most detailed concern Chesapeake Bay and Matagorda Bay, TX. In Chesapeake Bay, Winslow (1881) noted that the shape and area of eastern oyster beds were variable but that the length of a bed was usually greater than the breadth, with the greatest dimension usually in the direction of the current. Oysters tended to occur in long narrow ridges off the mouths of creeks and rivers. A century after Winslow's report, Haven and Whitcomb (1983) examined oyster reefs in the once productive James River, VA, a sub-estuary of Chesapeake Bay, and characterized four morphological reef types based on the reefs' surface outlines: 1) long transverse reefs that lay at right angles to the current; 2) longitudinal reefs in the upriver oyster grounds that were parallel both to the current and to the river's axis in shallow areas with fast tidal currents; 3) large irregular reefs that occurred throughout the river, with one component at right angles to the river's axis and the other parallel to the axis; 4) amorphous pancake reefs that occurred mostly downriver. It is not clear if these morphological types existed before commercial harvests began.

Moore (1907) reported that the oyster beds in shallow (<5m deep) Matagorda Bay, TX were of three types: 1) long reefs that were oriented at right angles to the currents, with crests that approached the water surface; 2) small, deep, somewhat circular or oval reefs ("lumps") in quieter waters that also reached to the water surface; 3) flat beds of no great thickness that did not extend much above the bay bottom and that appeared to result from culling activities by harvesters returning to harbor. Long, narrow reefs of the kind that Moore (1907) described as growing at right angles to the predominant tidal current were associated with rapid currents in silt-laden environments (common in bays and rivers of Texas, Louisiana, Alabama, and Florida, and in North Carolina rivers; Churchill 1920). By contrast, in open southern and Gulf waters subject to limited freshets, moderate current, and moderate silt load, oyster beds were often round or oval in outline (Churchill 1920). We will discuss the influence of water circulation and sediment on reef morphology later in this paper.

In his review of oyster biology, Stenzel (1971) categorized beds of eastern oysters as (1) string, (2) fringe, and (3) patch reefs, based on their shape and proximity to the nearby shore. String reefs have narrow crests that are often exposed at low tide, and most run at right angles out from the shore and are oriented normal to tidal ebb and flow. They are well developed in long, relatively narrow estuaries with straight sides, a configuration that allows tidal currents to flow parallel to the shore. These string reefs would include the long reefs of Matagorda Bay, TX (Moore 1907), the transverse intertidal reefs of North Carolina (Grave 1905), and the long transverse reefs in the James River, VA (Haven and Whitcomb 1983). Fringe reefs, which also lie nearshore but which develop in the direction of the current along the shoulder of an axial channel (Fig. 2), would include the longitudinal reefs of Winslow (1881) in Chesapeake Bay and of Haven and Whitcomb (1983) in the James River, VA. Patch reefs, which are found away from the shore and which usually have an irregular, compact form would include the oval reefs or "lumps" in Matagorda Bay, TX (Moore 1907) and the pancake reefs in the James River, VA (Haven and Whitcomb 1983). The large irregular reefs of Haven and Whitcomb (1983) appear to be a mix of string and fringe components.

Factors Influencing the Location and Morphology of Oyster Beds

Numerous factors influence the location and morphology of eastern oyster beds. The most important factor is probably suitable clean substrate, but others include sea level variations, salinity, tidal height, and water circulation as it influences delivery of larvae and sediment to the bed. In this section we consider the influence of sea level rise on oyster beds, discuss possible reasons for intertidal versus subtidal beds (including the influence of salinity), and evaluate the influence of water movement and sediment deposition on oyster bed morphology. In addition to the literature cited below, Bahr and Lanier (1981), Burrell (1986), and Kilgen and Dugas (1989) have provided broad overviews for particular geographic regions.

GEOMORPHIC DEVELOPMENT OF OYSTER BEDS

The fall and rise of sea level over geological time has had a major influence on the location and persistence of oyster beds (e.g., Kilgen and Dugas 1989). DeAlteris (1988) proposed a conceptual model of geomorphic development of a James River, VA oyster bed (Wreck Shoal), a relatively young bed that developed in the Holocene. Data from cores reveal that the bed first began on shallow sandy shoals in the James River valley as the sea encroached about 10,000 years ago. Thereafter the bed grew vertically at an estimated rate of 50 cm per century until about 1855 AD. This rate of rise kept pace with both sea level rise and the deposition of new sediment, but harvesting activities over the following 100 years lowered the reef surface by 1 m.

There are two important implications of DeAlteris' (1988) work relevant to our discussion. The first is that the modern location of oyster beds is often influenced by processes and geographies of the distant past; once these beds were established, they served as a favorable substrate for further settlement and so were self-maintaining. Managers seeking to rehabilitate oyster beds could focus on long-established beds that were productive until degraded by overfishing. The second important point is that, in the face of continuing sea level rise and continuing sediment deposition in estuarine habitats, commercial beds may be buried if a suitable substrate for settlement is not supplied to replace harvested shell.

INTERTIDAL VERSUS SUBTIDAL OYSTER BEDS

The dominance of intertidal over subtidal distributions of *Crassostrea virginica* from southern North Carolina to northeastern Florida has attracted much speculation as to its cause. Galtsoff and Prytherch (1927) and Galtsoff and Luce (1930) attributed the distribution pattern to preferential settlement by larvae in the intertidal rather than the subtidal zone. In Georgia, Galtsoff and Luce (1930) used wire bags of shells, brush, and natural shell found in situ to show a gradient of declining spat settlement from a peak near the low water mark to smaller numbers both higher on the tidal flat and below low water (a pattern that had been reported earlier by Dean 1892). They proposed that the peak at the low water mark was influenced by slack tidal currents. Slack water occurs at mid-tide near the mouths of most bays and rivers in the region, and they hypothesized that preferential settling of larvae occurred at that time as well.

A significant weakness in their argument is that, while it explains a decrease in spat settlement above mid-tide levels, it does not explain a decrease in settlement below the low water mark. We think it is more likely that settlement may have been hampered by lack of suitable substrate, higher turbidity, and increased predation in the subtidal zone, and by a shortened duration of exposure of larvae to cultch or an increased aerial exposure in the upper intertidal zone.

Other scientists related the distribution differences to salinity and predation. Battle (1892) remarked on the concentrations of raccoon oysters near ocean inlets in southern waters and wrote:

> *"...it may be laid down as a rule that as you approach the heads of the streams, where the specific gravity [salinity] is much lower, the [intertidal] beds along shore become less frequent and the type of oyster becomes poorer; but when this condition is reached one may look for and expect to find deep water oyster beds."*

Oemler (1894) provided examples of this general rule for moderate-salinity habitat in Georgia and South Carolina, and reported that oysters placed in high salinity water (salinity value not stated) in Georgia did not survive, a point reiterated by Ritter (1896) for oysters in Alabama and Mississippi. In Georgia, Oemler (1894) found that spat (< 3 mm) that had settled on subtidal shells suffered total mortality and that their upper shells were undamaged but easily dislodged by a gentle touch (Newell et al., [submitted]) found a similar situation for shells of spat preyed upon by small flatworms, *Stylochus ellipticus*). In South Carolina, Smith (1949) reported 100% mortality in spat that had been transplanted from the intertidal to the subtidal region. In Florida, Marshall (1954a) measured 91% mortality in oysters placed subtidally and unprotected in Alligator Harbor compared with 15% mortality in oysters placed in cages adjacent to the unprotected animals. Bahr and Lanier (1981) also implicated boring sponges that are abundant subtidally (and not intertidally). The sponges weaken oyster shell so that predators crush them into pieces that tend to be washed away and lost as settlement substrate.

In summary, it seems likely that the most important reasons for the persistence of intertidal and not subtidal oyster beds in South Atlantic estuaries are higher rates of predation (and possibly parasitism) and a lack of suitable habitat (cultch) within the subtidal zone. The upper distributional limit of intertidal beds may be limited by increasing aerial exposure (Moore 1907) or increasingly brief periods of possible settlement. Subtidal oysters become abundant within an estuary only when salinity is low enough (<20 ppt) to preclude or weaken predators (and perhaps parasites).

CIRCULATION AND OYSTER BED MORPHOLOGY

Early attempts to explain the morphology of unexploited oyster beds invoked a relationship between tidal current direction and the direction of fastest growth of the oyster bed. The most quantitative work was that of Grave (1905), who performed extensive studies to explain the morphology and location of natural oyster beds (divided into "reefs" and "tonging grounds") in the Newport and North Rivers in North Carolina. The "reefs" (long narrow ridges of raccoon oysters located intertidally) extended outward from the shore at right angles to the current. Grave (1905) proposed that they were formed by a process of preferential transverse development, beginning near projecting spits of land on the shore (Fig. 3a-c) where currents were fastest. The faster currents cleansed cultch of silt, whereas slower waters at the side of the bed dropped their entrained sediment on the cultch, inhibiting spat settlement or smothering spat. Over time, growth of the bed would occur mainly at the offshore end, with bed width remaining uniform as length increased. As the bed extended into the river, it would begin to obstruct tidal currents, strengthening the flow past the growing end. Circulation would slow and eddies would develop to an even greater extent along the sides of the bed toward the shore. As the bed grew it might "outcompete" an adjacent bed (Fig. 3d) which would cease to grow, as would the portion of the bed in quieter waters inshore (Fig. 3e).

Extension of the bed out to the river channel eventually would force prevailing currents to bend away from a shore-parallel path, leading to the formation of branches in the bed at right angles to the diverted current (Fig. 3d,e). Ultimately the amount of water being obstructed by the growing bed would increase to the point that some water would break through the bed, usually within a few meters from shore where ancestral oysters had died (Fig. 3f). Eventually the bed would break the water surface and an island with a fringe of living oysters would develop as described earlier.

As a working hypothesis, this explanation seems quite reasonable with one caveat. Slower currents along the sides of the bed towards the

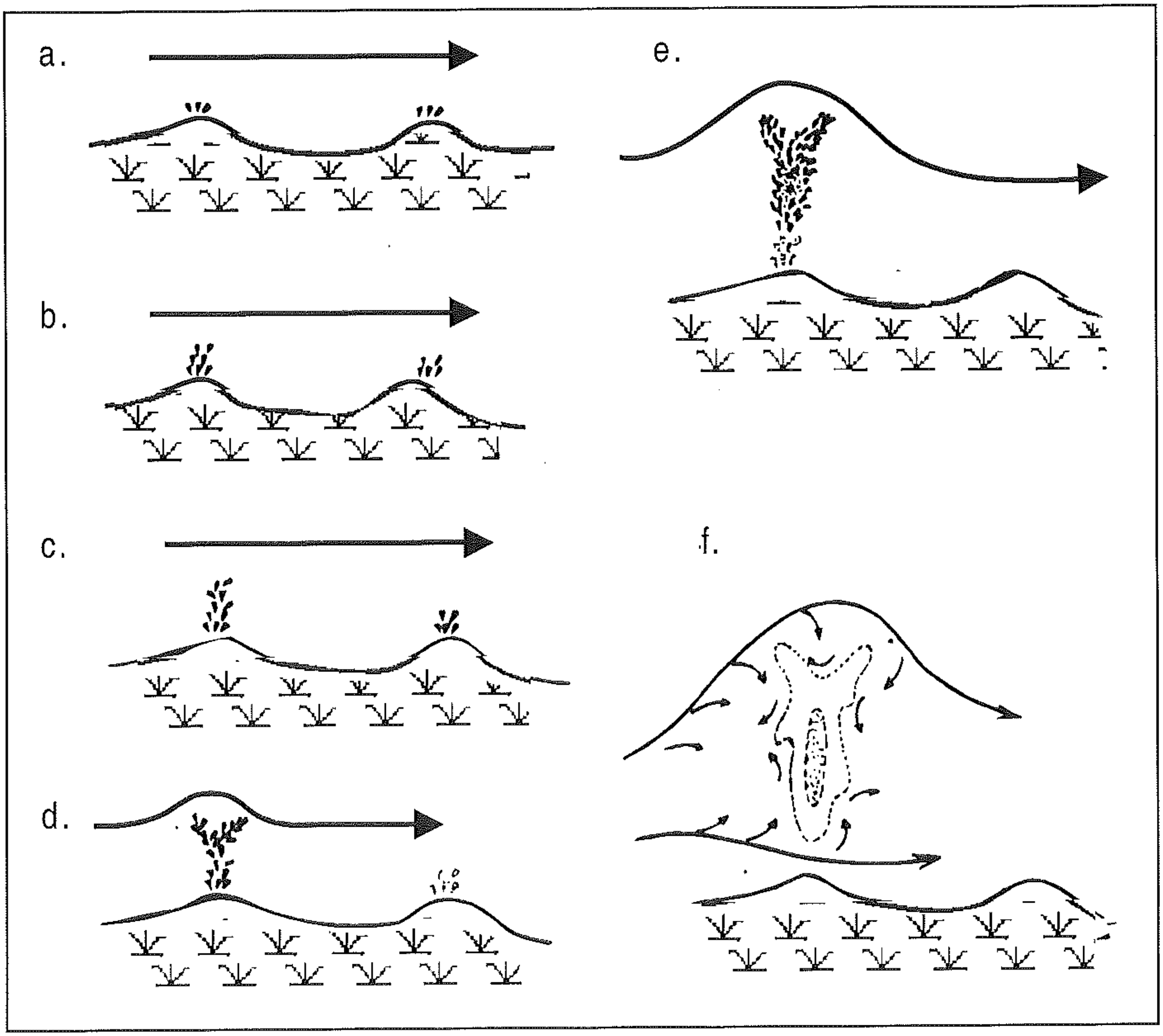

Figure 3. Grave's (1905) model of an eastern oyster bed developing from a spit of shoreline (with stylized marsh grass) at right angles to the current (solid arrows) (modified from Hedgpeth 1953). Dashed lines in (f) outline the bed and its central aerially exposed region of dead oyster shell and sediment.

shore and the base of the bed where it meets the sediments actually appear to result in enhanced spat settlement, as found for artificial reefs in the Neuse River, NC by Lenihan (in press). However, Lenihan also found higher sedimentation rates, lower growth rates, and higher mortality in the same low flow zones. The net result is the same, in that growth of the bed is enhanced in regions of higher current flow and lower sedimentation. However, it may be that the reason is greater survival and growth rather than greater settlement.

Freshwater inflow and asymmetrical tidal flow may explain the shape of the "long reefs" in Matagorda Bay TX described by Moore (1907). These long string reefs (apparently the oldest beds in the Bay) extended from the shore across the currents into deeper water (Fig. 4), with a crest that often broke the water's surface at low tide. The side of the bed that faced up-bay rose abruptly from the bay bottom and harbored the largest and best quality oysters. In contrast, the down-bay side facing the ocean sloped more slowly into the depths, with ridges or spurs of shell projecting seaward like artificial groins; oysters on the down-bay side were less abundant, markedly smaller, and in poorer condition than their counterparts on the up-bay side.

To explain this morphology in Matagorda Bay, Moore (1907) agreed with Grave (1905) that movement of the current past the bed's distal end kept that end free of sediment, enhancing spat settlement and survival and pro-

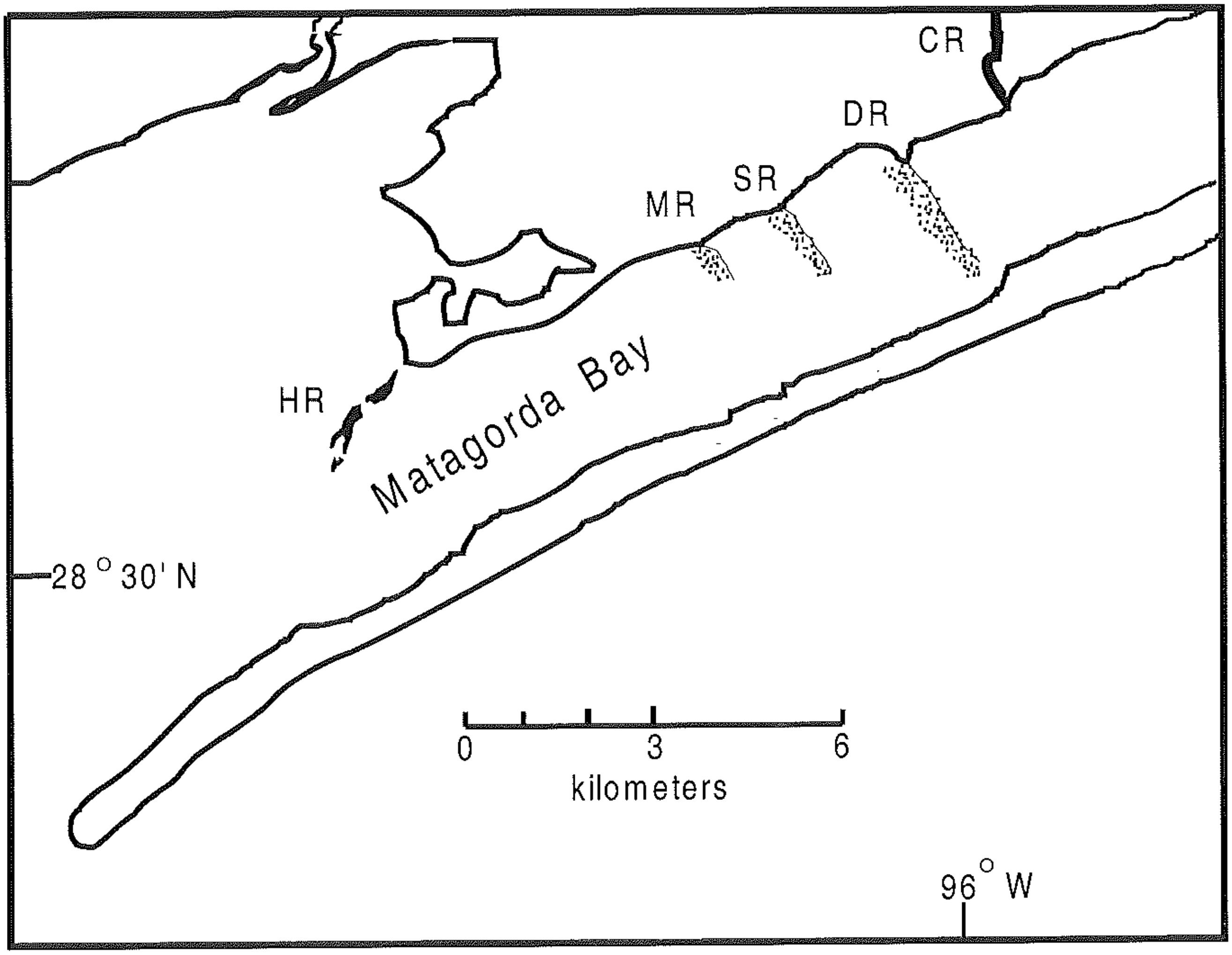

Figure 4. *Eastern oyster reefs studied by Moore (1907) in Matagorda Bay, TX. Abbreviations: HR - Half Moon Reef; MR - Mad Island Reef; SR - Shell Island Reef; DR - Dog Island Reef; CR- Colorado River (modified from Hedgpeth 1953).*

moting the outward growth of the reef. He explained the asymmetrical cross-section of the oyster reef by invoking flood-ebb asymmetries of the tidal currents and sediment loads. He stated that strong, turbid ebb currents (due to riverine inflows carrying high suspended sediment loads) accelerated over the reef, depositing sediments on both the upstream and downstream sides but keeping the top free of sediments. The less energetic, less turbid flood currents exerted much less influence on the reef, such that its morphology exhibited asymmetries more readily associated with a unidirectional flow (in the direction of the ebb) than with a reversing tidal flow. The asymmetrical reef morphology was most developed on the reef (Dog Island Reef) furthest up Matagorda Bay in the direction of the Colorado River (Fig. 4). Reefs found further down the bay away from the River were progressively more symmetrical. Moore's (1907) ideas are reasonable, with a slight modification in light of Lenihan's (in press) finding that the zones of highest current flow also were the zones of greatest survival and fastest growth. This would suggest that the asymmetrical morphology of the reef resulted from more rapid growth in the direction of strongest flow, namely the upstream top edge of the bed.

Fringe reefs, such as those observed by Winslow (1881), Stenzel (1971), and Haven and Whitcomb (1983), are an alternate possible linear bed morphology to string reefs. Fringe reefs develop in the direction of the current along the shoulder of an axial channel (Fig. 2), although Stenzel (1971) also considered oyster beds along the shoreline in very shallow water to be fringe reefs. We believe that the reasons for development of these two forms of fringe reefs may be different, and we concentrate on the channel edge form here.

At first glance, it is not clear why oyster beds should develop in two such distinct, orthogonal morphologies. Stenzel (1971) proposed that the fringe configuration was the result of larval settlement as a consequence of decreasing tidal velocity as the tide rose and water spread over the shelf. This is not a very satisfactory explanation. If it were valid, then one would expect to find fringe reefs in precisely the intertidal or shallow subtidal shelf locations where string reefs develop. The fringe reefs observed by Winslow (1881) and Haven and Whitcomb (1983) occurred entirely subtidally, in areas where tidal current directions essentially follow the isobaths. This is not to say that cross-isobath currents do not occur. Secondary circulations due to channel curvature (Bahr and Lanier 1981; Boicourt 1982; Keck et al. 1973), wind-forced upwelling, and internal tides (Sanford et al. 1990) may be present at certain times and places, and may exert significant influence on oyster bed location (Bahr and Lanier 1981; Keck et al. 1973). However, it is doubtful that these secondary circulations alone are responsible for the regular, persistent fringe reef morphology observed by Winslow (1881), and shown in Figure 2.

We propose rather that the fringe reef morphology is associated with oyster larval transport mechanisms in partially mixed estuaries, where an up-estuary net flow of more saline water in the channel is thought to be responsible for carrying older oyster larvae upstream (Pritchard 1953, 1954; Boicourt 1988). It is notable that Haven and Whitcomb (1983) described the fringe reefs in the James River as occurring in the upriver oyster beds, and it is also notable that both their observations and those of Winslow (1881) were in partially mixed estuaries. We hypothesize that fringe reefs are built preferentially because the channel edge provides the closest suitable substrate to the source of larvae being carried upstream at depth in the channel. Whether the larvae are carried over the channel edge by secondary circulations or are simply mixed into the upper layer at the point of intersection of the pycnocline with the bottom may not be as important as the fact that the channel edge harbors the first suitable substrate encountered by those larvae. Once oyster beds are established, this location becomes even more attractive to entrained larvae. Although this explanation seems to invoke passive deposition rather than active selection of settlement substrate, a review of larval settlement (Kennedy 1996a) indicates that both passive and active responses are involved. For example, because both increased temperatures and lowered salinities stimulate larval settlement (Lutz et al. 1970), larvae that are carried from the deeper, cooler, and more saline channel up into warmer, less saline upper-layer water may be stimulated to settle near the shelf edge.

Our hypothesis for the formation of subtidal fringe reefs in the upstream reaches of estuaries is supported by the recent work of Powell et al. (1995) in Galveston Bay, TX. Dredging of the Houston Ship Channel in Galveston Bay radically modified the circulation of the estuary, allowing enhanced upstream intrusion of salt water in the channel into regions that previously were unsuitable oyster habitat. Over 1000 hectares of new oyster bed have developed as a consequence, in a subtidal fringe reef morphology favoring the side of the channel with parallel-trending dredged sediment banks in 2-7 m of water depth. The dredged sediment banks offered higher elevations, and presumably swifter currents, and perhaps substrate for oyster settlement if oyster shell was present in the dredge spoil.

SUMMARY OF FACTORS AFFECTING OYSTER BED LOCATION AND MORPHOLOGY

Oyster bed location and morphology are affected by the complex interactions of several environmental factors and oyster larval behavior. The end product of these interactions may be morphologically distinct reef systems in different geographic regions or different zones of the same geographic region, or even morphologically distinct sections of the same reef. For example, the large, irregular reefs in the James River, VA (Haven and Whitcomb 1983), with one component at right angles to the river's axis and the other parallel to the axis, seem to be a mixed response to current patterns and the original reef morphology that was influenced by sea level rise. Characteristics of different sections within a given bed also may vary significantly in response to local conditions. DeAlteris (1989) discussed how spatial variations in bottom current flow and patterns of sedimentation produced "hard-rock" and "mud-shell" regions on the same oyster bed, and Moore (1907) described significant differences between the upstream and downstream sides of a single string reef.

We have explored several possible ways in which oyster beds may be organized and the factors that seem to be likely causative agents, basing our thinking on surveys and hypotheses extending back into the mid-19th Century. The different locations and morphologies are summarized in Table 1, along with our best estimate of the relationships between environmental factors and each of the location-morphology pairs. Expanding on the relationships identified in Table 1:

A. Suitable substrate and adequate larval supply are common factors important for all oyster bed development, and predation limits subtidal beds. These points are obvious, but worth re-emphasizing.

B. Channelized salinity intrusion (e.g., in a dredged shipping channel or typical partially-mixed coastal plain estuary) favors the development of subtidal fringe reefs. We hypothesize that this factor may have a negative effect on string reef and intertidal fringe reef development because the primary source of oyster larvae in the channel is relatively distant from the shoreline points at which these morphologies begin to develop.

C. High turbidity favors the development of string reefs because the flow-normal orientation of string reefs results in the greatest flow acceleration over their crests and around their outer ends, and consequently the best environment for reduced sedimentation, increased survival, and rapid growth. If reefs with other morphologies cause significant local flow acceleration, they may have the same effect, but this must be evaluated on a case-by-case basis.

D. Stratification and hypoxia are indicated as unfavorable influences on subtidal reefs because they may result in excessive exposure to low dissolved oxygen near the bottom or they may cut off a subtidal oyster bed from its upper

Table 1. Important environmental influences on oyster bed location and morphology; + signifies a positive influence, - signifies a negative influence, and a blank space signifies an unimportant influence on bed development.

Location	**Morphology**	**Environmental Factors**						
		Suitable oyster bottom	Adequate larval supply	Predation	Channelized salinity intrusion	High turbidity	Stratification and hypoxia	Prolonged aerial exposure
Intertidal	Fringe	+	+		-			-
Intertidal	String	+	+		-	+		-
Subtidal	Fringe	+	+	-	+		-[1]	
Subtidal	String	+	+	-	-	+	-[1]	
Subtidal	Patch	+	+	-			-[1]	

[1] Unless bed height is sufficient to keep oysters out of hypoxic zone

layer food supply. If water depths are shallow enough or reef heights are great enough, stratification and hypoxia may not affect subtidal beds adversely.

E. Prolonged aerial exposure always is a limiting factor for intertidal beds. The duration and extent of exposure become particularly limiting in northern climates with sub-freezing winter temperatures.

The lists in Table 1 are not exhaustive, nor are many of the relationships indicated there established as fact. Rather, we have attempted to lay out a framework upon which to build further investigations and which we hope may serve as a starting point for future management and rehabilitation efforts. Further recommendations for oyster bed management and rehabilitation are presented at the end of this paper. In the next section, we review past oyster rehabilitation efforts and their results, in the same spirit as we have considered environmental factors in this section.

Previous Rehabilitation Efforts

Early harvesting activities may have had positive effects on oysters and oyster beds. In Chesapeake Bay, Winslow (1881) reported that beds in Tangier and Pocomoke Sounds were more extensive 30 years after the fishery began, and that oysters were larger and finer even though catches were declining. He attributed these improvements to dredges and tongs breaking up the tightly consolidated virgin reefs and spreading raccoon oysters and shell over a wider area, thereby diminishing competition for food and providing increased surface area for larval settlement. As harvesting activity intensified however, beds were scraped or dredged until their vertical profile greatly diminished and the ratio of debris to living oysters increased (Winslow 1881; Brooks 1891); some beds disappeared completely. Oemler (1894) noted that the elevated configuration of a bed inhibited the deposit of silt and that the failure to cull over the beds undermined their future by removing the cultch needed for subsequent settlement by larvae.

Faced with these deleterious changes throughout the range of the eastern oyster, state and federal agencies and private planters sought to improve oyster habitat by deploying cultch (oyster shells were preferred) as a settlement substrate and by placing seed (pre-market-sized) oysters where they could grow to harvestable size (Table 2). Ingersoll (1881) reviewed oyster culture practices in Europe and North America, emphasizing Long Island Sound, where up to 250,000 bushels of shell were spread in a year

Table 2. Historical recommendations for placement of cultch and seed in eastern oyster fisheries.

Location	Bushels per acre	Additional recommendations	References
		CULTCH	
Long Island Sound	250	Add 200 tons coarse sand per acre; Add 30-50 bushels adults per acre	Ingersoll 1881
Chesapeake Bay	1000-1200	Plant cultch in mid-spawning season	Brooks 1891
None specified	250-500	Add 30-60 bushels adults per acre	Moore 1897
Newport & North Rivers, NC	2000-5000	More shells on softer bottom; not in rows	Grave 1905
Atlantic Canada	2000	Spread evenly, provides one-shell thick layer/acre	Kemp 1916
None specified	500	Spread evenly	Churchill 1920
S. Carolina	2000-5000	More shells on softer bottom	Galtsoff & Prytherch 1927
		SEED	
None specified	300-600	Spread evenly	Moore 1897
Atlantic Canada	500-800	Do not spread thickly	Kemp 1916
S. Carolina	500-800	Spread evenly	Galtsoff & Prytherch 1927

by one independent firm in Connecticut and where hundreds of thousands of additional bushels were added by other firms (Anonymous 1883). Muddy bottom in the Sound could be improved by adding coarse sand (200 tons per acre)[2] once every five years. Long Island planters spread about 250 bushels of cultch per acre on average (Brooks [1891] wrote that 1000 to 1200 bushels per acre were required in Chesapeake Bay). Planters knew that cultch that was placed in the water too early became heavily fouled, thus inhibiting settlement of larvae, so cultch was spread in the middle of the spawning season.

Summarizing oyster culture practices to date, Moore (1897) recommended an initial survey of conditions of microscopic oyster food over potential habitat and emphasized the importance of appropriate bottom material. He associated hard rocky ground, although it might be suitable for settlement of larvae, with poor food conditions and poor oyster growth, unless muddy bottom was nearby. He reported that

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[2] One ton = 0.9 metric tons; one acre = 0.4 hectare.

heavy-clay bottoms were also food-limited, loose sand was readily shifted by water movement and tended to bury oyster beds, and deep soft mud smothered cultch and oysters as they sank into it. A firm substrate covered with a few centimeters of soft flocculent mud was thought to be optimal for planting seed and cultch. If the mud was too deep, bivalve shells, gravel, or sand could make the bottom firmer. A properly prepared bottom need not have additional hard material added for 4 or 5 years, depending on rates of sedimentation and the ability of local currents to keep settlement surfaces relatively clean.

Moore (1897) suggested that once the bottom was prepared, seed to be planted should consist of separate individuals of uniform shape that were free of old shell, fouling organisms, and predators. About 300 to 600 bushels per acre was spread evenly over the prepared ground to avoid crowding. Subdividing the bed into a grid facilitated uniform distribution of seed.

Bottom used for spreading cultch should be firmer than that used for seed because a bottom that was too soft could lead to smothering of spat (Moore 1897). If hard bottom in shallow water did not have sufficient microscopic food, it might be suitable for spat settlement, with the spat later moved to a region that would support growth.[3]

There were disagreements about how cultch should be applied. Moore (1897) recommended that it be spread uniformly but Brooks (1891) recommended placing it in piles or ridges to establish secondary currents that would carry sediment away. Grave (1905) counseled against placing cultch in rows in the Newport and North Rivers, NC because the rows accumulated too much spat, which subsequently grew into raccoon oysters. An even distribution of cultch was preferable to avoid crowding of spat.

Field observations indicated that larvae often were arrayed in bands or belts as a result of circulation patterns (Moore 1897). Thus he recommended that cultch be placed in regions with currents, rather than in still water, to provide maximum exposure of larvae to cultch. Grave (1905) made experimental plantings in North Carolina and found that more spat (per 100 shells of cultch) settled on cultch placed at right angles to the current than on cultch placed parallel to the current.

Additional recommendations for rehabilitation were made as experience accumulated (Table 2). Up to 5000 bushels of shell per acre were recommended for some regions, depending on the bottom type (more shells on softer bottom). As for seed oysters, 500 to 800 bushels spread evenly over planted grounds seemed to be optimal.

The absence of adults from the vicinity of planted cultch had been correlated with unsuccessful settlement, and therefore 1 bushel of broodstock was usually included with every 5 to 10 bushels of cultch (at 250 bushels of cultch per acre) in Long Island Sound (Ingersoll 1881). Winslow (1881) also recommended that adults be placed with cultch in the direction of tidal currents late in the spring, and Moore (1897) supported the addition of 30 to 60 bushels of mature oysters per acre, using adults indigenous to the region being planted. The enhanced settlement associated with the presence of the mature oysters is likely due to chemical cues that stimulate settlement behavior (e.g., Fitt and Coon 1992; Turner et al. 1994). Zimmer-Faust (1995) reported that water collected above an oyster reef induced settlement of larval oysters, whereas water from an off-reef site did not. Thus, the addition of adults to planted cultch seems a reasonable practice.

Early efforts to rehabilitate oyster grounds often were very successful. Under satisfactory conditions in upper Barnegat Bay NJ, 100 bushels of seed were expected from the deposition of 20 bushels of cultch (Ingersoll 1881). Connecticut planters increased their harvests from rehabilitated grounds from about 300,000

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[3] In Chesapeake Bay (Kennedy and Breisch 1981) and Australia (Rochford 1952), there are locations where oysters are stunted and grow poorly, but where spatfall is consistently good, whereas there are other regions where oyster growth is good but spatfall is poor. The reasons for these differences are not known.

bushels in 1880 to nearly 1.5 million bushels in 1888 (Brooks 1891). Managers in Maryland estimated that 1 bushel of planted shells would yield 2 bushels of young oysters on beds at the mouth of the Patuxent River (Maryland Conservation Department 1924). Butler (1954) estimated that an acre of good habitat in the Gulf of Mexico could produce up to 900 bushels of oysters annually under optimal conditions.

Recommendations for Rehabilitation of Eastern Oyster Beds

Here we present general recommendations for oyster bed rehabilitation, based on our literature review of early studies of unexploited oyster beds and early experiences with oyster rehabilitation. Application or adaptation of the general principles drawn from our review need to be performed with an eye to regional differences discussed earlier in this paper. Managers using these recommendations need to apply them with an understanding of the particular environmental conditions of their local region that would affect rehabilitation efforts (e.g., MacKenzie 1996; Hargis and Haven [Chapter 23, this volume]). The decision to rehabilitate oyster grounds will depend greatly on the economic feasibility of doing so in the face of the diseases that currently plague the industry. However, Kennedy (1996b) has suggested that oysters living in rehabilitated conditions of adequate water flow, limited sedimentation, and suitable food may be more resistant to disease. If so, rehabilitation efforts may serve a prophylactic purpose in addition to re-invigorating an industry.

Long-term efforts at reconstructing oyster reefs should consider both the locations and morphologies of historical oyster beds and the factors responsible for those locations and morphologies. The fact that an oyster bed existed in a region before intensive harvesting disrupted its productivity can be taken as evidence that natural processes once were capable of sustaining that unexploited bed. Thus, if there have been no major changes in water circulation, sedimentation, disease, or potential predation, we recommend that sites and morphologies that were historically productive be rehabilitated before sites in "new" locations are established. However, if there have been major changes in the factors influencing oyster reef development and health, we recommend that new sites for potential rehabilitation be chosen based on the principles and factors identified here. This should be done in an experimental mode before committing to a final rehabilitation plan, because the relationships that we have put forward are for the most part hypothetical rather than established fact.

As an example, consider the case of an estuarine oyster fishery severely affected by salinity-associated disease. Managers charged with rehabilitation of the oyster population naturally look to the upstream limit of low salinity that can be tolerated by oysters for initial rehabilitation efforts. If the estuary has remained substantially unchanged in its circulation and sedimentation patterns since times before the onset of intensive oyster harvesting, and if the location of a healthy, long-lived oyster reef from those times can be identified, then that previous location offers a good starting point for rehabilitation efforts.

If such a location can not be identified or if the estuary has changed substantially in the intervening time period, then the factors identified in Table 1 should be considered when selecting an initial location and morphology for rehabilitation efforts. Thus, the upstream reaches of a partially mixed estuary might respond best to construction of subtidal fringe reefs along channel edges, of sufficient height to avoid hypoxic conditions and at appropriate depths for adequate food supplies. This essentially is what natural forces accomplished in Galveston Bay after construction of the Houston Ship Channel (Powell et al. 1995). Powell et al. (1995) point out quite clearly that location was the single most important factor in determining accretion or loss of oyster reefs in Galveston Bay after destruction of an ancient oyster bar and construction of the Ship Channel, both of which substantially modified the circulation in the Bay.

Historical records can indicate which regions were once better for spat settlement and which were better for growth (Rochford 1952, Kennedy 1996a). This will make clear whether the bed to be rehabilitated should receive cultch or seed oysters. Where spat settlement is the goal, the presence of oyster larvae should be evaluated (preferably over a number of spawning seasons) to ensure that a rehabilitation program has a chance of success; there is no point in applying shell where larvae are not present.

If construction of a productive bed of adults is desired, there appear to be few quantitative data on the numbers or density of adults required for satisfactory spawning or fertilization. Galtsoff et al. (1930) proposed a value of at least 6×10^4 oysters (>8 cm shell height) per hectare in Connecticut and Needler (1931) suggested that adult densities of 1000+ bushels per acre promoted mass spawning and improved fertilization in Prince Edward Island, Canada. The validity of these recommendations remains to be tested elsewhere.

Once a region is selected for rehabilitation, the characteristics of the bottom can be assessed visually by divers or by use of a remote video system (MacKenzie 1996). The bottom can then be modified by placement of sand, gravel, or shell in the quantities appropriate to the situation (Table 2). Similarly, cultch or seed can be deposited in the quantities established by oyster "farmers" in earlier years (Table 2), with indigenous adults added to the cultch to stimulate settlement.

Given the tendency for hypoxic or anoxic conditions to occur in modern estuaries, cultch or seed should be placed in configurations that will allow the settled spat or the seed to remain above the local hypoxic or anoxic water layer (Lenihan and Peterson 1998). The actual construction and configuration of the reef can be planned in light of the recommendations by Hargis and Haven (1999, Chapter 23, this volume) and Lenihan and Peterson (1998). These plans can be modified in light of the subsequent successes or failures of the rehabilitation efforts.

Rehabilitation of oyster beds will require that the area be protected from poaching. When harvesting is allowed, culling should be done over the reef. Finally, if oysters can be looked on as a crop to be farmed, rather than a resource to be hunted, practices analogous to common agricultural practices such as preparing the ground for the crop, allowing land to lie fallow if that is effective, developing strains selected for desirable traits such as disease resistance or rapid growth, and using efficient harvest methods could revitalize the industry.

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Oyster Bottom: Surface Geomorphology and Twentieth Century Changes in the Maryland Chesapeake Bay

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Abstract

Digital data sets depicting historical oyster bar locations and more recently surveyed oyster bottom were assembled for Geographic Information System (GIS) representation for the Maryland portion of Chesapeake Bay and synthesized with bathymetry and sediment data to assess changes in natural oyster reefs over a century time scale. Graphical examples show estimated changes in oyster bottom acreage for three locations within the Maryland portion of Chesapeake Bay. Overlay analysis was conducted utilizing two digitally reconstructed oyster bottom data sets: Yates' charted oyster bars and the Maryland Department of Natural Resources Bay Bottom Survey (circa 1982). Comparisons of bottom characteristics during the early and late twentieth century point to a high probability of loss of cultch. The patterns, and thus presumably the causes, of this loss appears to be specific to individual locales. Although specific examples of habitat loss can be identified, differences in methodology and interpretation of bottom character render such comparisons less than exact.

The accuracy and application of such comparative methodologies are put into perspective by the use of topographical techniques for a selected oyster region within the Tangier Sound area of Chesapeake Bay. Digital bathymetry from the twentieth century are compared to historical oyster bar delineations. Characterizations of oyster habitat (*bars, lumps rocks, reefs, bottom, beds, grounds*) are shown to represent various spatial formations related to the morphology and bathymetry of the habitat. In this light, restoration activities could be best applied after an understanding of the formative processes and reef types on a site-specific basis. The complex structural differences and gradations between fringing reefs and patch reefs need to be examined in relation to attempts to restore natural reef structure. Site-specific, detailed bathymetric and substrate analyses, coupled with historic data on reef habitat, can provide a foundation for setting oyster reef restoration criteria.

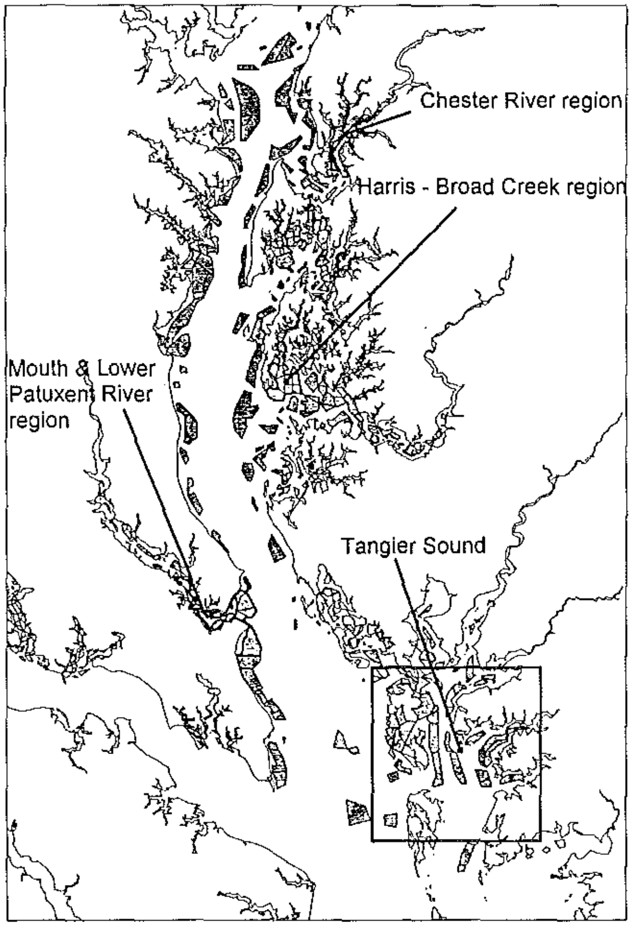


Figure 1. *The Maryland portion of the Chesapeake Bay showing Yates (1911) charted oyster bars and the three sub-tributaries where areal comparisons were performed. The boxed area is the Tangier Sound region where topographic data are presented. Sub-tributaries are the Middle Chester River, the Harris - Broad Creek region of the Choptank River, and the mouth and lower portion of the Patuxent River.*

Introduction

Declining oyster harvest in the Chesapeake Bay has been an issue of concern for over a century. Various combinations of overfishing, habitat loss, and more recently oyster diseases have been identified as causes of this problem. Habitat loss due to processes such as sedimentation and overharvesting may have contributed to widespread destruction of oyster habitat or reef structure. The exact extent of this loss has been difficult to document due to three major factors: 1) the large geographical extent of oyster growing region within Chesapeake Bay; 2) the difficulty of determining exactly what oyster density is considered as oyster bottom or habitat; and 3) the difficulty of directly comparing live oyster and cultch coverage documented in historic and recent surveys.

We have compared two historical data sets (Yates' [1911] oyster bar survey and Maryland Department of Natural Resources Bay Bottom Survey [circa 1982]) to determine site specific changes in oyster bottom between surveys of different time periods. These comparisons are hampered by different methods of data collection, but they serve well to documentation a clear habitat loss. Geographic Information System (GIS) technology was employed to prepare overlay analysis with these two digitally reconstructed oyster habitat data sets. In this way we can compare digital bathymetry data from the late twentieth century to Yates' oyster bar delineations from the first decade of this century. We present graphical examples to illustrate estimated changes in oyster bottom area for three locations within the Maryland Chesapeake Bay. Additionally, we used two historic bathymetric data sets (19th century charts of Almy [1856] and Winslow [1878] and mid-20th century charts from the Coast and Geodetic Survey for the Tangier Sound area of Chesapeake Bay to reconstruct the three-dimensional aspects of fringing reef topography.

Methods

OYSTER BOTTOM— COMPARATIVE COVERAGE 1908–1983

Three sub-tributary regions of the Maryland portion of the Chesapeake Bay, the middle Chester River, the Harris - Broad Creek area of the Choptank River region, and the lower Patuxent River region (Figure 1) were chosen for comparison of live oysters or cultch coverage between these two surveys. This selection was based on geographic coverage and data availability.

For each sub-tributary area, a two-dimensional comparison of existing oyster bottom was made between the Yates 1906 - 1912 surveys (Yates 1911), and the Bay Bottom Survey of circa 1982 (MD Depart. of Natural Resources, unpublished data). Yates' survey information produced corner bearings for named oyster bars, the dimensions of which were established by dragging a chain and recording vibrations (Graves 1912). The coordinates published by Yates (1911) were used to define polygons in a spatial data set.

The portions of the Bay Bottom Survey covering these same three geographic areas were digitized. All data for these sites were collected sometime between 1973 and 1984 utilizing a variety of gear types. Initial sampling for bottom type was conducted by patent tong grabs (L. Wright, MD DNR pers comm.). Later surveying was accomplished by interpretation of acoustic returns from a microphone towed over the bottom. Descriptions of the method(s) used to sample at specific sites are not available. Data were originally recorded as point information, which was later interpolated into a surface rendition of inked shadings on chart sized mylar sheets. These data were used to categorize the Bay bottom into six general substrate types: *hard bottom, mud, sand, sand with cultch, mud with cultch,* and *cultch*. We digitized these charts to produce spatial data sets of the six bottom types.

An overlay procedure utilizing GIS thematic mapping techniques produced direct areal comparisons of designated oyster bottom between the two time periods. Individually named oyster bars in the Yates' survey that were contiguous were grouped together and treated as single reefs. In the Chester River and the Harris - Broad Creek area, oyster bars were mostly adjacent, and little modification was required to produce large single units. In the Chester River, the river's central channel separates two distinct oyster bars on either side. In the Patuxent River, it was necessary to connect individual oyster bars into one continuous reef system. Because the individual bars comprising this system were sometimes separated by considerable distances, connections between oyster bars were made using thin reef bridges.

Selection of oyster bars for incorporation into the larger reef systems was done in a careful fashion. Arbitrary or selective truncation or separation of regions could cause strong bias in areal comparison between historic and recent surveys. In all cases, separations were made where natural breaks occurred in oyster bar topography.

Following creation of singular reef systems, the Yates' oyster region outline was smoothed by first converting the regional polygon outline to a polyline and using a spline technique (MapInfo® software) to perform smoothing. This resulted in an outline shape of reduced area that was more consistent with the smooth polygons of the Acoustic Survey, thus reducing artifacts caused by the large corner areas included within the Yates Survey. This smoothed area then was transformed back into a polygon data structure.

Bay Bottom Survey data were then overlaid on the Yates bars. Three of the six designated categories of Bay Bottom Survey bottom type were consistent with Yates' original designation of oyster bottom. These were the cultch, sand with scattered cultch, and mud with scattered cultch categories. Mud, sand, and hard bottom (deep water) categories were excluded as areas of oyster bottom. Comparisons were made between the Yates' areas and 1) the Bay Bottom Survey cultch bottom type and 2) a combination of cultch, sand with scattered cultch and mud with scattered cultch bottom types. Results are expressed as percent change between the recent and historic estimates.

TOPOGRAPHIC ASPECTS—TANGIER SOUND

Two different data sets were used to characterize three-dimensional relief in oyster habitat and compare changes over a half century time scale. Raw bathymetric survey data utilized by the Coast and Geodetic Survey for production of nautical charts were obtained for the Tangier Sound Region of Maryland and Virginia. Point data coverage was in an irregular grid format with points separated by approximately 30-200 m. These data sets were subjected to a TIN (Triangulated Irregular Network) transformation (ArcInfo® software) to produce a continuous surface from the original point data.

Following this procedure, points were resampled into a lattice (point based exact grid) data structure for use in contouring and three-dimensional surface representation. Contouring was performed on the lattice at 3 fathom intervals beginning at -1 ft. water depth. We also digitized older charted data from Almy (1856) and Winslow (1878). The Winslow (1878) data additionally depicted dense and scattered oyster bottom in Tangier Sound. The polygons representing "dense" oyster bottom were overlaid on these contours and a three-dimensional mesh was generated from the bathymetric data with Yates' oyster bars depicted over this representation. Visual inspections of these three-dimensional surfaces were used to assess large scale changes in topography in this region over the time interval between the Winslow and Coast and Geodetic surveys.

Results

Oyster Bottom—
Comparative Coverage 1911 and 1982

Chester River

Transformation of adjacent Yates bars on the two sides of the Chester River produced two distinct reef systems with all contiguous oyster bars contained within the smoothed outline (Figure 2a). Comparisons of the Bay Bottom Survey overlays for cultch, sand with scattered cultch and mud with scattered cultch with the smoothed Yates' bar showed good agreement with the cultch bottom type (Figure 2b). Furthermore, there was little change in areal coverage (<1%), with Yates' contiguous oyster bars falling within the boundaries of the later survey (Table 1).

The river channel segregates the oyster bottom into two fringing oyster reef systems, one on either side of the channel. The cultch bottom type from the Bay Bottom Survey was designated as *dense*, while sand with *scattered cultch* and *mud with scattered cultch* were lumped together as *scattered* for purposes of calculating Table 2. A combined category

Table 1. Aerial comparison of Yates contiguous oyster bars and "smoothed" object characterizations. Area measurements are expressed in m^2.

Location	Yates	Smoothed	Percent Change
Chester (Right Bank)	12,516,182	12,603,712	< 1%
Chester (Left Bank)	8,113,000	8,191,845	< 1%
Chester (Combined)	20,629,182	20,795,557	< 1%
Harris / Broad Creeks	29,488,002	28,840,182	9.7%*
Patuxent River	46,687,254	40,554,189	8.6%*

*Some of the original area depicted in Yates' survey was removed during the smoothing process because it did not fall within the boundaries of existing digitized mylar Acoustic Bay Bottom Survey charts.

Table 2. Percentage of the "smoothed" Yates' oyster bars covered by dense and scattered cultch in the Bay Bottom Survey at each of the three areas. The "inside" estimates lie within the smoothed bar boundaries; the "outside" estimates are outside of, but adjacent to, the Yates' oyster bars and are expressed as percent the Yates' area. See text for description of cultch types.

	Chester		Broad / Harris Creek	Patuxent River
	(Right)	(Left)		
Inside				
Dense	43	45	44	12
Scattered	25	25	29	20
Combined	68	70	73	32
Outside				
Dense	12	20	7	5
Scattered	22	13	7	7
Combined	34	33	14	13
Total				
Dense	55	65	51	17
Scattered	47	38	35	27
Combined	102	103	86	44

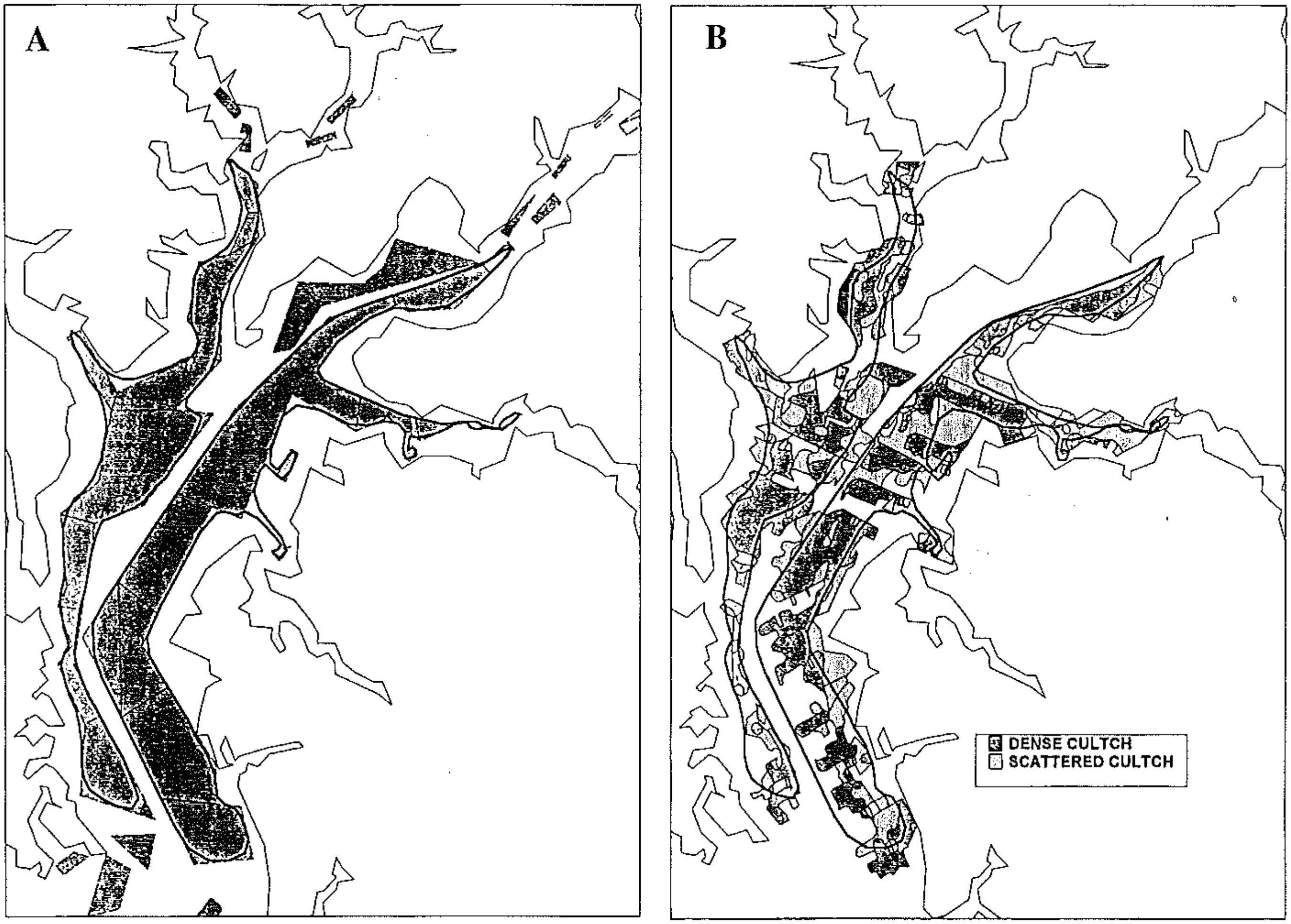


Figure 2-A. Middle Chester River, Yates oyster bar boundaries, and smoothed "objects" of oyster regions. Shaded objects indicate Yates oyster bars and the thick solid line represents the smoothed oyster bar object. B. Middle Chester River, Acoustic survey (circa 1976) cultch bearing sediment type overlays on grouped and smoothed Yates' bars. Only cultch bearing sediments are shown. Dark hatch represents "cultch" while lighter shading represents combined categories of "mud with shell" and "sand with shell". Other mapped bottom type polygons not representing cultch bearing bottom are shown in polygons with no shading. The thick, solid line is the same as in A.

groups both of these bottom types. Within the smoothed Yates' bar boundaries percentages of cultch types were similar between both sides of the river channel. Dense oyster bottom in the Bay Bottom Survey covered approximately 44% of the beds charted by Yates (1911) (Table 2). When both dense and scattered cultch coverage are included from the Bay Bottom Survey are compared to Yates' bar boundaries, this value increases to 68-70%. Interestingly, there was considerable shell substrate measured in the Bay Bottom Survey outside of the charted Yates bars. This ranged between 12% and 20% respectively on both sides of the river for the cultch category alone. With this additional area included in the total, combined dense and scattered oyster bottom between the two surveys was very similar (within 2.5%).

The largest noticeable loss of oyster habitat within the boundaries of Yates' bars was on the channel edge of the southeastern side of the Chester River. This once productive area was replaced by mud and hard bottom in the Bay Bottom Survey. The marked deep water cutoff of oyster bottom in the channel was similar between the two sampling periods.

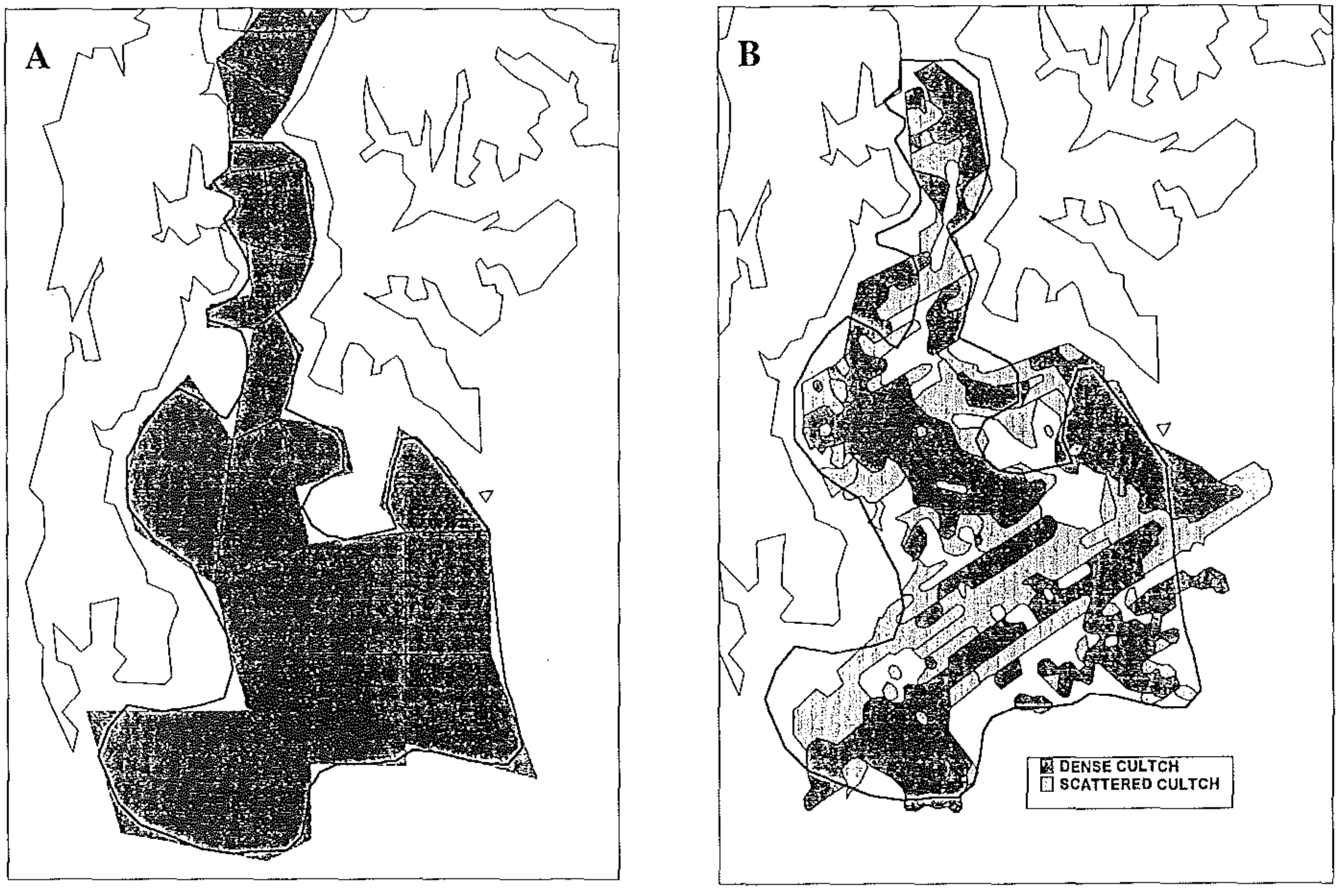


***Figure 3-A**. Harris - Broad Creek area, Yates oyster bar boundaries and smoothed "object" of oyster region. Note the need to truncate the upper Yates oyster bar due to lack of digitized acoustic data for this region. **B.** Harris - Broad Creek area, Acoustic Survey (circa 1976) cultch bearing sediment types overlaid on "smoothed" Yates bar object. (Data presentation as in Figure 2.)*

Harris-Broad Creek

Analysis was performed in a similar fashion on the Harris-Broad Creek reef system. Aggregation and smoothing of the Yates's survey data produced one clear oyster bar in this region as opposed to the two in the Chester River (Figure 3a). Differences in areal coverage between the original Yates' estimates and the "smoothed" oyster reef system in Table 1 resulted from truncation of the northern neck of the original Yates' bar. This was necessary because digitized Acoustic Bay Bottom Survey data were not available for this northern region.

As with the Chester River, there was strong visual correlation between Yates' survey results and the combined areal coverage of cultch and cultch mixed with sand and mud measured in the Bay Bottom Survey (Figure 3b). Noticeable absences in reef substrate were apparent within the central region of the smoothed reef system and along the southern border tending toward deeper water in the Choptank River. In both cases these areas were replaced by mud. Loss of cultch substrate was also apparent in the vicinity of the southern tip of Tilghman Island, where sand was documented in the Bay Bottom Survey.

This bar area showed loss of dense oyster bottom (44%) identical to that observed in the Chester River area (Table 2). A slightly higher percentage of scattered cultch put the combined cultch-bearing bottom types at 73% of the Yates survey. Cultch bottom outside of the charted Yates' bars within the Harris-Broad Creek region was 14% of the Yates' total bar coverage (Table 2.). When Bay Bottom Survey areal measurements of cultch-bearing bottom, both outside and inside of the charted Yates region,

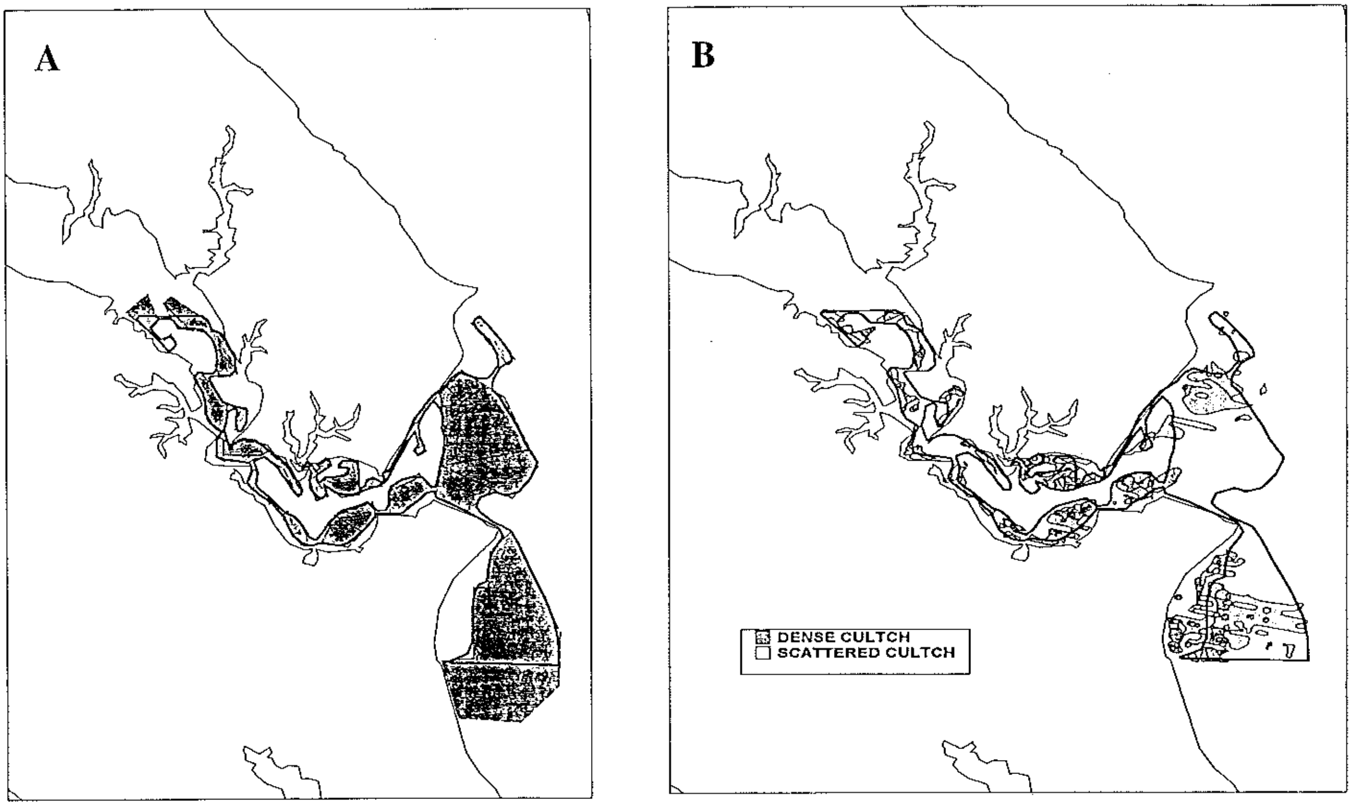
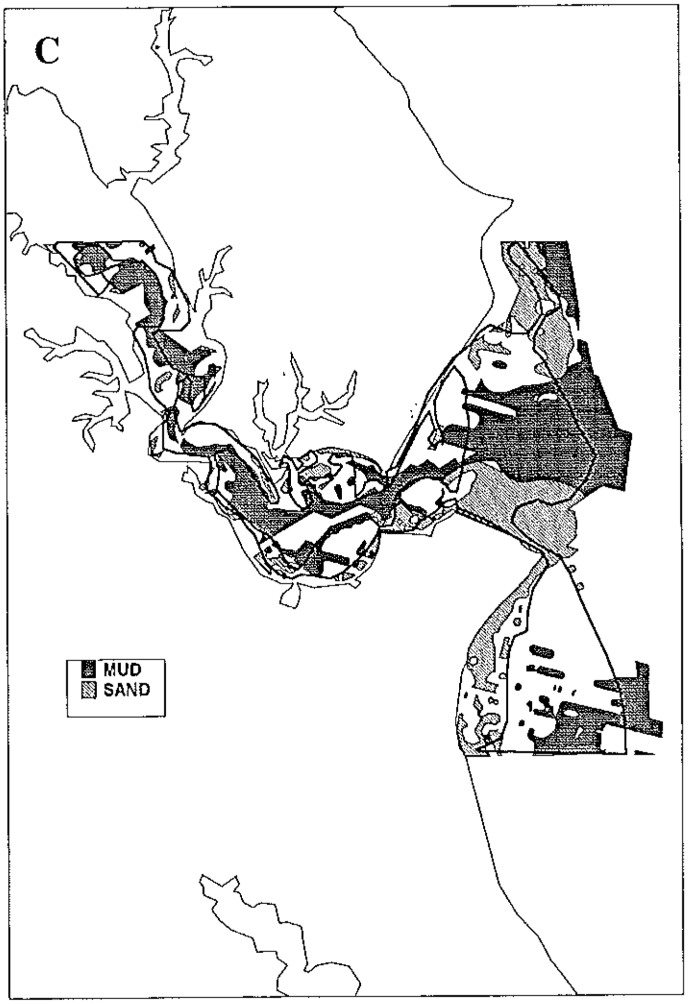


Figure 4-A*. Lower Patuxent River region, Yates' oyster bar boundaries, and smoothed "object" of oyster regions.* ***B****. Lower Patuxent River region, Acoustic survey (circa 1976) cultch bearing sediment type overlays on grouped and smoothed Yates bars. (Data presentation as in Figure 2.)* ***C****. Lower Patuxent River sand and mud deposition as charted in the Acoustic Bay Bottom Survey (circa 1976) overlaying Yates (1911) charted oyster bars.*



were combined, a total coverage that was 86% of the area estimated by Yates was observed.

Lower Patuxent River

In the Yates survey 19 independent non-adjacent oyster bar regions were charted in the selected area of the lower Patuxent River (Figure 4a). The integration of these independent regions into one continuous region is depicted in Figure 4a. Although connecting regions between bars were minimal, tabular comparison of the bar region object to selected contiguous Yates oyster bars is poor (Table 1). This discrepancy was again due to truncation. A portion of a large contiguous oyster bar (Cedar Point Hollow), south of the mouth of the Patuxent River (Figure 4a) was removed because of boundary limitations of the Bay Bottom Survey. Unlike the other two sub-tributary sites, the oyster bar

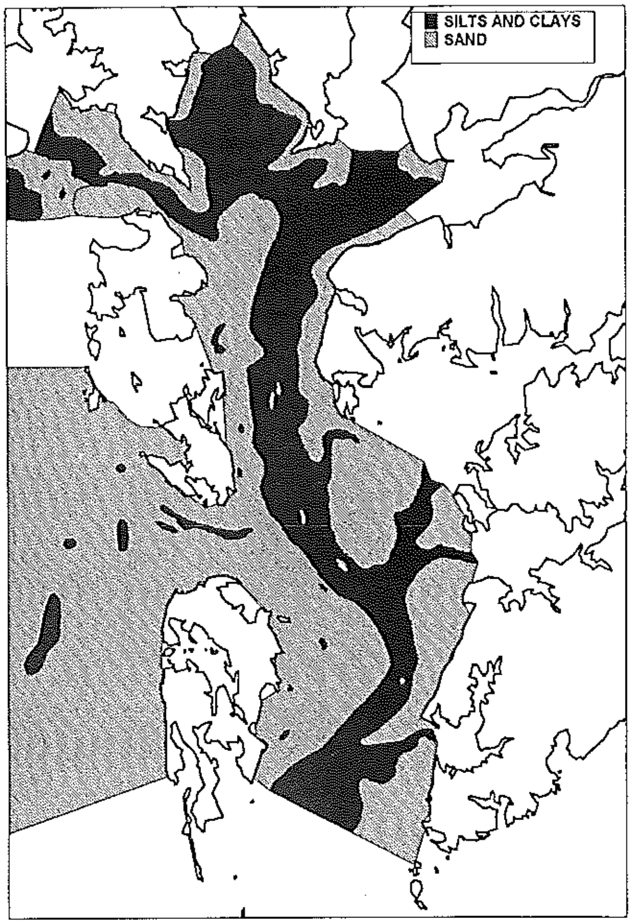


Figure 5. Tangier Sound surficial sediment characterizations.

region in the Patuxent River contains two highly divergent types of bar structure. Within the river proper, fringing reefs on both sides of the channel are apparent. At the mouth and outside the mouth of the river, broad expanses of patch oyster bottom are visible as charted by Yates.

Of the three sub-tributary sites examined, comparisons in the Patuxent River showed the least consistency between the two survey dates (Figure 4b). Positions of fringing oyster reefs (bars) along sides of the river were generally in agreement between the two time periods. Reef size, however, was greatly reduced in the 1970's from that at the turn of the century. Only 12% of the original Yates bottom area remained as dense cultch. With an additional 20% of scattered cultch mixed with sand or mud added to the totals, only 32% of total acreage charted by Yates remained. As with the Harris-Broad Creek Area, oyster bottom outside of the charted Yates boundaries was minimal (13% of Yates' bar coverage).

The Bay Bottom Survey indicated a potential reason for such a loss of bottom type. Both mud and sand deposits of (most likely) river borne sediments covered much of the original Yates bottom. Outside the mouth of the Patuxent River reduction in cultch bearing bottom was extreme. The Bay Bottom Survey clearly showed this effect to be due to a large plume of sand and mud extending over the Yates bars. This effect also acted upon the large oyster bar region to the south of the mouth of the river, again due to increases in mud, sand, and hard bottom. An interesting shift of oyster bottom to the shoreward side of the Yates bar in this vicinity was also an anomaly for which we cannot offer an explanation.

Topographic Aspect—Tangier Sound

Surficial sediment characteristics of Tangier Sound (Kerhin 1988) are clearly associated with the presence of a large river-cut channel traveling down the center of the Sound. To either side

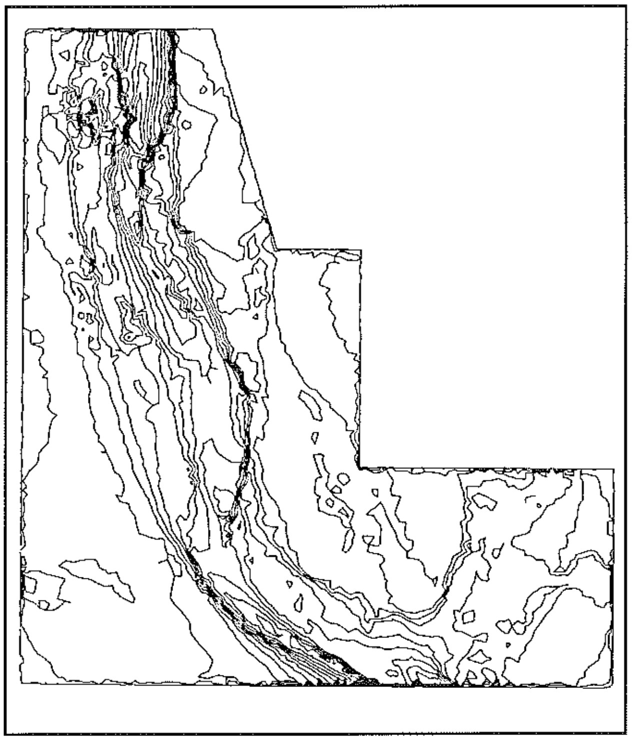


Figure 6. Bathymetric contours of Tangier Sound central channel. Steep contours of central channel are visible.

of this deep trench, sand is the only surface sediment. Within the trench, clay and silt fractions dominate (Figure 5). At its deepest portions this trench reaches almost 30 m, comparable to the depth of the Chesapeake Bay mainstem.

Figure 6 shows results of contouring for the 1931 - 1956 bathymetry data utilizing a lattice contouring procedure in ArcInfo. A visual comparison of these digital data with those of earlier Tangier Sound surveys (Almy 1856, Winslow, 1878) indicated strong agreement between the more recent and historic bathymetry. The depths of oyster regions have not changed visually between the three time periods.

Figure 7 shows the Tangier Sound region with the Yates charted oyster bars. These same bars are displayed along with dense oyster bottom coverage from Winslow's 1878 charts (Figure 8). Dense oyster bottom generally runs in a linear fashion along both sides of the deep mid-channel trench of Tangier Sound. Dense oyster regions to the landward sides of Tangier Sound in general extend no shallower than 4 m throughout the entire region. The charted bars extend to maximum depths of approximately 9 m.

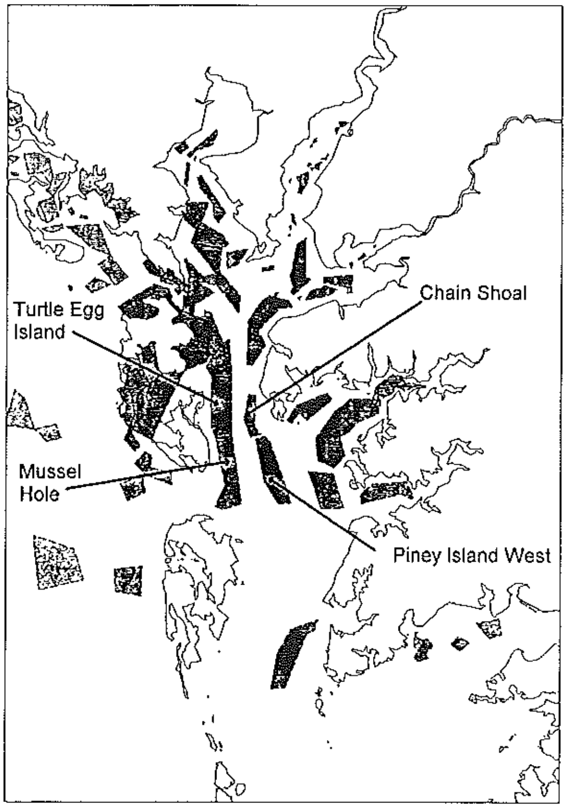


Figure 7. Yates oyster bars (1907) centered on the Tangier Sound region.

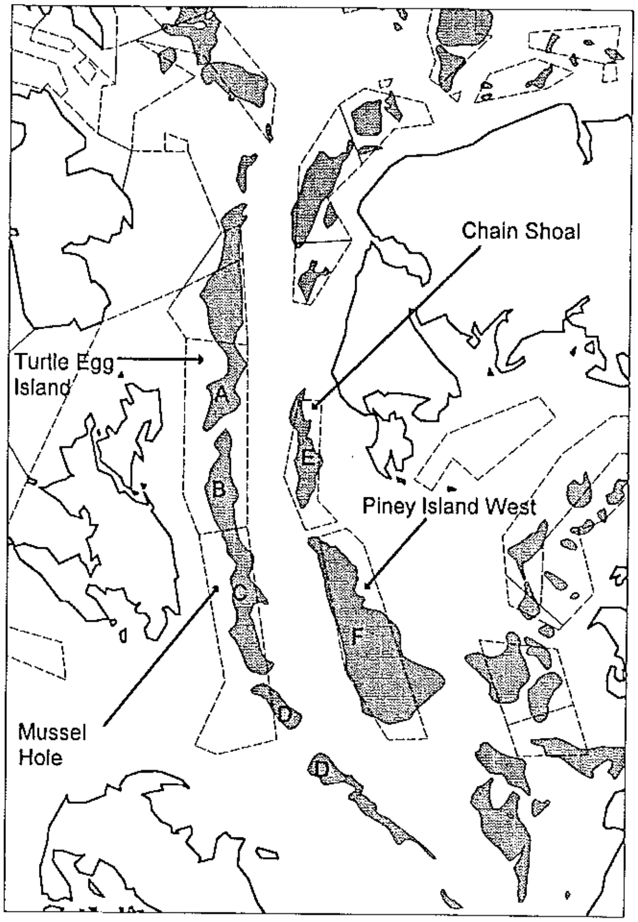


Figure 8*. Yates oyster bars (1907) in the central Tangier Sound region. Overlaid on these outlines are "dense" oyster regions as charted by Winslow 1878. Letters designate features specified in the Winslow chart: A. Turtle Egg Rocks; B. Mud Rocks; C. Mussel Hole Rocks; D. Terrapin Sands Rocks; E. Chain Shoal Rocks; F. Piney Island Bar.*

Prominent oyster reef feature of the Winslow era were described on his charts of the 1880's (Figure 8). On the western side of Tangier Sound and east of South Marsh Island was Turtle Egg Island Rock. To the south were Mud Rocks and Mussel Hole Rocks (in north to south sequence). Terrapin Sands Rocks were noted to the east of Kedges Straits. On the western side of the Sound's central deep channel the northernmost of Winslow's dense oyster regions was noted as Chain Shoal Rocks. South of this oyster area is a gap leading to the Manokin River at whose mouth lay the large oyster region Piney Island Bar.

A three-dimensional view of this same mid-channel trough looking from south to north is shown in Figure 9. Vertical scale has been exaggerated 25x to clearly show channel relief. At the top of the figure on the left hand side of the mid-channel, the topography of Turtle Egg Island Rock and Mud Rocks can be seen. These "rocks" are historic charted areas of dense oyster growth (Winslow 1878). Further to the south, the topography of Mussel Hole Rocks is apparent in these depictions. Chain Shoal Rock is evident to the upper right of the mid-channel (Figure 9).

Superimposed upon this topography are the outlines of Yates' turn of the century charting of the natural oyster bars. The two bars visible on the left side of the channel are Turtle Egg Island at the top, and Mussel Hole at the bottom. At the upper right of the figure, Chain Shoal is the only visible natural oyster bar. At the western side of the mid channel it should be noted that the Yates bar designations extend a great distance into the flat terrace region between the slope break of the edge and the shoreward areas. The large Mussel Hole oyster bar extend extensively to the west into the Kedges Strait region below South Marsh Island. A different three-dimensional perspective of recent bathymetry is shown in Figure 10. This view is looking from the northeast towards the southwest of the upper portion of Figure 9. Portions of Turtle Egg Island Rock and Mud Rocks are seen from a viewpoint looking across the central channel from the northeast. Clearly discernible in this terraced environment are the upward sloping face from the bottom of the channel and the flat back shore area behind a region designated as dense oyster bottom by Winslow in 1878. Note that very irregular surface features are common on the reef surface.

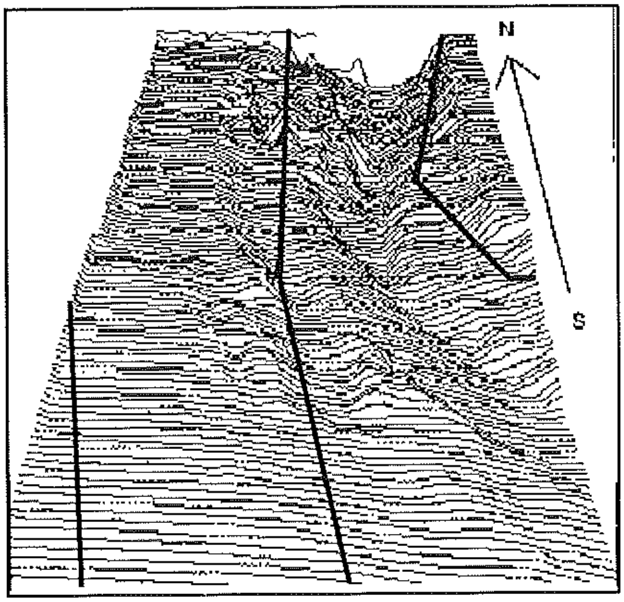


***Figure 9**. Tangier Sound central channel, a three dimensional view covering approximately 15 kilometers of channel length. View is approximately south to north. Vertical relief has been exaggerated 25 X to enhance relief. Data from recent surveys generated largely from the 1940's. Yates (1907) oyster bars are superimposed upon the topography.*

Discussion

OYSTER HABITAT—TWO DIMENSIONAL AREAL CHANGE

Direct comparisons between turn of the century and the early 1980's data for the purpose of estimating oyster habitat loss must be done cautiously. Surveying methods have not remained consistent over this timeframe. Yates (1911) clearly utilized economic criteria for determining what bottom should be considered natural oyster bottom (Graves 1912), by requiring that areas designated as oyster bars be capable of supporting the livelihood of oystermen. Although grabs samples were made during the Yates survey to confirm oyster presence on the bottom, there are no records that distinguish between dense and scattered cultch. Therefore, it is difficult to compare bottom types determined from the acoustic, diver, and patent tong samples from the Bay Bottom Survey to Yates' survey. We have taken particular care in this study to make comparisons only between spatially appropriate portions of these data sets and to examine the relationship between several bottom types in the recent survey and "oyster bottom" in the historic data.

Our results suggest that there has been significant oyster reef habitat loss during this century in the areas examined in this study. In all cases, dense cultch coverage (recorded as cultch bottom in the Bay Bottom Survey) was greatly reduced within the boundaries of Yates' oyster bars from the time of the Yates' survey to that of the Bay Bottom Survey. However, areal coverage does increase to 32-73% of that measured by Yates if scattered cultch in mud and sand is considered.

In the Bay Bottom Survey oyster bottom was found outside of the original Yates' oyster bar boundaries. If such bottom areas are added to a comparative total, one of the three regions examined (Chester River) shows a very slight increase in oyster bottom from the early to later part of the century. However, when peripheral cultch bottom is added to coverage values for the Patuxent River only 45% percent of cultch bottom estimated by Yates remains. In all cases where bottom area has clearly been reduced within the boundaries designated by Yates, mud or sand has replaced shell as the surface substrate. To what extent these mud or sand areas might have originally been within the bar areas at the turn of the century is unknown.

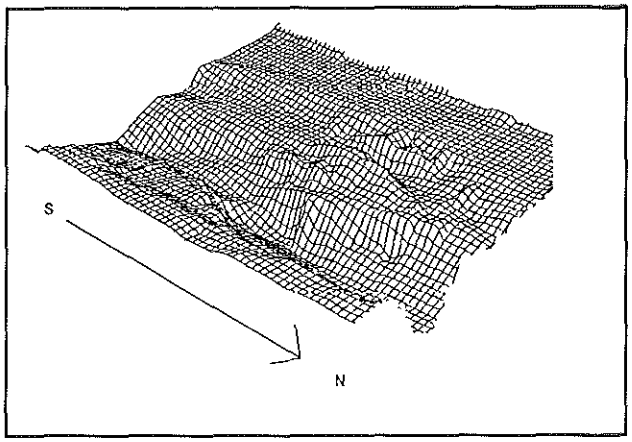


Figure 10. A three dimensional view of Turtle Egg Rocks from 1940's bathymetry. A viewpoint change and zoom from Figure 9. View is looking from northeast to southwest. Vertical scale exaggerated 25 X, to enhance relief.

Hypotheses explaining how cultch bearing regions have appeared outside of Yates' bar outlines could involve charting omissions, unexplained movement of cultch down the slopes of oyster bars, or the addition of new cultch material outside of original charted oyster bars. In the case of the Chester River, where harvesting has historically been by hand-tong, rather than dredge, such movement is unlikely. State shell planting programs may also have had some effects which we have not attempted to evaluate.

Large scale sedimentation processes may have influence bar topography and persistence at the mouth of the Patuxent River, where large plumes of sand and mud covering previously charted oyster bottom are apparent. The Yates survey may have exaggerated the oyster bottom area in this region, especially in the area directly eastward of the mouth of the river, where two county boundaries meet in an east-west direction.

A similar analysis performed on multiple oyster bars by Rothschild et al. (1994) estimated greater than 50% reduction in oyster habitat between the Yates' and Bay Bottom surveys. In their study, a decision was made not to include mud with scattered cultch as oyster bottom. In our analysis this category was included as oyster habitat, resulting in somewhat lower estimates of oyster bottom loss. In either case, the conclusion which emerges from these studies is that their has been a significant loss of oyster bottom habitat in the Maryland portion of Chesapeake Bay over the past century.

TOPOGRAPHIC CHARACTERIZATIONS

The foregoing has addressed changes in areal coverage and discussed some of the difficulties inherent in estimating long-term temporal changes. No less difficult is estimating historical changes in vertical relief in these habitats. Some variation in the topography of oyster habitat is implied by the common terminology used to characterize them: *lumps*, *rocks*, *reefs*, *bottom*, *beds*, and *grounds*, but these terms lack precision and historical trends have not been well documented. Three-dimensional digital reconstructions of 19th century charted data (Winslow 1878) and mid-20th century bathymetric data (Coast and Geodetic Survey, 1931-1956) help to visualize the topographic variation in oyster habitat.

The Tangier Sound region can be viewed in a bathymetric sense as a microcosm of the Chesapeake Bay mainstem, with a deep central riverine main channel flanked by prominent oyster growing regions and in-flowing tributaries (Figure 1). Various configurations of oyster reef or rocks are apparent, complementing the shapes examined with the three areal comparison sites.

Visually the historic bathymetry of this region (Almy, 1856; Winslow, 1878) and the more recent bathymetry (1931-1956) appear similar. Therefore, we considered the mid-twentieth century bathymetric rendition to provide a good model for the historic oyster bottom of the 1800's. When digitization is completed for all Almy and Winslow data however, some anthropogenic change may be apparent. One point of interest is that unlike intertidal reef structures noted in other East and Gulf Coast locations, as of 1856, the channel-bordering oyster rocks did not extend upward into the intertidal zone, but were submerged in close approximation to today's depth.

The central channel of Tangier Sound (Figure 9), shows a variety of topographically distinct bottom types found within Yates' charted oyster bars. The outlined top left oyster bar is called Turtle Egg Island. The adjoining lower bar is Mussel Hole. Visible to the east of the main channel and descending deeply into the trough is Chain Shoal. The topography of the *rocks* or dense oyster growing areas can be seen in relief on both sides of the channel.

At the central channel edge of Yates' Turtle Egg Island Rock and Mussel Hole Rock are fringing oyster reefs in a truly classic sense (Moore 1971). Characteristic of drowned river valleys and tributaries, tidal scour excavates the central channel and keeps it deep and free of oysters. The densest oyster populations are on the edges closest to the central channel. The appearance of irregular terrain along the main channel edges is suggestive of relict oyster deposits. These particular regions are associated with long-term historic oyster growth concurrent with sea level over the past several thousand years (see Hargis 1999, and Kennedy and Sanford 1999, Chapters 1 and 2, this volume). Prior to recent assaults on survival growth of oyster reefs are presumed to have kept pace with sea level rise, producing thick deposits of reef base oyster shell (DeAlteris 1988).

Each of the three Yates oyster bars visible on Figure 9 has some large percentage of flat terrain not typically associated with reef oysters. A large expanse of smooth bottom at the lower left of the figure leads to the opening of Tangier Sound to the mainstem of the Chesapeake Bay. Firm, sandy substrate in this area (Figure 5) should permit oysters to gain a foothold, forming reefs with a morphology referred to as patch reefs (Moore, 1971).

To the right of the axial channel of Tangier Sound, Yates' Chain Shoal oyster bar and (just off the figure) Piney Island West oyster bar lie submerged beneath the Manokin River's entrance into Tangier Sound. Winslow (1878) referred to this area as oyster bar rather than a rock, but used the latter term for other oyster features which flank the main axial channel. Here shallow water at the mouth of the river maintains a bar some distance inland from the fringing reef areas.

A similar situation is apparent on the large inland portions of Yates' Turtle Egg Island oyster bar visible at the upper left of Figure 9. Originating as a fringing reef type at the main channel edge, the oyster bar extends inland to a lagoonal area terminated by the coastline of South Marsh Island. Figure 10 gives a different aspect of this oyster rock (Turtle Egg Rocks) and backshore area looking from the northeast to the southwest. Viewed over the eastern edge of the main channel, the irregular surface of the western channel side of the oyster-reef forming rocks is apparent. A smooth sediment trap backshore reef area leading to the shoreline of

South Marsh Island is present but not apparent in the figure.

Viewing oyster reefs in such a three-dimensional spatially explicit context and replacing terms like *oyster rock* and *oyster bottom* with *patch reef* and *fringing reef-backshore lagoon* provide a clearer context for evaluating historical changes (see Kennedy and Sanford, 1999, Chapter 2, this volume).

IMPLICATIONS FOR MARYLAND OYSTER ENHANCEMENT ACTIVITIES

Comparisons of bottom substrate within the 20th century point to a high probability of loss of cultch on the Maryland bay bottom. The patterns of this loss appears to be specific to individualized locations. Therefore, large scale efforts to quantify habitat loss on a regional basis may be of interest, but detailed analysis of specific sites may be more relevant to habitat restoration efforts. In light of this, oyster reef restoration activities should directly address existing, as well as historical, bottom characteristics of a site. Structural differences in reef type (e.g., fringe and patch reefs) need to be considered in selecting restoration approaches. A detailed bathymetric examination in conjunction with analysis of historic bathymetric records should provide an important aide for successful oyster reef restoration.

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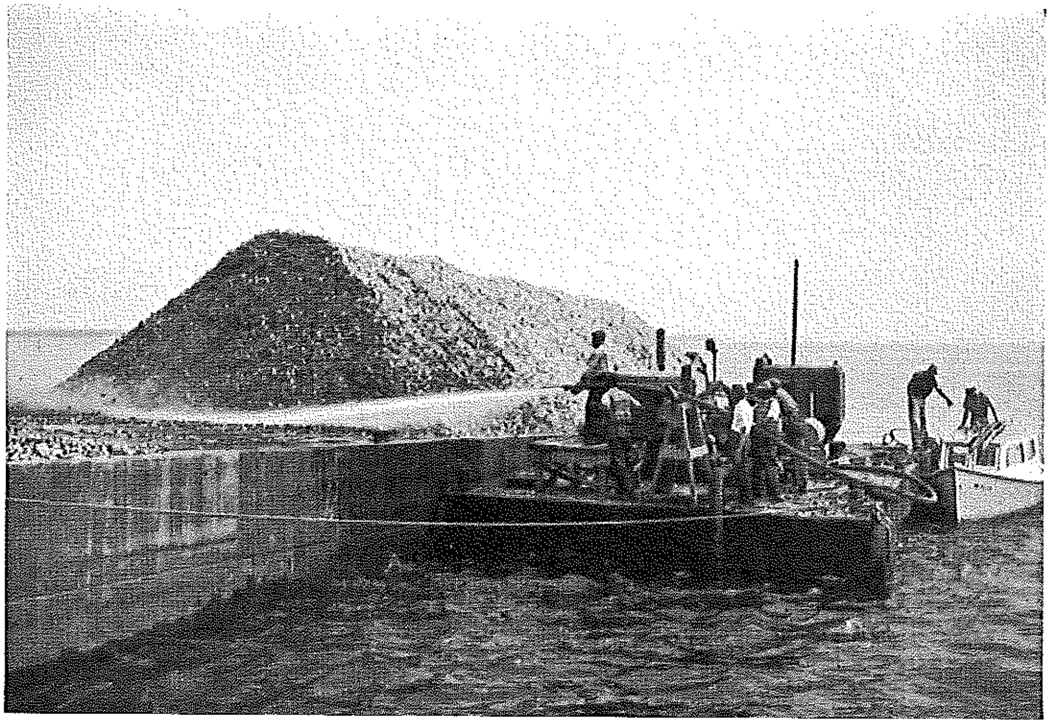
Part II
Synopsis of Ongoing Efforts



Chapter 4

Resource Management Programs for the Eastern Oyster, *Crassostrea virginica*, in the U.S. Gulf of Mexico... ...Past, Present, Future

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Abstract

Oyster reef habitat in the Gulf of Mexico has historically been managed by the states using a variety of methods and techniques. Most efforts have been directed at maintaining or increasing oyster habitat by replacing cultch that was lost as the result of harvesting, natural disasters, and other phenomena. Oyster shell and *Rangia* clam shell have been the most popular cultch materials. These shells most often have been mined from ancient reefs and other deposits, but the return of processed shell has also been a significant part of states' management programs, particularly in Florida. In recent years, limestone has become more widely used because adequate sources of oyster and *Rangia* clams are no longer available. States also have supplemented the productivity of reefs by relaying oysters from restricted areas to approved waters where, after purging, oysters can be harvested and marketed. Transplanting oysters from established, nearshore and intertidal reefs where setting propensities are high to grow-out areas on public reefs and private reefs has proven to be very successful. This practice of moving small, "seed" oysters is the primary component of the oyster management program in Louisiana.

Oysters also have been managed through user-directed practices. Gulf states have enacted various regulations including size limits, gear restrictions, area and season closures, and others to control harvests and to prevent depletion of reefs. User-directed and resource-directed practices employed by the Gulf states have been effective in maintaining a relatively stable fishery.

Introduction

State management of oyster resources began soon after statehood for most Gulf states (early to mid-1800s). Management evolved from user management to primarily an enforcement function that included tax collection, oversight of traditional industry operations to prevent poaching, and insurance of fair and equitable harvests, e.g., measuring sacks/barrels and culling. Today, management includes comprehensive practices for expanding, enhancing, and mitigating destruction of reef areas, as well as for protecting public health. In the Gulf states numerous management practices designed to maintain and increase production have been investigated and evaluated, despite fluctuating environmental conditions, pollution, illegal harvesting, and changes to the economic and social characteristics of their fisheries. These efforts have included both resource-directed and user-directed practices.

Perhaps the most important aspect of all states' programs has been the effort to replace and increase the amount of hard-bottom substrate using various cultch materials. Deposition of cultch materials began prior to state management programs. The oyster industry stockpiled processed oyster shells primarily during the winter processing months and scattered them over reefs during summer spawning months. Replenishment efforts by the industry continued after states developed management programs; however, these efforts diminished as alternative demands (mostly for roadbeds) for processed shells increased. Fluctuating landings, alternative uses, and increasing costs associated with collecting and stockpiling processed oyster shells forced states to seek alternative and more cost-effective cultch materials for their programs. Although different types of materials have been used for cultch, clam shell (*Rangia cuneata*) was used most often during the late 1960s, 1970s, and 1980s. Other materials that have been used include: dredged oyster shells, scallop shells, rocks, limestone chips, crushed concrete, and various experimental materials such as gypsum and coal fly ash, which are sometimes combined with cement.

As coastal populations increased rapidly, pollution (primarily from inadequate treatment of sewage) has forced harvest restrictions from many productive oyster reefs in the Gulf (Berrigan *et al.* 1991). To combat these losses of available reefs, states began to look at alternative ways to utilize oyster resources. In less-polluted, conditionally approved or conditionally restricted areas, various plans have been developed to allow seasonal or intermittent harvest when conditions are acceptable, e.g., there is minimal threat to human health from consumption of oysters. These plans include analyses of various factors that affect water quality including the proximity of reefs to known outfalls, rainfall, river stages, and other components. The primary strategy that has been employed to utilize oysters from closed or *restricted* areas is relaying to clean waters where, after an adequate purging period, oysters can be harvested for human consumption. States also have considered depuration, steaming, or otherwise cooking oysters from restricted areas; however, there are no approved facilities currently operating that utilize these techniques.

With the exception of Louisiana where oysters are predominantly harvested from private leases, most states' landings come from public reefs that are open to all fishermen. Although the other Gulf states have had laws allowing for the leasing of water bottoms for many years, the practice has been relatively unpopular until recently when most states began to allow relaying of oysters from restricted areas to private leases. In essence, leasing in most states fluctuates based on the availability of oysters on public reefs and in restricted areas. Leasing is favored when public supplies are low.

Although most states have experienced great variation in catches from year-to-year, and some have recorded an overall downward trend in landings, total Gulf production has remained relatively stable over the last 30 years (Berrigan *et al.* 1991). This stability may have resulted from innovative management strategies and funding mechanisms to combat losses of reef areas as the result of pollution and habitat degradation. Freshwater diversion in Louisiana, used to regulate salinity regimes, has been perhaps the boldest attempt to enhance environmental conditions and combat habitat losses. Currently, seven structures are operating, and two are planned. Most states have implemented size limits, sack limits, seasons, and area closures to prevent overfishing. All have worked with the industry, their respective legislatures, and others to continue successful, oyster resource management programs.

The purpose of this chapter is to describe oyster resource management programs in the Gulf states by providing an account of states' activities and management actions that have been used to increase or maintain oyster populations. Other activities that potentially could be used, or that could be intensified to improve existing programs are also discussed. This chapter also addresses the relative successes and failures of these efforts, and an attempt to project future programs to address expected needs of the fishery is included.

Methods

An oyster resource management program questionnaire and outline was developed by the authors and distributed to the Gulf states' representatives on the Oyster Technical Task Force of the Gulf States Marine Fisheries Commission. Task Force members were asked to use the outline to describe past, present, and future oyster resource management programs in their respective state. Primary questions focused on reasons for activities, the extent of the activities, benefits or losses, and prognoses for future activities. Responses were analyzed for Gulf-wide applicability and to determine state- or area-specific programs.

Results and Discussion

RESOURCE-DIRECTED MANAGEMENT PRACTICES

States have used numerous management strategies to increase the availability of oysters and thus increase production. These efforts have focused on maintaining and increasing reef acreage and employing alternative management practices to utilize oyster resources that were previously unharvestable. The following is a discussion of these techniques.

Cultch Deposition

Oysters require a hard, relatively unfouled substrate for setting. This substrate must also be sufficiently stable to resist subsidence, thereby preventing oysters from sinking as they grow. Cultch deposition, or planting as it is commonly referred to, is the most utilized management technique to provide suitable substrate that subsequently maintains or increases production. This practice has proven to be effective in replenishing oyster habitat that is lost as a result of fishing and shell dredging activities (Berrigan *et al.* 1991). Reef habitat is also lost as the result of pollution, filling, sedimentation, subsidence, flooding, and other natural disasters. If cultch is not replaced after being removed, buried, or fouled, available setting habitat is reduced, and overall production is diminished. Cultch planting is perhaps the most effective method to mitigate losses of reefs and increase productivity.

Success of cultch planting efforts is dependent on favorable conditions before, during, and after deposition, and short-term benefits are sometimes not observed due to fluctuating biological and physical parameters. Most states monitor temperature, salinity, and density of oyster setting (spat) on reefs before and after cultch deposition. Although these conditions are monitored, they are not necessarily used to time cultch planting but are primarily used to determine potential setting.

Cultch is usually planted during the oyster spawning season that occurs throughout the Gulf from early spring to late fall. In most areas, there are two peak spawning periods, one in the late spring/early summer and one in the mid-to-late fall. Cultch may be applied from April to October to take advantage of both peak periods. Operations may be suspended during mid summer especially in shallow areas where high temperatures would probably kill spat and young oysters.

Site selection is an important component of cultch planting programs, and sites are usually located on or near reefs that have historically produced commercial quantities of oysters. Bottom conditions, water depth, sediment types, turbidity, current patterns, salinity, temperature, and historical catch data are important factors to consider when determining which areas to plant. Planning and site selections also may include the recommendations from local oystermen. This information is valuable in identifying historically productive areas, and it is an important criteria for success.

Cultch planting can be a complex operation that involves mobilization of large amounts of equipment and personnel. Various techniques are used to apply cultch to obtain optimal results and to provide widest coverage. A thin layer of cultch is usually applied on existing reefs and in areas that have a firm bottom (i.e., hard, cohesive mud and shell), while a thick application that sometimes involves "piling" of cultch is used on softer substrates and areas where shell densities are low. Cultch may be dispersed from deck barges using high pressure "water cannons" to wash shells off as the barge is maneuvered slowly over the reef. This method provides for dispersion of shells in a thin layer over reefs. Draglines with clam buckets are used as well, especially in smaller, more shallow areas where deck barges cannot float or be maneuvered safely and effectively. This method also is used to restore reefs and create new ones; however, a large amount of cultch is required to produce the necessary elevation and to stabilize the area. In other areas, especially extremely shallow or narrow bodies of water, fishermen and their boats have been employed either voluntarily or under contract to deposit cultch.

When new cultch is needed on existing reefs, it is usually deposited in approximate densities of 100 - 150 yd^3/acre and broadcast in a thin layer over the reefs. In the 1970s and 1980s some states planted cultch in smaller quantities. Sometimes, depending on the type of material used and the bottom characteristics, cultch has been planted in densities of 250 yd^3/acre or more to form new reefs, add to existing fringe areas, or rejuvenate severely depleted reefs. Oftentimes, these efforts involved planting of cultch in layers to increase the relief and to compensate for subsidence. Increasing costs and decreasing supplies of cultch in recent years have forced most states to focus their efforts on maintenance and rehabilitation of existing reefs rather than on construction of new ones. Some construction, however, continues on fringe areas and in the close vicinity of existing, productive reefs.

Oyster resource restoration through the deposition of cultch has been shown to be a successful and cost effective management practice in the Gulf states (May 1971; Whitfield 1973; Dugas 1977, 1984; Hoffstetter 1981; Berrigan 1990; Perret *et al.* 1991; Berrigan *et al.* 1991). Because long-term benefits of cultch deposition programs have most often far exceeded the cost of planting (Whitfield 1973, Dugas 1988, Berrigan 1990), their success is reflected in part by the relative stability of Gulf-wide catches over the past 30+ years (Berrigan *et al.* 1991).

Cultch Materials

Although oysters will set on virtually any hard surface, the type of cultch material that is used depends upon its availability, cost, and ability to attract and retain oyster spat. Historically, oyster shells have most often met these criteria; however, in recent years clam shells (*Rangia cuneata*) have been used extensively. The following is a discussion of the materials that have been used, reasons for their use, amounts planted, results, and plans for future use.

Processed Oyster Shell In the past, processed shell or "shop shell" was one of the primary materials used in both public and private cultch planting programs. It was readily available in large quantities because of accessi-

Table 1. Processed oyster shell planting activities by Florida in Apalachicola Bay from 1970 through 1994.

Year	Volume (yd³)	Year	Volume (yd³)
1970	18,649	1982	6,501
1971	10,136	1983	14,030
1972	9,675	1984	26,164
1973	7,660	1985	13,949
1974	5,780	1986	26,801[1]
1975	5,055	1987	14,901
1976	DNP*	1988	9,104
1977	2,751	1989	10,013
1978	10,139	1990	7,297
1979	6,258	1991	DNP
1980	5,709	1992	2,100
1981	8,570	1993	6,250
		1994	2,363

**DNP - did not plant shell*
[1]Shell planted by Franklin County Seafood Workers Association in cooperation with the FDEP.
Source: FDEP

Table 2. Processed oyster shell planting activities by Florida in other areas from 1970 through 1991.

Year	County	Location	Volume (yd³)
1972	Santa Rosa	Escambia Bay	8,864[1]
1976	Bay	Bull Bayou	229
1976	Bay	Murray Bayou	664
1977	Bay	Bull Bayou	302
1977	Bay	East Bay	3,457
1979	Gulf	Indian Lagoon	1,440
1980	Bay	Bull Bayou	3,856
1985	Gulf	Indian Lagoon	2,516

Source: [1]Whitfield 1973 and FDEP

bility to processing plants, particularly in the northern Gulf where there were high-volume steaming and canning operations. Prior to the 1960s, processed shell was used extensively by agencies and oyster fishermen/processors often in cooperative programs to replace shell. Because of its broad, flat shape, processed shell served as a material of choice for new reef construction especially in relatively soft-bottom areas. These physical characteristics also made processed shell desirable for other uses (i.e., road construction and septic systems). Consequently, after the 1960s, much of the available processed shell was sold for other uses limiting its availability for cultch. Also, as production on the Atlantic coast declined in the 1980s, an increased market for shell stock (sack oysters) was created resulting in additional losses of processed shell.

Processed shell is currently being used to varying degrees by Gulf states, but it is usually a minor component of their overall management programs. Resource managers in all of the Gulf states recognized the potential benefits of using processed shell and have evaluated the effectiveness of the practice in their specific locales. When larger processors are located in close proximity to productive reefs, processed shell has been a significant cultch component for restoration in these areas. In most areas, however, the costs associated with collecting processed shell from numerous small processors and remote locations have caused economic constraints.

The Florida Department of Environmental Protection (FDEP) and its predecessor agencies have used processed shell in their management programs since 1949. Apalachicola Bay has historically accounted for over 90% of Florida's oyster landings, and the majority of processing activities occur in the nearby communities of East Point and Apalachicola. Consequently, resource managers in Florida have taken advantage of this concentration of harvesting and processing segments of the industry, and they have been more successful than the other Gulf states at developing and maintaining cost effective operations, including collecting, transporting, stockpiling, and dispersing processed shell. In turn, the FDEP has historically focused its efforts on maintaining the fishery in Apalachicola Bay. Tables 1 and 2 show the amounts of processed shell that have been planted in Apalachicola Bay and in other bays in Florida from 1970 to 1994, respectively.

Mississippi used large amounts of processed shell in its resource management program during the early and mid 1900s. The large concentration of processing plants in Biloxi, Mississippi, particularly steaming and canning operations, produced large quantities of shells. These shells were planted on public reefs by fishermen and factories in cooperative efforts with the Mississippi Department of Marine Resources (MDMR) and its predecessor agencies. Some shells were taken to Louisiana and planted on private leases in the eastern marsh area where processors had business ties with lessees. As canning operations declined in the mid 1900s, the availability of processed shells

Table 3. Processed oyster shell planting by Mississippi, 1960 through 1971 and 1988 through 1994. Locations unknown for shell planting prior to 1988. Other blanks indicate no activity or missing records (we were unable to determine which).

Year	Location	Volume (yds)	Cost ($/yd^3)
1960		4,392	
1961		1,470	
1962		1,280	
1963		1,661	
1964		875	
1965		290	
1966		8,202	
1967		6,824	
1968			
1969		6,642	
1970		*27,949	$3.72
1971		*16,018	
1988	Bang's Lake Reef		
	Biloxi Bay Reefs	1,396	
		1,680	
1989	Bay St. Louis Reef		
	Biloxi Bay Reefs		
	Bang's Lake Reef	757	
		1,736	
		1,021	
1990	Bay St. Louis Reef		
	Pass Christian Reef	1,332	
		1,013	
1991	Bay St. Louis/ Waveland Reefs	137	
1992			
1993	Pass Christian Reef	2,000	
1994		2,000	

*Includes some dredged reef shell
Source: MDMR

Table 4. Processed oyster shell planting by Alabama, 1940 through 1971 and 1989 through 1994. Cost estimates not available prior to 1989; blanks under shell volume again indicate no activity or missing records.

Year	Volume (yd^3)	Cost	Cost ($/yd^3)
1940	10,889		
1941			
1942	4,357		
1943			
1944	16,774		
1945			
1946	2,313		
1947	2,722		
1948	4,537		
1949	11,472		
1950			
1951	7,259		
1952	3,221		
1953	441		
1954			
1955	17,732		
1956			
1957			
1958			
1959			
1960	4,271		
1961	12,704		
1962	20,870		
1963	10,889		
1964	11,796		
1965	10,889		
1966	9,074		
1967	2,069		
1968	8,433		
1969	19,115		
1971	12,249		
1989	3,399	50,000	14.71
1990	16,589	397,250	*23.95
1991			
1992			
1993	5,961	85,850	14.40
1994	6,954	72,527	10.43

**Fishermen assisted with planting.*
Source: Swingle and Hughes (1976), Alabama Department of Conservation and Natural Resources (ADCNR)

diminished; from the mid 1970s to the mid 1980s, very little processed shell was used. Table 3 shows the historic use of processed shell in Mississippi.

Prior to 1970, Alabama planted processed shell almost exclusively in quantities averaging about 12,000 yd^3 per year during the 1960s. Clam shell was the cultch of choice during the 1970s, but shop shells again became the dominate cultch from 1989 through 1994 (Table 4). Most processed shells were planted in the Portersville Bay area, while clam shells have mostly been used at Cedar Point Reef. These locations are the two most productive areas in Alabama. Table 5 shows plantings in Louisiana from the 1950s and in 1994. Some earlier plantings were also recorded in 1912, 1917, 1941, and 1943 (Mackin and Hopkins 1962).

The use of processed shells by leaseholders is common practice in most Gulf States, especially for those lessees who are also processors. Although Texas has not utilized processed shell in its oyster management program, its lessees have relied heavily on this source of cultch. Currently, the 2,322 acres of private leases in Texas are controlled by approximately eight processors who return most of the shell to their leases. Likewise, processors that have leases in Apalachicola Bay rely heavily on processed shell. Alabama lessees also use processed shell almost exclusively; however, lessees in Louisiana and Mississippi have used very little processed shell to cultivate leases.

Table 5. Processed oyster shell planting activities by Louisiana, 1951 through 1953 and 1994.

Year	Area	Area Planted (acres)	Volume (yd^3)
1951	Caillou Lake	184	5,526
1951	Lake Felicity	46	1,381
1952	Caillou Lake	235	7,062
1953	Caillou Lake	140	4,210
1994	Hackberry Bay	18	1,784

Most Gulf states anticipate that their oyster management programs will be increasingly dependent upon processed shell due to the 1990 ban on clam shell dredging and the uncertain availability and cost of alternative cultch. To continue resource restoration efforts at current levels, states must rely on greater cooperation from the processing industry. Although most states have long benefitted from laws providing that all or a percentage of the shucked oyster shells are the property of the respective state, there are questions in some states concerning the ownership of oysters received from other states. Oysters harvested for the "half shell" market and sack oysters shipped out-of-state contribute to the decline in availability and increased costs of processed shell. To compensate for the loss of this valuable cultch material, Florida and some other states have examined alternative approaches to procure processed shell. Possible solutions include enacting legislation to institute taxes or fees on processed shell that is not returned for resource restoration. Fees collected in the form of a shell tax, bag tax, or other "buy back" programs could be used to fund collection and planting activities.

Dredged Oyster Shell Oyster shells have been dredged from ancient reefs that have been buried for centuries. Many such reefs may be hundreds of feet deep and reflect thousands of generations of oysters. Dredged shell, commonly called fossil, reef, or mud shell, is usually smaller, thinner, and more brittle than processed shell because it has been compacted over time; and the dredging operation tends to break up shell. Dredged shell has been used Gulf-wide for cultch because of its historic, high-volume availability and low cost. Although it was a popular material in the early to mid 1900s, it has been used to only a limited degree since the 1960s because of increasing environmental concerns regarding dredging operations and preference for *Rangia* shell and processed shell.

Shell dredging has historically occurred in coastal and estuarine areas of all the Gulf sates (Bouma 1976), but over the past twenty years, dredging operations have increasingly been restricted or eliminated. A portion of the Atchafalaya Bay is the only area still open, and it will likely be closed after 1995.

Table 6. Dredged oyster shell planting activities by Florida from 1972 through 1994.

Year	Location (County)	Bay	Volume (yd^3)	Cost ($\$/yd^3$)
1972	Santa Rosa	Escambia & East	1,775[1]	NA
1990	Santa Rosa	East	1,900	24.60
1990	Bay	West & East	2,400	24.60
1991	Santa Rosa	East	2,450	27.15
1991	Bay	West & East	2,920	27.15
1991	Okaloosa/Walton	Choctawhatchee	1,200	27.15
1992	Santa Rosa	Escambia	1,810	26.90
1992	Bay	West & East	2,140	26.90
1993	Santa Rosa	East Bay	1,728	27.35
1993	Walton	Choctawhatchee	2,438	27.35
1993	Bay	West	2,056	27.35
1994	Santa Rosa	East Bay	1,459	26.10
1994	Walton	Choctawhatchee	1,291	26.10
1994	Bay	West Bay	1,630	26.10

Source: Little and Quick 1976 and FDEP

Table 7. Dredged oyster shell planting activities by Louisiana from 1948 through 1961.

Date	Location	Area (acres)	Volume (yd^3)
1948	Mississippi Sound	88	2,627
1949	Lake Felicity	81	2,423
	Caillou Lake	99	2,978
1952	Halfmoon Lake	165	4,951
1953	Halfmoon Island	137	4,119
1954	Halfmoon Island	167	5,002
1955	Bay Boudreaux	161	4,819
1956	Black Bay	92	2,763
	Snake Island	91	2,725
	Petit Pass	140	4,211
1959	Petit Pass	220	2,127
	Halfmoon Island	71	16,570
1960	Grassy Island	321	14,858
	Bay Boudreaux	216	6,485
1961	Three Mile Bay	23	11,890
	Little Raccoon Island	228	6,840
1994	Caillou Lake	306	42,576
	Marsh Island		19,595
	Black Bay	708	29,655
	Bay Crabe	137	8,594
1995	Hackberry Bay	35	1,786
	Caillou Lake	700	70,902

Source: LDWF

Florida did not use appreciable quantities of dredged shell until 1990 when *Rangia* shell was unavailable (Table 6). Additionally, it has been primarily used in areas outside of Apalachicola Bay where processed shells are less available.

Louisiana utilized dredged reef shell on an intermittent basis from 1948 to 1961 (Table 7). Mississippi planted 3,342 cubic yards in 1981, 1,327 in 1991, and 5,500 in 1994; however, no other records were found. Likewise, no records were found regarding the use of this cultch in Alabama.

Texas mined reef shell from 1922 to 1983, and it was an important cultch material used for reef construction and enhancement during much of this period (Table 8). In the 1960s, dredging companies were required to mitigate their activities by supplying shell and constructing reefs in Galveston, Matagorda, and San Antonio Bays.

Future use of dredged shell is uncertain. As a result of environmental concerns, dredging companies are currently operating on a very limited basis, and they are not likely to expand in the near future. Texas is working with the

Table 8. Dredged oyster shell planting activities Texas from 1952 through 1982. Volumes planted and areas covered are listed by embayment.

Year	Galveston Trinity	Matagorda	San Antonio	Aransas	Corpus Christi	Upper Laguna Madre
1952[1]	87,806 yd^3 31.1 acres	0.0	0.0	0.0	0.0	0.0
1954	2,541 yd^3 0.9 acres	0.0	0.0	0.0	0.0	0.0
1957	180,693yd^3 64.0 acres	0.0	0.0	0.0	0.0	0.0
1958	28,516 yd^3 10.1 acres	0.0	0.0	0.0	0.0	0.0
1959	231,513yd^3 82.0 acres	0.0	0.0	0.0	0.0	0.0
1960	117,733yd^3 41.7 acres	0.0	0.0	9,882 yd^3 3.5 acres	0.0	0.0
1961	166,294yd^3 58.9 acres	87,523 yd^3 31.0 acres[2]	0.0	0.0	0.0	0.0
1962	152,460yd^3 54.0 acres	0.0	0.0	0.0	4,235 y^{d3} 1.5 acres	5,647 yd^3 2.0 acres
1963	28,516yd^3 10.1 acres	0.0	0.0	0.0	0.0	0.0
1964	95,993 yd^3 34.0 acres	0.0	0.0	0.0	0.0	0.0
1969	0.0	0.0	33,880 yd^3 12.0 acres	0.0	0.0	0.0
1973	0.0	0.0	96,840 yd^3 34.3 acres[3]	0.0	0.0	0.0
1974	0.0	448,910yd^3 159.0 acres	0.0	0.0	0.0	0.0
1976	0.0	0.0	37,550 yd^3 13.3 acres	0.0	0.0	0.0
1982	0.0	64,937 yd^3 23.0 acres	3,388 yd^3 1.2 acres	0.0	0.0	0.0

[1] *Year permit received for construction. Completion was at a later date which is unavailable at this time.*

[2] *1961-1982 construction period*

[3] *1973-1982 construction period*

Source: Lukens 1973

U.S. Army Corps of Engineers to negotiate the use of shell that is dredged during pipeline construction and the dredging of the Houston Ship Channel for oyster reef construction as mitigation measures. Future use will depend on alleviating environmental concerns followed by availability, cost, and suitability when compared with other available cultch materials.

Rangia Clam Shell Like dredged oyster shell, most *Rangia* shells have been produced from mining of ancient reefs in brackish water bays and streams. Most shells have been produced from the Lake Pontchartrain area of Louisiana, but some shells have been taken from other areas off Louisiana and from Mobile Bay, Alabama.

Table 9. *Rangia* shell planting activities by Florida from 1972 through 1989.

Year	Location (County)	Bay	Volume (yd^3)	Cost ($\$/yd^3$)
1972	Santa Rosa	Escambia & East	12,520[1]	NA
1973	Santa Rosa	Escambia & East	14,020[1]	NA
1984	Bay	West	3,006	16.65
1986	Franklin	Apalachicola	56,470	16.25
1986	Santa Rosa	Escambia	2,890	16.25
1986	Bay	East	1,895	16.25
1986	St. Johns	Salt Run	700	44.00
1987	Okaloosa/Walton	Choctawhatchee	1,925	13.89
1987	Santa Rosa	East	3,925	13.89
1987	Bay	West & East	3,170	13.89
1987	Franklin	Apalachicola	39,760	13.89
1988	Santa Rosa	East	2,333	19.24
1988	Bay	West & East	3,298	19.24
1989	Bay	West, East & North	4,850	21.88
1989	Santa Rosa	Escambia	2,050	21.88

[1]*Estimated from Little and Quick (1976)*
NA - Cost Not Available
Source: FDEP

Rangia shells were the preferred cultch material for enhancing and expanding existing reefs from the early 1960s through 1989. In addition to being a very cost effective cultch material, *Rangia* shells were readily available in large quantities. Other characteristics that made *Rangia* shells the cultch of choice included: (1) they can be easily and evenly dispersed; (2) they are less dense than oyster shell or limestone and thus can be used on relatively soft substrate without sinking; (3) they attract less-dense spat concentrations; (4) they produce more single, well-shaped oysters that are more attractive (for half-shell markets) and more easily shucked; and (5) they produce oysters that are more easily harvested and culled.

Florida used *Rangia* clam shells intermittently in its resource management program from 1960 to 1989 and relied heavily on shell imported from Louisiana from 1984 through 1989 (Table 9). Imported *Rangia* shells were commonly used in regions other than Apalachicola Bay where processed shell could not be economically recovered. Following Hurricane Elena in 1985, Florida used large amounts of *Rangia* clam shells to restore damaged reefs in Apalachicola Bay (Berrigan 1988). A detailed economic account of this restoration effort indicated that initial planting costs were recovered in two years (Berrigan 1990). Actual and estimated revenues from landings were used to calculate cost:benefit ratios of 1:2.3 to 1:3.5 after two years and up to 1:20.7 after ten years for each $1.00 expended to restore damaged oyster reefs.

Being in close proximity to dredging operations, Alabama, Mississippi, and Louisiana relied heavily on this source of cultch for reef restoration programs (Table 10 - 12). Several large planting efforts were initiated following natural disasters caused by hurricanes and flooding. In Alabama, *Rangia* shells were used almost exclusively from 1970 through 1987, and the Cedar Key Reef was the primary planting area (Table 10). Pass Marianne, St. Joe, Henderson Point, and Square Handkerchief

Table 10. *Rangia* clam shell planting activities by Alabama, 1970 through 1987.

Year	Location	Area (acres)	Density yds^3/acre	Volume (yd^3)	Cost (\$/yd^3)
1970				*9,309	
1971				11,249	
1972	Whitehouse Reef				
	Cedar Point Reef			*20,196	
				1,102	
1973				*573	
1974	Bouy Reef				
	Sand Reef			*15,183	
				15,184	
1975	Cedar Point Reef			*29,447	
1976					
1977					
1978					
1979	Cedar Point Reef			2,495	
1980	Bouy Reef	147	297	43,820	10.37
	Cedar Point Reef	566	100	56,396	10.37
	Kings Bayou Reef	50	287	14,331	10.37
	Sand Reef	29	293	8,455	10.37
1981					
1982	Little Pt. Clear Reef	10	63	627	12.00
	Shellbank Reef	50	96	4,782	12.00
	Cedar Pt. Reef	28	49	1,339	12.00
	Portersville Bay Reef	200	13	2,635	12.00
1983	Cedar Point Reef			5,570	[1]36.37
1984	Cedar Point Reef			28,148	13.50
	Portersville Bay Reef			1,503	13.50
	Sand Reef			3,584	13.50
	Bush Stake Shoals			1,355	13.50
1985	Cedar Point Reef			14,460	13.83
1986	Cedar Point Reef			84,402	13.67
1987	Cedar Point/Bouy Reef			22,588	10.90

*Contains some oyster shell

[1] Cooperative effort with industry

Source: Swingle and Hughes (1976) and ADCNR

Table 11. *Rangia* shell planting activities by Mississippi, 1970 through 1989.

Year	Location	Area Planted (acres)	Volume (yd^3)	Cost ($\$/yd^3$)
1970				
1971				
1972			5,354	
1973			5,317	
1974	Bay St. Louis/Waveland Reefs	2,500	9,476	
	Henderson Point Reef		6,947	
	Bayou Caddy Reef		7,320	
	St. Joe Reef		14,691	
1975			2,774	
1976				
1977			4,335	
1978			4,500	
1979	St. Joe Reef		6,083	9.00
	Bay St. Louis/Waveland Reefs		21,833	9.00
	Pass Christian Reef		37,973	9.00
1980	Bay St. Louis/Waveland Reefs		10,383	10.00
	Long Beach Reef		4,687	10.00
	Round Island Reef		2,358	10.00
	Whitehouse Reef		3,680	10.00
1981	Long Beach Reef		6,369	
	Whitehouse Reef		6,717	
1982	Henderson Point Reef		8,284	
	Long Beach Reef			
1983	St. Joe Reef		2,862	
	Henderson Point Reef		6,729	
	Pass Marianne Reef		1,425	
1984	St. Joe Reef		6,835	
	Henderson Point Reef		32,599	
	Long Beach Reef		1,795	
	Bay St. Louis Reef		3,053	
	Bayou Cumbest Reef		3,125	
1985	Square Hankerchief Reef			
	Henderson Point Reef		3,900	
1987	St. Joe Reef		2,892	
	Bay St. Louis/Waveland Reef		6,154	
	Bayou Heron Reef		1,000	
	Pass Christian Reef		771	
	Biloxi Bay Reef		10,059	
1988	St. Joe Reef		6,249	
	Bay St. Louis/Waveland Reef		4,175	
1989	Henderson Point Reef		3,616	14.79
1989	Pass Christian Reef		3,146	14.79

Source: MDMR

Table 12. *Rangia* shell planting activities by Louisiana from 1959 through 1994.

Year	Location	Area Planted (acres)	Volume (yd³)
1959	Black Bay	1,155	34,673
1960	Big Raccoon Island	329	9,880
1961	Bel La Pass	640	19,200
	Black Bay	845	25,370
1962	Snake Island	670	20,120
1966	Black Bay	550	19,533
	Bay Boudreaux	585	17,386
1967	Halfmoon Island	500	15,150
	Black Bay	549	18,183
1969	Calcasieu Lake	24	7,200
	Black Bay	772	23,160
	Three Mile Pass	446	13,380
1970	California Bay	360	8,901
	Caillou Lake	273	7,039
	Bay Crabe	742	21,668
	Bay Boudreaux	853	23,830
	Mississippi Sound	127	7,241
	Lake Pontchartrain	8	400
1973	Hackberry Bay	450	22,500
1974	Bay Gardene	676	33,800
	Lake Borgne	468	23,400
1975	Caillou Lake	174	10,698
	Bel La Pass	237	11,850
1977	Black Bay	200	10,000
1978	Bay Gardene	15	750
1979	Bay Gardene	59	2,950
	Bay Boudreaux	1,017	50,850
	Lake Borgne	390	19,500
	Black Bay	508	25,400
	Black Bay	598	29,900
	Caillou Lake	458	24,998
1981	Black Bay	660	33,000
	Bay Gardene	300	15,000
1983	Black Bay	650	32,500
	Caillou Lake	435	19,527
	California Bay	150	7,500
1984	Caillou Lake	307	24,353
1989	California Bay	136	18,579
1994	Hackberry Bay	23	1,785

Source: LDWF

reefs in the western portion of Mississippi Sound received the majority of *Rangia* shells planted in Mississippi (Table 1). Louisiana has been the largest user of *Rangia* shells, and they have been distributed over the largest amount of reef acreage (Table 11).

Rangia shells have never been mined in appreciable amounts in Texas; consequently, they have only been available from out-of-state sources. Added transportation costs to obtain *Rangia* shells from Louisiana have precluded their cost-effective use when other cultch, primarily dredged oyster shells, were locally available. Texas used *Rangia* shells in 1989 to rehabilitate existing reefs in San Antonio Bay where approximately 8,258 yd³ were planted over nearly 161 acres.

Because of environmental concerns, access to large deposits of *Rangia* shell in Louisiana was restricted in 1989. Although limited dredging activity was permitted in 1992 and 1993, available supplies have been insufficient to meet resource management needs. In the future, dredged *Rangia* shell will likely become a smaller component in restoration efforts, unless access to larger supplies is permitted.

Calico Scallop Shell Calico scallop shell is an excellent cultch material that is often an unused by-product of local fisheries in Florida. Scallop shell has been most plentiful on Florida's Atlantic Coast and only recently available on the Gulf Coast. Scallop shell has proven to be a good substrate when planted on firm bottoms and on intertidal shoals. Their low density and large surface area to volume ratio appear to reduce subsidence under conditions that might bury denser cultch materials. The use of scallop shell as a cultch material has been dependent upon: (1) the "boom or bust" nature of the scallop fishery; (2) the proximity of scallop processing plants to locations where oyster resource development projects are planned; and (3) restrictions regulating the disposal of shell after they have been processed. Consequently, scallop shell has only been used in Florida on an intermittent basis from 1978 through 1994 (Table 13).

The cost effectiveness of using scallop shells may be very good, depending on the proximity of the source to the planting area and means of delivery. In Florida, the cost of scallop shell has ranged from $1.00 (on-site) to $12.50 (delivered) per cubic yard. The FDEP has increased its efforts to recover processed scallop shell since 1992, and has entered into cooperative agreements with processing plants to remove and stockpile shell. Resource managers in Florida anticipate greater reliance on scallop shells in restoration programs as the availability of other materials declines. Scallop shells are not generally available in other Gulf states.

Limestone Since 1989 when dredging operations for oyster shell and *Rangia* shell were almost completely eliminated, states have begun to look at limestone as a potential low-cost source of cultch. Limestone is available in large quantities in parts of Florida and Texas, and former shell dredgers and suppliers in Louisiana have begun to market limestone from the Southeastern U.S. They also are supplying an ancient coral reef limestone from Mexico that is less dense than domestic limestone.

Chatry *et al.* (1986) compared the relative success of limestone in producing oysters to *Rangia* shells and found almost a two-fold increase in spat setting success for limestone. On established, relatively hard reefs, limestone has proved to be a very effective cultch material. Because limestone is more dense than most shell materials, it is not favored as cultch on relatively soft bottoms where it has a greater tendency to subside.

Although limestone is available in Florida, it has not been used extensively for cultch because it has been more expensive than dredged or processed oyster shells. The FDEP used limestone on a limited basis from 1972 through 1980, and they are currently evaluating the effectiveness of ½" to 1" limestone aggregates (Table 14).

Texas has not used limestone in its resource management program. Alabama has only used coral reef limestone in an experimental planting in 1993; and although it proved to be a successful cultch, its cost ($19.00/yd^3) was not competitive with available oyster shell. Mississippi has used limestone (Kentucky) only on an experimental basis, planting approximately 103 yd^3 in 1990. Louisiana has done experimental testing of limestone (Chatry *et al.* 1986), and subsequently planted about 1,000 yd^3 (Kentucky) in Black Bay in 1981. Louisiana also planted 1,741 yd^3 (Kentucky) over 23 acres and 1,743 yd^3 (coral reef) over 27 acres, both in Hackberry Bay in 1994. At least three lessees in Louisiana have utilized the coral reef limestone on their leases, but they are not currently using it be-

Table 13. Calico scallop shell planting by Florida from 1978 through 1994.

Year	Volume (yd^3)	Location	County
1978	765	Indian River	Brevard
1984	2,200	Salt Run	St. Johns
1988	700	Salt Run	St. Johns
1989	800	Salt Run	St. Johns
1993	555	East Bay	Bay
1993	4,412	Apalachicola Bay	Franklin
1994	550	East Bay	Bay
1994	7,841	Apalachicola Bay	Bay

Source: FDEP

Table 14. Limestone aggregate plantings by Florida from 1972 through 1992.

Year	Volume (yd^3)	Location	County
1972	1,987	Indian River	Brevard
1974	1,745	Shired Island	Dixie
1974	2,291	Shell Island	Citrus
1976	922	Indian River	Brevard
1977	782	Indian River	Brevard
1980	117	Salt Run	St. Johns
1992	50[1]	East Bay	Bay

[1] experimental planting for evaluation
Source: FDEP

cause of the large supply of seed oysters that are available.

Although limestone has been used only on a limited basis in recent years, future usage is likely to increase in all states. In recent years, limestone has been slightly more expensive than previously used *Rangia* shells or dredged oyster shells; however, as limestone becomes more available and shells are less available, the cost effectiveness will probably reverse. Since limestone poses no environmental problems and there are few cost-effective, alternative materials for cultch; limestone is almost guaranteed to be a significant cultch material in many areas of the Gulf.

Crushed Concrete Although crushed concrete has been used in experimental tests, the only reef application was in Louisiana. In 1994, 1,746 yd^3 were planted in Hackberry Bay.

Coal Fly-Ash Aggregate The recent elimination of shell dredging and the increasing supplies of coal fly-ash with limited means of disposal have created an opportunity for producing an oyster cultch material (fly-ash aggregate). Fly-ash aggregate has been produced by combining fly-ash (a by-product of coal-combustion and power-generating plants) with small amounts of cement and water. Other binders, as well as fly ash mixtures alone, also have been used. These materials have been forged into various shapes to provide the most attractive surfaces for oyster spat in different regions.

In the Gulf, three test plots have been planted in Galveston Bay and one in Mississippi. Houston Lighting and Power Company in conjunction with Texas A&M University developed the first test plots, and the results of this research are presented by Baker *et al.* (in press). Mississippi Power Company developed a 50 yd^3 test plot off Waveland, Mississippi, in 1990. Three additional test plots (350 yd^3 each) are scheduled for September/October 1995, two off Biloxi and one off Ocean Springs, at a cost of \$16.54/yd^3 (J.R. Herring, personal communication).

Tests of fly-ash aggregate have shown some success in catching and retaining oyster spat. Environmental concerns regarding leaching of heavy metals and other potential pollutants have, however, limited its production and use. Testing of specific coals and specific plant's fly-ash has reduced environmental concerns and increased interest in this form of cultch (Alden et al. 1996). If an environmentally safe fly-ash aggregate can be produced in sufficient quantities and proves to be cost effective, it could potentially be used by Gulf states in their management programs.

Re-exposing Cultch

Various techniques have been used to re-expose buried shell in an effort to increase spat sets and oyster production. A pasture harrow was used on *Crassostrea gigas* reefs in Washington State resulting in a five-fold increase in subsequent spat set (Sayce and Larson 1966). On the Atlantic Coast, heavy logs sometimes with spikes and lime were once used to re-expose cultch and remove fouling organisms. Now a hydraulic escalator is being used in Virginia to re-expose buried shell (Wesson et al. 1999, Chapter 8, this volume). Efforts in the Gulf have been mostly limited to tilling with modified, but traditional, commercial dredges with the bags removed (Eckmayer 1976). These practices have been limited and mostly experimental, but in Florida, specially designed "drags" have increasingly been used; and they are becoming an important part of oyster management programs in many areas.

Utilization of Oysters from Restricted Areas

The number of productive oyster reefs that are located in waters where shellfishing for direct-to-market sale is prohibited has increased substantially in the past 20-30 years. Harvesting prohibitions on these reefs have been implemented in response to changes in classifications of growing waters to avert public health problems associated with contamination and pollution and to minimize the potential for water-borne and shellfish-borne illnesses.

Harvesting areas where water quality does not meet national standards for direct-to-market sale of shellfish have been characterized as prohibited and restricted. Oysters may be harvested from restricted areas when waters are not grossly polluted for the purpose of relaying and depuration only. Oysters in these areas generally exhibit normal growth, but they are often underutilized because they cannot be harvested for direct-to-market sales.

Oysters filter large volumes of water while feeding and respiring; consequently, they are capable of concentrating many water-borne contaminants and potential toxins that may cause or contribute to serious public health concerns. This process is reversed, however, when pollution levels in water filtered by oysters are diminished. Relaying and depuration are two processes through which oysters purge themselves of accumulated contaminants. In relaying projects oysters are purged in state-approved harvesting areas, whereas in depuration projects oysters are purged in closed seawater systems. Relaying and depuration offer a practical means for utilizing a previously debilitated resource.

Relaying The term relaying in this paper describes a management strategy that involves moving oysters from restricted harvesting areas to approved harvesting areas. During relay projects, juvenile and adult oysters are relocated from public reefs to other public reefs or to private leases that are approved for harvesting. The relocation sites remain closed to harvesting for approximately 15 days. Relaying activities require special operating procedures to prevent relayed oysters from being diverted to direct-to-market sales. They may include added documentation and supervision, special permits, licenses and bonds, increased surveillance and enforcement, and more thorough record keeping.

Relaying also may include the practice of obtaining seed stocks from restricted growing areas. In this management strategy, seed stocks are relocated to more favorable harvesting areas

Table 15. Oyster relaying activities by Florida, 1971 through 1994.

Year	Location (county)	Volume (yd^3)
1971	Levy	
1972	Santa Rosa	239
1973		
1974		
1975		
1976		
1977		
1978		
1979		
1980		
1981		
1982	Frankin	1,701[1]
	Wakulla	417
1983	Franklin	2,083
	Dixie	208
	Levy	208
1984	Franklin	1,099
	Wakulla	167
	Levy	417
	Bay	83
1985	Dixie	364
	Bay	167
	Santa Rosa	12
1986	Dixie	546
	Bay	83
1987	Franklin	128
	Santa Rosa	74
	Levy	565
	Dixie	781
	Wakulla	333
1988	Franklin	805
	Dixie	540
	Wakulla	874
1989	Franklin	578
	Levy	1,001
	Dixie	1,917
	Wakulla	1,495
1990	Dixie	2,770
	Levy	1,210
	Wakulla	1,189
	Franklin	1,264

Continued on next page

Table 15 *Continued.*

1991	Dixie	2,950
	Franklin	805
	Wakulla	1,108
	Levy	250
	Levy	764
1992	Wakulla	104
	Dixie	1,271
	Levy	1,740
	Dixie	344
1993	Wakulla	167
	Levy	1,421
	Franklin	924
1994	Wakulla	687
	Levy	1,064
	Dixie	1,562
	Franklin	

Source: Futch (1983)[1] and FDEP

and allowed to grow to marketable size. Because seed stocks that are relayed may not be marketable for many months or years, rapid depuration is a less important aspect of this management practice, and there is reduced danger to public health from poaching.

Relaying as a public and private management practice is less common than cultch deposition, but various forms of relaying have been practiced in each of the Gulf states. In Texas and Louisiana, relaying from restricted public reefs to private leaseholds (public to private) has been an important component of oyster resource management. In Louisiana, oyster seed stocks also may be relayed from restricted public reefs to other public reefs that are developed as seed grounds, and subsequently, oyster stocks are relocated from the seed grounds to private leaseholds (public to public to private). This unique method of relaying seed stocks is a component of extensive oyster mariculture operations in Louisiana. Additionally, relaying provides an alternative management practice for leaseholders in Louisiana who operate leases that are situated in waters that may be classified as conditionally approved or restricted. In many instances, leaseholders may relay stocks between leases (private to private) in order to harvest oysters from the lease parcels that meet harvesting criteria. In Mississippi, Alabama, and Florida, relaying from restricted public reefs to private leaseholds has been a less frequent practice. Relaying practices have occurred in Galveston Bay, Texas (public to private); the Calcasieu public tonging reef (public to public); Lake Pontchartrain and Vermilion Bay, Louisiana (public to private); Mississippi Sound, Biloxi Bay, Bay of St. Louis, and Pascagoula Bay, Mississippi (public to public and public to private); Mobile Bay, Alabama (public to public and public to private); and Escambia Bay, North Bay, Apalachicola Bay, Oyster Bay, and Suwannee Sound, Florida (public to public).

Florida has perhaps the most extensive relaying program of the five Gulf States. Table 15 shows the volumes of oysters relayed by Florida from 1971 through 1994. Mississippi has been the second most frequent user of this management practice (Table 16); however, Texas lessees have relayed the greatest volume of oysters (Table 17). Alabama has only employed this technique in three years since 1980 (Table 18), and Louisiana has only relayed oysters infrequently, opting to use available resources for shell planting on seed grounds used in its extensive transplanting program for seed oysters.

In most Gulf states, relaying is conducted during periods when public reefs are closed to harvesting for the season, or in some cases closed because of public health concerns or catastrophic events, such as floods or hurricanes. In Texas, seasons are established strictly for relaying when the public harvesting season is closed; and in Florida, relaying is conducted primarily as a cooperative management program during the summer months when the harvest season is closed.

In Texas, Louisiana, and Mississippi, relaying has been accomplished using dredges for initial oyster harvests, whereas in Florida relaying has been carried out exclusively by hand tongs and by hand. Both tongs and dredges are used in relaying operations in Alabama. Re-

Table 16. Oyster relaying activities by Mississippi, 1968 through 1993.

Year	Location		Volume (yd^3)
	From	To	
1968		4,194	
1969		1,324	
1970		221	
1971		883	
1972			
1973		5,518	
1974			
1975			
1976			
1977	Biloxi Bay Reefs	Whitehouse Reef	2,659
1978	Biloxi Bay Reefs	Whitehouse Reef	3,733
1979	Biloxi Bay Reefs	Whitehouse Reef	3,057
1980	Biloxi Bay Reefs	Whitehouse Reef	743
	Graveline Bayou	Round Island Reef	305
	Pascagoula Bay	Round Island Reef	743
	Graveline Bayou	Round Island Reef	305
	Pass Christian Reefs (closed)	Pass Christian Reefs (open)	667
	Biloxi Bay Reefs	Long Beach Reefs	476
			3,239
1981	Biloxi Bay Reefs	Whitehouse Reef	1,133
1982			3,311
1983			662
1984			441
1985			441
1986			883
1987			
1988			
1989			
1990	Pascagoula Bay	Bangs Lake/Heron Bayou Reefs	1,022
1991	Pascagoula Bay	Bangs Lake Reef	1,193
1992	Pascagoula Bay	Graveline Bayou	1,210
1993	Pascagoula Bay	Bangs Lake Reef	1,270

Source: MDMR

layed oysters may be placed directly on the bottom or into containers for the depuration and grow-out period (Hofstetter 1977, Supan 1983, Quast *et al.* 1988, Berrigan *et al.* 1991). On-bottom relaying generally includes unculled oysters, while operators generally cull oysters to

Table 17. Oyster relaying activities by Texas lessees, 1978 through 1994.

Year	Location	Volume (yd^3)
1978	Galveston Bay	10,057
1979	Galveston Bay	8,655
1980	Galveston Bay	5,551
1981	Galveston Bay	12,772
1982	Galveston Bay	8,317
1983	Galveston Bay	20,219
1984	Galveston Bay	18,601
1985	Galveston Bay	20,045
1986	Galveston Bay	34,456
1987	Galveston Bay	22,790
1988	Galveston Bay	19,334
1989	Galveston Bay	11,969
1990	Galveston Bay	20,944
1991	Galveston Bay	15,084
1992	Galveston Bay	14,597
1993	Galveston Bay	10,604
1994	Galveston Bay	10,375

Source: TPWD

legal-harvest size prior to placing them into containers (Supan 1983).

Relaying accomplishes several important objectives for oyster resource managers, including increased product quality, decreased public health risks, increased revenues, and enhancement and restoration of oyster habitat. At times when production from principal reefs is marginal or poor, relaying may be essential for maintaining landings. Relaying protects public health by providing a safe product for harvest while reducing oyster stocks that may be potentially targeted for illegal harvest. By utilizing oyster resources that might be otherwise lost to the shellfish industry, resource managers can increase landings and revenues through both public and private harvests. Additionally, cooperative management programs to relay oysters may provide employment and incomes for participants during periods when the harvesting season is closed. Disadvantages to relaying include: the requirements for more stringent law enforcement and documentation, mandatory closure periods, and conflicts between resource users.

The cost effectiveness of relaying is dependent upon several important factors, including stock availability, harvest effort, and the distance that the relayed stocks must be transported. Current landings and values of harvestable stocks are also critical elements in an operator's decision to relay oysters. Because relaying often requires additional effort and costs for transport and reharvest, it is most commonly undertaken when oyster landings from public reefs are in decline. In some locations, where the availability of cultch material is limited and seed stocks are available, relaying for the purpose of restoring depleted resources may represent the most cost-effective and feasible practice.

Like many other oyster management practices, relaying activities have been funded through state appropriations, federal assistance programs, and by the private sector. Numerous oyster relay programs have been financed using federal funds allocated through Public Law 88-309 (the Commercial Fisheries Research and Development Act), emergency assistance acts and Public Law 99-659 (the Interjurisdictional Fisheries Act). In Florida, relay projects in several coastal counties have been conducted using special category appropriations and trust funds allocated for oyster resource development. Relaying will probably remain a significant component of Gulf states' resource management programs because numerous restricted areas are likely to remain closed while continuing to produce oysters. Also, relaying is perhaps the most cost-effective means of utilization.

Depuration Depuration is a process involving the placement of bivalve shellfish in a controlled, clean-water environment for cleansing. This resource management strategy is employed to utilize shellfish from restricted areas. Its use is also directed at producing the highest quality product with the lowest health-related risks. This distinction of a safe or purified product is needed to increase consumer confidence, increase market values for this specialized product, and expand or create new markets, thus making the value-added process cost effective.

Depuration has been successful and cost effective in some of the clam fisheries of the U.S. It has not been demonstrated using oysters from the Gulf of Mexico; however, there have been a few attempts by private industries and some cooperative, experimental operations involving industry, state agencies, and various institutions.

Various technologies have been used to design equipment and facilities to maintain constant, clean-water conditions that are necessary to meet National Shellfish Sanitation Program (NSSP) guidelines. Primary components of these systems have been biological filters coupled with ultraviolet irradiation and/or ozone diffusion.

In the early 1980s, pilot operations developed in both Louisiana and Texas. These facilities were not successful because they could not meet NSSP depuration standards. Without this special product label their oysters had to compete with public-reef or lease-produced oysters; consequently, these operations were not cost effective and later closed. In Florida, experimental operations have developed from cooperative efforts among the industry in the Apalachicola Bay and Cedar Key areas, the FDEP, and the Institute of Food and Agricultural Science of the University of Florida. Although these pilot operations have shown some success, depuration has not been demonstrated to be commercially successful.

Although depuration will probably become more important to the utilization and management of oysters as more reefs are closed due to health risks, numerous concerns will have to be addressed before it becomes a successful practice. First, the technology is available to depurate oysters, but its effectiveness in removing viruses and *Vibrio* spp. that may be present in oysters currently harvested from approved areas needs to be documented. Second, facilities must be located, inspected and monitored to ensure that the environment is protected from plant discharges and to prevent illegal operations. Other concerns are based on product liability depending on how it is labeled.

Alternative Treatments Alternative treatments that could be used to eliminate pathogenicity in oysters from some restricted areas are irradiation and heat processing, e.g., canning. Canning was a popular processing procedure in the northern Gulf, particularly Mississippi,

Table 18. Oyster relaying activities by fishermen in Alabama, 1980 through 1994.

Year	Location		Volume (yd^3)	Cost
	From	To		
1980	Dauphin Island Bay	Dauphin Island Bay	226	
	Dauphin Island Bay	Portersville Bay	87	
	Cedar Point Reef	Bush Stake Shoals	5,087	
			5,400	$119,252
1982	Dauphin Island Bay	Cedar Point Reef	2,189	
	Coden/Bayou LaBatre	Portersville Bay	607	
			2,796	$61,800
1986	Point Clear/Harlinger's Island and Gaillard Island Reef	Portersville Bay	1,185	$82,221[1]

[1] Includes personnel and administrative costs of the Alabama Department of Conservation and Natural Resources.
Source: ADCNR

during the early to mid 1900s. Reductions in the use of this technique probably resulted from increasing value and reduced supply of oysters for the raw stock market, coupled with advances in refrigeration technology.

Irradiation using gamma radiation is a relatively new, experimental method used to reduce the bacteriological content of oysters. In 1991, testing began under a cooperative project in the Gulf among the University of Florida, the Institute of Food and Agricultural Science and Vindicator, Inc. (private company). Testing continues; however, further work is needed to evaluate the effectiveness of irradiation in eliminating bacteria. Other factors that need to be evaluated include: shelf-life, organoleptic qualities, consumer acceptance, labeling requirements, and cost effectiveness. Although none of these methods are currently acceptable under NSSP guidelines, demonstration of their effectiveness in eliminating health risks could permit their use in the future, especially if more areas become restricted.

Transplanting

Transplanting is one of the older management strategies utilized by the five Gulf states, and its usage dates to the mid 1800s in Louisiana. Transplanting is distinguished from relaying in that it involves moving oysters from one approved or conditionally approved area to another, whereas relaying is usually conducted from a restricted area to an approved area.

Transplanting typically has involved moving either small seed oysters or market-sized oysters. Seed oyster transplantation involves moving small, submarket oysters from areas where settlement is generally high to areas where conditions are highly conducive for growth (grow-out areas). This practice has primarily been used in Louisiana, where nearshore public reefs, also called seed grounds, have been planted with cultch by the LDWF, and lessees using dredges later transport seed oysters to private leases. These seed reefs are simultaneously worked for direct-market harvest of legal-sized oysters. This cooperative management practice is a major component of Louisiana's oyster industry, and average annual yields are approximately 80% of the total state landings (Keithly and Roberts 1988). The amounts of transplanted oysters are not available.

In Florida, and to a very limited degree the other Gulf states, naturally producing near shore and intertidal reefs have been tonged, dredged, or hand picked for seed oysters that are then transplanted to other public reefs. In many of these areas the setting propensity is great; however, conditions for growth are poor. High setting densities, especially on intertidal reefs, cause crowding that slows growth. Also, intermittent exposure to air during low tides reduces feeding time and further inhibits growth. Transplanting operations break up these reefs and promote better setting in the future. These activities also break-up clusters of oysters that, when relocated to deeper waters, grow more rapidly and reach market size sooner.

Transplanting operations for seed may include varying amounts of market-sized oysters; however, their relocation is not the primary purpose of this management strategy. Targeting market-sized oysters for transplanting is another aspect of transplanting that has primarily been employed when a destructive event is imminent. Examples may include anticipated flooding, impending pollution resulting from an oil or chemical spill, or planned developments such as channel construction, maintenance dredging, and bridges.

Transplanting programs have been conducted by state agencies, fishermen, and processors, or through cooperative efforts. Alabama, Mississippi, and Texas have seldom used this strategy, and its usage has primarily come when a disastrous event was anticipated. Louisiana and Florida, however, have employed transplanting regularly, but these programs are distinctly different. In Florida, transplanting has been conducted in a cooperative manner between the FDEP and local oystermen's associations. The department contracts and supervises operations. This effort involves letting of contracts, defining criteria for harvesting and planting locations, delineation of specific locations, inspection of the quantities and condition of oysters, compliance monitoring, and reporting of results. The local associations advise local industry of projects (i.e., starting dates, areas to be worked, schedules, delays, etc.) and recruit and pay participants. They also assist the department in delineating locations for harvesting and planting and in monitoring project activities. The amounts of oysters transplanted by Florida are shown in Table 19.

In Florida, transplanting programs are critical to production in areas where there is limited productive habitat. At times, production in these areas may depend entirely on transplanting stocks. Cooperative transplanting operations also provide a source of income to local fishermen during seasons when direct-market harvesting is closed. Other benefits of transplanting programs include the potential for establishment of new reefs and greater user awareness of and involvement in the management of oyster resources.

Transplanting will probably continue to be an important part of the resource management programs in Louisiana and Florida. These efforts have proven to be economically successful and socio-culturally acceptable partly because of the unique biological conditions in areas of Florida and special traditional deployment in Louisiana.

USER-DIRECTED MANAGEMENT PRACTICES

In addition to directed efforts to increase oyster production, states have developed programs that target users. Most of these strategies are regulatory practices that have been used to control harvests and provide optimum benefits from the available public resources. Leasing programs, however, have provided users with the opportunity to create, expand, and manage their own resources. The following is a discussion of these practices.

Table 19. Oyster transplanting activities by Florida, 1971 through 1994.

Year	Location (county)	Volume (yd^3)
1971	Levy	1,421
1972	Levy	1,761
1973	Levy	4,107
1974		
1975	Levy	3,125
1976		
1977	Levy	2,878
1978		
1979	Dixie	669
	Levy	2,441
1980		
1981	Dixie	735
	Levy	1,710
1982	Wakulla	1,438
1983	Franklin	3,190
	Wakulla	3,530
	Dixie	577
	Levy	2,177
1984	Franklin	740
	Wakulla	1,351
	Levy	1,853
	Bay	1,402
1985	Wakulla	1,997
	Levy	1,868
	Bay	875
1986	Franklin	924
	Levy	1,858
	Wakulla	2,170
	Bay	697
1987	Levy	1,186
	Wakulla	1,399
1988	Franklin	1,763
	Levy	3,852
	Dixie	533
1989	Franklin	3,585
	Levy	988
	Wakulla	761
1990	Levy	2,100
1991	Franklin	3,038
	Levy	1,683
1992	Wakulla	1,330
	Dixie	226
	Levy	431
	Franklin	812
1993	Wakulla	1,253
	Levy	42
	Dixie	1,481
	Franklin	2,249
1994	Wakulla	833
	Levy	862
	Franklin	648

Source: FDEP

Table 20. Oyster lease acreage by parish for Louisana (various years) and number of leases and acreage for 1994.

Parish	1980-1981	1981-1982	1988-1989	1990-1991	1991-1992	Number of Leases	Acreage of Leases
St. Bernard	69,011	70,467	73,928	69,118	72,861	1,130	72,339
Plaquemine	81,632	84,194	128,088	142,871	152,997	3,767	154,462
Terrebonne	42,595	43,025	51,813	53,530	55,033	1,826	64,544
Jefferson	19,775	20,085	26,651	25,268	22,526	602	20,782
LaFourche	15,657	15,119	16,930	18,870	17,851	598	19,722
St. Tammany	940	940	818	381	383	4	383
Vermilion	720	520	6,088	6,630	7,338	25	7,338
St. Mary	543	497	585	0	519	7	519
Iberia	889	1,484	23,368	22,693	21,369	58	21,369
Jefferson/LaFourche				1,987	1,813	39	1,731
Jefferson/Plaquemine				938	838	14	1.091
LaFourche/Terrebone				116	126	9	341
Plaquemine/St. Bernard				498	563	9	563
Terrebone/ St. Mary				177	177	1	7,338
Iberia/Vermilion				2,317	2,317	4	2,322
Total	231,762	236,331	328,269	345,394	356,711	8,093	367,615

Leasing

Leasing of water bottom for the production of oysters has a long history in the Gulf. Most states enacted laws to allow leasing of submerged public lands in the late 1800s to the early 1900s. Leases of bottom under riparian right laws predates state leasing programs. Although leasing was popular in the early 1900s, the number of leases has generally declined in most states except Louisiana where the number of leases has increased. The cause for the decline is unknown; however, poaching and the availability of oysters on public reefs are possible reasons. Also, since most states' laws have precluded leasing of productive water bottom, failed attempts to establish reefs at alternative, less productive sites could have resulted in reductions in lease renewals. Most state laws regarding public leases have also required that they be actively cultivated, or the leases are revoked. This factor has caused a "seesaw" effect with regard to the number of active leases in some states. (Lease acreage increases when public reef production decreases, and vice versa.)

Florida began its leasing program in 1913, and subsequently approved about 1,200 leases. Approximately 150 leases covering about 2,000 acres are currently active. Most leases are on the east coast, and only 20 leases totalling 747 acres are located in the Gulf. Ten of these leases (656 acres) are in the Apalachicola Bay system. Approximately 5-10% of Florida's annual landings come from leases.

Currently, Alabama has no state issued oyster leases. About 25 leases to riparian bottoms are active; however, the acreage is unknown, and their contribution to annual harvest is insignificant. Mississippi currently has only eight active leases covering 547 acres and one riparian lease of unknown acreage. Following a 1977 law that allowed leaseholders to relay oysters from restricted to approved areas, over 50 leases covering 5,000 acres were approved from 1977 to 1979. Subsequently, lessees relayed a large but unrecorded amount of oysters, and once these relay areas were depleted, most leases were dropped.

Some of Louisiana's parishes began leasing bottoms in 1885, and the state took control of the program in 1902 (Mackin and Hopkins 1962). The number and acreage has steadily increased since the mid 1970s, and a six-year moratorium was instituted in the mid 1980s. Presently, over 3,000 people hold over 8,000 leases to over 367,000 acres (Table 20). The average lease size is 36 acres, and most leases are located in the eastern half of the state. Historically, over 80% of Louisiana's total production has come from leases.

Texas began leasing oyster bottoms in 1895 (Hofstetter 1977); however, the amount of acreage leased has varied considerably over time (Table 21). Currently there are 43 leases to 2,322 acres in Galveston Bay, and these are controlled by about eight individuals most of whom also operate processing facilities. The average size of a lease is 54 acres. Harvests from leases currently account for approximately 28% of Texas' total commercial production. This harvest is primarily obtained from relaying oysters from restricted areas to leases. Texas currently has a moratorium on the issuance of new leases.

Leasing has been an effective tool in managing oyster populations. Through leasing, fishermen and processors gain an ownership right to oysters and some authors have suggested that such rights may help to increase and stabilize production (Loosanoff 1954, Dyer and Leard 1994).

The relatively stable leasing programs in Louisiana, Texas, and Florida will probably continue in the future. As more public reefs become restricted for direct-to-market harvesting, leasing will probably increase in popularity for relaying purposes in other areas and other states.

Size Limits

Size and bag limits have been used by all Gulf states to regulate direct-to-market landings (Berrigan *et al.* 1991). Size limits have been effective in providing the most-desirable and sellable product and in preventing overharvest of reefs. Bag limits have been used mainly to extend the harvest season and maintain higher prices when supplies within a given state were low.

Closed Seasons

Closed seasons and areas have been used to prevent overharvesting and to allow other management strategies (e.g., cultch planting and transplanting) to be conducted. Special open seasons have occasionally been established in approved waters to allow harvesting of oysters in peril from flooding or other imminently destructive events. They have been instated in restricted and even prohibited areas to allow removal of oysters that could cause health problems due to illegal harvests.

Table 21. Acreage of oyster leases in Texas, various dates.

Year	Area (acres)
1907	6,486
1919	609
1930s	2,289
1956	92
1967	910
1977	1,832
1987	2,356
1995	2,322

Source: TPWD

Gear Restrictions

Gear restrictions also have been instituted to control the rate of harvest and to limit damage to sensitive reefs. Alabama and Florida have restricted harvest from all public reefs to hand tonging and direct hand harvesting. Mississippi, Louisiana, and Texas have designated certain reefs for dredging and others for tonging, but most reefs have historically been dredged.

Limited Entry

Limited entry is perhaps the most restrictive user-directed strategy; however, none of the Gulf states has formally adopted such regulations. Some access restrictions have been informally instituted through leasing in Louisiana and Texas. In Louisiana, approximately 80% of the annual production comes from leasing, and most of the more favorable areas

Table 22. Oyster resource development program funding for Florida, 1981 through 1995.

County	1981	1982	1983	1984	1985
Bay (EB)	$	$	$	$	$ 50,000
Bay (WB)					50,000
Dixie		15,000		15,000	
Franklin	[1]33,961	[1]32,436	[1]32,436	60,000	100,000
Levy		35,000		35,000	
St. Johns					25,000
Wakulla			50,000	40,000	35,000
Total	$ 33,961	$ 82,436	$ 332,436	$ 150,000	$ 300,000

County	1986	1987	1988	1989	1990
Bay (EB)	$ 32,000	$ 34,000	$ 34,000	$ 32,000	$ 32,000
Bay (WB)	32,000	34,000	32,000	32,000	32,000
Bay (NB)				[2]50,000	
Dixie	10,000	15,000	21,000	21,000	52,000
Franklin	50,000 [3]295,000 [1]917,897		47,500	47,500 [2]150,000	52,200 [4]36,650
Levy	50,000	55,000	47,500	47,500	52,200
Santa Rosa	50,000	55,000	47,500	47,500	52,200
St. Johns	25,000	25,000	25,000	25,000	
Wakulla	50,000	55,000	47,500	47,500	52,200
Walton		27,000			
Total	$ 1,512,897	$ 300,000	$ 300,000	$ 500,000	$ 361,650

County	1991	1992	1993	1994	1995
Bay (EB)	$ 40,400	$ 32,000	$ 31,000	$	$
Bay (WB)	40,400	32,000	31,500	47,500	57,500
Bay (NB)					
Dixie	104,400	55,250	52,250	52,500	55,000
Franklin	64,400 [4]65,500	55,250 [4]104,400	40,000 [4]104,400	52,500 [4]134,400	55,000 [4]104,400
Levy	104,400	55,250	52,500	52,500	55,000
Okaloosa/Walton	33,400				25,000
St. Johns					
Santa Rosa	67,400	55,250	52,500	42,500	57,500
Wakulla	40,000	40,000	40,000	40,000	45,000
Walton			75,000	37,500	
Total[5]	$ 559,800	$ 429,400	$ 479,400	$ 459,400	$ 454,400

[1] P.L. 88-309

Source: FDEP

[2] Special Appropriation

[3] Office of Governor

[4] Apalachicola Bay Conservation Trust Fund

[5] Not included in these totals is approximately $250,000 per year fro the administration functions of the Shellfish Assessment and Enhancement Section of the FDEP of which about $100,000 is used to directly support shellplanting and oyster relocation efforts.

have been privatized for many years. In Texas, approximately 28% of the annual production comes from leases, and there is currently a moratorium on new leases.

SUPPORT FOR RESOURCE MANAGEMENT PROGRAMS

The Gulf States have received financial support for oyster resource management from various sources. The earliest programs were primarily supported by the industry with in-kind contributions of shells, boats, and labor to plant cultch and transplant or relay oysters. Shell taxes, tag and license fees, and lease charges have also been used for many years. Other financial support has come from the oil and gas industries from mitigation fees, excise taxes, and lease charges. State general funds, fines for violations, legal judgements, donations, other mitigation fees, and federal funds (primarily P.L. 88-309 and P.L. 99-659) have also contributed to resource management programs.

Florida has relied on a number of funding sources for its resource management programs. Nonfederal funds have come primarily from legislative appropriations; however, special and federal funds have helped support the program (Table 22).

Table 23. Oyster resource management program funding for Alabama, 1980 through 1994[1].

	Funding $		
Year	**State**	**Federal**	**Total**
1980	19,252	[2]1,350,000	1,369,252
1981			
1982	[3]171,996		171,996
1983	[4]151,867		151,867
1984	12,000	[2]464,000	476,800
1985	100,000	100,000	200,000
1986	64,375	[2]1,153,774	1,218,149
1987	1,985	[2]246,213	248,198
1988			
1989	[4]50,000		
1990	[4]397,250		
1991			
1992			
1993	85,850		
1994	72,527		

[1] Administrative costs for the ADCNR including sampling, monitoring, and enforcement, and others are not included.
[2] P.L. 88-309
[3] Oil and Gas Windfall
[4] Legislative Grant
Source: ADCNR

In Alabama, most of the recent support for oyster resource management has come from P.L. 88-309 disaster funding following hurricanes in 1979 and 1985 and flooding in 1983. Major state sources have been legislative grants, oil and gas windfalls, and general/special funding (licenses, tag fees, etc.). Most of the funds have been spent planting shells (Table 23).

Since 1970, Mississippi's oyster resource management program has mainly consisted of shell planting and relaying, and a number of funding sources have been used. Federal disaster funds from P.L. 88-309 were used to plant shells following hurricanes in 1969, 1979, and 1985, and after flooding in 1973 and 1983. State funds have primarily come from legislative appropriations; however, in recent years license fees, shell taxes, fines, and other special fund sources have contributed to the program (Table 24).

Historically, Louisiana's funding for oyster resource management has almost exclusively been used for shell planting on seed reefs. Federal funds especially disaster funding from P.L. 88-309 have been the dominant source since the early 1970's; however, state general funds and special funds from oil and gas industry, lease fees, fines, and other sources have been used (Table 25). Additionally, Louisiana spends more than $1,000,000 each year for monitoring, lease surveys, enforcement, and other activities related to oyster management.

Table 24. Oyster resource development program funding for Mississippi, 1970-1994.

Year	State[1]	Federal	Total
1970	$ 25,992	$ 77,976	$ 103,968
1971	14,896	44,690	59,586
1972	26,770		26,770
1973	54,175		54,175
1974	67,259	201,777	269,036
1975	19,418		19,418
1976			
1977	43,350		43,350
1978	45,000		45,000
1979	178,820	444,750	623,570
1980	85,160	158,310	243,470
1981	130,860		130,860
1982	109,050		109,050
1983	110,160		110,160
1984	158,482	462,216	620,698
1985	107,578		107,578
1986	8,830		8,830
1987	132,264	[2]160,000	292,264
1988	192,076		192,076
1989	152,720		152,720
1990	62,340		62,340
1991	26,600		26,600
1992	24,200		24,200
1993	65,400		65,400
1994	40,000		40,000

[1] State costs for shell planting and relaying are unknown; however, they are estimated based on estimated costs from known P.L. 88-309 projects in the 1970s and 1980s. Relaying costs estimated from amounts in Table 16 are probably higher than these estimates. Administrative and monitoring costs are not included.
[2] Sport Fish Restoration Program funds used to plant shells for low-profile fishing reefs near oyster reefs.
Source: MDMR

Table 25. Oyster resource management program funding for Louisiana, 1992-1995.

Date	Funding		
	Federal	State	Total
1992-1993	$689,320	$144,192	$833,512
1993-1994	$630,509	$132,407	$762,916
1994-1995	$3,033,928	$120,264	$3,154,192

Source: LDWF

Funding for direct oyster reef restoration, rehabilitation, and enhancement of public reefs in Texas has only been available three times since at least the early 1970s (Table 26). The TPWD has received both state and federal funding for direct monitoring of oyster reefs; however, this funding declined from approximately $134,000 in 1986 to less than $100,000 in 1990. Only about $43,000 was available in 1994, and this trend has caused a corresponding decrease in the number of samples taken.

Conclusions

State resource management programs have been responsible for helping sustain oyster production in the Gulf for many years. Although pollution and habitat destruction have eliminated numerous productive, near-shore reefs, innovative efforts have been developed to construct new reefs and increase production from remaining reefs. Unlike the Atlantic Coast, production in the Gulf has been relatively stable, and this stability is due in part to these programs and the efforts of fishermen, processors, and dealers. It is anticipated that future programs will continue to use the strategies outlined in this document, and they will likely include new components to address needs and problems with the fishery as they arise.

Table 26. Oyster resource restoration and rehabilitation program funding for Texas, various years.

Year	Area	Source	Funding
1988-1992	Corpus Christi Bay	State Appropriation	$100,000
1988-1989	San Antonio Bay	Federal - P.L. 99-659	$194,000
1990-1991	Galveston Bay	Federal- P.L. 99-659	

Source: TPWD

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Oyster Habitat Restoration: A Response to Hurricane Andrew

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Abstract

Hurricane Andrew crossed the central Louisiana coast, just east of Atchafalaya Bay, August 25-26, 1992, passing through the state's most productive oyster grounds. Sustained winds near the center of this storm were 130 mph for several hours, causing Gulf water storm surges. Resettlement of displaced marsh sediment and accompanying vegetation killed live oysters and destroyed suitable oyster habitat.

In July, prior to the storm, oyster density samples were taken on all of the State's public oyster grounds as part of a regular oyster monitoring program. At that time, oyster densities in the area where the storm would go ashore were the highest observed in the state (20-140 live oysters$\cdot$m^{-2}). The week following the storm, density samples were conducted to determine the extent of the oyster damage. Mortalities were severe on all public grounds along the central coast, as post-storm densities dropped to 0-24 live oysters$\cdot$m^{-2}. In addition to the impact studies on the public oyster grounds, a sampling program was initiated to estimate damages on private leases from Vermilion Bay to the Mississippi River where concentrations of oysters were known to occur. Mortalities exceeded 25% in most of the impacted areas and often exceeded 75%.

In response to the damage done by Hurricane Andrew, the Louisiana Department of Wildlife and Fisheries developed and executed an oyster habitat restoration program on public oyster grounds. Restoration efforts, using federal disaster relief funds, were initiated in the spring of 1994, included sonar location of surviving oyster reefs; dredge cleaning (removal of silt overburden) and cultch replenishment. Approximately 2,000 acres of shell reef were uncovered through dredging areas identified in the surveys. Available cultch material was deposited over 1,252 acres of water bottom in five different water bodies and these areas were closed to commercial harvest for one year. A sampling program on restored oyster grounds nine months after restoration efforts indicated excellent recovery of the impacted area.

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Introduction

Oyster (*Crassostrea virginica* [Gmelin]) production in Louisiana over the past ten years has averaged nearly 10 million pounds annually with a dockside value of approximately 23 million dollars. The 1991 landing of 7.2 million pounds was valued at over 19 million dollars dockside. Louisiana production generally ranks first among the Gulf States, and first or second in the United States.

The Louisiana oyster industry is labor intensive, employing many people in coastal communities. The Department of Wildlife and Fisheries has annually issued approximately 2,200 oyster harvester licenses. The oyster industry is not only tremendously important to the local economy, it also contributes significantly on a national scale.

The oyster producing waterbottoms in Louisiana include both state-managed public oyster grounds and privately-managed leased areas. The public oyster grounds include most of the state's traditional, naturally productive reef areas, and their management is primarily mandated by law to provide seed oysters for bedding on private grounds. Fluctuating environmental conditions (salinity and dissolved oxygen) and oyster lease locations in coastal Louisiana result in inconsistent production of seed oysters on many leased areas. To provide oyster leases with a source of young seed oysters and thereby maintain a stable source of oysters available to the market, the Department maintains and manages "Public Seed Grounds" at several locations along the Louisiana coast (Figure 1). These areas are periodically opened to harvest and licensed fishermen are allowed to move seed to private leases and to harvest legal size oysters.

During the early morning of August 25, 1992, Hurricane Andrew crossed the Louisiana coast just east of Atchafalaya Bay, passing

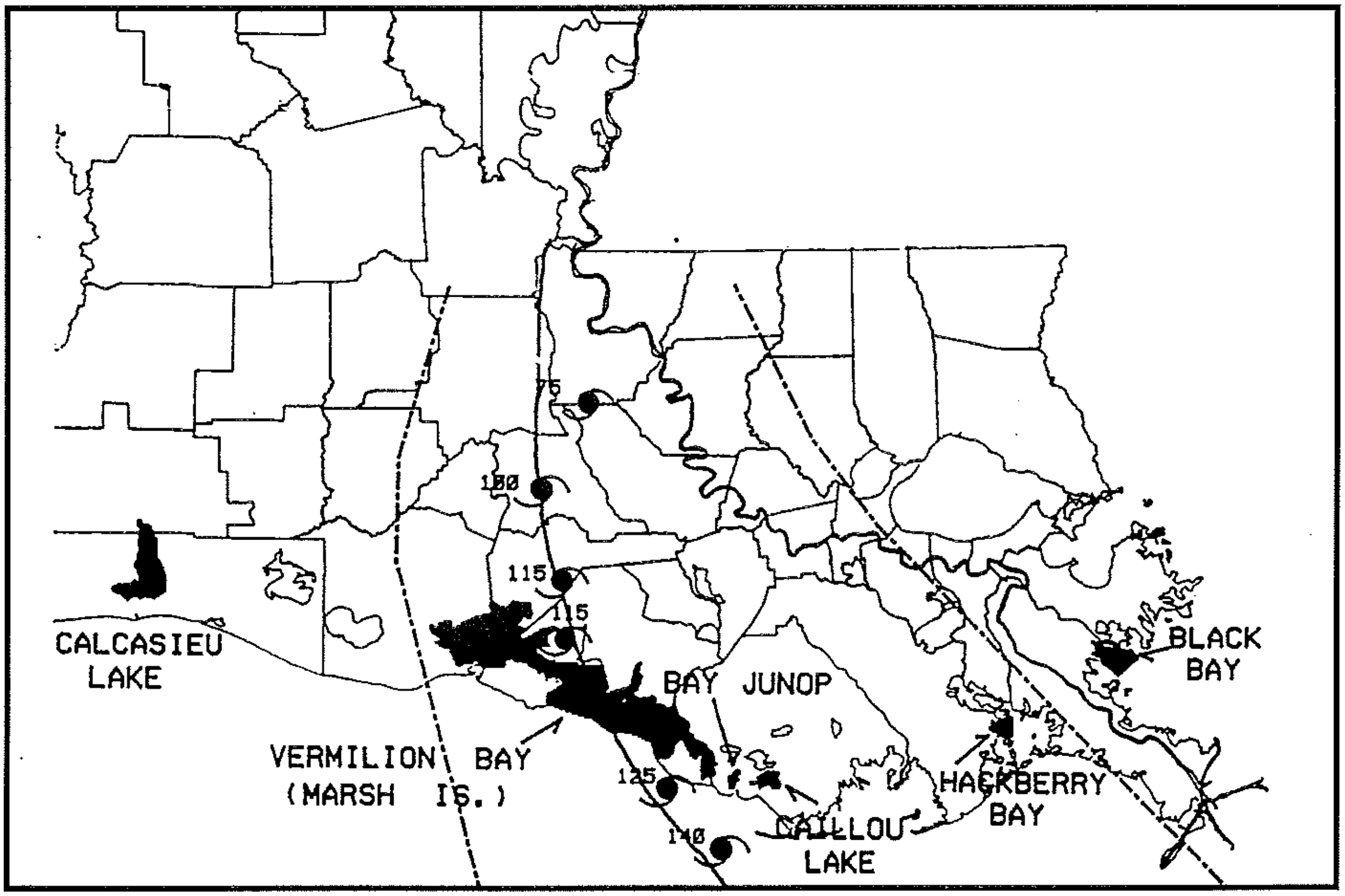

***Figure 1.** Public Oyster Seed Grounds (filled in black) and track of Hurricane Andrew.*

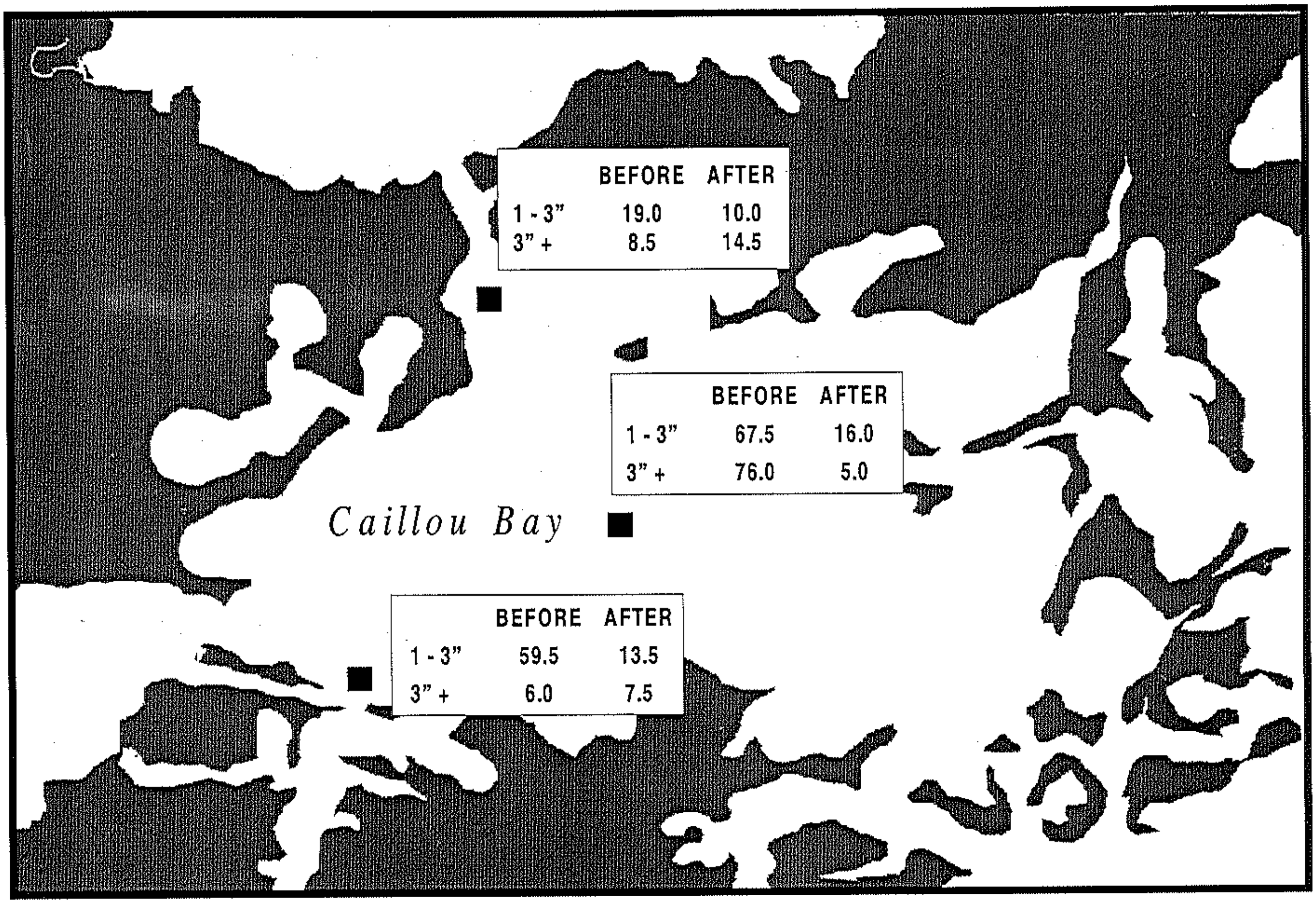

***Figure** 2. Callou Lake oyster beds, with oyster densities ($\#\bullet m^{-2}$) before and after Hurricane Andrew. (Sizes indicate oyster size classes.)*

through several of the public oyster grounds (Figure 1). Sustained winds near the center of this Category 4 storm were 130 mph for 5 hours or longer, causing a storm surge in excess of 20 feet at the shoreline. These surges displaced huge amounts of marsh sediment and accompanying vegetation and re-deposited them throughout the various water bodies in the area. Some of the state's most productive oyster reefs and oyster populations were within these bodies of water and many were buried by the transported sediment. Oyster density samples were taken in July, prior to the storm, as it is done annually on all of the State's public oyster grounds as a part of the regular sampling program. At that time, oyster densities in the area where the storm went ashore were the highest observed in the state. The week following the storm, oyster density samples were taken to determine the extent of oyster damage (Figures 2 and 3). Mortalities were severe on all public grounds along the central coast. The most significant damage to the oyster resource was a direct result of silt and vegetation deposited on the reefs that killed oysters and destroyed suitable oyster habitat.

In addition to the impact studies on the public oyster grounds, a sampling program was initiated to estimate damages on privately

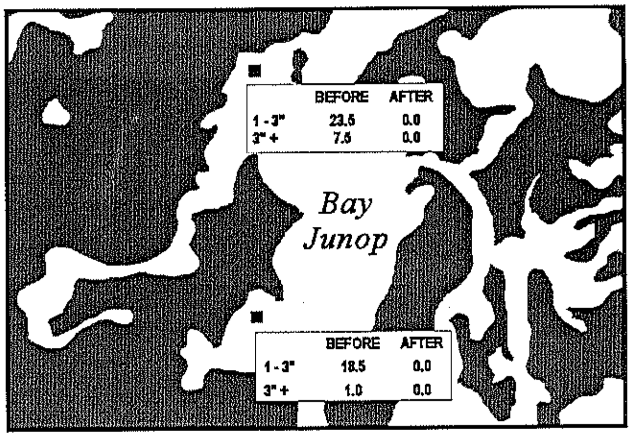

***Figure** 3. Bay Junop oyster beds with oyster densities ($\#\bullet m^{-2}$) before and after Hurricane Andrew.*

owned leases. Coastal Louisiana was divided into 12.25 square mile (3.5 miles by 3.5 miles) grids from the Vermilion Bay area to the Mississippi River Gulf Outlet on the east side of the Mississippi River. Within each grid, one dredge sample was taken where concentrations of oysters were known to occur. Mortalities exceeded 25% in most of the impact area, and often exceeded 75%. The assessed value of the damage to the impacted area was over $26 million; this does not reflect the long-term impact of lost habitat necessary for future production. The greatest damage from Hurricane Andrew was between Bayou Lafourche to the east and St. Mary Parish to the west. The documented environmental impact led the Louisiana Dept. of Wildlife and Fisheries to seek Federal funding for a restoration program.

Materials and Methods

The were two primary objectives in the Department's restoration effort: cleaning buried reefs and replacing lost cultch. It was the Department's intent to restore oyster habitat in Caillou Lake and Bay Junop, the most heavily impacted water bodies in the state (Figure 1).

Since oyster larvae will not attach to substrates covered by loose sediments the purpose of cleaning buried reefs was to re-expose pre-existing oyster reef covered by silt and vegetation. (Galtsoff, 1964). The preferred method of clearing buried oyster reefs after environmental catastrophes, particularly hurricanes, has been described by MacKenzie (1977).

Contractors were selected to work over the covered reefs using dredges without bags in order to remove sediments from the reef and to shift the shell, exposing clean surface for the future setting of oyster larvae. Selection of precise location of cleaning sites was made based on water currents at the time of cleaning.

The purpose of depositing artificial cultch was also to enhance shellfish habitat and to provide a clean surface for setting of oyster larvae. A contractor was selected to plant oyster cultch. The location of planting was selected from among those public oyster grounds shown in Figure 1. Selection of the precise location was made based on water currents and tide at the time of planting, by review of historical production in the area, and by the input of oyster fishermen familiar with the area. Those areas with sediment overburden and in need of cleansing were staked off with PVC poles.

The success of the restoration effort was evaluated by a shell assessment program. Oyster densities were determined in Caillou Lake and Bay Junop from m^2 samples. Sites for sampling were randomly chosen within the impacted areas and the contents of m^2 quadrates were retrieved by SCUBA. Oysters were grouped into 0-1", 1-3", and >3" size classes and enumerated.

Results and Discussion

CLEANING BURIED REEFS

Forty-one Contractors were hired to clean 350 acres in Bay Junop and 1,430 acres in Caillou Lake. Cleaning began June 1st in both Caillou Lake and Bay Junop, Terrebonne Parish. On that day, 25 of the larger boats were assigned to Caillou Lake, and 15 of the smaller boats were assigned to Bay Junop. The vessel size differences were simply assigned because of the shallower waters of Bay Junop.

SHELL PLANTING

Cultch restoration was only possible in Caillou Lake due to the shallow depth of Bay Junop. The cultch used for reef restoration was subject to the following requirements.

1. Cultch had to be clean.
2. Cultch had to be crushed and could not be larger than 1-1/2" in diameter with no more than 5% by volume of fragments, pieces, fines, or shells smaller than 3/8" in diameter.
3. The Louisiana Department of Wildlife and Fisheries reserved the right to have its representatives inspect all cultch at the loading site and each barge-load will be checked at the planting site. All small and large particles in excess of the

allowed 5% were deducted from the total project cost.

Cultch material consisted of reef shell substrate that had been dredged from Atchafalaya Bay. Cultch was loaded onto barges, towed to Caillou Lake, and washed overboard using a high pressure water hose (@ 90 p.s.i. on a 1.25 inch nozzle). This high pressure jet of water is directed against the shells in a manner to spread them in a thin, even layer for a distance of 20 to 50 feet from the barge. Throughout the operation, the barges were maneuvered over the planting location in a fashion so that cultch covered the entire area to the needed density as determined by supervising Wildlife and Fisheries personnel.

The shell plant which occurred on the Caillou Lake began on June 9, 1994 and was completed on July 14, 1994. A total of 42,576 yards^3 of reef shell were deposited on a total of 306 acres of water bottom at three locations in Caillou Lake. The north plant began on June 9 and ended on June 16 with 9,641 yards^3 deposited on 96 acres. The mid plant began on June 17 and ended on July 6 with 18,414 yards^3 planted. An additional 3,791 yards^3 were planted on July 13 and 14 for a total of 22,205 yards^3 planted on 129 acres to complete the mid plant. The south plant began July 7 and ended July 12 with a total of 10,728.77 yards^3 planted on 81 acres. The average cost of cultch and spreading was \$20.93•yard^{-3}.

Oyster reef survey data eight months after bed restoration and cultch placement indicated excellent recovery. Prior to the passage of the hurricane, oyster densities in Caillou Lake ranged from 19 to 67.5 1-3" oysters and 6-76 >3" oysters/m^2. Following the storm, oyster densities ranged from 10-16 1-3" oysters and 5-14 >3" oysters•m^{-2}. Samples were collected in February 1995, 8 months after cultch placement. Oyster densities indicated a good fall set and ranged from 5 to 81 oysters•m^{-2} (0-2") (Figure 4). Oyster densities on the cleaned sites had returned to pre-storm levels. The economic benefits of this restoration project are under evaluation.

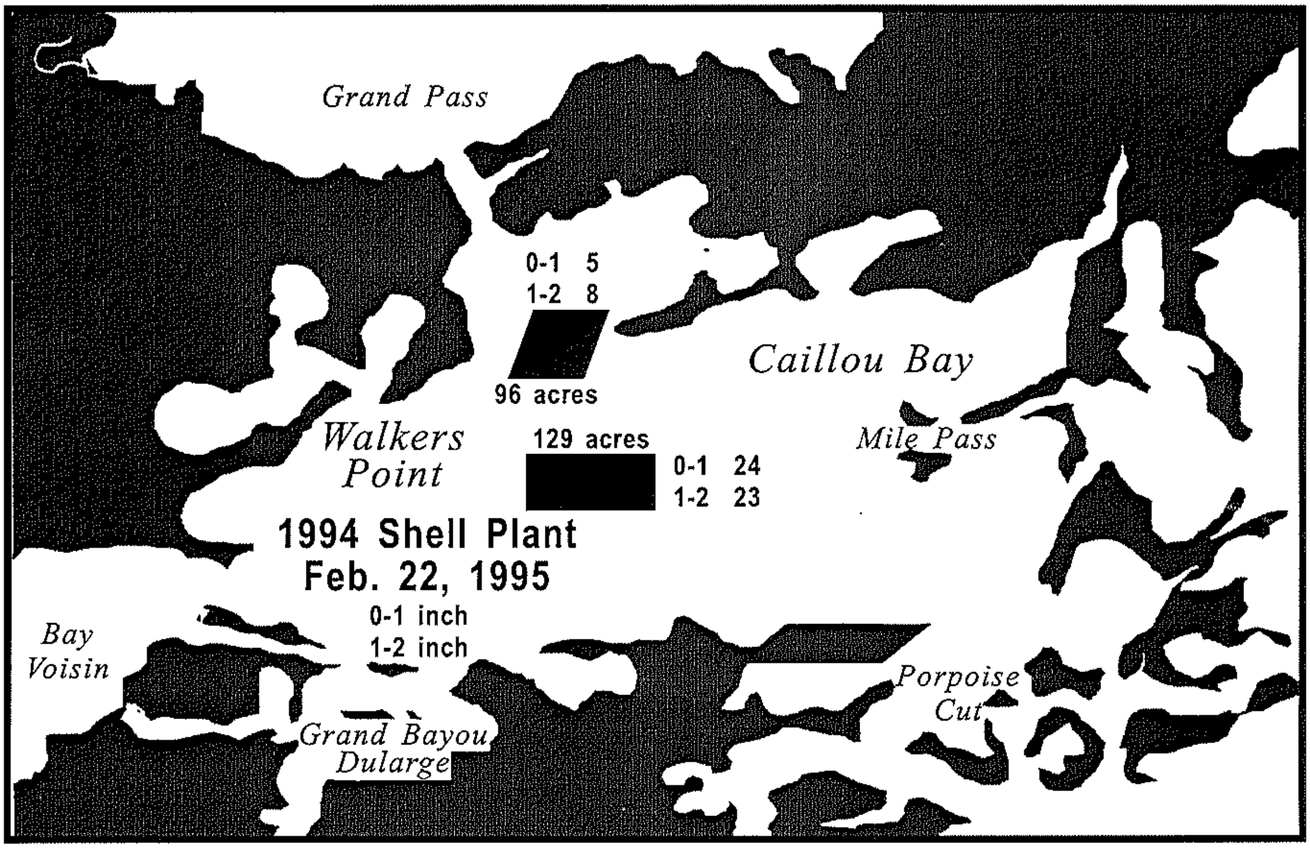

Figure 4. Oyster abundance after shell planting in Callou Lake.

Table 1. The Benefit/Cost ratio of planting oyster shell in Louisiana 1973-1983. Cost- cost of planting shell; Sacks- number of sacks harvested from the shell plant area; Retail Price-retail value of harvested oysters per sack; Remm- total value of harvested oysters.

Year	**Cost**	**Sacks**	**Retail Price**	**Return**	**Benefit/Cost**
1973	$275,000	204,783	$10.00	$2,048,000	7.4:1
1979	$1,750,000	639,081	$10.00	$6,391,000	3.7:1
1981	$1,000,000	332,722	$12.00	$3,993,000	4:1
1983	$1,250,000	490,070	$12.00	$5,881,000	4.7:1
1989	$275,000	34,884	$20.00	$697,000	2.5: 1

PREVIOUS RESTORATION PROJECTS

Since 1926, the state of Louisiana has deposited over 750 thousand meters^3 of cultch material on public seed grounds and reservations to create new reef areas or increase production of existing reefs (Perret and Chatry, 1988; Perret et al., 1991). Louisiana has received funding to rehabilitate oyster habitat after natural disasters formerly under Public Law 88-309 program and currently under the Interjurisdictional Fisheries Act Program, administered by the U.S. Department of Commerce's National Marine Fisheries Service. All funds were used to purchase cultch material, LDWF matched the Federal funding by providing support for labor and logistics. Through the 309 program, funding was secured in the amounts of:

1. $100,000 for rehabilitation and restoration of the oyster seed grounds following Hurricane Betsy (1965);
2. $176,388 for rehabilitation of natural oyster seed grounds damaged by Hurricane Camille (1969);
3. $275,000 for rehabilitation of natural oyster seed grounds destroyed by a natural disaster (i.e., flooding caused by the Mississippi River in 1973); and
4. $1,000,000 for rehabilitation of natural oyster seed grounds destroyed by a natural-disaster (i.e., flooding in 1979).

Successful cultch plants in Louisiana have had high benefit/cost ratios (Table 1). The $275,000 received in 1973 resulted in a large return to the oyster industry. Two-thirds (39,059) of the 61,367 yard^3 of the shells were deposited in the Bay Gardene Oyster Seed Reservation. As a result, the oyster industry harvested approximately 84,621 barrels (1,000,000+ pounds of meat) from the shell plant area. Applying the 1973 value of $10.00 per sack, the plant produced a benefit in excess of 2 million dollars to the oyster fishery. Other shell plants also produced benefits to the fishery greatly exceeding their original cost.

The results of previous shell plants indicate that a monetary return of at least 4:1 (benefit/cost) can be expected dockside. This ratio does not include an economic multiplier that reflects the additional increase in value that occurs as the oysters make their way through the market to the consumer. The benefit of cultch planting is expected to continue to grow over the years as a result of continued production.

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Chapter 6

Oyster Restoration in Alabama

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Abstract

Oyster reef restoration in Alabama consists almost entirely of shell planting, although seed oyster planting was common until the late 1960s. Private seed plantings were recorded from the 1880s but were poorly documented. Significant amounts of shell were planted on public reefs historically and private shell plantings continue at a modest level on riparian bottoms. However, no public bottoms are currently leased by the state to private citizens for planting. The first public plantings took place around 1910. A succession of oyster commissions, state and federal legislation, and entities of the Alabama Department of Conservation and Natural Resources have directed public reef restoration since that time. Eight legislative acts from 1910 to 1961 required the return of various percentages of oyster shells for replanting. The 1961 Act required oyster buyers either to replant 50% of all oyster shells removed from Alabama waters or to pay the state the value of the shells plus planting costs. The act proved unenforceable until the addition, in 1987, of a $0.25 per sack oyster tag. The tag provided a method of determining the amount of shell owed by each buyer and of providing the funds for shell planting.

Alabama currently has about 1,240 ha of public oyster reef, and it is estimated that another 24,000 ha of bottom are suitable for planting. Managers have relied on the economics of oyster production to rationalize oyster restoration expenses and have not made an issue of the potential ecological benefits, nor has there been much research to help support such a position.

Recent research by state biologists indicates that fossil coral is a good substitute for oyster and clam shell, but the costs make it uneconomical at this time. University researchers have investigated off-bottom culture of cultchless oysters in bags, bottom culture of remote set oysters, hatchery techniques, natural spat settlement patterns and the natural variables that control growth. Several oyster culture methods have potential in Alabama but remain underdeveloped. The ecological benefits and costs of oyster culture in Alabama have not been addressed.

Introduction

Physical conditions on Alabama oyster reefs are dominated by the Alabama-Tombigbee River system which has the fourth largest discharge in the U. S. (mean = 1,800•m^{-3}) and reaches more than 7,000•m^{-3}•sec^{-1} during flood conditions (Schroeder 1979). During low river flow, tides and winds overcome the freshwater discharge and allow high salinity waters from the Gulf of Mexico to reach the reefs. The reefs survive in a precarious balance between periods when the water is too fresh for survival and periods of high salinity when predators such as the oyster drill (*Thais haemastoma*) can decimate the stock (Eckmayer 1979).

Alabama currently has 1,240 ha of public reefs (May 1971) and the areal extent (Fig. 1) is similar to the 1,256 ha found in 1894 (Ritter 1896). However, Bell (1952) estimated that there were 2,392 ha of public reef in Alabama. Discrepancies between these surveys are attributed to methodology and interpretation, although it is known that one reef was altered by channel construction (May 1971).

Oyster production in Alabama was reported sporadically from 1880 to 1948 and yearly thereafter (Fig. 2). Landings have averaged 419,753 kg since 1880 and, for the period 1991-1994, landings have averaged 357,226 kg with a mean annual ex-vessel value of $1.1 M.

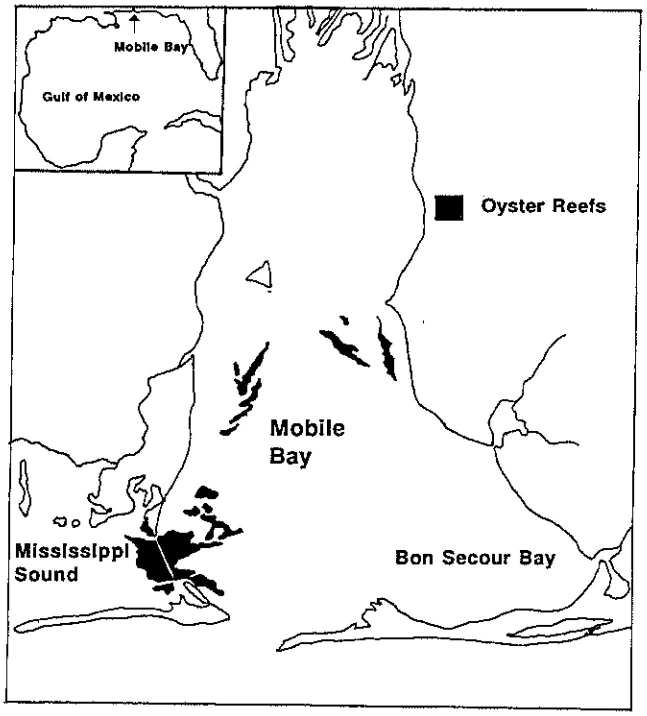

Figure 1. Location of oyster reefs in Mobile Bay, Alabama.

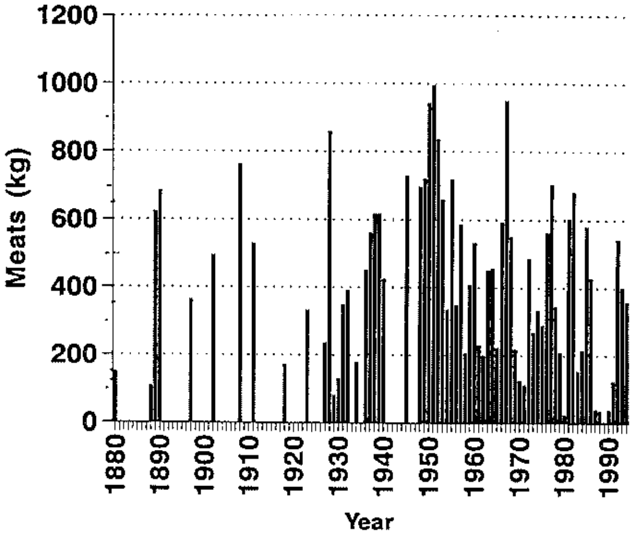

Figure 2. Alabama Oyster Landings, 1880 - 1994.

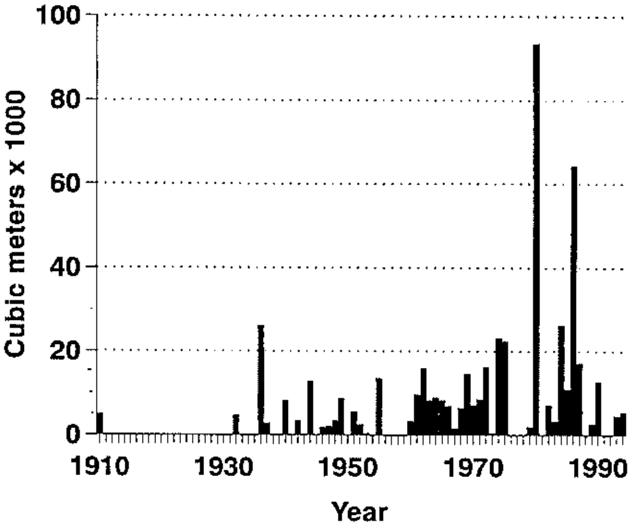

Figure 3. Public Shell Planting in Alabama, 1910 - 1994.

Alabama has three categories of oyster grounds: oyster riparian bottom, leased bottom, and public reefs. All tidally influenced subtidal bottom belongs to the state. However, in 1872 the state legislature created oyster riparian bottom which allow a waterfront property owner or his lessee the exclusive right to plant and gather oysters out to 545 m from shore. This riparian right can only be obtained when the area is surveyed, marked, and registered with the Alabama Department of Conservation and Natural Resources, Marine Resources Division (MRD). Approximately 24,000 ha are available to be claimed as riparian bottom. Natural reefs found within a riparian oyster claim remain public reef by law. The state can also lease non-riparian public bottom for oyster culture. As many as 1,600 ha have been leased in the past. The third category is comprised of existing public reefs. These areas are afforded special legal protection including prohibition of dredges (hand tong harvesting only), a 75 mm shell height limit, (often) daily catch limits and half-day harvests during the summer.

Oyster Reef Restoration

Oyster reef restoration has taken place in Alabama since at least the 1880s (Durrenberger 1992). Accounts from this early period do not always distinguish between planting seed oysters and planting shell, so it is difficult to determine how much planting activity simply involved moving oysters around compared to replacing shell or adding new shell to the bottom. Apparently most, if not all, of the planting was privately funded and took place on riparian oyster bottoms.

The first Alabama oyster commission was established by the state legislature in 1909 and abolished in 1915. The commission planted 4,830 m^3 of shell sometime between 1910 and 1915 and transported an unknown amount of seed oysters to an experimental plot (Swingle and Hughes 1976). Since 1910, oyster or clam shells have been planted in public waters 43 times in volumes ranging from 450 m^3 to over 93,000 m^3 (Fig. 3). Funding for planting efforts has come from a variety of sources including the state legislature, federal grants, various oyster taxes, and royalties from shell dredging (Swingle and Hughes 1976). Additionally, eight legislative acts from 1910 to 1961 required the return of various percentages of oyster shells from state processors for planting. It is not clear how effective these past requirements were in supplying shells for restoring oyster reefs. May (1971) noted that the 1961 Act was unenforceable and thus ineffective in providing oyster shells for planting.

From 1980 to 1987 Alabama utilized clam shell (*Rangia cuneata*) as cultch material and planting efforts were of greater magnitude. Funding was largely by federal monies and planting contracts were established by competitive bid. Planting efforts over this period are summarized in Table 1.

Environmental concerns sharply curtailed clamshell dredging in Mobile Bay during the late 1980s and eliminated this material as cheap, readily available cultch. Diminished federal funding forced Alabama not only to seek new cultch material but also new revenue sources to maintain its oyster restoration efforts. Low

Table 1. Alabama clam shell plantings from 1980-1987

		Funding ($)			
Year	m^3	State	Federal	Total	Cost/m^3 ($)
1980	93,480	19,252	1,350,000	1,369,252	14.64
1981	—	—	—	—	—
1982	7,1311	71,996	—	171,996	24.11
1983	3,325	151,867	—	151,867	45.67[1]
1984	26,289	12,000	464,800	476,800	18.14
1985	10,988	100,000	100,000	200,000	18.20
1986	64,145	64,375	1,153,774	1,218,149	18.99
1987	17,166	1,985	246,213	248,198	14.45
Total	225,524	521,475	3,314,787	3,836,262	—

[1] Oystermen were paid to plant shell

production from public reefs from 1987-1989 prompted the state legislature to provide funds for planting in 1989 and 1990. In 1989 funds were used to transport shells donated by oyster shops, while the labor for planting was provided by a local oystermen's association. Funds in 1990 were used to purchase oyster shell and to pay oystermen for planting.

Funding of shell planting was partially shifted to the industry with the passage of a sack tagging law in 1987 that required a $0.25 tag on each sack of oysters. The industry was also tapped as a source of cultch material in 1991, when a long dormant law (the 1961 Act) was revived. The 1961 Act required oyster buyers that purchased Alabama oysters to replant 50% of the shell. An agreement was reached with the shop owners that if they donated 100% of their Alabama oyster shell, the Alabama Department of Conservation would be responsible for shell transport and planting. This agreement has proven successful with most shops donating not only their Alabama shell but also shell that is trucked in from other Gulf states. At present, Alabama has far more oyster shell available than funds to pay for transportation and planting.

Enough funds from oyster tag sales were accumulated (supplemented by money provided by the Alabama Marine Resources Division) to fund oyster reef restoration efforts in 1993 and 1994. Contracts were established by competitive bid for transporting and planting shell. Alabama shell planting efforts since 1989 are summarized in Table 2.

In addition to the public reefs, there are currently 27 recognized private beds in Alabama. These beds are on the previously described riparian oyster right bottoms and no records of shell planting are available. Of the 27 riparian beds, few exceed two ha in size and only two consistently produce commercial-size oysters. Private oyster production in Alabama exceeded the harvest from public reefs only once in the last 25 years. Alabama law also provide for the leasing of state-owned oyster growing bottoms; however, no one has leased any state oyster bottom in 15 years.

Table 2. Oyster shell acquired from oyster shops and planted on Alabama reefs, 1989 - 1994.

Year	Planted (m^3)	Cost ($)	Cost/m^3 ($)
1989	2,660	50,000	18.80
1990	12,691	397,250	31.30
1993	4,560	85,850	18.82
1994	5,320	72,527	14.20
Total	25,231	605,627	____

Research

Planting shell to restore oyster reefs has long been considered a positive management measure, but there have been few quantitative studies in Alabama to justify the practice. May (1971) noted that 340 m^3/ha shells planted on barren bottom produced 121,000 oysters/ha. More recently MRD personnel evaluated clamshell planting. Post planting dredge tows were taken from 1984-1988 to assess spat set success. The results of these tows are found in Table 3. Successful spat sets can be traced to many factors; however, location was most likely responsible for successful plantings in 1983 and 1985 since a historically productive section of the main reef was planted in those years. In other years, attempts were made to expand potential harvest areas by planting in marginal or low productive habitat but had little success.

Since oyster shell may become scarce or expensive, MRD personnel have investigated archeological coral as an alternative cultch material. It was found that a test plot of coral had a spat setting success comparable to a nearby test plot containing oyster shell (Tatum 1994). However, the price of coral ($25•$m^{-3}$) is not currently competitive with oyster shell.

There have been limited efforts over the years to transport oysters from areas closed to public harvest by the state health department, from areas scheduled to be renovated (dredged, filled, etc.) and from areas virtually inaccessible to tonging for reasons of depth or sea conditions to locations open and accessible to public harvest. Analysis of these efforts indicate the costs were high relative to the benefits.

Temporal and spatial distribution of oyster spat have also been studied and the information is relevant to locating appropriate sites for shell planting. Hoese et al. (1972) monitored 15 stations for oysters set in Mobile Bay and Mississippi Sound and found low spat set ($<1\text{-}2 \bullet \text{m}^{2} \bullet \text{d}^{-1}$) in the southeastern and central part of Mobile Bay, higher sets ($5\text{-}10 \bullet \text{m}^{-2} \bullet \text{d}^{-1}$) in the southwestern area of the Bay and eastern Mississippi Sound. High spat sets ($100\text{-}200 \bullet \text{m}^{2} \bullet \text{d}^{-1}$) were reported in the western Mississippi Sound. Unpublished studies at the Dauphin Island Sea Lab, Alabama support these findings. Researchers at MRD documented a bimodal spat setting pattern within each year over a three-year period. The earliest initial setting peaks were in June and July while the latest secondary setting peaks were in October and November. Temperature and salinity appeared to be important factors affecting the time of the set.

Oyster culture is another area of research that is related to oyster reef restoration. May (1969) concluded that string culture using oyster shell produced good growth in Mobile Bay (from 10 mm to 77 mm in 12 months); however, high costs and loss of oysters from the strings discouraged further study. Eckmayer (1983) reported that hatchery-reared oysters planted on the bottom in the southeast corner of Mobile Bay (Bon Secour Bay) all died within seven months. Mortality was probably due to freshwater flooding.

Interest in oyster culture was renewed in 1989 when production from natural reefs hit a historic low (4,300 kg) due to drought conditions. At that time, the Auburn University Marine Extension and Research Center (AUMERC) began a small oyster culture research program aimed at enhancing oyster production in Alabama. Initial research focused on growing cultchless oysters in bags on racks in a fertilized pond. Oysters grew rapidly to 34 mm in 56 days with low mortality, but were only 50 mm after one year (Wallace and Rouse 1993). Subsequently, fertilized ponds have been used only as nurseries prior to placing oysters in Mobile Bay for growout.

Table 3. Evaluation of Alabama clamshell plantings from 1983-1987.

Date Planted	Date Evaluated	# Shells Examined	% Shells with Spat
06/27–07/14/83	05/18/84	625	29.0
07/07–07/07/84	05/01/85	6510	1.6
09/09–09/13/85	04/29/86	360	19.0
07/31–08/24/86	08/10/87	2619	0.4
06/11–06/17/87	06/28/88	1929	1.5

Three basic culture techniques have been examined to date: cultchless oysters in horizontally suspended bags, cultchless oysters in bags on racks, and remote set oysters (set on whole oyster shell) in trays on the bottom. Oysters in horizontally suspended bags reached harvestable size (75 mm) in 16 months (Wallace et al. 1994). These oysters were grown in an area of Mobile Bay where there has been very little natural oyster production. A local oyster processor is continuing with this technique and has recently test-marketed "farm-raised Bon Secour oysters". Cultchless oysters grown on racks averaged 71 mm (range = 49-99 mm) while remote set oysters on the bottom averaged 82 mm (range = 57-110 mm) after 16 months (Rouse et al. 1993). Neither of these culture techniques have been adopted in Alabama.

Current mariculture studies include: production of triploid oysters using pressure and nitrous oxide, prevention and control of fouling in suspended bag culture, disease in cultured oysters, and polyculture of shrimp and oysters in ponds. The Dauphin Island Sea Lab is conducting experiments in cooperation with AUMERC to assess which areas in Mobile Bay possess the necessary conditions for good oyster growth by examining a suite of biotic and abiotic factors at different locations.

Oyster reef restoration in Alabama is driven by the desire to maintain commercial oyster production. Benefits to the Mobile Bay ecosystem derived from oyster reefs are taken for granted by fishermen, managers, and scientists, but arguments for oyster reef restoration are rarely, if ever, made on an ecological basis. It is unlikely that the general public understands the attendant benefits of maintaining oyster reefs. Public educational efforts may help justify continued expenditures for shell planting and other oyster reef enhancement projects.

The more sophisticated forms of oyster culture such as cultchless oysters grown in bags would not seem to fall within the scope of traditional oyster reef restoration and may not have the same ecological value. However, oysters in suspended bags or on racks still filter large volumes of water, provide habitat for some typical oyster reef organisms (xanthid crabs, blennies, gobies, etc.), and contribute to the natural spat set.

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A History of Oyster Reef Restoration in North Carolina

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Abstract

North Carolina has extensive intertidal and subtidal habitat with approved shellfish growing waters; however, historical harvest levels have generally been modest compared to larger producing areas such as the Chesapeake Bay. Mechanical dredging and removal of shell resources have degraded natural reef habitats over the past century. State efforts to restore oyster habitat and enhance oyster fishery production have a long history dating back to the beginning of this century. These efforts have relied primarily upon planting a variety of natural cultch materials, including oyster, clam and scallop shells, as well as limestone marle. Additionally, some relaying of wild seed oysters has been conducted. The history of this effort and some of its limitations are discussed in this chapter. Recent increases in cultch planting capabilities together with greater attention to the siting and configuration of these cultch plantings may hold promise for more successful restoration efforts in the future.

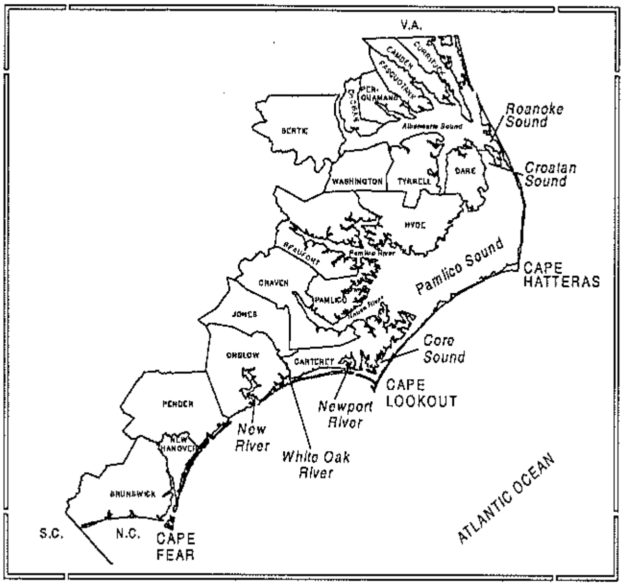

Figure 1. Coastal North Carolina.

Introduction

In North Carolina, oysters are found from extreme southeastern Albemarle Sound near the northern end of Roanoke Island southward through Croatan, Roanoke, and Pamlico sounds and in the estuaries of the southern part of the state to the South Carolina border (Figure 1). They are found at varying distances up the major drainage basins depending on long-term rainfall. North Carolina ranks second only to Louisiana in approved estuarine shellfishing waters indicating that by at least one general measure there is some potential for oyster production (Figure 2). However, North Carolina has never been a major oyster producing state (Figure 3). Even though the size of North Carolina's estuaries rivals the Chesapeake Bay, the State's oyster production more closely resembles its smaller southern neighbor South Carolina.

North Carolina's oyster stocks are composed of both intertidal and subtidal populations. The intertidal populations are characteristic of the oyster stocks of the South Atlantic Bight and exist primarily between the mean low and high water marks. These intertidal populations are found principally from Cape Lookout southward. However, notable exceptions are the subtidal oyster rocks found in the Newport, White Oak, and New river systems. Other scattered subtidal populations are found in some of the larger systems farther south. North of Cape Lookout, oyster resources are almost exclusively subtidal. This region is primarily influenced by wind driven tides, and intertidal oysters are found only in close proximity to inlets.

Historically, oyster harvesting practices have varied little in North Carolina. Mechanical harvesting of oysters is conducted almost exclusively with oyster dredges. This gear is allowed in portions of Pamlico Sound and its tributaries. The area closed to oyster dredging is shown in Figure 4. Hand harvest methods include hand tongs, hand rakes, and by hand. Hand tongs are generally used in shallow subtidal areas. Hand rakes and actual picking up by hand are normally used in intertidal areas. Some specialized uses of rakes and modified tongs occur in subtidal areas. Hand methods are allowed in all approved harvest waters during the open season.

In an effort to increase oyster harvests, the area opened to oyster dredging in North Carolina gradually expanded from its beginnings late in the 1880s until 1955. Since 1955, available mechanical harvest area has declined due to efforts to protect finfish and crustacean nursery areas, sea grass beds and oyster habitat from bottom disturbing fishing practices. Primary nursery areas important for development of juvenile populations of estuarine dependent species were closed to oyster dredging in 1977.

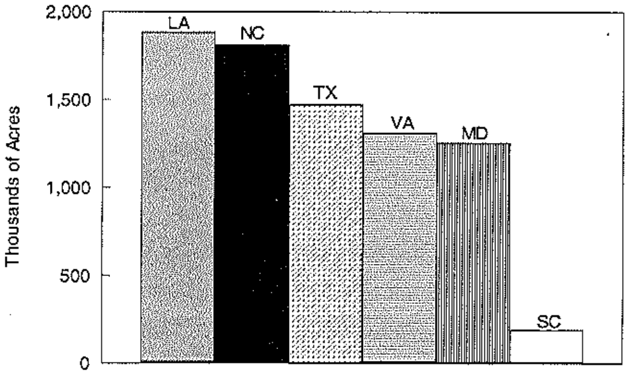

Figure 2. Acreage of approved or conditionally approved estuarine shellfish growing waters by state - 1990. Source: The National Register of Classified Estuarine Waters, NOAA, National Ocean Survey.

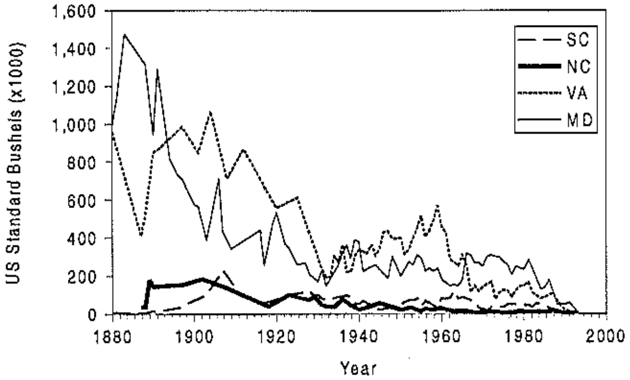

Figure 3. Historical oyster landings for Maryland, Virginia, South Carolina, and North Carolina.

Dr. Al Chestnut, Director of the UNC Institute of Fishery Research, (1955) described the oyster rocks of Pamlico Sound as consisting of a thin layer of shells and oysters on firm bottom. Both Chestnut (1955) and Lt. Francis Winslow, US Navy surveyor, (1889) reported finding once highly productive areas in Pamlico Sound where intensive harvesting left only widely scattered oysters and little or nothing to provide a substrate for spat attachment. Current investigations reveal that the same processes exist today. Therefore, restoration of the oyster resource will require elimination of practices that destroy oyster habitat and reconstruction of degraded oyster rocks. North Carolina's Oyster Rehabilitation Program was originally conceived as a means of expanding an already valuable oyster industry. A review of the program may provide insight into why it failed to achieve that goal and where it should be directed in the future.

History

The origins of North Carolina's public oyster reef enhancement program were overshadowed by the State's efforts to develop private oyster culture and profit from the high market demand for oysters during the late 1800s and early 1900s. These attempts at private oyster culture were patterned after programs in more northerly states but never succeeded in North Carolina due to lack of available seed oyster resources and lack of adequate laws protecting oyster growers. The first oyster cultch plantings on public bottoms were state-sponsored tests to prove the feasibility of private oyster cultivation in certain North Carolina waters.

Grave noted while conducting some of these demonstration projects on oyster culture, "that if the natural beds were strewn with shells at some time during the summer months, they could easily be made to produce many times the amount of oysters taken from them" (c.f. Pratt 1911). He further concluded that since the natural beds were public property, the planting of shells might be done by the State.

Experimental oyster cultch plantings began in 1900 and resulted in oyster harvest on those sites by local oystermen. Although there are no references to a direct link to these experiments, it may not be coincidental that North Carolina passed its first law allowing the expenditure of state funds to plant oysters and cultch materials shortly after these experiments in 1903 (Thorsen 1982). Even though the statutory authority existed to plant cultch materials and seed oysters on public bottoms, available records indicate that activity did not begin until 1915. Even then, early cultch planting efforts were limited.

The probable reason for limited efforts to increase public oyster productions was attempts

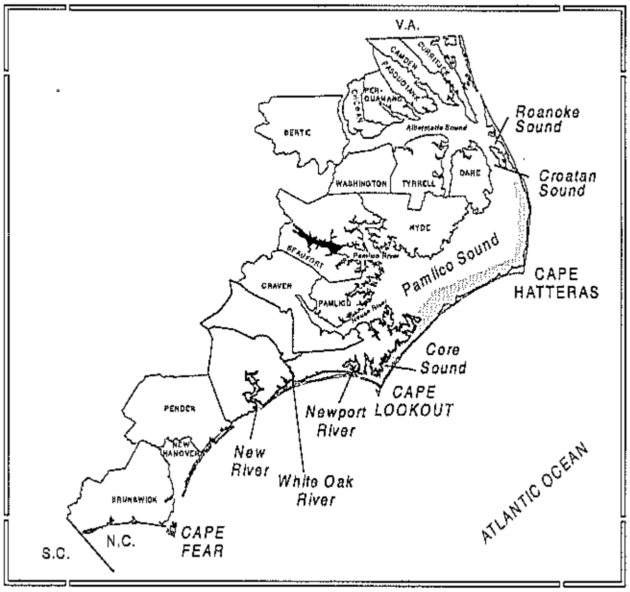

Figure 4. Current areas closed to oyster dredging (hatched) and Primary Nursery Areas (black).

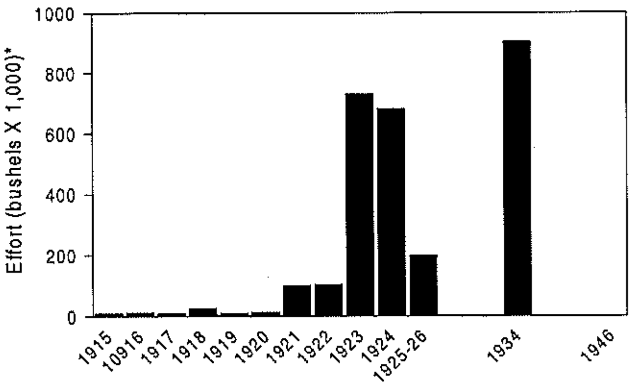

*Figure 5. Known N.C. Oyster Restoration Efforts 1915-1946 (*Effort includes cultch material and seed shellfish).*

by the State to begin a large private oyster culture industry. A survey of oyster grounds by Lt. Francis Winslow from 1886 to 1888 found that nearly 700,000 acres of potentially productive oyster bottom existed in North Carolina (Winslow 1889). The State wanted to raise revenues by passing legislation to allow private cultivation of these areas for oysters. Approximately 50,000 acres of oyster franchises were granted for private oyster production. However, the legislation did not sufficiently protect the oyster growers and private oyster cultivation was minimal (Pratt 1911). After several additions and revisions to the statutes, ending around 1913, the state apparently turned its attention to enhancing public ground oyster production.

Although only 8,000 acres of natural oyster rock were identified in that early Winslow survey, oysters were still among the top three fisheries products in value for North Carolina during the early 1900s. Attempts to increase oyster production began slowly with between 10,000 and 12,000 bushels of shells planted each year between 1915 and 1920 (Figure 5). Due to the excellent results of these plantings, the Fisheries Commission Board requested and obtained $10,000 in funding for each of the next two years for oyster enhancement work, and approximately 100,000 bushels of shells and seed oysters were planted per year in 1921 and 1922 (Thorsen 1982).

The Fisheries Commission Board convinced the Governor that these types of plantings were all that was needed to build a large oyster industry and a plan to expand the public harvest industry was devised. A sum of $500,000 was appropriated for the 1923/24 biennium to plant seed oysters and shells that were anticipated to support oyster harvesters for many years (Thorsen 1982). The $500,000 was used to plant seed oysters and shells totaling 730,812 bushels in 1923 and 682,692 in 1924. The 1.4 million bushel total was distributed more than sixty-four sites. These plantings were credited for a 472,431 bushel increase in oyster landings in 1924. However, the increase in landings was probably caused as much by an increase in market price and new shipping methods as by increased supply (Thorsen 1982).

Between 1926 and 1947 only one reference to oyster resource enhancement activities can be found (Figure 5). In 1934, 825,000 bushels of seed oysters and 78,567 bushels of shells were planted and the areas were closed until 1936 (Chestnut 1951). This is the largest annual oyster enhancement project in North Carolina history. Landings doubled to around 800,000 bushels during the year these sites were opened to harvest.

The lack of continuity for the oyster program during this period could have resulted from a typhoid scare associated with oyster consumption in 1924, the inception of a profitable bay scallop fishery in North Carolina during that time period, and the effects of the Great Depression. Unless there was special funding by the legislature, the oyster planting efforts during the 1926 through 1946 period were probably meager due to dependence on oyster tax revenues. Chestnut (1955) reported that the seed oyster plantings he made in 1954 were the first major attempt since the 1930s. Even though state officials believed their efforts gave all the impetus necessary to create a viable oyster industry, oyster landings continued to decline (Thorsen 1982). A new oyster canning industry began in the early 1940s and may have inspired creation of a special oyster commission by Governor Cherry in 1946. The legislative act that resulted from the commission's recommendations contained many landmark changes in oyster management in North Carolina (Chestnut 1955).

This effort to revive the state's oyster industry was known as the Oyster Rehabilitation Program. Of particular interest were the provisions for an ongoing, large-scale program for planting shells and seed oysters on natural oyster beds, a tax on oysters to support the program, a requirement that oyster shuckers contribute 50% of their shell material to the program, a 50 cents per bushel tax on shell stock shipped out-of-state, and an initial appropriation of $100,000 to begin the program. The legislation encouraged the establishment of instate oyster shucking houses, and shells that had been used for lime, chicken feed, and road beds were now used as oyster cultch.

The cultch planting program began almost immediately and three sites were planted during the summer of 1947. During the first ten years of the program, 838,088 bushels of shell and 350,734 bushels of seed oysters were planted (Chestnut 1955). The appropriated monies were soon exhausted, however, because landings and the attendant tax collections did not increase. The landings may have been impacted by the intense hurricane activity which occurred in the mid 1950s in North Carolina or by insufficient habitat restoration efforts. Chestnut supervised the North Carolina Oyster Rehabilitation Program at the time and found that North Carolina's program planted an amount of shell in one decade equal to the amount planted by the State of Virginia in just one year of its ongoing program. Maryland was planting even more shell at a rate of more than two million bushels annually during the mid 1950s (Chestnut, unpublished memo). Both Virginia and Maryland were harvesting millions of bushels of oysters during this period. Chestnut requested and received an annual appropriation from the 1956 legislature of $80,000 with the intent of increasing North Carolina's Oyster Rehabilitation efforts to 500,000 bushels per year. The annual appropriation was increased to $130,000 per year in 1972 and an additional $50,000 was added in 1977 to bring the total to $180,000. In 1979, a $400,000 total was approved for annual funding (Munden 1981). The North Carolina Oyster Rehabilitation Program currently operates on a total annual budget of approximately $700,000 (Table 1).

North Carolina's seed oyster and cultch planting totals from 1947 through 1994 are shown in Figure 7. Between 1954 and 1971, the planting of seed oysters was carried out on a large scale and seed oyster planting totals exceeded cultch plantings eight times during that period. Seed oysters were transplanted by local fishermen using traditional harvest methods to gather the oysters. Payments were made based on the distance the oysters had to be transported and the degree of difficulty in obtaining the oysters.

A reduction in the amount of available cultch coupled with the reluctance of Hyde and Pamlico county fishermen to move seed oysters created a shift in oyster habitat enhancement efforts to the southern coastal counties (Onslow, Pender, New Hanover, Brunswick) in the late 1950s (Figure 8). The intense harvest pressure, fast growth characteristics and abundance of labor for transplanting convinced officials at the N.C. Division of Marine Fisheries (henceforth referred to as the Division) that more return on the investment could be realized from restoration efforts in the southern coastal area. However, landings soon began to decline and by 1970 the Division renewed its efforts in Pamlico Sound while maintaining the programs in the southern area. The historically high oyster

Figure 6. *Changes in Legislative Appropriations for the N.C. Oyster Rehabilitation Planting Program.*

Year	Annual Appropriation
1956	$80,000
1972	$130,000
1977	$180,000
1979	$400,000
Current	$700,000

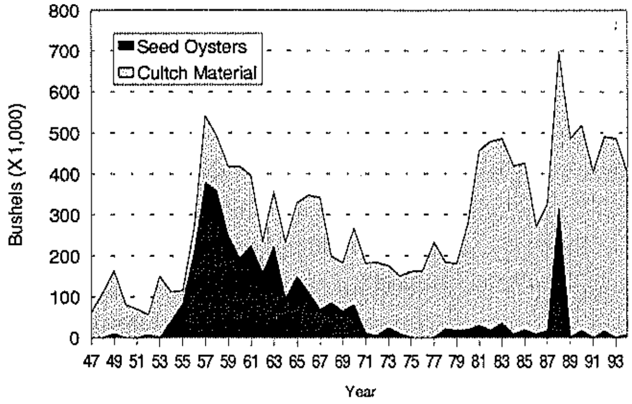

Figure 7. North Carolina Oyster Rehabilitation Activities 1947-1994. (Data are stacked to show cumulative total.)

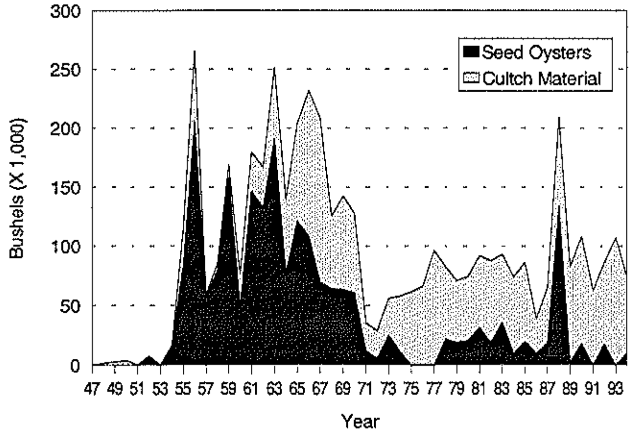

Figure 8. Southern Area Oyster Rehabilitation Activities 1947-1994. (Data are stacked to show cumulative total.)

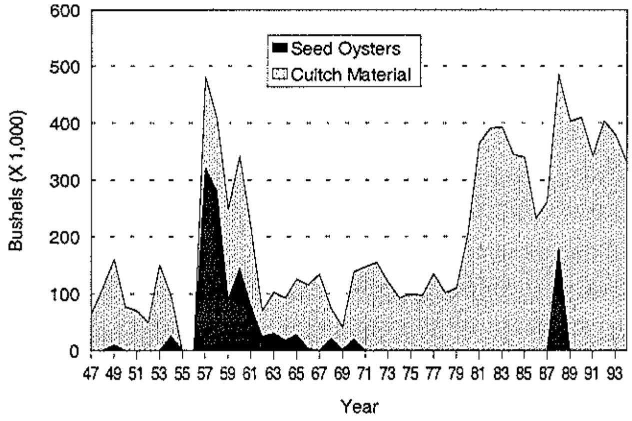

Figure 9. Northern Area Oyster Rehabilitation Activities 1947-1994. Data are stacked toshow cumulative total.

production potential of Pamlico Sound and the problems with pollution closures and loss of habitat due to development in the southern area probably influenced the return to more geographically balanced attempts at enhancing the oyster fishery. The corresponding decline and subsequent increase in effort in the northern area are shown in Figure 9.

Since 1970, North Carolina has relied almost exclusively on cultch planting as a means of enhancing oyster production. Cultch plantings reached a high of 499,920 bushels in 1990. An exception to this trend occurred from 1978 through 1983 when the Division developed a mechanical seed oyster harvester and completed controlled polluted stock relay from several areas in the southern counties (Godwin 1981). Initially, the results of the program appeared very positive with efficient harvesting and low oyster mortality. Subsequently, it was learned that most of the areas harvested for seed oysters had not recovered five years after serving as a seed source, and mechanically harvested oysters for relay have been used sparingly in recent years. Since the early 1980s, the Division's position has been to concentrate primarily on cultch plantings for direct harvest and use small-scale, high quality transplanting programs in areas with low harvestable resource and readily available polluted seed. The transplanting programs utilize commercial fishermen employing hand harvest methods. There is no program currently in place to replant the polluted seed source areas.

During a rare occurrence of Red Tide during 1997-88, relaying oysters was used as a means to employ fishermen prevented from working by the shellfishing closures. Shellfishermen relayed 355,890 bushels of material during 1988 under this program (Figure 9). The majority of these fishermen appeared to participate in the program only for the $1.00 per bushel that they received, and cared little about the quality of the product they provided. The state was not equipped to handle the 484 relayers and was often overrun with oysters, shells, and mud. Due to the poor execution of the project and subsequent oyster disease problems, very little benefit was realized from the effort.

Most of the recent oyster reef restoration effort is conducted in the large bays around Pamlico Sound and in smaller protected tributaries in the other estuaries (Figure 10). There has been little change in the areas used for restoration efforts except where shellfishing closures have occurred. Almost all of the sites selected in the Pamlico Sound area are "new" plantings where cultch is placed on basically barren sediments. Cultch and seed oyster areas in the southern area are frequently replanted after harvesting takes place because the harvest often leaves little substrate for future growth and good sites are limited. As can be seen from the distribution of sites, the tendency is to spread Oyster Rehabilitation efforts over a large area. The most consistent guidance the program has received over the years is to put the shells where the fishermen want them. That guidance leads to many sites and smaller effort per site.

Annual, advertised public meetings are held at various locations to give the public input into the selection of Oyster Rehabilitation sites. An effort is made to acquire names and telephone numbers from participants so that they can be contacted and invited to participate in the site evaluation and cultch planting activities. Since other fisheries are in peak periods of operation in the summer months when shell is planted, few fishermen respond to the invitation.

Criteria evaluated at the prospective sites include physical factors such as sediment types, currents and exposure to possible storm damage as well as habitat considerations such as historical productivity, salinity patterns and current shellfish concentrations. These concerns are addressed by reviewing past data and by sampling with a sounding pole and oyster dredge over the intended site. Compatibility with other fishing activities, including trawling, hydraulic clam harvesting and long haul fish seining, is also considered in selecting sites. Cultch plantings can be made totally useless by disturbances from towed gear.

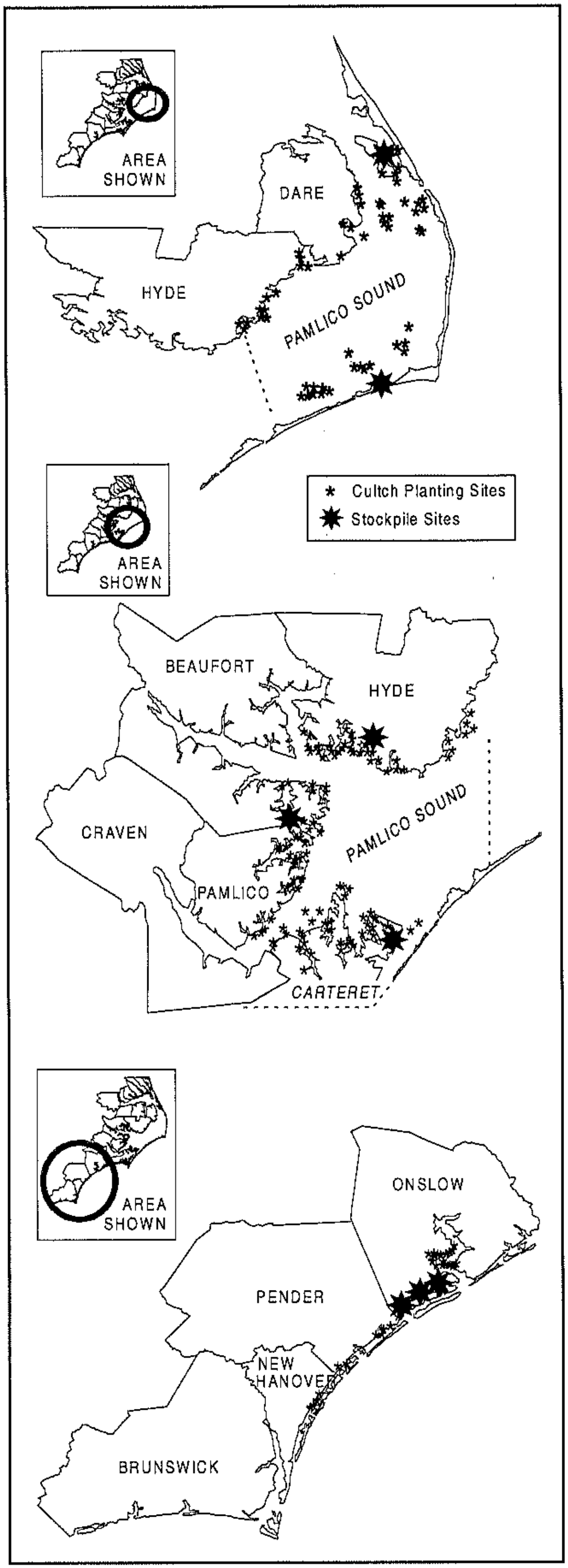

Figure 10. North Carolina oyster cultch planting sites 1990-94.

During the early years of the program, cultch plantings were predominately oyster shell with occasional use of bay scallop (*Argopecten irradians*) shells. Most of the annual supply of oyster shells come from the Gulf of Mexico. Oysters were imported for shucking at the rate of about 200,000 bushels per year. In 1968, the Division began using marl, a sedimentary rock mined in the coastal area, because shell supplies did not meet planting needs. Also, in 1968, North Carolina attempted to utilize dredged shell deposits identified in Currituck and Albemarle sounds. Local governments opposed the activity and, although other attempts were made, no locally dredged shell has ever been used in North Carolina waters. The lack of an abundant, inexpensive cultch source such as dredged shell contributed to the small scale of North Carolina's Oyster Rehabilitation Program.

Beginning in 1973, the Division began planting calico scallop (*Argopecten gibbus*) shells, as large quantities were being imported from Florida fisheries for shucking in North Carolina. However, shucking operations eventually moved to the Florida coast and shells currently are available only during periods when Florida shucking houses are overloaded and from a small fishery which occurs off the North Carolina coast near Cape Lookout. Small amounts of sea scallops (*Placopecten magellanicus*) also came into use about the same time period. Shucking at sea now disposes of most of those shells. The sea scallop shells had poor characteristics for oyster cultch.

The latest addition to the cultch material supply for North Carolina has been surf clam (*Spisula solidissima*) shell first tried in 1981. Surf clam shell is brittle and post shucking handling often reduces the shell to small pieces. The small pieces create low profile mounds and siltation is a problem. Therefore, it is used sparingly as oyster cultch. However, surf clam shell creates excellent hard clam (*Mercenaria mercenaria*) habitat, because the small pieces provide excellent protection from predators. North Carolina has not experimented with tire chips, fly ash, or manufactured cultch materials. The Division experimented with using large pieces of overburden from local phosphate mining operations composed of marl, fossil bones, and coral during 1993 and 1994. Spat settlement on the new material was similar to marl during the first year of trials. However, the effort was abandoned after the 1994 season because the phosphate company did not wash the product to specifications and could not supply the projected volume.

Prior to 1954 all of the oyster resource enhancement activities were conducted on an individual contract basis with local fishermen. Beginning in 1954, the state began planting oyster cultch materials with its own equipment. The state initially procured a forty-foot wooden barge which was loaded using wheel barrows and towed with Fisheries Law Enforcement Patrol vessels. The shells were washed overboard using high pressure water pumps. Capacity of the barge was estimated at 2,000 bushels of oyster shells. In 1968, the state began experimental plantings using marl hauled on the same small wooden barge. The first two years of experiments were successful and a tug and steel barge were hired to conduct the northern area marl plantings in 1970. It is significant that this was the first use of a bulldozer to push the cultch off the barge in large piles. Recent research comparing cultch planting methods found that cultch planted in mounds associated with offloading by bulldozers received significantly higher spatfall than cultch planted with water pressure which showed lower relief (Ortega et al. 1990).

Most of the best cultch planting bottoms lie at a depth of six to eight feet in the smaller tributaries of Pamlico Sound. The draft of the tug and barge did not allow planting at that shallow depth. In 1972, an increase in the annual Oyster Rehabilitation appropriation of $50,000 and a one-time federal grant of $80,000 allowed the state to purchase a 110-foot former Hatteras class ferry for cultch planting operations and ended the use of tugs and barges (Munden, pers. comm.). The ferry was originally a military landing craft designed for beaching and shallow water operation. The vessel's fully loaded draft was only 3.5 feet which made it ideal for the traditional planting areas (Munden 1975). Due to the success of previous plantings using the bulldozer and because of the necessity of having sides on the vessel due to loading procedures, the practice of dumping shells overboard in piles was continued. The same year, a 50-foot self-propelled, steel-hulled barge was procured for use in the southern area cultch plantings. The vessel was fitted with special outdrive units which could be tilted to gain access to the very shallow waters of the southern area estuaries. The practice of blowing the shells off with water pressure continued on this vessel.

Recent Advances and Future Directions

The two vessels purchased in 1972 have been sold, but the Division continues to operate vessels with similar characteristics to meet the requests of the oystermen for cultch plantings. North Carolina Marine Fisheries now operates six steel-hull, diesel powered vessels which are operated by fourteen employees. Two of the vessels are 115-foot former military landing craft which still utilize the dumping method of cultch distribution. The other four vessels are designed for shallow water operation and use the water pressure method to plant cultch. The two smallest vessels have outdrives that can be tilted to allow fully loaded operation in approximately 2 feet of water. The other two vessels have inboard propulsion and can operate, loaded, in about 40 inches of water.

The smaller vessels typically plant cultch on intertidal areas or in the head waters of coastal creeks and bays. The intertidal areas produce the typical elongated oysters in high densities that are harvested at low tide. The other areas planted with the shallow draft vessels respond to a fishery for high quality, mostly single oysters that are harvested with hand tongs and long handled rakes primarily in shallow, calm waters. The low density cultch planting method mimics the natural growing conditions in these areas.

The landing craft usually plant along the edges of the middle portions of the bays. The recommended planting bottom in these areas is often a narrow band of mixed sand and mud sediments that lies between the shallow, hard, near-shore sediments and the soft sediments of the middle of the bay. The cultch planting sites therefore tend to be long and narrow. The vessels are not anchored but are maneuvered slowly or allowed to drift over the selected site. The cultch is pushed through scupper doors or dumped over the side with a crawler/loader having a one cubic yard bucket. Cultch that is dumped by the bucket makes small mounds which may reach two feet in height and six feet in diameter (Munden 1981). Cultch that is pushed through the large scupper doors makes long rows up to six inches high. Cultch planting densities are estimated at between 1,000 - 5,000 bushels per acre for all methods and types of bottom.

A study of oyster recruitment success on restored sites was conducted during 1988-90 (Ortega et al. 1990). Results of the study indicated that oyster recruitment was higher at the deeper cultch planting sites in the Pamlico Sound area. The southern coastal area was not studied. The report made several recommendations including planting shell later in the fall to coincide with highest oyster recruitment and concentrating plantings at the program's deeper selected sites. The authors also concluded that there was too much variation in spat settlement to make accurate spatset predictions and that recruitment of oyster spat seemed to be declining.

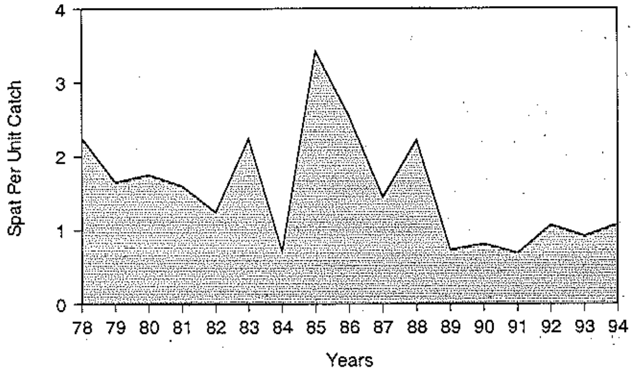

Figure 11. Northern Area Average Spatfall 1978-1994.

Marine Fisheries has a program for sampling cultch sites for three years after planting. Random samples of thirty shells are collected at each site. Data are available continuously since 1978 for most sites (Figure 11). Chestnut (1955) sampled several of the sixty-four planting sites created between 1947 and 1954 using methods similar to those used today. The general range of spatfall was similar to findings since 1978. Typically, both sets of data show an average of zero to five spat per shell with a few sites having up to an average of twelve spat per shell. However, in that seven-year span (1947-54) with only sixty-four sites, Dr. Chestnut reported five sites in Pamlico Sound with an average of more than twenty spat per shell. Only one site out of 800 sampled since 1978 has exceeded that average.

In summary, the primary goals of North Carolina's oyster restoration efforts have been to simply grow oysters for harvest. The approaches and mechanics of the program have increased in scale but have remained relatively unchanged for nearly fifty years. Recent research indicates construction of high profile oyster restoration sites increases oyster survival and growth. Other research indicates that the oyster habitat may have greater value for other species than for oysters. It appears that efforts at oyster production would have been better utilized if creation of optimum oyster habitat had been the goal rather than simply providing cultch for spat attachment and subsequent harvest.

Recently opportunities for habitat creation projects have occurred. The first true oyster reef habitat restoration project in North Carolina occurred in 1992/93 when 13 acres of oyster producing habitat were created as out-of-kind mitigation for the loss of 16 acres of estuarine bottoms and 1.5 acres of wetlands in Roanoke Sound. An attempt was made to recreate a low profile oyster rock known locally as the half-moon rock by planting 65,000 bushels of cultch material. Marine Fisheries is monitoring the site as part of the mitigation agreement with the U.S. Army Corps of Engineers.

More recently the Division has performed mitigation projects for the North Carolina Department of Transportation and additional projects to create more than 70 acres of oyster rock habitat is planned with the Corps of Engineers. Research is continuing on how to best construct these sites to provide effective oyster habitat.

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Oyster Restoration Efforts in Virginia

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Abstract

Long-term restoration of the Virginia Oyster resource has been assisted by a series of governmental and regulatory initiatives. Following the 1990 Blue Ribbon Panel the Virginia Marine Resources Commission set as goals that the oyster resources and oyster fishery would be so managed as to achieve (a) no net loss of existing standing stock of the native oyster over the next five years, and (b) a doubling of the existing standing stock of the native oyster over the next ten years. The 1994 Chesapeake Bay Aquatic Reef Plan and Oyster Fishery Management Plan both recommended the creation of 5,000 acres (2024 hectares) of oyster reef habitat during the 1995-2000 period. Practical progress toward this goal has been made through the development of several programs including direct application of substrate (cultch) to extant oyster reefs to facilitate settlement and recruitment, enhancement of reefs of the Seaside of the Eastern Shore by exhumation of buried shell, and construction of elevated reef structures in the Virginia subestuaries of the Chesapeake Bay. Efforts in the James River have included subtidal berm type structures capped with shell and a reef constructed entirely of shell. A shell reef has been constructed in the Piankatank River, and construction of several more is planned. All reefs remain as broodstock sanctuaries. Continuing management is supported by quantitative stock assessment.

Overview of Blue Ribbon Oyster Panel Recommendations

Years of intensive harvesting, habitat destruction, pollution, and disease related mortalities have reduced Virginia's oyster population to less than 1% of that of only 35 years ago (Table 1, Fig. 1, also see Hargis 1999, Chapter 1, this volume). Many attempts have been made to limit harvest and to facilitate restoration projects; however, industry and political objections have reduced most efforts to insignificance. In 1990, the Governor, Lawrence Douglas Wilder, convened a Blue Ribbon Oyster Panel, staffed by the Virginia Marine Resources Commission (VMRC), to develop plans to restore the oyster resource and the oyster industry. This panel, composed of commercial fishermen (watermen), seafood processors, politicians, economists, and scientists developed a plan and presented it to VMRC in November 1991. The Plan (Appendix 1), with the exception of a recommendation for the introduction of non-native oysters in Virginia waters, was adopted in May, 1992. In addition, two long range goals developed by the Commission itself were adopted to guide oyster management and restoration in Virginia for the next ten years.

These goals were:

1) The Commonwealth's resources and oyster fishery shall be so managed as to achieve no net loss of existing standing stock of the native oyster over the next five years.
2) The Commonwealth's resources and oyster fishery shall be so managed as to achieve a doubling of the existing standing stock of the native oyster over the next ten years.

The goals and recommendations of the plan were well conceived, significant, and reasonable, but success in oyster restoration remains uncertain. The depleted state of the extant oyster stocks dictate that any recovery will be extremely slow in rate and limited to those areas where stocks remain in sufficient numbers to be reproductively active. For example, the James

Table 1. Oyster Ground Production.

Year	Public Landings (Bushels)	Private Landings (Bushels)	Total
58	586,304	2,926,750	3,513,054
59	703,915	3,347,170	4,051,085
60	699,420	2,553,275	3,252,695
61	781,783	2,237,736	3,019,519
62	227,921	1,815,001	2,042,922
63	278,830	1,652,880	1,931,710
64	576,857	1,223,549	1,800,406
65	615,864	1,605,759	2,221,623
66	605,982	1,188,633	1,794,615
67	226,855	587,105	813,960
68	262,996	790,483	1,053,479
69	227,577	621,463	849,040
70	192,187	818,943	1,011,130
71	281,001	836,014	1,117,015
72	260,241	928,404	1,188,645
73	157,890	394,121	552,011
74	374,522	424,277	798,799
75	403,737	491,860	895,597
76	397,209	475,159	872,368
77	312,539	320,711	633,250
78	512,687	394,692	907,379
79	590,533	441,082	1,031,615
80	608,880	465,896	1,074,776
81	704,848	472,465	1,177,313
83	329,492	361,792	691,284
84	334,749	247,525	582,274
85	308,392	318,660	627,052
86	328,338	386,665	715,003
87	501,075	279,872	780,947
88	325,527	194,654	520,181
89	165,061	107,612	272,673
90	88,635	73,983	162,618
91	59,883	52,109	111,992
93	34,355	30,182	64,537
94	7,401	28,134	35,535

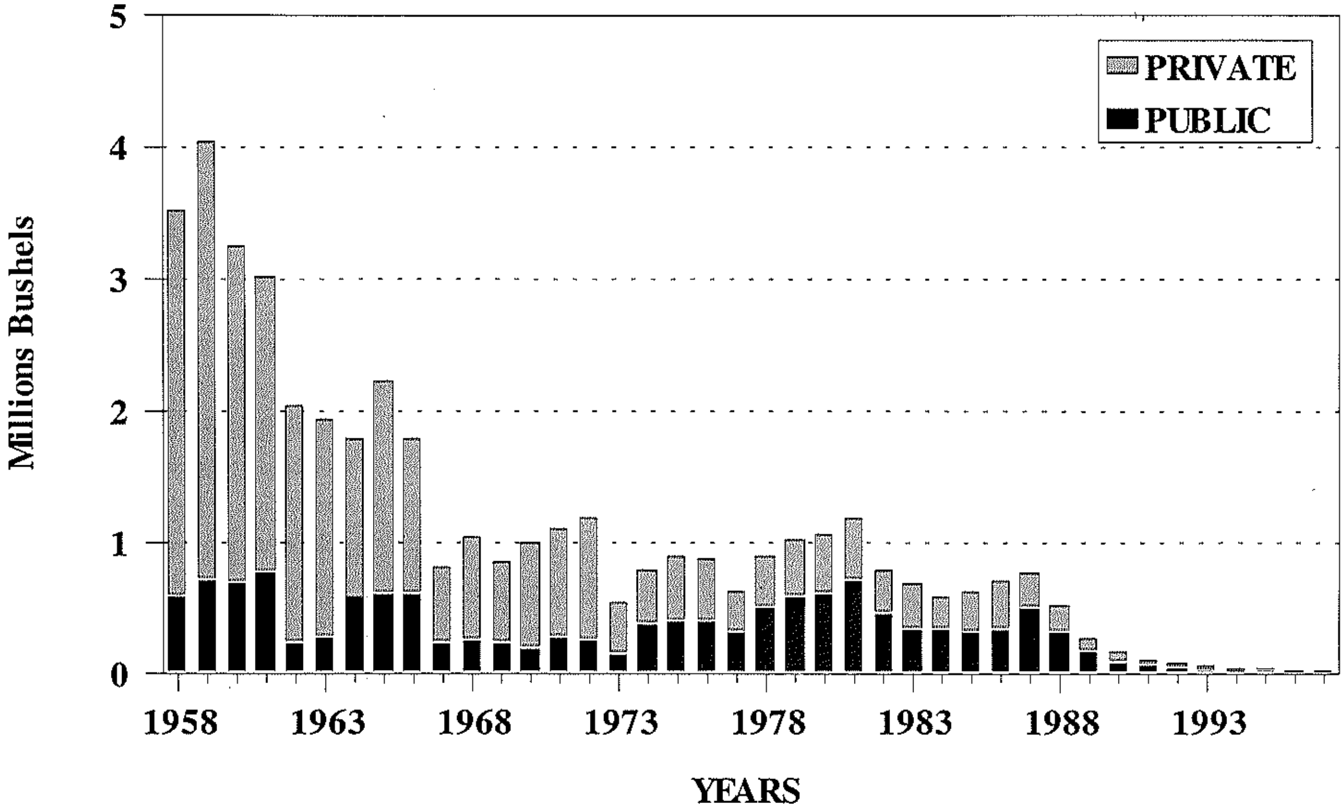

Figure 1. Oyster ground production, public and private.

River continues to exhibit limited annual recruitment, but that in the lower Rappahannock River is sparse to absent. We lack current knowledge of brood stock genetic diversity, and must contend with the possibility that this may have been reduced by the major decrease in population size over the past three decades. Successful spawning may be limited by low extant densities of reproductive oysters in many locations. Disease prevalence and intensity remains weather driven and unpredictable. Political pressures impeding scientific and long-term management are still strong. All of these factors combine to make the substantial ten year recovery goal extremely difficult to achieve.

Stock Assessment

The first recommendation of the Blue Ribbon Oyster Panel called for the establishment of a computer database system and fishery independent stock assessment methods to monitor both population trends and the success of replenishment efforts. Both VMRC and the Virginia Institute of Marine Science (VIMS) have monitored Virginia's oyster resources for many years with dredge surveys. These surveys provided qualitative information that Virginia's oyster population levels were closely reflected by landing records. In 1993, a patent tong based stock assessment project was funded by the Chesapeake Bay Stock Assessment Committee (CBSAC) and was begun in the James and Rappahannock Rivers. The project was repeated in 1994 for the James and Rappahannock Rivers with the addition of areas on the Seaside of the Eastern Shore. Standing stock estimates are now available for all of these areas. As we have suspected from dredge surveys, except for a small area of the upper James River, standing stocks of oysters in Virginia's portion of the Chesapeake Bay are at low levels. In the small area of the upper James, several oyster bars are still relatively healthy, and exhibited a small increase in the standing stocks from 1993 - 1994 in this area. Fishery independent quantitative stock assessment of the historically important

Table 2. Changes in Virginia Harvesting Regulations, 5/3/95.

	1992	1993	1994
Chesapeake Bay			
Daily Time Limit	None	12:00 noon	CLOSED
Season Limits	Oct 1 - Mar 31	Oct 15 - Dec 31	
Tong Limits	None	18'	
Cull Law	3" mkt, 4 qts shell	3" mkt, 4 qts shell	
Quota	None	None	
James River			
Daily Time Limit	None	12:00 noon	12:00 noon
Season Limit	Oct 1 - May 31	Oct 15 - Apr 30	Oct 1 - Apr 30
Tong Limit	None	18'	18'
Cull Law	mkt 2-1/2", 4 qts shell seed no size, 10 qts shell	mkt 3", 4 qts shell seed no size, 6 qts shell	mkt 3", 4 qts shell seed no size, 6 qts shell
Quota	None	mkt 6,000 bu. seed 80,000 bu.	*seed 120,000 bu.
Seaside, Eastern Shore			
Daily Time limit	None	None	None
Season Limit	Oct 1 - Mar 31	Oct 15 - Mar 31	Oct 1 - Dec 31
Cull Law	No size, 6 qts shell	mkt 3", 4 qts shell seed no size, 6 qts shell	mkt 3", 4 qts shell seed no size, 6 qts shell
Summer Harvest - Private Grounds	Allowed	Allowed, permit required	Allowed, permit required

* Originally 80,000 bu, raised to 120,000 bu when quota completed in February

oyster bars throughout Virginia's Bay and tributaries is now effected on an annual basis as a joint VMRC-VIMS program. This stock assessment method is invaluable for making rational management decisions; however, employing the resultant data in the management process has required a significant continuing effort to explain the employed methods and their statistical basis to both the oyster industry and the regulatory body, the VMRC itself.

Harvest Restrictions

The most dramatic and potentially most productive restoration activity in Virginia has been the closure of most the Chesapeake Bay to harvest and the restriction of harvesting in the remaining areas. Many of these restrictions were implemented directly in response to recommendations of the Blue Ribbon Oyster Panel; however, others were added due to the low natural recruitment in 1993 and 1994, and the low standing stocks observed in the patent tong survey. Prior to the 1993 oyster harvest season, harvesting regulations were promulgated that implemented a 12:00 noon daily time limit, 18 ft (5.45 m) hand tong limit, an increase in the minimum size for market oysters from 2.5 inches (62.5 mm) to 3 inches (76 mm) maximum dimension, reduction in shell tolerance for harvests, shortened seasons, and harvest quotas (Table 2). The most significant conservation measure was the 12:00 noon daily time limit along with a reduction by half of the season length (October 15 - December 31) for the Chesapeake Bay. Season length remained from October through April in the James River; however, a 6,000 bushel market oyster and 80,000 bushel seed oyster quota was set. On the Seaside of the Eastern Shore, a 3 inch (76 mm) cull limit was implemented for the first time on market oysters, in addition to some controls on the summer harvests of oysters.

At the completion of the 1993 - 1994 oyster season, neither market nor seed quotas were reached in the James River, only 361 bushels of oysters were harvested in all other areas of Virginia's Chesapeake Bay, and less than 1600 bushels of oysters were harvested on all of the Seaside of the Eastern Shore. Harvest restrictions were, therefore, tightened further for 1994-1995. Quotas were maintained in the James River. The harvest season length on Seaside was shortened and ended on December 31 instead of March 31. For the first time, market harvest on all other public grounds in the Chesapeake Bay were closed. There was very little natural spat set (recruitment) in 1993 and 1994. Greater than normal rainfall levels in 1993 and 1994 reduced disease related mortality and allowed excellent survival of the 1992 year class of recruits. The 1994-1995 harvest closure protected this critically important component of the population so that it was available to spawn in the summer of 1995. Had this timely closure not occurred the size of the spawning stock would have been depleted with negative implications for the ability of the resource to recover in a timely manner. Long-term rehabilitation is and probably will continue to be challenged by industry and its political supporters to open the harvest season to take advantage of a single, large years classes when they occur. Such pressure must be resisted when there remains no evidence of significant recovery in all year classes towards the previously described long term goal.

Re-evaluating Shell Placement and Seed Transplanting

The Blue Ribbon Oyster Panel recommended reexamination of past replenishment strategies and evaluation of the cost-benefit ratio of future projects. Replenishment programs in Virginia over the past 35 years have focused on moving shell and transplanting seed oysters to enhance harvest. Watermen have always been employed in Virginia to harvest and transplant seed oysters. The transplanted oysters were usually available for harvest the same year. The program had notable deficiencies. Little attention was directed to the probability of disease transfer with transplant of seed oysters. Such transfers undoubtedly occurred because the best seed producing areas were the higher salinity areas which had the highest disease incidence. In addition, almost all of the shell planting efforts have been directed towards the questionable practice of creating new oyster bars rather than towards the maintenance of the natural oyster bars of the state. Most natural oyster bars are maintained by the hydrodynamic and bottom characteristics of their unique location (see Hargis 1999, Kennedy and Sanford, 1999, Chapters 1 and 2, this volume). By contrast it is usually very difficult and expensive to build and maintain new bars in areas where oysters are not naturally present.

The movement of seed oysters is expensive and has a high financial risk caused by fluctuating disease prevalence and unpredictable freshwater events. Seed oyster movement is very complicated in that oysters produce the greatest and most dependable spat sets in moderate to

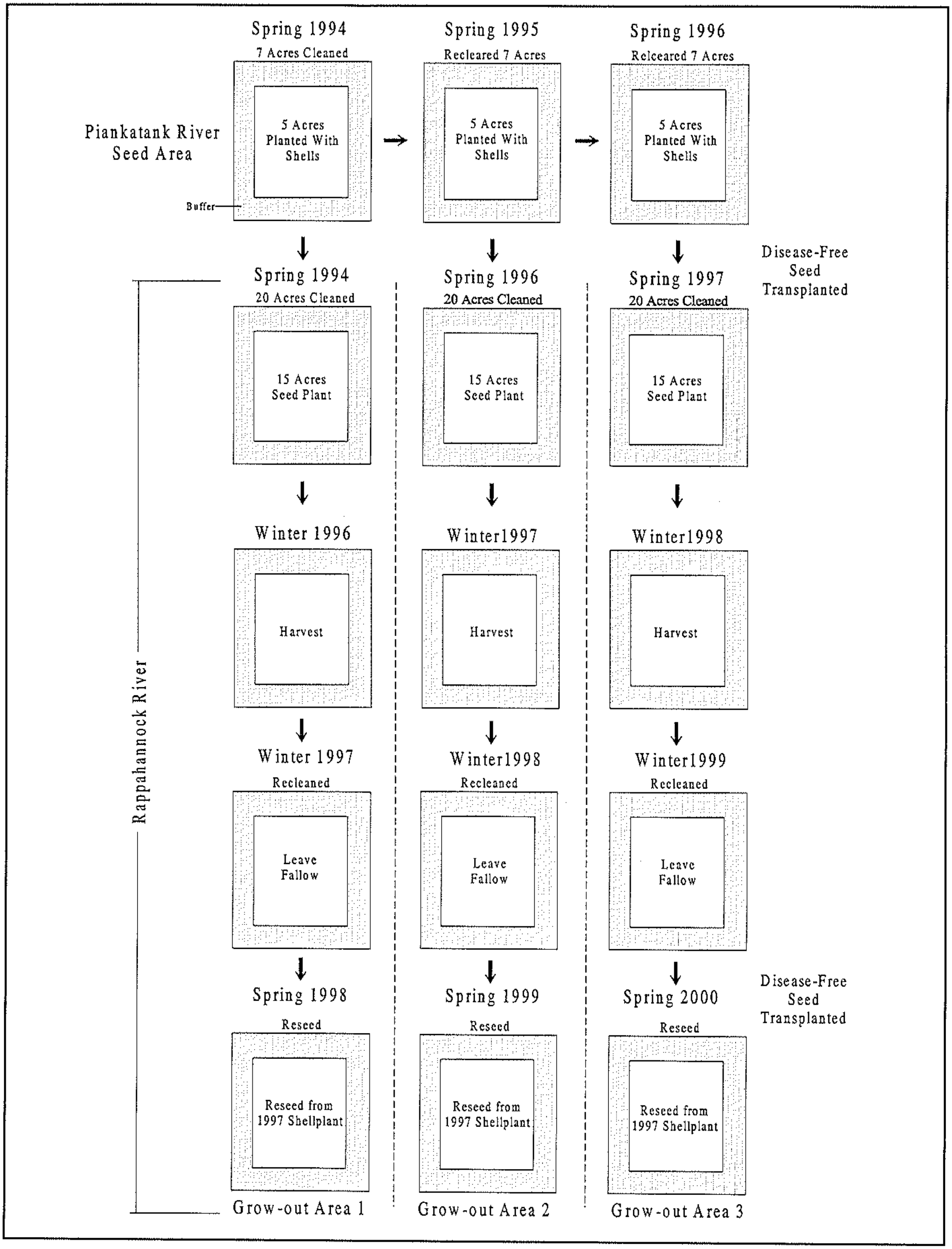

Figure 2. *Protocols and design for seed planting and harvest schedule for Piankatank and Rappahannock Rivers.*

high salinity waters but disease inhibits these oysters from reaching market size. If such seed is moved from the high salinity areas to lower salinity areas with attending lower disease pressure, the seed grows very slowly and is vulnerable to freshwater related mortality. In 1994 and 1995, the replenishment program in Virginia received two Oyster Disease Research Grants from the National Oceanic and Atmospheric Administration (NOAA) Office of Sea Grant to develop and test protocols that can use the advantages of higher salinity for spat set and oyster growth, while at the same time reducing the impacts of the oyster disease environment. These protocols have adapted past recommendations from oyster disease scientists by cleaning shell and seed beds prior to any replenishment activity as a method to reduce the impact of resident endemic disease (Fig. 2). The studies are continuing; however, current information demonstrates that removing live oysters and shell from a shell plant area prior to shell planting has resulted in disease-free seed that can be transplanted in the winter of the first year. Seed oysters are subsequently transplanted to other grow-out bed areas that again have been cleaned prior to the seed being placed on the bottom.

Reconstructing Reefs

Researchers have stressed for years the importance of maintaining cultch and reef height on the natural oyster rocks in Virginia (Haven et al. 1978; Hargis and Haven 1999, Chapter 23, this volume); however, their advice was, until recently, never heeded. Two new shell application projects have been directed towards restoring cultch on natural oyster rocks by two strategies. The first project was to lightly sprinkle shells at a rate of 500 - 1000 bushels/acre on the natural oyster rocks in the upper James River. This project began with 250,000 bushels of surf clam (*Spisula solidissima*) shells in 1994. The procedure was controversial with watermen who feared this would result in burial of living oysters; however, results demonstrating greatly improved spat sets (recruitment) on the lightly shelled natural rocks impressed almost all of the antagonists. The cultch on the critically important seed-oyster-producing bars in the James River is extremely thin, generally less than 10 L m^{-2} or a mean shell layer thickness of 2.5 cm when shells were evenly distributed (Wesson and Mann, unpublished data), and the addition of clean cultch more than doubled the natural spat set on almost all of the areas that were subjected to shell application.

The second project was carried out on the Seaside of the Eastern Shore, where cultch on many of the natural intertidal oyster bars is at low density or absent. The reef footprint and contour still exists; however, the bottom is barren of shell. In 1993, the replenishment program began concentrating shell restoration efforts on areas with almost no cultch or live oysters on bars which appeared to have the correct bottom contour. Concurrently, a hydraulic excavating machine was adapted to turnover and exhume shell of former oyster reefs when a layer of sand or sediment had covered the shells. Results of shell planting and hydraulic excavation have been very successful when proper elevation in relation to tidal height is achieved. Most disturbingly, it appears that many, if not all of the natural reefs on Seaside have been harvested to such an extent that they are now below an optimal tidal elevation for natural recruitment and survival. If the reef profiles are too low, neither cultch restoration method will be successful unless the entire reef elevation is raised.

Reef restoration was a major recommendation of Virginia's Blue Ribbon Oyster Panel. In 1994 the Governor of Virginia, George F. Allen, signed the Chesapeake Bay Aquatic Reef Plan and Oyster Fishery Management Plan, both of which call for the creation of 5,000 acres (2,024 hectares) of oyster reef habitat during the next five years. Historical accounts indicate that during colonial times many oyster rocks in Virginia were exposed at low tide, but after years of harvesting most reefs are just "footprints" of former elevations in excess of 1m below mean low water (MLW) (see Hargis 1999, Chapter 1 this volume). Any level of significant reef restoration will therefore be a very substantial reconstruction effort and is likely to be extremely expensive.

In 1993, the VMRC Oyster Replenishment Program began two projects to investigate both the value of reef structures for the survival of the oyster as well as methods by which reefs could be constructed. The first project was in the Piankatank River (Figures 3 and 4), a small coastal plain estuary classified as a "trap-type" estuary (Andrews and Ray 1988) because setting is more intensive and localized due to a circular closed water movement pattern (this is in contrast to the large flushing type rivers like the Rappahannock.). In the "trap type" estuaries, spat settlement has remained relatively high even with the decline in the population of oysters. The 1993 project began with construction of an intertidal oyster reef made entirely from shucked oyster shells. Shells were loaded on barges at shucking houses, moved by tugboat to the Piankatank River, and deployed by water cannon. The reef was constructed parallel with the direction of tidal movement on the footprint of an old oyster reef. Water depths were approximately 2 m at high tide and oyster shells were deployed until visible on the surface. Approximately 207,000 bushels of oyster and clam shells were deployed in a 300 m long by 30 m wide high reef structure in 1.8 - 2.0 m depth that consisted initially of 22 individual intertidal mounds. The Piankatank typically has an 0.5 m tidal range. All 22 mounds were covered at high tide and exposed to some degree at low tide. This reef project had a total cost of $137,908 or $460 per linear meter of reef structure.

Since building reefs with shells which are transported from land

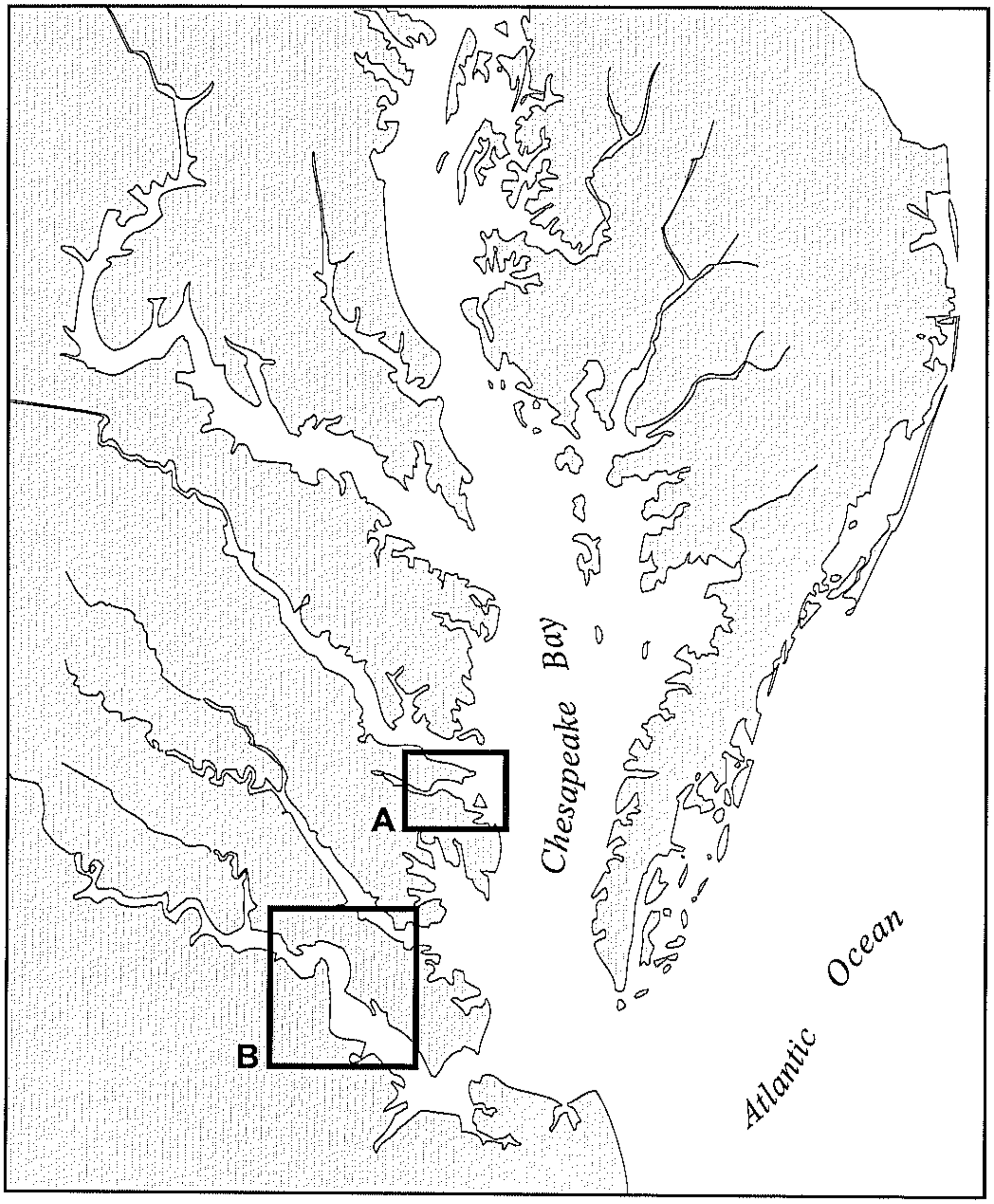

Figure 3. Chesapeake Bay with regions of the Piankatank (A) and James (B) Rivers, indicating reef restoration sites.

appears very expensive for significant restoration efforts, a second construction technique was tested at Wreck Shoals in the James River (Figure 5). At Wreck Shoals, historical bathymetric and oyster survey information was examined to select an area that would have both firm bottom and high buried shell content. Marine construction proposals were then solicited to build, using the bottom substrate, 7,575 linear m (25, 000 linear feet) of 1.2 - 2.0 m tall reef structures in water depths of approximately 3.0 m. Specifications limited the depth that contractors could dig when building the reef structures. Several methods were proposed, and the successful bidder used a clam shell dredge on a barge. Thirteen parallel berms were constructed in a pattern similar to field furrows. The cost for this project was $251,887 or approximately $33/linear meter. After construction, 80,000 bushels of clam shell cultch were spread on the reef area, which covered a total of approximately 50 acres. This increased the final cost to approximately $39/linear meter of reef. This appears to be the most cost effective method of constructing significant amounts of reef structures.

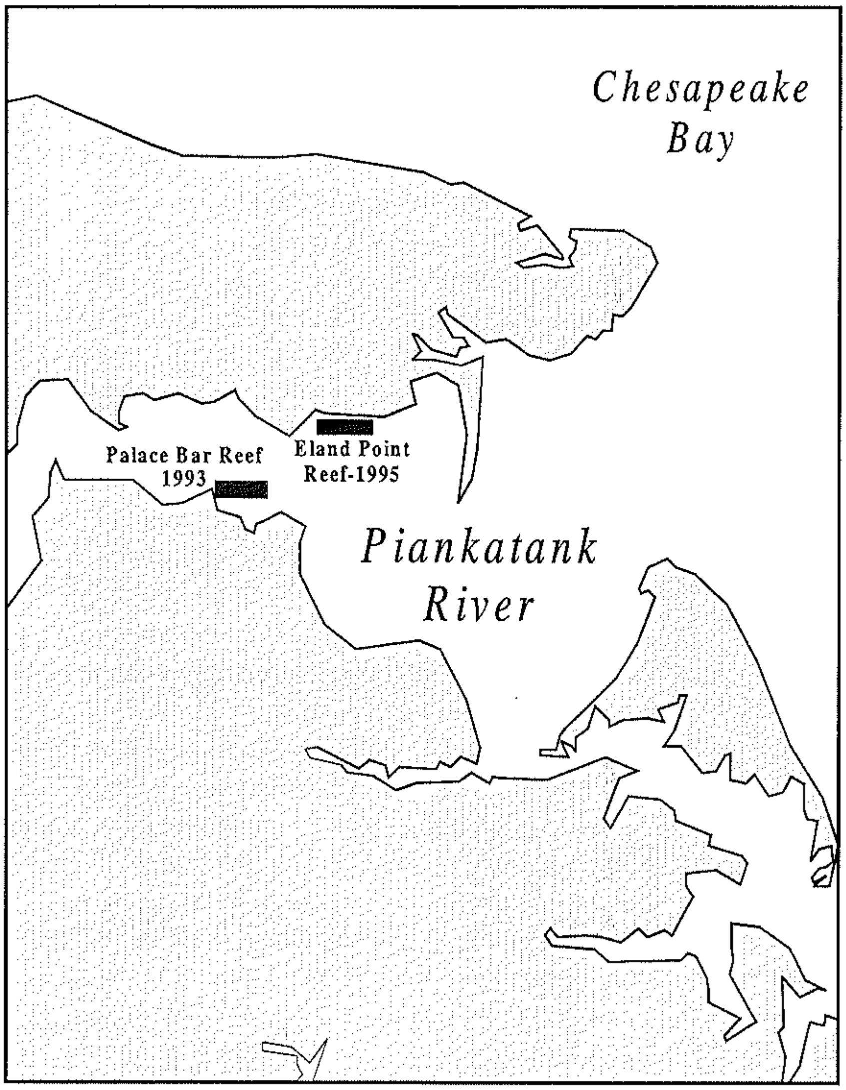

Figure 4. Reef restroation sites in the Piankatank River, Virginia.

Both of the 1993 reef projects were in historic oyster habitat with moderate salinity (15-20 ppt), where modest settlement and recruitment potential still exists, both oyster diseases are present and should give long-term information on disease mortality. Oyster spat sets were light in both areas in the summer of 1993 and 1994; however, small and market oysters are now apparent on both sites. In the fall of 1994 mean oyster density on the Piankatank Reef was five times higher than on the Wreck Shoals Reef. The larger population of oysters on the Piankatank River Reef may have resulted from the greater thickness of oyster cultch which may have increased the survival of the young oysters; however, many differences in the reef sites may have contributed to these differences, including but not limited to reef configuration, substrate material, geographic location, brood stock abundance and water depths. Intensive monitoring continues at both of these sites.

A third reef structure in Virginia was proposed and funded by the Environmental Protection Agency (EPA) Chesapeake Bay Program in 1994. As proposed, the reef would have been constructed on historic oyster bottom in the James River slightly upstream from the Wreck Shoals reef (Figure 5). The method as originally proposed and funded was to use marine construction equipment to build 9,100 linear m (30,000 liner ft) of subtidal oyster reef using bottom substrate. As proposed, the project would have examined the orientation of the reef structure in relation to tidal flow direction by building the reef in a pattern similar to the "spokes of a wheel" radiating from a hub. The project had been through scientific peer review and a successful construction bidding process; however, in May, the approved site and methodology were challenged by local watermen.

As a consequence of this challenge, the project was delayed and a committee of watermen and fisheries managers was appointed to choose a new site and review the methodology. After examining several sites in the James River, the committee chose a site on barren, shifting, sandy bottom, on the public (Baylor) oyster grounds inshore of Rocklanding Channel near Mulberry Point (Figures 3, 5 and 6). In many ways, the committee decision stood in opposition to the principles of the funded project. There were no living oysters on the construction site, although oyster beds were upriver and downriver of the site. The annual records for salinity on the site varied from a minimum of 0 ppt to a maximum of around 12 ppt, but averaged 5 - 10 ppt. Neither Dermo (*Perkinsus marinus*) nor MSX (*Haplosporidium nelsoni*) were suspected to cause mortality in this area; however, oysters were subject to freshets. Tidal currents in the area were high on both ebb and flow. It is not known why the oysters did not exist on this site; but a majority of the committee believed that if substrate was placed at this site in a reef structure, oysters would colonize the reef. The committee also decided to change the construction method. As originally proposed, marine construction equipment would mound bottom materials on site to create the reefs and then cap the structure with shell veneer. The committee recommended the

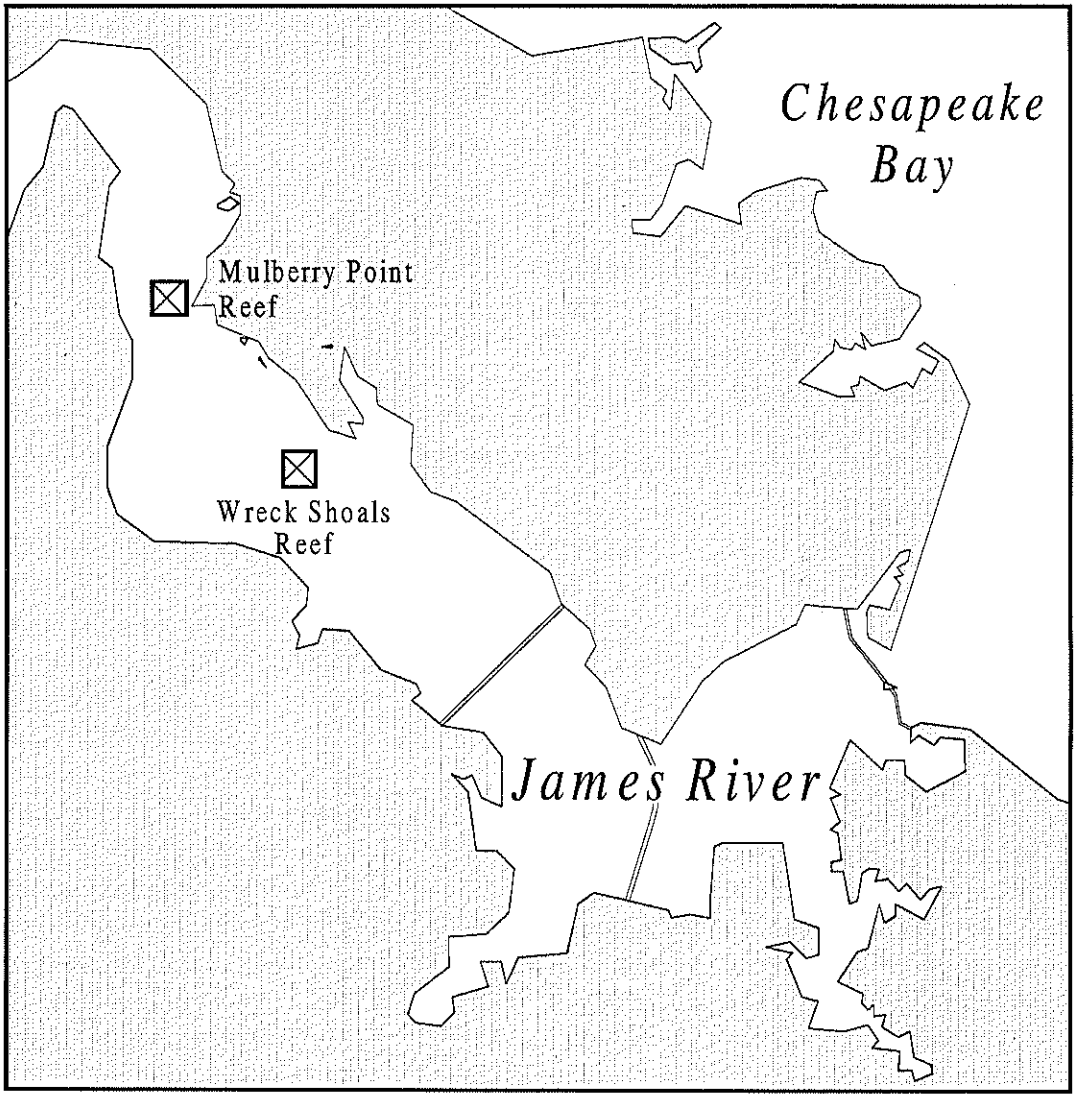

Figure 5. Reef restoration sites in the James River, Virginia.

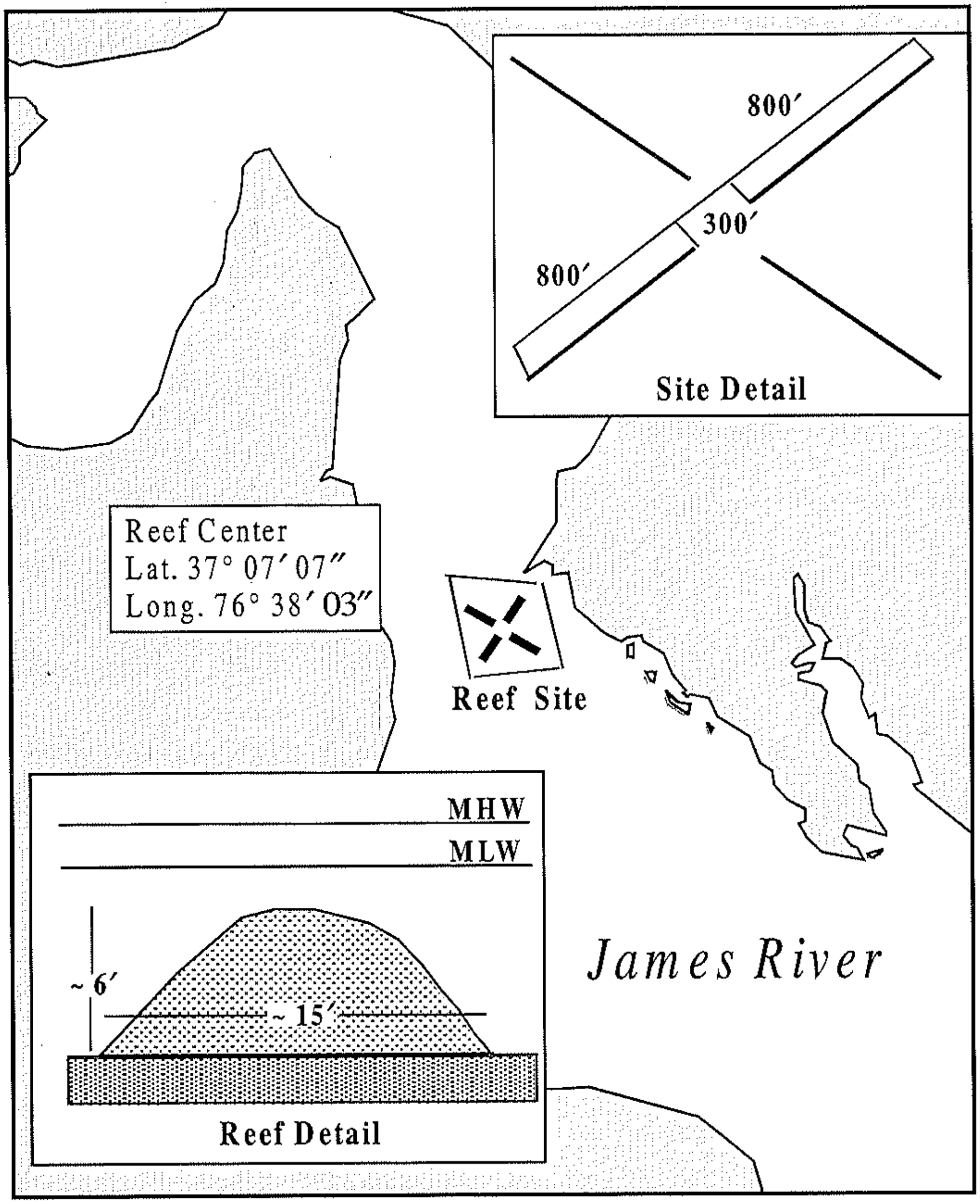

Figure 6. Mulberry Point Reef in the James River, Virginia.

construction of the reef from deployed shell material. Shells would be purchased from oyster and clam houses and come by barge to the site. Since the costs of the shell method was much more than the bottom construction method that was originally proposed, the design of the reef was simplified. Only four lines of reef structure were surveyed and marked for deployment in an orientation where two lines were approximately parallel with the tidal flow and two lines were approximately perpendicular to the tidal flow (Figure 6). Water depths at the site varied from 1.6 - 3.5 m MLW.

Construction began on August 17 and was completed on September 23, 1994. During each deployment of shells, a barge was placed in a parallel position adjacent to one at the lines which had been marked by flags. A spud barge with a crane held the shell barge in place. A water cannon on the shell barge was maneuvered with a "bobcat" loader and shells were washed off one side for the entire 45 m length. Each barge completed 45 - 60 m of mound approximately 2 m tall and 5 - 6 m wide. A total of 920 linear m of structure was completed with lines 1 (255 m) and 4 (255 m) being partially intertidal and line 2 (240 m) and 3 (170 m) being entirely subtidal. A total of 302,390 bushels of shells was placed in reef structures at an average cost of $0.95/bushel or $312.67/linear meter of reef. In recent years, spatfall has occurred in the James River between late July and mid-September. Delay in the site selection process of the new reef resulted in the construction late in the oyster setting season. Thus it was not surprising that very little oyster settlement was observed during the year of construction.

The success of the 1993 effort in the Piankatank River reef encouraged a more supportive political attitude towards reefs in that

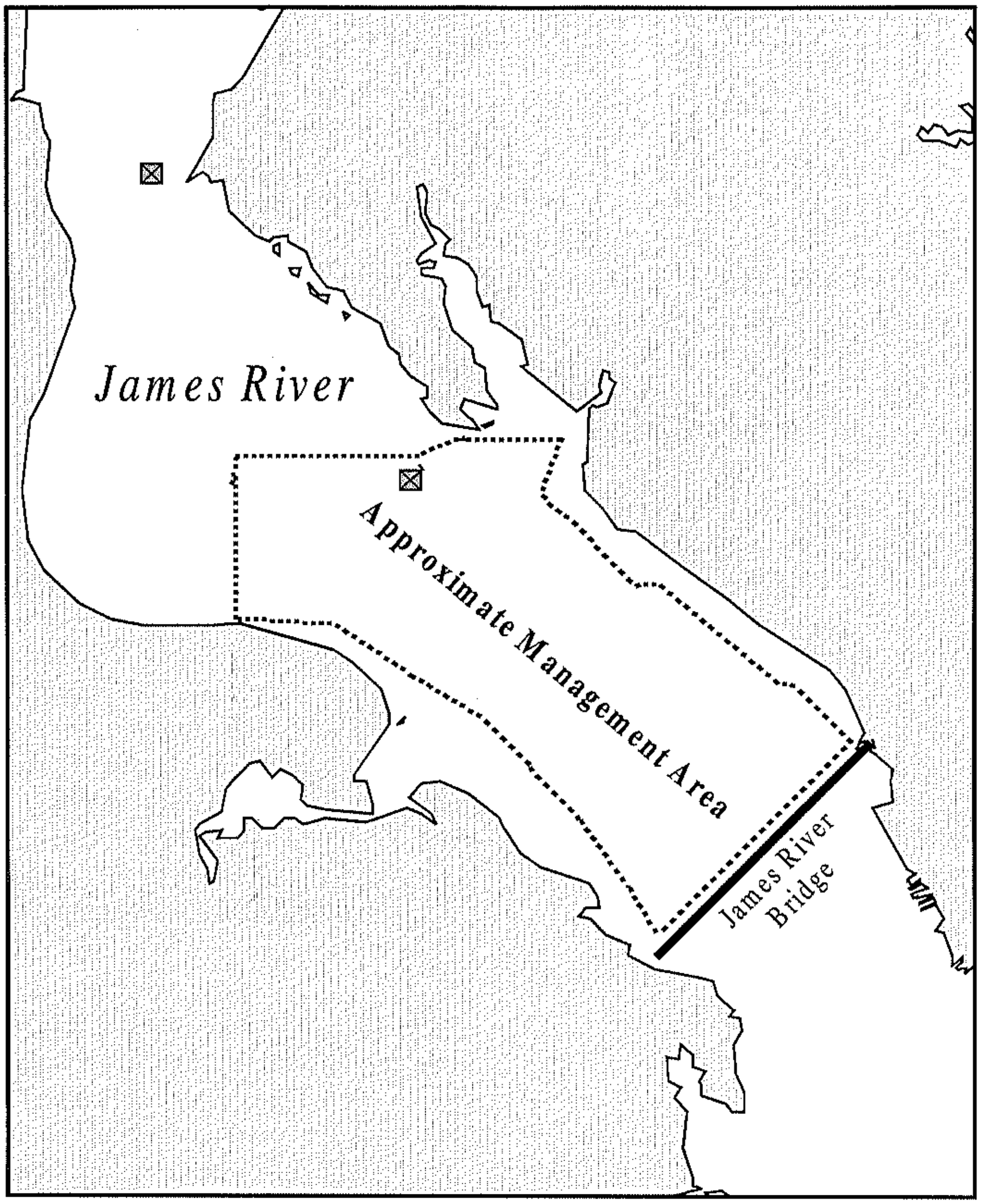

Figure 7. Oyster sanctuary area in the James river, Virginia.

area, and in 1995 another EPA Chesapeake Bay Program Grant project was funded to continue the investigation of created reef habitat in that location. The 1995 grant was for $245,907 for further reef construction using oyster shells. Three reef construction locations (Figure 4) were chosen for the bottom consistency (old shell and hard bottom), and for depths that are 2 - 2.5 m MLW so that the reefs can be mounded to an intertidal height. The recorded oyster spat set in the Piankatank River in 1993 and 1994 were the lowest in the 1977-1994 period. It is possible that broodstock density has reached such a low level that reproductive success in even this type of estuary has been compromised. The objective of the multiple reef project is to investigate the possibility that several thriving reef populations of oysters could, in aggregate, rebuild the spawning capacity of the entire river system.

All reef structures built in Virginia are closed to oyster harvesting and will remain sanctuaries for broodstock restoration. In addition, the Blue Ribbon Oyster Panel recommended setting aside oyster sanctuaries in several river systems throughout the Bay. To date, one large sanctuary in the James River has been designated (Figure 7). Currently, this area has very limited oyster population, and was therefore unimportant to the oyster industry. Restoration of the oyster resource in Virginia, which has been invigorated by the joint efforts of the Blue Ribbon Oyster Plan and by achievable long-term goals set by the Marine Resources Commission, is slowly progressing in a positive direction. Oyster recovery will only be accomplished by the combination of a commitment to long-term management, protection of a stable and growing broodstock population, and by controlling harvest limits to only the small surplus production of a precariously small oyster resource.

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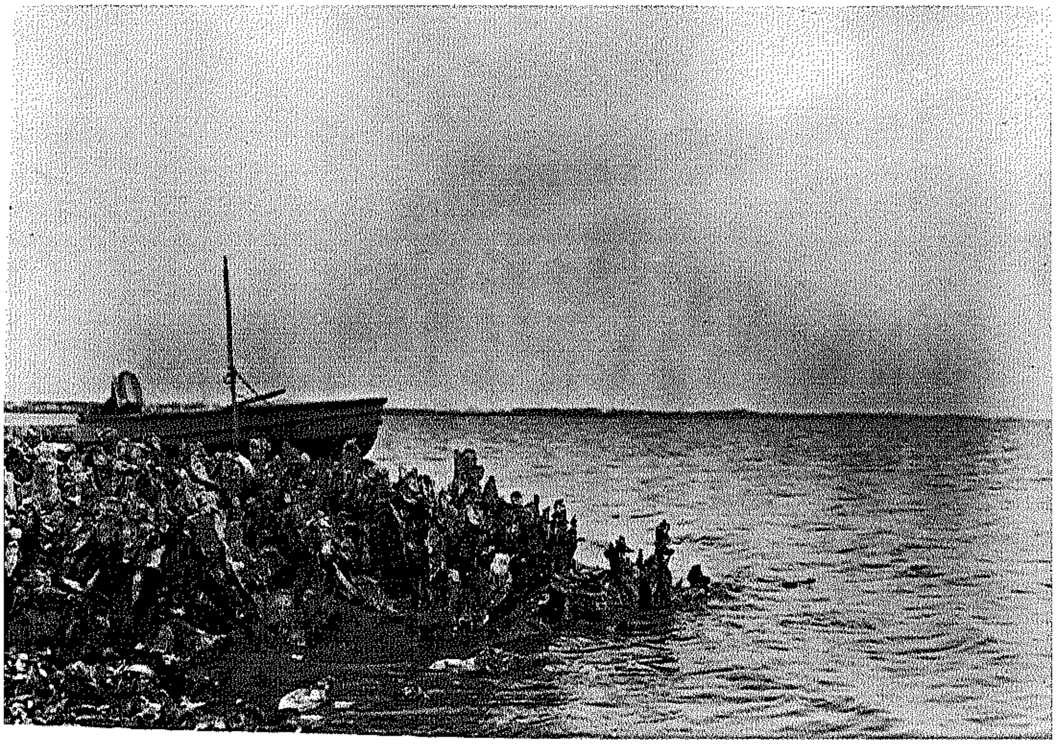
Part III

Reef Morphology and Function--Questions of Scale



Chapter 9

Intertidal Oyster Reef Studies in South Carolina: Design, Sampling and Experimental Focus for Evaluating Habitat Value and Function

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Abstract

In South Carolina, where tidal amplitude is approximately 2 m, over 95% of the oysters grow intertidally rather than subtidally, making them very different from reefs that have received intensive study elsewhere (e.g., Chesapeake Bay). By forming extensive biogenic reefs, *Crassostrea virginica* can be considered a keystone species, often generating the only three-dimensional structural relief, both as living organisms and dead shell on unvegetated soft-bottoms. Whether these intertidal habitats are functionally analogous to submerged aquatic vegetation (SAV) or marsh, especially where SAV nursery habitats are absent (i.e. South Carolina), is an important question. A past focus of oyster research has been directed toward enhancing oyster harvests; however, our understanding of the role of intact reefs on ecosystem function is limited (but see Dame and Libes 1993). Additionally, many states where oysters are commercially harvested, minimally require cultch (shell) replanting; however, no rigorous experimental data presently exist for optimizing shell placement or evaluating the effectiveness of this practice for reef restoration efforts.

Our long-term studies of the oyster ecosystem are designed to: (1) evaluate the utilization of reefs by transient and resident species; (2) examine the tempo and mode of intertidal oyster reef recruitment and succession using rigorous statistical designs; (3) aid in the development of habitat quality criteria; (4) formulate strategies for habitat management of these living resources; and (5) utilize the information to develop restoration and mitigation methodologies. Two study sites were selected, one at a relatively pristine oyster flat, the other at a developed (impacted) area near a marina/condominium complex. Three replicate intertidal experimental reefs per site (each ~24 m^2) have been constructed of 156 subunits. We have now established sampling protocols and developed and conducted efficiency tests for sampling transient and resident faunas associated with experimental and adjacent natural reef substrates. Over the next 4-6 years, we will be following reef development, collecting continuous environmental data and comparing contaminant levels and oyster disease status, along with other life history parameters on both natural and adjacent experimental reefs. By initiating and following the reef development over an extended period, we will be able to explore and model potential changes in reef habitat status and function with reef succession.

Key Words: intertidal; oyster reef; habitat function; habitat quality; management; Southeast; keystone species; *Crassostrea virginica*

Introduction

Historically, the major charge of environmental agencies has been to manage natural resources in order to protect human health and accommodate their continued use (Grumbine 1994). More recently, this objective has been redefined and broadened to include ecosystem health, integrity or natural functioning as an integral part of ecosystem management (Costanza et al. 1992; Grumbine 1994). Unfortunately, this concept is ill-defined and hotly debated among managers and biologists and therefore difficult for resource managers to evaluate, based on available data and simple criteria. Recently Grumbine (1994) has reviewed this issue and provided five specific goals to maintaining ecosystem integrity, including: (1) maintenance of viable populations; (2) ecosystem representation; (3) maintenance of ecological processes; (4) protection of species; and (5) ecosystem evolutionary potential and accommodation of human use, given all of the above. Many of the above goals involve long-range planning and major financial commitments, and agencies generally lack the resources to tackle these complex issues. Additional confusion arises when compromises are sought on how to restore habitats through mitigation in ecosystems where the structural and functional attributes of those habitats are poorly understood (Bohnsack 1991; Bratton 1992).

Estuarine habitats have inherent value beyond their simple consumptive worth, including a variety of direct and indirect ecosystem scale benefits/services and non-consumptive uses (e.g., Reimold et al. 1980; Officer et al. 1982; Anonymous 1994; Grumbine 1994 and references therein). In recent years, researchers and managers have endeavored to understand how various nearshore vegetated and unvegetated habitats contribute to the productivity and health of coastal ecosystems (Ruiz et al. 1993 and references therein). There is an immediate need for this information, as many of these habitats are subjected to extensive anthropogenic perturbations that may seriously restrict their distribution, areal extent (e.g., commercial harvesting, coastal development, Anonymous 1990; Thayer 1992) and natural functioning (e.g., food, shelter, enhanced water quality) provided to local ecosystems (e.g., Smith et al. 1988; Fonseca et al. 1990; Moy and Levin 1991; Bell et al. 1993; Brown-Peterson et al. 1993; Allen et al. 1994). As these habitats become impacted (degraded), the need to understand the influence of environmental stress from pollutants on ecological processes (Farrington 1983; Bayne et al. 1985; Sindermann 1990) and to rank their "value" or importance of critical habitats becomes ever more pressing. For example, we know that seagrasses, salt marshes and macroalgae serve as refuge or nursery habitats for shrimp, crabs, lobsters, fishes, molluscs, and a host of other species (e.g., Tabb et al. 1962; Loesch 1965; Thayer and Stuart 1974; Thayer et al. 1978; Heck and Orth 1980a, 1980b; Heck and Thoman 1984; Zimmerman and Minello 1984; Zimmerman et al. 1984; Marx and Herrnkind 1985; Costello et al. 1986; Herrnkind and Butler 1986; Thomas et al. 1990; Wilson et al. 1990; Coen and Heck 1991; Wenner and Beatty 1992; Garcia-Esquivel and Bricelj 1993; Peterson and Turner 1994; Smith and Abele 1994).

Throughout its extensive geographic range, the American oyster, *Crassostrea virginica*, is unique in its ecological role in that it forms living subtidal and intertidal reef structure in the estuary that supports, in turn, a host of other associated organisms generally not found in surrounding sand or mud habitats (Dame 1979; Bahr and Lanier 1981; Klemanowicz 1985; Stanley and Sellers 1986; Zimmerman et al. 1989; Posey et al. this volume). Oyster reefs can have important direct and indirect effects through their tremendous processing capacity as filter feeders, removing sediments and affecting hydrodynamic flow (e.g., Heck 1987; Haven et al. 1978; Newell 1988; Dame 1993; 1999, Chapter 18, this volume; Dame and Libes 1993; Dame et al. 1984a,b; Harsh and Luckenbach 1999, Chapter 18, this volume) and through the creation of new habitat structure (e.g., Bahr 1974; Dame 1979; Stanley and Sellers 1986; Zimmerman et al. 1989). Recent studies in

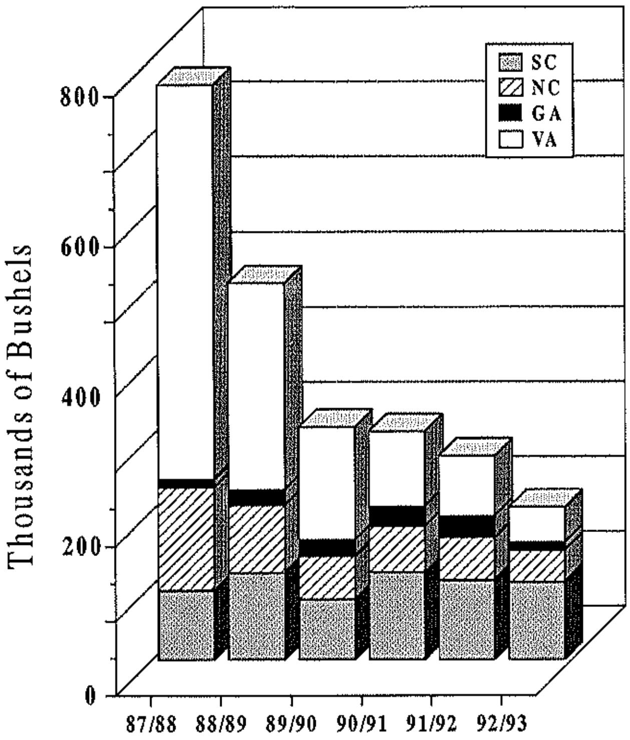


Figure 1. *Oyster landings in thousands of U.S. bushels from 1987-1993 for South and North Carolina, Virginia and Georgia. Note that for 1992-93, South Carolina landings roughly equal the other three states combined. Data from SCDNR Office of Fisheries Management, Shellfish Section, W. Anderson).*

Chesapeake Bay further support the notion that oyster-dominated ecosystems are critical in sustaining overall ecosystem production and natural functioning (e.g., Heck 1987; Newell 1988; Ulanowicz and Tuttle 1992; Gerritsen et al. 1994; Rothschild et al. 1994). Correspondingly, results from bivalve introductions into San Francisco Bay demonstrate how these non-native additions can significantly alter community composition and ecosystem trophic structure (e.g., Carlton et al. 1990; Nichols et al. 1990; Kimmerer et al. 1994).

Human activities, in concert with natural phenomena, have greatly affected the distribution and abundance of oysters in the U.S. In many areas, oyster production has declined precipitously in recent years due to many causes including: (1) diseases, (2) physical disturbance by storms, oyster harvesting or human traffic, (3) over-harvesting, (4) nutrient enrichment through runoff, (5) natural predators, (6) alteration of natural flow regimes and salinity patterns; (7) removal of appropriate habitat for new recruits and (8) cannery closings due to a labor shortage (e.g., Haven et al. 1978; Officer et al. 1982; Stanley and Sellers 1986; Newell 1988; Anonymous 1989; Rothschild et al. 1994; W. Anderson SCDNR pers. comm.). Today, there is essentially no oyster production in Delaware Bay and production from Maryland has drastically decreased. Virginia, once the leading producer of oysters in the United States, now harvests less than 50,000 bu, compared with more than 3 million bu in 1960 (Fig. 1). In fact, in 1992-93 more oysters were harvested in South Carolina than in North Carolina, Georgia and Virginia combined, with nearly 100,000 bu reported (Fig. 1, SCDNR).

In the southeastern U.S. (portions of South Carolina, North Carolina, Georgia and Florida), oyster reefs are a conspicuous feature of the intertidal zone in most estuaries, yet much remains to be studied about how these extensive intertidal habitats (Lunz 1960; Dame 1979; Bahr and Lanier 1981; Stevens 1983) contribute to the broader functioning of the inshore ecosystems in which they occur (cf. Zimmerman et al. 1989 for the Gulf of Mexico). Bahr (1974) and Dame and coworkers (e.g., 1984a,b, 1993 and references therein) have demonstrated convincingly that intertidal oyster reefs contribute both physically and biologically (e.g., nutrient recycling, particle flux and hydrodynamic flow) to ecosystem functioning. In South Carolina, over 95% of the oysters grow intertidally (SCDNR-OFM data) often adjacent to emergent vegetation, with macrotides greater than 1-2 m (see Monbet 1992), making them very different from extensively studied subtidal oyster reefs elsewhere, for example in Chesapeake Bay. Since they form the basis for a structurally complex habitat, *Crassostrea virginica* can in many ways be considered a keystone species (sensu Paine 1966) that dominates these reefs as both living and dead oysters. By forming extensive biogenic intertidal reefs, this species often provides the only three-dimensional structural relief in an otherwise unvegetated, soft-bottom benthos. In areas normally devoid of naturally occurring hard substrate, the many crevices and expansive surface area found within an oyster reef provide the only source of shelter and attachment for numerous small invertebrates (e.g., Dame 1979; Bahr 1974; Klemanowicz 1985; Powell 1994). Although there are no seagrasses in South Carolina, there are abundant salt marshes and intertidal oyster reefs (Lunz 1955, 1960; Collier and McLaughlin 1983, Burrell 1986) in higher salinities. The function and value of SAV and *Spartina*-dominated salt marsh has been the subject of numerous studies (e.g., see above and Thayer et al. 1978; Weinstein 1979; Orth and Van Montfrans 1990; Thomas et al. 1990; Wilson et al. 1990; Kneib 1991; Wenner and Beatty 1992; Peterson and Turner 1994). Whether intertidal oyster reef habitats are functionally analogous to SAV or emergent vegetation, especially where critical SAV nursery habitats are historically absent (i.e. South Carolina and Georgia), is an important question. However, we presently lack sufficient information to determine how oysters, as the keystone species of the reef system (C. B. Jones et al., 1994), function in a broader sense. Interactions between oysters and the various life history stages of reef-associated motile and sessile fauna (e.g., Bahr and Lanier 1981; Osman et al. 1989; Zimmerman et al. 1989; Powell 1994), which may alternate ontogenetically between consumer and prey (e.g., juvenile and adult crustaceans and fishes), are further complicated by the fact that intertidal reefs (often with fringing marsh) vary, both spatially and temporally, in their developmental succession (Bahr and Lanier 1981).

Although intertidal oyster reefs are a prominent habitat in South Carolina, almost nothing is known about how these extensive areas contribute to the broader functioning of the inshore South Carolina waters in which they occur, with the exception of their nutrient cycling and metabolism by Dame's group (1993 and included references). However, information is lacking on the value of oyster reefs as habitats for young and adult fishes, crabs and shrimps, which may be associated with reefs at high and low tide (cf. Weinstein 1979; Zimmerman et al. 1989; Orth and Montfrans 1990; Thomas et al. 1990; Ruiz et al. 1993 for other submerged habitats). Anecdotal data for South Carolina indicate that fishes such as anchovy and silversides are attracted to oyster reefs because of their complex three-dimensional structure, which provide them with a refuge from fish predators (e.g., spotted sea trout and paralichthid flounders). These large predators migrate to oyster reefs on flood tides to feed, as do sheepshead, black drum and red drum, which consume small crabs and shrimp that reside in and around reef structure. Preliminary studies by our group have documented invertebrate densities exceeding 750 macrofaunal individuals/m^2 of reef habitat (Knott and Coen unpublished data). Oyster reefs in high salinity waters are also an important habitat for juveniles of several important fish species such as sheepshead, gag grouper and snapper, as well as stone crabs (Wenner and Stokes 1984; R. Beatty unpublished data). The association of these commercially-important species with oyster reefs further enhances their value as critical habitats in South Carolina's estuaries.

Much of the focus of past research has been directed toward enhancing oyster harvests (e.g., using shell and seed repletion programs). For example, most states that harvest oysters require cultch (shells or artificial substrate) replanting. Nevertheless, to our knowledge, no scientifically defendable data exist on optimizing shell placement or evaluating the efficacy of this historical practice for community restoration (Ulanowicz et al. 1980; MacKenzie 1983; Abbe 1988; Haven et al. 1978; Brodtmann 1991, Lenihan, 1996). Anecdotally, there is some notion that oyster shell alone may not support an associated reef fauna that is functionally equivalent to one with live oysters (Puffer and Emerson 1953; Arve 1960; Bahr 1974; also see Bohnsack 1991 for other artificial reefs).

In summary, the research described here will address critical habitat restoration issues relating to: (1) whether these extensive intertidal oyster reefs play a critical role in the surrounding ecosystems and hence, may be viewed as a keystone habitat, and (2) whether oyster reefs are analogous to other structured (vegetated) habitats, that may act as juvenile or nursery habitats. Integral to the study's goals is the development of a conceptual model of intertidal reef functioning. Intertidal oyster reefs may similarly have an analogous function as a prey refuge, especially in the southeastern United States, where little or no SAV occurs (Archambault et al. 1990; Orth and van Montfrans 1990; Wilson et al. 1990, Ruiz et al. 1993; R. Beatty unpublished data). Rigorous experimental data to address these basic and applied questions are currently not available, but they must be developed before we can hope to decipher the relationship between habitat quality (or health) and fisheries production. Details of the design and data collection procedures, along with some preliminary results are presented in this chapter in the hope that they can serve as a framework for the design and implementation of management strategies.

CURRENT RESEARCH AND MANAGEMENT FOCUSES

The mission of the South Carolina Department of Natural Resources (SCDNR) has recently been broadened to include advocacy for and stewardship of all of the state's natural resources. That responsibility encompasses development of policies and programs for conservation, management, utilization and protection based on sound resource assessment, monitoring and research. DNR's Marine Resources Division (MRD) is responsible for the state's marine resources and includes its Marine Resources Research Institute (MRRI) and Office of Fisheries Management (OFM).

Currently OFM is involved in oyster management/research through: (1) use of the department's R/V Oyster Catcher II, a unique intertidal mechanical harvester for relay and resource assessment (Collier and McLaughlin 1983; Klemanowicz 1985; Burrell et al. 1991; Coen 1995); (2) development of an interactive Geographic Information System (GIS) for mapping the location of intertidal oyster resources throughout South Carolina, incorporating oyster resource, with other land use/environmental data; (3) monitoring of shell planting/cultivation (including technology transfer); and (4) commercial/aquaculture permitting and leases.

At the SCDNR's MRRI we have recently (since 1994) undertaken a 6 year multidisciplinary research program that is designed to generate experimentally-derived data to aid in: (1) evaluating the utilization of oyster reefs by important estuarine species; (2) examining the rate and timing of intertidal oyster reef recruitment and succession (cf. Bell et al. 1991); (3) the development of habitat quality indices for oyster reefs and other estuarine systems; and (4) assessing and recommending measures for current and future habitat management programs governing these living marine resources, including development of restoration and mitigation plans (cf. Thayer 1992).

The primary objective of this research is to determine whether intertidal oyster reefs function as critical or nursery habitats in coastal ecosystems in the southeastern United States. Our focus will be intertidal reefs, a dominant southeast habitat, although some of our results may have applications for subtidal systems elsewhere in the U.S. Another major objective is to evaluate empirically how oyster reefs function within their respective ecosystems and how observed habitat quality affects reef function. We will accomplish this by examining experimental oyster reefs established at sites that differ in habitat quality. Currently, the South Carolina Marine Resources Division has extensive GIS information on oyster resources and MRRI already has baseline physical and biological data from nearby sites (e.g., EMAP, Charleston Harbor Project). This database will provide useful information for making critical decisions on habitat value, provided information exists on how these habitats function.

Our research poses several general questions that are relevant in determining nursery habitat value: (1) Are intertidal oyster reefs functional analogues of SAV or emergent vegetation, in that they support diverse and productive communities? (2) In areas where SAV is absent, do oyster reefs have enhanced value beyond a harvestable resource? (3) Are food and structure the critical parameters in assessing comparative habitat value? (4) Do reefs from developed (or impacted) areas function in the same manner as those in undeveloped environments? (5) Is reef function affected by exposure to pollution despite the continued existence of intact reef structure? (6) Can we predict these differences *a priori* using either environmental or faunal (epifaunal or infaunal) census data? By addressing these sorts of questions we can begin to understand, rank and protect these resources. This work as part of a multi-year program is designed to allow adequate time for placement, recruitment of oyster spat and development of replicate oyster reefs at the experimental sites, the evaluation of intra- and inter-year variation in reef development and inhabitants and assessment of oyster population dynamics and effects of habitat quality through analysis of disease and reproductive success. We will develop a conceptual model of oyster reef function at developed (impacted) and undeveloped reference sites, synthesizing empirical data generated on overall oyster reef population and community parameters.

Procedures/Methodologies/ Questions

STUDY SITES AND REEF FABRICATION

To standardize site characteristics we attempted to choose areas with similar salinity regimes, bed grades, base sediments, wave disturbance, adjacent oyster communities and intertidal heights. We selected two sites, one from a developed (or impacted) area and one from a more pristine, control (or reference) area to evaluate experimentally how oyster reefs function within their respective ecosystems and how observed habitat quality parameters may affect observed reef function. We have operationally defined developed to include sites with significant anthropogenic input adjacent to heavy industry, shipyards, marinas, those with chronic low D.O. and/or demonstrated elevated contaminant levels.

Our experimental design consists of the two sites, each with three replicate experimental reefs (Figs. 2A & 2B). The two sites chosen were Toler's Cove Marina and Inlet Creek. The reefs are 24 m^2, approximately the size of a natural oyster reef in these areas. This size is adequate for the number of samples necessary (156 subunits, Fig. 2B) to assess how reef development (or community structure) influences associated invertebrate and vertebrate communities over the long-term period of this study (perhaps 6 yrs). Three paired experimental and natural reefs were located within each site (see Fig. 2A). A minimum distance of approximately 5 m was maintained between the reefs to reduce disturbance from adjacent reef sampling (e.g., transient fauna collections). The six intertidal experimental oyster reefs were constructed in October, 1994. Overall, our reef design utilized over 8.66 tons of material (shell and trays), using 936 perforated plastic trays filled with washed oyster shell. The trays (0.46 x 0.31 x 0.11 m, Fig. 2B) were lined with 1.3 mm fiberglass window screening to retain resident macrofauna during retrieval. Trays were filled with oyster shell (approx. 8 kg each) to a standard height of approximately 0.11 m. Trays (=quadrats) provided initial support to the reef and were used in numbers sufficient to avoid repeated sampling and disturbance of areas sampled previously. Utilizing standard-sized quadrats to form the reef allows replicate sampling of resident fauna over time. Thus, sampling over extended periods (years) will not disturb an excessive portion of established total reef area (see reviews by Connell and Keough 1985, Sousa 1985).

Historically, much of our understanding of oysters has been derived from invoking likely explanations of field observations. Since numerous alternative scenarios are possible, this process is often referred to as "weak inference" (Platt 1964). Alternatively, manipulative experiments are preferable because of the inherent process of prediction. The process whereby clear hypotheses are proposed and valid tests are conducted is similarly referred to as "strong

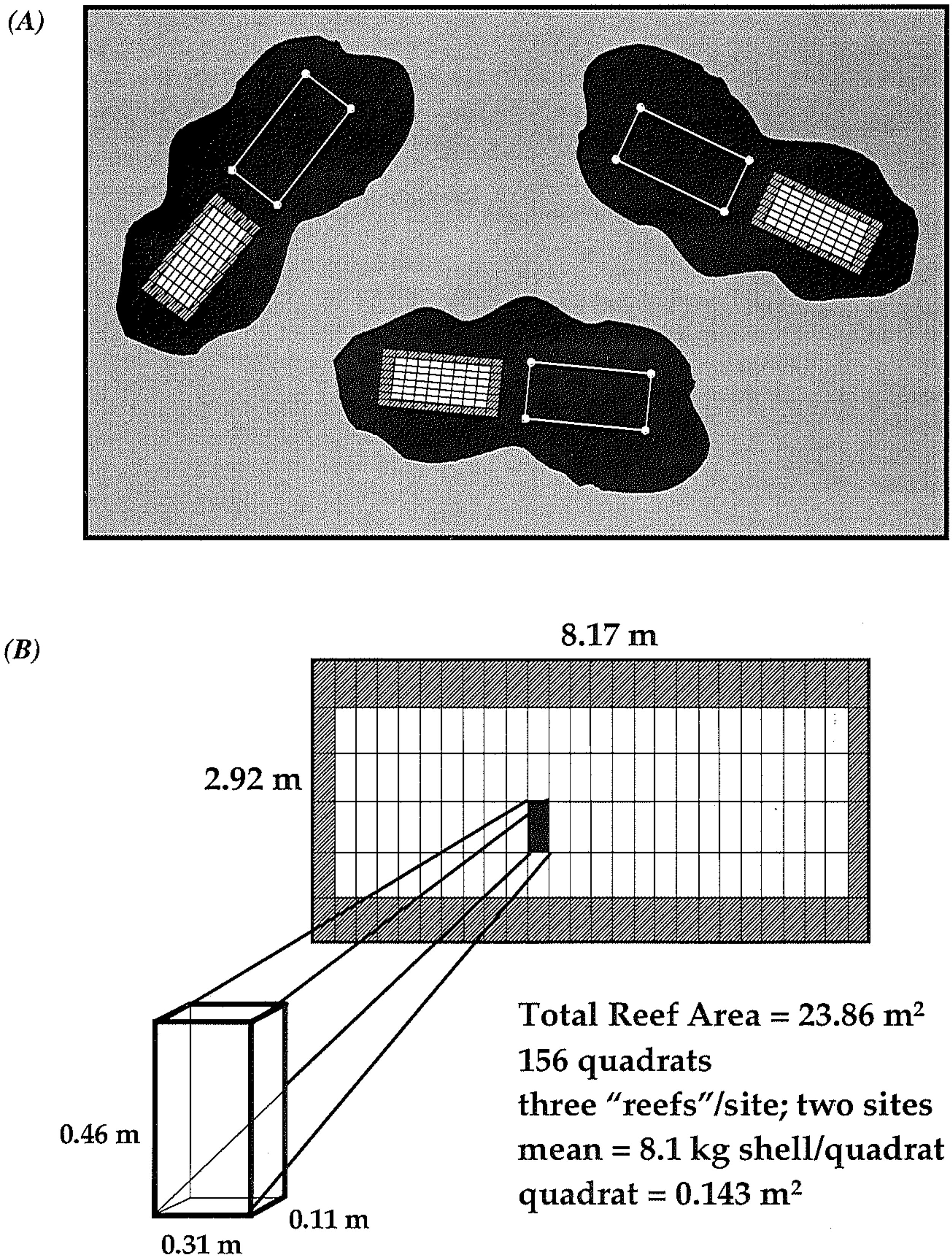


Figure 2. *(A) Layout of experimental and natural reefs at each of the two sites. Paired (n = 3, experimental and natural) reefs are spatially separated, but within the same "mound", reducing disturbance from adjacent reef sampling. Reefs are approximately 24* m^2*, each consisting of 156 subunits. The adjacent natural reef area of identical size is staked only.*
(B) Schematic of a single experimental oyster reef showing pertinent dimensions and other relevant information (total quadrats, mean shell weight/tray, etc.). Shaded peripheral area ("edge") will not be sampled to avoid potential edge effects.

inference" (Platt 1964; Hairston 1989). This rationale is the basis of the research plan described below.

LONG-TERM SITE CHARACTERIZATION: PHYSICAL FACTORS AND CONTAMINANTS

The major questions that will be initially addressed are: (1) Do major differences exist in physical/biological factors between reference (control) and developed sites? and (2) Do these differences correlate with any community, species and population attributes (e.g., oyster reproduction/condition and diseases, larval supply, diversity)?

Environmental Data Collection

In order to characterize the two sites prior to reef fabrication, periodic turbidity and chl *a* samples were taken, beginning at late flood and continuing through the full ebb tidal cycle until the next flood on September 22, 1994 ($n = 2$ per sampling approx. every 2 h). Relative tidal cycle changes (amplitude, time differentials, etc.), currents, depths, and various environmental variables (Dissolved Oxygen [D.O.], salinity, temperature and pH) were sampled every 10 min with a Hydrolab Datasonde 3s™.

Continuous (every 48 min) *in situ* near bottom, subtidal environmental data (D.O., temperature, salinity, pH, depth) using two Hydrolab Datasonde 3s™ and discrete sampling of chl *a* and total seston (modified from Strickland and Parsons 1977) are being conducted to assess potential differences in environmental parameters among sites. Dissolved oxygen (D.O.) for example, is of fundamental importance to fish, shellfish and other aquatic biota. Many estuarine organisms can tolerate short exposures to low D.O. concentrations; however, prolonged exposure to D.O. concentrations less than 60% of saturation may result in reduced growth and reproduction, mortality and altered behavior (e.g., Breitburg 1990). The increasing prevalence of low D.O. concentrations in some estuaries is one of the major symptoms of declining coastal environmental quality (Kuo and Neilson 1987, Stanley and Nixon 1992). Discrete water samples will be taken just above oyster beds at high tide to quantify total seston and chl *a*, as an indirect measure of food quantity (Berg and Newell 1986; Judge et al. 1993).

Contaminants

Oysters are excellent organisms with which to evaluate bioaccumulation of contaminants, because they concentrate metals and some chemicals to several orders of magnitude above ambient levels from surrounding waters and sediments. As sedentary organisms, they integrate chemical pollution in a given area over time (Farrington 1983); however, in wild populations, the ages of the organisms are unknown, and difficulties in interpretation of the data are complicated by variations in gonadal development and reproductive investment. These problems can be circumvented by the use of immature/juvenile pre-reproductive organisms and the deployment of laboratory reared organisms of known age (Phillips 1980, Widdows 1985). Immature organisms are the most appropriate stage to measure contaminants, since accumulation rates are related to age (e.g., Boyden 1974; Ringwood 1991).

Sediment toxicity bioassays will include replicate ($n = 3$) Microtox^{R} solid-phase and pore-water tests on natural sediment cores from the two sites using the luminescent bacteria *Photobacterium phosphoreum* as a test organism (Bulich et al. 1992). These tests have been used for toxicological evaluations in aquatic environments and standard methods have been developed. Sediments will also be screened for selected metals (Cd, Ar, Cr, Cu, Pb, Hg, Al, Zn) and polycyclic or nuclear aromatic hydrocarbons (PAHs) using standard EPA methods. We are especially interested in the potential for leachates from pressure treated lumber (CCA) and TBTs at Toler's Cove Marina (see Wendt et al. 1995, Wendt and Levisen unpublished data).

Concentrations of selected metals (see above), PAHs and pesticides (e.g., DDE, Chlordane, Lindane, Diazinon) will be analyzed to determine if there are differences in contaminant exposures between the reference and developed sites that may explain observed inconsistencies in growth, reef development, habitat quality, etc. Tissues will be examined from pooled oysters (3-4 cm), taken from adjacent wild populations, and also from first year recruits to the experimental reef. To eliminate a potential genetic component, common stock laboratory-reared specific pathogen free (SPF) oysters (Hadley et al., 1996) will also be deployed at each site in June (see below). All samples for analysis will be collected in October (growth, diseases and contaminants).

The accumulation of contaminants in selected organs (e.g., fish livers) by transient and resident fishes and decapods that recruit to the experimental reefs will also be determined in future years. Although it is difficult to interpret data from motile organisms, species that exhibit habitat fidelity (resident species such as gobies or blennies) will be analyzed. Samples of oysters, fish, or shrimp will be homogenized and subsamples will be taken for the various analyses. Tissues for metal concentrations will be digested with nitric acid and analyzed by atomic absorption spectrophotometry. PAHs and pesticides will be extracted from tissue digests and analyzed by gas chromatography.

RECRUITMENT AND COMMUNITY DEVELOPMENT

In the past, most efforts to evaluate intertidal reef communities have focussed on that faunal component which remains within the reef matrix during low tide exposure (Bahr 1974; Bahr and Lanier 1981; Dame 1979; Klemanowicz 1985). Exclusive examination of this portion of the reef fauna (operationally defined here as the **resident** fauna), however, does not completely characterize the organisms associated with the reef during submergence. Rather than ignoring the larger mobile animals (e.g., fishes and decapods) that make transitory use of reefs and often feed on the resident fauna during high tide (hence termed the **transient** fauna), we are employing two different sampling methods that will allow us to adequately quantify these two different faunal components (transients and residents).

This research focuses on the following major questions: (1) Do resident macrofaunal communities on our experimental or natural reefs differ between the developed and reference sites? (2) Are the resident community convergence (or divergence) rates between experimental and natural reefs similar at the two sites? (3) Does the transient (fish and decapod) community change as a function of habitat complexity (i.e. as reefs mature)? and (4) Do transient community species composition and/or abundance patterns differ between the developed (impacted) and control sites?

Resident Fauna

The species composition, density and succession of resident macrofaunal communities on experimental reefs is being monitored and compared between the developed and the control sites, in order to evaluate the functional role of intertidal oyster reefs as sites offering shelter and food. Three quadrats (Fig. 2B) are selected randomly from each of the three experimental reefs at each site bimonthly (total of 9/site). Trays are lifted from the reef during the period of exposure using an elevated scaffold, to avoid disturbing reefs (and sinking in mud). Upon return to the lab, tray contents are then emptied onto a large 0.5 mm mesh sieve for sorting, where shell material is separated and rinsed thoroughly with freshwater, removing all organisms other than firmly attached solitary species (e.g., barnacles, serpulid worms) or encrusting colonial species (e.g., bryozoans). Sieved contents are preserved in 10% buffered formalin with rose bengal and returned to the laboratory for sorting, faunal identification and enumeration. After rinsing, trays with original shell are maintained in running seawater raceways, prior to replacement in their original position within the reef, where they are avoided during future sampling. This maintains reef size and integrity over time for transient faunal use.

During each sampling of experimental reefs, three equivalent samples are also collected from natural reefs, exclusive of the adjacent paired reefs sampled for transients (Fig. 2A) in order to

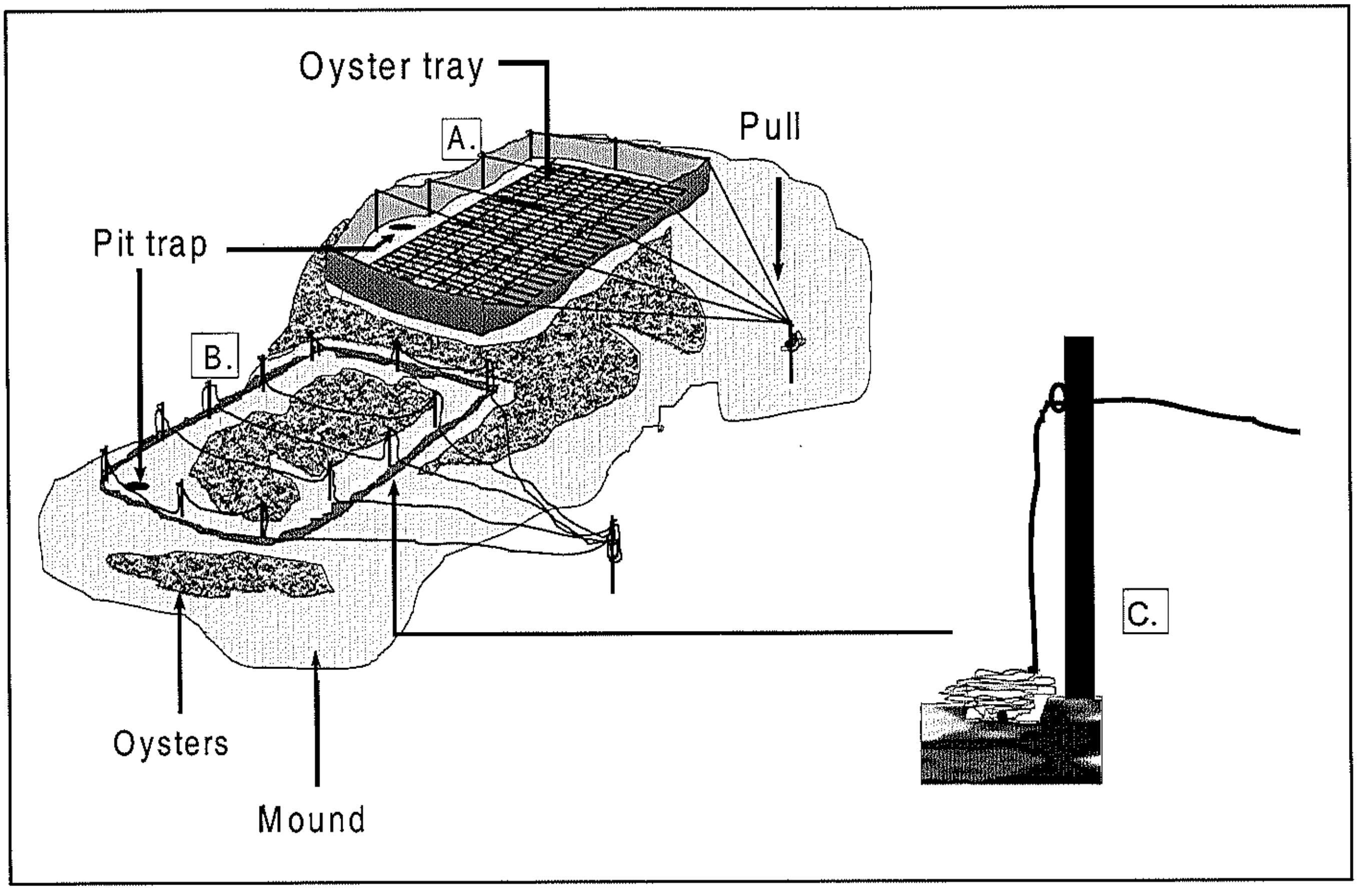


Figure 3. Individual reef mound (three/site) containing a pair (experimental and natural) of reefs. An experimental reef (A) (with the lift net up) and a natural reef (B) (with the lift net prior to triggering). Prior to sampling, the net is folded over the lead line and the buried cable in a shallow trench (C), and covered with sediment. Each of the five pull lines is attached to the top of the net, and threaded through an eye bolt in the pole (see also Wenner et al. 1996).

avoid disturbance and significant depletion over the extended life of this project. Natural reefs will be sampled by placing an identically sized quadrat (reef plastic tray without bottom) at randomly assigned oyster reef locations within each site. All oysters and sediment are then removed to a depth of 11 cm. These samples are then processed as described above.

The above sampling design allows us to compute sample variance estimates among- and within-sites and sampling intervals using nested-ANOVAs. These statistical procedures will be used to test the significance of differences in the abundance and diversity of faunal associates on developed versus control reefs, and they will also facilitate an evaluation of the convergence (or divergence) of the natural and experimental reefs over time.

Transient Macrofauna

To our knowledge, only Bahr (1974), Crabtree and Dean (1982), Powell (1994, diver visual censuses only) and R. Beatty (unpublished data, MRRI) have previously attempted to quantify transient intertidal or shallow subtidal oyster reef macrofauna. Powell (1994) observed numerous pinfish (*Lagodon rhomboides*) and several sheepshead (*Archosargus probatocephalus*) at high tide. Beatty collected 48 fish and decapod species in traps placed on reefs in a polyhaline South Carolina tidal creek, including juvenile gag grouper, sheepshead and various snapper species. Adult and juvenile gobies, blennies and toadfish, and stone crabs (Wenner and Stokes 1984) appear to be somewhat restricted to reef structure. Red drum (*Sciaenops ocellatus*) are also common among reefs during submergence (C. Wenner pers.

comm.). On most southeastern intertidal oyster reefs, negligible visibility (< 10-15 cm) precludes visual censuses (cf. Powell 1994 for North Carolina).

We are quantitatively sampling transient fishes and decapod crustaceans using a modification of the flume-weir described by Kneib (1991). This collection device is particularly effective for non-destructive sampling of large areas of a structurally-complex habitat, and it is an efficient method of determining habitat use by non-resident nekton species. Although Kneib (1991) noted that the use of a flume-weir in habitats with little or no emergent structure could bias results, we expect that our modifications will avoid such bias for several reasons: 1) we will not be installing a permanent boardwalk around the flume netting, thereby avoiding shading of the sampling area; 2) the oyster reef is a structured habitat, so additional submerged structures should not cause excessive avoidance or attraction by nekton; and 3) escapism should be minimized if nets are pulled upwards from a submerged position (hooking on top of each post), rather than as in previously reported flume usage (McIvor and Odum 1986, Wenner and Beatty 1992) where the lead line was lowered. We also employed removable plywood scaffolding to further minimize disturbance during reef sampling.

Our modification (see Fig. 3, Wenner et al. 1996) of Kneib's (1991) flume weir consists of a 3.2 mm (1/8") mesh block net 2.44 m high (supported with ten permanent eye-hooked posts), attached at the base to a fixed buried cable which completely encloses an experimental or adjacent natural oyster reef area. Net panels weighted with chain are fitted snugly and cable-tied to the buried cable residing within a trench surrounding the reef areas to be sampled. Nets are then carefully placed around each reef area at low tide such that they could be raised from a remote station (30-35 m away) at slack high tide. The upper edge of each net is quickly raised by five guide lines and then hooked to perimeter posts. Water-filled collecting pits are excavated in the lowest portion of the enclosure and are used to concentrate and collect most of the nekton as the tide receded. Collection baskets with 3.2 mm (1/8") mesh are placed in each pit and fitted with removable covers. The covers are to avoid creating a deep pit in the sampling site and are removed at slack high tide. After the tide recedes, pits and nets are carefully censused twice by each net crew (total of four) and all organisms collected from the pits (Fig. 3) and the surrounding lower net-sediment margin are preserved in 10% formalin and returned to the lab for enumeration and identification to species. Due to the large numbers of grass shrimp encountered, it is necessary to subsample and estimate the number of *Palaemonetes vulgaris* and *P. pugio*. When the total weight in a sample is less than 60 g wet weight, all individuals are counted and identified. However, when mass exceeded 60 g, 10% by weight are removed, and 50 randomly selected specimens from the 10% subsample are identified to species, enumerated and reweighed. The ratio of number and weight for each species in the subsample to weight of the total sample is used to compute estimates of total number in the sample. Seasonal bimonthly flume collections will be made during spring, summer and fall of each year, the period when transient species make maximum use of salt marsh creeks (e.g., Weinstein 1979).

Because the above sampling method has been used primarily in vegetated intertidal marshes rather than oyster reefs, we tested the efficiency of the method at two paired experimental and natural reefs at Inlet Creek on daytime low tides from March 21-23, 1995. At high slack tide, nets were raised as described above so that each reef was completely surrounded. We then placed 50 mummichogs (*Fundulus heteroclitus*) whose anal fin had been clipped and 50 stained (alcian blue, 1 g/l distilled water, Coen et al. 1982) *Palaemonetes* into each of the netted areas. At the ensuing low tide when all water had drained from the reefs, organisms were collected from each pit trap and the perimeter around the base of each net was carefully censused for any additional animals trapped there. Five paired replicate trials were made for experimental and natural reefs.

OYSTER LIFE HISTORY AND POPULATION PARAMETERS

This research focuses on the following major questions: (1) Are there among- and within-site differences in oyster spat recruitment, post-settlement survivorship or growth? (2) Does habitat quality influence oyster survival or condition (physiological)? (3) Are there differences in specific life history parameters between natural and experimental oyster populations due to habitat quality factors? and (4) Are MSX and Dermo disease patterns observed on experimental and natural reefs at the two sites similar to those observed elsewhere with respect to epidemiology, mortality, etc.?

Oyster Recruitment

In South Carolina, oyster overcrowding in the intertidal, as a consequence of intense spat settlement, rapid growth and resulting competition for space, often leads to clustered formations, consisting of individuals whose growth form is greatly modified within these elongate and densely packed aggregations. In barnacles, this overcrowding condition can often result in significant mortality under certain physical conditions (Barnes and Powell 1950; Bertness 1989). The potential for a similar scenario will be examined on our experimental reefs.

Settlement on larval collectors will be monitored biweekly from April to October each year (with replicate plate replacement) to determine the availability of oyster larvae, and identify settlement peaks at the two sites. Modified replicate collectors for intertidal use on reefs (e.g., Osman et al. 1989; Crosby et al. 1991; Ortega and Sutherland 1992; O'Beirn et al. 1994; O'Beirn et al. 1996) are being employed (3 panels/stand; 3 stands/site). Settlement studies will be repeated each year, since large year to year recruitment variations are typical for southeastern oysters (Ortega and Sutherland 1992). Growth and mortality will also be assessed on experimental reefs using several different oyster "outplanting" strategies (e.g., bags or trays of marked individual oysters).

Growth and Condition Indices

Growth and reproduction represent end-products of metabolism that can only occur when resources exceed basal metabolic needs. Reductions in these potential fitness components can be due to variations in energy resources or adverse environmental conditions that affect metabolic efficiency. Growth rates typically vary within and among sites as a function of environmental conditions, tidal height and related food supply (quantity, chl *a* and quality; Dame et al. 1984; Berg and Newell 1986; Judge et al. 1993), position within the bed and oyster density (see Stanley and Sellers 1986; Ortega and Sutherland 1992; Austin et al. 1993).

Recent studies have indicated that in tidal creeks populated by oysters, oxygen levels commonly fall below 2 mg/l during the summer (observed diurnally during nighttime low tides), but the effects on juvenile oysters are unknown. Reduced growth rates and individual mortality of juveniles under hypoxic and anoxic conditions have been reported (Austin et al. 1993; Baker and Mann 1994, Osman pers. comm.). However some of these studies were conducted under continuously low D.O. conditions and the relevance of periodic (3 to 6 h) exposures to depressed oxygen levels is unknown. Environmental data (see above) collected as part of this study (D.O., salinity, temperature, pH, contaminants, etc.), may provide valuable insights into this problem.

During the first year of study, we will simultaneously collect data on condition indices, reproductive state and sex ratios of natural oysters at the two sites, in conjunction with oyster disease (Dermo and MSX) studies (see below). Monthly samples of 25 (5 x 5 replicate reefs/site) oysters will be collected to determine disease status and epidemiology, physiological condition indices. During the second year, oysters that recruited to the experimental reefs in year 1 will be sampled in addition to those from natural reefs. Each oyster will be scrubbed clean of epibionts and its shell height and whole wet weights will be recorded. Each oyster will be opened and shell and tissue abnormalities noted (Howard and Smith 1983). For condition indices, soft tissue will be removed from each oyster and shell and tissue dried at 60°C for 48 h. Condition index will be determined by the methods of Crosby and Gale (1990) and Rainer and Mann (1992) using the equation: Condition Index (CI) = dry soft body tissue (g) x 1000/ internal shell cavity capacity (g). A qualitative gonadal scoring technique will also be employed (Ringwood 1988).

Specific-pathogen-free (SPF) oysters (20-30 mm) from Marine Resources Research Institute's hatchery-raised stock (Hadley et al. 1996) will be outplanted (early summer) over experimental and natural sites and monitored each year. The rapid growth rates of deployed young oysters will enable an estimation of potential growth rates. Size, tissue weights, and shell weights will be determined. At least 100 juvenile oysters will be place in each replicate bag (n = 4) per reef (experimental and natural) site. Depending on SPF oyster size and availability, we will be examining individuals in bags weekly to biweekly for individual mortality. Disease status will be carefully monitored as described below. Growth rates within and between sites and tidal heights will be measured monthly in the field.

Disease Epidemiology

The oyster pathogens *Perkinsus marinus* and *Haplosporidium nelsoni* (the causative agents of Dermo and MSX, respectively) have recently decimated oyster production (reviewed in Sindermann 1990). Disease virulence usually increases with age, size and exposure duration (Sindermann 1990). We will sample monthly, as above, 25 oysters/site to examine *Haplosporidium* and *Perkinsus* epidemiology among seasons and sites. We will then examine the interaction between physical/environmental factors and diseases as they might be useful indicators of habitat quality and health. We can then generate a long-term database of disease prevalence and infection intensity (Ford and Haskin 1982) tracking oyster diseases in both experimental and natural areas at the two sites. Previously, a relationship has been established between environmental stress (e.g. temperature and salinity) and Dermo and MSX in the northeast (see reviews by Ford and Haskin 1982; Haskin and Ford 1982; Sindermann 1990; O'Beirn et al. 1994). The seasonal epidemiology of MSX in South Carolina remains undetermined, as it has only recently been identified from multiple sites (Bobo et al. 1996, 1997). We will examine whether or not environmental factors such as temperature and salinity are correlated with disease as noted earlier in Delaware and Chesapeake Bays and the Gulf of Mexico (Ford and Haskin 1982; Haskin and Ford 1982; Austin et al. 1993).

Using the monthly oyster samples mentioned above (see Growth and Condition Indices section) we will examine incidence and distribution of these two diseases on natural and experimental reefs at both the control and developed (or impacted) sites (cf. Barber et al. 1988; Crosby and Roberts 1990; Crosby et al. 1991; Fisher et al. 1995; Oliver et al. 1995). Disease occurrence can be evaluated simultaneously with oyster's physiological indices, using techniques outlined by Crosby and Gale (1990). We will also compare disease incidence in outplanted oysters from our hatchery stock to evaluate epidemiological differences between outplanted SPF-oysters and naturally settled oysters.

The prevalence and intensity of *Perkinsus marinus* and *Haplosporidium nelsoni* will be examined following standard methods (Preece 1972, Ford and Haskin 1982; Howard and Smith, 1983, Burrell et al. 1984). The level of infection for *Perkinsus* will be scored for each oyster as a disease code number which ranges from 0 (uninfected) to 6 (heavily infected, Quick and Mackin 1971). Prevalence (the percent infected) and intensity (weighted incidence) of each sample will be calculated. Weighted incidence will be determined after Quick and Mackin (1971), where Weighted Incidence (WI) = sum of disease code numbers/number of oysters. Previous work in South Carolina suggests that infections can be very patchy (Crosby and Roberts 1990; Bobo et al. 1996, 1997).

Haplosporidium nelsoni prevalence will be ascertained by histopathological methods (Preece 1972; Howard and Smith 1983). Histopathology will be used to confirm the presence and location of *H. nelsoni* within oyster tissues.

Preliminary Results and Discussion

STUDY SITES AND REEF FABRICATION

For this project, the two sites chosen were Toler's Cove Marina and Inlet Creek. Toler's Cove Marina is a moderate-sized marina (approx. 138 boat slips) located within a small tidal creek (depths to 3 m). The marina is part of a residential condominium development located adjacent to a heavily traveled roadway over the Ben Sawyer Bridge near Charleston, South Carolina. The marina is bordered by an extensive salt marsh habitat (primarily *Spartina alterniflora*), which is closed to shellfish harvesting. Contaminant and oyster growth data have been previously obtained from this site (Van Dolah et al. 1992; Wendt and Levisen unpublished data) and an adjacent reference creek. In 1989, Wendt and Levisen (unpublished data) found significantly higher sediment levels of TBT, Cu, and Pb and lower D.O. values, at Toler's Cove as compared to a nearby control site. Macrofaunal abundances (mostly polychaetes) were consistently lower at Toler's Cove versus their nearby reference site. The second site selected for our study is a tidal creek site within the upper reaches of Inlet Creek, a relatively pristine control (reference) site with extensive oyster flats, a large marsh buffer (primarily *Spartina alterniflora*) and relatively little adjacent development. The two sites are approximately 3.2 km apart, straight line distance. Both sites, which are located off the Atlantic Intracoastal Waterway (AIW) are dominated by fine sediments (pluff mud), often >75% silt/clay with little or no sand (Wendt and Levisen unpublished data for Toler's Cove).

The two sites were studied prior to reef fabrication on September 22, 1994. The initial measurements for this temporally-limited suite of physical/biological variables suggested that the two sites did not differ substantially from one another. Ebb and flood duration, turbidity, temperature and relative primary productivity (as measured indirectly by chl *a* concentration) were similar. Bottom D.O. values were consistently lower at Toler's (albeit < 2 mg/l D.O.) than at Inlet Creek throughout the day, and salinities converged at the two sites until near low tide, when they diverged somewhat (2-3 ppt). Replicate oyster samples were also taken at the two sites for initial evidence of *Perkinsus marinus* and *Haplosporidium nelsoni* prevalence/intensity (n = 5 from each of 5 distinct mound for a total of 25/sites). No significant differences were noted for *P. marinus* intensity within a site; however, significantly greater mean intensities (P = 0.005) and prevalences (P = 0.008) were detected at Toler's Cove; for *H. nelsoni*, prevalence was greater at Toler's Cove also.

Specific oyster reef flats were chosen for experimental reef construction at each site, based on position, ease of access and an intertidal area sufficient in size to include the experimental reef and an equivalent area naturally populated with oysters. The two areas were spatially separated, so that sampling on one would not disturb the other (see Fig. 2A). Sites were prepared for experimental reef fabrication by removing all oysters/shell from within an area equivalent to reef size (roughly 8.2 x 2.9 m). Corners of the equivalent natural area were staked so that it would not be disturbed. Three replicate reefs were constructed at each site over several weeks in October, 1994.

LONG-TERM SITE CHARACTERIZATION

Shortly after the reefs were constructed, continuous measurement of environmental variables was initiated at the two sites, for comparison of water quality and physical variables (Figs. 4 and 5). Monitoring instruments are now in their 16th week of deployment (with appropriate intervening lab downtime, approximately 2-3 days every 2 weeks), and a considerable database has been developed regarding the hydrographic characteristics of the sites. Comparison of the means (over 6 deployments) of selected water quality variables revealed only minor differences between sites (pH: 7.89 Toler's vs. 7.82 Inlet; Salinity: 28.0 ppt Toler's vs. 28.4 ppt Inlet; Temperature: 13.7°C Toler's vs. 13.4°C Inlet).

Bottom dissolved oxygen (D.O.) levels did not differ significantly between the two sites and were generally high (>70% saturation, often >100%). Minimum D.O. levels may be a more biologically relevant measure of water quality than mean values, and the minimum D.O. recorded during our 48-min sampling intervals remained above 46% (temperature-adjusted saturation) at both sites during the relatively cool months of November through March, 1994-95.

At times, some of the hydrographic parameters were clearly influenced by tidal circulation, as illustrated by the regular variation in salinity shown in Figure 4. Dissolved oxygen also varied with the tides, but in a more complicated manner than salinity. In a pattern that was repeated at both sites during several deployments, D.O. minima and maxima tracked the semi-diurnal tide level very closely for several days (see Fig. 4, Jan 12-17), but this period was followed by an abrupt shift to a diurnal D.O. frequency, with the D.O. maximum coinciding with a late afternoon or evening low tide and the minimum occurring during nighttime low tides.

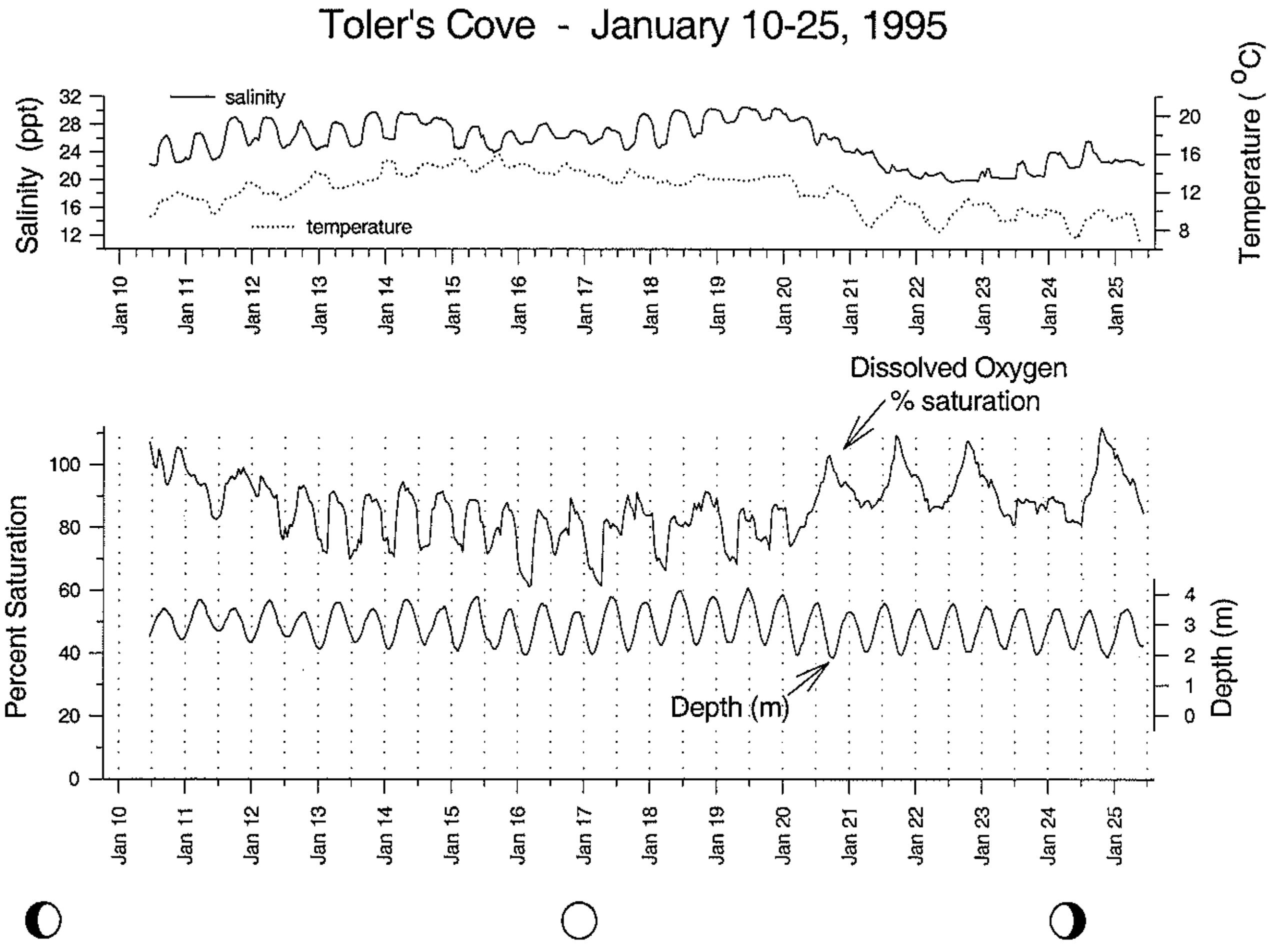


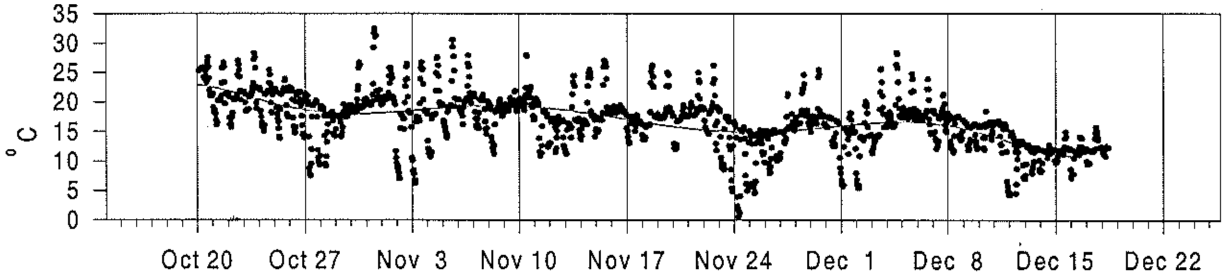
Figure 4. Physical and environmental data recorded every 48 min during a 2-week Hydrolab deployment at Toler's Cove. Salinity, temperature (subsurface) and D.O. (% saturation) are shown, along with relative depth readings that show tidal periodicity.

The causes underlying this shift in periodicity of DO are unknown; however it has also been observed in nearby shallow marsh creeks by Holland and Riekerk (pers. comm.).

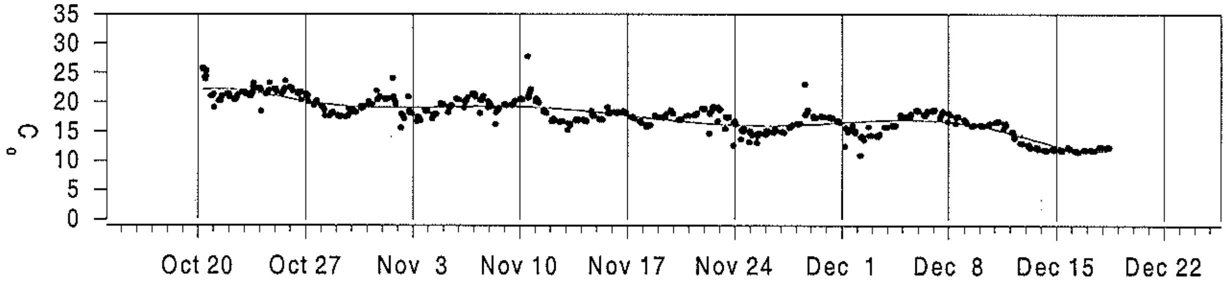
To better assess conditions experienced by organisms that remain on the intertidal oyster reefs during their emergence, we attached additional temperature sensors (Hobo-Temp I sensor/logger from Inset Corp.) directly to one of the experimental reefs at each site. These instruments provided a continuous record of temperature readings with the same 48-min frequency as the subtidal water quality measurements (Fig. 5). Since depth readings made by the Datasonde 3s were not sufficient to determine the actual times of reef emergence, we used predicted tide levels (NOAA) to separate measurements that were made during submergence (Fig. 5b) and exposure (Fig. 5c). Because tidal predictions only roughly estimated tidal height at the sites, we used a conservative approach in constructing the data sets plotted in Figure 5, deleting all records when the predicted level was less than 1.07 m for Figure 5b and deleting those greater than 0.61 m for Figure 5c. With the exception of a few possible misclassifications (Fig. 5b), this analysis clearly shows that the temperature range experienced on the intertidal reefs is considerably more variable (1-32°C) than that which would have been encountered by an exclusively subtidal oyster (12-24°C).

Temperatures at Toler's Cove Reefs - Oct 20 through Dec 18, 1994

(a) Reef Temperatures during Exposure and Submergence



(b) Reef Temperatures during Submergence Only



(c) Reef Temperatures during Exposure Only

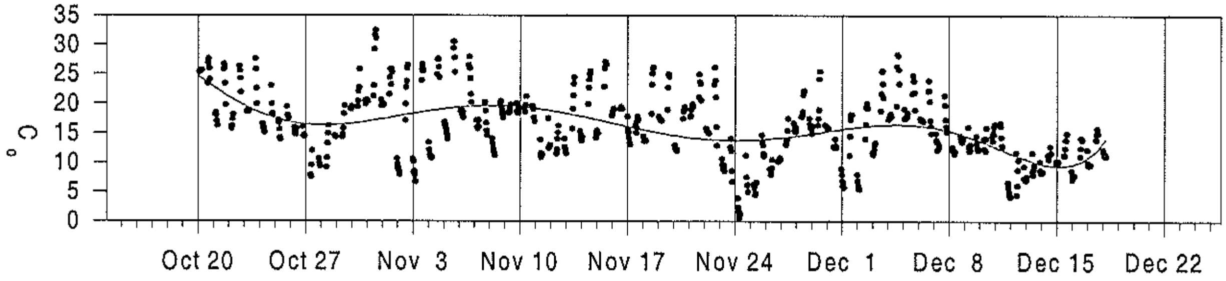


Figure 5. *Two month record of intertidal reef temperatures (48 min intervals) measured by a Hobo™ temperature sensor attached directly to one of the intertidal reef quadrats at Toler's Cove. Note the difference in variability of temperatures encountered during submergence (b) and those experienced by intertidal oysters during periods of exposure (c).*

Table 1. Abundance of resident macrofauna in pilot studies using oyster trays deployed in Clark Sound to test methods (n=2).

	Individuals per Tray					
Duration in Field	71 days		170 days		261 days	
	Mean	StdErr	Mean	StdErr	Mean	StdErr
Nereis succinea	33.5	11.5	45.5	1.5	51.0	2.0
Marphysa sanguinea	-	-	-	-	1.0	1.0
Leitoscoloplos fragilis	-	-	-	-	2.0	0.0
Streblospio benedicti	5.5	4.5	-	-	8.0	2.0
Heteromastus filiformis	-	-	-	-	1.0	1.0
Oligochaeta	4.0	4.0	1.0	0.0	6.5	0.5
Geukensia demissa	-	-	0.5	0.5	-	-
Acarina	2.5	2.5	-	-	0.5	0.5
Cassidinidea lunifrons	-	-	2.0	0.0	-	
Melita nitida	25.5	8.5	32.5	11.5	6.0	2.0
Alpheus heterochaelis	1.5	1.5	-	-	2.0	2.0
Brachyuran megalopae	1.0	1.0	-	-	2.5	2.
Panopeus herbstii	17.5	1.5	12.0	3.0	15.5	0.5
Eurypanopeus depressus	25.0	8.0	16.5	2.5	29.0	1.0
Xanthidae (< 4 mm)	56.5	24.5	71.5	2.5	49.5	19.5
Uca pugnax	-	-	-	-	0.5	0.5
Insecta	-	-	-	-	0.5	0.5
Diptera	2.0	0.0	-	-	0.5	0.5
Mean number of taxa per tray	8.0	1.0	6.5	0.5	11.0	2.0
Mean number of individuals per tray	174.5	61.5	181.5	12.5	176.0	28.0

Such differences in exposure to temperature extremes are likely to have profound effects on intertidal oysters, compared with those oysters on subtidal reefs found elsewhere, with regard to such aspects of oyster condition and health including: (1) reproductive periodicity, (2) disease susceptibility, and (3) response to anthropogenic stress. Environmental factors (e.g., elevated salinity and temperature) have already been shown to increase oyster susceptibility to *Perkinsus marinus* and *Haplosporidium nelsoni* (Burrell et al. 1984; Barber et al. 1988; Gibbons and Chu 1989; Crosby and Roberts 1990; Littlewood and Ford 1990; Sindermann 1990; Austin et al. 1993; Ewart and Ford 1993). Additionally, southeastern intertidal *Crassostrea* races in macrotidal areas (> 2 m) may be physiologically predisposed, through selection, to counter the effects of long periods of exposure and starvation, whereas subtidal populations/ races may be more adversely affected by such environmental extremes.

RECRUITMENT AND COMMUNITY DEVELOPMENT

Resident Fauna

Initial pilot studies with smaller reefs (fabricated with identical materials) at another field site yielded large numbers of recruiting/immigrating invertebrates. Trays deployed in the field for 71-261 days (December to September, 1993-1994) had mean densities of approximately 180 resident organisms per tray composed of on average 6-11 total recognizable taxa (Table 1). Xanthid crabs (primarily *Panopeus herbstii* and *Eurypanopeus depressus*), peracarid crustaceans, and polychaetes dominated the resident recruits. Experimental and natural reefs at the two study sites were sampled for the first time in late March, 1995. These samples have not been enumerated or identified at this time.

Transient Fauna: Flume Efficiency

From March 21-23, 1995 we evaluated the efficiency of sampling transients with the modified flume nets at two paired experimental and natural reefs at Inlet Creek on daytime ebb tides. No significant difference was detected between the mean number of individual *Fundulus* (mummichog) or *Palaemonetes* (grass shrimp) recaptured on natural and experimental reefs (Fig. 6; *t*-test: *Fundulus*, P = 0.37; *Palaemonetes*, P = 0.34). Although not significantly higher, the percent of individuals recaptured was greater on the natural reefs, with 68% of the *Fundulus* and 58% of the *Palaemonetes* recovered. On the experimental reefs, 54% of the *Fundulus* were recovered, while only 44% of the *Palaemonetes* were recovered (Fig. 6). The additional structure created by the trays and complete coverage by oyster shells on experimental reefs undoubtedly provided more refuges and natural depressions (=pits) than the patchy structure on natural reefs, thereby reducing capture efficiency.

Transient Fauna: Censuses

In March we also conducted our first transient sampling trials using flume nets on paired reefs (experimental and natural) at Inlet Creek. Over the course of three days, five replicate runs were made on these paired reefs. Species collected by flume nets on the experimental and natural reefs included ten finfish and seven decapod crustacean species (Table 2). The grass shrimps, *Palaemonetes pugio* and *P. vulgaris*, and juvenile spot, *Leiostomus xanthurus*, numerically dominated collections from both experimental and natural reefs.

Table 2. Abundance of transient decapod crustaceans and fishes inhabiting experimental and natural oyster reefs at Inlet Creek during March 1995 high tide flume net sampling.

	Experimental Reefs		Natural Oyster Reefs	
	n=5		n=5	
Decapoda	Mean	StdErr	Mean	StdErr
Callinectes sapidus	0.8	0.4	1.2	0.6
Palaemonetes vulgaris	463.2	162.4	558.8	245.0
Palaemonetes pugio	461.4	228.7	414.2	119.9
Panopeus herbstii	0.6	0.2	0.4	0.4
Eurypanopeus depressus	0.2	0.2	0.6	0.4
Panopeus obesus	0.2	0.2	–	–
Uca pugilator	0.2	0.2	–	–
Fishes				
Leiostomus xanthurus	24.0	6.2	34.8	7.2
Paralichthys lethostigma	0.4	0.4	0.2	0.2
Brevoortia tyrannus	0.8	0.8	0.6	0.6
Gobiosoma bosci	2.8	1.2	0.8	0.4
Gobionellus boleosoma	0.2	0.2	–	–
Anchoa mitchilli	0.2	0.2	–	–
Cyprinidon variegatus	0.2	0.2	–	–
Fundulus heteroclitus	0.4	0.2	1.0	0.6
Menidia menidia	–	–	0.2	0.2
Menidia beryllina	–	–	0.4	0.4

On the natural reefs, 12 species were collected in aggregate, while on experimental reefs, 15 species were observed (Table 2). Similarity in species composition between samples from control and experimental reefs was examined by calculating a percent similarity index defined as follows:

$$\% \text{ Similarity} = \Sigma_i(\min x_{iC}, x_{iE}) \text{ where:}$$

x_{iC} = percent abundance of species i in pooled samples from the control reefs and

x_{iE} = percent abundance of species i in pooled samples from the experimental reefs.

Overall percent faunal similarity exceeded 92% between experimental and natural reefs. The mud crab *Panopeus obesus*, the fiddler crab *Uca pugilator*, the goby *Gobionellus boleosoma*, the bay anchovy, *Anchoa mitchilli* and the sheepshead minnow, *Cyprinodon* *variegatus* were collected exclusively on the experimental reefs. The silversides, *Menidia menidia* and *Menidia berylina*, were only collected on the natural reefs.

The results, obtained in March represent preliminary sampling of transient reef dwellers.

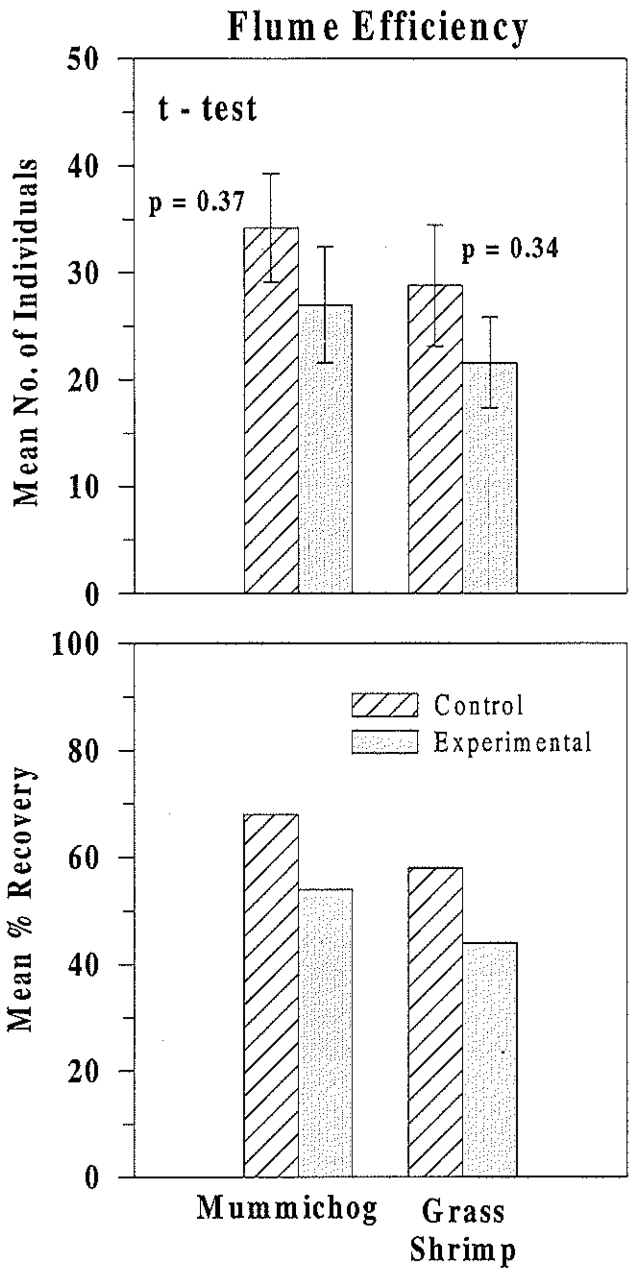


***Figure 6.** Recapture efficiency of flume net sampling of transient reef inhabitants. The study was conducted at two paired experimental and natural reefs at Inlet Creek on March 21-23, 1995. No significant difference was detected between the mean numbers (± 1 S.E.) of individual* Fundulus *or* Palaemonetes *recaptured on the natural and experimental reefs. Percent of individuals recaptured also shown (see methods section for details).*

They are based on a single site, Inlet Creek. Subsequent seasonal sampling on natural and experimental reefs at the two sites will provide quantitative information previously not available for intertidal, or for that matter subtidal, oyster reefs. The above methods and preliminary results (Wenner et al. 1996; Coen et al. unpublished data) indicate that we can quantitatively sample the transient fauna which utilize these important estuarine habitats. This technique provides us with the ability to assess: (1) relative importance of trophic linkages among neighboring habitats (e.g., Randall 1965; Ogden et al. 1973; Heck and Wetstone 1977; Bray et al. 1981; Ambrose and Anderson 1990; Powell 1994); (2) value of intertidal oyster reefs for important estuarine species (thereby promoting their protection, non-consumptive use; Reimold et al. 1980) and; (3) whether oyster reefs are analogous to other structured (vegetated) habitats, that act as juvenile or nursery habitat refugia (cf. Heck and Orth 1980b, Heck and Crowder 1991; Orth et al. 1984; Zimmerman et al. 1989; Ruiz et al. 1993).

OYSTER LIFE HISTORY AND POPULATION PARAMETERS

Disease Epidemiology

Since September 1994, we have been collecting monthly samples of native oysters from Inlet Creek (control) and Toler's Cove Marina (developed site) for determination of the shellfish pathogens *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX). *Perkinsus* prevalence (% infected) and weighted incidence (mean infection intensity, Quick and Mackin 1971 scale) have typically been higher at the Toler's marina site than at the Inlet creek site since sampling began (Fig. 7). With one exception, *Haplosporidium* prevalences (% infected) have been consistently greater at Toler's (developed site) than at Inlet Creek (Fig. 8). With the onset of higher temperatures we are already observing high *Perkinsus* prevalences. Overall, prevalence and infection intensity have both been higher at the marina site than at the Inlet Creek site.

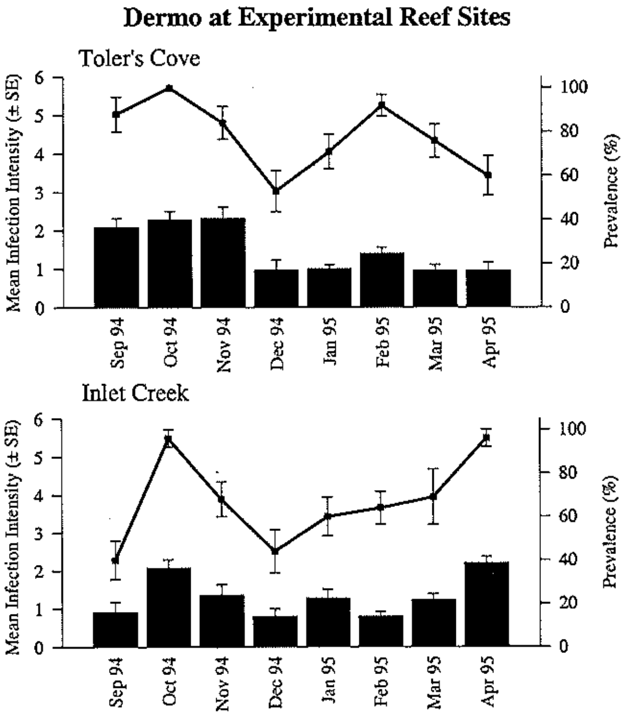


Figure 7. *Prevalence and intensity of* Perkinsus marinus *(Dermo) in oysters from Inlet Creek (reference site) and Toler's Cove Marina (developed site) (n = 25/site, 5 replicate samples of 5 oysters).*

We know little about how intertidal oyster populations in the southeastern United States may differ from their northern subtidal counterparts. Disease epizootiology in intertidal oysters may be quite different from that for subtidal populations. Although intertidal oysters have reduced exposure to water-borne disease agents, the additional stress of intertidal existence (see above and Fig. 5) could render oysters more susceptible to invasion by pathogens. At this time, little is known regarding epizootiology of *Perkinsus marinus* in intertidal populations, and nothing is known about *Haplosporidium nelsoni* in this regard. Focused epidemiology studies at these two sites should yield a better understanding of the interaction between diseases and environmental/pollutant effects (Bobo et al. 1997).

CONCLUSION

Although the research and associated questions presented here are still very much in progress, we suggest that the techniques developed specifically for addressing this unique and very different macro-intertidal oyster ecosystem will enable a determination of its functional importance in habitat creation in southeastern estuaries. By experimentally comparing oyster reef function and species utilization between natural and experimental reefs (at both developed and reference or control sites), we will provide valuable insight into deciphering the complex relationship between habitat quality and fisheries production.

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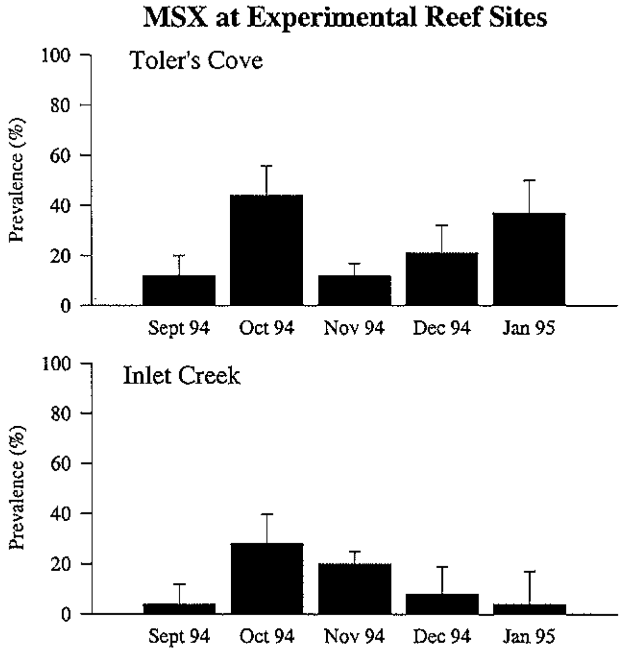

Figure 8. *Prevalence of* Haplosporidium nelsoni *(MSX) in native oysters from Inlet Creek (reference site) and Toler's Cove Marina (developed site) (n = 25/site, 5 replicate samples of 5 oysters).*

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Small-Scale Patterns of Recruitment On A Constructed Intertidal Reef: The Role of Spatial Refugia

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Abstract

Traditional oyster repletion activities have utilized a two-dimensional approach to shell (substrate) deployment to attain maximal coverage in subtidal locations with little consideration for optimal thickness of deployed shell and tidal elevation. Vertical dimensionality may play a vital role, however, in the establishment and persistence of oyster communities. Therefore, a three-dimensional oyster reef was constructed in the Piankatank River, Virginia, and settlement and mortality patterns of oysters were recorded from June of 1993 through September of 1994. The reef was constructed entirely of oyster shell on the footprint of an historical reef, and extended from 2.5 m below mean low water (MLW) to 0.75 m above MLW. The reef covered an area approximately 150 x 30 m, with numerous sections, varying from 2 - 20 m^2 in area, exposed at low tide. In both intertidal and subtidal locations settlement and subsequent mortality (recruitment) were monitored both at the surface of the reef shells and within the interstices of the reef at depths of 10 cm. Settlement was greater in subtidal locations, and no difference in settlement intensity between surface and subsurface environments was detected. Survivorship rates along the intertidal-subtidal continuum varied temporally, but for most of the year, were highest at MLW, where physical and predatory influences rarely are that severe. Oysters which attached to subsurface substrate benefitted primarily from refugia from temperature extremes in intertidal locations and from relief from predation in subtidal environments. We suggest the moderation of these biological and physical stresses both within the reef interstices and within the low intertidal zone plays an instrumental role in increasing survival: even minor submergence within the reef and small changes in vertical elevation provide relief from scorching summer and freezing winter air temperatures and furnish protection from predators, most notably crabs and flatworms. In practical terms these results proffer an important lesson: both reef tidal elevation and substrate thickness provide microscale refugia for settlement and survival of early oyster life history stages.

Introduction

Traditional oyster replenishment programs have focused on spreading thin veneers of substrate suitable for larval settlement over coastal and estuarine bottoms or over foundations of less ideal substrates to maximize areal coverage. In general, such activities have been driven by the practicality of deploying very large volumes of shell, a commodity of increasing value, at greatest cost efficiency and with reasonable speed, usually with the subsequent intent of retrieving either juvenile (seed) oysters or market size oysters. The end product of this approach, a two-dimensional subtidal carpet of shell and live oysters, has little resemblance to the intricate, three-dimensional reef communities that often extended out of the water at low tide and that oysters once formed naturally in the Chesapeake Bay before man's intervention (Hargis 1997). In light of rapidly declining oyster stocks in the Chesapeake Bay, a concerted effort to re-establish natural oyster communities by constructing artificial reefs has been made by repletion agencies. The ultimate goal of such projects is to rejuvenate dwindling local oyster populations.

Presently, we know little about constructing reefs which are most advantageous for oyster settlement and survival. From the cumulative literature on oyster biology, we know that reefs grew by accretion over time periods of hundreds to thousands of years in a process aided substantially by the preferred settlement of metamorphically competent oyster larvae on shells of the adult oyster. We also know that the physical environment, in the form of currents, tides, and sedimentary forces, practically dictate the perimeter size and the features of the reef. However, we remain ignorant of a number of details, and as a result, there are a number of practical questions, fundamental to an organized approach to reef construction, which are without answers. For example, for a known location what size and shape should the reef be, and can we obtain guidance on this question from current "footprints" of formerly intertidal reefs? Is tidal elevation an important factor to consider when constructing reefs? Given that shell is a valuable commodity, can other substrates be used to construct reefs? How thick should substrate layers be and how should they be applied?

In this study, we focus on the issues of substrate thickness and tidal elevation. Naturally forming reef systems have some degree of vertical dimensionality that allows for the settlement and subsequent survival of dense populations of oysters at distinct bands along the tidal continuum. Furthermore, natural reef environments have numerous interstitial microhabitats that offer both physical and biological refugia. Both tidal elevation and interstitial habitats may play integral roles in artificial reef ecosystems as well, and may be important factors to consider when constructing reefs for rejuvenation efforts. Thus, within a constructed reef setting, we have set out to determine if 1) tidal elevation influences oyster recruitment processes (settlement and subsequent post-settlement survival); 2) if subsurface interstitial environments are beneficial for survival; and 3) if oysters are even capable of settling within these environments when reefs are constructed of oyster shell. Specifically, we address these areas by measuring settlement and post-settlement mortality of *Crassostrea virginica* at two substrate levels (reef surface and 10 cm below reef surface) and at various tidal heights ranging from +30 cm above mean low water (mid/high intertidal zone) to -90 cm below MLW (mid subtidal zone) on a constructed intertidal reef.

Methods

STUDY SITE

The study was conducted in the Piankatank River, a subestuary of the Chesapeake Bay located in Virginia, at a site which once supported a highly productive natural intertidal reef system, but at the time of reef construction, contained only a remnant shell footprint of the natural pre-existing reef (Fig. 1). The Piankatank River is ideal for artificial reef construction because it once supported a pro-

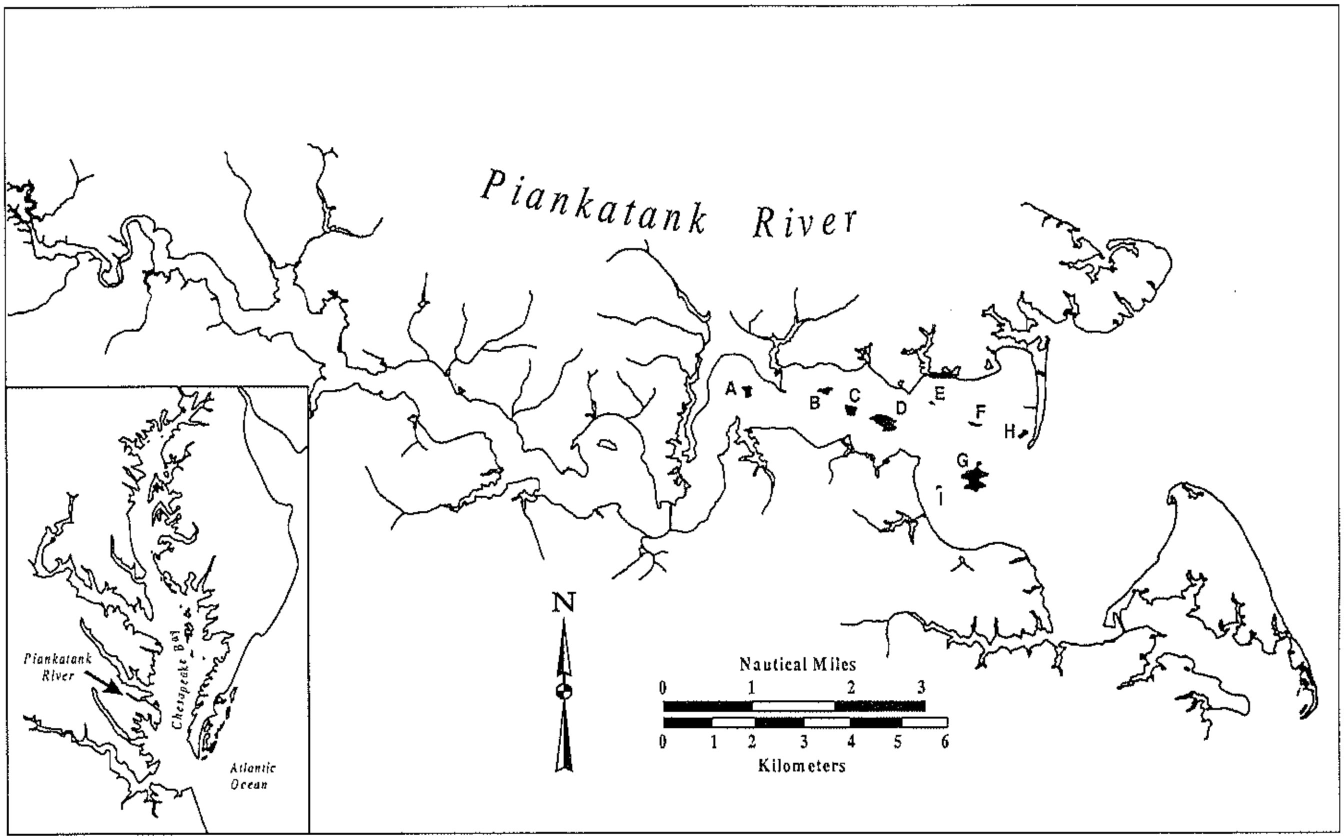


Figure 1. Map of Piankatank River showing the site of reef construction (D) and location of other nearby oyster reefs (A, B, C, E, F, G, H, I)

ductive adult oyster population, has a high abundance of oyster settlement (Morales-Alamo and Mann 1996), there is no commercial oyster fishery, and there is virtually no industry or agricultural development within the watershed. During the course of this study, water temperature at the site varied from 0.5 - 30 °C, salinity ranged from 8 - 20 ppt, and tidal range was small (mean range = 36 cm).

Reef Construction

The reef was constructed in June 1993 by the Virginia Marine Resource Commission (VMRC). The construction procedure involved the deployment of aged oyster shells from barges using a high pressure hose. The shells were discharged in an area approximately 150 x 30 m, which were the approximate footprint dimensions of the historical reef. After completion, the reef consisted of numerous sections, varying from 2 - 20 m^2 in area, exposed at low tide, and extended from 2.5 m below mean low water (MLW) to 0.75 m above MLW. The majority of the reef, however, did not extend much deeper than 1.0 m below MLW or much higher than 0.35 m above MLW.

Sampling Procedure

The reef was sampled in both 1993 and 1994. During the 1993 sampling period 2 of the 12 principal intertidal hummocks comprising the reef system were focused on: one on the reef periphery completely exposed to wave action and currents and a second situated near the middle of the reef partially shielded from wave action and currents. These hummocks were sampled using a transect approach, whereby samples were collected along upstream and downstream transects on each of the two mounds during each period of sampling. Transects were carefully marked on the reef to prevent resampling. Along each transect four tidal heights were considered: 30 cm above MLW, MLW, 45 cm below MLW, and 90 cm below MLW.

During the 1994 sampling period, after data from the previous year were analyzed and we had a preliminary understanding of the reef system, a randomized approach was used which was more geographically expansive and statistically powerful. In this method, eight hummocks were partitioned into 64 x 20 cm plots using rope and reinforced bars, and experimental sites were selected randomly across all eight mounds. Four of the 12 primary hummocks were not considered because ice scouring during the '93-'94 winter eroded the hummock apices, resulting in the loss of substantial intertidal substrate. In this randomized approach, three tidal heights were considered: 25 cm above MLW, MLW, and 90 cm below MLW. The high intertidal height was lowered slightly to accommodate as many intertidal hummocks as possible in the sampling procedure, and one of the subtidal heights, 45 cm below MLW, was eliminated to incorporate more replication. In addition to tidal height another factor, substrate level, was considered. To document the effects of substrate level, samples were collected both at the reef surface and 10 cm below the reef surface.

During both years of sampling, non-destructive and destructive sampling were employed from June through September to assess settlement/early recruitment within the reef ecosystem. Non-destructive sampling involved the weekly placement of oyster shells in open-topped, 64 x 20 cm, rubber coated 1 inch wire mesh trays secured to the reef surface by reinforced bars. In 1993 a surface layer of 20 shells was placed weekly in single level trays which were fixed spatially to the reef at all four tidal height designations along upstream and downstream transects at each of the two mounds. The concave and convex side of all 20 shells within individual cages were examined for recently settled oyster larvae (spat) using a dissecting scope, and a spat total per cage was recorded. In 1994 three-tiered trays containing 30 shell upper and lower levels, which were spaced 10 cm apart, and a 40 shell intermediate level were buried into the reef substrate until the upper level was even with the reef surface. Each week trays were placed at 12 different, randomly selected plots (four plots for each of the three tidal heights). Both surfaces of shell found in the upper and lower tiers were examined for spat, and a surface layer spat total and a deep layer spat total were recorded at all 12 weekly selected plots.

Destructive sampling involved the weekly placement of 64 x 20 cm quadrats on the reef surface, the removal of a layer of shell, and the subsequent examination of both shell surfaces for spat. This sampling technique provided an index of cumulative spatfall on the actual reef substrate and accounted for any early post-settlement mortality losses. In 1993 the quadrats were placed at all four tidal heights along upstream and downstream transects chosen on each of the two mounds. To prevent resampling, successive samples collected over time were taken along transects which were immediately adjacent to previously sampled transects. During this period only a surface layer spat total per plot was calculated. Plots used in 1994 destructive sampling were selected randomly across all eight remaining intertidal mounds. As with 1994 non-destructive samples, four plots were selected randomly each week at all three tidal heights. At each plot, a surface layer of shell and a layer 10 cm beneath the reef surface, easily distinguishable from the surface layer by its brown detrital film, was extracted and examined for spat. This allowed for the calculation of both weekly surface and weekly deep spat totals for all 12 plots.

To determine if oysters which settled along these spatial gradients would survive, oysters of various age classes were tracked throughout the fall, winter, and summer months. On August 12, 1993, oyster larvae were set on clean oyster shells in densities of 5-25 spat per shell at the Virginia Institute of Marine Science Oyster Hatchery. Shells containing spat were placed in Vexar mesh bags (100 shells per bag), and spat were reared in hatchery systems to sizes comparable to oysters found on the reef. On September 26, 1993 the mesh bags were placed on the reef at the same 4 tidal heights designations used in the 1993 settlement monitoring program along two distinct transects on each of the two hummocks. On October 14 and November 11, 1993, and May 5, 1994 25 shells were haphazardly selected from each bag, which was shaken vigorously prior to selection, and shells were photographed with an Olympus OM camera equipped with a 50 mm macro lens. Recent spat scars on each shell were noted and proportional mortalities (# scars per shell / # live oysters at the start of each sampling period) were calculated.

Over the summer of 1994, a different method that considered all intertidally exposed hummocks at the reef site and two year classes of oysters was used to document mortality. One year class consisted of hatchery oysters set on oyster shell on May 16, 1994 in the VIMS Oyster Hatchery, whereas the other year class consisted of a well mixed sample of oysters used in the previous experiment. For each year class, 30 oysters present collectively on 15 randomly picked shells were numbered using paint markers and were placed on either the upper or lower level of 32 x 20 cm, three-tiered, 1 inch mesh cages. Both upper and lower levels, which were 10 cm apart, were filled with shell containing live oysters, but the middle level was filled with 20 shells devoid of live organisms. To keep densities within the 15 shell assemblages as constant as possible, the physical removal of oysters in high density communities was sometimes necessary.

At each of the three tidal heights considered in the 1994 settlement study, eight plots were selected randomly for each year class. At each plot (2 year classes x 3 tidal heights x 8 plots = 48 total plots), cages were buried into the reef substrate until the upper layer was even with the reef surface. The cages were held in place with a reinforced rod. Photographs of labelled oysters were taken in the field with a Nikonos V camera equipped with a close-up lens and focusing frame at 28 day intervals in June, July, August, and September. Estimates of the number of blue crabs and mud crabs present within the upper and lower tiers of each cage were recorded in the field, whereas the number of flatworms present within the two levels were measured from photographs. To enhance photographic clarity and reduce fouling, a 3 HP gasoline powered Homelite water pump was used in the field to clean labelled oysters and cages. Proportional mortality values per layer of each cage were computed for each sampling interval.

STATISTICAL ANALYSIS

The argument may be made that 1993 settlement and mortality samples collected over time were not independent, since successive samples were taken from either spatially fixed areas, spatially connected plots, or from the same population of organisms. To account for this, analyses of variance (ANOVA) with repeated measures on time were performed on each data set. To satisfy assumptions of homogeneity, all settlement data were log (x +1) transformed and proportional mortality data were arcsine transformed. When no significant interactions between the within factor, time, and any other factor were detected, 3-way fixed factor (factors: tidal height, mound, and time) ANOVAs were performed. Significant main effects were examined using Student-Newman-Keuls (SNK) tests.

Linear correlations were performed first on surface and deep samples collected in the 1994 settlement and mortality studies to determine if a relationship existed between the two substrate levels. If no significant relationship was detected in the correlation analysis, substrate level was treated as a factor in further statistical procedures. When significant relationships were detected, paired sample t-tests were used to determine if differences existed between surface and deep samples. A mean value for surface and deep data was calculated when no significant difference between the substrate levels was detected, and further analyses were performed on these mean values.

ANOVAs were performed on 1994 nondestructive and destructive log (x+1) transformed settlement data, and all differences between means were revealed using SNK multiple comparison tests. Multivariate repeated measures ANOVAs were performed on arcsine transformed mortality data collected in 1994. All significant between factor effects were analyzed using SNK multiple comparison tests, whereas significant within factor effects were examined using Newman-Keuls procedure (pp. 527-528, Winer 1991).

Results and Discussion

The majority of data analyzed in this study suggest that small-scale spatial changes, such as 30 cm shifts in tidal elevation or 10 cm changes in substrate depth, strongly influence the processes of oyster settlement and post-settlement survival. Rather than go into an exhaustive examination of the data, we feel that it would be more constructive (and hopefully more interesting), to present representative examples from the data which illustrate and reinforce key microscale effects within constructed reef settings. For a more comprehensive treatment of the data, please see Bartol and Mann (1997) and Bartol et al. (1999).

Settlement of oyster larvae in a constructed reef environment is heavily dependent on the tidal elevation of the reef substrate. Within the shallow water (≤ 2.5 m) reef system considered in this study, settlement increased with tidal depth. This is most clearly seen in the non-destructive settlement studies, where settlement intensities both in 1993 and 1994 were greatest at -90 cm (Fig. 2). This finding is consistent with several other studies conducted in non-reef environments. For example, greater subtidal settlement rates have been documented by McDougall (1942) using unglazed hearth tiles, Chestnut and Fahy (1953) using clam shells suspended in baskets, and Roegner and Mann (1990) using hatchery-reared larvae exposed to field conditions in microcosms. Nichy and Menzel (1967), who placed oysters on clothmats of mesh within a reef ecosystem, also observed greatest settlement/early recruitment within the subtidal zone.

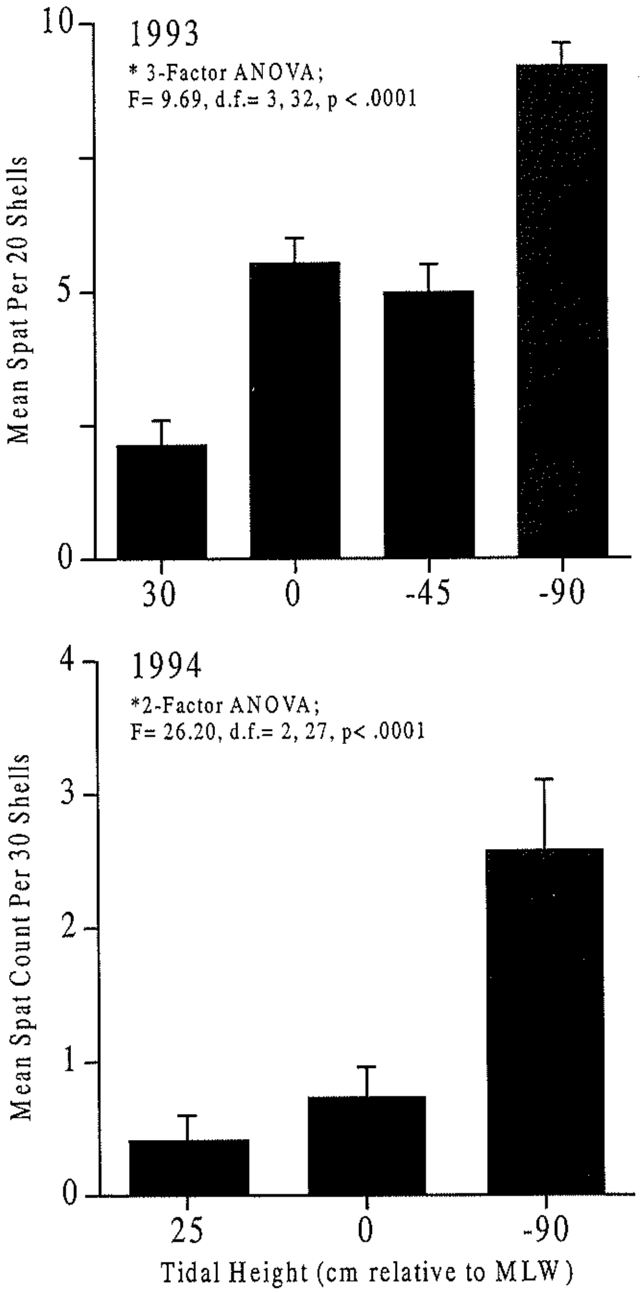
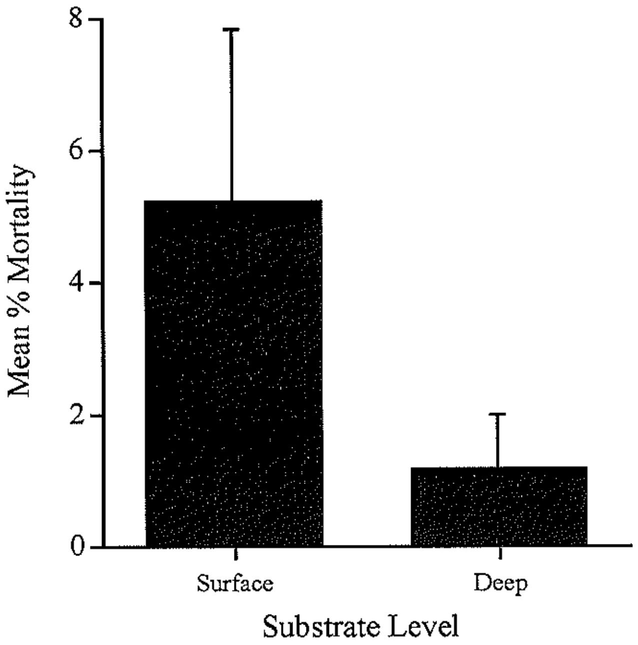


Figure 2. *Mean* C. virginica *spat counts recorded in the 1993 and 1994 non-destructive settlement studies. Error bars denote +1 S.E.*

The higher rates of subtidal settlement observed in this study were likely a result of several factors. Submergence time may have been one. Oyster larvae in the water column were exposed to subtidal substrates substantially longer than to intertidal substrates, and as a result, had a wider time window in which to set. Submergence time alone, however, did not account for the observed differential settlement. Kenny et al. (1990) found that settlement intensity is not a direct function of submergence



*1-Factor ANOVA; F=4.86, d.f.=1,12, p=.047

Figure 3. *Mean percent mortalities of* C. virginica *reared in 1993 residing at the + 25 cm tidal height during the June/July sampling period. Error bars denote +1 S.E.*

time, especially in the high intertidal zone where settlement is often lower than predicted and the low intertidal zone where settlement is generally higher than predicted . Vertical segregation of oyster larvae in the water column also may have contributed to elevated subtidal sets because oyster late stage pediveliger larvae are more abundant near the benthos than at the surface or within the midwater region (Carriker 1951, Kunkle 1957, Haskin 1964, Baker 1994). Furthermore, because late stage competent to set larvae are negatively phototactic (Cole and Knight-Jones 1939, Ritchie and Menzel 1969, Shaw et al. 1970) and prefer areas of lower wave energy when setting (Ortega 1981, Abbe 1986), they may have actively sought subtidal habitats where light intensities and wave stress are reduced.

Surprisingly, no significant differences in settlement were detected between surface and deep substrates at any of the tidal heights considered (Paired t-tests > .05). One concern, however, was that low settlement rates (mean weekly destructive/non-destructive settlement over a three-week settlement period = 0.5 - 3.5 spat per 30 shells) may have dramatically lowered the statistical power of the paired t-tests. Although this may be a true, a thorough examination of the of the data sets revealed no trend in greater settlement for either substrate depth at any of the tidal heights considered. Therefore, we concluded that larval settlement was not impeded by shell down to depths of 10 cm on artificial reefs composed of oyster shell.

Oyster larvae may have settled 10 cm beneath the reef for a number of reasons. Some of the oyster larvae may have actively attached to subsurface substrate because again they prefer darkened conditions when setting (Ritchie and Menzel 1969) and areas of reduced wave action (Ortega 1981), but also because they seek out environments where flow is low, crevices are abundant, and substrates are not heavily fouled (Abbe 1986, Bushek 1988, Michener and Kenny 1991). A plethora of microhabitats offering reduced flow and sheltered, crevice abundant residence were present within the fabric of the reef, and these habitats were considerably less infested with algal growth and barnacles, altogether making them highly suitable for larval settlement. It is also feasible that because water currents are substantially reduced beneath the reef surface, the interstices served as sediment traps and entrained oyster larvae, which are not thought to be proficient swimmers. Although it is not clear from this study what mechanism, active and/or passive transport of larvae, is responsible for subsurface settlement, it is clear that larvae are capable of settling within the reef interstices and are not impeded by shell down to depths of 10 cm. This is quite remarkable considering that there may be 20 or more shells layers within the 10 cm space.

Although oyster larvae are capable of settling beneath the reef surface, can they survive in these environments? Results from this study suggest that oysters not only survive in these environments, but survive better there during certain times of the year. For example, oysters reared in 1993 that resided at the reef surface at the +25 cm tidal height experienced significantly higher mortalities than oysters residing below the surface from mid June through mid July (Fig. 3). During this period air temperatures were the highest of the year, averaging just

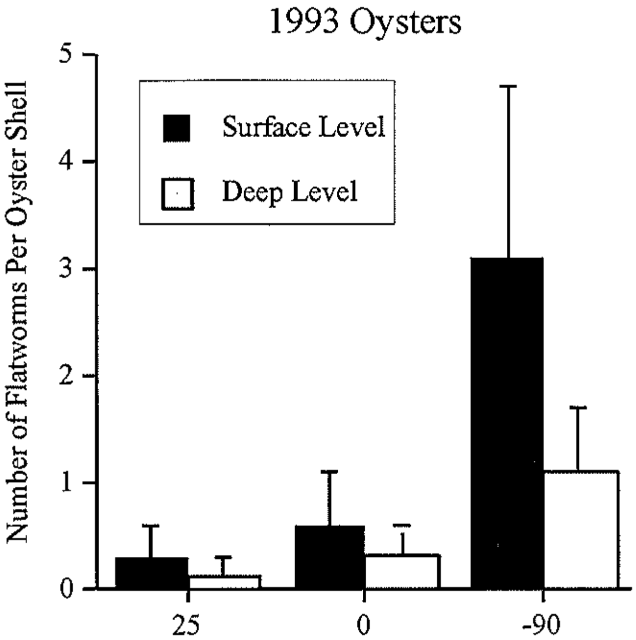


Figure 4. *Mean cumulative percent mortalities from June through September, 1994 for the '93 year class oysters residing at the -90 cm tidal height. Error bars denote +1 S.E.*

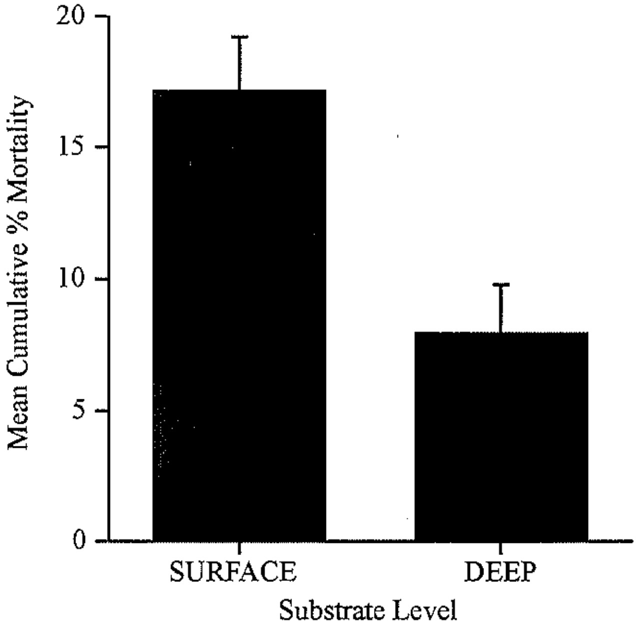


Figure 5. *Mean number of flatworms (*Stylochus elliptus*) recorded on shells for the '93 year class oysters residing at three tidal elevations (25 cm above MLW, MLW, and 90 cm below MLW) and two substrate levels (surface, 10 cm below the surface). Error bars denote +1 S.E.*

over 28 °C. It is likely that oysters beneath the reef surface benefitted from a shading effect from overlying oysters and shell, and as a result resided in a cooler, moister, more hospitable environment than surface dwelling oysters. In fact, temperature measurements recorded in a subsequent study conducted in July 1995 revealed temperatures 10 cm below the reef surface were 11 °C lower than at the reef surface within the intertidal zone. In natural reefs oysters grow vertically in highly populous clusters, and these aggregated settlements provide mutualistic refuge from solar radiation for all oysters in the community (Bahr and Lanier 1981). Since dense assemblages of vertically growing oysters may take many years to become established, subsurface residence may be critical for the survival of intertidal oysters residing in recently constructed reef systems.

A further example of beneficial subsurface residence is found at the -90 cm tidal height. At this height, significantly higher surface mortalities were detected for oysters reared in 1993 over the entire three month summer sampling session (Fig. 4). Although the two most deleterious predators, oyster drills and seastars, were absent at the reef site because of low salinities, the flatworm *Stylochus elliptus*, the mud crabs *Panopeus herbstii, Eurypanopeus depressus, and Rhithropanopeus harrisii*, and the blue crab *Callinectes sapidus* were present, and all are known to contribute to oyster mortality (Landers and Rhodes 1970, Abbe 1986, Littlewood 1988, Eggleston 1990, Baker 1994). These predators were found within cages at surface and deep layers at all tidal heights, but were most abundant at the reef surface and at subtidal depths based on field measurements. For example, in August there was 3.1±1.6 (S.E.) flatworms per shell found on 1993 oysters residing at the reef surface at the -90 cm tidal height, which was more flatworms per shell than any other tidal height/substrate depth designation (Fig. 5). Flatworms and mud crabs were probably the most deleterious because they were highly abundant at the study site and were not restricted by the mesh of the experimental cages. Although adult blue crabs may not have been able to enter the cages, they were able to prey

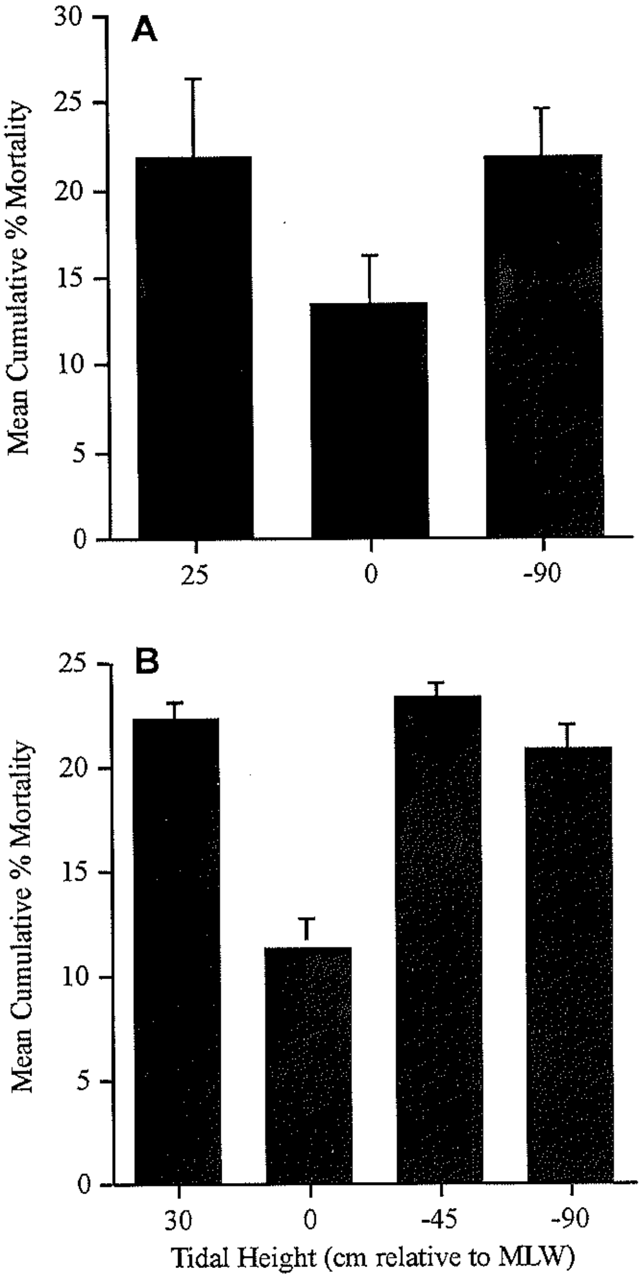


Figure 6. Cumulative percent mortalities for A) the '94 year class of oysters from June-September, 1994 and B) 3-week old oysters from September - November, 1993. Error bars denote +1 S.E.

upon the numerous oysters which grew through the cage mesh.

Of the three tidal heights examined, surface residing oysters survived best at MLW throughout the summer (June-September). For example, oysters belonging to the 1994 year class and dwelling at the MLW tidal height had a cumulative percent mortality of 12 % over the summer compared with mortalities of 22 % and 23 % recorded at the +25 cm and the -90 cm tidal heights, respectively (Figure 6a). Beneath the reef surface within the reef interstices, there was no detectable difference in mortality along the intertidal-subtidal continuum. This may have been because physical and biological environments were relatively stable within the fabric of the reef regardless of tidal elevation. During the fall oysters situated at MLW had a cumulative percent mortality of 13 %, which again was significantly lower than mortalities recorded at other tidal heights (Figure 6b).

Oysters residing at MLW during the summer and fall probably experienced less predation pressure and fouling than subtidal oysters as a consequence of aerial exposure, but did not suffer from significant heat and respiratory stress like mid to high intertidal oysters because they are not aerially exposed for extended periods of time. This is consistent with the findings of McDougall (1942), Chestnut and Fahy (1953), McNulty (1953), Nichy and Menzel (1967), Arakawa (1980), and Littlewood (1988), where high oyster survival in the mid to low intertidal zone was observed as a result of reductions in predation pressure, physical stresses, sedimentation, and/or competition for space.

Oysters situated at MLW did not fare as well during the winter months. Mortality rates at MLW and higher in the intertidal zone were 95-100 % , whereas mortality rates at the -45 and -90 cm tidal heights were on the order of 25 % (Fig. 7). These mortality rates, especially at MLW, were likely atypical and a result of the coincidence of an unusually brutal winter and the presence of a young population of oysters (oysters were 4 months old at the onset of the winter). From December of '93 through March of '94 air temperatures dropped below freezing 28 days, which is very unusual for Virginia. Oysters less than 1 year old are especially vulnerable to freezing conditions because they put much of their energy into growth and maintenance rather than into the storage of glycogen, a preferred substrate for anaerobic respiration,

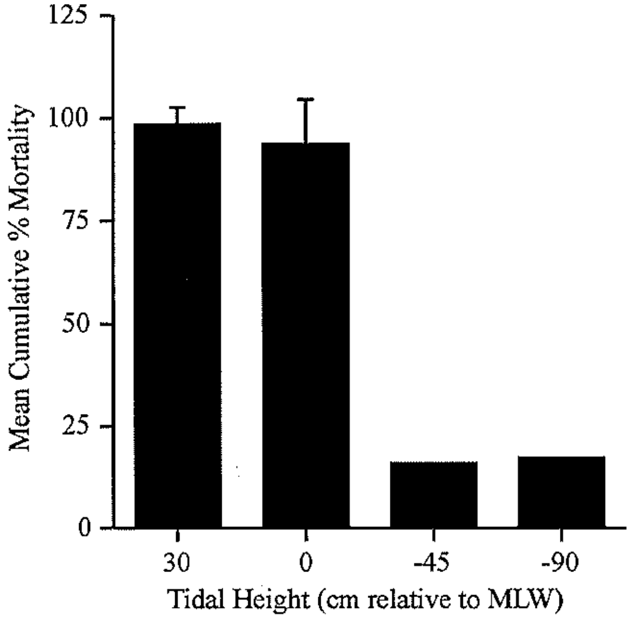


Figure 7. *Cumulative percent mortality of juvenile oysters residing at 30 cm above MLW, MLW, 45 cm below MLW, and 90 cm below MLW from November, 1993 -May, 1994. Error bars denote +1 S.E.*

and thus are less capable of environmental isolation (Holland and Spencer 1973). In a separate study conducted by the authors over the '94-'95 winter, oysters of a similar age (5 months) and oysters 15 months old residing at MLW experienced winter mortalities between 15 and 20 % This is evidence that the mortality rates observed over the '93 - '94 winter were exceedingly high.

It should be made clear that the above winter mortalities only reflect oysters at the surface substrate layer, since oysters beneath the reef surface were not measured during the winter months. It was interesting to note, however, that oysters within one cage buried 15 cm beneath the reef surface in the intertidal zone during the '93 -'94 winter (not depicted in the graph), had mortlities of 50 %. This is substantially lower than intertidal mortalities recorded at the surface. Furthermore, visual inspections of "natural set" oysters in underlying intertidal environments revealed higher below surface survivorship. These observations suggest that residence below the reef surface may not only provide refugia from high temperatures and predators during the summer and fall, but may also provide relief from ice and wind during the winter months.

To recap briefly, settlement/early recruitment of oyster larvae are greatest subtidally, and settlement intensities at the reef surface and 10 cm below the surface are similar. During the summer and fall, subsequent post-settlement survivorship is maximized at MLW; during the winter, mortality of surface dwelling intertidal oysters may be substantial. Survivorship patterns may differ on a smaller spatial scale as well. Submergence 10 cm within the reef provides an important refuge both for intertidal oysters during periods of peak solar exposure (June/July) and for subtidal oysters during periods of intense predation pressure (summer and fall). Furthermore, there is some evidence to suggest that subsurface residence may be beneficial for oysters living in the intertidal zone during the winter months.

In practical terms these results proffer an important lesson: microscale variability should not be ignored when constructing reef systems. Adding merely 1 m of vertical topography onto a constructed reef system so that it may extend marginally out of water at low tide may elevate survivorship substantially, especially if the addition of substrate provides a spatial refuge from intense predation and fouling. This was clearly demonstrated in this study during the summer and fall when mortality rates were lowest at MLW. Unfortunately since mortalities recorded over the winter were a product of unusual circumstances, this study fails to provide a representative comparison between summer, fall, and winter mortalities, which, of course, would be useful in determining whether summer/fall survivorship benefits outweigh mortality losses over the winter. As a result, we cannot provide a definitive answer as to whether building intertidal reefs will maximize survival. Nonetheless, we have shown that tidal elevation does affect settlement and post-settlement survival and that determining the tidal elevation at which recruitment is maximized for a given geographic setting before deciding on a reef elevation is a necessary exercise if survivorship is to be maximized. Substrate depth also should be considered. The veneer level of shell over a base substrate in reef construction should be thick enough to provide microscale refugia for settlement and survival of early life history stages. Based on the results of this study, the substrate should be at least 10 cm thick and allow for subsurface colonization. Finally, the most important advice we offer to reef builders is to be aware that the issues of settlement and mortality in relation to biological and physical environments are determined by microscale variability rather than larger scale uniformity, and the macroscale patterns observed in the field are the sum of these microscale events.

Acknowledgements

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Chapter 11

Perspectives on Induced Settlement and Metamorphosis as a Tool for Oyster Reef Enhancement

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Abstract

In most habitats, oyster larval settlement and metamorphosis is both temporally and spatially restricted. Active efforts to restore oyster reefs will be enhanced by understanding the factors which govern larval habitat selection and how these parameters can be manipulated to promote settlement and metamorphosis at the desired place and time. L-DOPA is known to be a potent inducer of oyster settlement which mimics endogenous neural signalling. The time course and kinetics of the effects of L-DOPA are useful for chemical manipulation of oyster settlement and metamorphosis. A model is presented which addresses relevant aspects of artificial and natural induction and their relationship to environmental stimuli. We present the results of a flume trial demonstrating the effectiveness of planting oyster beds by pre-treating larvae with L-DOPA then releasing them onto a shell bed in flowing water. Then we present the application of these laboratory results to a limited field trial of dispersing L-DOPA-treated larvae onto planted shell beds from a boat outfitted with a sled which disperses the larvae directly to the bottom. The specific successes and failures of these trials demonstrate the promise and problems of this approach to reef restoration.

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Introduction

Oyster populations along the mid-Atlantic coast of North America have declined dramatically over the past two centuries, due to disease, pollution and primarily overfishing (Horton and Eichbaum 1991). The decrease in oyster populations has affected both the ecology and economy of the Chesapeake Bay. Because of the compromised populations and health of oysters in the Chesapeake Bay and other areas, active management and intervention are needed to restore the oyster reefs (Hargis and Haven 1999, Chapter 23, this volume).

Strategies for restoring oyster reefs can involve several levels of manipulation. First, existing reefs can be managed to eliminate stresses leading to declines in population size such as overfishing, pollution and sedimentation. Secondly, the quantity and quality of substrate available for natural larval set can be increased by planting shell, developing artificial cultch material and construction of artificial reefs. Thirdly, oyster spat may be set and hardened on shore prior to being planted in the field. Lastly, natural larval populations can be supplemented with hatchery-reared larvae to enhance recruitment to specific reefs. This chapter addresses laboratory and field experiments related to understanding the factors which govern larval habitat selection and how these factors can be manipulated to promote settlement and metamorphosis at the desired place and time.

In most habitats larval settlement and metamorphosis are both temporally and spatially restricted. Therefore larvae do not set randomly on any available surface, but there is some degree of selection. Historically, oyster larvae have been shown to set in response to an array of physical and chemical cues, which may be associated with the substratum (texture, orientation, chemistry), dissolved in the water column (chemical), or part of the physical environment (light, gravity) (for review see Crisp 1967; Bonar et al. 1985).

There are two general approaches to increasing larval recruitment using chemical inducers. The first involves *substrate modification*, to make it more attractive to larvae. For example, larval "flypaper" has been developed to attract larvae to settle and metamorphose on specific substrates (Jensen and Morse 1990; Morse et al. 1994). Similarly, oyster shells have been coated with specific types of bacteria to enhance settlement (Weiner et al. 1989; Prieur et al. 1990). The second approach to increasing larval recruitment involves *larval modification*, such that application of appropriate chemicals are used to induce settlement and metamorphosis, as has been shown for a variety of molluscs (Morse et al. 1979; Hadfield 1984). Specifically, oyster larvae can be treated with L-3,4-dihydroxyphenylalanine (L-DOPA) to enhance setting (Coon et al. 1985).

In this paper we propose a strategy for reef restoration based on larval modification: treatment of hatchery-reared oyster larvae with chemical inducers of settlement behavior followed by dissemination of the larvae to shell beds where they will attach and metamorphose. First, we will summarize laboratory experiments which were used as a justification for the specific methods employed in the field. Secondly, we present a model which explains the relationship between external cues, internal neurotransmitters and second messengers, and subsequent metamorphosis. Finally, we demonstrate how laboratory technology can be adapted for field application of chemically-induced larvae to oyster reefs.

Experimental Basis

The first critical laboratory finding was that treatment of oyster larvae with a solution of L-DOPA would induce settlement behavior. When competent eyed larvae are exposed to L-DOPA they exhibit the classic stereotyped settlement behavior as defined previously in the literature (Cranfield 1973; Coon et al. 1985), including swimming with the foot extended, then crawling in increasingly more localized patterns and finally cementing to the substratum. The response time of the larvae depends on the concentration of L-DOPA used (Fig. 1).

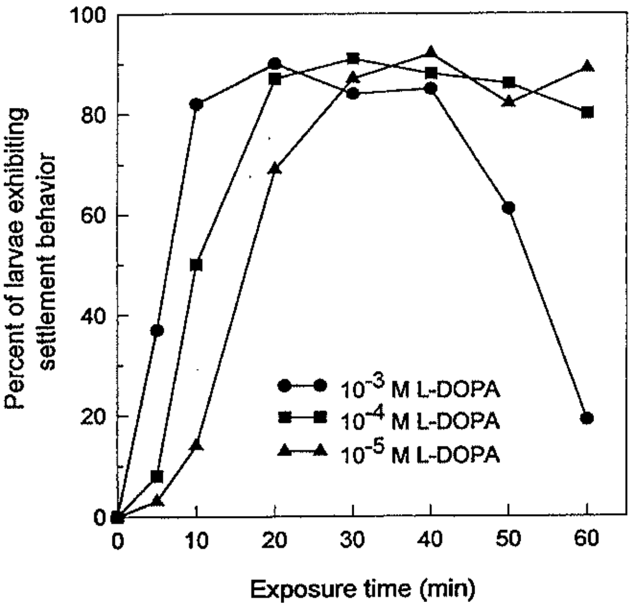

***Figure 1.** Settlement behavior of larvae of the oyster* Crassostrea gigas *in response to L-DOPA as a function of time and L-DOPA concentration. Larvae (25-50 per well) were exposed to the indicated concentrations of L-DOPA in wells of a 24-well cluster dish. Larval behavior was monitored with a dissecting microscope for 30 sec intervals at the times given. Larvae which actively extended their foot beyond the margin of the shell, whether swimming or crawling, were scored as exhibiting settlement behavior.*

Three attributes of the larval response to L-DOPA are particularly important for use in hatchery and field situations. First, settlement behaviors occur within about 10 min of the addition of L-DOPA and continue for over 1 hour. Second, a high percentage of the treated, competent larvae respond to L-DOPA, typically 80-90%. Third, over half of the larvae exhibiting settlement behavior in these experiments subsequently metamorphosed (Coon et al. 1990a). L-DOPA by itself, with no larval contact with the substratum, does not end in metamorphosis, as demonstrated by gluing larvae to glass needles to suspend them above the substratum (Bonar et al. 1990). This suggests that substrate cues are required for attachment and metamorphosis (Coon, in preparation).

Another chemical inducer of settlement behavior in the laboratory is ammonia (NH_3)(Coon et al. 1992). Metamorphosis is seldom seen in laboratory experiments involving ammonia, probably because the larvae quickly habituate to ammonia (typically less than 20 min) (Coon et al. 1990b; Fitt and Coon 1992). Like the response to L-DOPA, typically 80-90% of the competent larvae show settlement behavior.

A third category of chemical inducers are the gregarious settlement factors which recruit larvae to habitats near adult or juvenile conspecifics; these factors are thought to be released by oysters as dissolved chemical cues (Bayne 1969; Hidu 1969; Tamburri et al. 1992). Bacteria are also known to release soluble compounds which induce settlement behavior (Fitt et al. 1990; Zimmer-Faust and Tamburri 1994).

Theoretical Background

A conceptual model of oyster settlement and metamorphosis, detailing intrinsic responses of oyster larvae to external stimuli, is presented in Figure 2 (see also Bonar et al. 1985).

In this presentation the following four points are important:

1. L-DOPA is not the environmental inducer, but enters the larva and triggers the natural signal transduction pathway downstream from the natural environmental cues. This is essentially the same pathway by which L-DOPA is converted

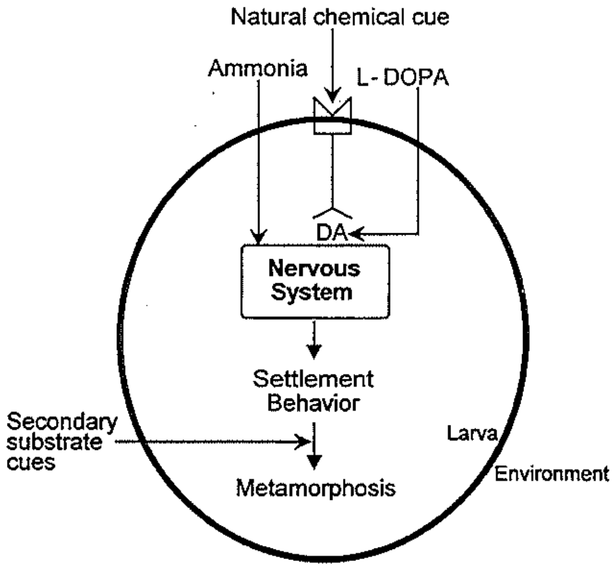

***Figure 2.** A conceptual model of oyster larval response to environmental cues relevant to settlement and metamorphosis. DA=dopamine.*

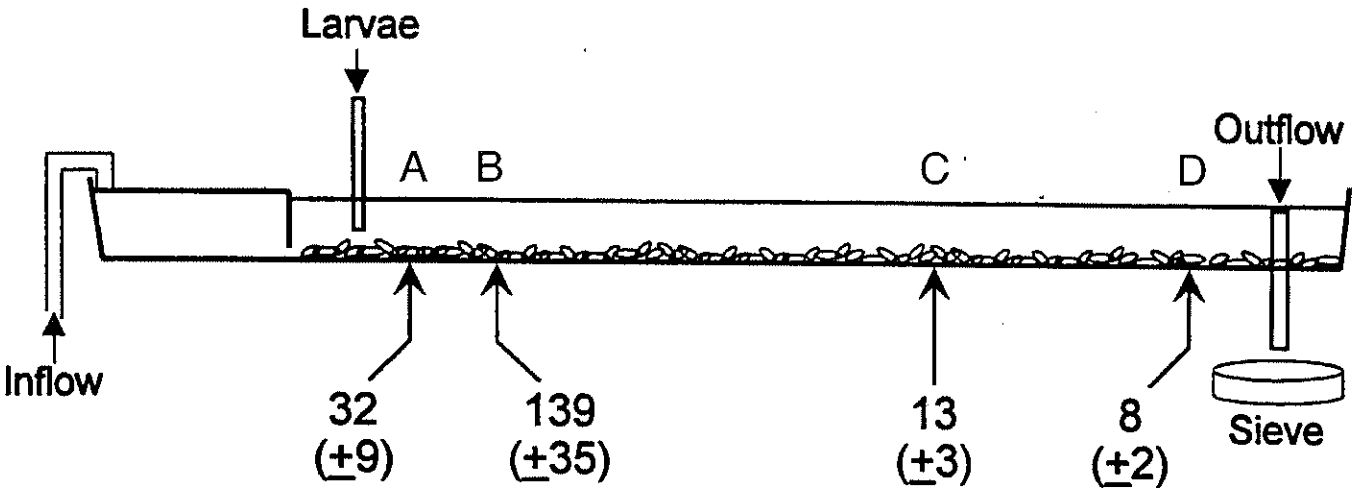

Figure 3. Schematic diagram of a preliminary flume trial designed to test the feasibility of planting treated larvae in the field. The number of spat per shell was counted 5 days after planting of treated larvae. Data are mean (± s.e.m.) number of spat on 10 shells from each location, counted top and bottom. Areas: A = 0-15 cm from beginning of shell; B = 15-45 cm from beginning of shell (this is the planted area); C = 150-180 cm downstream of planted area; D = within 15 cm upstream of outflow.

to dopamine (DA) in the brains of Parkinson's patients after passing through the blood-brain barrier.

2. The pathway through which the natural inducer interacts with the larva is currently unknown, but is thought to trigger the same downstream pathways as in larvae exposed to L-DOPA.

3. Ammonia appears to bypass the pathways utilized by the natural environmental cue and to bypass the pathway that involves L-DOPA. The mechanisms of action of ammonia on oyster larvae probably involves a rapid change in intracellular pH and subsequent depolarization of neural membranes.

4. The model shows that secondary factors associated with the substratum come into play once larval settlement behavior progresses far enough to include contact with the substratum. Larval crawling behavior includes a series of well-characterized behaviors during which the larva traverses a progressively more localized area of the substratum (Cranfield, 1973; Coon et al., 1985). The larva may resume swimming during these phases if the substratum is inappropriate, thus one may presume that the larvae is sensing the substratum while it is crawling.

Thus a paradigm was established in which larvae treated with L-DOPA would be induced to crawl on, and perhaps "explore", substrates available to them, and if the substratum was appropriate, the larvae would cement and metamorphose. Ammonia was considered inferior to L-DOPA for this application because of the rapid habituation of the larvae.

Field Applications

PRELIMINARY FLUME OBSERVATIONS

In order to assess the practical applicability of laboratory experiments to the field, and to estimate how far the induced larvae would travel before attaching and metamorphosing in flowing water characteristic of an estuarine environment, a simple flume trial was conducted. The flume was 3.66 m long by 0.91 m wide, and the bottom was covered with a double layer of aged oyster shell which was allowed to sit in the flume overnight with flowing water (Fig. 3). Filtered (15 μm) estuarine water flowed through the flume at a mean depth of about 10 cm covering the shells (15 cm total depth in the flume), with a velocity of 1.5 cm•s^{-1} (measured 2 cm above the shells in the middle of the flume), then passed through an 87 μm collection screen at the end of the flume. Larvae (4.2×10^5 competent larvae caught on a 209 μm Nitex screen) were treated with 10^{-4}M L-DOPA in 2 liters of ambient estuarine water (plus 2 ppt NaCl to increase density) for 15 min before being added to the flume at the upstream end. The larvae were added by pouring them into a funnel attached to a 1" diameter PVC pipe that ended 2 cm above the shells; larvae were added across the width of the flume between 15 and 45 cm from the beginning of the shells. When added, most of the larvae were exhibiting active search/crawl behavior, some were swimming with their foot extended forward and some were swimming normally. During the addition to the flume, almost all larvae sank immediately to the bottom; in addition, many larvae had to be dislodged from the treatment container by swirling the water. Direct observation indicated that disturbed larvae resumed settlement behavior within 1 min of returning to non-agitated conditions.

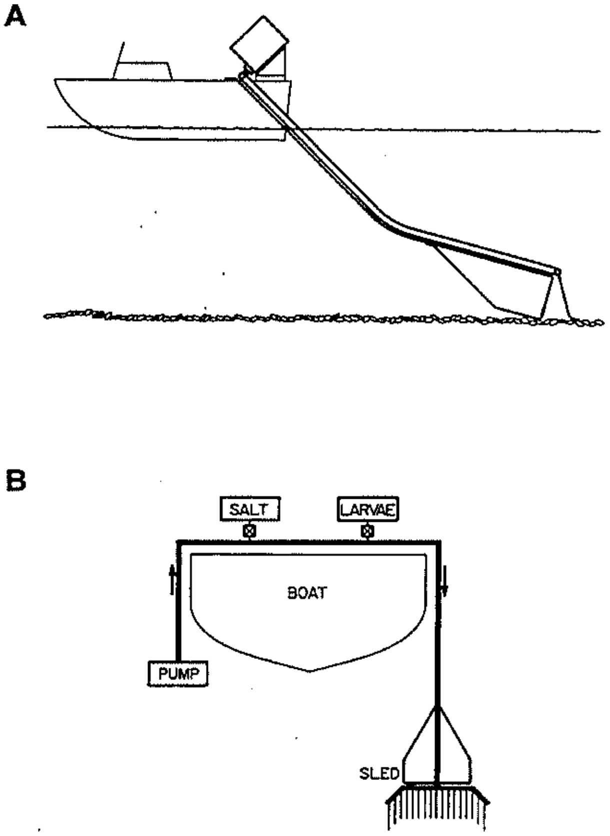

Figure 4. Schematic diagram of larval planting apparatus used for planting induced larvae onto shell beds for restoration of oyster reefs. (A) Side view of the boat towing a modified dredge ("sled") over a shell bed. Tanks were mounted on a wooden rack at the rear of the boat. (B) Rear view of the boat showing sequential addition of salt, then treated larvae, into a stream of ambient estuarine water being pumped from one side of the boat. The larvae passed down the tube and were distributed through a manifold attached to a modified dredge being towed behind the boat.

Initial observations found many larvae crawling actively over the tops and bottoms of shells and on the bottom of the flume, with very few swimming. About 1% of the larvae were caught in the sieve at the outflow of the flume within the first 2 hours, and few were caught subsequently. Five days after the larvae were added to the flume, shells from various distances from the release point were sampled and the number of attached and metamorphosed animals counted. A total of 1925 spat were counted and no significant difference was found between the number set on the convex versus the concave surface of the shells. Figure 3 shows that 90% of the spat found were on shells within the release area or just upstream. This indicated that induced larvae would attach quickly to available shell before being carried away by the current.

Remote Setting of Chemically-Induced Larvae in the Field

An apparatus was constructed for chemically treating and releasing larvae onto submerged shell beds from a boat (Fig. 4). This apparatus consisted of a pump on one side of the boat, which drew water up to where 2 ppt of salt solution was added to increase the density. Larvae were treated for about 20 min with 10^{-4}M L-DOPA in ambient estuarine water in a tank on the boat, then fed into the high-density water before being pumped at about 32 liters per minute down a tube to a specifically-designed sled. The sled, which was dragged behind the boat, consisted of an oyster dredge modified by removing the teeth and bag. Attached across the back of the sled, off the bottom, was a 4 foot long PVC pipe outfitted with 16 small fittings at 3 inch intervals. Each fitting was attached to a 50 cm long length of aquarium tubing which dangled on the ground when the sled was dragged. The effect was to deliver the treated larvae from the boat directly to the shellbed surface (Fig. 4). Shell beds were established by Maryland DNR and monitored for spat prior to the introduction of induced larvae.

In the data presented here 12 million larvae were planted on September 7, 1989, over an area 100m long by 15m wide (Fig. 5A). Six months following this planting, the treated area and 3 adjacent control areas were collected by oyster dredge (Fig. 5A). Four independent one-quarter bushel samples from each area were collected and all spat and oysters measured and counted (Fig. 5B,C). Control areas contained a unimodal size-frequency distribution of oysters, with few individuals less than 20 mm in length (Fig. 5B), which was substantially the same distribution found prior to planting (data not shown). In contrast, the experimental plot had a bimodal distribution with the largest number of individuals in the <20 mm size class, suggesting that these small spat were derived from the planted larvae (Fig. 5C).

While these results clearly show differences between control and experimental areas, some issues remain regarding interpretation. First, there was no control area that was planted with larvae that had not been treated with L-DOPA. This was not included because past experience from the hatchery and field has shown that larvae are not likely to set immediately unless they have been treated. In addition, the cost of the L-DOPA treatment is so inexpensive (about $0.40 of L-DOPA per million larvae compared to a market value of over $100.00 per million larvae) that the cost not to treat was considered prohibitive. Second, we have not definitively demonstrated that the small spat that were found in the experimental area were derived from the planted larvae. There is a possibility that there was a highly focussed natural spat set that coincided in time and space with the experimental planting, but there was no evidence from the size frequency distributions of this occurring previously in this area. In the future, larvae could perhaps be marked (genetically, or with tetracyclin, etc) so that they would be distinguishable from natural set. Third, this apparent success occurred on a shellbed that already contained established adult oysters and that had been put in place several years earlier. Would the results have been the same on a freshly emplaced shellbed?

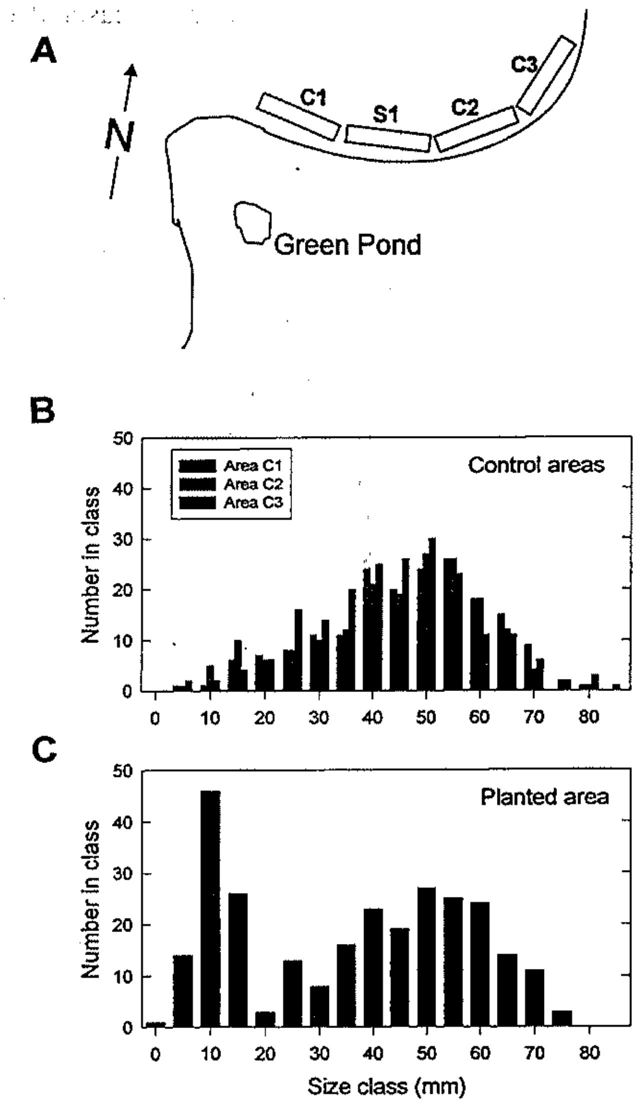

Figure 5. *Details of a planting conducted at the Green Pond site in the St. Mary's River just south of St. Mary's College between Church Point and Chancellor's Point. (A) A map of the planted area showing the planted site (S1) and the three control sites (C1, C2, C3). Each plot was 100 m long by 15 m wide. (B) Data from sampling the control areas 6 months after the planting. Four independent one-quarter bushel samples were collected, counted and summed for each sample. (C) Data from sampling the planted area (S1) at the same time and using the same techniques as for the control areas.*

In fact, this technique was attempted several other times without being able to demonstrate enhanced set. In most cases, there were obvious reasons for this. For instance, one area was so silted over within 6 months after introducing the larvae that essentially all shells were buried by anoxic sediments, pointing to the need for more research on currents, tides and historic reef patterns in future experiments. In another location, all of the shells were completely covered with colonial bryozoans to such an extent that any spat that had set would have been smothered. Clearly timing and location of shell plantings are critical to the potential success of remote setting experiments.

Discussion

The primary alternative to the field-planting method outlined in this paper is traditional remote setting in which hatchery-reared larvae are set onto cultch in tanks, hardened, then out planted. There are insufficient data at this point to quantitatively compare the two approaches, but if only a small percentage of field-planted larvae survive to adults, this technique will be significantly less expensive than remote setting since there is much less labor and equipment involved. A major disadvantage of field-planting larvae is that there is less control over the environment and therefore more opportunities for things to go wrong. In addition, larval and spat mortalities would be expected to be higher with field-planting. The cost of larvae compared to labor and equipment will be matter of scale. Field planting could be adapted for much larger scale than remote setting. Clearly, there are many more parameters that could be considered and optimized for the field-planting technique, but much of this future work will be relevant to specific local conditions and would therefore benefit from trials at many localities. In spite of technical obstacles, the data demonstrate the potential for application of hatchery-reared and chemically-induced larvae to oyster reef restoration.

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Chapter 12

Processes Controlling Local and Regional Patterns of Invertebrate Colonization: Applications to the Design of Artificial Oyster Habitat

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Abstract:

The colonization of artificial reefs by benthic invertebrates will be influenced by both regional and local processes. For sessile species, the regional pool of available species coupled with the processes affecting the spatial and temporal distributions of their planktonic larvae will have a strong influence on colonization. The regional species pool sets the overall limits on colonization and larval availability determines the initial order and abundances of colonizing species. These in turn can determine interactions within and among species and set both short- and long-term patterns of abundance. However, the local physical and biological environment can severely alter this regional control. Local physical factors such as strong currents or biological factors such as the presence of predators of larvae, new recruits, or juveniles may prevent the colonization of many species. Therefore, it is important to examine the integration of regional and local processes and how they might affect the communities of oyster reefs.

In studies conducted at sites along 25 km of the southern California coast we found that the colonization and community development of sessile invertebrate communities is very dynamic with species composition and dominance constantly changing. However, consistent differences existed between sites separated by 3-10 km. In addition sites as little as 100 m apart also displayed consistent differences in diversity and species composition. For example, substrates placed on existing reefs developed different communities than those only 100 m removed from the reef. Thus even along an open coast, local differences can result in extreme differences in the types of communities that develop and the success of particular species.

In more recent studies conducted in southern New England we have found that both small and large predators can completely control recruitment onto a reef. When these predators are present, a community

dominated by bryozoans develops and when they are absent the community is dominated by ascidians. These differences can be at sites separated by much less than 1 km and the community dominance patterns appear to be permanent.

Overall, these studies suggest that local conditions can have a dominant effect on recruitment, colonization, community development, and species dominance. Once established, local communities may contribute to their long-term persistence. Thus the placement of new or artificial oyster habitat near or far from existing reefs can greatly influence their success. Management efforts (in terms of oysters as well as the associated community) may have their greatest influence during the early stages of the reef's development. After the establishment of a more or less stable local community, it may be extremely difficult to change it.

Introduction

Regardless of composition, structure, or size, the creation of artificial oyster reefs results in the placement of new, uncolonized habitat into the natural environment. Unless this new habitat is seeded with oysters or other species when established, its colonization will be controlled by both regional and local processes. For sessile species that are permanently attached as adults (such as oysters), colonization will depend on the production of recruiting larvae. This production will, in turn, depend on the regional pool of reproductively active populations coupled with the processes affecting the spatial and temporal distributions of their planktonic larvae. For motile species such as crabs, emigration of adults and juveniles onto the reef may also contribute to colonization.

The regional pool of available species sets the upper limit on colonization (Osman and Dean 1978). The temporal and spatial distributions of larvae produced within the region will cause variations in the availability of these motile stages at any site and thus determine both the initial order and abundances of colonizing species (e.g. Grosberg 1982; Olson 1985; Roughgarden et al. 1985; Gaines and Roughgarden 1987; Gotelli 1987; McShane et al. 1988; Robertson et al. 1988; Todd et al. 1988; Farrell et al. 1991; Hurlbut 1991; Minchinton and Scheibling 1991; Le Fevre and Bourget 1992; Stoner 1992; Carlon and Olson 1993). These in turn can determine dominant interactions within and among species and set both short- and long-term patterns of abundance. For example, in seasonal environments large variations in relative and absolute larval abundances among species can cause very different patterns of larval settlement (e.g. Osman 1977, 1978; Sutherland and Karlson 1977). Artificial reefs established in one season may be exposed to an entirely different pattern of colonization than adjacent reefs exposed 3 months later or earlier.

Despite the existence of strong regional patterns in larval availability, the local physical and biological environment can severely alter this regional control. Local physical factors such as strong currents (Shanks and Wright 1987; Farrell 1991) or biological factors such as the presence of competitors or predators of larvae, new recruits, or juveniles (Meleikovsky 1974; Keough and Downes 1982; Cowden et al. 1984; Young and Gotelli 1988; Holm 1990; Andre et al. 1993; Osman et al. 1992; Osman and Whitlatch 1995a,b) can prevent the colonization of many species. Likewise, the strong competitive dominance of one or more species, can result in reefs being dominated by one or few species, despite local environmental differences. Therefore, it becomes necessary to examine the integration of regional and local processes and how they might affect the communities of oyster reefs.

There is a particular relevance in understanding colonization processes to the establishment of artificial reefs. Unlike natural reefs, these structures have no history or native fauna. They are of a predetermined size and are placed at chosen sites at selected times. Thus important factors such as their location, season of deployment, and size all can be controlled. Location can be controlled not only in terms of the physical environment, but also with regard to how contiguous or isolated they are to existing reefs. The effects of natural reefs can be both positive in supplying recruits and immigrants and negative in allowing more ready access of predators, competitors, or parasites of desired species. Timing of deployment can also determine order of early colonization and thus the development of the community (Osman 1977; Sutherland and Karlson 1977). Size will ultimately regulate the number of species, population sizes, the permanent presence of larger species, and ultimately the long-term persistence of the community that develops (Osman 1978).

Finally, understanding colonization processes is important to the specific goal of establishing reefs with productive oyster populations. Examining colonization processes recognizes that the communities of reefs are dynamic, with continuous immigration of new individuals into local populations as well as new species and the mortality of existing individuals and the local extinction (loss) of species (Osman 1982). The life history of each species will influence how dynamic these processes of loss and gain are. The oyster with permanently attached juveniles and adults and a long-lived planktotrophic larval stage is ultimately more dependent on regional production of new individuals for the local reef population than species in which the offspring of local populations can colonize the reefs on which they were produced and thus contribute to the growth and persistence of the local population.

Thus our goal in this paper is to examine and contrast the potential contribution of both regional and local processes to the colonization of reefs, the long-term dynamics among the species forming the reef community, and the persistence of populations and communities. Our focus will be the sessile invertebrate communities common to all types of reefs and other hard substrata.

Methods

To illustrate the importance of regional and local controls on the colonization of reefs we will compare the relevant results of two studies designed to examine colonization processes within sessile invertebrate communities. As part of both studies, clean experimental substrates were deployed at field sites and natural recruitment coupled with interactions among the species present were allowed to control colonization, community development and species dominance. Although occurring on much smaller (but replicated) substrates, the processes investigated were a microcosm of what will occur on larger artificial reefs placed in any marine or estuarine body of water.

STUDY 1 - CALIFORNIA

The first of the research projects was a three year study conducted along the coast of southern California. The original intent of this study was to examine the effects of the San Onofre Nuclear Generating Station on epifaunal communities. However, because similar long-term colonization experiments were conducted at 20 sites spread along 15 km of coastline, this study allows us to examine both broad regional and local site effects on recruitment and subsequent effects on community development.

Ten of the 20 stations were located on two transects away from the outfall of the power plant. These transects were parallel to the coast, one north and one south of the outfall (see Osman 1982 for map). Permanent stations were located at 50, 100, 200, 400, 800, and 1600 m north and 50, 100, 800, and 1600 m south of the discharge. In general these stations were in 6-9 m of water in areas of mixed muds and sands. Sparse patches of cobbles and boulders occurred along the north transect and in the vicinity of the discharge. Because these stations were not near any existing reef area, substrates placed at them can be used to represent artificial reefs established in areas away from existing reefs.

Another 10 stations were located farther offshore in 12-14 m of water, in or near three

Macrocystis pyrifera kelp forests. Because kelp generally establishes in areas that can be characterized as reefs, these stations can be used to examine the effects of an existing reef on invertebrate colonization. At the start of the study, at least three stations were established in each kelp forest, one inside, one on the edge, and one 500 m outside of the forest. Changes in the spatial extent of the forests led to the reestablishment of one station at a new location. Within three months of the start of the study, regression of the southern forest (Barn) resulted in all three stations being located outside. In October 1979 (16 mo into the study) a fourth station was established inside the forest and some substrates from the old inside station were moved to it. The original three stations were in areas eventually covered by sediments and the fourth station was on a low-profile bedrock reef.

In the middle kelp forest (San Onofre) growth and regression of the kelp forest caused the inshore edge and outside stations to fluctuate between being characterized as edge or outside. A fourth station was included in this forest at a site on the offshore edge. This station was in an area of very small cobble which were unsuitable for the attachment and persistence of large kelp plants. Thus, this station was unaffected by fluctuations in the size of the forest. Substrate within the San Onofre kelp forest was mixed cobble, sand, and boulders.

The northern kelp forest (San Mateo) included three stations all whose characterization remained stable throughout the study. This kelp forest was on a stable rock reef and fluctuated little in size. The inside station was on the reef, the outside station was in muddy-sand, and the edge station was at the permanent boundary between these two substrate types.

Four identical colonization experiments were conducted at the 20 stations. In all the experiments artificial substrates were used to mimic naturally occurring hard substrate. The five main experiments consisted of the continuous exposure of identical substrates for the length of the study. Experiments were initiated during the first week of June, September, and December 1978, and March and November 1979. Substrates were 100 cm^2 panels made of asbestos-concrete (Transite). These were attached to flexible field racks that held them 0.5 - 1.0 m above the bottom. In all the experiments, only the surface of the panel facing the seafloor was analyzed. A minimum of three replicate panels were used in all experiments at all sites.

All sampling was nondestructive. Panels were collected by divers, placed in coolers of aerated seawater, and transported to the laboratory. In the laboratory panels were held in a 2000 l closed seawater system for 2-7 days. During this time each panel was photographed, carefully surveyed for all species present, and then the abundances of dominant sessile species were estimated using a randomly placed grid of evenly spaced points (1/cm^2) and counting the number of points falling on each species. After the panels were analyzed they were returned to the field racks. Panels were nominally sampled every six weeks. After the first six sampling periods, the large number of panels made it impossible to sample all substrates this frequently and sampling was reduced for some experiments and stations. Most substrates, however, were analyzed every 6-10 weeks. All panels remained in the field at least six weeks between sampling times.

In addition to the colonization experiments, invertebrate recruitment was measured by exposing two clean panels for each six week sampling period at each site. All individuals of all species on these panels were counted to estimate recruitment rates.

During this study approximately 350 species of sessile invertebrates, 50 species of small motile invertebrates, and 50 genera of macroscopic algae were recorded on the experimental substrates. Sessile invertebrates were represented by ten different phyla with colonial groups such as sponges, hydroids, bryozoans, and ascidians generally being spatial dominants.

STUDY 2 - CONNECTICUT

The second study was begun in 1992 and conducted in eastern Long Island Sound near Groton, Connecticut. The research was an extension of earlier work conducted in Vineyard Sound, Massachusetts (Osman et al. 1990, 1992) as well as at the Groton site (see Osman et al. 1992 for map). Our earlier research indicated that predation on newly-settled individuals of several species, particularly ascidians, had the potential to control the development of the epifaunal community by eliminating the recruitment of prey species. Thus the research was designed to test in the field whether local differences in the abundance of predators could consistently control the persistence of dominant species. Based on our previous work, the major predators included two small snails, *Mitrella lunata* (<5 mm) and *Anachis lafresnayi* (<15 mm) and the wrasse *Tautogolabrus adspersus*. In addition both adults and juveniles of species such as the crab *Libinia emarginata* and the seastar *Asterias forbesi* were present, as well as other small predators, and their effects were also examined.

The study was conducted at two sites near the mouth of the Poquonnock River. The first site was near a breakwater at Avery Point just inside the mouth of the river. The second site was offshore of Pine Island, just outside of the river's mouth (see Osman and Whitlatch 1995 for map).

Experiments were conducted at both sites using artificial pilings that were 75 cm tall, 28 cm diameter. The pilings were constructed using pieces of PVC pipe secured upright to weighted frames. Preliminary experiments indicated that the artificial pilings successfully mimicked both pilings and natural boulders in terms of the types and abundances of invertebrates colonizing them. In a pilot study these pilings and substrates attached to them accumulated in 3-12 mo an epifaunal and macroalgal community indistinguishable from adjacent boulders.

In each experiment 100 cm^2 PVC panels attached to replicate pilings were used as sampling units. However, the pilings themselves were the unit of replication in all experiments. In most experiments four piling treatments were used with five pilings/treatment and 1-4 panels/piling. Treatments were:

1) open pilings, exposed to all predator guilds,

2) caged (1 cm^2 mesh) pilings which excluded all but the snails *Mitrella* and *Anachis* and other small predators (extensive tests for potential cage artifacts were negative),

3) screened (1 mm^2 mesh) pilings which excluded all predators, and

4) partially screened pilings to control for artifacts resulting from the possible environmental changes (e.g. reduced flow) inside the screened treatments. These partially screened pilings had a 5 cm band at their bottom that was free of screening but protected by the 1 cm^2 mesh used in the caged treatment. Thus they created the same environment used in the screened treatment, but allowed access by small predators. If artifacts were unimportant, then these treatments would have effects similar to that of caged treatments.

Each experiment was conducted with 1 of 3 life-stages of an epifaunal species: 1-3 day-old recruits, 2-3 wk-old juveniles, or adults. Initially, clean panels were exposed to larvae of the chosen species in the laboratory or the field. After exposure panels were hung beneath a raft at the Avery Point breakwater site until individuals or colonies had reached the proper life-stage. During this time the panels were 'gardened' periodically to remove all other species. Prior to being used in an experiments, the panels were cleaned of all other species, counted, photographed, and then haphazardly assigned to treatments. In each experiment panels were exposed for 3-6 d and then retrieved and photographed. Estimates of mortality and growth were made by comparing the initial and final photographs using computer-assisted image analysis.

To examine effects of the local environment on long-term colonization, panels were exposed on caged and uncaged pilings and panel racks suspended above the bottom at both sites and examined monthly. After time periods of one week to one month, sets of panels were reciprocally transplanted between sites. The transplants tested whether the post-recruitment processes of the local environment had stronger effects on the community than differences in initial recruitment. The caged pilings were designed to exclude large benthic invertebrate predators and fish and the suspended racks excluded both small and large benthic predators. Preliminary analyses of these panels suggested that the greatest effects were seen between treatments during the first month of the study and these are the data examined in this report.

Results

CALIFORNIA

Recruitment-We used the recruitment data from all 20 stations to examine whether there were spatial differences in recruitment. We hypothesized that if recruitment was random along the open coastline of southern California, then we should not see any consistent differences among the sites in recruitment. That is, during any sampling period the random variation in larval distribution among the 20 sites would be expected to result in one or more sites being significantly different. However, we would also expect that over the length of the study, all sites should receive similar numbers of recruits. Therefore, we used the recruitment data for 23 species collected over all 18 sampling periods to test whether they exhibited any consistent differences among stations.

In analyzing each species, we eliminated any sampling periods in which the species failed to recruit at any of the stations. Also, because the recruitment data were not normal and strong seasonal variability in recruitment could result in some sampling periods having a disproportionate effect on mean values, we ranked all the samples within each sampling period. A one-way ANOVA was then conducted on the ranks using the data for all sampling periods.

The species analyzed included the sponge *Leucosolenia eleanor*, the hydroids *Bougainvillia glorietta* and *Obelia dichotoma*, the bryozoans *Parasmittina* sp., *Rhynchozoon rostratum*, *Celleporaria brunnea*, *Tubulipora tuba*, *Bugula longirostrata*, *Bugula neritina*, *Membranipora* sp., and *Callopora circumclathrata*, the barnacles *Balanus pacificus*, *Balanus tintinnabulum*, *Balanus trigonus*, and *Balanus* spp., the polychaetes *Sabellaria cementarium*, *Sabellaria gracilis*, *Chone minuta*, and *Eupomatus gracilis*, and the bivalved mollusks *Chama pellucida*, *Pododesmus cepio*, and *Hiatella arctica*. For each of these species we conducted four separate analyses with some stations either not included or stations pooled by habitat or location. In the first analysis all stations were included, but ten were grouped as Inshore (transect) stations and ten were grouped as Offshore (kelp forest) stations. In the second analysis we examined the ten Inshore stations separately, pooling the stations by four categories: Inshore Far North and South (>400 m from the power plant outfall) and Inshore Near North and South. The third analysis examined the ten kelp forest stations using three Kelp Forest categories: Inside, Edge, or Outside. Finally, the three stations in the San Mateo Kelp Forest were examined separately. This kelp forest was chosen because the distinctions between inside, edge, and outside were most consistent throughout the study.

The results of the four sets of analyses are shown in Table 1 and it is clear that there were more significant differences among the stations than one would expect by chance. In the comparison of inshore and offshore stations, 13 of the 23 taxa examined recruited in significantly higher numbers inshore than offshore. Only seven of the taxa exhibited no differences among the stations and three recruited in significantly higher numbers at offshore stations. No clear inshore-offshore patterns emerge from these analyses in terms of taxa or larval dispersal ability. Taxa with long-lived planktotrophic larvae (e.g. barnacles) and short-lived lecithotrophic larvae (e.g. many bryozoans) exhibit no distinct differences in the spatial variability in their recruitment patterns.

Table 1. Analysis of recruitment at the 20 stations along the southern California coast. Lines connect groups of stations with no significant difference based on a 1-way ANOVA of ranked recruitment data. Within each analysis stations were ranked within each of the 18 sampling periods and these rankings were used in the ANOVA's. Symbols are: NN = Inshore North transect Near the power plant outfall, NF = Inshore North transect far, SN = Inshore North transect Near, SF = Inshore South transect Far. Numbers are the mean recruitment in number of individuals per sampling period.

SPECIES	**INSHORE - OFFSHORE**	**INSHORE TRANSECT**	**KELP FORESTS**	**SAN MATEO KELP**
Leucosolenia eleanor (PORIFERA)	IN OFF .4 .3	SN NN NF SF .1 .1 1 .1	OUT EDGE IN .5 .1 .1	OUT EDGE IN .1 .1 .1
Bougainvillia glorietta (HYDROID)	OFF IN .1 0	SN NN NF SF 0 0 .1 . 2	OUT IN EDGE .2 .1 0	EDGE IN OUT .1 .1 .1
Obelia dichotoma (HYDROID)	OFF IN .6 .6	SN NN SF NF .6 .6 .7 .6	OUT IN EDGE .8 .6 .5	OUT EDGE IN .7 .7 .6
Alcyonidium parasiticum (BRYOZOA)	IN OFF .3 .03	NN SF SN NF .3 .2 .1 .3	OUT EDGE IN .1 0 0	
Parasmittina sp. (BRYOZOA)	IN OFF 2 1	NN SN NF SF 2 1 1 0	IN OUT EDGE 12 4 2	IN EDGE OUT 17 1 0
Rhynchozoon rostratum (BRYOZOA)	IN OFF .6 .2	NN SN NF SF .6 .4 1.2 .1	IN OUT EDGE .3 .1 .3	IN EDGE OUT .3 0 0
Celleporaria brunnea (BRYOZOA)	IN OFF .3 .3	SN NN NF SF .2 .1 .6 0	IN EDGE OUT .5 .4 0	IN EDGE OUT .6 .1 0
Tubulipora tuba (BRYOZOA)	OFF IN 1.6 0		EDGE IN OUT 2 3 1	IN EDGE OUT 4 .3 .1
Bugula longirostrata (BRYOZOA)	IN OFF 2.4 1.2	SN NN SF NF 2 1 .7 .4	OUT EDGE IN 4 0 0	
Bugula neritina (BRYOZOA)	IN OFF .3 0	SN NN NF SF 1 .2 .2 0	OUT EDGE IN 0 0 0	
Membranipora sp. (BRYOZOA)	IN OFF 1.1 .7	SN NN SF NF 3 1 1 .4	OUT EDGE IN 1 .1 .1	OUT EDGE IN 4 0 0

Table 1. Continued.

SPECIES	INSHORE - OFFSHORE	INSHORE TRANSECT	KELP FORESTS	SAN MATEO KELP
Callopora circumclathrata (BRYOZOA)	IN OFF .6 0	NN NF SN SF 4 1 .3 0	EDGE IN OUT .1 .1 0	IN EDGE OUT .1 0 0
Balanus pacificus (BARNACLE)	OFF IN 4.4 .5	SN NN SF NF .7 .7 .6 .1	OUT EDGE IN 4 3 2	EDGE OUT IN 5 1 0
Balanus tintinnabulum (BARNACLE)	IN OFF 26 18	NN SN NF SF 29 19 50 3	IN EDGE OUT 193 80 7	IN EDGE OUT 337 178 12
Balanus trigonus (BARNACLE)	OFF IN 1.8 1.4	NN SN SF NF 2 3 2 1	EDGE OUT IN 2 1 3	EDGE OUT IN 4 .4 .2
Balanus spp. (BARNACLE)	OFF IN 5 4	SN NN NF SF 30 33 56 8	IN EDGE OUT 207 90 14	IN EDGE OUT 349 190 15
Sabellaria cementarium (POLYCHAETE)	IN OFF 1.2 .5	NN SN NF SF 2 1 1 .2	EDGE IN OUT .8 .6 .5	EDGE IN OUT 1 .2 .1
Sabelllaria gracilis (POLYCHAETE)	IN OFF 2.6 1.4	NN NF SN SF 2 4 2 2	EDGE IN OUT 2 2 2	EDGE IN OUT 2 .5 .4
Chone minuta (POLYCHAETE)	IN OFF .2 0	NN SN NF SF .3 .1 .2 .1	OUT EDGE IN .1 .1 0	EDGE OUT IN .2 .1 0
Eupomatus gracilis (POLYCHAETE)	IN OFF 31 .5	NN SN NF SF 59 36 9 8	OUT EDGE IN .5 .4 .2.	IN OUT EDGE 7 .3 .3
Chama pellucida (MOLLUSC)	IN OFF .1 0	NN SN NF SF .1 0 .1 0	OUT EDGE IN .1 0 0	
Pododesmus cepio (MOLLUSC)	OFF IN .2 0	SN NN SF NF 0 0 .1 0	EDGE OUT IN .3 .1 .2	EDGE OUT IN .3 .1 .1
Hiatella arctica (MOLLUSC)	IN OFF 2.9 .7	NN NF SN SF 3 6 1 2	IN EDGE OUT 2 1 1	IN EDGE OUT 2 2 .6

However, when inshore and kelp forest stations were examined separately, we found several distinct patterns. In the analysis of recruitment among inshore stations, 15 of the 23 species recruited in significantly higher numbers at the sites nearest the power plant outfall. Of these species, the serpulid polychaete *Eupomatus* shows the most distinct pattern (Figure 1). The large volume of water discharged at the outfall coupled with the entrainment of adjacent bottom waters, in effect, exposed substrates near the outfall to greater volumes of water than those farther away. Thus the outfall could represent a physical condition that would result in higher numbers of larvae available for recruitment at sites near it. Except for the bryozoan *Tubulipora*, which never recruited at inshore sites, the remaining seven species showed no significant differences among stations. As with the inshore-offshore patterns, the dispersal ability of the different taxa had no obvious affect on the observed recruitment patterns.

Finally, in the two analyses of the offshore Kelp Forest stations fewer species exhibit significant spatial patterns of recruitment. For the analysis of all ten kelp forest stations, 12 species showed no significant differences among stations outside, inside, or on the edge of the forests, while ten species showed no differences among the three San Mateo Kelp Forest sites. Of those species displaying differences, only one (the barnacle, *Balanus trigonus*) was significantly higher at the kelp forest edge. The recruitment of the remaining species either decreased from the outside to the inside of the kelp forests or increased along the same transect. In most cases species that were signifi-

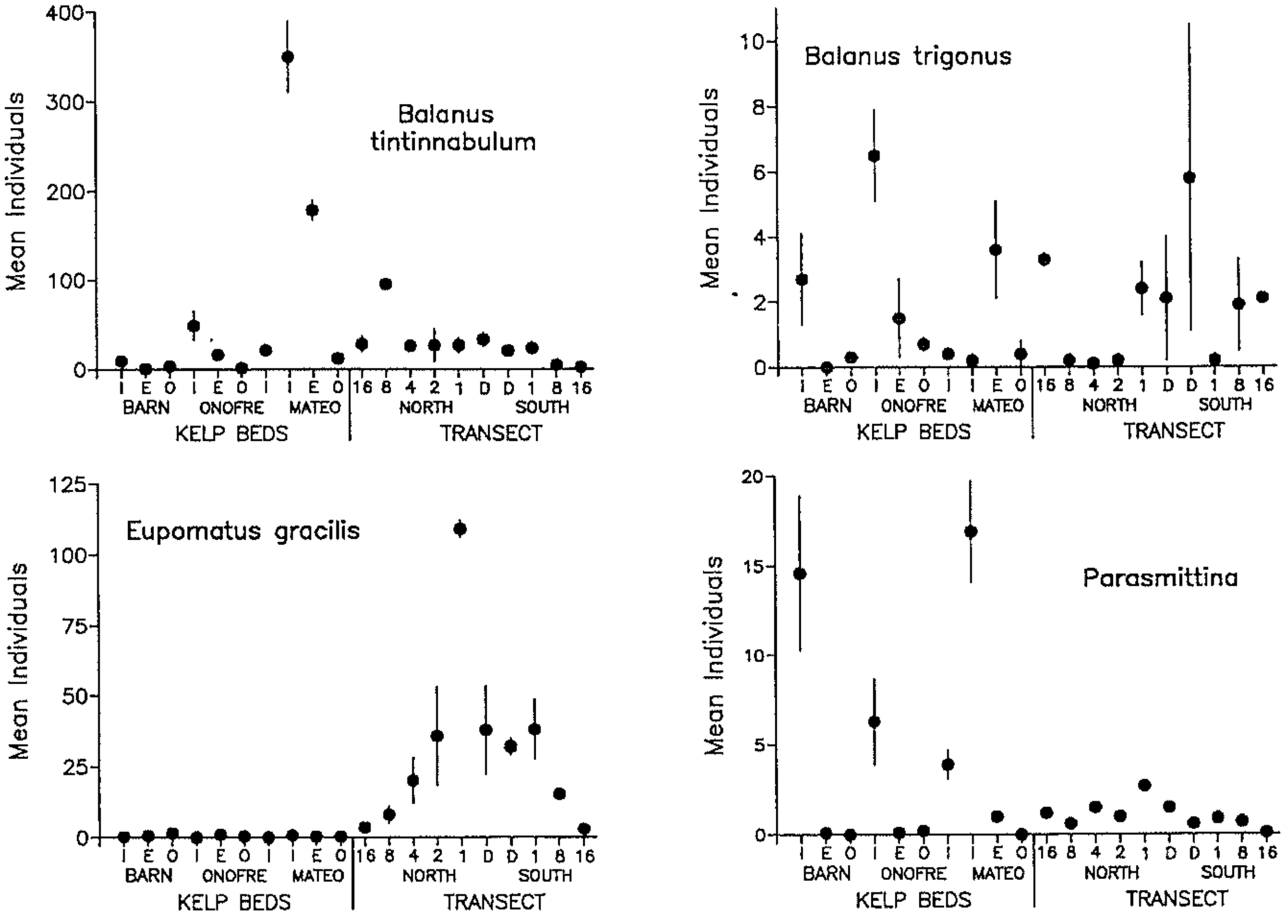

Figure 1. Mean recruitment of four species at the 20 stations along the southern California coast. Shown are the 10 kelp forest sites and the inshore transects north and south of the outfall of the San Onofre Nuclear Generating station. Kelp forest stations are shown by forest (Barn, San Onofre, or San Mateo) and by location (Inside, Edge, Outside). Transect stations are arranged north to south from 1600 m to 50 m (D) from the discharge.

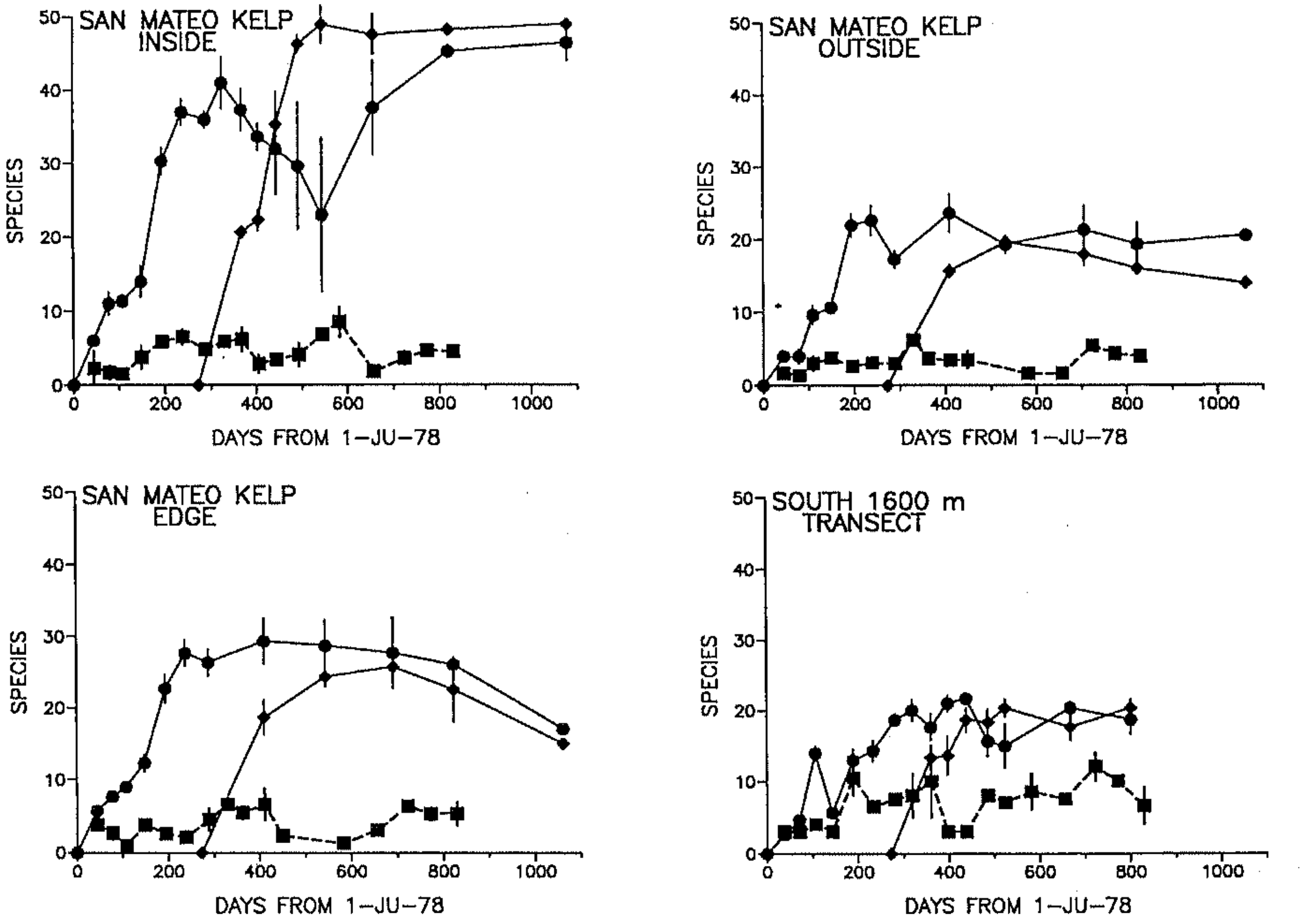

Figure 2. Colonization curves for the 3 San Mateo Kelp Forest stations and the Inshore Transect station 1600 m South of the Outfall. Curves show the mean cumulative number of species on panels initially exposed in June 1978 (Circles) and March 1979 (Diamonds). Mean recruitment (Squares) is also shown.

cantly higher inside kelp forests were ones with short-lived, poorly dispersing larvae (e.g. the bryozoans *Parasmittina*, *Rhynchozoon*, and *Tubulipora*) and those most abundant outside were species with longer-lived larvae (e.g. *Obelia*, *Chama*) or larvae more commonly found inshore (e.g. *Alcyonidium*, *Bugula longirostrata*, *Chone*, *Eupomatus*). However, exceptions such as *Balanus tintinnabulum* which recruited in significantly higher numbers inshore as well as inside kelp forests, were found.

Regardless of the particular patterns the recruitment data do show that significant differences can occur consistently between different sites. Recruitment was measured over a 2.5 year period and many of the species exhibited significant differences between inshore and offshore sites, along the inshore transects, and in relationship to kelp forests. For the most part patterns did not reflect differences in life-history among the species. The inshore transect data do suggest that patterns of water movement (artificially induced by a power plant outfall) can have broad effects on the recruitment of most species. The offshore kelp forest data also suggest that the recruitment of some poorly dispersed species may be influenced by the proximity of reproducing adults. That is, some bryozoan species that produce short-lived larvae recruited in higher numbers inside kelp forests (where adults are most abundant) than outside. However, species with long-lived larvae (e.g. *Balanus tintinnabulum*) exhibited a similar pattern. Nonetheless, it is clear that the location of artificial reefs can have a great effect on the level of recruitment of a variety of species. The next question is whether such differences in

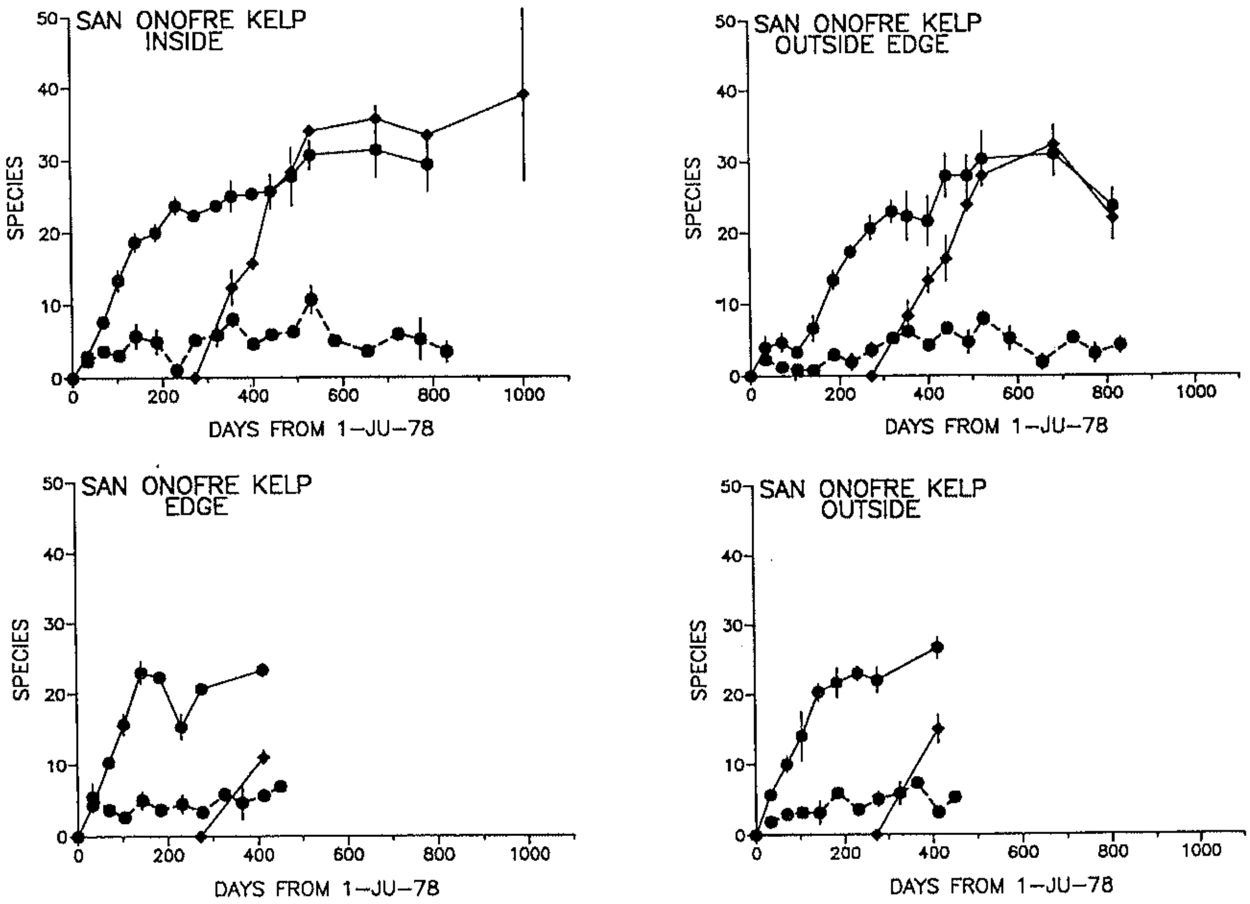

Figure 3. Colonization curves for the 4 San Onofre Kelp Forest stations. Symbols the same as Figure 2.

recruitment can influence the community development on reefs placed at different locations.

Colonization and Community Development - The California colonization data can be used to address the long-term effect of reef location on community development. Figures 2-5 contrast the changes in species abundance on long-term colonization panels at different sets of stations. For each station the number of species on panel series initially exposed in June 1978 and March 1979 are shown as well as the number of species on recruitment panels exposed each sampling period. In general, species abundance at most stations reaches an asymptote after 1-2 years, representing an equilibrium between the rate of the continuing recruitment of new species and the local extinction or loss of species already present. In addition, the June and March series at each station generally equilibrate at the same number of species, while series at different stations often reach very different levels of species abundance. However, recruitment in terms of number of species does not exhibit large differences among the stations.

Figure 2 contrasts colonization at the three San Mateo Kelp Forest Stations as well as the 1600 m South Inshore transect station. There is a striking difference between the station inside the kelp forest where panels accumulate almost 50 species/panel with the station outside the kelp forest with 20 species/panel. The outside station also did not differ from the inshore transect station, while panels at the kelp forest edge station reached species abundance levels intermediate between the inside and outside stations. There is a clear indication from these data that the distance a station was from adult populations producing new recruits (i.e. the natural reef inside the kelp forest), influenced the number of species that could be maintained on any substrate.

Figure 3 contrasts similar data for the San Onofre Kelp Forest. Although the patterns are less clear (sampling at two of the stations was halted after 1.5 years), there is a similar suggestion of a higher number of species inside the kelp forest than outside with the inside edge station being similar to the outside station and the offshore edge station being similar to the inside station. The San Onofre Kelp Forest did not have a well-defined central reef and hard substrate was more scattered than in the San Mateo forest. Hence, the patterns are not as distinct and the inside station reached only 40 species/panel.

Similar data for the Barn Kelp Forest are plotted in Figure 4. The influx of large amounts of sediment at these sites resulted in the burying of the reef and loss of the kelp forest at the three original sites. Some substrates were transplanted to a new station inside the kelp forest on the remaining reef. It seems clear that species abundances at all three original sites never exceeded more than 25 species/panel. However, when panels were transplanted onto the reef, the number of species increased to levels similar to those found inside the other kelp forests. These data again suggest that the location of a reef may be critical in the type of community that develops.

Finally, Figure 5 contrasts colonization data for four stations along the inshore transect. The proximity of stations to the power plant outfall does seem to result in elevated recruitment and, consequently, a higher diversity of species on the panels. Thus, regardless of the process, it would appear that the location of an artificial reef will have a direct effect on recruitment and the number of species that can accumulate. Obviously the location can also influence the rate of loss of species as a consequence of the presence of predators or changes in overall environmental conditions that would influence mortality.

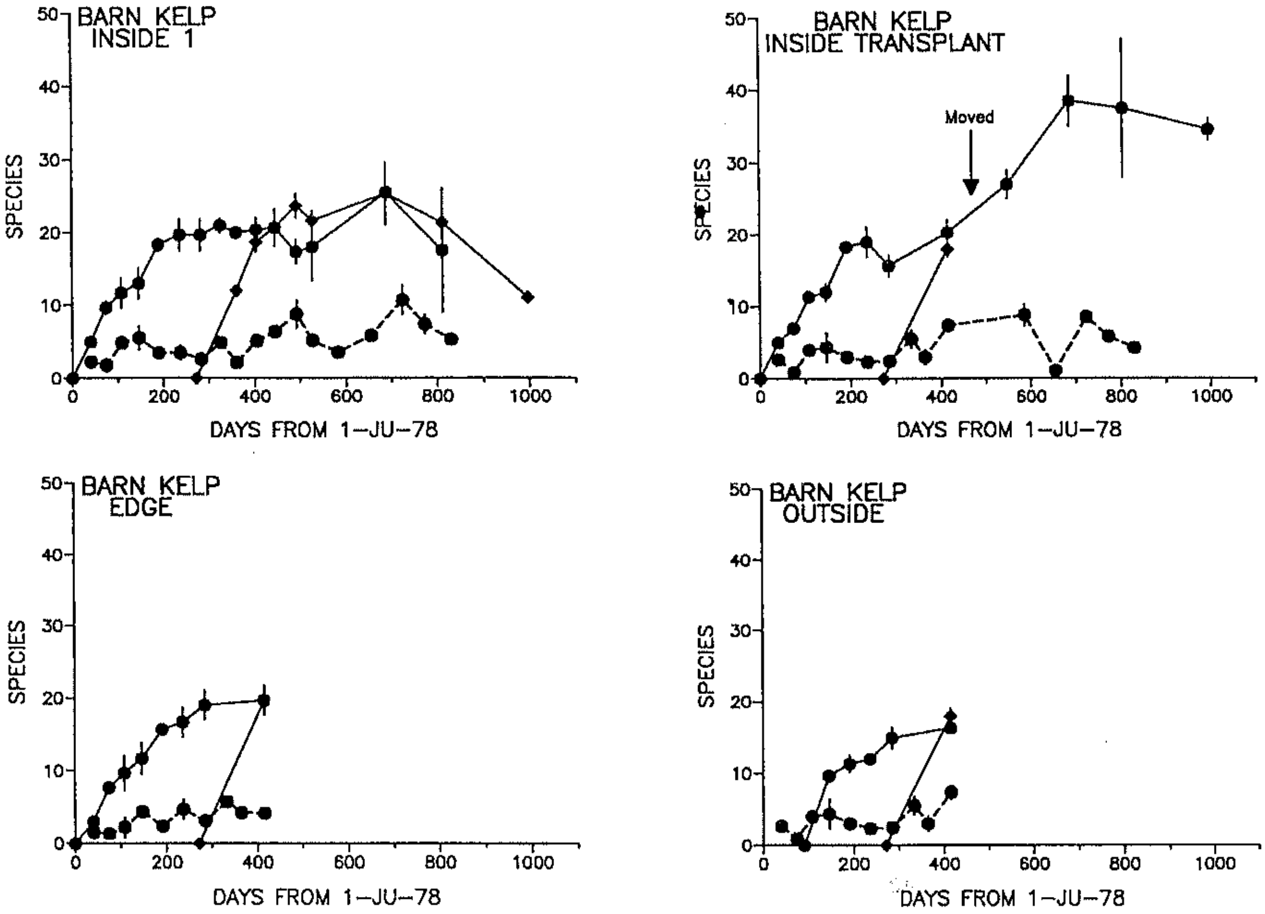

Figure 4. Colonization curves for the 4 Barn Kelp Forest stations. The Transplant site was established in 1979 at a site not covered by sediments and panels from the Edge and Outside sites were moved to it. Symbols the same as Figure 2.

Differences between the sites were not only seen in the number of species colonizing the substrates, but also in the dominance relationships among the species present. Figure 6 shows the similarity among 12 colonization panels exposed at the inshore transect station 1600 m north of the power plant discharge. The panels are from series initially exposed during four different seasons from the summer of 1978 to the spring of 1979. What is clear from Figure 6 is that regardless of when substrates were placed at this site, the bryozoan *Alcyonidium parasiticum* dominated the panels, resulting in a high degree of similarity between all substrates. This contrasts sharply with the pattern of dominance at the station inside the San Mateo Kelp Forest (Figure 7). For a similar series of panels at this site, the clonal polychaete *Salmacina tribranchiata* dominates summer and fall series while the bryozoan *Parasmittina* sp. dominates the winter series. The spring series is split between panels dominated by *Parasmittina* and a panel dominated by *Salmacina*. In addition, the dominance on the spring series (as well as on one summer panel) is fairly weak resulting in 4-6 species sharing the dominance. Thus, even though individual substrates at this site may become dominated by one or a few species, different substrates are dominated by different species, which is usually dependent on colonization history. For example, the lack of dominance by *Salmacina* on the one summer panel resulted from the mutualistic hydroid *Zanclea* colonizing *Celleporaria* colonies and preventing *Salmacina* dominance (Osman and Haugsness 1981).

This difference among stations can also be seen in Figure 8, which contrasts winter panels exposed at the inshore sites 1600 m north and south of the discharge with panels exposed at the same time in the San Onofre Kelp Forest

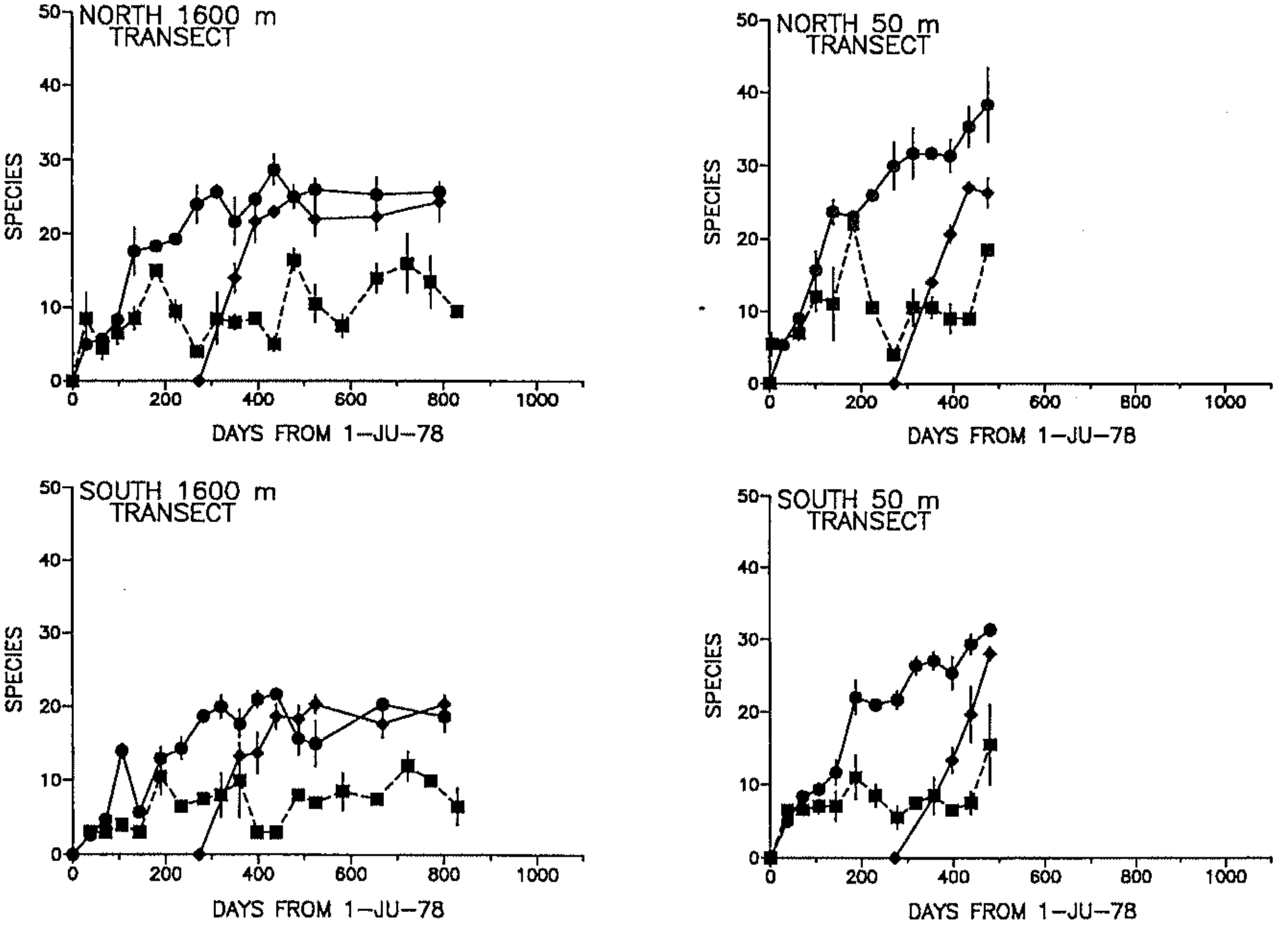

Figure 5. Colonization curves for 4 Inshore Transect stations. Symbols the same as Figure 2.

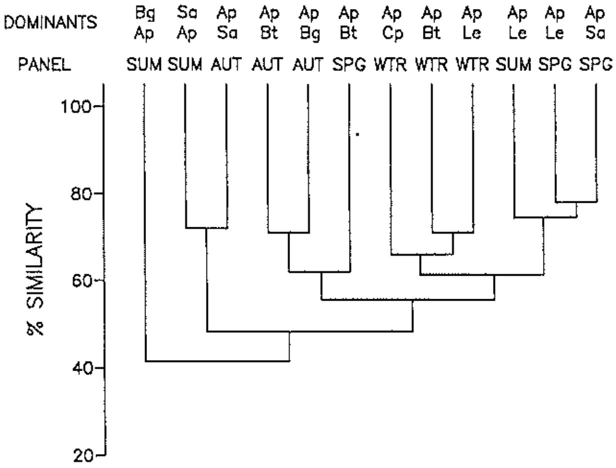

Figure 6. Similarity among 12 panels from the Inshore Transect station 1600 m North of the Outfall. Panels are identified by the season in which they were initially exposed. The dominant species are the most abundant species (in % cover) that together cover at least 50% of the panel surface. Species symbols are: Bryozoans Ap - Alcyonidium parasiticum, *Cp* - Cryptosula pallasiana, *Ps* - Parasmittina sp., *Cb* - Celleporaria brunnea, *Cc* - Callopora circumclathrata, *Sa* - Scruparia ambigua, *Hydroids Bg* - Bougainvillia glorietta, *Od* - Obelia dichotoma, *Barnacles Bt* - Balanus tintinnabulum, *Sponges Le* - Leucosolenia eleanor, *Polychaetes St* - Salmacina tribranchiata, *and +2 - 2 additional species, +4 - 4 additional species.*

inside and offshore edge stations. Even though the 2 inshore sites were at opposite ends of the inshore transects and 3.5 km apart, they were all dominated by *Alcyonidium* and showed a high degree of similarity. The substrates at the kelp forest stations were also much more similar to each other than to panels at the inshore station. However, there was much more variability in dominance and only one pair of panels dominated by *Celleporaria* were more similar to each other than all of the inshore panels.

Thus, from the California studies it seems clear that substrates placed at different locations can develop very different communities depending on recruitment differences and the effects of these differences on community development. These differences occur despite the fact that the deployment of the substrates was identical. Even though background larval availability may be regionally determined, the local sites, both in terms of the physical environment and the communities already present, can have a strong effect on the type of community that develops. Local differences can result in huge differences over a small scale (inside to outside of a kelp forest). Conversely, similarities among inshore stations suggest that where local conditions are fairly similar (except for sites near the power plant discharge), distant sites can develop remarkably similar communities. In applying these results to the establishment of artificial oyster reefs it seems clear that the local placement of the reef will be critical to the kind of community that develops.

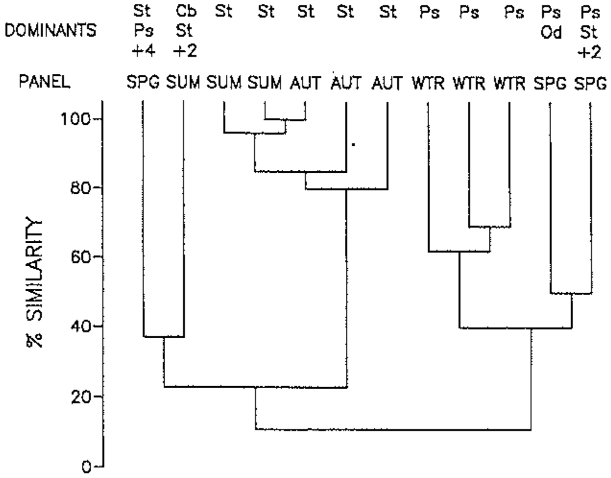

Figure 7. Similarity among 12 panels at the station inside San Mateo Kelp Forest. Symbols the same as Figure 6.

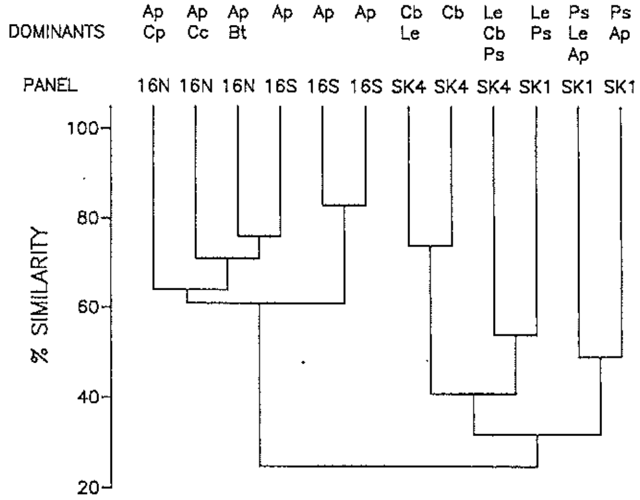

Figure 8. Similarity among winter panels from the 1600 m N and 1600 m S stations on the inshore transect and panels from inside (SK1) and the offshore edge (SK4) stations of the San Onofre Kelp Forest. Symbols the same as Figure 6.

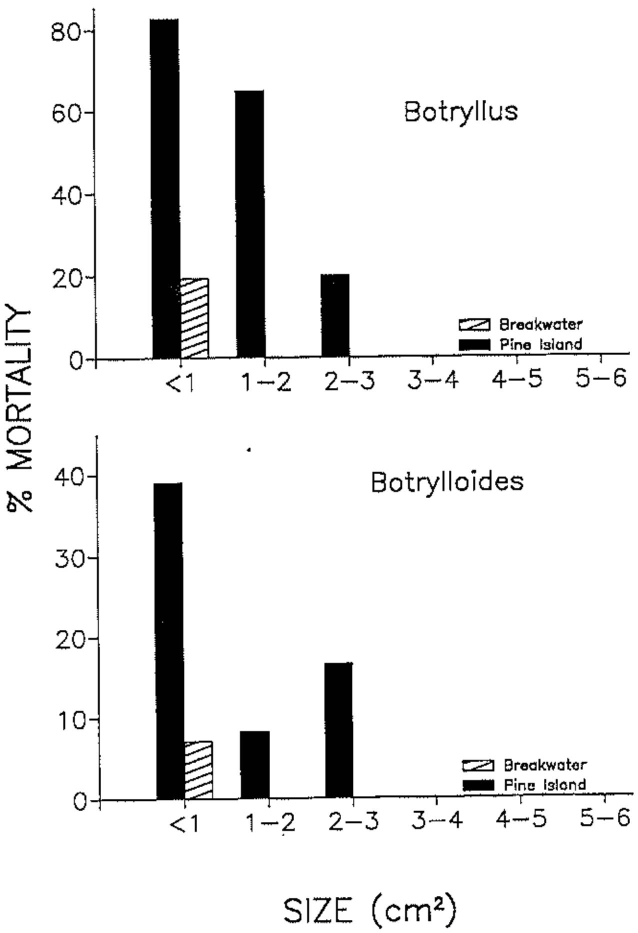

Figure 9. Mortality of recruits and juveniles of Botryllus *and* Botrylloides *at the Connecticut Pine Island and Breakwater sites.*

CONNECTICUT

Even though the Connecticut study was conducted over a much smaller spatial scale than the California study, the results support the same general conclusions found in California. The two Connecticut sites showed extreme differences in recruitment, resulting from local differences. As we have shown in previous studies (Osman et al. 1990, 1992; Osman and Witlatch 1995), the major difference between the two field sites was the presence of predators at the Pine Island site that preyed mostly on new recruits and juveniles of several ascidian species.

The difference between the two sites can be seen in Figure 9 which contrasts the mortality of recruits and juvenile colonies of the ascidians *Botryllus* and *Botrylloides*. The mortality of the smallest sizes of both species was much higher at the Pine Island site where the predators were present. As in other studies, the mortality of *Botryllus* in the presence of predators was much higher than that of *Botrylloides*.

The effects of the different guilds of predators at the Pine Island site on four representative species can be seen in Figure 10. The pattern of mortality for new recruits of the colonial ascidians, *Botryllus* and *Diplosoma* suggest that recruits of these species are extremely vulnerable to the small predators that can get to pilings inside the field cages. The mortality for both species is reduced only in the full-screen treatment. The exclusion of larger predators (fish and large invertebrates) in the caged and partially-screened treatments had little effect in reducing mortality. The pattern of mortality for the 2-week-old juveniles of the solitary ascidian, *Ciona* contrasts sharply with the patterns for *Botryllus* and *Diplosoma*. The mortality of *Ciona* was only high in the open treatment, suggesting that predation by fish (and possibly larger invertebrates) represents an extremely important source of mortality. Finally, juvenile colonies of the colonial bryozoan, *Cryptosula*, show almost no mortality in any of the treatments, suggesting little effect of predators on this species. Thus, these transplant experiments demonstrate that recruitment can be very different between stations; in this case resulting from the presence of several guilds of predators at one station. These predators differentially remove new recruits and juveniles of several dominant species and this results in local recruitment patterns dominated by different suites of species. Thus artificial reefs colonized by such predators would develop a very different community than reefs devoid of such predators.

The community effect of such local phenomena can be seen in the preliminary results of the colonization experiments (Figure 11). Panels exposed at the Breakwater site for one and two weeks were then transplanted to the Pine Island site. The resulting mortalities after 1 week exposure at the Pine Island site are contrasted. The mortality of *Botryllus*, *Botrylloides*,

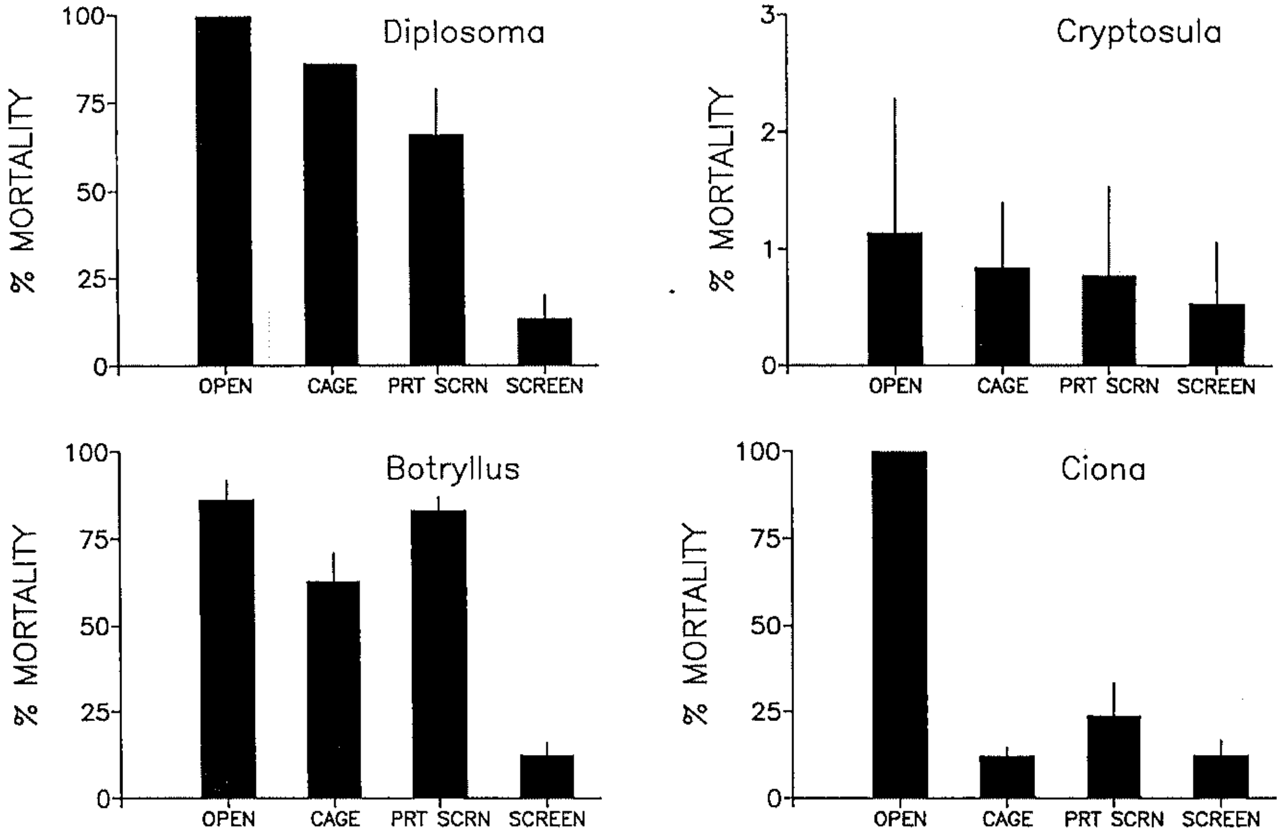

Figure 10. Mortality of recruits and juveniles of 4 different species in piling experiments conducted at the Pine Island site. Species are: the colonial ascidians Diplosoma macdonaldi *and* Botryllus schlosseri, *the solitary ascidian* Ciona intestinalis, *and the bryozoan* Cryptosula pallasiana. *Treatments are: Open Pilings, Caged Pilings, Partially Screened Pilings, and Screened Pilings. Bars are mean mortality for each treatment (± S.E.).*

Balanus, and *Cryptosula* on the colonization panels exhibit a similar pattern of high mortality on Open and Caged treatments and much lower mortality on substrates on a rack suspended above the bottom. Since the caged treatments excluded fish and benthic predators (but not *Mitrella*, *Anachis*, and other small predators) and the racks excluded all benthic predators, it appears that the recruitment of these species was reduced by the small predators. On the other hand, the arborescent bryozoan *Bugula* and the solitary ascidian *Molgula* on panels transplanted

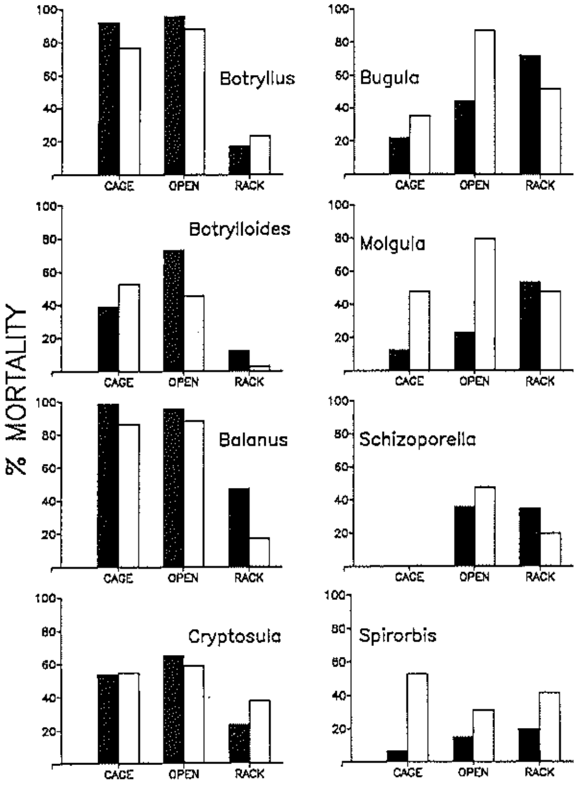

Figure 11. Mortality of 8 species in colonization experiments. Panels were transplanted from the Breakwater site after 1 and 2 weeks. Mortality after exposure at the Pine Island site is contrasted among the 3 treatments. Black bars - one week transplant series, White bars - 2 week transplant series. Mortality was measured after 1 week exposure at the Pine Island site.

after one week suffered their highest mortality on the suspended racks while on 2-week-old panels they exhibited their highest mortality on open pilings. These data suggest that fish, which had access to both treatments, reduced the recruitment of these species. Finally, encrusting bryozoan *Schizoporella* and serpulid polychaete *Spirorbis* exhibited no regular pattern among the treatments, suggesting that predators may have had little influence on their post-settlement mortality. It is also important to note that these two species are consistent dominants at the Pine Island site.

Discussion

The results of both the California study and the Connecticut study strongly suggest that local conditions can have a very strong influence on the recruitment of a wide variety of species. In turn, these differences in recruitment can affect the development of the community and eventually which species are dominant and the degree to which they dominate the local habitat. The local mechanisms controlling recruitment and community development are varied. For example, physical differences such as the inshore-offshore differences in southern California or the increased recruitment near the power plant outfall can be important. Proximity to existing populations (inside to outside of kelp forests) or the presence of predator communities (Connecticut) can have consistent and long-lasting effects on recruitment and species dominance.

It is also important that local conditions and processes affected a broad range of species. Although taxa with short-lived larvae, such as bryozoans and ascidians, are much more likely to be influenced by the proximity of adult populations, species with long-lived larvae (e.g. *Balanus tintinnabulum*) were also influenced by kelp forests. Vulnerability of recruits to predation also spanned a wide range of taxa and life-histories (e.g. Figure 11).

The implications of these results for the planning and locating of oyster reefs seems clear. If one of the goals of the reefs is to establish a naturally rich community of associated species, then the locating of a reef must be carefully considered. Proximity to existing reefs may govern the colonization rates of many species. The season when a reef is established can also influence the order in which species arrive and this can have long-term consequences on dominance or even whether late-arriving species can survive. For example, the establishment of predator populations could preclude the successful recruitment of some species. As we have seen in our Connecticut studies, differences in communities on reefs can remain for long periods of time with the local reproduction of poorly dispersing species and strong effects of locally abundant predators controlling dominance. In this sense, the community that develops on a reef may have an exceedingly strong influence on the ability of other species to become established. Once established, communities may persist for a long time.

There are also implications for the oysters themselves. Local conditions may have an equal or greater importance to the overall abundance of available larvae in determining the successful recruitment of oysters onto a reef. The presence of predators or parasites on the reef as well as sedimentation or hypoxia may control success much more than the supply of larvae. Locating reefs away from existing reefs may reduce the diversity of the reef community, but it may also reduce sources of mortality for the oysters themselves. Thus, if production of oysters is a primary goal, rather than the establishment of oyster reef habitat, the siting and location of the reefs may be very different.

Although there are many unanswered questions about the relative importance of different phenomena and processes, the creation of oyster reef habitat must incorporate a consideration of the local processes that are likely to govern each reef's short- and long-term success. Simply placing substrate on the bottom, regardless of its nature, is not oyster reef restoration.

Acknowledgment

The California study was supported by grants from the Marine Review Committee of the California Coastal Zone Commission and the Connecticut study was supported by grants from the National Science Foundation (OCE 9101615 and OCE 9123890). Maryland Sea Grant (RWO) and Connecticut Sea Grant (RBW) supported the authors' attendance at the symposium on Oyster Reef Habitat Restoration. J. Haugsness, J. Deacon, C. Mann, R. Day, and R. Smith assisted with field and laboratory work in California and P. Mitchell, A. Frese, R. Stankelis, M. Holt, C. Cooper, B. Lussier, J. Siemon, M. Vega, and A. Gordon assisted in the Connecticut study. We wish to thank the organizers of the symposium for inviting us to participate and present our ideas. This is Contribution Number 304 of the Marine Sciences and Technology Center, University of Connecticut.

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Chapter 13

Oyster Reefs As Metapopulations: Approaches for Restoring and Managing Spatially Fragmented Habitats

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Abstract

An intrinsic feature of oyster reef habitats is their fragmented spatial structure. In order to develop an understanding of how physical and biological processes influence the distribution and abundance of organisms on reefs, it is important to recognize this spatial complexity and how it influences oyster population productivity and persistence. Viewing reef habitats in a metapopulation framework ("a population of populations", Levin, 1970) provides a construct to begin assessing the relative contribution of within- and between-reef dynamics and identifying potential demographic "bottlenecks" in the oyster's life cycle. In this article we present a simple metapopulation demographic model for *Crassostrea virginica* which identifies the importance of source areas (e.g., seed beds, productive local habitats) to the contribution of population dynamics within a given region. Results of model simulations also indicate local reef habitat harvest reserve areas can protect against catastrophic collapse of a regional fishery. The identification of sub-populations within a regional landscape which contain productive populations of oysters and habitats which are recognized as good oyster setting areas will also provide resource managers with information on how to establish new or restore existing reef habitats in order to maximize regional shellfish production.

In contrast to the more conventional emphasis on local population dynamics, the metapopulation framework focuses attention on the processes of dispersal between sub-populations, and the variability of recruitment and post-settlement processes affecting populations within and between local habitats. Despite the potential of broad-scale dispersal at the regional scale, oyster recruitment tends to be highly variable over different spatial scales. Information on larval dispersal ability between various sub-populations is very important when establishing the size and spacing of reef habitats. The persistence of sub-populations is also dependent on the nature of local biotic and abiotic interactions. Given there are few tested approaches that enable us to recognize the limitations of scaling up local interactions, caution is advised in trying to predict regional population dynamics from the study of a limited number of local sub-populations.

Introduction

The importance of spatial structure affecting the dynamics of natural populations is generally widely accepted among population ecologists (Kareiva 1986), and there is need for a thorough understanding of spatially-related population processes when considering restoring and managing oyster reef habitats. An intrinsic feature of these habitats is their fragmented spatial structure. The organisms inhabiting reefs are likely influenced by reef size, morphology and position as well as the degree of interconnectiveness and spatial arrangement of individual reef patches within a given region. Because of habitat patchiness, factors affecting local population dynamics of reef inhabitants may not necessarily be similar to processes influencing regional dynamics. Permanent or transient physical or biological differences among sites cause local variation in the mortality and reproductive rates of reef inhabitants.

The population dynamics of sessile organisms inhabiting marine reefs can best be viewed as a suite of sub-populations in which the various local groups of inhabitants are interconnected by larval dispersal between the sub-populations. Organisms like oysters that broadcast gametes into the water column serve to break the connection between reproduction and recruitment at the local scale and add to the connectivity among the sub-populations. While the "glue" which mixes the sub-populations together is larval dispersal, the degree of interconnectivity between populations is not always a simple function of spatial proximity between sub-populations (e.g., Osman and Whitlatch 1999, Chapter 12, this volume, and references therein). Attention, therefore, must be directed to assessing the ecologically-relevant spatial scales of recruitment variability. In addition, the interplay of recruitment dynamics and local post-settlement interactions within sub-populations becomes a key feature in order to describe the population dynamics and persistence of reef organisms. Local dynamics can be exceedingly variable in space and time, can be dependent upon relatively small-scale differences in the biotic and abiotic environment (e.g., Osman and Whitlatch 1999, Chapter 12, this volume).

Population ecologists have formalized the description of spatially-explicit population dynamics by invoking the use of the term *metapopulation* dynamics. This term is used to describe the dynamics of spatially fragmented sub-populations of organisms which are linked by dispersal of individuals between the sub-populations (e.g., Kareiva 1990 and Hanski and Gilpin 1991 for reviews). While the metapopulation concept is more than 25 years old (Levins 1970), it has gained renewed interest in the ecological and conservation literature. With continued human-induced habitat fragmentation of plant and animal populations, greater emphasis has been directed to describing specific requirements of species in local habitat patches necessary to maintain regional population persistence (e.g., Quinn and Hastings 1987; Rolstad 1991; Quinn and Karr 1992; Hanski and Thomas 1994). In addition, for many species of marine benthic organisms local reproductive output and recruitment are frequently poorly coupled and knowledge of regional patterns of recruitment variability are necessary in order to fully assess local population dynamics (e.g., Roughgarden et al. 1985; Roughgarden and Iwasa 1986).

There are a variety of metapopulation models, ranging from "mainland-island" concepts in which all migration occurs from a "mainland" to "island" or habitat patches (e.g., MacArthur and Wilson, 1967) to habitat patches of all the same size with no outside migration (e.g., Levins, 1970). As noted by Hanski and Gyllenberg (1993) most natural metapopulations likely fall somewhere between the two extremes. From the viewpoint of marine populations associated with reef habitats, a convenient metapopulation structure is to view individual local populations within a regional landscape as a loosely connected collection of "source" and "sink" sub-populations (e.g., Pulliam 1988; Pulliam and Danielson 1991). This conceptual framework is somewhat analogous to the more traditional view of characterizing specific reef habitats as "good" and "poor" recruitment sites or "productive" and "non-productive" sites (e.g., Moore 1911; Marshall 1954; Haven and Whitcomb 1983, 1986). For reef habitats, the various sub-populations of sessile oysters within a region are connected by dispersing of larvae. The reproductive output of adults in sink habitats is insufficient to balance local mortality, and the persistence of these sub-populations is dependent upon external supply of recruits from other sub-populations. In contrast, segments of the regional population living in source habitats are capable of providing sufficient quantities of new recruits to maintain sub-population persistence in both sink and source habitats. Other sub-populations can act as both source and sink habitats, receiving recruits from source patches and contributing recruits to sink sub-populations.

In this paper we examine the utility of viewing reefs as spatially fragmented habitats by introducing a generalized metapopulation demographic model for the American oyster, *Crassostrea virginica*. Our primary intent is to illustrate how the source-sink framework can be used to better assist our understanding of the population dynamics of organisms inhabiting reef systems. Our approach examines differences in population vital rates (e.g., survivorship, fecundity) and measures of population performance (e.g., population growth rate) as a function of availability of source habitats. We are particularly interested in assessing the relative role that differences between source and sink sub-population availability have on regional oyster population dynamics and persistence.

Viewing populations of reef organisms in a metapopulation framework defines an interacting group of assemblages of organisms in which population dynamics are closely linked with the processes of establishment and extinction of sub-populations. The study of metapopulation dynamics, therefore, is essentially the study of the conditions under which colonization and extinction are in balance coupled with factors affecting these two processes. Implicit to the source-sink concept are the assumptions that dispersal of individuals between sub-populations must be non-random and that processes affecting local post-settlement population dynamics must be spatially variable. If dispersal between the various sub-populations is so high that all the recruits become entirely mixed with each other or if local post-settlement mortality patterns are similar for all sub-populations, one can more easily treat all of the sub-populations as a single unit rather than invoking the use of a metapopulation framework to describe population dynamics. In a companion article (Osman and Whitlatch 1999, Chapter 12, this volume), we present several examples which illustrate the recruitment dynamics of a variety benthic reef invertebrate species at 20 different locations positioned along a 25 km portion of the coastline in southern California. Collectively, results of this work were consistent with the supposition of non-uniform recruitment which is characteristic of a metapopulation structure. Reef invertebrate recruitment was highly variable over space and time and displayed little spatial coherence among sampling stations, even at relatively small spatial scales (e.g., stations located hundreds of meters apart). These dynamic recruitment patterns existed regardless of length of the dispersal phase of a particular species.

To examine the second assumption related to metapopulation dynamics, we present results which examine the effects of variability in the density of different oyster life stages on patterns of post-settlement growth and mortality. Our previous work on post-settlement interactions has primarily focused on the examination of competitive interactions between oyster larval and juvenile stages with other species of sessile invertebrates (e.g., ascidians, bryozoans, barnacles). Field and laboratory studies have generally demonstrated that inter-specific density-dependent competitive interactions can negatively effect oyster larval recruitment (Osman et al. 1989) and significantly reduce juvenile oyster growth (Zajac et al. 1989; Osman et al. 1990). These interactions can have important consequences on the dynamics of oyster population (Whitlatch and Osman 1994).

Methods and Approach

A. METAPOPULATION MODELING

A simple metapopulation model for *Crassostrea* was developed in order to incorporate demographic variability between source and sink sub-populations and how this variability influences population dynamics within a particular region. The model consists of spatially distinct source and sink sub-populations of oysters which are all reliant upon a common larval pool for the recruitment of new individuals to the sub-populations. The model, therefore, places emphasis on the demographic responses within sub-populations and how they vary as a function of local conditions. Demographic variability of the sub-populations was analyzed using life cycle graphs (e.g., Hubbell and Werner 1979; Caswell 1989); a graphical technique which depicts a species' life history as a series of nodes which represent particular stages in the life cycle which are appropriate for estimating vital rates.

Figure 1 depicts a graphical representation of the oyster source-sink demographic model. The model consists of five year-classes (nodes) of oysters inhabiting both source and sink sub-populations. The nodes are connected by arrows depicting transition probabilities of survivorship (P_x) into the next node and reproductive output (F_x) from a node. Since there is presently no complete life table for a specific *Crassostrea* population, estimates of P_x and F_x values for inclusion in the model were obtained from a generalized oyster life table compiled by Malinowski and Whitlatch (1988). In addition, estimates of *Crassostrea* larval survivorship are also presently unavailable; and we estimated survivorship rates for this life stage to be $10^{-6}\%$. Galtsoff (1964) reported the combined survival of *Crassostrea* larvae and juvenile stages to be $10^{-8}\%$ while others have found the combined survivorship of larvae and juveniles for a variety of marine benthic invertebrates typically ranges from $10^{-5}\%$ to $10^{-9}\%$ (Rumrill 1990). Since age-specific survivorship and fecundity schedules of natural populations can be habitat-specific and vary considerably over relatively small spatial scales (e.g., Caswell and Werner 1978; Zajac and Whitlatch 1989; Horvitz and Schemske 1995) we included a small amount of variability (10% variance) in the transition probabilities in some of the model simulations. It should be noted that our primary intent is to provide general examples of the source-sink metapopulation framework rather than attempting to model the dynamics of a specific oyster population.

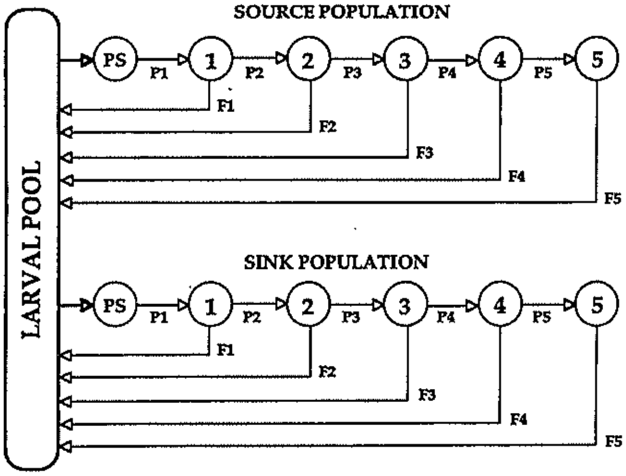

Figure 1. A simple demographic-based metapopulation model of the oyster Crassostrea virginica. *The model consists of source and sink populations which are dependent upon a common larval pool for the recruitment of new individuals to the sub-populations. Nodes (oyster life stages: PS = post-set; 1-5 = year classes 1-5) are connected by arrows which depict transition probabilities for survivorship between nodes (P_x values) or contributions of the reproductive (F_x values) output of each node. See text for further description.*

The resultant oyster population matrices were solved for $\ddot{e}_m$ (the dominant eigenvalue of the transition matrix) which was used as a currency to evaluate potential population growth for a given population within a particular region (e.g., Caswell 1989 and references therein). $\ddot{e}_m$ is also a measure of average fitness of individuals living in a given region (Fisher 1930; Charlesworth 1980; Caswell 1989) and is equal to e^r; where r is the intrinsic rate of increase in a population. Therefore, values of $\ddot{e}_m$ greater than unity indicate population increase, or in the present case, favorable conditions for population growth within a regional population. Values below one indicate population decline and $\ddot{e}_m$ values at unity indicate population equilibrium. Comparisons of $\ddot{e}_m$ values were used to provide relative measures of regional demographic responses to variations in the availability of source and sink habitats.

An analysis of the relative importance of each of the parameters in the life cycle matrices, with respect to $\ddot{e}_m$, can be accomplished by sequentially changing single parameters in the matrix and observing their relative effect on $\ddot{e}_m$. An alternative and more straightforward procedure, known as sensitivity analysis, has been developed by Caswell (1978; 1989) and uses the stable age distributions and reproductive values (right and left eigenvectors of the matrix, respectively) to assess the sensitivity of $\ddot{e}_m$ to changes in fecundity and survivorship. For these analyses we elected to use the elasticity index (Caswell et al. 1984; de Kroon et al. 1986) which is a measure of proportional sensitivity; each parameter being a product of the sensitivity with the actual transition value divided by the population growth rate. Elasticity values are useful in assessing how relative changes in individual life history parameters (e.g., changes in survivorship and fecundity) affect population growth rate. Elasticities are readily comparable among life history stages since they are scaled by the magnitudes of the transitions themselves.

B. Post-Settlement Studies

Field work to examine oyster post-settlement survivorship and growth was conducted in the western drainage branch of Tom's Creek, a small tidal estuary located along the western boundary of Hammonasset State Park, Madison, CT. Creek waters drain into eastern Long Island Sound and the lower portion of the estuary has historically been used as a grow-out habitat for juvenile oysters. Sediments at the study site consist of firm sandy-muds; and common benthic organisms found in the area include other bivalves (e.g., *Mercenaria mercenaria*, *Mya arenaria*, *Mytilus edulis*) and several species of decapod crustacean predators (e.g., *Carcinus maenas*, *Panopeus herbstii*) and polychaeteous annelids (e.g., spionids, nereids, orbiniids).

To conduct the experiments on the effect of adult oyster density on spat growth and survival, adult oysters were spawned and spat were set on 100 cm^2 roughened PVC panels. Panels were placed in a filtered running seawater system and after 5 days spat were enumerated and transported to the study site in seawater-filled coolers. Individual substrates were attached to the centers of shallow, plastic-coated wire mesh (mesh size 16 cm^2) trays. The trays were 0.5 m^2 in surface area with sides 8 cm high. The trays were designed to retain adult oysters or oyster shell while minimizing obstruction of physical (e.g., water flow) and biological (e.g., competitors and/or predators) processes which could affect spat growth and mortality during the course of the experiment. Experimental substrates with oyster spat were exposed to four different treatments, each with ten replicate trays: live adult oysters or dead oyster shells placed in the trays at "low" (10-15 per tray) or "high" (30-35 per tray) densities. Individual trays were haphazardly placed in the main channel of the creek, each approximately 2-3 m apart, at a water depth of -0.5 m MLW. Spat growth and survivorship were censused over a three month period from 21 August to 12 November. Censused panels were retrieved at low tide and transported to the laboratory in seawater-filled coolers. The number of live oysters on each panel was counted, and using a dissecting microscope fitted with an ocular micrometer the longest dimension of ten randomly selected oysters on each panel were measured. After censusing, panels were returned to the field and attached to their respective trays within 24 hr.

Early results indicated the oyster spat experienced significant predator-related mortality (e.g., chipped and cracked shells), and a second series of experiments was deployed to assess the extent of density-related mortality of juvenile oysters at the study site. Juvenile oysters (aver-

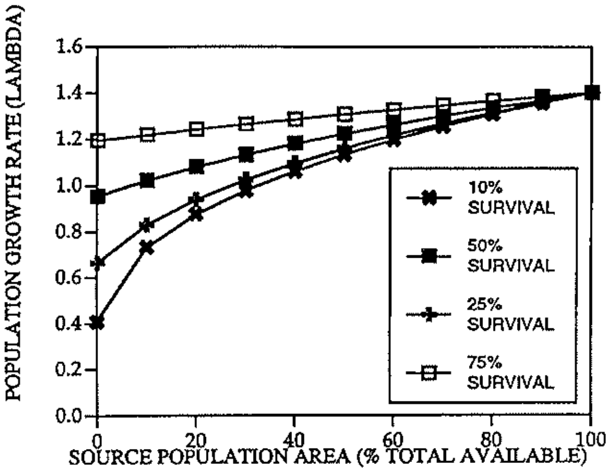

Figure 2. The relationship between regional oyster population growth rate (lambda) as a function of changes in the availability of source habitat for the demographic-based metapopulation model shown in Figure 1. Post-set and juvenile stage oyster survivorship values in sink sub-populations were reduced 10-75% relative to the mortality schedules of the two life stages in source sub-populations.

age length: 15 mm) were placed in 1 m^2 trays (similar in design to those described previously with bottoms lined with 1 mm plastic mesh). The juvenile oysters were deployed at three different densities (10, 50 and 100 individuals per tray), each with five replicates in trays which were left open to crustacean predators or had 2 cm mesh wire mesh tops which were fastened to the sides of the trays. Trays were haphazardly placed 1-2 m apart in the main channel on 1 September and were retrieved on 5 October. Upon retrieval the number of oysters in each tray was counted and examined to determine potential sources of mortality (e.g., drilled shells from carnivorous snails, chipped shells from crab foraging).

Results and Discussion

A. Oyster Metapopulation Modeling

Figure 2 summarizes the results of modeling in which we examined how differences in the vital rates of oysters found in source and sink sub-populations can affect regional oyster population growth rate. In this case survivorship values for post-set and juvenile stage oysters in sink sub-populations were reduced 10-75% relative to the mortality schedules of similar life stages residing in source sub-populations. As one would expect, the regional oyster population growth rate can be greatly influenced by the percentage of available source sub-populations, particularly when early stage oyster mortality in sink sub-populations is high. More interesting is the finding that regional population growth rate is not always a simple linear function of the amount of available source sub-populations. When oyster post-set and juvenile stage mortalities in sink sub-populations are high relative to source sub-populations, small changes in the amount of source sub-populations can result in very large reductions in regional $\ddot{e}_m$ (Fig. 2). These results emphasize that significant reductions of source sub-populations can result in population growth rates less than unity and potentially lead to regional population extinction.

Figure 3 illustrates the effects of the inclusion of a relatively small amount of demographic variability (10% variance in P_x values for post-set and juvenile stages) in transition probability input values in the metapopulation model. Regional population growth rates can be

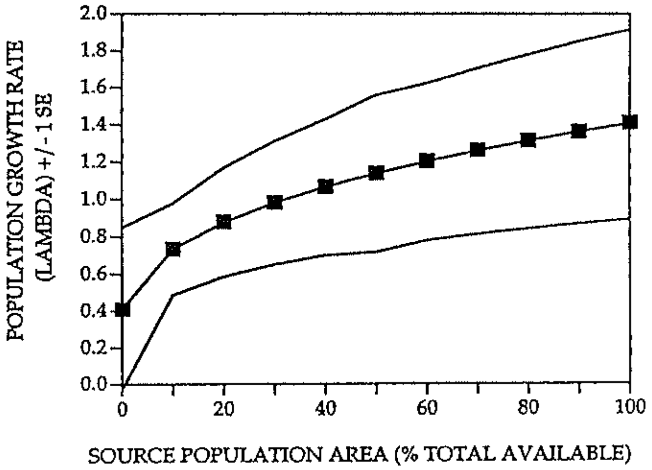

Figure 3. The effect of a 10% variance in vital rates of source and sink sub-population matrices on the relationship between regional and changes in the availability of source habitat for the metapopulation model. Lines around the population growth rate trajectory represent 95% confidence limits.

quite sensitive to variability in oyster vital rates, particularly when the available amount of source population area is relatively low and early stage mortality is high. The figure further illustrates that when source population abundance is low only a relatively small amount of among sub-population variability in early life stage vital rates can potentially lead to extinction of the entire regional oyster population.

In addition to presenting a more realistic description of processes affecting the population dynamics of reef organisms, the source-sink metapopulation framework also provides insights into strategies for establishment, management and harvesting of reef habitats. For instance, our model predicts reef populations are particularly susceptible to catastrophic collapse as gradually increasing habitat destruction or harvesting pressure drops populations below the densities necessary to insure adequate recruitment from source sub-populations. Efforts directed to the development of databases on the quantity and quality of source sub-populations and their degrees of connectiveness to sink sub-populations will provide resource managers with information on where to place new reefs and which habitats are the most likely candidates for reef restoration. In addition, identifying good recruitment habitats and assessing the degree of spatial variability in reef productivity also provides a rationale for assessing which reefs should be left opened to harvesting and which should be left as refugia to supply new recruits to other sub-populations within a particular region.

The sensitivity analysis (using elasticities) which examines how regional population growth rate is affected by changes in survivorship and fecundity of oysters in source and sink sub-populations is shown in Figure 4. The analysis indicates $\ddot{e}_m$ is most sensitive to changes in early oyster life stage survivorship while older oyster life stages contribute proportionately less to population growth (Fig. 4a). This pattern exists regardless of the relative contribution of the two different sub-population types, although the relative contribution of each life stage to $\ddot{e}_m$ varies as a function of the abundance of the source and sink sub-populations. For instance, as the availability of source habitat decreases, early oyster life stage survivorship becomes increasing important in affecting $\ddot{e}_m$. A similar life stage-specific pattern exists for oysters living in sink populations, with early stages survivorship contributing proportionately more to $\ddot{e}_m$ than older life stages. The sensitivity of population growth rate to the survivorship of early life stages appears to be a common feature of a variety of marine benthic invertebrate species (e.g., Malinowski and Whitlatch 1988; Zajac and Whitlatch 1989; Zajac 1991).

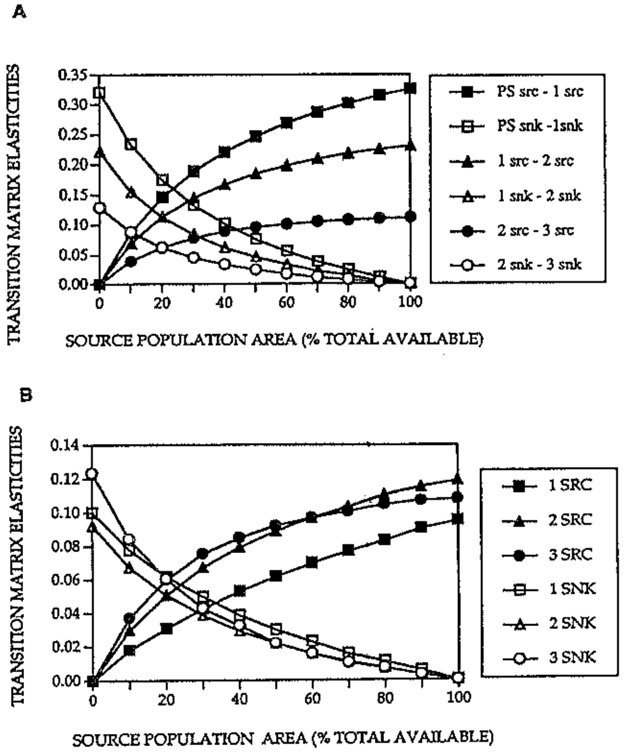

Figure 4. The relationship between the proportional sensitivity (elasticity) of population growth rate to oyster stage-specific changes in (A) survivorship and (B) fecundity. PS SRC-I SRC = transition from post-set to first year in source sub-population; I SRC-II SRC = transition from first to second year in source sub-population; II SRC-III SRC = transition from second to third year in source sub-population. Similar notation for sink (SNK) sub-population. See text for further explanation.

Compared to survivorship elasticity values, the affects of changes in oyster fecundity on population growth rate were both smaller and less variable between oyster life stages in both source and sink sub-populations (Fig. 4b). For example, comparison of the proportional sensitivity of $\ddot{e}_m$ to changes in survivorship with respect to fecundity indicates that population growth rate is 2-3 times more sensitive to the former. Larval and early post-settlement mortality rates of oysters are typically very high (e.g., Galtsoff 1964) and exceedingly large increases in reproductive output are needed to mimic the consequence of only relatively small increases in early life stage survivorship. This life history feature has also been found for other species of commercially important shellfish (Malinowski and Whitlatch 1988).

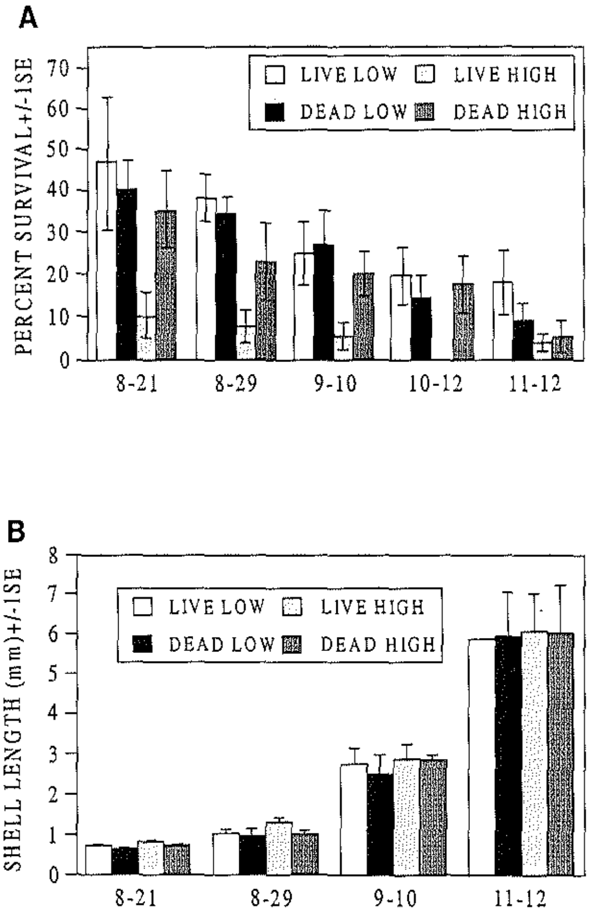

Figure 5. *Experimental results on the effects of two different densities of alive adult (Live low; Live high) and dead adult (Dead low; Dead high) oyster shells on oyster spat survival (see text for details of experimental design). A = average percent spat survival. A repeated measured analysis-of-variance (arc-sin transformed data) indicated the "High live" treatment was significantly ($p<0.05$) different from the other three treatments, except for the last sampling date. No significant differences in spat survival were found among the other three treatments using a Duncan's test after the ANOVA. B = average spat shell length. A repeated-measured analysis-of-variance (untransformed data) indicated no significant differences between treatments during the experiment.*

Results from the sensitivity analysis can be used to begin developing an ecologically-based rationale for size-specific harvesting strategies in the sink and source sub-populations. For instance, results indicate that harvesting should be concentrated on those life stages that contribute the least to $\ddot{e}_m$ (e.g., older life stages). In addition, a far greater return will be gained from management practices directed at increasing early life stage survivorship (e.g., reducing juvenile oyster mortality, enhancing the quality and quantity of recruitment habitats) than from other alternative management practices (e.g., adult "spawner" plantings, free-planting of juveniles). Identifying the relative contribution of the shellfish life stages to population growth also provides a quantitative measure for determining minimum harvest size. As Malinowski and Whitlatch (1988) have pointed out, the reproductive value (e.g., the relative "usefulness" of an individual in a given life stage as a parent in the future [e.g., Fisher 1930; Mertz 1971; Caswell 1980]) of oysters peaks in early life and fecundity is size-related and remains high throughout adulthood. Given these life history traits, care should be taken to avoid harvesting pre-reproductive individuals from any of the sub-populations.

B. OYSTER POST-SETTLEMENT INTERACTIONS

The effects of adult oyster density on the survivorship and growth of newly settled oyster spat is summarized in Figure 5. Results indicate that post-settlement spat survival was significantly reduced in treatments containing high numbers of living oysters when compared to low densities of adults and low and high densities of dead oyster shell (Fig 5a). The treatments containing low densities of living adult oysters and the two densities of dead shells all showed similar spat mortality patterns. While juvenile oyster mortality was negatively affected by high densities of adult living oysters, the growth rate of the newly settled spat did not significantly differ among the various treatments during the experiment (Fig. 5b). Examination of the shells of the dead spat indicated that most of the mortality was due to predation by crabs (chipped and cracked shells) and to a lesser degree by carnivorous gastropods (bored shells). None of the adult oysters died during the experiment, and less than 1% of the shells had margins which appeared to be chipped. Also, there was no obvious evidence that intra-specific competitive interactions between adult and post-set oysters contributed to different levels of spat mortality.

Several studies have demonstrated that the intensity of crab predation is often positively related to shellfish prey density (e.g., Elner and Hughes 1978; Boulding and Hay 1984; Eggleston 1990). In our experiment it appears the predators were responding to variations in the densities of living adult oysters rather than simply the presence of shell material placed in the experimental trays. Crabs may be able to detect patches of high prey density from a distance and selectively forage there. Prey detection through chemoreception is common for crustacean predators (e.g. Pearson et al. 1979). Once attracted to the high density patches of living oysters, between-treatment variations in predator foraging (either through differences in predator number or by individual predator foraging intensity) could lead to observed dissimilarities in oyster spat mortality. Oyster adult-mediated, dependent-density foraging by crustacean predators was, therefore, probably the cause for between-treatment variability in spat mortality.

The finding of predator-mediated density-dependent oyster mortality was also confirmed in our experiments which compared the survivorship of three densities of juvenile oysters placed in cages which excluded predators and trays in which predators had access to the oysters (Fig. 6). While juvenile oyster mortality did not vary with density in treatments excluding predators, we found evidence of density-dependent mortality in treatments exposed to predators. Mortality was more than two times higher in treatments containing 50 and 100 oysters m^{-2} than the treatment containing 10 oysters m^{-2}. Between 80-100% of the recovered dead shells were either chipped or cracked, suggesting most of the mortality of juvenile oysters was the result of crab foraging.

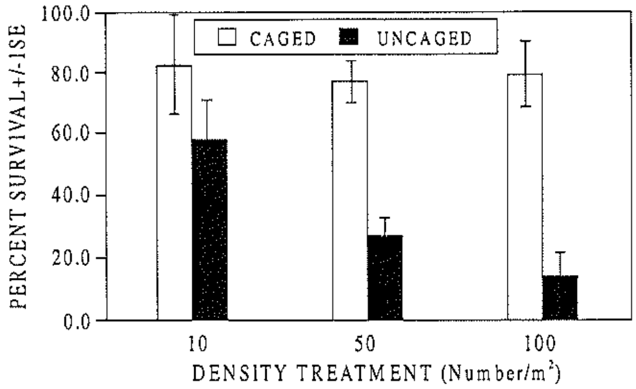

Figure 6. Mortality of juvenile oysters planted at three different densities in trays with and without cages to exclude predators (average percent survival; error bars represent 1 standard error).

Density-dependent mortality in post-set and juvenile oysters is consistent with other studies which have demonstrated a relationship between the density of bivalve prey and predator foraging behavior (e.g., Peterson 1982; Lipcius and Hines 1986; Eggleston 1990). Understanding the role that predation processes play in affecting post-settlement survival of organisms has an important impact on strategies used in the establishment and management of reef habitats. For example, density-dependent survival of juvenile oysters will tend to diminish the long-term effects of annual fluctuations in recruitment. High intensity oyster "sets" will be compensated by increased rates of predation. This suggests that adult densities within a habitat may be much more dependent on the pattern of predator response to increasing prey density at a particular site than the relative degree of recruitment success into that habitat. Intuitively, we would expect there to be strong selection pressures to increase the intensity of recruitment of juveniles into habitat patches but density-dependent survival of juveniles would tend to prevent high densities of juveniles resulting from episodes of dense recruitment from persisting into adulthood. Oysters are a relatively long-lived species, however, that display highly variable age distributions between local habitats suggesting that the relative role of recruitment and predator-mediated density-dependent survival in the persistence of individuals within local habitats may vary considerably.

If density-dependent post-set and juvenile mortality is a common feature of oyster populations, resource managers should place an emphasis on assessing both the spatial and temporal dynamics of recruitment as well as patterns of post-settlement mortality for all oyster life stages. For example, local oyster recruitment success may be dependent upon local adult density. This can result in temporal and spatial shifts on the local population structure and as a consequence a given local population may potentially vacillate from a source sub-population to a sink sub-population and then back again. Density-dependent interactions at the sub-population level may also cascade between different spatial scales due to the inherent patchiness of reef habitats (e.g., Wu and Levin 1994).

Conclusions

The population dynamics of species inhabiting spatially fragmented habitats involves the study of the distribution of individuals among habitats and habitat-specific demographic rates (Pulliam and Danielson 1991). Oyster populations occur as distinct local populations which are weakly connected by larval dispersal. While it has been possible to identify "productive" and "non-productive" reef habitats within a given region, it is not necessarily clear whether between-reef differences in productivity are a consequence of variability in the colonization processes or are the result of differences in post-recruitment growth and survivorship. Despite the potential of broad-scale dispersal at the regional scale, oyster recruitment is often temporally and spatially variable within- and between-sites (e.g., Loosanoff 1966; Abbe 1986; Kennedy 1986). The degree of connectiveness between sites is not simply a function of proximity of sub-populations and is not always easily measured at the appropriate spatial scales. Local variations in post-settlement processes can also contribute substantially to organism survivorship and growth. For example, our experimental studies on artificial reefs in southern New England revealed that local persistence of populations was highly dependent upon life history characteristics of resident and colonizing species, population age-(size) structure of residents and the nature of local interactions with predators and competitors (Osman and Whitlatch 1999, Chapter 12, this volume).

The use of a metapopulation demographic framework for assessing the population dynamics of oysters inhabiting reefs centers on the critical processes impacting the distribution and abundance patterns of different life history stages, thereby promoting identification of potential demographic bottlenecks in the oyster's life history which contribute to population performance. While the results of our model suggest that harvest refugia have the potential of providing valuable protection against catastrophic collapse of a regional oyster fishery, determining the optimal size and spacing of harvest refugia obviously requires more investigation and will depend on the nature of local and regional variability of larval dispersal and post-settlement mortality. Quinn et al. (1993) have developed a metapopulation model for the red sea urchin (*Strongylocentrotus franciscanus*) which points to the importance of larval dispersal ability when establishing the size and spacing of marine reserves. They conclude that a management strategy to avoid over-harvesting red sea urchins while maintaining sustainable yields would be to establish multiple non-fished reserves which are spaced more closely than the average larval dispersal distance of the invertebrate. Unfortunately larval dispersal of benthic invertebrates is highly variable in space and time and difficult to measure the appropriate spatial and temporal scales. With the development of new methods for labelling and tracking invertebrate larvae (see Levin 1990 for a review), however, it may be possible to directly estimate the degree of inter-connectiveness of various sub-populations of oysters within a particular region.

How scale influences population dynamics and persistence is a critical but poorly understood area in population and community ecology (e.g., Levin 1992). Identifying what are the limits to extrapolation from small-scale studies, how processes interact across scales and how we develop new techniques for incorporating scale into ecology are also important questions for population biologists and resource managers. Given the fragmented nature of reef systems, coupled with the high degree in the variability of recruitment and post-settlement mortality patterns, we should proceed with caution when trying to predict regional population dynamics of reef organisms from small-scale studies of a limited number of local sub-populations. At present there are few tested approaches that enable us to recognize the limitations of scaling up from small-scale studies to the level of a specific region (but see Rastetter et al. 1992; Schneider 1994). Recent developments in the use of spatial patch dynamic models (e.g., Caswell and Etter 1993; Wu and Levin 1994) appears to be powerful and promising approach for viewing ecological systems as mosaics of interacting patches which occur at distinct spatial and temporal scales.

Acknowledgments

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Chapter 14

Application of Landscape Ecological Principles to Oyster Reef Habitat Restoration

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Abstract

This paper incorporates recent theoretical and empirical advances in population and landscape ecological principles to provide a conceptual framework for guiding oyster restoration efforts aimed at shell repletion, habitat replacement with new reefs, and the establishment of broodstock sanctuaries. Specifically, it addresses the following questions: (1) what are the management goals in terms of restoration efforts?; and (2) what spatial arrangement (e.g., reef location, size and shape) of oyster habitat best meets these management goals? The management goals of oyster restoration may include, but are not limited to, maximizing: (1) recruitment to the fishery; (2) spawning output; (3) biodiversity (i.e., species diversity of the oyster reef community); and (4) water filtration. These goals are not mutually exclusive, and managers should strive to simultaneously maximize as many goals as possible on a per unit area basis. The concepts of metapopulation dynamics and source versus sink habitats are used as a framework for defining the best location for establishing oyster habitat within an estuarine tributary or water basin, whereas landscape ecological principles concerning habitat fragmentation provide a framework for defining the most productive spatial arrangement and size of oyster patches. Recent experimental results concerning fertilization success in free spawning invertebrates should also be used to guide efforts aimed at quantifying the effects of within-patch oyster density and dispersion on fertilization success. This paper highlights important management considerations in oyster restoration efforts, and provides a series of examples and testable hypotheses, based on modern ecological principles, for designing restoration efforts that maximize specific management goals. Such a conceptual approach should be applicable to a wide variety of coastal systems.

Introduction

The mechanical destruction of eastern oyster (*Crassostrea virginica*) habitat by fishing and mining practices during the last century, combined with the recent prevalence of disease and reduced water quality, has lead to the catastrophic decline of oyster populations throughout the East and Gulf coasts of the United States. The remaining populations consist of low vertical profile crusts of living oysters overlying a sediment-covered base of reef material (Mann et al. 1991; Rothschild et al. 1994). These crusts are often limited to low salinity sanctuaries from disease (Mann et al. 1991). Recommendations for restoring oyster habitat along the East and Gulf coasts of the United States include: (1) changes in current management practices (e.g., an increase in minimum size limits); (2) introduction of non-endemic, disease-resistant oysters (e.g., *Crassostrea gigas*); (3) large-scale shell repletion efforts; (4) building "new" reefs with natural or artificial shell (e.g., pellets made from coal combustion by-products); and (5) the establishment of broodstock sanctuaries that are closed to fishing, which would presumably enhance recruitment success (Mann et al. 1991; Rothschild et al. 1994). This paper incorporates recent theoretical and empirical advances in population and landscape ecology to provide a conceptual framework for guiding oyster restoration efforts aimed at shell repletion, habitat replacement with new reefs, and the establishment of broodstock sanctuaries. Specifically, it addresses the following questions: (1) what are the management goals in terms of restoration efforts?; and (2) what spatial arrangement (e.g., reef location, size and shape) of oyster habitat best meets these management goals? The concepts of metapopulation dynamics and source versus sink habitats are used as a framework for defining the best location for establishing oyster habitat within an estuarine tributary or water basin, whereas landscape ecological principles concerning habitat fragmentation provide a framework for defining the most productive spatial arrangement and size of oyster patches.

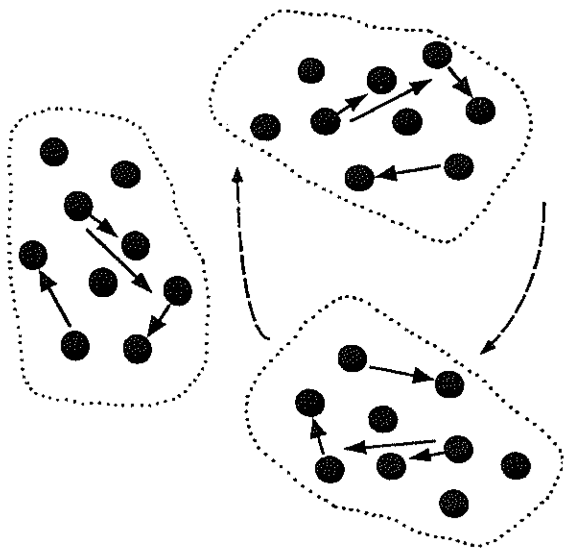


Figure 1. Schematic of metapopulation concept illustrating larval dispersal between patches within a metapopulation. Dots denote patches; the dotted-line around the dots denotes a population; the small arrows between dots denotes larval dispersal between patches; and the broken arrows between populations denotes potential larval "leakage" between populations within the metapopulation.

Background Information

METAPOPULATION DYNAMICS AND SOURCE VERSUS SINK HABITATS

The types, quality and spatial arrangement of habitat patches within a landscape influences the distribution and abundance of populations (Pulliam 1988; Pulliam and Danielson 1991; Hanski 1994). Within fragmented landscapes, many species exist as metapopulations, facing possible extinction in certain patches, but persisting regionally by dispersal into neighboring patches (Fig. 1; Levins 1969; Hanski 1994). The concept of metapopulations (Levins 1969) is particularly applicable in marine systems, where dispersive stages in populations with complex life cycles (i.e., species with ≥2 developmental stages requiring spatially separated habitats) connect spatially separated populations or subpopulations. This notion of connectivity through the larval phase is well suited to organ-

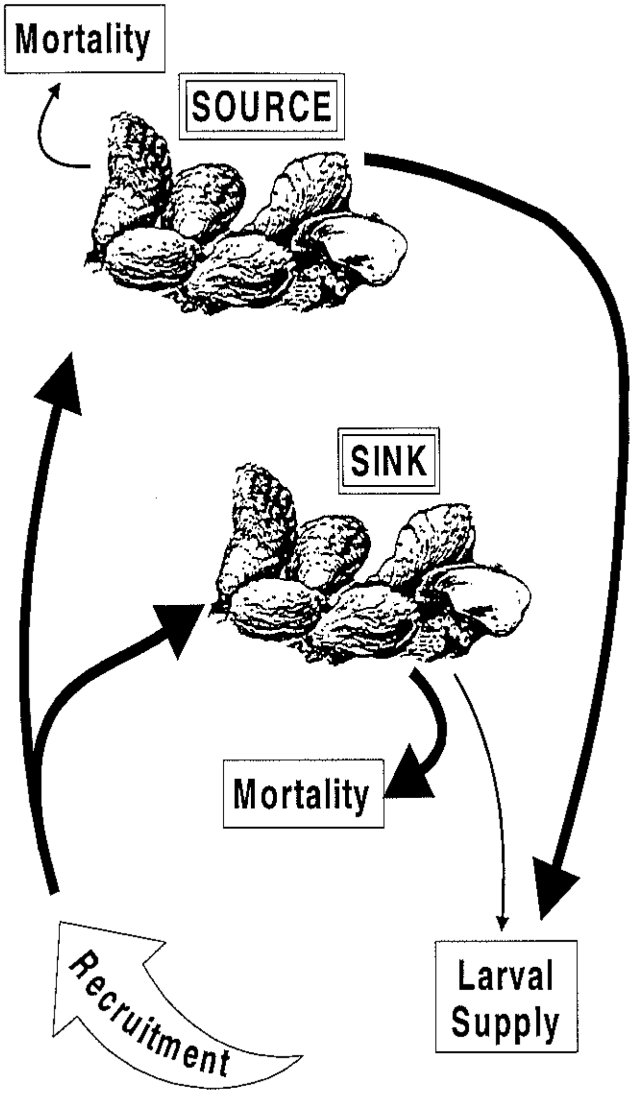


Figure 2. Schematic of source and sink concept. One habitat is a source such that recruitment is sufficient, mortality low, and reproductive output is high, thereby making it a critical habitat for population persistence. The other habitat is a sink because mortality is high, reproductive output is low, despite adequate recruitment.

isms such as oysters, which as juveniles and adults are permanently attached epibenthic animals.

The long-term survival of metapopulations can be strongly affected by the spatial and temporal distribution of suitable habitat patches. Populations living in high quality habitats (referred to as "source" habitats) have birth rates greater than death rates, whereas populations living in poor quality habitats ("sink" habitats) have birth rates that are less than death rates (Fig. 2). The viability of metapopulations depends on the existence of sufficient high quality habitats, but a large fraction of the individuals may live in the sub-optimal habitats (Pulliam 1988). The determination of critical habitat needs of such species requires identification of source and sink habitats. These concepts have largely been ignored by marine ecologists and fishery biologists, yet their incorporation into investigations of the distribution and abundance of marine populations is essential because they integrate recruitment processes, habitat utilization, and factors influencing demographics of critical life history stages of a species. The key components of this approach include (Fig. 2): (1) recruitment to the habitat from a spawning stock, (2) habitat-specific mortality rates, and (3) dispersal from or into distinct habitats. These processes are emphasized in most studies, yet their habitat-specific impact on population variation and connectivity between habitats have rarely been emphasized or quantified.

The potential consequences of not determining source and sink habitats are great, and include:

- a lack of information on the relative significance of various habitats in the population dynamics of a species, thereby precluding proper emphasis of habitat conservation or enhancement efforts, particularly when limited funds require emphasis on a subset of available habitats; and
- inappropriate conclusions on the importance of various factors, such as recruitment, habitat quality or predation, in the population dynamics of a species, particularly when those conclusions are based on a few relatively well-studied areas.

The benefits of sufficient attention this concept include:

- an ability to identify critical habitats for a population, thereby allowing concentration of funding and efforts in those habitats;
- a broad and integrative conceptualization of population dynamics, encompassing the processes and controlling factors of re-

cruitment, survival, growth and dispersal within a unifying framework; and

- a comprehensive theory dealing with the key ecological aspects necessary for development of sound management strategies.

LANDSCAPE ECOLOGICAL PRINCIPLES

Landscape ecology provides a theoretical framework for the detection and quantitative analysis of spatial patterns, and is defined as the study of processes occurring across spatially heterogenous habitat mosaics and the biotic responses to the resulting patterns (Robbins and Bell 1994). This definition may include either floral (e.g., seagrass) or faunal components (e.g., oyster reefs), or a combination of both as the defining elements of a landscape. Although the principles and concepts of landscape ecology are based in terrestrial systems, the techniques being developed are also directly applicable to the marine environment. For example, the large spatial scale provided by landscape techniques will benefit marine studies by (Robbins and Bell 1994): (i) forcing examination of patterns across a variety of spatial scales, leading to the possible identification of self-similarity across scales; (ii) providing a framework to assess the effects of habitat fragmentation upon recruitment success and extinction of marine organisms; and (iii) providing theory for designing marine reserves and in habitat restoration attempts.

In terrestrial systems, the equilibrium theory of island biogeography (MacArthur and Wilson 1967) and the species-area relationship have been used extensively as a theoretical framework for designing landscape experiments, formulating conservation policy, and in designing nature reserves. These principles are used to predict the optimal size of reserves to maximize the number of species, and to project species extinction rates as a function of habitat fragmentation. The application of these principles to conservation biology has received wide and conflicting attention in terrestrial systems (Diamond and May 1981; Kindlmann 1983; Beckon 1983; Boecklen and Gotelli 1984; Tillman et al. 1994; Lomolino 1995). A frequently debated prediction is whether a single large reserve will contain more or less species than several small reserves of the same total area, the so-called SLOSS (Single Large Or Several Small) debate (Fig. 3). The general prediction from terrestrial systems is arguably increased species abundance and diversity with increasing habitat area (small perimeter:area ratio), and decreased abundance and diversity with increasing detrimental edge effects (i.e., increased perimeter:area ratio; see review by Saunders et al. 1991; Robinson et al. 1995; but see Kindlman 1983 and Lomolino 1995 for contrasting views).

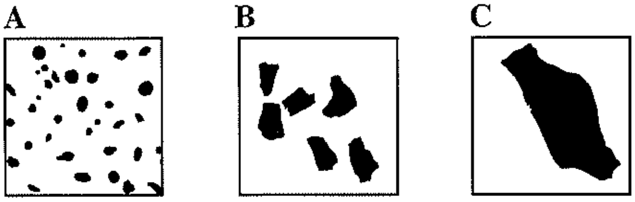


Figure 3. Schematic illustration of the so-called SLOSS (Single Large or Several Small) concept. Each figure (A,B,C) represents the same overall habitat area, but with different levels of fragmentation.

These general predictions from terrestrial systems provide a striking contrast to those from a limited number of studies in marine systems, which suggest increased recruitment and high species richness in small patches with high perimeter:area ratios. Recent studies in seagrass systems suggest that many small seagrass patches may increase the overall probability of encounter by larvae, thereby increasing overall recruitment to a patch compared to larger patches (e.g., Bell et al. 1987, Sogard 1989, Worthington et al. 1992, McNeill and Fairweather 1993, Eggleston et al. 1998, but see Bell et al. 1995 for an example with disproportionately high algal accumulation rates on large versus small patches). These observations prompted one research team to propose a seagrass conservation strategy that attempts to preserve discrete seagrass beds within a larger area, rather than preserve one large contiguous bed (McNeill and Fairweather 1993). A similar habitat management strategy was proposed for conserving breeding waterbird populations in Florida Bay, USA (Erwin et al. 1995). Increased recruitment of barnacles into small versus large habitat patches has also been observed in rocky shore habitats (Paine and Levin 1981, Sousa 1984). The hypothesized mechanism for these rocky shore observations was similar to that posed for seagrass habitats; increased probability of interception of larvae by the patch edge in small versus large patches (Paine and Levin 1981, Sousa 1984).

Fragmentation of the terrestrial landscapes also produces a series of remnant vegetation patches surrounded by a matrix of different vegetation or habitat types. Two primary effects of this are alteration of the microenvironment within and surrounding the remnant (e.g., changes in physical stresses such as radiation, wind, and water), and the isolation of each fragment from other remnant patches in the surrounding landscape (Saunders et al. 1991). Thus, in a fragmented landscape, there are changes in the physical environment as well as biogeographic changes. Most discussions of fragmentation have focused on biogeographic aspects, whereas the physical aspects have received little attention (Saunders et al. 1991). The response of biota to physical and biogeographical changes are further modified by factors such as remnant size, shape and isolation (Saunders et al. 1991, and see below).

LANDSCAPE PERSPECTIVE OF OYSTER HABITATS

Both subtidal and intertidal oyster reefs possess a suite of spatial and ecological characteristics that make them amenable to the direct application of terrestrially-based landscape concepts and techniques. For example, oyster reefs range in size from small, fragmented intertidal reefs of less than 1 m^2, to continuous subtidal reefs that extend over 1 km. The morphology of oysters also varies considerably, ranging from small, cup-shaped oysters that form low relief subtidal reefs (Mann et al. 1991), to thin-shelled, elongate oysters that make up narrow strands of intertidal reefs that extend outward from the shore at right angles to the current, or along the shore (Kennedy and Sanford 1999, Chapter 2, this volume). Reef expansion occurs through oyster growth and enhanced larval settlement on large conspecifics (Kennedy and Briesch 1981, Haven et al. 1978), whereas reef reduction is due to habitat destruction from fishing and mining practices, and the death of reef assemblages due to disease, predation, and sedimentation events (Eggleston 1988, Armstrong et al. 1989, Osman et al. 1989, Mann et al. 1991, Rothschild et al. 1994, Hargis and Haven 1999, Chapter 23, this volume).

Oyster reefs also exhibit a hierarchical arrangement of structure over spatial scales ranging from millimeters to kilometers. At the millimeter to centimeter scale, individual juvenile oysters (i.e., spat) are typically attached to a large piece of oyster shell cultch (or other hard substrate) to form a clump. Individual clumps are arranged into discrete patches that typically range from one to more than 100 m diameter. Most state-funded shell replenishment efforts have operated at the patch scale of 1-100 m (Haven et al. 1978; Marshall et al. 1999, Chapter 7, this volume; Wesson et al. 1999, Chapter 8, this volume). Oyster patches, in turn, are arranged into reefs that may extend over kilometer-wide areas. Oyster reefs can then be placed within a larger coastal landscape containing a mosaic of seagrass, salt marsh, mangrove, and unstructured soft-bottom habitats. Although information on the interdependence of these habitats is scant, this knowledge is critical to our understanding of population dynamics of numerous commercially and ecologically important estuarine-dependent species, as well as our understanding of energy flow within an ecosystem context.

Conceptual Approach

WHAT ARE THE MANAGEMENT GOALS OF OYSTER HABITAT RESTORATION?

A major challenge to oyster reef restoration efforts with limited funding and personnel is to replenish or build new oyster habitats that maximize management goals. Thus, it is critical that management goals be clearly defined before restoration efforts begin. The management goals of oyster restoration may include, but are not limited to, maximizing: (1) recruitment to the fishery; (2) spawning output; (3) biodiversity (i.e., species diversity of the oyster reef community); and (4) water filtration. These goals are not mutually exclusive, and managers should strive to simultaneously maximize as many goals as possible on a per unit area basis.

Efforts aimed at maximizing recruitment to the fishery would strive to enhance larval settlement, growth and survival. Suitable substrate for settling larvae could be added in areas where the production of larvae and spat settlement are known to be high. Settlement could be further enhanced by insuring that reefs composed of oyster shell cultch include live oysters. Growth and survival could be enhanced by constructing high vertical relief reefs as described by Lenihan et al, 1996. A series of broodstock sanctuaries would help maintain the natural size structure and sex ratio of certain populations or subpopulations, thereby enhancing reproductive output to a given metapopulation (Kennedy 1983, Rothschild et al. 1994). The broodstock sanctuary should be located in areas of historically high larval production.

Oyster reefs also support extensive and often diverse assemblages of species (Wells 1961, Breitburg 1999, Chapter 16, this volume; Cohen et al. 1999, Chapter 9, this volume; Posey et al. 1999, Chapter 15, this volume), that, in turn, provide the base levels of food webs that eventually support commercially and ecologically important finfish and crustaceans. In systems lacking seagrasses, oyster habitats may represent the only major structural refuge (Eggleston et al., 1998, Posey et al. 1999, Chapter 15, this volume). Oyster reefs also have the potential to dominate energy and nutrient flow within shallow coastal environments. For example, a review of many estuarine ecosystems indicates that oysters and bivalves in general have the potential to directly control phytoplankton biomass through grazing (Cloern 1982; Carlton et al. 1990; Dame 1999, Chapter 18, this volume). Moreover, oysters filter out other suspended solids, depositing them as pseudofeces, thereby improving water quality. Thus, oyster restoration goals must look beyond the immediate economic benefits of producing harvestable oysters, and establish strategies for maintaining a diverse and stable food web, and improving water quality by reducing the impact of eutrophication.

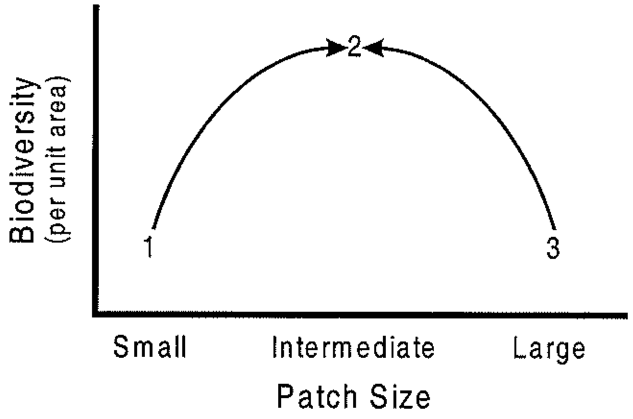
WHAT SPATIAL ARRANGEMENT (E.G., REEF LOCATION, SIZE AND SHAPE) OF OYSTER HABITAT BEST MEET THESE MANAGEMENT GOALS?

A hierarchical approach to addressing this question should initially involve defining the target population or subpopulations that are most likely connected through the larval phase; i.e., the metapopulation. This will help to establish the requisite spatial bounds within which to define source versus sink habitats. There is ample evidence in the literature to suggest that the dynamics of certain marine organisms should be examined according to a metapopulation conceptual framework (e.g., oysters: Haven et al. 1978; Whitlach and Osman 1999, Chapter 13, this volume; bay scallops, *Argopectin irradians concentricus*,: Peterson and Summerson 1992; reef fishes: Doherty and Fowler 1994; Man et al. 1995). From an oyster perspective for example, various tributaries of the Chesapeake Bay often vary in the timing and magnitude of oyster settlement, with low annual variability consistently observed in certain locations (e.g., seaside of the eastern shore of Virginia, bayside of the eastern shore) and high variability in others (e.g., York and Rappahannock Rivers) (Haven et al. 1978). Historically, in the Chesapeake Bay, the James, Piankatank and Great Wicomico Rivers have displayed the highest annual settlement rates (Haven et al. 1978). Coherence in oyster population dynamics within a given tributary suggests that individual tributaries be viewed as metapopulations (Fig. 1), and managed on a tributary by tributary basis.

Similarly, basin-scale coherence in the population dynamics of the bay scallop has been observed in North Carolina. In this case, a large-scale red tide (*Ptychodiscus brevis*) event that lasted from October 1987 to February 1988 had a catastrophic impact on bay scallop populations within three sounds inside Beaufort Inlet (Peterson and Summerson 1992). Although the impact was limited to the two generations present at the time (1987-88 and 1988-89 year classes), the subsequent three year classes remained extremely depressed (Peterson and Summerson 1992). A positive stock-recruit relationship for the bay scallop suggests that these populations may be recruitment limited at low densities (Peterson and Summerson 1992). Patterns of adult and recruit abundance were strikingly coherent within a particular sound, with densities in Core Sound relatively high, Back Sound relatively low, and Bouge Sound extremely low (Peterson and Summerson 1992). Basin-scale coherence in the population dynamics of the bay scallop suggest that individual water basins may serve as metapopulations, with attendant dynamics driven by the abundance of spawning adults. Management efforts can now focus on enhancing spawning stock biomass within a given metapopulation or water basin (Peterson and Summerson 1992).

In terms of oyster restoration efforts, **how does one establish biologically meaningful spatial bounds for a given tributary or basin?** The most rigorous approach would be to use a three-dimensional, hydrodynamic model to simulate larval trajectories under realistic environmental conditions and larval durations, then examine the subsequent distribution and abundance patterns of settlers. The spatial bounds described by the distribution of settlers would theoretically define the metapopulation. Modeling results could then be refined by field measures of larval supply and settlement. This approach is being used to model the transport and fate of oyster larvae in the James River, Virginia (Hamrick 1992). In North Carolina, a three-dimensional hydrodynamic model (PALPAM1) has been configured to examine physical coupling between the Albemarle, Pamlico and Croatan Sounds (Pietrafesa and Janowitz 1991, Lin 1992). This model has been used to predict larval transport and settlement of blue crab (*Callinectes sapidus*) postlarvae under varying meteorological conditions (Xie and Eggleston, unpubl. data). For systems where hydrodynamic models are unavailable, the simplest solution would be to design oyster restoration efforts on the basis of individual tributaries or water basin.

Once the spatial bounds have been assigned to a particular metapopulation, the next question is, **how does one identify source versus sink habitats for shell repletion or reef construction efforts?** Identification of source versus sink habitats (Fig. 2) requires that the following demographic characteristics be measured in a range of sites: (i) larval supply; (ii) settlement; (iii) post-settlement growth and survival; and (iv) fecundity. Larval supply could be measured by towing or mooring plankton nets over a particular habitat (e.g., Wood and Hargis 1971; Seliger et al. 1982), or, in areas with pronounced salinity stratification, by using a suction pump (e.g., Mann 1988). Relative rates of larval settlement can be measured with weighted strings of oyster shells suspended off the bottom (e.g., Haven and Fritz 1985), or by measuring spatfall on natural oyster beds. A simple approach for measuring growth and survival uses a mark-recapture technique (e.g., Eggleston 1988). In this approach, natural densities of cultch and attached oysters are removed from the seafloor by divers and placed in a flow-through seawater system. The cultch is then marked with marine epoxy and assigned a unique identification number. The number of spat and corresponding sizes are then recorded, and the entire sample, including fouling organisms, are replaced on the seafloor for approximately three weeks (Eggleston 1988). A three week sampling period allows for reestablishment of the natural fouling community and natural levels of sedimentation, yet accounts for



1 = Species abundance and diversity is relatively low at small patch sizes due to frequent disturbances in the form of predation and sediment transport. Recruitment may be high due to increased probability of encounter of the patch edge by larvae due to high perimeter:area ratio.

3 = Species abundance and diversity is predicted to decrease at high patch sizes due to low recruitment (low probability of larvae encountering patch) associated with a reduced perimeter:area ratio, and the increased spread of disease, even though large patches are predicted to contain low predation pressure and high habitat diversity.

2 = Intermediate levels of habitat area are predicted to contain the highest species abundance and diversity, as well as reduced predation pressure and physical stress (e.g., sedimentation), compared to small patches, and a high perimeter:area ratio compared to large patches, thereby enhancing recruitment.

Figure 4. *Hypothesized relationship between oyster abundance or biodiversity per unit area, and habitat fragmentation (patch size).*

temporal variation in growth and mortality rates (Eggleston 1988). A protocol for quantifying temporal and spatial variation in fecundity of oysters is described in Cox and Mann (1992). In this case, fecundity values are obtained as direct estimates of the number of eggs in the gonad (Cox and Mann 1992). In terms of management goals that attempt to maximize fisheries production and eventual contribution to the spawning stock, source versus sink habitats will be identified by their significantly higher or lower abundances and fecundity of adult oysters, respectively. With respect to water filtration goals, estimates of water filtration rates in source versus sink habitats could be determined through previously published estimates on the relationship between filtration rate and body size (Doering and Oviatt 1986; Powell et al. 1992 and references therein).

Once source and sink habitats have been identified, **how does one determine the oyster patch size, shape, abundance, and isolation that best maximizes management goals?** There is no empirical answer to this question as of yet; however, a mechanistic-based relationship between species diversity per unit area and patch size is shown in Figure 4 to to guide sampling and experimental efforts. This relationship predicts that oyster density or species diversity of the oyster community (i.e., biodiversity) will be highest at intermediate levels of habitat fragmentation, irrespective of spatial scale, and that biodiversity will increase with habitat diversity, and decrease with patch isolation. The parabolic relationship between habitat fragmentation and biodiversity (Fig. 4) is analogous to the "intermediate disturbance" hypothesis used in community ecology (e.g., Connell 1978, Hixon and Brostoff 1983). Thus, in addition to conserving overall habitat area, the conceptual model (Fig. 4) suggests a conservation strategy to preserve discrete oyster patches within a larger area, rather than conserve a single, continuous habitat area. Based on the findings from a limited number of studies in marine systems which indicate high species diversity in small patches (e.g., Bell et al. 1987, Sogard 1989, Worthington et al. 1991, McNeill and Fairweather 1993), an alternative hypothesis is that oyster density and species diversity per unit area in oyster reefs will be highest in small than large patches (but see Eggleston et al. 1999 for an example of a disproportionate reduction in faunal density and diversity in small versus large patches of oyster shell.

Several mechanisms are hypothesized as important in defining the relationship between patch size and biodiversity, including: (i) larval and postlarval settlement (recruitment);

Table 1. Summary of factors and hypothesized effects of oyster habitat fragmentation on biota.

Factor	Hypothesized Effects
1. Patch shape	This is the most critical factor for relatively small patches; shape determines perimenter:core ratio (edge effects). For example, long, thin patches have proportionally more edge than square or round patches, and are more vulnerable to detrimental edge effects (e.g., increased physical stresses, predation pressure, etc). Increased perimeter:edge ratio may be advantageous in marine systems by increasing encounter rates of the patch edge with settling larvae.
2. Patch size	The smaller the patch size, the greater the influence that external factors will likely have (e.g., physical stresses, predation,etc.). Larger patches have a larger core area that is relatively unaffected by environmental and biotic changes associated with the edges. Increased perimeter:edge ratio associated with smaller patch sizes may be advantageous for larval recruitment in marine systems as described for 1.
3. Patch isolation	In terrestrial systems, the ability of a species to colonize an isolated patch depends on the distance between patches and nearby undisturbed areas (island biogeographic theory). Isolation may or may not be important for marine species with planktonic larvae. However, isolation may be important in slowing the spread of disease through a metapopulation. Patch isolation may also limit predation if predators have difficulty locating a patch.

(ii) habitat diversity; (iii) physical fluxes such as sedimentation; (iv) predation; and (v) disease. The predicted relationship between these mechanisms, biodiversity, and habitat fragmentation are described in the legend of Figure 4. The predicted responses of biota to patch size, shape, and isolation are shown in Table 1. If one views the primary impact of habitat fragmentation as the loss of habitat continuity, then different organisms will perceive the same scale of fragmentation as affecting the continuity of their habitat in different ways. For organisms operating at the same scale, several general predictions have been made (Lord and Norton 1990): (i) finer scales of fragmentation will have a greater affect on smaller organisms; and (ii) finer scales of fragmentation will affect specialists more than generalists. The hypothesized responses of marine organisms to oyster habitat fragmentation at three spatial scales is shown in Table 2.

For many free-spawning invertebrates, sperm can become quickly diluted after release in the water, leading to concentrations below which fertilization is unlikely (e.g., Pennington 1985, Denny and Shibata 1989, Levitan et al. 1992). Because fertilization success is dependent on the concentration of eggs and sperm, the distribution and abundance of spawning conspecifics may play an important role in zygote production and overall reproductive success of the population. In instances where the management goal includes enhancing or insuring production of oyster broodstock, it is critical that one examines fertilization success of eggs as a function of within-patch density and dispersion of oysters (e.g., Levitan et al. 1992).

Caveats

Oyster populations fluctuate substantially in abundance at various scales of time and space. Thus, it is important to recognize that spatially distinct metapopulations may be inter-connected during certain years and not others, and that the location of source and sink habitats may change over time. Moreover, source and sink habitats undoubtedly represent extremes in a continuum,

Table 2. Summary of hypothetical sampling areas, patch sizes within areas, sampling techniques, and potential faunal groups responding to habitat fragmentation at various spatial scales.

Area of Site	Patch Sizes within Site	Sampling Techniques	Organisms Responding to Fragmentation*
25m X 25 m Small; S)	0.25 m^2 - 4m^2	Excavation by hand, or suction sampling	Crab megalopae, Postlarval fish, Bivalves; Relatively sedentary amphipods, shrimp, gastropods, polycheates
50m X 50m (Medium; M)	4 m^2 - 625 m^2	Suction sampling, Infaunal cores	Settlement stages; Sedentary and mobile early juvenile stages of estuarine-dependent species; Small mobile crustaceans, gastropods, etc.
500 m X 500 ma (Large; L)	0.25 ha - 10 ha	Beam trawls, Suction sampling, Infaunal cores	Juvenile crabs and fish

* Sources on organism mobility for predicting the effects of fragmentation at various spatial scales included Howard (1985), Sogard (1989), Shirley and Wolcott (1991), Worthington et al. (1992), McNeill and Fairweather (1993), Martin-Smith (1994), Eggleston (1995), (Eggleston et al. 1999).

with intermediary habitats where recruitment input and spawning output are nearly in balance. The identification of source and sink habitats is further complicated by high variation in recruitment and mortality, which may overwhelm habitat-specific patterns in these factors. Nevertheless, several recent and ongoing studies highlight the persistence of source populations in certain habitats. For example, measurements of larval abundance, postlarval settlement, and juvenile and adult abundance patterns of the Caribbean spiny lobster at four separate locations in the Exuma Cays, Bahamas (Lee Stocking Island, Warderick Wells, Cat Island, Eleuthera; each located ca 50 km apart), indicate that high annual postlarval supply to Cat Island over the past three years, is consistently decoupled from adult abundances there, and that Lee Stocking Island, Warderick Wells, and Eleuthera serve as persistent sources of spawning stock (Lipcius et al. 1997). Given historical consistency of the production of oyster larvae and spat in certain geographic locations (e.g., James and Piankatank Rivers, Virginia) and not others (York River, Virginia), it is not unreasonable to suggest that certain locations or habitats within a tributary serve as persistent sources of spawning stock for the entire tributary.

Another concern regarding the proposed conceptual approach, is the lack of information on the spatial scale at which habitat fragmentation might impact oyster recruitment success or biodiversity (Eggleston et al. 1999). One approach would be to test the relationship depicted in Figure 4 with a range of patch sizes typically deployed by shell replenishment efforts (e.g., 1-100 m^2). The use of a wide range of patch sizes would help insure that there would be a detectable effect of patch size on oyster recruitment success or biodiversity. Another useful approach, particularly when field data are scant and replication is difficult, is to employ mathematical models to simulate a population's response to landscape changes. One of the most promising approaches in this regard is the use of spatially explicit population models (SEPMs) (Dunning et al. 1992; 1995). Spatially explicit models have a structure that specifies the location of each object of interest (organism, population, habitat patch) within a heterogeneous landscape, and therefore the spatial relationships between habitat patches and other features of the landscape (e.g., landscape boundaries, other patches) can be defined. Since the spatial layout of the landscape is explicitly incorporated, the models can be used to indicate how populations or communities might be affected by changes in landscape composition (e.g., relative or absolute amount of habitat types, isolation of habitat types) (Dunning et al. 1992; 1995). For example, the potential effects of changing habitat on species persistence could be assessed by systematically varying habitat features (e.g., size, shape, and spacing of habitat patches), and measuring subsequent population size (e.g., Pulliam and Danielson 1991; Lamberson et al. 1994). However, SEPMs require habitat-specific, empirical information about demography, dispersal behavior, and habitat selection of the organism(s) being studied to initially parameterize a model. Thus, the use of SEPMs will require close collaboration between modelling and field restoration efforts.

Another concern is the lack of quantitative information on the effects of oyster habitat fragmentation on the resilience of oysters and other organisms to harvesting impacts, as well as the relationship between oyster patch size and commercial harvesting efficiency. For example, if relatively small oyster patches exhibit the highest spawning output on a per unit area basis, but are physically decimated during typical harvesting activities, larger patches sizes would be required. Moreover, harvesting efficiency would likely be lowest in areas with numerous small patches compared to an area with one large patch. Spatially explicit models may also include non-biological parameters to examine the response of economic variables. For example, the economics of oyster harvesting can be integrated with the ecological consequences of varying habitat spatial arrangements to determine the economic costs of certain conservation strategies (e.g., Costanza 1991; Liu 1993). Beyond these caveats and potential solutions, this paper highlights important management considerations in oyster restoration efforts, and provides a series of testable hypotheses, based on modern ecological principles, for designing restoration efforts that maximize specific management goals. Such a conceptual approach should be applicable to a wide variety of coastal systems.

Conclusions and Recommendations

Two central problems facing oyster habitat restoration efforts are deciding (1) what are the management goals of the restoration effort?, and (2) what location, number, size, and shape of oyster patches best meet these management goals? Management goals may include, but are not limited to, maximizing: (1) recruitment to the fishery; (2) spawning output; (3) biodiversity; and (4) water filtration. These goals are not mutually exclusive, and managers should strive to simultaneously maximize as many goals as possible on a per unit area basis. Modern landscape ecological principles provide a conceptual basis for predicting what spatial arrangement of oyster habitat would best meet these management goals. A hierarchical application of landscape principles would first involve setting spatial bounds on the target metapopulation. This step is necessary in the identification of source habitats within which to focus restoration efforts. Once the existence and location(s) of source habitats has been identified, restoration efforts should aim to replenish or build discrete oyster patches within a larger area, rather than a single continuous habitat area. This conservation strategy is based on the prediction that the density of oysters and species diversity within the oyster community is maximized at intermediate levels of oyster patch sizes. These predictions are based on a review and synthesis of empirical tests of landscape ecological principles in both terrestrial and marine systems. In this case, several mechanisms are hypothesized as important in defining a parabolic relationship between patch size and oyster density or biodiversity: (i) larval and postlarval settlement (recruitment); (ii) habitat diversity; (iii) physical fluxes such as sedimentation; (iv) predation; and (v) disease. These hypotheses should be field tested across a range of space and time scales during the initial phases of oyster restoration efforts.

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Use of Oyster Reefs as Habitat For Epibenthic Fish and Decapods

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Abstract

Although oysters are well known as an important shellfish resource, recent research has emphasized their potential importance as habitat for other estuarine species. The 3-dimensional structure of oyster reefs may provide refuge and foraging habitat in a manner similar to vegetated areas. We examined the use of intertidal oyster beds by epibenthic decapods and fish in southeastern North Carolina through low tide quadrat sampling as well as sweep net sampling and diver observations when the beds were submerged. Laboratory mesocosm studies examined the potential importance of predation in explaining preferential use of oyster patches by the grass shrimp, *Palaemonetes pugio*. Several fish and decapods were observed more abundantly over oyster beds compared to adjacent sandflat areas, with significantly greater use by grass shrimp, pinfish, and blue crabs. Laboratory studies indicated significantly greater use of oyster patches by grass shrimp in the presence of a predatory fish compared to treatments with no fish or a non predatory fish. These results indicate that oyster habitats are important for epibenthic decapods and fish and emphasize the need to manage oyster reefs not only for their direct fishery value but also as habitat for other species.

Introduction

Management of oyster reefs has generally concentrated on their importance as a commercial fishery. While among the most important shellfish resources in the United States, oyster reefs also serve an important ecological role as a structural habitat in an otherwise low relief system. Other structural habitats, such as seagrass beds, salt marshes, and rock reefs, are utilized as refuge sites by a variety of decapods and fish (Welsh 1975, Kikuchi 1980, Heck and Thoman 1981, Thayer et al. 1984, Stevenson 1988, Posey and Ambrose 1994). Because they tend to concentrate many smaller organisms, such structural habitats may also serve as foraging areas for larger predators (Summerson and Peterson 1984, Posey and Ambrose 1994), with potential indirect effects on fauna in adjacent habitats (Posey 1991). This combination of refuge and forage functions has led to the recognition of the importance of seagrass beds and salt marshes as nursery habitats for many commercially important species. However, seagrasses have a limited distribution along the east coast of the United States, being largely absent from southeastern North Carolina through Georgia, and the upper intertidal distribution of salt marshes makes them available for only a short period each tidal cycle. Along the southeastern coast of the United States, oysters may provide one of the primary structural habitats in the low intertidal and subtidal. Thus, they may comprise a critical refuge and forage habitat for epibenthos.

Many studies of oyster habitats have concentrated on the epibenthos attached to shell or fauna residing permanently in the shell matrix (Wells 1961). Oyster shell provides habitat for a diverse array of barnacles, sponges, hydrozoans, bryozoans, and tunicates (Wells 1961) as well as resident motile fauna such as grapsid and panopeid crabs (Meyer 1988). However, use of oyster reef habitat by transient species such as blue crabs, paneid shrimp, and fish, which facultatively use the reefs for only limited periods, is less well understood. This partly reflects a concentration on the shellfish resource function of oyster reefs and partly reflects the difficulty of sampling these habitats with nets or traps. Despite logistical problems, several studies have utilized pop nets, sweep nets, traps, or direct observation to examine use by selected transient crustaceans and fish. Observations using these techniques suggest that many ubiquitous species such as grass shrimp, *Palaemonetes pugio*, juvenile blue crabs, *Callinectes sapidus*, and bottom dwelling or demersal fish, may preferentially utilize oyster reefs compared to adjacent sand bottom habitat (Wells 1961, Castel et al. 1989, Townsend 1991, Powell 1994). The mechanisms causing these patterns are unclear, but are proposed to be related to food availability and/or refuge.

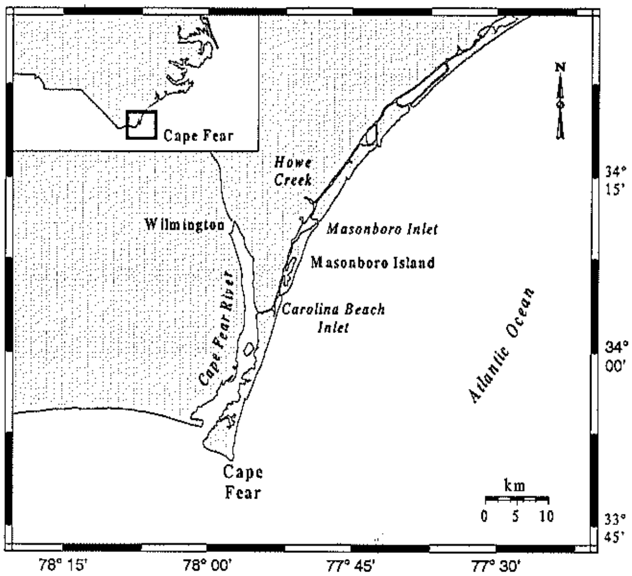

***Figure 1.** Location of Masonboro Island and Howe Creek sampling sites in southeastern North Carolina*

Here we present results from several field sampling techniques and laboratory mesocosm studies to: 1) document use of intertidal oyster reefs by transient decapods and fish, and 2) determine the potential importance of predation in regulating decapod usage patterns.

Methods

A. FIELD OBSERVATIONS

Field sampling to observe epibenthic use of oyster beds was conducted near Masonboro Island, southeastern North Carolina (Fig. 1). Oyster reefs in this area are primarily intertidal, with reefs often occurring as distinct patches 2-10 m in diameter. Sediments are predominantly fine sands, with salinities generally above 30 ‰ in the areas studied. Southeastern North Carolina lacks permanent seagrass beds and *Spartina* marshes predominate only in the high intertidal, with most of the intertidal being unvegetated sandflat.

Mobile epifauna remaining on oyster reefs at low tide were observed using quadrat samples. Ten 20 cm x 20 cm quadrats were randomly selected within replicate oyster reefs. Within each quadrat, all the shell matrix and 2 cm of underlying sediment was removed, placed in a 5 gallon bucket, and then elutriated through a 2 mm mesh screen. Adjacent sandflat areas were sampled at the same time in the same manner, sieving the top 4 cm of sediment. All mobile epifauna were identified to species. Sampling was conducted bimonthly from April 1992 through July 1993.

Sampling fish and mobile decapod use of oyster beds at high tide, when the reefs are inundated, presents special problems. Standard seine or trawl sampling is not easily conducted within an oyster reef because of snagging on shells. As part of a broader effort, we used a combination of sweep net sampling and diver observations to obtain qualitative assessments of the relative use of oyster and adjacent sandflat habitats. Sweep net sampling was conducted at three oyster reef and adjacent sandflat areas near the mouth of Howe Creek, 1 km north of Masonboro Island, North Carolina. Sweep sampling was conducted monthly during 1990 (January 1990 through January 1991) and again in Fall 1991 (September through November 1991). Standardized sweeps, 15 m long, were made with a 40 cm wide x 25.4 cm height x 0.16 cm mesh Duraframe Intermediate D-type net (Townsend 1991). Sweep protocol involved holding the net against the bottom at a 70° angle and lightly bouncing it along the bottom at a moderate walk. Bouncing prevented the net catching on oyster shell when sampling in a reef. Sweeps were made at peak flood and ebb periods on spring tides at 15 cm, 30 cm, 45 cm and 60 cm water depths. Starting depths and habitat types were alternated. Analysis of Variance was conducted to compare oyster and non-oyster habitat use by common taxa, blocking for depth and tidal period effects (3-way ANOVA with habitat, depth, and tidal period as main effects with no interaction terms). Because of the 9-month separation between sweep net studies, analyses were conducted separately for 1990 and 1991 time periods.

In addition to sweep net sampling, diver observations were conducted to estimate usage by larger fish and decapods that may be able to evade sweep nets. One diver was positioned on an oyster reef and a second diver was approximately 3 m away from the reef. Divers made 3 observations, 10 minutes per observation, on each of 4 consecutive days. Divers switched positions during each observation period to reduce problems associated with diver bias. During these observations water clarity was generally in excess of 2 m and each diver recorded any fish or decapods crossing a line extending 1 m in front of them and parallel to the reef edge. Observations were repeated in July, August, and September 1993. Differences in abundance between reef and off-reef locations were compared using a paired t-test on log-transformed data for each month, summing the 12 observations taken during each 4 day period.

B. LABORATORY STUDIES

Laboratory experiments were conducted to determine the potential role of predation in regulating use of oyster reefs by decapods and the relative preference for oyster patches compared to other potential refuge habitats (shallow water and seagrass patches). Within North Carolina coastal areas, shallow water, seagrass beds, and oyster reefs all represent potential refuges relative to open water. Experiments were conducted within paired 208 l tanks (following Posey and Hines 1991). One tank was used as a fish addition (either predatory or non-predator fish) and the other was a non fish control. Separate no-fish controls were always

Table 1. Design of laboratory experiments

A. Habitat combinations offered in laboratory mesocosm experiments (all habitat combinations had open, deep water in addition to the refuge habitats listed).

Habitat Combination	Refuge Habitat Types Available		
	Shallow	Oyster	Seagrass
I	●	●	
II	●	●	●
III		●	●

B. Experimental treatments presented for various habitat combinations.

Habitat Combination	Treatment			
	Predatory Fish	No Fish Control	Non-predatory Fish	No Fish Control
I	7 reps w/ mummichogs	7 reps w/o fish	N/A	N/A
II	7 reps w/ mummichogs	7 reps w/o fish	7 reps w/ white mullet	7 reps w/o fish
III	7 reps w/ mummichogs	7 reps w/o fish	7 reps w/ white mullet	7 reps w/o fish

run as pairs with each fish addition replicate. Within the tanks, one of the following three combinations of shallow water, seagrass, and oyster refuges was offered: 1) shallow water, 2 depths of oyster (see below), no seagrass, 2) shallow water, 2 depths of oyster and 2 depths of seagrass, and 3) oyster and seagrass at one depth with no shallow area. These combinations allowed observation of grass shrimp use of oyster patches in relation to other potentially co-occurring refuge habitats. When a shallow water refuge was present, the tank was divided into 5 zones (Fig. 2): 1) a 2 cm depth shallow area, 2) a transitional slope from shallow to intermediate depths, 3) a 14 cm intermediate depth zone, 4) a transitional slope from intermediate to deep zones, and 5) a 44 cm depth deep zone. When present with shallow water, oyster and seagrass patches were placed opposite of each other in the intermediate and deep zones. When only oyster and seagrass refuges were offered, they were placed at opposite ends of the tank in 44 cm depth water. Oyster patches were formed from 12 cleaned, large shells, arranged in a 30 cm x 10 cm x 23 cm pyramid. Seagrass refuges were formed from 42 strands of floatable green ribbon with a width of 0.7 cm and length equaling water depth (either 14 cm or 44 cm depending on location). The strands were tied together on a 2 cm base, covering a 500 cm^2 area at the surface of the tank (700 strands•m^{-2}).

Grass shrimp, *Palaemonetes pugio*, were used as test organisms because they are an ubiquitous estuarine species that has been shown to use oyster reefs on a facultative basis (Wells 1961, Townsend 1991). They are also important intermediate predators as well as prey for larger fish and crabs. Experimental protocol involved placing 20 grass shrimp, 30-35 mm total length, in both fish addition and control

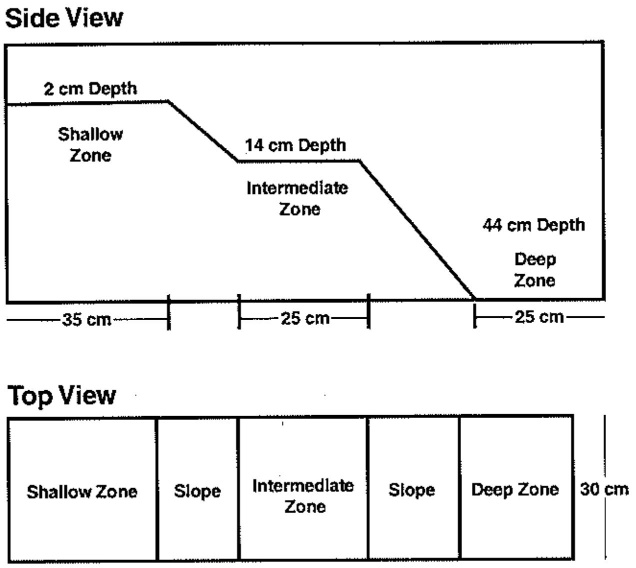

Figure 2. Design of laboratory mesocosm tanks. Shown is a tank presenting shallow water, intermediate, and deep depth zones.

tanks. After a 12 hour acclimation period, 2 fish, either mummichogs, *Fundulus heteroclitus*, (predators) or white mullet, *Mugil ceramus*, (non predatory fish) were added to one tank. Shrimp distribution in the refuges were monitored at 6 hour intervals and the final numbers of shrimp in each type of refuge after 24 hours, as well as in open water or on the bottom, was recorded. To minimize observer effects all observations were made from behind a opaque plastic blind. Shrimp did not appear to dramatically change distribution with observer presence and all observations were made instantaneously. Both shrimp and fish were held in 208 l tanks and were fed commercial fish food before use (animals were not held for more than 1 week before use). No shrimp or fish were used twice. Seven replicate trials were run for each fish type/refuge combination. Mummichogs were tested with all 3 refuge combinations while white mullet were tested with shallow water/seagrass/oyster and seagrass/oyster (deep depth only) combinations (Table 1). Relative use of a refuge habitat in the presence and absence of a fish was analyzed with a one-way ANOVA comparing abundances in a habitat type between fish addition and control treatments, blocking for experimental pairs (paired fish addition and control tanks). To eliminate problems associated with non-independence of distributions among habitats, only use of refuges was compared with no analysis of open water areas (which comprised the majority of the bottom area of the tanks). An F-max test was used to test homogeneity of variances before analysis and a log-transformation applied when heterogeneous variances were found.

Results

A. Field Observations

During both 1990 and 1991, grass shrimp, *Palaemonetes pugio*, were the most abundant organism taken in sweep net sampling. Grass shrimp were significantly more abundant over oyster reefs than adjacent sandflat areas during 1990 (Fig. 3, F=5.95, p<0.02). Although marginally not significant (F=3.51, p<0.10), a consistent pattern of greater numbers over oyster reefs was also observed for grass shrimp in 1991 (Fig. 3). Other taxa which were captured in sweep net samples included blue crabs, *Callinectes sapidus*, brown shrimp, *Penaeus aztecus*, and mummichogs, *Fundulus heteroclitus*. Although all of these taxa had

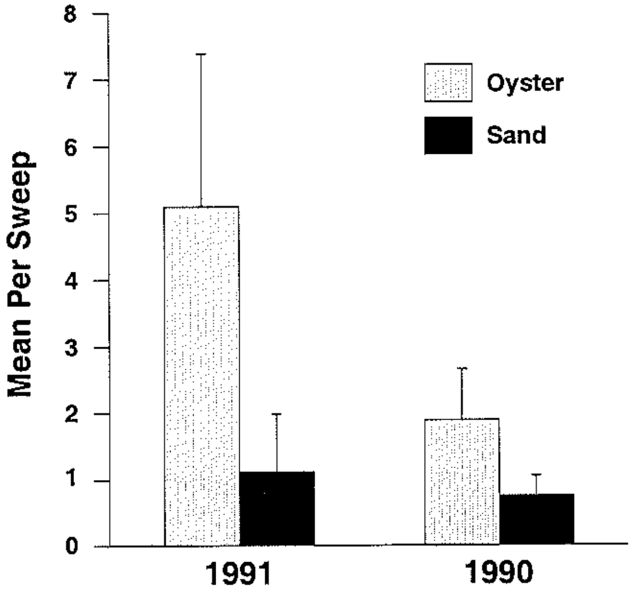

Figure 3. Abundances of grass shrimp collected by sweep net sampling over oyster and adjacent sandflat areas during 1990 and 1991 sampling periods. Shown are means + 1 SE.

Table 2. Abundance of mobile epifauna collected during low tide quadrat sampling in oyster reefs. Numbers indicate mean abundance per season (n=20 for each season, SE given in parentheses).

Species	Spring 1992	Summer 1992	Fall 1992	Winter 1993	Spring 1993	Summer 1993
Panopeus herbstii	1.75 (0.76)	2.9 (1.25)	1.5 (0.65)	0.6 (0.25)	3.2 (0.85)	4.3 (1.5)
Callinectes sapidus	0.37 (0.24)	0.15 (0.12)	0	0.05 (0.05)	0.3 (0.21)	0.2 (0.13)
Clibanarius vittatus	0.15 (0.11)	0.1 (0.1)	0	0	0.2 (0.15)	0.1 (0.1)
Palaemonetes pugio	0.45 (0.32)	0.5 (0.5)	0.5 (0.35)	0.35 (0.35)	0.01 (0.13)	0
Hexapanopeus augustiformis	0.05 (0.05)	1.2 (0.6)	0.15 (0.30)	0.2 (0.15)	0.35 (0.2)	1.7 (0.72)
Alpheus heterochelis	0.1 (0.1)	0.2 (0.2)	0.25 (0.13)	0	0.2 (0.15)	1.3 (1.01)

greatest absolute abundance within the oyster beds, these additional taxa were not common enough and abundances too variable to allow statistical comparison between oyster and non-oyster habitats.

A variety of taxa were observed during diver observations, including pinfish, *Lagodon rhomboides*, sheepshead, *Arcosargus probatocephaleus*, blue crabs, *Callinectes sapidus*, flatfish, *Pleuronectes* spp., and mummichogs, *Fundulus heteroclitus*. All of these taxa were observed more commonly over oyster beds than open sandflats, but only pinfish were observed with sufficient regularity to allow statistical analysis. Pinfish were the most abundant epibenthic organism observed by divers on all dates (Fig. 4) with significantly more pinfish observed over oyster beds than adjacent sandflats (t=11.65, 11 d.f., p<0.0001).

As expected, low tide quadrat sampling indicated significant use of oyster beds by a variety of taxa even after the beds were exposed (Table 2). These included resident reef organisms such as *Panopeus, Clibanarius*, and *Hexapanopeus* as well as transient taxa such as *Callinectes sapidus* and *Palaemonetes pugio*. Although abundances varied seasonally within the reef, with greatest numbers of most taxa during spring or summer, none of these species were ever collected in quadrat samples taken on sandflat areas outside the reef.

B. Laboratory Studies

In the absence of fish (control treatments) there was greater use of structural habitats (oyster and seagrass) than shallow water areas, but little difference in use among structural refugia. In treatments offering only shallow

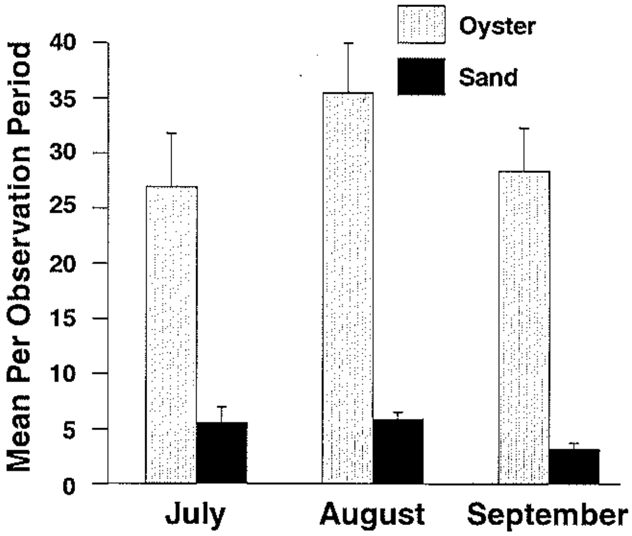

Figure 4. Abundances of pinfish from diver observations over oyster reefs and adjacent sandflat areas. Shown are the mean number of fish (+ 1 SE) observed during 12 ten minute observation during each month.

Table 3. Mean number of shrimp (out of 20 total) in refuge habitats offered in laboratory mesocosms. When oyster and seagrass refuges were offered at both intermediate and deep depths, the mean number over all depths is given.

		Fish Addition			Control		
Fish/Refuges Presented		**Shallow water**	**Oyster**	**Seagrass**	**Shallow water**	**Oyster**	**Seagrass**
mummichog:	shallow water/oyster	0.2	5.6	--	0.6	3.6	--
	shallow/oyster/seagrass	0.4	4.5	0.05	0	2.7	3.3
	oyster/seagrass	--	9.4	1.8	--	4.1	3.1
white mullet:	shallow/oyster/seagrass	0	1.0	5.7	0	1.0	6.6
	oyster/seagrass	--	2.8	3.2	--	2.2	5.0

water and oyster refuges, 18% of shrimp were found within the oyster patches and 3% in shallow water (Table 3) of controls, suggesting some preference for oyster patches relative to shallow water in the absence of predators. When all 3 refuges were offered, 9% were found in oyster, 25% in seagrass and 0% in shallow water of control treatments. When only seagrass and oyster were offered, 16% were in oyster and 20% in seagrass.

The addition of predatory mummichogs was associated with significant differences in the use of these refuge habitats, especially a shift towards use of oyster patches. In the presence of mummichogs, there was significantly greater use of oyster habitat compared to controls for all combinations of refuges offered (Table 4). There was either little increase or a significant decline in the use of other refuge habitat types (Table 4).

There was little effect on habitat use with the addition of white mullet. As with the mummichog experiments, seagrass was the most commonly used habitat in the absence of fish (Table 3). However, unlike the mummichog experiment, there was no difference in habitat use between white mullet and control treatments (Table 4).

Discussion

Oyster reefs represent the primary structural habitat in the low intertidal and shallow subtidal of southeastern North Carolina. Our field observations support the idea that in addition to obligate oyster reef residents, such as mud crabs, these reefs are utilized by a variety of transient species that occupy the reef in a facultative fashion, including grass shrimp, blue

Table 4. Comparison of refuge use between fish addition and control treatments. Numbers indicate F-values from a 1-way ANOVA, blocking for experimental pairs, comparing shrimp numbers in each refuge type between control tanks and fish addition treatments. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$, NS-no significant difference. Where a significant difference occurred, (+) indicates greater use of habitat in fish addition treatments and (-) indicates lower numbers of shrimp in the habitat in fish addition treatments.

Fish/Refuges Presented		**Shallow water**	**Oyster**	**Seagrass**
mummichog:	shallow water/oyster	2.76^{NS}	.86** (+)	---
	shallow/oyster/seagrass	8.93**(+)	15.47***(+)	126.76***(-)
	oyster/seagrass	---	48.23***(+)	9.82 **(-)
white mullet:	shallow/oyster/seagrass	0	0	0.23^{NS}
	oyster/seagrass	---	0.1^{NS}	2.94^{NS}

crabs, and certain fish. These species can be found in a variety of habitats throughout the estuary and presumably use oyster reefs intermittently as a refuge or foraging location. Transient epibenthic decapods and fish may reside in the reef matrix throughout the tidal cycle or only utilize the reefs when they are submerged. These results are consistent with other studies of selected decapods and fish. Grass shrimp have been reported with higher densities in North Carolina oyster reefs compared to non-structural habitats (Wells 1961, Townsend 1991). Gobies and juvenile blue crabs have also been noted utilizing reef habitats (Breitburg 1992). Striped bass and certain other predatory fish may hover near reef patches and utilize them as a foraging site (Breitburg 1999, Chapter 16, this volume).

Laboratory studies suggest that, for grass shrimp, predator avoidance may be an important mechanism leading to preferential use of oyster reef habitats. Although fewer shrimp used oyster patches relative to seagrass or open water areas in the absence of predators, there was a significant increase in residence within oyster patches in treatments with a predator compared to controls. Such shifts were not observed for alternative refuge habitats (shallow water and seagrass). Furthermore, this increase was not observed in treatments containing a non-predatory fish, white mullet, relative to controls.

Structural habitats in general are important refuges for estuarine decapods and fish. Since they may concentrate many small fish and shrimp, they are also important forage sites for larger predators and may be associated with indirect trophic effects on smaller benthic infauna. This phenomenon is well documented from rock reefs (Posey and Ambrose 1994) and from vegetated habitats such as seagrass beds and salt marshes (Summerson and Peterson 1984). Seagrasses are known to be an important habitat for many decapods and juvenile fish and may form an important nursery for certain commercially important shellfish and finfish (Kikuchi 1980. Heck and Thoman 1981). Additionally, use of seagrass beds by intermediate predators, such as shrimp and juvenile crabs, may indirectly lead to reductions in abundances of infauna in the adjacent sandflat areas. Because they are only inundated on a periodic basis, use of salt marshes by decapods and fish is more sporadic, but several studies have still indicated the potential importance of these areas as foraging and refuge sites (Talbot and Able 1984, Miltner et al., 1995).

Our work and other research on the epibenthic community associated with oyster reefs indicate that oyster habitat may function similarly to other structural habitats, with regional variations in its importance potentially dependent on co-occurrence of other habitat types. As a result, oyster reefs may play a critical role as a primary refuge habitat in certain systems. From a management perspective, this indicates the need to manage oyster reefs not only for their direct shellfish resource value, but also as a potentially important nursery habitat. As such, oyster reefs may have similar functions, and need to be considered in similar ways as seagrass, marsh, or rock reef habitats.

Acknowledgments

Field sampling for this project would not have been possible without help from John Caskey and Amy Innes. Joseph Gammel and Ken Riley helped with laboratory studies. This research was supported by a faculty development grant from the University of North Carolina at Wilmington (to M. Posey), a development grant from North Carolina Sea Grant (M. Posey), and a grant from the Cooperative Institute of Fisheries Oceanography (M. Posey).

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Are Three-Dimensional Structure and Healthy Oyster Populations the Keys to an Ecologically Interesting and Important Fish Community?

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Abstract

Oyster reefs provide important habitat for a fish assemblage that is both ecologically interesting and important to the estuarine food web. These fishes are dependent on oyster reefs to varying degrees for feeding, reproduction and shelter from predators. Among the most dependent are the small resident fishes that attach their eggs to unfouled, articulated oyster shells. This resident oyster reef fish assemblage is unusual in the high degree of similarity of both the temporal patterns of recruitment and the diets of newly recruited juveniles. Larvae of the naked goby, the most abundant benthic fish in many mesohaline Chesapeake Bay oyster reefs, occur in sufficiently high densities during summer to be important grazers of zooplankton. The naked goby also has the highest recruitment rate recorded for any reef fish world-wide. In addition to the resident fishes, oyster reefs are extensively utilized by more widely ranging fish species. However, limited research involving visual observation in Chesapeake Bay and many other estuaries, and the difficulty of sampling this habitat with traditional nets, has likely led to our underestimating the importance of oyster reefs to many of these highly mobile fishes. For example, counts and observations conducted with scuba indicate that striped bass, especially juveniles, are very abundant on oyster reefs. Some individuals appear to remain in limited areas within reefs and forage on oyster reef fishes, especially on naked goby larvae aggregating near structures.

Oyster reef restoration and construction efforts have the potential to enhance local abundances of reef fishes. Reefs that develop "healthy" oyster populations will provide a continual supply of nest sites for resident fishes. Reefs that support large populations of mobile invertebrate infauna and epifauna will provide prey for both resident fishes and larger, more transient, bottom-feeding species. Enhancing topographical relief within reefs will attract oyster reef fish larvae by creating downcurrent low flow zones that allow larvae to remain on reefs and settle to the benthos. Reefs that extend to near the water surface and into shallow nearshore areas will also provide refuges for fish when oxygen concentrations in deeper areas of reefs decline to lethal levels. It is important that the requirements of fish populations and oysters on reefs are not likely to be in conflict; many of the same strategies proposed to enhance oyster populations will also improve the habitat for fishes.

Introduction

A wide variety of fishes utilize estuarine oyster reefs for feeding, shelter from predators, and for reproduction. The most abundant of these fishes are small benthic species that are cryptic in both coloration and behavior, and use oyster shells for nest sites. However, oyster reefs are also utilized by more widely ranging fish like spot (*Leiostomus xanthurus*) and black drum (*Pogonias cromis*), which feed on benthic invertebrates, and by some of the top predators in estuarine systems such as striped bass (*Morone saxatilis*), which feed on the benthic fishes and crabs found in and among the shell substrate.

Although the degree of dependence on oyster reefs varies widely among fish species, both the decline of oyster reefs in many estuaries and oyster reef restoration efforts have the potential to influence populations of many estuarine fishes. These fishes will potentially be affected by oyster reef management and restoration efforts regardless of whether the consequences to fishes are implicitly considered (e.g. Chesapeake Bay Program: CBP 1993, 1994), or the reefs are managed only to maximize oyster production. The goals of programs designed to create complete oyster reef communities, and those designed to maximize oyster production are not necessarily in conflict; however, many of the factors that are likely to enhance oyster recruitment, survival and growth should also enhance fish populations.

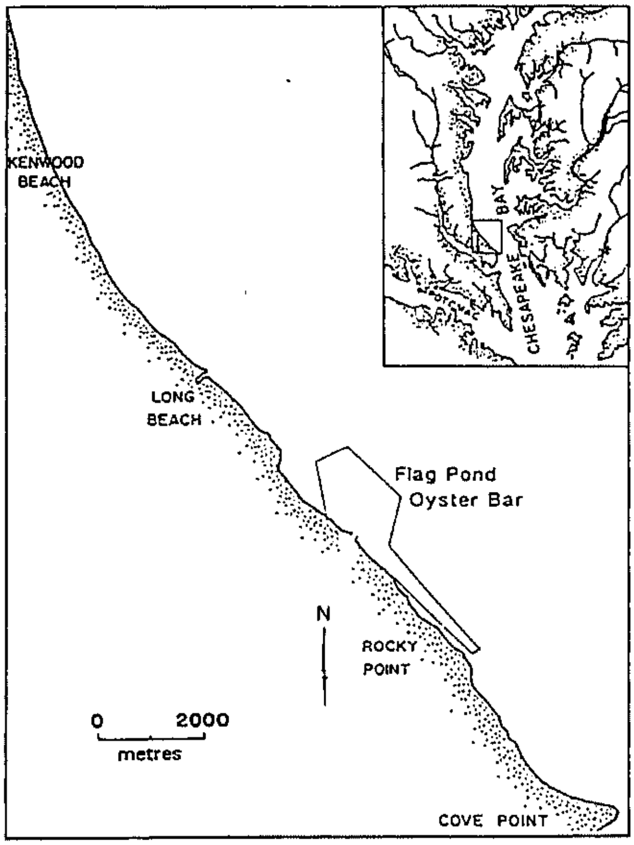

Figure 1. Flag Pond oyster reef. Physical conditions and biota are not significantly affected by the nearby Calvert Cliffs Nuclear Power Plant (Heck 1987).

The goal of this paper is to suggest some of the reasons that oyster reef fishes should be considered in restoration efforts, and to discuss how various methods for oyster reef restoration may affect oyster reef fish populations. To do this I draw on visual observations and field experiments conducted during 1985-1994 in mesohaline reefs in Chesapeake Bay. Because most of the fish species discussed have broad geographic ranges and the factors that affect their abundance deal with the general health and physical configuration of oyster reefs, the information in this paper should be relevant to reef management and restoration in many of the Atlantic and Gulf of Mexico estuaries of the United States.

Oyster Reef Fish Ecology And The Structure of Oyster Reefs

FLAG POND OYSTER REEF

Many of the observations and field experiments described in this paper were conducted on the Flag Pond oyster reef, located 7 km north of Cove Point, MD on the western shore of the Chesapeake Bay (approximately 38°25'N, 76°25'W; Fig. 1). During the summers of 1985-1994, research assistants and I dove extensively to sample fishes and monitor dissolved oxygen and flow at Flag Pond. The Flag Pond oyster reef consists of approximately 81 ha of extant oyster bar and rock substrate extending from the shore for approximately 0.3-1.0 km at water

Table 1. Fishes at Flag Pond oyster reef. Species listed as facultative residents appear to be represented by at least some individuals that remain on the oyster reef for several months. Some species listed as transients may actually be facultative residents. However, they are highly mobile within the reefs, and the duration of residency of individuals has not been studied.

Oyster Reef Resident Fishes	Facultative Residents	Transients
naked goby *(Gobiosoma bosc)*	black sea bass *(Centropristis striata)*	striped bass *(Morone saxatilis)*
skilletfish *(Gobiesox strumosus)*	northern pipefish *(Syngnathus fuscus)*	summer flounder (juv.) *(Paralichthys dentatus)*
striped blenny *(Chasmodes bosquianus)*	Atlantic spadefish *(Chaetodipterus faber)*	winter flounder (juv.) *(Pleuoronectes americanus)*
feather blenny *(Hypsoblennius hentz)*		spot *(Leiostomus xanthurus)*
oyster toadfish *(Opsanus tau)*		pinfish *(Lagodon rhomboides)*
		inshore lizardfish *(Synodus foetens)*
		American eel *(Anguilla rostrata)*
		striped burrfish *(Chilomycterus schoepfi)*
		Atlantic silverside *(Menidia menidia)*

depths of 1-6 m. Oyster (*Crassostrea virginica*) shell provide fairly continuous bottom cover, interspersed with patches of sand and sediment, as well as low consolidated sandstone outcroppings and rocks (mostly <1 m diameter and <0.5 m high). Outcroppings and rocks, which are generally covered with oysters and other sessile invertebrates, provide three-dimensional physical structure within the oyster reefs and alter near-bottom flow. These structures become more prevalent shoreward, with continuous shell and sediment seaward. Flow at Flag Pond is bidirectional with predominant flood tides towards the NNW (ca 334°; Browne & Fisher 1988) and ebb tides towards the SSE. Salinity, temperature, and oxygen fluctuations, as well as the oyster reef fish community are described in Breitburg (1990, 1992). Bottom temperatures and biota at the study site are not affected by operation of the nearby Calvert Cliffs Nuclear Power Plant (Heck 1987).

Densities of oyster reef fishes described below were estimated in one of three ways. Numbers of demersal larvae of the naked goby were estimated visually. Densities of small oyster reef fishes were estimated from collections made by suctioning fish isolated within 0.26 m^2 metal cylinders, or by allowing fish to colonize 0.35 m^2 fiberglass trays filled with 1 l of sand and 4 l of oyster shell (Breitburg 1992).

OYSTER REEF FISH ASSEMBLAGE AT FLAG POND

The fish assemblage found in the Flag Pond oyster reef during late spring through early autumn includes species that vary widely in their dependence on oyster reef habitat. These fishes comprise three general categories: (1) resident oyster reef fishes, which are dependent on oyster reefs as their primary habitat, (2) facultative residents that are generally not wide ranging, but utilize a variety of structured habitats, and (3) transients that can be quite abundant at times but are wide ranging at least as adults (Table 1).

The "resident oyster reef assemblage" at Flag Pond includes four small species – the naked goby, skilletfish, striped blenny and feather blenny – as well as the larger oyster toadfish. All of these species are highly dependent on oyster reefs, and utilize this habitat for feeding, shelter and reproduction. Resident oyster reef fishes feed primarily on benthic invertebrates, but also prey on benthic fishes. They are cryptic in their behavior, tending to shelter under and among oyster shells, especially when predatory fish are present.

The four smaller resident oyster reef species attach their benthic eggs to the insides of unfouled, articulated oyster shells. Naked gobies, striped blennies and skilletfish appear to be particularly dependent on this resource. It is important to consider that a "healthy" population of oysters would be expected to have a continual, low level of mortality of a variety of sizes of individuals, and thereby provide a continual supply of nest sites for these fishes. In contrast, shell plants, reefs where disease kills oysters before they are large enough to be used by fish, and artificial structures not colonized by large bivalves, may not provide adequate reproductive habitat for these species. Furthermore, addition of shell or dredging the reef during the spring through late summer-to-early autumn breeding season could disrupt reproduction of these fish by burying nests, breaking apart articulated shells or scaring off males guarding their eggs.

Unlike the smaller species, oyster toadfish attach their eggs to the undersides of larger substrates including rocks and consolidated oyster shells. Oyster toadfish do not have planktonic larvae, and males guard their offspring until they leave the nest at 20 mm standard length (SL). Because they do not produce widely dispersing larvae, oyster toadfish may be more useful as indicators of local contaminant conditions than other estuarine fish species. No studies of which I am aware have tagged young-of-year oyster toadfish and returned them to the reefs from which they were caught. However, it would not be surprising if the egg through juvenile stages remained within a single oyster reef at least until water temperatures decline in autumn. Adults appear to have a strong tendency to return to their home reef when removed and relocated (Schwartz 1974).

ECOLOGICAL IMPORTANCE OF A RESIDENT OYSTER-REEF FISH TO ESTUARINE DYNAMICS

Some members of the resident oyster reef assemblage may be ecologically important because they are sufficiently abundant to play significant roles in estuarine trophic interactions. Naked goby larvae are typically either the first or second most abundant fish larvae in mesohaline areas of Chesapeake Bay tributaries during summer, and rank second only to bay anchovy larvae in the mainstem Bay. Densities above the pycnocline in the Patuxent River typically average 5 to 10 ind m^{-3} during late June through mid-August, with peak densities on the order of 50 to 60 larvae m^{-3} (e.g. Shenker et al. 1983, Keister et al. unpubl). Average densities of over 200 naked goby larvae m^{-3} have been reported from the North Inlet estuary in South Carolina (Allen and Barker 1990).

Perhaps because of their abundance, naked goby larvae are, at times, the most important prey of juvenile striped bass (Markle and Grant 1970). Also because of their abundance, naked goby larvae may crop a nontrivial portion of copepod production in Chesapeake Bay tributaries. Feeding rates vary among species of larval fishes. For example, yellow perch (*Perca flavescens*) larvae consume approximately 21% of their body weight each day (Mills and Forney 1983). In contrast, 200 µg dry wt. bay anchovy (*Anchoa mitchilli*) larvae consume approximately 50 *Artemia* sp. nauplii$\cdot h^{-1}$ or 6 µg nauplii$\cdot h^{-1}$ at prey densities of 50 nauplii$\cdot l^{-1}$ (Houde and Schekter 1980). If larvae feed 14 $h \cdot d^{-1}$, this would equal 42% of body weight$\cdot d^{-1}$. Personal experience rearing both species suggests that feeding rates of bay anchovy are greater than that for naked goby larvae. Assuming an intermediate feeding rate of 30% of body weight$\cdot d^{-1}$, and using an estimate of 6 µg dry weight for *Acartia tonsa* (Heinle 1969), an 8 mm SL, 2000 µg dry weight naked goby larva would consume approximately 100 copepods$\cdot ind^{-1} \cdot d^{-1}$. This is similar to the feeding rate of 17 dph striped bass larvae feeding on copepods at prey densities of 50 ind$\cdot l^{-1}$ (Chesney 1986). If

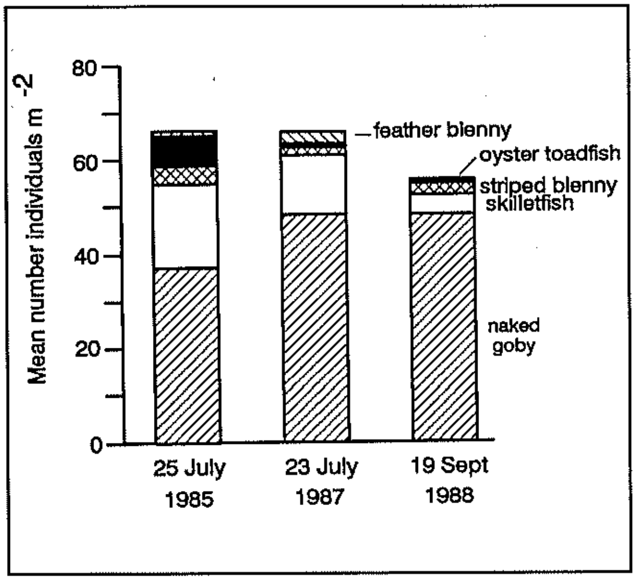

Figure 2. Mean densities of oyster reef resident fishes during peak sampled density in three years. Data are means of 5-10 samples per sample date.

summer densities of naked goby larvae sufficiently large to feed on mesozooplankton are approximately 2 ind·m^{-3}, and these larvae range in size from 6-10 mm SL, consumption of copepods and copepodites would be on the order of 50-400 ind·m^{-3}·d^{-1}.

Estimates of grazing by gelatinous predators indicate that predation by naked goby larvae on zooplankton may be comparable to that of sea nettles and ctenophores, which are recognized as important grazers in the Chesapeake Bay system (e.g. Purcell 1992, 1994a). Summer standing crops of planktonic copepods and other mesozooplankton in surface waters of tributaries and the mainstem Bay during July has been estimated at 1,000 to 55,000 ind·m^{-3} (e.g. MDE 1992, 1993). At copepod densities of 25,000 ind·m^{-3}, a 60 mm bell diam individual sea nettle feeding at 27°C would be expected to consume approximately 200 copepods·d^{-1} (from equation in Table 4 in Purcell 1992). At typical surface layer densities of 0.2 sea nettles m^{-3} (e.g. Purcell et al. 1994b, Keister et al. unpubl) sea nettles should therefore consume approximately 40 copepods·m^{-3}·d^{-1}. At typical surface layer field densities of 1 ind·m^{-3} (Purcell et al. 1994b, Keister et al. unpubl) and copepod densities of 25,000 ind·m^{-3}, ctenophores would consume approximately 1600 copepods·d^{-1} (Purcell et al. 1994b). However, during mid-summer, ctenophore densities can be substantially lower than 1 ind·m^{-3}.

Ultimately, naked gobies and other oyster reef fishes that survive the larval stage settle to the benthos, primarily to oyster reefs. By doing so, they transport carbon and nitrogen from the water column to the benthos. The result of these high recruitment rates is high densities of resident oyster reef fishes (Fig. 2), averaging as many as 60 or more ind·m^{2}, with populations heavily skewed towards the young-of-year class.

Recruitment rates of naked gobies on Flag Pond are typically 1-2 orders of magnitude higher than maximum recruitment rates recorded for coral reef fishes or other temperate reef fish species. In field experiments conducted during 1994, we recorded 24-h recruitment rates averaging as high as 34.1±4.9 ind·m^{-2}·d^{-1} (n=16 0.35 m^{2} recruitment trays), and an average of 9.1±2.9 ind·m^{-2}·d^{-1} during late July - late August (n=13 sample dates). This would result in an average recruitment rate of 272 ind·m^{-2}·month^{-1}. Comparable experiments have not been conducted on other oyster reefs. However, these high rates are not likely to be unique to either Flag Pond or the Chesapeake Bay system because higher larval densities have been recorded elsewhere (e.g. Allen and Barker 1990).

REEF CONSTRUCTION AND THE SIMILARITY OF SPECIES

Resident oyster reef fishes are also interesting and unusual from an ecological standpoint because of the similarity in the temporal patterns of recruitment, and the diets of benthic juveniles of the four most abundant species. A consequence of this similarity, however, is that the timing of reef construction or rehabilitation efforts, and the degree to which reef restoration affects prey for newly settled fish, may strongly affect the resident oyster reef fish assemblage in its entirety. Three years of sampling at the Flag Pond oyster reef indicate that peak recruitment for all of the most abundant resident oyster reef fishes occurs within the same brief period

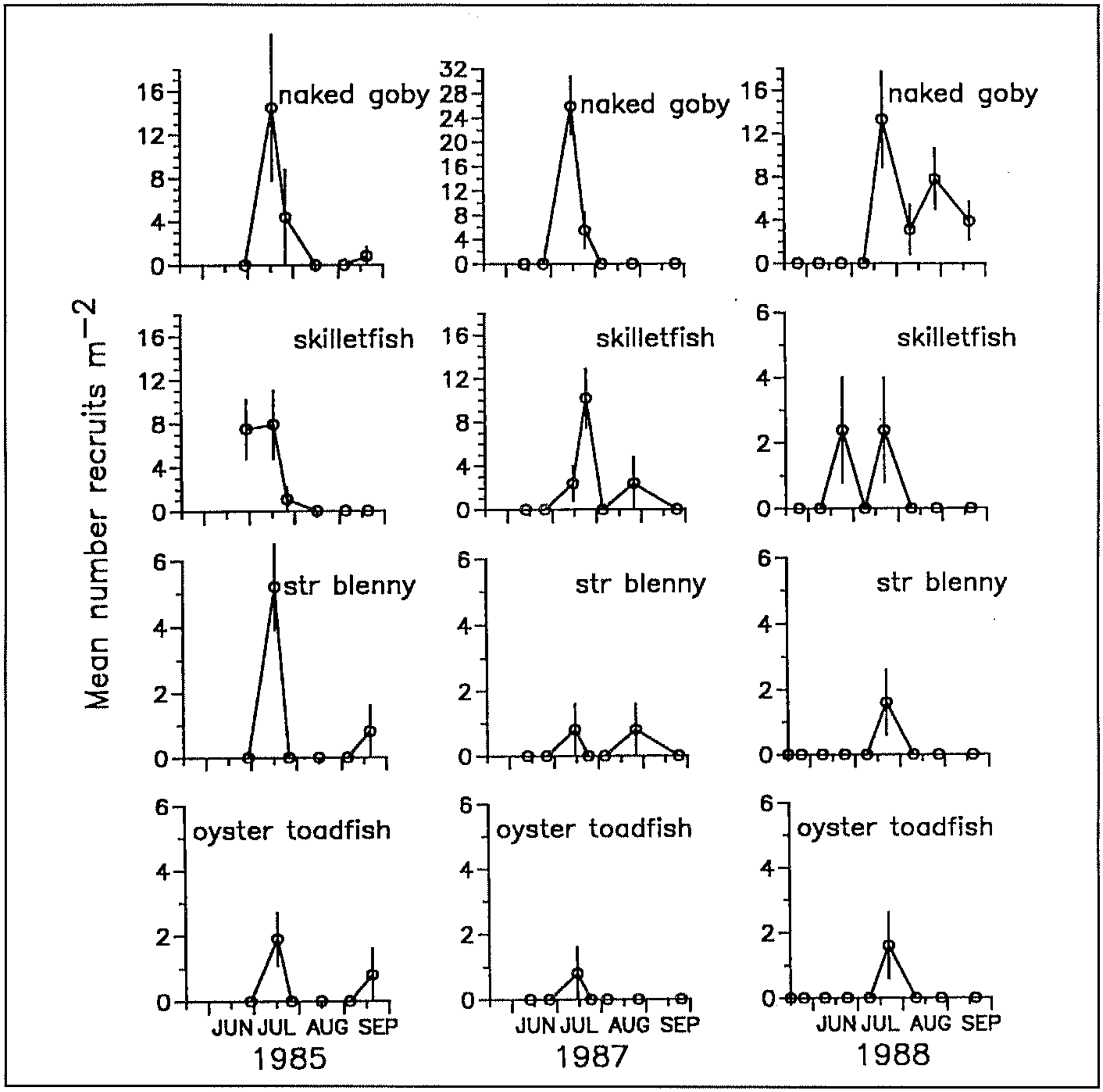

Figure 3. Mean number of recruits ≤ 2 weeks postsettlement m^{-2} in the Flag Pond oyster reef during 3 years of sampling. Sampling was conducted biweekly through most of the recruitment season. Numbers of recruits 2 weeks postsettlement for each species were calculated based on minimum sizes of individuals collected in samples and estimates of growth rates. For oyster toadfish these numbers represent individuals that have likely left their nest 2 weeks before being collected. Data are ±1SE of 5-10 samples per date. str blenny = striped blenny.

during mid-summer (Fig. 3). If reefs are disturbed during this peak recruitment period, or if reef construction occurs after this peak, recruitment of the entire assemblage may be reduced for that year. In subsequent years, however, this initial timing will likely have little or no residual effect. Furthermore, until the overwintering behaviors of these fishes are better understood, the consequences and benefits of disturbing oyster reef habitat at various times of the year will be difficult to predict.

The combination of high recruitment rates (described above) and the similarity in diets of the juvenile oyster reef resident species may make the way that reefs affect benthic invertebrate assemblages of more long-lived conse-

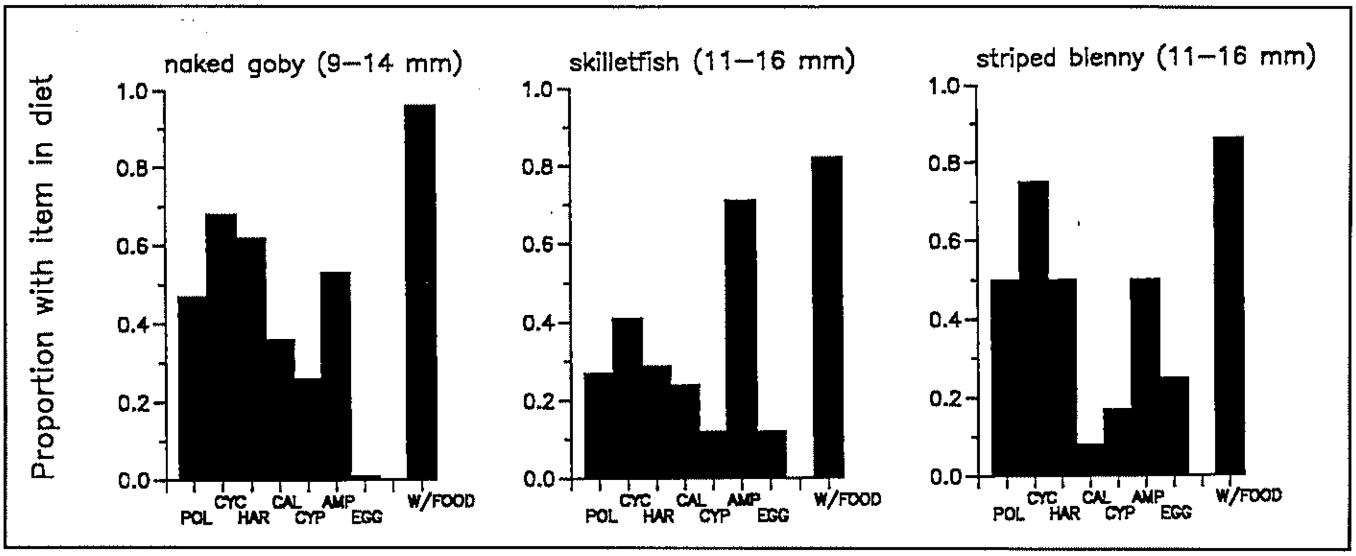

Figure 4. Diets of oyster reef fishes estimated to be 2 weeks postsettlement. pol = polychaetes, cyc = cyclopoid copepods, har = harpacticoid copepods, cal = calanoid copepods, cyp = barnacle cyprids, amp = amphipods, egg = fish egg, w/food = proportion of fish with prey in their gut.

quence. All resident species are similarly dependent on benthic and demersal invertebrate prey. Diets of similar sized, 2 week postsettlement naked goby, skilletfish and striped blenny include the same array of polychaetes, copepods, barnacle cyprids, amphipods and fish eggs (Fig. 4). Diets of slightly larger, 20-25 mm SL, juveniles of these fishes are also similar and overlap with diets of similar-sized oyster toadfish (Fig. 5). Dissimilar-sized individuals of all of these species will eat each other, and naked gobies are also known to prey on smaller conspecifics (Nero 1976, Breitburg et al. 1994, Breitburg unpubl. data). Artificial reef structures and the height and dimensions of shell plants are sometimes purposefully designed to modify water flow, sedimentation and other physical properties that may influence the recruitment or growth of oysters. These same factors can affect the behavior, recruitment and abundance of prey of juvenile oyster reef fishes (e.g. Jumars and Nowell 1984, Palmer 1986, Butman 1989). Structures that are less readily colonized by invertebrate prey may thus decrease recruitment or growth rates, or increase cannibalism and predation within the resident oyster reef fish community.

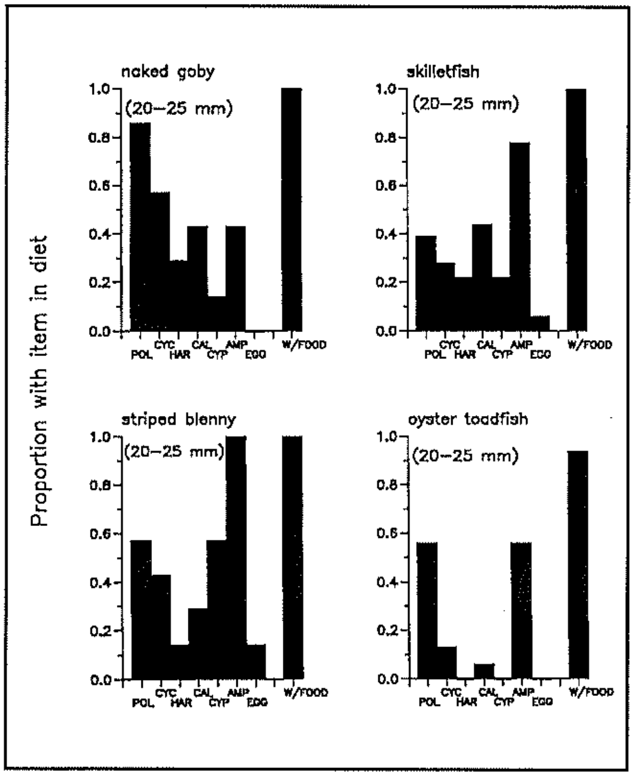

Figure 5. Diets of oyster reef fishes similar in size to that of oyster toadfish 2 weeks after leaving their nest. Abbreviations for diet items are the same as those used in Fig. 4.

RECRUITMENT AND SURVIVAL OF OYSTER REEF FISH AND THE THREE-DIMENSIONAL STRUCTURE OF OYSTER REEFS

The three dimensional structure of oyster reefs will affect the spatial distribution of demersal naked goby larvae on reefs, the spatial distribution of settlement of naked gobies (Fig. 6), and perhaps the overall abundance of this fish species (Breitburg et al.1995). This structure can result from rehabilitation efforts or the natural relief that historically developed on unfished oyster habitat. Rocks and other structures create areas of reduced flow velocity on their downcurrent sides. Naked goby larvae aggregate in these downcurrent low-flow zones. For example, only 6% of the substrate measured on transects in the Flag Pond oyster reef consisted of structures that protrude more than 15 cm above the basal shell substrate, but over 90% of the schools of ≥10 larvae were located adjacent to these structures (Breitburg 1991). When the size and position of rocks were manipulated, larger numbers of larvae associated with larger rocks, which created larger downcurrent low-flow zones (Breitburg et al. 1995). Furthermore, larvae were nearly always within the downcurrent low-flow zone, and were never upcurrent of rocks even though planktonic prey were more abundant in the upcurrent position. This attraction of larvae to low flow zones created by structure is reflected in the spatial distribution of settlement; most naked gobies settle adjacent to structures and in positions that during a portion of the tidal cycle would be within these downcurrent low flow zones (Breitburg et al. 1995). Other experiments designed to examine the response of naked goby larvae to flow and structure indicate that these structures may also create habitat that is heavily used by young-of-year striped bass (see below).

In areas subject to low dissolved oxygen concentrations, reefs that extend to or near the surface, or along the bottom to shallow areas where oxygen concentrations remain suitable, potentially increase survival of oyster reef fishes and crabs (see also Lenihan et al., this volume). The behavioral response of oyster reef fishes to oxygen concentrations that approach lethal levels is to move upward onto rocks or other structures that protrude above the surrounding substrate and to migrate shoreward (Breitburg 1992). Xanthic crabs and blue crabs (*Callinectes sapidus*) climb upward onto rocks, buoy lines, and other structures. These behavioral responses can allow benthic fish and crabs to move into water depths with higher oxygen

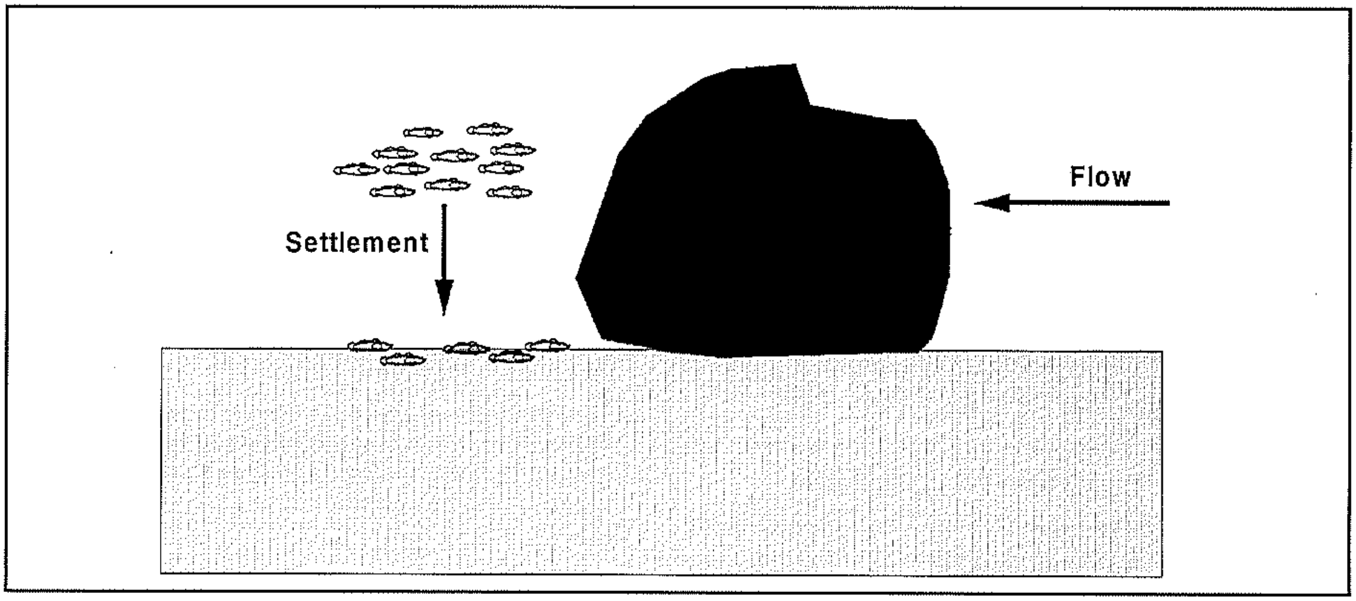

Figure 6. The spatial distribution of naked goby larvae and settlement of naked goby to the benthic oyster reef habitat. Demersal larvae aggregate downcurrent of structures that reduce flow velocity at least during portions of the tidal cycle when current velocities exceed the sustained swimming speed of larvae. Most larval settlement occurs in these downcurrent "flow shadows" created by three-dimensional structure within the oyster reef.

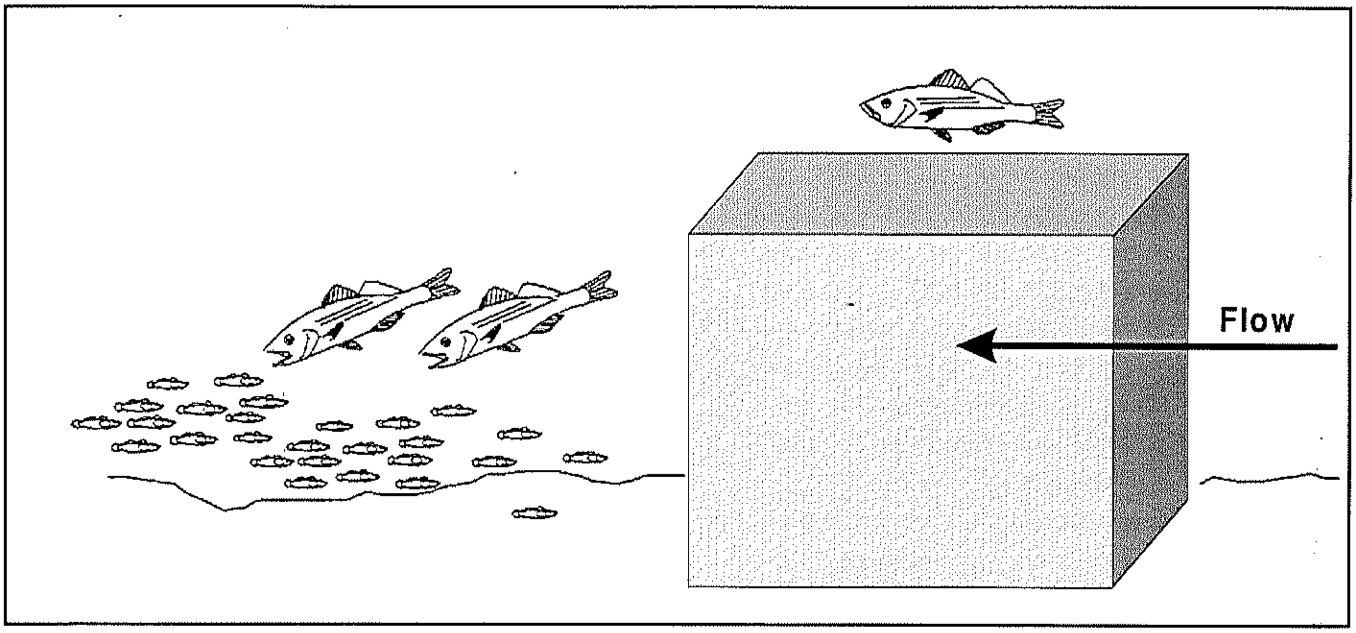

Figure 7. Illustration of cube experiment testing effects of flow on naked goby larvae. Young-of-year striped bass hovered above cubes and fed on larvae.

concentrations and can sometimes substantially increase survival (Breitburg 1992). Relatively flat oyster reefs that do not extend shoreward to shallow water depths will not provide a refuge during low dissolved oxygen events.

ARE OYSTER REEFS IMPORTANT HABITAT FOR STRIPED BASS?

The limited research involving visual observations on oyster reefs in the Chesapeake Bay and elsewhere, and the difficulty of sampling oyster reefs with bottom trawls, has likely led to our underestimating the importance of oyster reefs to many of the highly mobile fish species. For example, my observations while diving at Flag Pond indicate that densities of striped bass, especially juveniles, are extremely high on oyster reefs. Since Chesapeake Bay striped bass populations have begun to recover, I have often seen >50 individuals during a 1-hour dive covering an extremely limited area. Some individuals, especially young-of-year and age class 1+ fish, appear to remain in limited areas within reefs and forage on oyster reef fishes, especially on naked goby larvae aggregating near structures. Other striped bass, especially larger fish, occur in schools of up to several hundred individuals.

None of my oyster reef research has focused specifically on striped bass. However, two instances when striped bass abundances were estimated illustrate their abundance on oyster reefs. Both of these counts were pre-planned, i.e. we did not initiate the count because of high densities on a particular date. First, during summer 1993, I conducted an experiment using 33 x 33 x 33 cm cubes designed to separate the effects of flow and structure on aggregating behavior of naked goby larvae (Breitburg unpublished data). Seven of the 12 cubes monitored on 26 July 1993 had young-of-year striped bass hovering within a few cm above the top of the cube, for a total of 20 striped bass per 1.3 m^2 of cube top area (Fig. 7). These young-of-year were actively feeding on the naked goby larvae that aggregated in large numbers along the downcurrent side of the complete cubes (some cubes had open sides to allow water to pass through unimpeded). In addition to the young-of-year that remained associated with the cubes, large numbers of larger juvenile and subadult striped bass actively swam above, beside and between the cubes.

Second, during 1994 research assistants and I did 5 min counts of numbers of striped bass and other piscivorous fishes swimming 50 cm above the substrate that passed over 0.35 m^2 recruitment trays adjacent to, and 2 m distant from, large rocks (approximately 80-100 cm in diameter perpendicular to the prevailing flow direction). Four trays (upcurrent/downcurrent, adjacent/distant) were counted simultaneously, each by a different diver. Averages of 4.4 and 1.9 observations of juvenile striped bass per 5 min were counted for trays distant from, and adjacent to rocks, respectively (n=8 trays per distance category). Most of the striped bass were probably 1+ year class individuals. Although it is impossible to estimate densities of striped bass from these counts because some individuals likely swam over the trays more than once, it is clear that the abundance of these fish is sometimes sufficiently high for them to be important predators within this oyster reef.

Conclusions

No studies of which I am aware have examined the direct or indirect effects of resident oyster reef fishes on oysters or mobile fauna in oyster reef communities (as of the submission date of this manuscript.) Similarly, although we know that many of the more transient fishes, including a number of commercially and recreationally valuable species, utilize oyster reefs, we do not know the importance of oyster reefs to these transient fishes on either the individual or population level. Excluding issues of water quality, we cannot answer the question: Would we have fewer or smaller striped bass, spot, pinfish, etc., if there were no oyster reefs in Chesapeake Bay? Nor do we know the type or magnitude of effects of these transient fishes on the oyster reef community. Clearly these are major gaps in our understanding of oyster reef communities that could have important management implications.

The part of the fish:oyster reef relationship that is evident, however, is that an ecologically interesting and important assemblage of resident fishes is dependent on a healthy oyster population for habitat and reproduction. The methods used for reef enhancement and rehabilitation and for the construction of artificial reefs are likely to influence their suitability for these fish species. One important feature of reef construction, also singled out as important to oysters themselves (see Bartol and Mann 1999, Chapter 10, this volume) is likely to be the extent and type of three-dimensional structure created. In addition, reefs must provide shelter from predators, sites for egg attachment, and suitable habitat for prey.

Acknowledgments

Many people helped with the field- and lab studies summarized here. I would especially like to thank B. Albright, W. Yates, T. Loher, C. Pacey, J. Smallwood, C. Jordan, and J. Pahl. This research was funded by University of Maryland Sea Grant awards R/DO-1B and A/DO-1B to D. Breitburg, and NSF grants OCE-9102641 and OCE-9103877 to D. Breitburg and M. Palmer.

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Chapter 17

Materials Processing by Oysters in Patches: Interactive Roles of Current Speed and Seston Composition

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Abstract

Filtration rates for oysters have typically been measure in still water laboratory experiments and ecosystem-level effects estimated by extrapolation. With the exception of *in situ* measures of oyster filtration by Dame (1999, Chapter 18, this volume and references cited therein) these estimates have failed to account for the effects of hydrodynamic effects on oyster filtration rates and on physical redistribution of particles. In this chapter we report on a series of experiments conducted in a recirculating seawater flume designed to address the effects of flow speed and seston composition on filtration rates in a bed of oysters. In six separate experiments ninety oysters were arranged in the bed of the flume, flow speed adjusted to one of eight levels (0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7 or 22.0 cm s^{-1}), seston added to the flume and particle concentrations upstream and downstream of the oyster bed determined from vertically-arrayed samples. Four experiments investigated the effects of each flow speed on the filtration of a unialgal diet, while two experiments utilized the algal diet in combination with inorganic particles. Control experiments sought to estimate the effects hydrodynamic effects on particle distribution by measuring "filtration" rates over beds of ninety pairs of empty oyster valves. Our findings reveal effects of flow speed and, less evidently, seston composition on particle filtration by oysters. More importantly, our results point to the importance of hydrodynamically-mediated particle redistribution of particles over patches of oysters, and portend sampling difficulties associated with quantifying oyster filtration rates in the field.

Introduction

There is increasing evidence that benthic, filter feeding bivalves may control water quality in shallow water systems. Benthic filter feeding bivalves have been shown to be the primary control of phytoplankton biomass in regions of the Potomac River, the Saint Lawrence River, and the south San Francisco Bay (Cloern, 1982; Cohen et al., 1984; Frechette et al., 1989). Phytoplankton concentrations were reduced 40 to 60% by the filtration activity of a dense bed of Asiatic clams, *Corbicula fluminea,* in the Potomac River (Cohen et al., 1984). Bio-deposition of fine ($<3\mu m$) particles by the Eastern Oyster, *Crassostrea virginica*, has been shown to be seven times faster than by gravity alone (Haven and Morales,1966). Estimates of the material processed by a bed of bivalves have been used to extrapolate the potential ecological effects of the filtering activity on estuarine water quality (Dame 1999, Chapter 18, this volume).

The decline of the primary filter feeder in the Chesapeake Bay may have lead to system wide ecological changes. At one time the Eastern Oyster, *Crassostrea virginica*, was the dominant suspension feeder in the Chesapeake Bay ecosystem. Based on historical densities of *C. virginica*, Newell (1988) calculated that, prior to 1870, the oyster population could filter the entire volume of the Chesapeake Bay in 3.3 days, the estimate for the same activity in 1988 was 325 days. In a model of carbon flux in the mesohaline reaches of the Chesapeake Bay, 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 the decrease in planktonic primary productivity and the increase in benthic primary productivity may have the potential to reduce eutrophication in the Chesapeake Bay.

Fundamental to assessing the system level effects of bivalve filtration are reliable estimates of filtration rates in the field. Most filtration rate measurements have been based upon solitary bivalves in small scale experiments with minimal water flow, usually just stirring to keep algae in suspension, and minimal turbidity (e.g. Palmer 1980, Gerdes 1983, Riisguard 1988). The efficacy of extrapolating directly from rates measured on a few oysters in the laboratory to filtration rates of an oyster reef in the field has not been generally established. Dame (1999, Chapter 18, this volume and earlier work cited therein) has made *in situ* measures of materials processing by oysters in tidal creeks which indicate that they may have a controlling influence on benthic-pelagic coupling.

Two factors likely to affect oyster filtration capacity are seston composition and flow speed. In laboratory studies low concentrations of suspended sediments (20 mg kaolinite L^{-1}) apparently do no affect filtration rate on algae (Urban and Kirchman, 1992), but high clay and silt concentrations (100 and 700 mg L^{-1}, respectively) have been shown to affect pumping activity of *C. virginica* (Neilson et al., 1976).

Growth of non-siphonate bivalves has been negatively correlated with increasing flow speeds, presumably as a result of an associated decrease in filtration efficiency (Wildish and Kristmanson 1985; Wildish et al. 1987; Eckman et al. 1989; Grizzle1992). Since growth rates were inhibited at flow speeds > 1 cm s^{-1} for *Crassostrea virginica* (Grizzle 1992), it is expected that there is a negative relationship between increasing flow speed and filtration rate (Wildish and Saulnier 1993).

The filtration capacity of a bed of bivalves depends not only on the filtration capabilities of each animal, but also on current velocity, turbulent mixing, and the density and spacing of organisms. Monismith and co-workers (1990) have shown that refiltration can have a negative effect on the filtration capacity of an infaunal bivalve bed. Metabolic wastes and decreased food concentration in the waters overlying downstream portions of the bed may reduce filtration activity and total food availability. Vertical mixing may redistribute particles in the water column, ameliorating near bed depletion (Officer et al. 1982; Frechette et. al. 1989).

However, for dense assemblages of epifaunal suspension feeders "skimming flow" (Nowell and Church 1979) may reduce particle flux through the patch. The hydrodynamic effects of such patches will depend upon organism density, spacing, and flow velocity.

Time variances in filtration activity among each individual oysters in a group may figure prominently in the overall filtration capacity of the group. Riisguard (1988) and Loosanoff (1958) reported that any oyster that was not open or actively filtering was not included in their results. Palmer (1980) reported filtration rates that ranged from 0 to 5.47 L g^{-1} hr^{-1} and that the percent time each oyster spent filtering water ranged from 49 to 91%. However, Newell (1988) estimated that oysters filter for 23 hours each day at the continuous rate of 5 L g^{-1} hr^{-1}. Filtration rates that do not reflect time variances in oyster filtration will not only overestimate the filtration rates of individual oysters, but will lead to an overestimation of the filtration capacity of an oyster bed.

Small-scale filtration experiments do not account for the complex interactions of flow, suspended particulate matter, seston depletion, resuspension, and refiltration on the filtration rates and feeding behavior of *Crassostrea virginica*. Turbulent mixing and seston depletion across the bed are apt to have antithetical effects. Extrapolation of system-level effects may be improved by evaluation of the effects of environmental factors such as flow speed and seston composition on filtration rates. In addition, estimating the proportion of the population feeding at any one time has important ecological consequences.

Here we report on a series of flume experiments designed to incorporate variation in flow speed and seston composition over a bed of oysters into the measurement of oyster filtration. Evaluating oyster filtration capacity under conditions of turbulent mixing and seston depletion allows for the interplay of both hydrodynamic and biotic factors. Our findings revealed some expected relations between flow speed and feeding activity, and considerable variation in the relationship between flow speed and filtration rates. Unexpectedly, our results reveal considerable variation associated with physical redistribution of particles and underscore the difficulties with making meaningful estimates of seston depletion due to oyster filtration in the field.

Materials and Methods

FLUME DESCRIPTION

All experiments were conducted in a recirculating seawater flume, located at the Virginia Institute of Marine Science's (VIMS) Eastern Shore Laboratory. The main flume channel, constructed of Plexiglas®, is 5 m long and 0.60 m wide (Fig. 1). For these experiments, a smaller channel, 18.7 cm wide and 220 cm long, with an attached seston sampler was inserted in the flume channel (Fig. 2). Prior to each experiment, the flume was filled with seawater filtered through four filters in series: two sand-charcoal pool filters and two 20 µm pore diameter cartridge filters wrapped with 1 µm cloth filter. Flow across the flume bed was pressure driven from a constant level in the head tank and velocity controlled through a combination of an inflow gate valve and a vertical louvered exit weir. At the head of the flume, two collimators in series reduced the scale of turbulent eddies in the flume. The flume has been calibrated such that freestream velocities can be selected using dial adjustments on the inflow valve and regulating the depth with the exit weir. (See Orth et al., 1994 for a fuller description of the flume.)

Water depth was maintained at a constant 10 cm and freestream velocities ranged from 0.65 – 22.0 cm/s (see below). Throughout the experiments flow Reynolds numbers ($Re = ud/v$; where u=freestream velocity, d=water depth, v=kinematic viscosity) ranged from 528 to 17,886 and thus spanned a range from laminar to fully rough turbulent. Froude numbers ($Fr = u/[gd]^{1/2}$; where g=gravitational acceleration), which relate the relative strengths of gravitational and viscous forces and are typically less than unity in estuarine boundary flows (Nowell and Jumars, 1984), ranged from 7 10^{-3} to 2.2 10^{-1}

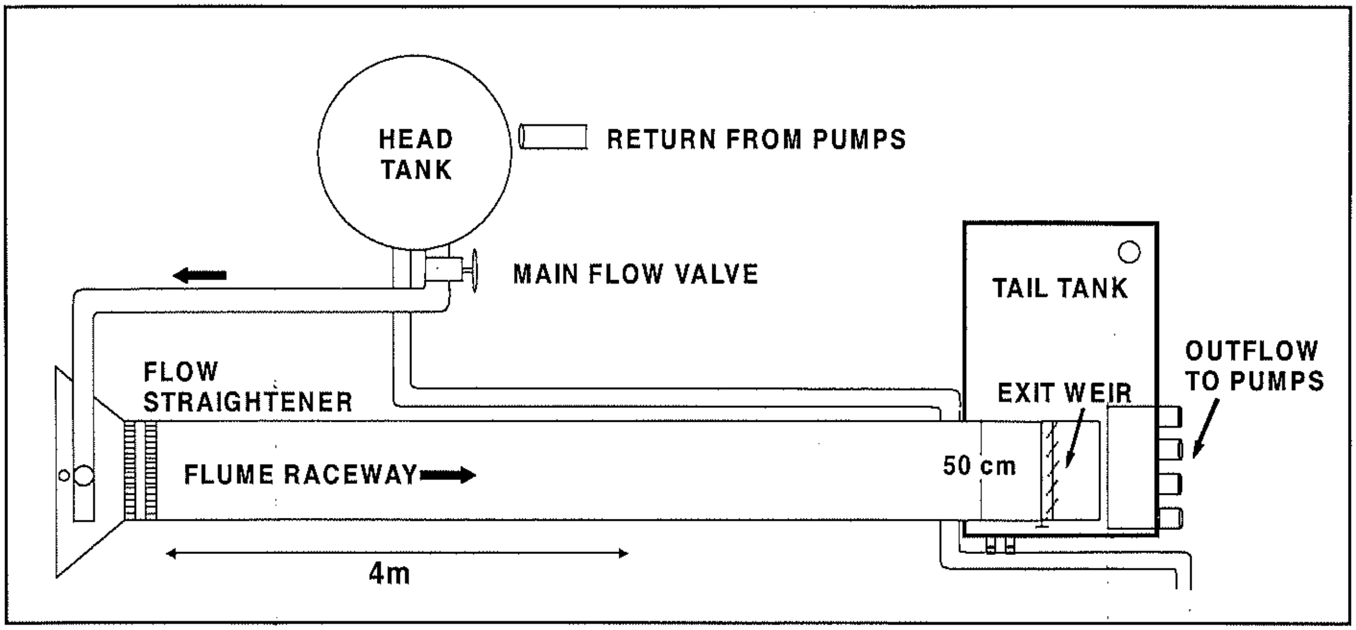

Figure 1. *Recirculating seawater flume located at VIMS' Eastern Shore Laboratory.*

across all experiments. Values computed using Schlichting's Four-fifths Law (Schlichting, 1967) revealed that the boundary layer over the smooth Plexiglas® bed was fully developed within 0.4 m downstream of the collimators at the maximum flow of 22 cm s^{-1}, well before the leading edge of the oyster bed.

OYSTERS

All oysters used in these experiments were spawned at the VIMS hatchery and maintained in floating rafts at field sites until use. Three cohorts were used in these experiments: oysters used in E1, E2 and E3 were from a cohort spawned in 1991; oysters used in E4 and E5 were from a 1992 cohort; and, E6 oysters were spawned in 1993. Prior to use in the flume experiments all fouling organisms were removed from shell exteriors. At the termination of each experiment all oysters were measured for shell height and ash-free dry weight and condition index was determined as ash-free dry weight of soft tissue (in mg)/shell height (in mm).

EXPERIMENTAL DESIGN

Flume experiments were designed to measure the filtration rates of the algae *Thalassiosira weisflogii* by a bed of oysters under different flow speeds and to measure the effect of an inorganic component on the filtration rates. Prior to the initiation of the experiments, the oysters were brought in from the field and maintained on flow-through seawater tables. Each oyster was numbered to allow for monitoring of individual feeding behavior throughout the experiments.

Ninety oysters were placed within the constrained flume channel in 30 staggered rows of three oysters each with their beaks facing into the flow and allowed to acclimate for a minimum of 24 hrs. Freestream velocity in the flume was adjusted to one of eight treatment levels: 0.65, 1.0, 2.1, 4.2, 6.0, 10.4, 13.7, and 22.0 cm s^{-1}. Monocultures of the unicellular diatom *Thalassiosira weisflogii* alone and in combination with kaolinite were added to the flume by a gravity-fed system in quantities sufficient to establish a nominal concentration in flume of $1 \cdot 10^5$ particles ml^{-1}, with kaolinite (when used) accounting for 10% of the total particles added to the flume. At each flow speed within an experiment, particle concentrations were measured upstream and downstream of the bed of oysters and the change in the concentration of these particles across the bed was computed as described below.

Four replicate experiments (designated E1, E2, E3, and E4) estimated filtration rates at each of the eight flow speeds on *T. weisflogii* alone and two replicate experiments (E5 and E6) included kaolinite in the seston. Each replicate experiment made use of a separate batch of oysters drawn from the stocks held in the field. Additionally, for each seston type, control (dead oyster) experiments were conducted to measure the change in particle concentrations due to hydrodynamically-mediated deposition and resuspension of particles. In these controls, oysters shells were filled with lead shot, glued shut, and substituted for live oysters. Three replicate control experiments were conducted using *T. weisflogii* alone (C1, C2 and C3) and one (C4) using algae + kaolinite.

Each experimental replicate began with a different flow speed to separate the effect of the sequence of flow speed from the effect of flow speed on the filtration rates. The flume was adjusted to the desired flow and allowed to stabilize for several minutes before the addition of algae (and kaolinte) to the head box. The first sampling period was begun after the oysters had been exposed to the algae for 10 min and samples were collected continuously for 20 min thereafter. Five min after termination of the first sampling period, a second sampling was begun. At the end of the second sampling period the additions of algae and kaolinite were terminated and chlorophyll *a* and particle concentration determined as described below.

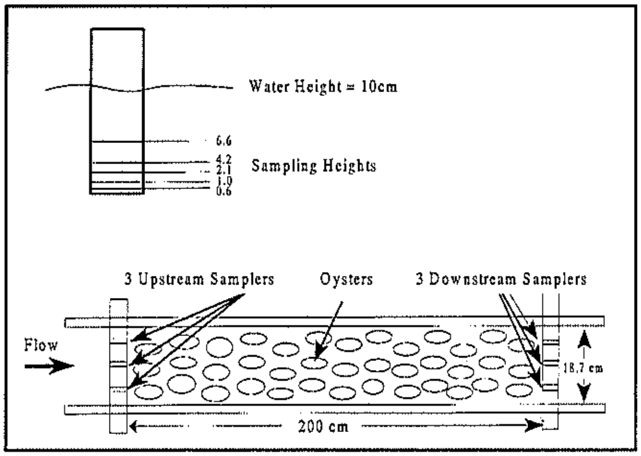

***Figure 2.** Sampler Diagram.*

During each sampling period and for a one hr period after the cessation of algae additions, the type of feeding behavior exhibited by each individual oyster was monitored and scored as (1) not feeding, (2) open (and presumably feeding) or (3) open and producing feces (certainly feeding).

DETERMINATIONS OF CHLOROPHYLL AND PARTICLE CONCENTRATIONS

Water samples for seston characterization in the flume were collected upstream and downstream of test oyster beds using a seston sampling apparatus with ports arrayed laterally across the channel and vertically through the water column (Fig. 2). Three vertically arrayed samplers, constructed of thin Plexiglas® with beveled edges, were evenly spaced across the channel and the upstream and downstream edges of the test section. Each sampler had 5 vertically arrayed ports located at 0.6 cm, 1.0 cm, 2.1 cm, 4.2 cm and 6.6 cm above the flume bed (see Fig. 2). A logarithmic scale was chosen for the placement of the sampling ports to reflect the theoretical particle distribution above the bed in shearing flow. Water samples collected at each port were gravity fed through Tygon® tubing (i.d. = 300 μm) into individual sampling vials, the heights of which were adjusted such that flow speed through the tubing approximated flow speeds in the flume channel, thereby minimizing bias in particle sampling. The entire apparatus, including seston samplers and the 18.7 cm wide channel, comprised the test section in these experiments and was positioned were approximately 2 meters downstream of the collimators.

The three samples collected at a given height were pooled, yielding a total of 5 vertically-arrayed upstream and 5 downstream samples for each collection period. Five ml of each sample was removed, filtered through a 0.45 μm-filter and chlorophyll *a* determined with *in vivo* fluorescence as described by Strickland and Parsons (1968). The remainder of the sample was used to determine particle concentrations of

Thalassiosira weisflogii and kaolinite with a Coulter counter following procedures outlined in Strickland and Parsons (1968). The counter was configured to count particles in the size range of 2 to 40 µm; *T. weisflogii* cells are approximately 16 µm in diameter, while 77.3% of the Kaolinte particles were < 2 µm. Thus, by analyzing at two different threshold settings we were able to distinguish the particle types. Further calibrations were established using direct counts under light microscopy with a hemocytometer. Filtration rates were computed using estimates of algal cell concentrations determined in this manner.

COMPUTATION OF FILTRATION RATES

Coughlan's (1969) equation for filtration rates in still water was adapted and used to calculate filtration rates of the oyster bed in flowing water as follows:

Eq. 1A

$$m = \frac{V \dfrac{\ln C_1}{\ln C_2}}{nt} - a$$

V - total volume of suspension
C_1 - concentration upstream
C_2 - concentration downstream
n - biomass of oysters
t - time
a - control particle change rate determined in a control experiment with no live organisms

Eq. 1B

$$a = \frac{V \dfrac{\ln C_1^{\prime}}{\ln C_2^{\prime}}}{n^{\prime} t}$$

V - total volume of suspension
C'_1 - concentration upstream in control experiment
C'_2 - concentration downstream in control experiment
t - time
n - number of oyster shells x mean biomass of live osyters

Each term in the above equation was adapted to calculate filtration rates for these flume experiments. Time (t) represents the residence time of a water parcel over the oyster bed and was computed as the length of the test section, 200 cm, divided by the freestream velocity. The volume of suspension was calculated from the dimensions of the constricted area of the flume in which particle change was being measured. The term *a* in still water experiments represents the settling rate of seston in the absence of grazers. In the flume experiments conducted here this term accounts for the redistribution of particles due to the physical presence of oyster shells. These rates were derived from the control experiments using dead oyster shell. For comparative purposes both *n* and *n'* in Eq. 1a and 1b, respectively, were converted to biomass using the ash-free dry weights measured for the live oysters.

Three filtration rates were calculated using the follow numbers of oysters: (1) m_a, all 90 oysters in the flume (2) m_o, the number of oysters that were open [a liberal estimate of the number of oysters feeding] and (3) m_f, the number of oysters that produced feces [a conservative estimate of the number of oysters feeding].

Finally, to better clarify seston dynamics within and above the bed of oysters, for analytical purposes we partitioned the water column into two regions and calculated filtration rates for each. The samples from the lowest two samplers (0.6 and 1.0 cm) measured the change in particle concentration for the area essentially within the oyster bed, while the upper region samples (2.1, 4.2, and 6.6 cm above the bed) measured the change in particle concentration in the region at the top of and above the bed.

RESULTS

PARTICLE CONCENTRATIONS

Measured particle concentrations in the flume ranged from 3.056×10^3 to 8.150×10^4 particles ml^{-1} over all experiments and samples.

Table 1. Morphometrics of oysters and oyster shells used in each experiment and control. Values are means (and standard deviations). Tissue weight is expressed as ash-free dry weight. Condition index is as defined in the text.

Experiment	Shell Height (mm)	Shell Width (mm)	Tissue Weight (g)	Condition Index
E1	65.2 (5.8)	20.6 (2.3)	-	-
E2	66.1 (5.7)	21.4 (2.5)	0.271 (0.101)	4.15 (1.00)
E3	65.3 (6.2)	21.0 (2.2)	-	-
E4	64.6 (6.4)	17.9 (2.0)	0.471 (0.192)	7.22 (2.70)
C1, C2, C3	67.7 (7.3)	21.7 (2.8)	-	-
E5	63.9 (6.4)	18.9 (2.4)	0.625 (0.256)	9.73 (3.70)
E6	70.9 (3.9)	19.7 (1.4)	1.055 (0.197)	14.90 (2.80)
C4	66.8 (7.3)	21.2 (2.6)	-	-

Regression analysis of chlorophyll *a* concentrations vs estimates of algal particle concentration varied between the experiments with algae alone (Particle concentration = -0.348+ 0.002 Chl *a*; R^2=0.85; n=417) and algae + Kaolinte (Particle concentration = 8.68 + 0.002 Chl *a*; R^2=0.69; n=192) in the intercept, but not the slope of the relationship. This indicates that our approach in distinguishing between algal and inorganic particles, while a bit conservative (i.e., it discounted a fixed amount of algae), did not bias our determinations of relative concentrations.

OYSTERS

The mean shell height of oysters used in the various replicate experiments ranged from 63.9 mm to 70.9 mm, with the group used in E6 significantly larger than those used in the other experiments (Table 1). Ash-free dry weight samples for E1 and E3 where lost during processing, so the mean weight for E2 oysters (which did not differ in shell height) was used in the calculation of filtration rate. The condition index of the oysters used in E6 exceeded that of all other groups of oysters.

FEEDING BEHAVIOR

Oyster feeding activity, as measured by the percentage of oysters open and the percentage producing feces, was highly variable (Fig. 3). Feeding activity varied markedly between

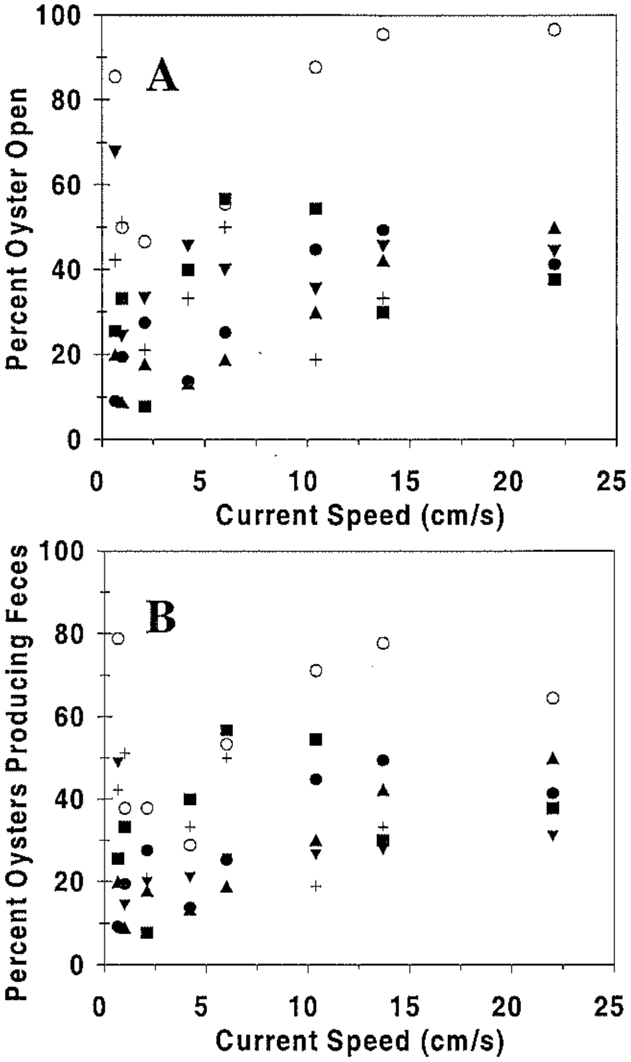

Figure 3. Oyster feeding behavior vs current speed. (A) Percentage of oysters open at each current speed by experiment. (B) Percentage of oysters producing feces at each flow by experiment. (■ = *E1,* ● = *E2,* ▲= *E3,* + = E4, ▼ = E5, ○ = E6.)

Table 2. One-way ANOVA's of the effects of the daily sequence of flow speeds and the sequence throughout the entire experiment on oyster feeding behavior (measured as the numbers of oysters open and the numbers producing feces.

	SS	d.f.	F	P
Effect of Daily Flow Sequence on				
1. Number of oysters open	201 .14	2	0.4753	0.628
2. Number of oysters producing feces	331.33	2	1.1773	0.328
Effect of Experimental Flow Sequence on				
1. Number of oysters open	997.96	7	0.6344	0.727
2. Number of oysters producing feces	893.91	7	0.7467	0.636

groups of oysters used in the various experiments, with a greater number of oysters in E6 feeding (Fig. 3). Two-way fixed factor ANOVA's without replication, using flow speed and experiment as factors, revealed significant effects of experiment on the percentage of oysters open ($F = 9.9690$, d.f. = 5, $p < 0.0001$) and the percentage of oysters producing feces ($F = 6.0490$, d.f. = 5, $p = 0.0004$). However, when E6 was removed from the analysis neither the percentage of oysters open ($F = 1.930$, d.f. = 4, $p = 0.1331$) nor the percentage producing feces ($F = 1.2134$, d.f. = 4, $p = 0.3273$) varied with experiment. Feeding behavior was not affected by the sequence in which flows were offered over the course of the day or throughout the experiment (Table 2).

PHYSICAL REDISTRIBUTION OF PARTICLES

Estimates of changes in particle concentration between the upstream and downstream edges of the "dead" oyster bed reflect physical redistribution of particles throughout the water column. "Filtration" rates in the region within the bed for the control experiments (i.e., term *a* in Equations 1A & B, which equates with physically-mediated particle redistribution) were approximately zero (Fig. 4a) and did not vary linearly with flow speed ($r^2 = 0.11$, $n = 24$, $p = 0.11$). In the region above the bed *a* varied considerably, but not consistently, across experiments (Fig. 4b) and again there was not a statistically significant linear relation with flow speed (r^2=0.01, n=24, p=0.68). Since the relationship between the control rates and flow speed was neither significant nor evident, a value of zero was chosen to be used for the control rate in the calculation of the live oyster filtration rates.

FILTRATION RATES

Filtration rate estimates obviously varied depending upon the numbers of oysters used in the calculations, with the lowest estimates derived from using all 90 oysters in the bed and the highest values using only those oyster producing feces (Table 3). Because our primary focus here is on the filtration capacity of a bed

Table 3. Mean (and standard deviations) of filtration rates for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4) and *T. weisflogii* in combination with Kaolinite (E5 & E6). Filtration rates are computed using all oysters (m_a), only oysters open during the experiment (m_o) and only oysters producing feces (m_f).

	Filtration Rate (L g^{-1} hr^{-1})	
	Within the bed	Above the bed
Algae alone	m_a: 0.73 (1.46)	m_o: 1.88 (3.28)
	m_f: 2.37 (4.08)	m_a - 4.10 (9.87)
	m_o: -8.60 (22.27)	m_f:-11.88 (29.15)
Algae + Kaolinite	m_a: 0.50 (0.87)	m_o: 0.89 (1.92)
	m_f: 1.35 (3.06)	m_a: 2.95 (2.30)
	m_o: 5.57 (4.92)	m_f: 8.329 (8.01)

of oysters, subsequent results are reported for m_a (all 90 oysters), but we will discuss the implications of these different rates below. The negative values in the region above the oyster bed in the experiments using algae only (Table 3) indicate an increase in suspended particles at the downstream end of the bed. Summary plots of mean filtration rates (m_a only) vs current speed reveal differing patterns within and above the bed and between diet types (Fig. 5).

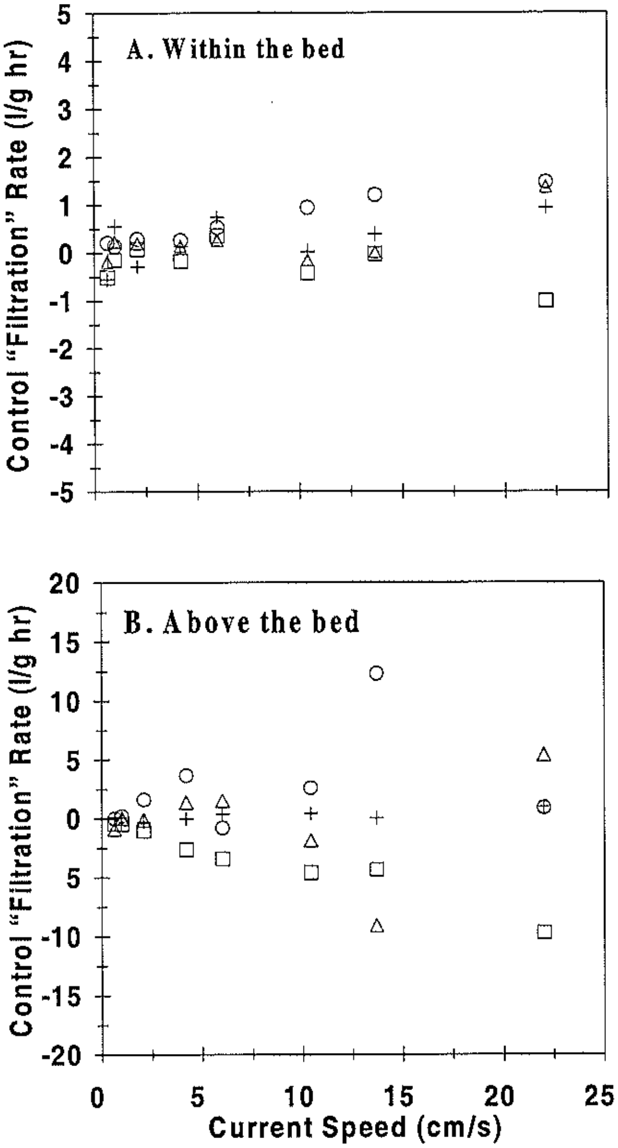

Figure 4. "Filtration" rates vs flow speed for control experiments using dead oysters in the (A) lower region within the oyster bed and (B) upper region above the oyster bed. Control rates are reported as l filtered per g ash-free dry weight of oyster per hr; positive values indicate the removal of particles across the bed of oysters and negative values indicate particle generation. The symbols ❑, O, △, and + indicate experiments C1, C2, C3 and C4, respectively.

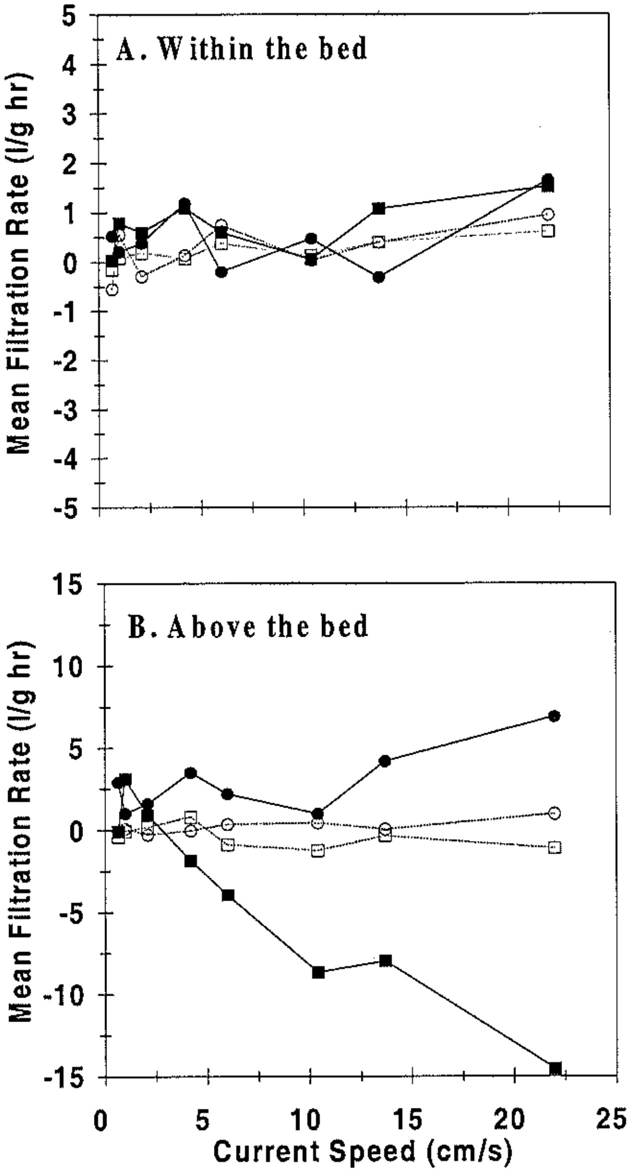

Figure 5. Mean filtration rate vs current speed (A) within the bed and (B) above the bed of oysters. ❑ = dead oyster control, algae only diet; O = dead oyster controls, algae + Kaolinite diet; ■ = live oysters, algae only diet; ● = live oysters, algae + Kaolinite diet.

Table 4. ANOVA's of the effect of flow speed on filtration rates (m_a) within the oyster bed for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4).

Experiment	Source	DF	SS	F	P
E1	Flow speed	7	16.38	5.01	0.019
E2	Flow speed	7	12.43	0.42	0.862
E3	Flow speed	7	6.57	2.26	0.138
E4	Flow speed	7	47.04	1.91	0.192

The relationship between filtration rates within the bed and current speed varied between the four experiments (Fig. 6a). Two-way ANOVA indicated that there was asignificant difference in the filtration rate among experiments (d.f.=3, F=8.1, P=0.001), but no significant effect of flow speed (d.f. = 7 F=0.1, P=0.566). Thus, the effect of flow speed on filtration rates within the oyster bed were analyzed separately for each experiment. In E2, E3, and E4, flow speed did not have a significant effect on the filtration rates (Table 4). Only in E1 were there significant differences in the filtration rates for the eight flow speeds (Table 4). While there was a trend towards more negative rates with greater flow speed in E1, Tukey's a posteriori multiple comparison test revealed that this relationship was not monotonic (Table 5).

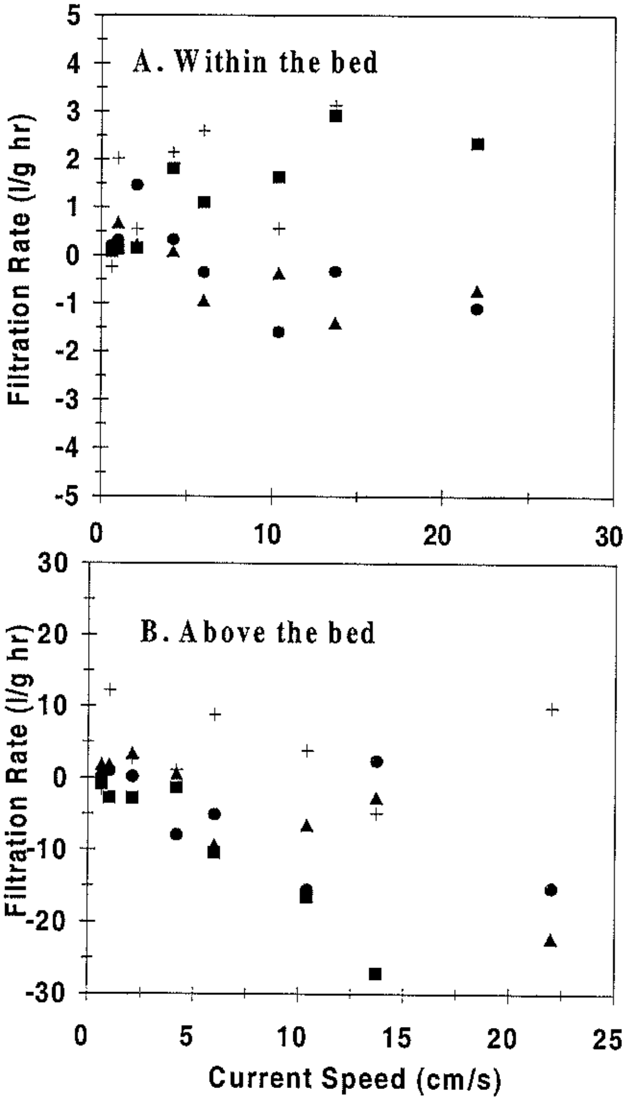

Figure 6. Filtration rates vs current speed in experiments using algae only diets (A) within the oyster bed and (B) above the oyster bed. (■ = E1, ● = E2, ▲= E3 & + =E4).

Table 5. Tukey's a posteriori multiple comparison test of filtration rates (m_a) within the oyster bed in experiment E1. (Flow speeds for which filtration rates were not significantly different are grouped in a single column and denoted by *.)

Flow speed (cm/s)	Homogeneous groups	
0.65	*	
1.0	*	
2.1	*	*
4.2	*	*
6.0	*	
10.4	*	*
13.7		*
22.0	*	*

Filtration rates in the region above the oyster bed varied between experiment, flow speed and

Table 6. Two-ANOVA of the effects of experiment and flow speed on filtration rates (m_a) above the oyster bed for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4).

Source	DF	SS	F	P
Experiment (A)	3	1953	32.6	<0.0005
Flow speed (B)	7	1953	14.0	<0.0005
A*B	21	2322	5.5	<0.0005
Error	32	639		
Total	63	6868		

the interaction of the two (Fig. 6b and Table 6), so the data set was partitioned by experiment and the effects of flow speed on filtration in this region analyzed using one-way ANOVA's (Table 7). Flow speed was thus revealed to have an impact on filtration rate estimates in three of the four experiments which used algae only diets. A posteriori multiple comparisons within these three experiments revealed that oysters within an experiment generally had similar filtration rates at flow speeds < 6 cm s^{-1} and similar, but more negative, rates > 6cm s^{-1} (Table 8). Though there were exceptions, measured filtration rates at flows < 6 cm s^{-1} were approximately zero, while rates at flows > 6 cm s^{-1} were negative, indicating particle redistribution into the region above the bed.

Discussion

The filtration capacity of an oyster bed is not solely a function of the cumulative filtration rate of the oysters, but is a composite of biological and physical processes. Particle distribution and concentration within the water column are functions of the vertical mixing, horizontal advection, resuspension, settling, and filtration by the oysters. Dame et al. (1984) suggested that removal of particulate carbon by an oyster reef was greater than expected by biofiltration alone and suggested that physical factors may have been important.

Table 7. ANOVA's of the effect of flow speed on filtration rates (m_a) above the oyster bed for experiments with *Thalassiosira weisflogii* alone (E1, E2, E3 & E4).

Experiment	Source	DF	SS	F	P
E1	Flow speed	7	2020	14.17	0.001
E2	Flow speed	7	743	12.86	0.001
E3	Flow speed	7	1022	5.02	0.019
E4	Flow speed	7	490	3.15	0.065

In these experiments, particle reductions were not of the magnitude expected from totaling filtration rates reported for individual oysters in static flow conditions. Using Newell's (1988) estimate for oyster the filtration rate of 5 L hr^{-1} gm^{-1}, the expected filtration capacity of the entire bed of oysters used in these studies would have been 75 ml sec^{-1} and should have reduced particle concentrations from 63% to 2% for the lowest to highest flow speed. Factors which may have contributed to the measured rates being lower than expected were 1) the effect of water flow on changes in particle concentration across the oyster bed, 2) the reduced number of oysters feeding at any one time, and 3) time variance in the filtering activity of each individual oyster.

The significance of flow-mediated effects is evident from the particle concentration profiles upstream and downstream, both within and between experiments in this study. The control

Table 8. Tukey's a posteriori multiple comparison test of filtration rates (m_a) above the oyster bed in experiments E1, E2 & E3. (Flow speeds for which filtration rates were not significantly different are grouped in a single column and denoted by *.)

Flow speed (cm/s)	E1					E2	E3
	Homogeneous groups			Homogeneous groups		Homogeneous groups	
0.65	*			*		*	
1.0	*			*		*	
2.1	*			*		*	
4.2	*			*	*	*	
6.0	*	*		*	*	*	*
10.4		*	*	*	*	*	
22.0			*		*		*

experiments, using oyster shells, provide an estimate of the effect of flow speed on the change in particle concentration across the oyster bed in the absence of filtration. In the water column upstream of the oyster bed a logarithmic particle profile describe by the Rouse equation is expected. Upon encountering the bed, particles in the lower region are uplifted by turbulent eddies, increasing particle concentrations above the bed. We had anticipated that a relation between flow speed and particle redistribution in the control experiments would have been evident. However, the observed pattern varied sufficiently between control experiments (Fig. 4) such that the "average" pattern did not reveal a significant effect of flow speed. We are not certain of the cause of this variation, but suspect that subtle differences in the placement of the 90 oysters within the bed (recall that each control experiment involved the placement of 90 different oyster shell pairs) resulted in differing turbulence patterns. It seems unlikely that our two 20-min sample collection periods were inadequate to average over normal variations in particle concentrations associated with turbulent fluctuations.

Between experiment variance in filtration rates increased with increasing flow speeds and was greatest in the upper region filtration rates. This increase reflected the increased turbulence generation associated with increasing flow speed. The negative filtration rates were not a result of a generation of particles downstream, but were due to turbulent redistribution of particles. The relocation of particles and the non-uniform effects of turbulence on particle concentration contributed to the differences in filtration rates between experiments.

Oyster bed configuration appears to have affected particle dynamics as indicated by the significant differences in the control rates of C1, C2, and C3. Although the oysters were all placed in 30 staggered rows for each experiment, the bed morphology was subtly different between experiments. In experiments with live oysters variation in the bottom topography between each batch was further enhanced by the number of oysters open and their location within the bed.

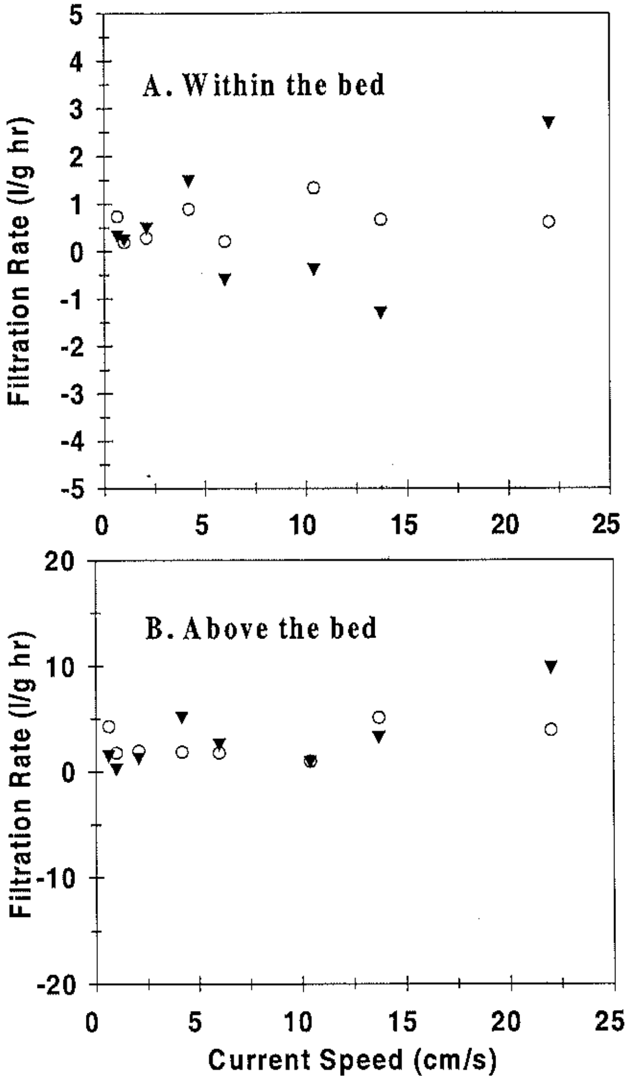

Figure 7. Filtration rates vs current speed in experiments using algae + Kaolinte diets (A) within the oyster bed and (B) above the oyster bed. (▼ =E5, ○ =E6).

The non-uniform particle redistribution due to turbulent mixing may have obscured some of the biological impact on particle concentration. Filtration rates reported here within the oyster beds at low flow speeds are within the range of previously reported rates (Haven and Morales-Alamo, 1970; Powell et al., 1992; Luckenbach et al., 1993; Sellner et al., 1995). These rates are also approximately the same as the "lower curve" rates which Powell et al. (1992) believed best represent the filtration rates in the field. Although there were not significant differences between the filtration rates and the control rates, abundant fecal production by the oysters indicated that large amounts of particles were being removed from the water column by the filtration activity of the oysters. It appears that the biotic factors were not of sufficient strength to produce filtration rates that would be significantly different from control rates in these experiments.

Using feces production and shell gape as indicators of feeding activity, we observed a positive relationship between oyster feeding activity and flow speed, and flow speeds up to 22 cm sec^{-1} did not inhibit oyster feeding activity in these experiments. This is counter to the findings of Grizzle et al. (1992) who found a negative relationship between growth rates of *C. virginica* and flow speeds greater than 1 cm s^{-1}, suggesting inhibition of feeding activity at higher flow speeds. This apparent difference may be due to differences in experimental design between the two studies. Oysters in the experiment by Grizzle et al. (1992) were placed with the hinge facing into the direction of flow, whereas in this study, oysters were placed with the beak facing into the direction of the flow. The orientation of the *Argopecten irradians concentricus* has been shown to affect the pressure exerted by the external water on the inhalant region (Eckman et al., 1989) and the same may be true for *C. virginica.* At sufficient flow speeds, external water pressure may exceed the inhalant-exhalant pressure differential and have a negative effect on the filtration rates. External flow pressure on the inhalant region of an oyster within the bed will be affected by the mean flow field and by local flow variations. In the context of these flume experiments, we lack sufficient details of the flow environment to estimate these impact on filtration rates.

We expected to observe the greatest depletion in the near-bed environment within the oyster bed at low flow speeds, both because of low advective flux and minimal turbulent mixing of particles from upper layers. That this was not clearly the case suggests either that turbulent mixing rates where sufficient at all flows to resupply oysters with particles or (more likely) that physical mixing processes generally obscured the effects of oyster filtration. Further, if biological processes predominated, we would expect that in the region above the oyster bed, at least up to a point, filtration rate would have increased with flow speed, because turbulent mixing would bring more particles in contact with the oysters. In fact, the reverse pattern was generally observed, at least for the algae alone diet, indicating that physical redistribution of particles was primarily responsible for the observed pattern. Turbulence generation due to the bottom roughness of the oysters tended to redistribute particles upward above the bed.

Food quality has been observed to have variable effects on bivalve feeding rates. Urban and Kirchman (1992) speculated that suspended inorganic matter may actually increase ingestion of certain organic particles by decreasing particle rejection. At high concentrations of inorganic particles ingestion may be reduced as pseudofecal production increases, but the effects on measured filtration rates are unclear. In the current study, there was no evident effect of inorganic particles on the filtration rates measured within the oyster bed. The pattern observed above the bed differs somewhat from that in the algae alone diets in that filtration rates were uniformly positive. This may be the result of reduced resuspension of the heavier inorganic particles or merely a reduced sample size relative to the algae alone diets (two vs four experiments).

These experiments were designed to provide greater dynamic similarity to natural oyster habitats than previous experiments on oyster filtration rates. They nevertheless represent a gross over simplification of the hydrodynamic regime associated with an oyster reef. Moreover, the biotic component of these experiments–a single size-class of oysters in a uniform spatial arrangement–represents a considerable simplification of a natural reef. Yet, it is still apparent that the interaction of a bed of oysters with the surrounding water column is the result of a complex of hydrodynamic and biotic factors. As interest grows in restoring oyster reefs for the ecosystem services which they provide, including particle filtration, our findings should serve both as a warning about the difficulties of measuring particle depletion in the field and the importance of improving *in situ* filtration estimates. Reconciling these difficulties will be necessary for improving estimates of filtration rates by individual oyster reefs and estimating system-level ecological of oyster restoration.

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Oyster Reefs as Components in Estuarine Nutrient Cycling: Incidental or Regulating?

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Abstract

A review of many estuarine ecosystems shows that oysters and bivalves in general have the potential to directly control phytoplankton biomass through grazing. This possible control is evident when bivalve clearance time is less than estuarine water mass turnover time. The extremes are typified by systems with slow water exchange times and modest bivalve populations, i.e., the Chesapeake Bay of the past, and those with rapid water mass turnover and massive populations of bivalves, i.e., North Inlet, S.C. The latter systems often depend on the coastal ocean as a source of phytoplankton, while the former systems use phytoplankton generated within the system.

Few studies have addressed the role of oysters in estuarine nutrient cycling. In this role, the nutrients released by the bivalve system are thought to provide an indirect control on the phytoplankton through nutrient enrichment. On oyster reefs the nutrient release is almost twice the magnitude of simple bivalve excretion and is probably the result of decomposition processes in the adjacent organically enriched sediments. Although field observations of nutrient enrichment associated with oysters are sparse, computer simulation models support this role for oysters in estuarine ecosystems.

Oysters and oyster reefs as systems have the potential to short circuit pelagic food webs and speed up nutrient cycling. Also, because of the large quantity of longer lived biomass stored in oyster reefs as opposed to that of zooplankton in pelagic dominated systems, reefs may, through time, stabilize nutrient cycling in estuarine ecosystems and thus support a more sustainable system.

Introduction

Bivalve molluscs not only remove materials from the water column or benthic-water interface, but as a result of feeding and metabolism, they generate both particulate and dissolved materials that have an impact on both benthic and pelagic habitats. Thus, specific high quality organic constituents in the form of plankton, detritus and amino acids are consumed as food, processed, deposited as feces or pseudofeces or excreted as fundamental nutrients to the water column where they can be utilized by the plankton. Bivalves may play an important role in the cycling of nutrients within these systems because they often form dense assemblages or communities of organisms in shallow ecosystems. In this paper, the role of oysters in nutrient cycling will be examined.

Theoretical Background

Early studies by Liebig (1840) indicated that biologically essential elements (bioelements or nutrients) could limit the production of organisms. Rather than a single limiting bioelement, it is frequently more complex interactions that limit ecosystems. The flux or cycling of essential materials is necessary for the continuity and stability of any living system and often provides a good indicator of metabolic activity and energy pathways through food webs. Thus, the study of nutrient cycling is a major strategy in the analysis of ecosystems (Pomeroy 1970).

Initially, the role of macroconsumers in total ecosystem function was viewed from the context of energy flow. Kitchell et al. (1979) showed that large animals can influence nutrient cycling through physical/chemical processes not directly reflected by energy flow. They summarized these processes into two general mechanisms of influence: translocation and transformation. In systems dominated by bivalve filter feeders, nutrients are moved from the water column to the benthos and back mainly through the pumping action of the animals. These translocated or retained nutrients can be distributed in ways that influence the total production rates of the system as a whole. Bivalves may also transform nutrients by changing their chemical complexity and by changing the particle size distribution in the water column. Normally, particulate organic matter is consumed and dissolved inorganic materials are released as a part of bivalve metabolic processes. In addition, some bivalves may filter different portions of the suspended particulate size spectrum that in turn may change surface to volume relationships. Finally, small particles in the water column are aggregated into the bodies of benthic bivalves and the relatively large size particles of their feces and pseudofeces.

There are four aspects of nutrient cycling: (1) nutrient limitation of primary production; (2) recycling of nutrients and the mechanisms of recycling; (3) chemical complexity; and (4) stoichiometry (DeAngelis 1992). Nutrient limitation of primary production is common in all ecosystems and may be compensated for by internal recycling. In addition, the degree of system openness, as determined by the imports and exports of nutrients and when compared to the quantities of elements being recycled, is an important property at the ecosystem level. The cycle of each element is different from all others in its specifics, and some, like nitrogen, are very complex involving several different compounds. Finally, chemical stoichiometry relates to the proportions of various elements, usually C, H, O, N, P and S in a substance. These proportions are quite regular within groups of organisms and generally mean that one or more of these elements will be kept in short enough supply in the pool of available nutrients in an ecosystem to be limiting.

By examining nutrient cycling in ecosystems dominated by bivalves (Fig. 1), two basic types of feedback, negative and positive, are evident. Grazing or the consumption of primary producers by bivalves can be considered part of a predator-prey system where the bivalves benefit from eating the primary producers while the primary producers are reduced through consumption. As one component benefits and the other is negatively affected, this direct effect is referred to as negative feedback or deviation-

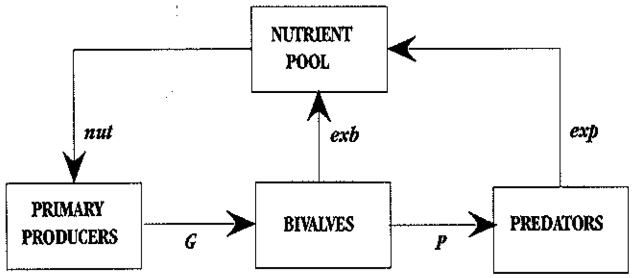

Figure 1. *A simple diagram of nutrient cycling in bivalve dominated systems.* ***G*** *= grazing;* ***P*** *= predation;* ***exb*** *= excretion by bivalves;* ***exp*** *= excretion by predators;* ***nut*** *= nutrient uptake by primary producers.*

counteracting. There is a general consensus in ecology that negative feedback regulation occurs to the degree that it normally keeps populations and communities from going completely out of control, although it may not always be strong enough to prevent sizable fluctuations (DeAngelis et al. 1986).

Positive feedback is an indirect effect in bivalve systems where the filter feeders utilize the nutrients in the primary producers and in turn the primary producers use the nutrients excreted by the bivalves. Both components benefit, but systems may respond to this feedback by reinforcing the change or effect in the direction of the deviation. Positive feedback amplifies changes and may result in boom or bust scenarios. DeAngelis et al. (1986) have made four generalizations about positive feedback: (1) the very existence of a positive feedback loop increases the complexity of the system through the network of nutrient flows and connections; (2) the positive feedback loop accelerates change within the system, i.e., bivalves short circuit the food web turning over nutrients more rapidly and making them available to the plankton for more production; (3) this type of feedback typically exhibits threshold effects where the mode of behavior of the system suddenly changes; and (4) systems that have major positive feedback loops may be fragile and the collapse or loss of one of the components can destroy the feedback loop, i.e., if the bivalves or the plankton is lost from the system then the feedback loop and its features may be lost. Fragility may not always be a problem in bivalve systems as there are often redundant pathways and components, multiple bivalve and plankton species, that protect the system from collapse.

Nutrient Cycles

In the this section, nutrient cycling in oyster dominated systems will be discussed for specific elements. In the case of carbon and nitrogen, there are atmospheric (gaseous) forms that make these cycles more open. While in others, phosphorous and silicon, the cycles are more closed because they do not have an important gaseous form.

Carbon

Both inorganic and organic carbon are processed and stored by marine bivalves. Inorganic carbon is found in substantial amounts in the sea compared to the atmosphere and the land. Much of this carbon is present as dissolved inorganic carbon and forms a complex equilibrium reaction that buffers the pH of seawater (Valiela 1984). One component of this buffer system is calcium carbonate in the form of crystals in bivalve shells and structural components of other organisms, e.g., corals. In some groups, e.g., giant clams, their symbiotic relationship to zooxanthellae leads to the control of the carbonate buffer system within the clam and may enhance their ability to lay down calcium carbonate crystals. As the cycling and storage of inorganic carbon take place on longer time scales than most ecosystem processes, this aspect of the carbon cycle will not be addressed here.

CARBON FLOW WITHIN OYSTER REEFS

Photosynthetically active organisms can rapidly take up dissolved inorganic carbon and produce organic carbon that bivalves can utilize as food. This aerobic processing of organic carbon in marine systems with a significant oyster component will be the focus of our discussions.

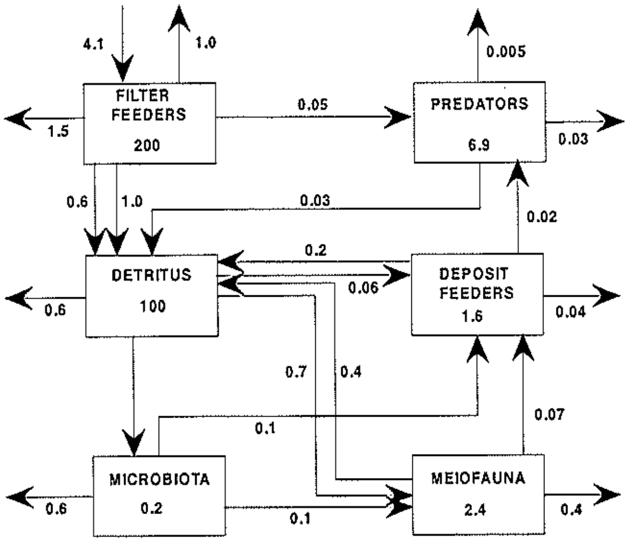

Figure 2. *Carbon flow through an intertidal oyster reef in South Carolina. Flows =* $gC\ m^{-2}\ d^{-1}$*, States =* $gC\ m^{-2}$*.*

In many studies of the role of bivalves, energy flow and carbon cycling are used more or less synonymously (Baird and Milne 1981, Dame and Patten 1981). In the energy flow rendition of these systems, different forms of inputs and outputs, i.e., light energy, tidal energy, respiration, fecal production, etc., may not be distinguished. For example (Fig. 2), oyster reefs have long been recognized as communities of organisms interacting with themselves and with their estuarine environments (Dame and Patten 1981). These systems influence estuaries both physically by removing suspended particulate material and changing current patterns, and biologically by removing phytoplankton and producing large quantities of oyster biomass. In addition, the structure of the reef provides habitats for many sedentary and mobile organisms.

The oyster reef as conceived by Dame and Patten (1981) has 6 major components: filter feeders, detritus, microbiota, meiofauna, deposit feeders, predators. Their conceptualization is for an intertidal oyster reef in South Carolina and at an average annual water temperature of 20 °C. For simplicity and as supported by over 20-years of observations on the North Inlet, South Carolina system, their oyster reef is assumed to be at steady state (Inputs = Outputs). As in natural reefs, the epibenthic portions of the reef are dominated by the filter feeders, in this case *Crassostrea virginica* and *Brachedontes exustus*, and the rest of the system is sedimentary.

Based on Dame and Patten's (1981) calculations, this oyster reef consumes 4.2 $gC\ m^{-2}\ d^{-1}$ or about 1,514 $gC\ m^{-2}\ y^{-1}$ making it one of the most heterotrophic natural systems known. The filter feeders couple the reef to the water column and this allows them to function both as grazers of phytoplankton and as suspended particulate detritus feeders. As there is little evidence that the filter feeders in the oyster reef utilized detritus as a food source, it is assumed that they simply deposit this material and it can then be utilized by other organisms in the reef.

In the Dame and Patten (1981) synthesis, the oyster reef is strongly heterotrophic with food and waste carried in or taken away by the tides. Carbon deposited by the filter feeders is processed by a subsystem of organisms living in the sediments. An analysis of the carbon flows within the system clearly shows the separation of the filter feeders from the rest of the system because there are no carbon feedbacks to the filter feeders from the rest of the system. Although there are numerous feedback pathways in the sediment portions of the system, only 11% of the material entering the reef is recycled with the remaining amount moving through the surface components of filter feeders, detritus and predators. In the Dame and Patten (1981) analysis, the filter feeders clearly controlled the system, but the predators, mainly mud crabs, also exerted control over the detritus, microbiota and meiofauna components.

The Dame and Patten (1981) conceptualization of carbon flow through an intertidal oyster reef was built from the bottom-up using physiological and population data on constituent organisms. Later field studies by Dame et al. (1989) used portable plastic tunnels to determine the input and output fluxes of the various forms of carbon, nitrogen and phosphorus to an intertidal oyster reef in North Inlet. This group deployed the tunnel over a living oyster reef every 10.2 days (33 tidal cycles) over a single year and using regression estimation techniques

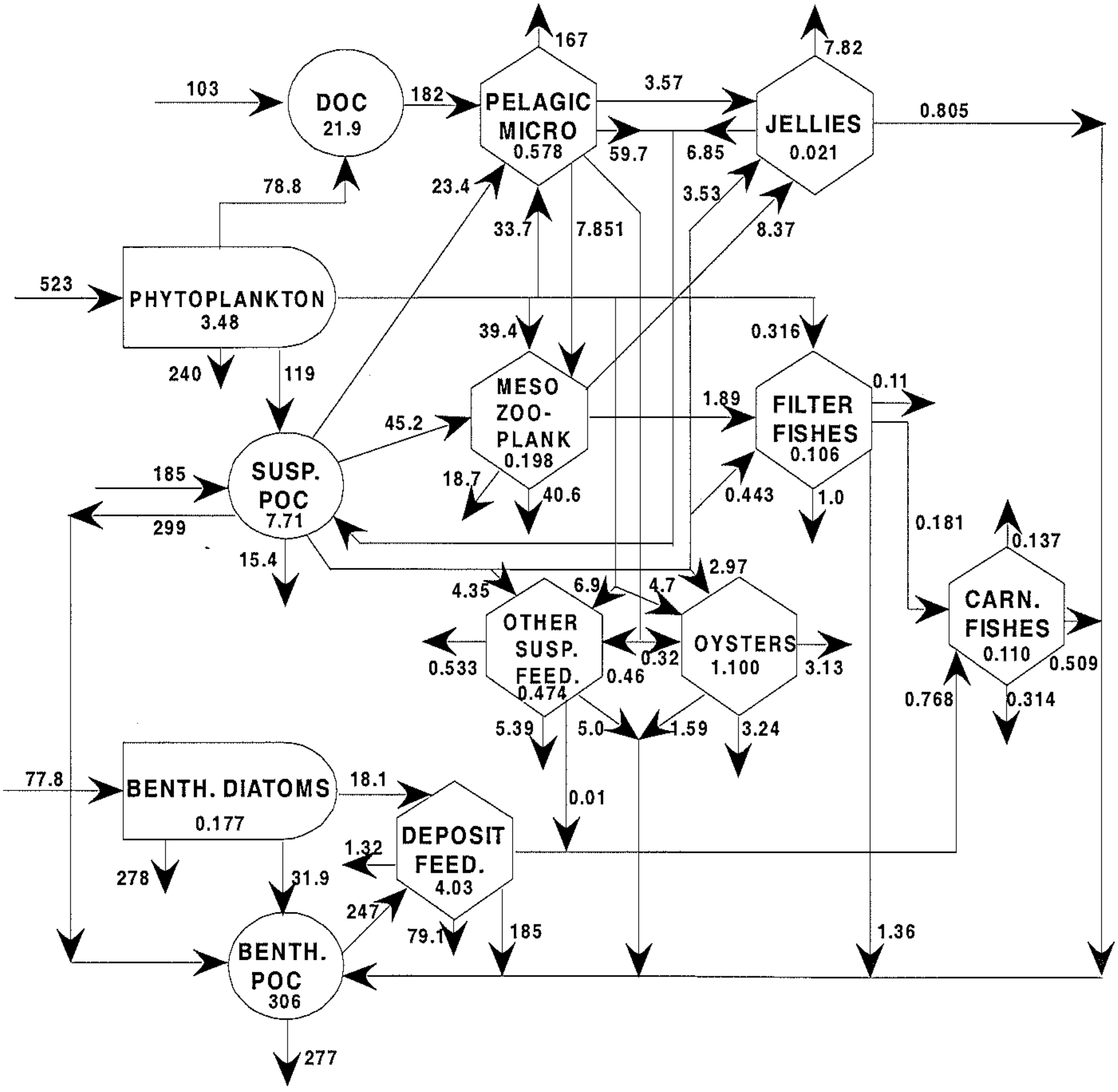

Figure 3. *Carbon flow through Chesapeake Bay. Flows = gC m^{-2} yr^{-1}, States = gC m^{-2}. (After Ulanowicz and Tuttle 1992)*

computed an annual carbon uptake of 1,200 gC m^{-2} y^{-1}. A value that is reasonably close to that estimated by Dame and Patten (1981) of 1,514 gC m^{-2} y^{-1}. In the tunnel study, the oyster reef was considered to be a black box and the fluxes of POC and DOC were observed. POC was taken up by the oyster reef on 95% of the observed flooding tides and released on 63% of the ebbing tides. The POC fluxes were probably the net result of both biofiltration and the physical processes of sedimentation and resuspension on the oyster reef. The DOC component was released on 63% of both flooding and ebbing tides. This constituent can be taken up by filter feeders as a nutritional subsidy in the form of amino acids (Manahan et al. 1982; Stephens 1982; Wright 1982) and can be excreted as urea, amino acids and uric acid (Hammen et al. 1966). In addition, other organisms on the reef, such as bacteria and algae, can

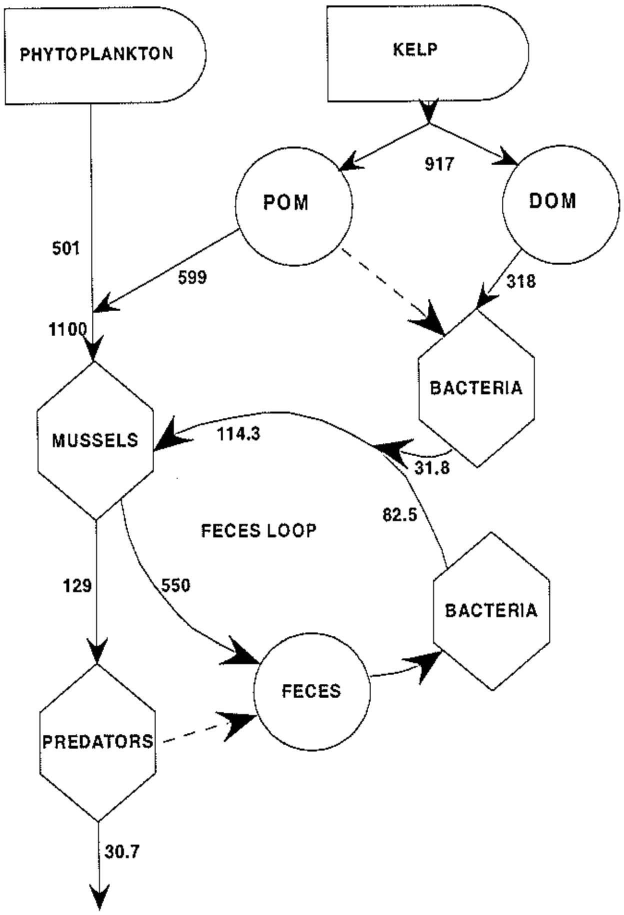

Figure 4. Carbon flow and cycling through a kelp bed community off South Africa. Flows = gC m^{-2} yr^{-1}. (After Newell and Field 1983).

take up and release DOC (Valiela 1984) and increased water velocities may increase the release of DOC from benthic systems (Boynton et al. 1981).

OYSTERS AND CARBON FLUX IN ECOSYSTEMS

At a higher level of complexity, Ulanowicz and his colleagues have developed a series of carbon flow models for Chesapeake Bay that include oysters and bivalves as major components (Baird and Ulanowicz 1989, Baird et al. 1991, Ulanowicz and Tuttle 1992). Their original conceptualization of carbon flow in Chesapeake Bay (Baird and Ulanowicz 1989) was composed of 36 components that they thought were significant. These components included water column and benthic primary producers, decomposers, oysters and other filter feeders, deposit feeders, numerous different fishes and predators. An aggregated form of this model was subsequently developed that had 13 components (Fig. 3) and was used to address specific questions about the role of oysters within the Chesapeake Bay ecosystem (Ulanowicz and Tuttle 1992).

The Ulanowicz and Tuttle (1992) depiction of carbon flow through the Chesapeake Bay ecosystem is similar to that of Dame and Patten (1981) for an oyster reef in that the filter feeders (oysters) receive no feedback flows. This approach has also been used for systems dominated by mussels feeding mainly on phytoplankton (Warwick et al. 1979, Baird and Milne 1981, Rodhouse et al. 1981). However, Newell and Field (1983) described carbon flow for a kelp bed system with a significant component of filter feeding mussels, *Aulacomya ater*, that were potentially consuming 9% of their carbon input in the form of bacteria generated from the decomposition of kelp detritus (Fig. 4). This positive feedback of carbon via the decomposer loop and back to the bivalve filter feeders may be more common to mussel dominated systems as Wright et al. (1982) have shown that mussels can filter and consume smaller (bacteria size) particles than oysters. Based on the available information, carbon flow in oyster dominated systems does not appear to have any clearly identifiable positive feedback flows.

GRAZING CONTROL OF CARBON FLUX

The potential control of coastal ecosystem phytoplankton populations through bivalve grazing has been intensely debated for many years (Dame et al. 1980, Cloern 1982, Officer et al. 1982, Nichols 1985, Alpine and Cloern 1992). System level grazing by bivalves has been studied in numerous ecosystems and an expanded comparison of the initial list developed by Smaal and Prins (1993) is presented in Table 1. System clearance time is calculated as a function of bivalve filtration of the total water volume in the ecosystem and compared to water mass residence time. Also, bivalve dry body biomass is related to system water volume as

Table 1. A comparison of system clearance time by bivalve filter feeders to water volume residence time.

System	Symbol	Dominant Bilvalve	Volume 1^{06} m^3	Biomass: Volume g m^3	Clearance Time (d)	Residence Time (d)	Clearance: Residence Ratio	Reference
Asko	AS	Mussels	4000	0.4	99	10^4	0.01	Kautsky & Wallentinus 1980 Kautsky & Evans 1987
S.San Francisco Bay	SSF	Various	2500	2.5	0.7	11.1	0.06	Cloern 1982
Eastern Scheldt	ES	Mussels Cockles	2740	3.1	3.7	40	0.09	Smaal et al. 1986 Dame et al. 1991
Chesapeake Bay, PAST	CBO	Oysters	27,300		3.3	22	0.15	Newell 1988
Bay of Brest	BB	Various	1480	7.4	2.8	16.7	0.17	Hily 1991
Marennes-Oleron Bay	MO	Oysters	675	4.2	2.7	7.1	0.38	Heral et al. 1988 Bacher 1989
Ria de Arosa	RA	Mussels	4335	1.6	12.4	23	0.54	Tenore et al. 1982
Western Wadden Sea	WW	Mussels	4020	3.7	5.8	10	0.58	Dame et al. 1991
North Inlet	NI	Oysters	22	15.4	0.7	1.0	0.70	Dame et al. 1980
Narragansett Bay	NB	Clams	2385		25	27	0.93	Kremer and Nixon 1978
Sylt,	SY	Mussels	7.2	21.7	2.1	0.5	4.20	Asmus et al. 1990
Delaware Bay	DB	Oysters	19,420		1278	97	13.17	Biggs and Howell 1971
Chesapeake Bay, PRESENT	CBP	Various	27,300		325	22	14.78	Newell 1988

suggested by Dame et al. (1991). When ecosystem clearance time (CT) is plotted versus water mass residence time (RT), those systems above the diagonal (CT/RT>1) probably do not exhibit grazing control, while those systems below the diagonal probably do have some potential for grazing control (Fig. 5). In North Inlet, for example, the oysters can potentially clear the system of phytoplankton in 0.7 days while the water residence time is somewhat longer at 1 day.

Smaal and Prins (1993) propose that the impact of bivalve filter feeders extends to various spatial scales. These scales are the level of the bivalve bed, the estuary or bay, and the land-ocean interface. In those systems with low bivalve biomass to water volume ratios, i.e., current Chesapeake Bay, Delaware Bay and Narragansett Bay, the residence time of the water mass is less than that of the potential clearance time and thus bivalve influences are probably limited to the level of the bed or community.

Systems with higher bivalve biomass to water volume ratios cleared larger volumes of water in less time than the water mass turned over. In these systems, i.e., Asko, Eastern Scheldt, Western Wadden Sea, Marennes-Olerón, etc., bivalve regulation of phytoplankton biomass was much more likely at the level of the bay or estuary when dry body bivalve biomass was in the range of 2 to 8 g m^{-3} and residence times were long.

Phytoplankton biomass in short residence time systems could still be regulated if bivalve biomass/volume is high, > 8 g m^{-3}, as in North

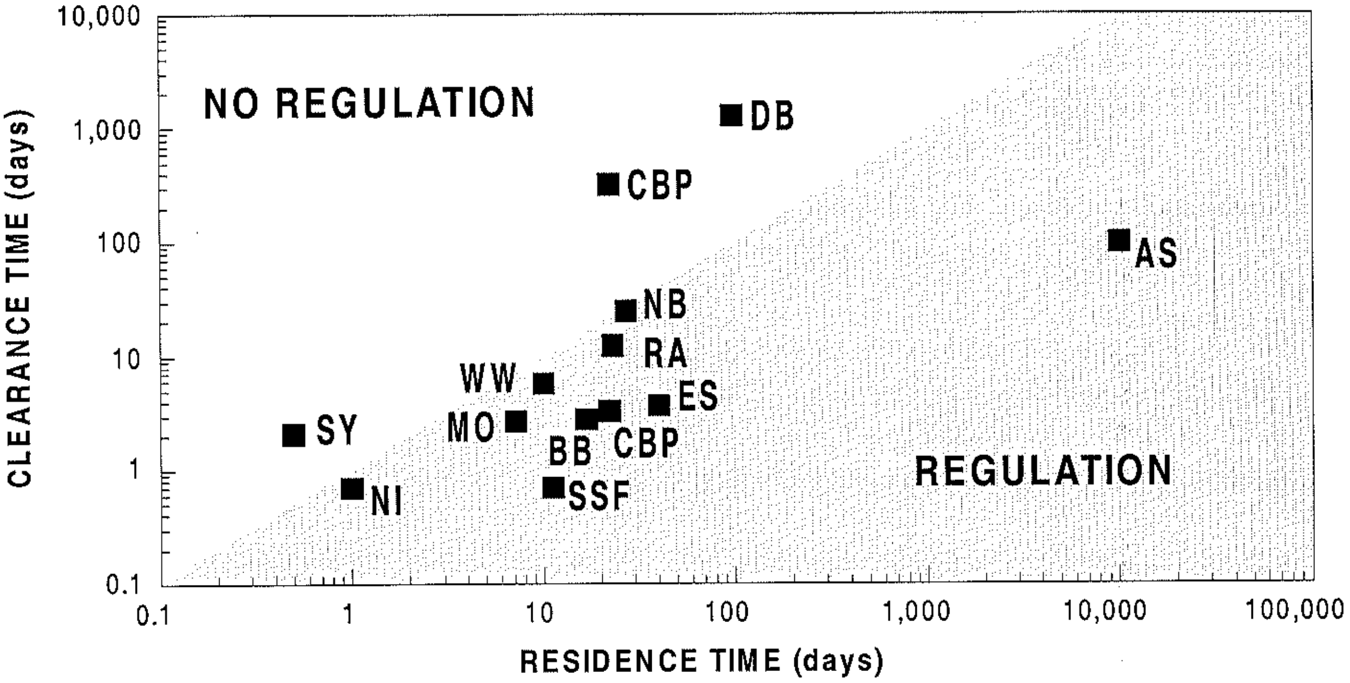

Figure 5. Residence time of water mass plotted against bivalve clearance time. (Symbols define in Table 1).

Inlet and Sylt. In these systems, bivalves appear to consume more phytoplankton biomass than is produced within the system. Thus, these systems function more like feedlots with food being imported from the adjacent ocean to support high heterotrophic activity within their shallow tidal creeks and flats.

Chesapeake Bay was once heavily dominated by bivalve filter feeding, but through overharvesting, disease and changes in the surrounding landscape this system has changed to a planktonic one (Newell 1989). The switching from benthic-pelagic coupling to a planktonic system is but one way bivalves have been involved in changing the nature of a coastal system. In Ria de Arosa of Spain (Tenore et al. 1982) and Marennes-Olerón of France (Heral et al. 1988), we find the reverse case where the artificial culture of dense populations of bivalves has moved these systems towards dominance by benthic bivalve filter feeding. From an ecosystem perspective, it would be informative to know if such switching can occur naturally and if it does what the system advantages and disadvantages are. I suggest that in a biodiversity context, planktonic grazing and benthic bivalve filter feeding are simply redundant components in the processing of suspended particulate material in coastal waters. However, when conditions favor benthic filter feeding, i.e., shallow flowing water, sufficient substrate, and sufficient phytoplankton, these systems will dominate because their food chain is shorter, they take advantage of tidal energy subsidies to receive their food, and their longer life span stabilizes systems over longer time periods with a greater variety of environmental cycles.

NEGATIVE FEEDBACK AS A STABILIZING INFLUENCE

The strong coupling of benthic filter feeding bivalves to phytoplankton in the water column via grazing is a negative feedback loop in the consumer-producer (predator-prey) model. Such negative feedbacks should be a stabilizing influence on their ecosystems because they counter act deviations in the functional attributes of the system. Bivalve filter feeders may be especially stabilizing because (1) they are permanently in the ecosystem, (2) their filtration rates do not level off with increasing food availability, and (3) their biomass turns over at a low rate (Herman and Scholten 1990). Unlike predator-prey cycles in the plankton, the permanent presence of long lived bivalves ensures that no time lags occur between the appearance of food and the grazing activity of the animals. The bivalves are always waiting to feed, slowly starving during the winter and immediately grazing when primary production starts in the spring. The absence of a time lag may ensure that the phytoplankton cannot reach a level where effective grazing control becomes impossible.

Nitrogen

Nitrogen is an element that undergoes numerous transformations in addition to state changes as it cycles through the environment. After carbon, nitrogen may be the most important element to living organisms, especially those that live in marine and coastal environments where nitrogen may be limiting (Sprent 1987). Compared to carbon that has only one inorganic form, nitrogen has several that play important roles in environments where bivalve filter feeders may be dominant components. It is probably this diversity of forms and states that has retarded the development of nitrogen budgets for ecosystems in general and coastal systems in particular (Nixon and Pilson 1983). Therefore, it is not surprising that observations of nitrogen processing by bivalve filter feeders in general and oysters in particular is incomplete for most systems studied.

In many systems, inputs of new nitrogen, nitrogen from fixation, is not sufficient to support the needs of primary production. In these cases, particulate organic nitrogen is recycled by the release of inorganic nitrogen by heterotrophic consumers, e.g., oysters. Usually this inorganic nitrogen is ammonium and often this form of nitrogen is preferentially taken up by phytoplankton. Bivalves may also release dissolved organic nitrogen in the form of amino acids and urea (Hammen et al. 1966) that can also be used by phytoplankton (McCarthy 1980). Thus, in the nitrogen cycle in coastal waters, benthic bivalves can short-circuit pelagic nutrient processing and rapidly recycle nitrogen. The nitrogen feedback loops between the bivalves and the phytoplankton are both positive (inorganic nitrogen regeneration) and negative (grazing). This discussion will focus on the uptake and release of nitrogen by oyster dominated systems.

The first direct evidence that bivalve filter feeders could influence nitrogen fluxes at the ecosystem level came from Nixon et al. (1976). In their study of the Bissel Cove salt marsh embayment in Narragansett Bay, a bed of *Mytilus* was observed to excrete 4 to 5 mM ammonia m^{-2} h^{-1} at 15 °C. These authors hypothesized that blue mussels in this system import large quantities of suspended particulate nitrogen and export large amounts of ammonia to the adjacent offshore water.

It was not until the application of portable plastic tunnels (Dame et al. 1984) and domes (Boucher and Boucher-Rondoni 1988) that *in situ* measurements of nitrogen uptakes and releases were conducted on oyster reefs in tidal channels. A major objective of each of these studies was to observe the material fluxes across oyster beds in as realistic manner as possible.

The initial tunnel work was conducted on intertidal oyster reefs, *Crassostrea virginica*, in North Inlet, SC and is summarized in Dame et al. (1989). The simultaneous fluxes of various forms of nitrogen were measured every 10.2 days for a year (Table 2). A striking observation of this study was the considerable variation in material fluxes from one observed tidal cycle to the next. This variability was attributed to tide to tide differences in ebb and flood velocity patterns. In addition to the general net flux pattern of uptake of particulate nitrogen (negative feedback) and release of dissolved nitrogen (positive feedback), the observed fluxes were almost always an order of magnitude greater than scaled-up estimates from laboratory data. These high flux rates strongly suggest a major role for oysters in ecosystems where they are abundant. When scaled-up to the marsh-estua-

Table 2. Yearly nitrogen and phophorus budgets for an intertidal oyster reef in North Inlet, SC. Units in gN m^{-2} yr^{-1} or gP m^{-2} yr^{-1} (after Dame et al. 1989).

Constituent	Flood Tide	Ebb Tide	Net
Total Dissolved Nitrogen	-116*	91	-25
Ammonium	-58*	-67*	-125*
Nitrite + Nitrate	0.3	-1.3	-1.0
Dissolved Organic Nitrogen	-136*	263*	127
Particulate Nitrogen	472*	-250	222
Total Nitrogen	275*	-86	189
Ortho-phosphate	1.4	-9.1	-7.7
Particulate Phosphate	156*	-86	70
Total Phosphorus	136*	-38*	98*

* Flux significant at 5% level
+: Uptake (no sign indicated)
-: Relelase

rine basin, the oyster reefs are by comparison the largest and only significant source of ammonium within this part of the North Inlet system (Dame et al. 1991). The turnover time for ammonium as calculated from oyster reef release is about half that of the water mass residence time. This relationship implies that the oyster reefs are influencing ammonium concentrations in North Inlet.

In the large tidal range estuaries of North Brittany, France, Boucher and Boucher-Rodoni (1988) and Boucher-Rodoni and Boucher (1990) investigated the role of the oyster, *Crassostrea gigas*, in nutrient fluxes. Using relatively low densities of oysters in domes, they found that the oysters contributed about 15 to 40% of the ammonium and urea within the chambers. They also noted that the actual material fluxes associated with the oysters were always greater than potential estimates.

The nitrogen excreted by bivalves and released by organically enriched adjacent sediments can have a major influence on the microalgae in oyster culture facilities (Robert et al. 1982, Maestrini et al. 1986). These researchers found that the microalgae seem to have adapted to the high concentrations of ammonium, nitrate and organic nitrogen in these culture ponds. Normally, high concentrations of ammonium inhibit the uptake of other nitrogen sources by algae, but the threshold of ammonium inhibition is much higher in these pond algae than in pelagic or neritic species, allowing them to assimilate other sources of nitrogen simultaneously with ammonium.

In order to directly assess the role of oyster reefs on nutrient cycling in tidal creeks, Dame and Libes (1993) developed a design to experimentally manipulate these systems. In their experiment, nutrient concentrations in creeks with oysters were compared to creeks with oysters removed using a BACI (before, after, control, incident) design (Underwood 1994). The amount of oyster biomass to water volume in each creek was standardized to that of the North Inlet system (3.8 g m^{-3}) and the bank-full volume of each creek was determine by hypsometric characterization. After a before manipulation calibration run of 1-month, oysters were removed from half of the creeks and the daily concentrations of nutrients were monitored for 2-months. With regard to nitrogen, ammonium and total nitrogen concentrations were found to be significantly higher in creeks with oysters when compared to creeks without oysters. It clearly and directly supports the previous suggestions that dense populations of oysters can and do significantly influence the amounts and types of nitrogen in tidal waters, and that these bivalves may play a major role in material cycling in these systems.

Phosphorus

Phosphorus is one of the essential elements in living organisms and plays a fundamental role in the metabolic processes of energy transfer, respiration and photosynthesis. In marine environments, phosphorus is found in living organisms, in the water column as dissolved inorganic phosphorus (usually orthophosphate), dissolved organic phosphorus and particulate phosphorus. In sediments, particularly anaerobic sediments, the chemistry of phosphorus can be complicated (Valiela 1984).

The first studies of phosphorus and marine bivalves used the radioactive isotope of phosphorous (P^{32}) to determine uptake and utilization (Ronkin 1950, Pomeroy and Haskin 1954). The earliest evidence that bivalve filter feeders could play an important role in mineral cycling at the ecosystem level came from Kuenzler's (1961) study of the phosphorus budget of the salt marsh mussel in Georgia. Kuenzler concluded that although these bivalves moved about 1% as much energy as bacteria in the salt marsh system, they are probably more important as remineralizers than consumers as a result of their high rates of filtration and deposition.

To date only two studies have focused on the role of oysters in processing phosphorus at the ecosystem level. Sornin et al. (1986) examined the role of intensively cultured *Crassostrea gigas* in the phosphorus cycle in Marennes-Olerón Bay of France. These investigators found that oysters removed about 50% of both total and assimilable phosphorus from the water column of the bay with most being deposited in the sediments. As earlier described, Dame et al. (1989) determined the phosphorus budget for an intertidal oyster reef, *Crassostrea virginica*, in South Carolina (Table 2). There was a significant uptake of total phosphorus with most of that being particulate (negative feedback). Only 8% of the total phosphorus uptake on the SC reef was released as orthophosphate (positive feedback) as compared to 3% by the less dense community in Marennes-Olerón Bay. The expected N:P Redfield ratio is 16 and for the SC reef the ratio for the uptake fluxes is about 2. Thus, the oyster reef appears to be taking up proportionally more phosphorus than nitrogen or carbon (Dame et al. 1989). Therefore in the oyster dominated systems studied to date, these animals seem to remove considerably more phosphorus from estuarine waters than would be expected. Oyster reefs may be significant components in retaining phosphorus - a constituent that unlike nitrogen and carbon has no gaseous state and can only enter the estuary via land runoff or import from the coastal ocean.

Table 3. A summary of system nutrient cycling control by oyster reefs.

Nutrient	**Feedback Loop** (+)	 (-)
Carbon	No	Direct
Nitrogen	Indirect	Direct
Phosphorus	(Maybe)	Direct

Conclusions

In coastal ecosystems with dense populations of oysters, these filter feeders remove large quantities of suspended particulate organic materials (negative feedback) and remineralize them into forms that are readily utilized by phytoplankton (positive feedback). The remineralization process is amplified by the reef system, in that, feces and pseudofeces enrich the sediments surrounding the oysters and the microorganisms in these sediments effectively double the remineralization rates to the reef. These processes short-circuit the typical pelagic food web and move carbon, nitrogen and phosphorus through these ecosystems at much faster rates. As a consequence of these material flows, both negative and positive feedback loops are established (Table 3) that potentially increase the productivity and stability of estuarine ecosystems. In essence, oyster reefs increase the functional and structural sustainability of their ecosystems.

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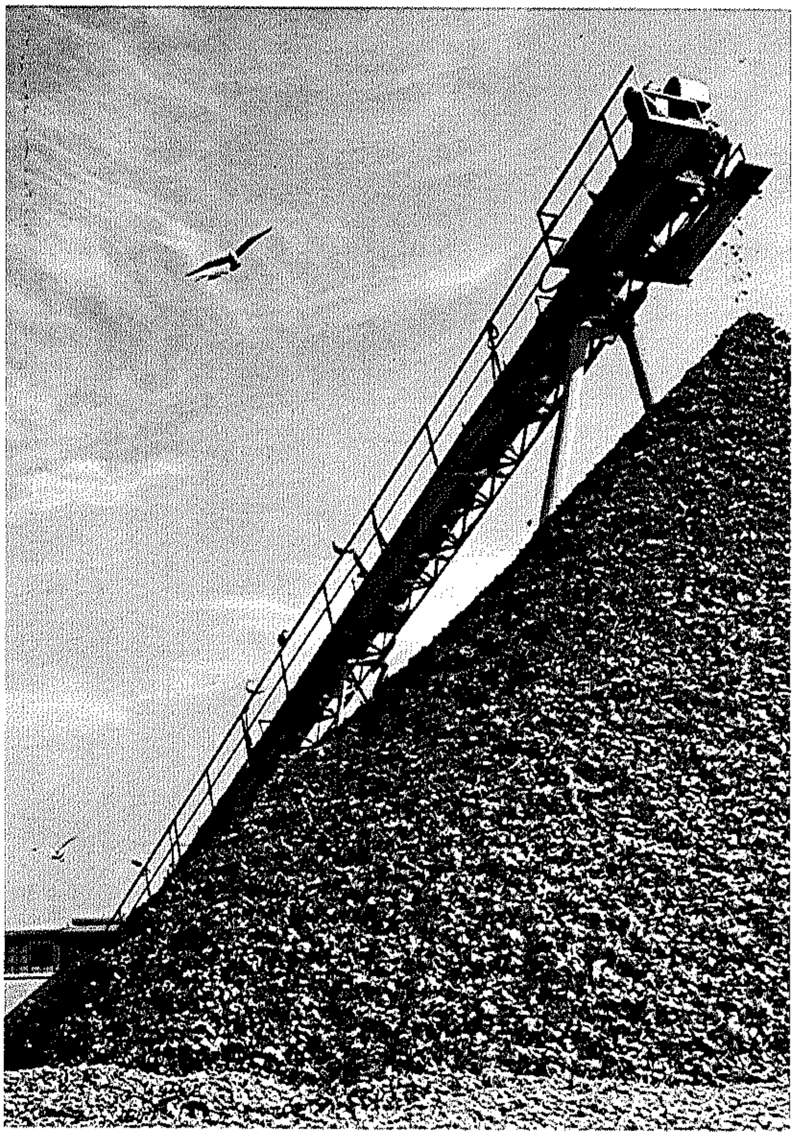
Part IV
Alternative Substrates



Chapter 19

Use of Dredged Material for Oyster Habitat Creation in Coastal Virginia

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Abstract

Dredging can have a beneficial effect on oyster habitat when the placement of the dredged material is effectively managed to help provide the bottom structure necessary to develop an oyster reef. Construction and maintenance of the Waterway on the Coast of Virginia (WCV) by the U. S. Army Corps of Engineers (Corps) has provided a number of examples of this process, both serendipitous and deliberate. The historical development of reefs that evolved from the random overboard placement of dredged material and the subsequent leasing of these areas for oyster cultivation is reviewed. A monitoring plan for the development of a reef in Swash Bay using maintenance dredging material is also described including pre- and post-dredging hydrographic surveys, surface sediment distributions, and shellfish surveys.

After one year, the benthic communities at the recently used placement site, the historical placement site and an unimpacted area in Swash Bay were compared using the Benthic Assessment Method (BAM) to determine short-term impacts. The historical and unimpacted sites had very similar values while the recently used site was somewhat lower. Consequences of continued success in developing oyster reefs in close proximity to a dredged channel are addressed with a suggested management plan that involves rotating the placement among a number of sites. This would allow for the continued maintenance of both the channel and the adjacent oyster reefs.

Introduction

Properly managed, dredged material has the potential to be an important resource in the management and enhancement of oyster fisheries by providing the foundation material for the construction of new or the restoration of old reefs. This can be particularly important in areas like the Seaside of the Eastern Shore of Virginia (Figure 1) where natural oyster reefs in the back barrier bays are primarily intertidal and raised one to two feet above the surrounding flats (Haven et al. 1981). Higher elevations are necessary for oyster production on the Seaside. Intertidal exposure appears to improve survival of the oysters by minimizing their exposure to disease and predators (M. Luckenbach, personal communication). In fact, intertidal oyster reefs have developed serendipitously on dredged material placement sites on the WCV (Priest, 1994). Dredged material has also been used in Maryland for the construction of a subtidal reef that was subsequently planted with oyster shell cultch to initiate development of the reef (Earhart et al, 1988 and Clarke et al. 1999, Chapter 21, this volume).

The WCV is an 85 mile long portion of the Intracoastal Waterway that extends north to south through the barrier bays and channels along the Seaside of Virginia's Eastern Shore (Figure 1). Maintenance of this waterway involves the regular dredging of approximately nineteen shoals and several ancillary channels with an average annual volume of over 300,000 yd^3 (VIMS and VMRC 1994). While many different placement options are used for dredging these shoals, the most commonly used option is overboard hydraulic discharge in open water adjacent and parallel to the channels. With repeated usage these sites can begin to emerge in a series of intertidal sand and shell hummocks that are often colonized by oysters naturally.

Local watermen soon realize the value of these areas for the cultivation of oysters and start leasing them from the State. By comparing the locations of previously used placement areas shown on the Corps project maps and the oyster lease records maintained by the Virginia Marine Resources Commission (VMRC), we have been able to determine that at least thirteen different sites have been leased subsequent to their use as placement areas for the WCV and its ancillary channels. This leasing can present a serious management problem because it usually eliminates that area as a future placement site. Consequently, new sites have to developed and approved which can become problematic due to engineering considerations or adverse environmental impacts. This situation actually occurred in Swash Bay where the placement area that had been used since 1957 was leased in 1985 and was no longer available as a placement area. As a part of the approval process for a new placement site, a management plan for the Swash Bay channel was developed with three goals in mind, 1) to use the dredged material to build an oyster reef, 2) monitor its development as a model for other channels and 3) to plan for the future placement needs.

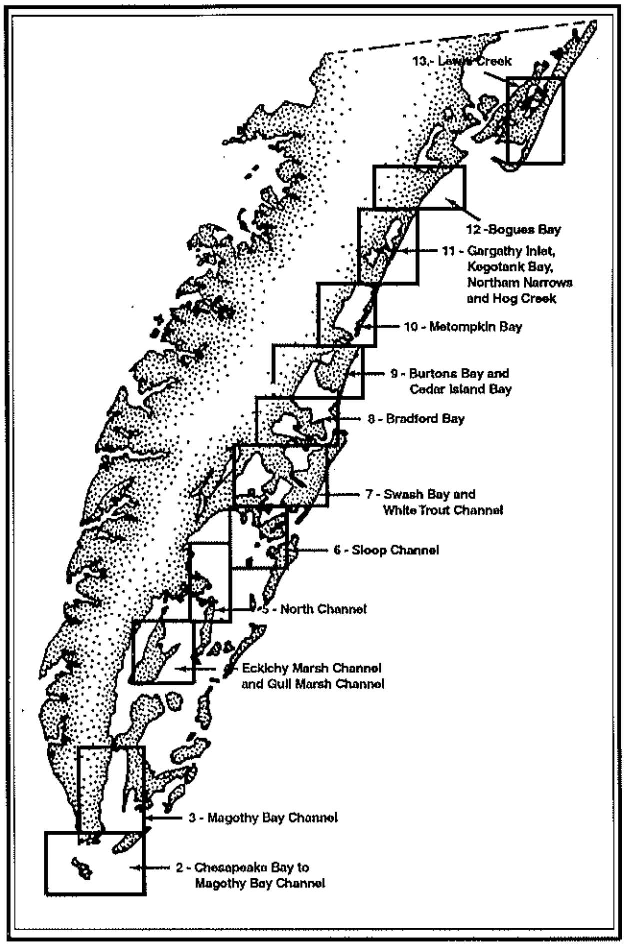

Figure 1. Waterway on the coast of Virginia showing segments maintained by Corps dredging.

A major concern in this approval process is the tradeoff that inevitably occurs when one type of habitat, shallow subtidal soft-bottom, is converted to another, intertidal mud/sand flat. Both are still part of the marine ecosystem, but their ecological roles can be completely different. The question of whether these changes are good, bad or indifferent always begs to be answered.

The circumstances in Swash Bay presented a unique opportunity to address the resource tradeoff question in addition to monitoring the evolution of the dredged material placement area. Swash Bay has all of the components that might be used to evaluate both the short and long term effects of the dredged material placement on benthic communities. It contains an area of recently deposited material, old reef areas greater than ten years old that have developed on dredged material, and previously undisturbed bottom.

Since the existing reefs developed from dredged material have evolved over a number dredging episodes and involved varied sediment characteristics and placement methods, their ontogeny cannot be reconstructed with any certainty. Hence this study was designed to begin the process of documenting the intentional development of an oyster rock using the dredged material from Swash Bay. This will be accomplished by continuing to place the material in the same area until such time as a substantial portion of the area becomes intertidal (the initial threshold has been proposed at approximately ten acres). Once the intertidal elevations have been reached the Corps will endeavor to plant the dredged material with shell cultch to stimulate the development of an oyster reef on the site. During the interim VMRC has agreed not to lease the bottom as long as it is an active placement area for the channel. The Virginia Institute of Marine Science (VIMS) and the Corps are monitoring conditions at the placement site before, six and eighteen months after the first dredging episode as a part of the management plan. VIMS is to document changes in the shellfish community and surface sediment conditions, while the Corps is to provide periodic bathymetric surveys of the placement area to describe changes in the physiography of the sediment mound.

The purpose of this study is primarily to determine the existing shellfish resources, i.e. the molluscan fauna, the amount of surficial shell, and the nature of the surface sediments in the placement area and document the changes that occur after the initial dredged material placement. Additionally, an effort was made to evaluate the short- and long-term impacts of the placement on the benthic communities in Swash Bay.

Methods

The new dredged material placement area is a 1000 ft^2 (93 m^3) square centered 1500 ft (457 m) east of the southern portion of the project channel (Figure 2). The area was surveyed by the Corps in March 1992 to established the pre-dredging bathymetry at the site. The channel was dredged during March and April of 1993. Post-dredging surveys were

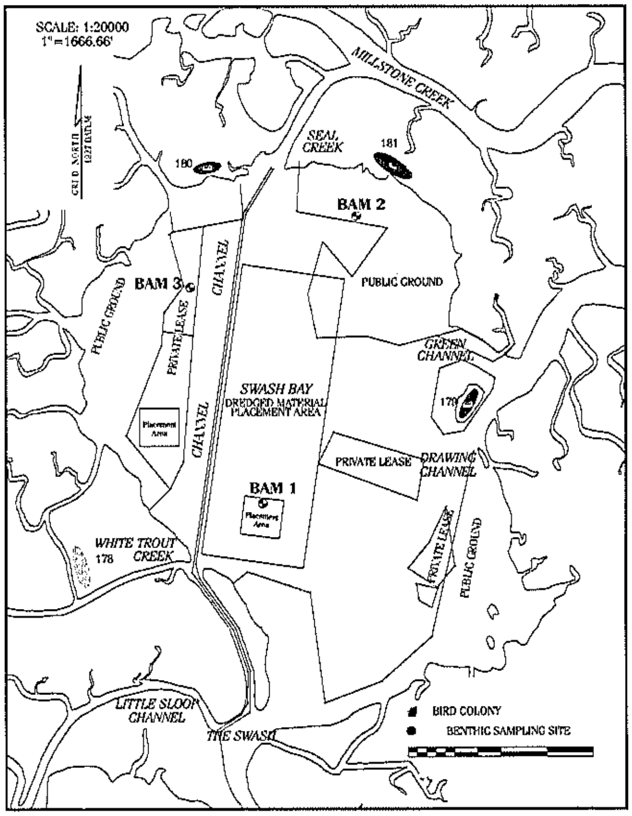

Figure 2. Swash Bay Vacinity.

conducted in July 1993 and September 1994 to document changes that have occurred in the bathymetry of the placement area. These surveys were conducted with a vessel mounted recording fathometer linked to a differential Global Positioning System (G.P.S.) to determine location.

A sampling grid was established on the placement area with 25 stations on 250 ft. centers forming a 5 x 5 grid. In addition, a short transect with four stations 250 ft. apart was established extending east from the middle of the eastern side of the placement area (Figure 3). Each station was located by a Corps survey crew in both 1992 and 1993.

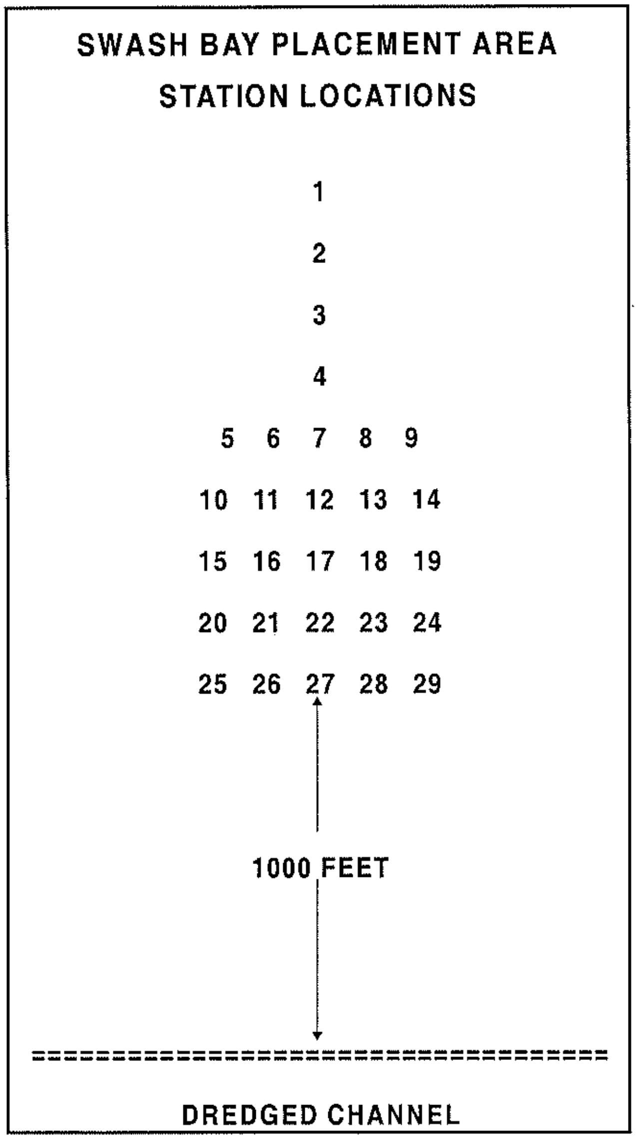

Figure 3. Schematic of station locations for Swash Bay placement area

Each of the 29 stations was sampled using randomly placed 0.25 m^2 circular quadrat deployed by divers. All of the material to a depth of 15 cm was removed with a 76 mm diameter suction dredge fitted with a 5 mm mesh bag over the discharge. Each bag was labeled, secured, placed on ice, and returned to the lab for live-sorting for benthic fauna. The material in each bag was sieved through a 5 mm mesh screen. All mollusks and other large fauna retained on the screen were preserved in 10% formalin for later identification. The shell material retained on the screen was placed in a graduated jar and its volume in cubic centimeters was estimated.

A surface sediment sample was collected at each of the 29 stations and analyzed for percent sand in 1992 and percent sand, silt and clay in 1993 using standard sieve and pipette procedures.

Numerous rapid bioassessment methods have been developed to evaluate and detect anthropogenic stress, disturbance and change in benthic communities. The Benthic Assessment Method (BAM), was recently developed at VIMS by Diaz and Maxemchuck-Daly (in prep) for use in soft-bottom estuarine habitats. This index is based on the premise that healthy areas contain diverse well-developed communities dominated by large deep-dwelling organisms. The benthic community is evaluated and given a score based on the functional lifestyle, size, depth of occurrence and biomass of the fauna present. In general, low scores reflect disturbed or stressed habitats and high scores indicate productive established habitats. BAM scores for Virginia estuaries typically range from 0 to 8 (Diaz and Maxemchuck-Daly, in prep).

The BAM method was used to compare the benthic communities at the recently used placement site (BAM 1), one that was over ten years old (BAM 2), and a previously undisturbed site (BAM 3) (Figure 2). Each of these habitats was sampled in June 1994 approximately one year after the most recent dredging episode. Three replicate samples were taken at each site to assess the average condition.

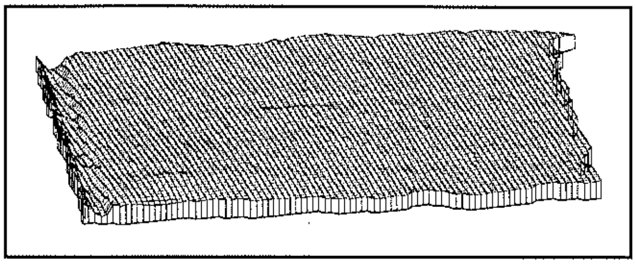

Figure 4. Topography of Swash Bay Placement Area, March 1992.

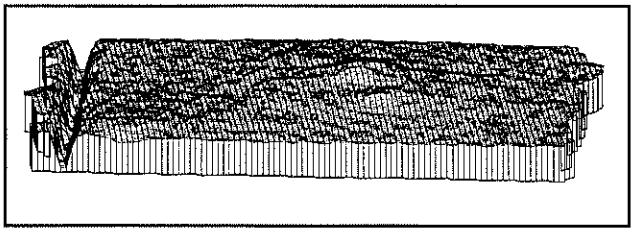

Figure 5. Topography of Swash Bay Placement Area, July 1993.

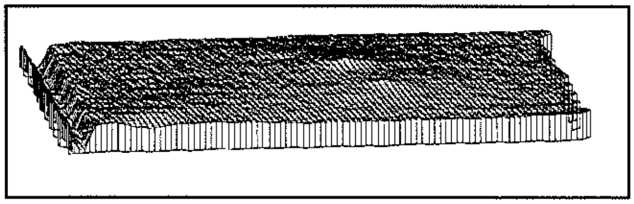

Figure 6. Topography of Swash Bay Placement Area, September 1994

The benthic macrofaunal samples were obtained using a Wildco 15 cm x 15 cm x 30 cm box core (225 cm^2 surface area) which penetrated the sediment to a depth of at least 15 cm. In the field, the box core sample was divided into 0-5 cm and >5 cm fractions. Both fractions of the box core sample were sieved separately on a 500 μm Nitex mesh screen. Material retained was fixed in 10% buffered formalin with a rose bengal stain. In the laboratory, samples were washed in fresh water and organisms were removed from the sediment and detritus and sorted into major taxonomic groups using a binocular dissecting microscope. The formalin preserved wet weight was determined to the nearest 0.1 mg.

Results

The most recent dredging of Swash Bay occurred in April 1993 when 111,000 yd^3 of maintenance material was removed from the channel and placed in a 1000 ft^2 area centered 1500 feet east of the southern end of the channel (Figures 2 and 3). Pre-dredging sediment sampling indicated the material averaged approximately 6% sand (Century Engineering, 1983). The pre-dredging bathymetric survey (Figure 4) depicts a relatively flat shallow subtidal area that was approximately 1.5 ft. (45.7 cm.) deep at mean low water. The mean tide range at the site is approximately 4 ft. (1.2 m). When the area was bathymetrically surveyed three months after the dredging in July 1993, two small mounds of material are noticeable above a much larger mound of lower relief (Figure 5). Based on this survey, the Corps calculated that the volume of the dredged material mound was approximately 82,000 yd^3 which represented 74% of the material dredged. The placement area was surveyed again in September 1994 approximately 17

Table 1. Summary of monitoring parameters for the Swash Bay Dredged Material Placement and Reference Areas.

		% Sand		**Shell Volume (cc/quadrat)**		**Total Mollusks (#/quadrat)**	
		1992	**1993**	**1992**	**1993**	**1992**	**1993**
Placement Area	Mean	13.7	11.4	49.9	9.2	7.7	4
(Stations 5-29)	Range	22-5	49-2	300-5	25-1	101-0	21-1
Reference Transect	Mean	35	32.3	57.5	47.5	6	5.5
(Stations 1-4)	Range	54-20	51-3	125-5	150-5	13-0	9-2
Combined Value	Mean	16.7	14.3	51	14.4	7.5	4.2
(Stations 1-29)	Range	54-5	51-2	300-5	150-1	101-0	21-1

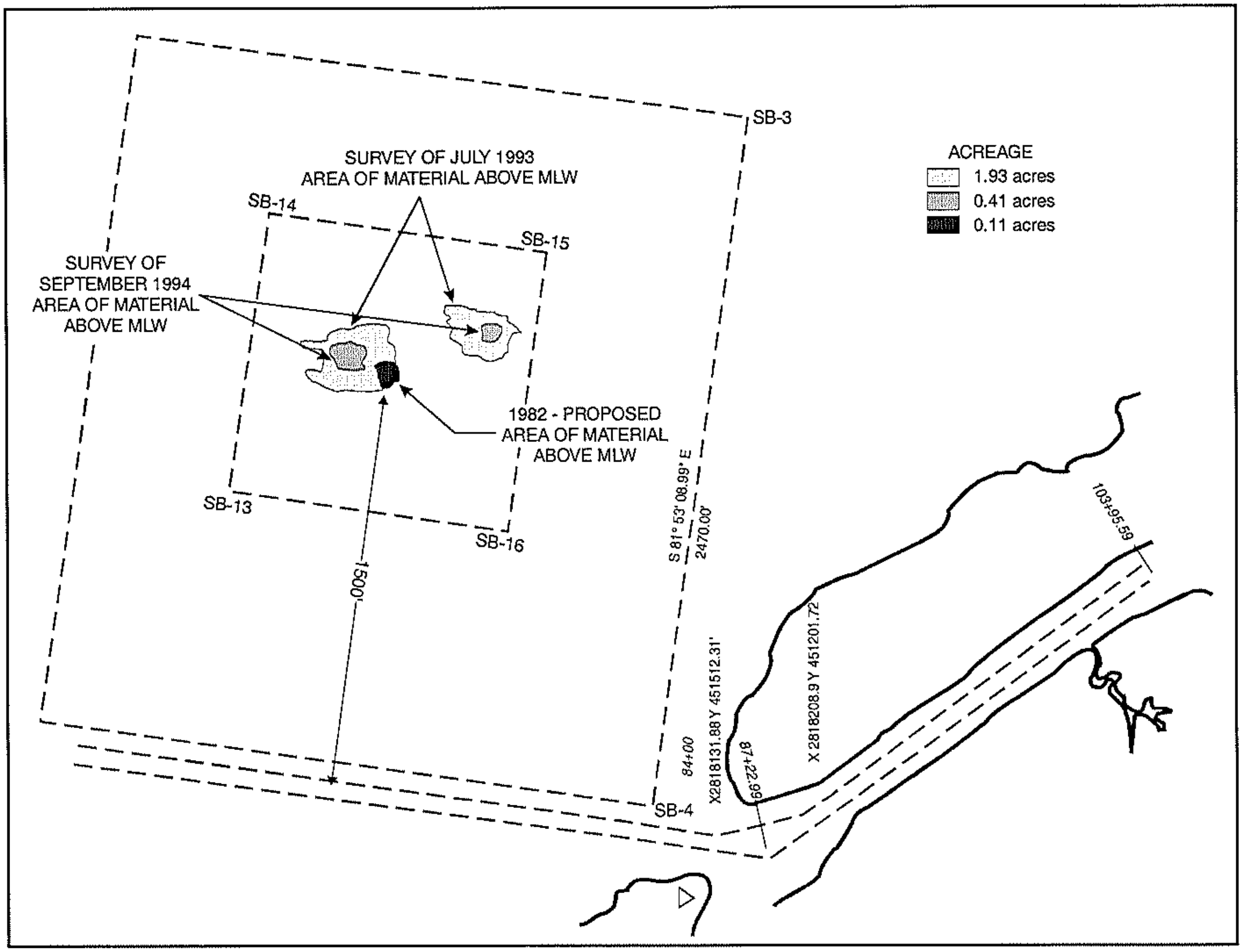

Figure 7. Bathymetric survey results for Swash Bay Reef showing intertidal portion.

Table 2. Mollusks identified from the Swash Bay Dredged Material.

Species	1992	1993
Andara ovalis	1	3
Crepidula fornicata	2	1
Cylichna sp.	0	10
Eupleura caudata	0	1
Ilyanassa obseleta	177	38
Mecoma balthica	8	20
Macoma tenta	10	38
Mercenaria mercenaria	3	0
Tagelus plebius	15	11
unid mussel	0	1

months after the dredging (Figure 6). The two small mounds were still evident and the volume was calculated to be 75,000 yd^3 which represents 68% of the original material dredged.

The Corps originally estimated in the Swash Bay Management Plan that approximately 0.11 acres (445 m^2) of the placement area would become intertidal after the first dredging cycle. According to the July 1993 bathymetric survey, the intertidal area was approximately 1.93 acres (7811 m^2). Fourteen months later when the area was resurveyed in September 1994, the intertidal area had been reduced to 0.41 acres (1660 m^2) (see Figure 7).

The results of the surface sediment, shell volume and total mollusks sampling over the grid established on the placement area are

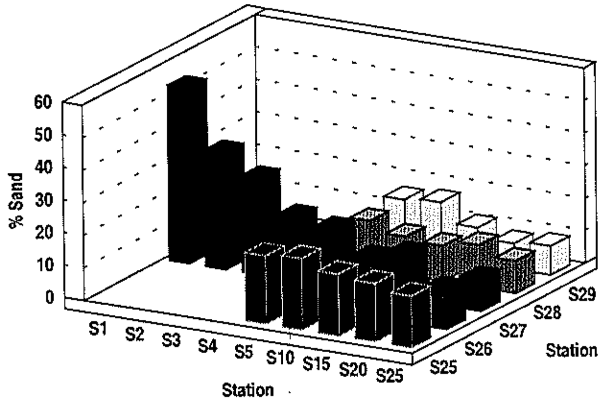

Figure 8. Sand composition by station before dredging, 1992.

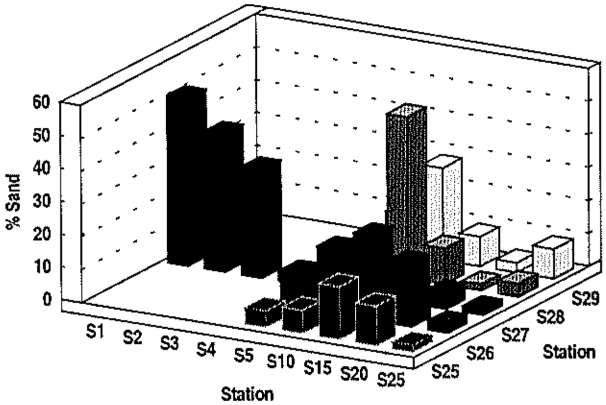

Figure 9. Sand composition by station after dredging, 1993.

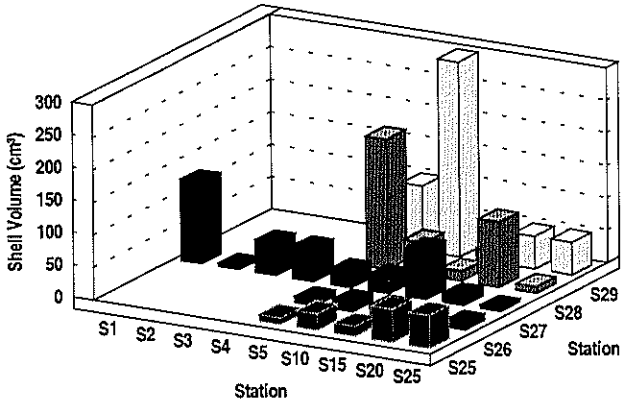

Figure 10. Shell volume by station before dredging, 1992.

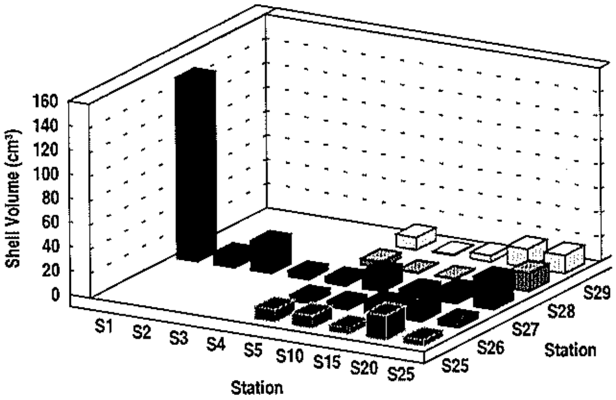

Figure 11. Shell volume by station after dredging, 1993.

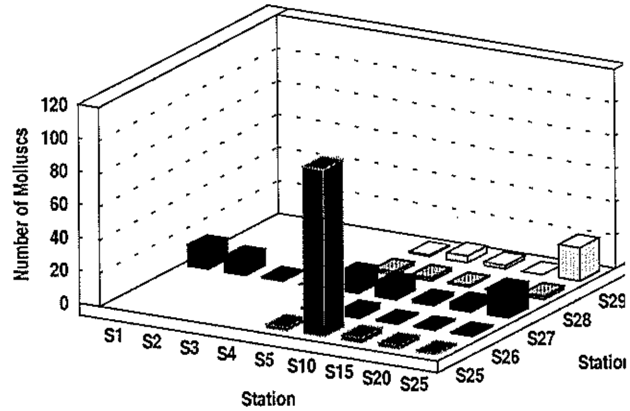

Figure 12. Number of molluscs by station before dredging, 1992.

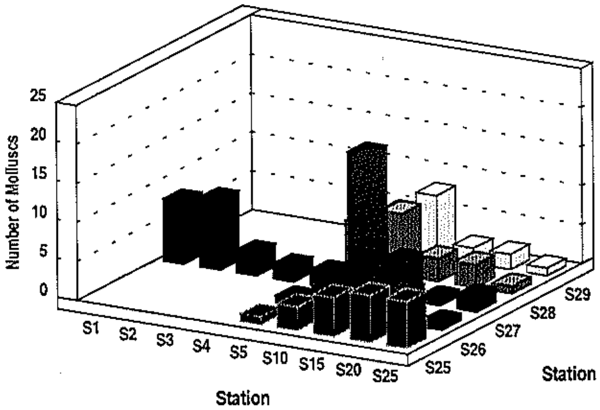

Figure 13. Number of Molluscs by station after dredging, 1993.

summarized in Table 1. These data are also graphically compared by station for both before dredging, 1992, and after dredging, 1993 in Figures 8-13. The specific data on the mollusks recovered are presented in Table 2.

The surface sediments in the placement area prior to the dredging ranged from 5-22% sand with an average of 13.7% in 1992. After dredging in 1993, the average percent sand was only slightly lower at 11.4%. The range, however, had increased considerably to 2-49%. The reference transect (stations 1-4) sand percentages changed very little from 35% in 1992 to 32.3% in 1993. The range increased slightly from 20-54% in 1992 to 3-51% in 1993. The highest percentages of sand after the dredging were located in two areas near where the pipeline discharge occurred, and the lowest percentages were found around the perimeter.

The average shell volume in the placement area dropped substantially between 1992 and 1993 from 50 cm^3/quadrat to 9.2 cm^3/quadrat. The range of shell volumes was also reduced from 5-300 cm^3/quadrat to 1-25 cm^3/quadrat. The reference transect average shell volume stayed virtually the same 57.5 cm^3/quadrat vs. 47.5 cm^3/quadrat and maintained similar ranges.

The only commercially important shellfish that were found in the placement area during the quadrat sampling were three hard clams, *Mercenaria*. None were found in the placement area after the dredging. Overall, the number of

Table 3. Swash Bay B.A.M. Results - June 1994.

Site	Replicate	Core Section	Is fauna present in >5cm section?	Is fauna in >5cm section large?	Fauna lifestyle	Section biomass (g)	Total biomass (g)	% biomass in >5cm section	Total BAM score*	Comments
New Displacement Area	1	0-5cm	yes (1)	yes (1)	Small burrowers (1)	1.330	2.0137	34% (2)	(5)	
		>5cm				0.6807				
	2	0-5cm	yes (1)	yes (1)	Long-lived large fauna (2)	0.5582	1.9984	72% (3)	(7)	Large Nereis
		>5cm				1.4402				
	3	0-5cm	yes (1)	yes (1)	Small burrowers (1)	0.5613	1.0661	47% (2)	(5)	
		>5cm				0.5048				
Undisturbed Area	1	0-5cm	yes (1)	yes (1)	Long-lived large fauna (2)	0.4827	7.0717	93% (4)	(8)	Large Nereis
		>5cm				6.5890				
	2	0-5cm	yes (1)	yes (1)	Long-lived large fauna (2)	0.6338	3.9136	83% (4)	(8)	Large Nereis
		>5cm				3.2798				
	3	0-5cm	yes (1)	yes (1)	Small burrowers (1)	0.2770	2.1408	87% (4)	(7)	
		>5cm				1.8638				
Old Placement Area	1	0-5cm	yes (1)	yes (1)	Small burrowers (1)	0.6379	4.2831	85% (4)	(7)	
		>5cm				3.6452				
	2	0-5cm	yes (1)	yes (1)	Long-lived large fauna (2)	10.5559	14.7868	29% (2)	(6)	Large Nereis holothuroidea
		>5cm				4.2309				
	3	0-5cm	yes (1)	yes (1)	Long-lived large fauna (2)	0.4273	13.1988	97% (4)	(8)	Large Nereis small Mercenaria
		>5cm				12.7715				

Total BAM Score interpretation:

0-1	Poor habitat, seriously disturbed
2-3	Moderately disturbed or stresses habitat
4-5	Slightly disturbed to moderately disturbed habitat
6-8	Good habitat

Table 4. Surface sediment characteristics at the Benthic Assessment Method sites in Swash Bay.

		% Gravel	% Sand	% Silt	% Clay
BAM1	New Placement Site (n=3)	-0-	9.5	53.7	36.7
BAM2	Undisturbed Site (n=1)	-0-	9.6	57.5	32.9
BAM3	Old Placement Site (n=2)	0.2	24.6	43.1	32.2

mollusks in the placement area appears to have decreased from an average of 7.7/quadrat in 1992 to 4/quadrat in 1993. These data are somewhat skewed by one quadrat that had 101 snails, *Ilyanassa obseleta.* If this quadrat is eliminated from the analysis the numbers per quadrat become 4.0 and 3.8 for 1992 and 1993, respectively. A summary of the species and numbers found in the quadrats is given in Table 2. The relationship between the number of mollusks and the percent sand at each station after the dredging is depicted in Figure 14.

The results of the BAM sampling at the new placement area, undisturbed site and the old placement areas in Swash Bay are provided in Table 3. The averages of the BAM scores for the three replicate samples at each site are as follows: the new site, 5.7, the old site, 7.0, and the undisturbed site, 7.7. The grain size analyses of the surface sediments at each of the BAM sampling sites are given in Table 4.

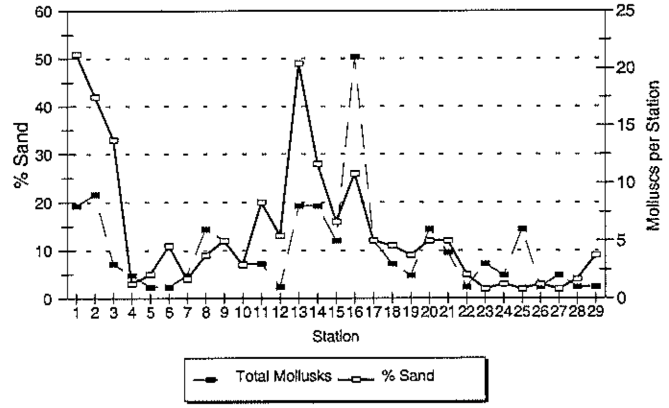

Figure 14. Sand composition and mollusc abundance by station.

Discussion

Little is known of the intermediate behavior of dredged material mounds resulting from repetitive overboard placement in shallow subtidal areas along the WCV. This behavior is greatly influenced by the volumetric increases and the bulk density reductions that occur in the dredged sediments as a result of the hydraulic dredging process. The subsequent volumetric reductions resulted from consolidation of the sediments and losses due to erosion from wave action and tidal currents (Halka et al. 1991; Panageotou and Halka 1994). Compaction of the underlying fine-grained sediment may also be a factor in the bathymetric changes observed.

When the Swash Bay channel was last dredged in April, 1993, approximately 111,000 yd^3 of material that averaged approximately 6% fine sand was pumped into the placement area (Century Engineering 1983; VIMS and VMRC 1995). Similar fine-grained sediments were reported to increase in volume by a bulking factor of 1.7 when hydraulically deposited in depths from 3-17m in the upper Chesapeake Bay (Halka et al. 1994). Three months later, the after dredging survey at the Swash Bay Placement Site indicated there was approximately 82,000 yd^3 of material in the area or approximately 74% of the original volume of material dredged. The survey in September, 1994 indicated 75,000 yd^3 remained; an additional loss of 8% for a total of 66% remaining after 17 months. Halka et al. (1991) reported losses from 39-63% of the material deposited after 18 months. At depths greater than 3m, Halka et al. (1994) attributed ½ to ⅔ of the losses to erosion and a ⅓ to ½ to consolidation.

The distribution of sand in the surface sediments corresponds with the location of the discharge pipe, the movement of which was intentionally constrained to maximize the accumulation of the limited amount of sand available in the dredged material. The amount of sand away from the immediate vicinity of the discharge was lower than the original levels and was suggestive of the sediment sorting that occurs around the discharge point. This process will be repeated in the future to manage the placement of the sand in an attempt to develop a reasonably stable foundation for the placement of cultch to initiate the development of an oyster reef.

The amount of surface shell in the placement area was extremely low and indicative of the existing soft-bottom community. The amount of shell was even less after the dredged material was deposited. The only exceptions are two small shell areas at the discharge points that were so small that neither was included within any of the sampling locations.

The original purpose of this study was to determine the extent of any oyster or hard clam resources located within the placement area. The reasons were twofold. First, if there was any significant shellfish resource, it would have been prudent to relocate the placement area to avoid displacing the existing resource. Second was the need to establish baseline information on the existing resources in the placement area so that future changes could be recognized and logically attributed to the dredged material placement and subsequent management efforts.

Since no oysters and only a very limited number of clams were found, and the sampling protocol was aimed only at very large organisms, it was decided that all of the mollusks retained would be used to compare the benthic community between sampling periods. The similarity of the molluscan communities before and six months after the dredging appears to indicate a fairly rapid recovery from the dredged material placement. The reasons for this rapid recovery are not specifically known but could be attributed to factors such as the lack of predators on the new site, the structure or "edge effect" provided by this mound of material on an otherwise flat bottom and the introduction of the relatively coarse-grained material into a area dominated by soft-bottom communities. The contribution by the vertical migration of the pre-dredging benthos is not known, but it was probably only a factor on the perimeter of the mound because the center was so thick and the change in sediment type so dramatic as to preclude most vertical migration (Hirsh et al. 1978). The relationship between the numbers of mollusks and the percent sand would appear to indicate that recolonization was an important factor because the deposit was thickest in the high sand areas.

The BAM analysis also appears to indicate a fast short-term recovery rate for the benthos in the placement area with an average score of 5.7. This would put the community in the mildly disturbed category just six months after eliminating virtually the entire benthic community at the site. The old site that has not been used in over ten years had an average score of 7.0 which ranked it among the more valuable communities. This would seem to connote that the prognosis for long-term recovery at the impacted site is also good. The undisturbed site scored 7.7 out of a possible 8.0 and served as reference for the other sites.

Conclusions

1. The intertidal area created by the dredged material placement decreased from 1.93 acres three months after dredging to 0.41 acres seventeen months after dredging.
2. The molluscan fauna displayed very little change six months after dredging as compared to pre-dredging conditions.
3. The amount of surficial shell decreased over the majority of the placement area, exclusive of the small shell pile at the discharge locations.
4. The distribution of sand in the surface sediments changed dramatically after dredging reflecting the hydraulic sorting process from the pipeline discharge.

5. The benthic community in the placement area appears to have had a good short-term recovery as reflected in the BAM values. The long-term prognosis is also good as indicated by the BAM values obtained at the historical placement site.

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Alternatives to Clam and Oyster Shell as Cultch for Eastern Oysters

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Abstract

The effectiveness of clamshell (*Rangia cuneata*) (Gray, 1831), limestone (Tennessee and Mexican), gravel, concrete, and cement-stabilized gypsum (gypment) as substrate for settlement of the eastern oyster, *Crassostrea virginica* (Gmelin, 1791), was compared in field and laboratory experiments. Oyster set on limestone in a 1990 field experiment was significantly ($p<0.05$) greater than on clamshell; Tennessee limestone, clamshell, and concrete attracted significantly more spat than did gravel. In a 1990 laboratory experiment, oyster set on clamshell and Tennessee limestone was significantly greater than on concrete, and all substrates were significantly superior to gravel. Limestone should prove to be an economically feasible, biologically acceptable, and environmentally benign alternative to clamshell. Solubility tests showed no significant difference between initial and final weights of gypment after exposure to flowing seawater for two months. A 1991 field experiment showed that gypment and Mexican limestone attracted significantly ($P<0.05$) more spat per dry liter of cultch than did clamshell. A 1991 laboratory experiment showed no significant difference among gypment, Mexican limestone, and clamshell in larval attracting capabilities. Gypsum, therefore, can be stabilized with cement and is as good or better than clamshell at attracting spat.

KEY WORDS: *Crassostrea virginica*, oysters, cultch, clamshell, *Rangia cuneata*, limestone

Introduction

The rehabilitation and restoration of oyster habitat requires cultch which is economically feasible, biologically suitable, and environmentally benign. Biologically suitable cultch will recruit oyster larvae, provide a firm bottom for adult oyster survival, and promote the development of a diverse biological community. The loss of oyster habitat is due to a variety of natural and manmade processes. These include changes in salinity which shift productive zones into areas which lack suitable substrate, harvesting at a rate which exceeds reef accretion, and excessive sedimentation which may kill adult oysters and prevent larval recruitment (Dugas 1988; Soniat et al. 1991). Oyster reefs have important economic and ecological functions - as a hard substrate for larval recruitment and oyster seed production, as a firm bottom for the cultivation of commercial oysters, and as a habitat for associated organisms. Reef rehabilitation and construction can emphasize any combination of these functional roles. In Louisiana, the interest is in cultch on public grounds to maintain reefs for the production of seed oysters, and in substrate on private leases to increase the firmness of the bottom for the cultivation of commercial-sized oysters. The Louisiana oyster industry is based on a public/private cooperative. The state maintains the seed grounds and provides oyster seed; oystermen transplant the seed to private leases for growth and subsequent harvesting. The Louisiana Department of Wildlife and Fisheries deposits large amounts of clamshell (*Rangia cuneata*) on seed grounds as cultch for oyster larvae. Clamshell has been the preferred material since the mid 1960's due to low cost, availability, and suitability. Areas with firm, stable bottoms and favorable salinities are chosen as cultch plant sites (Dugas 1988). The main source of clamshell has been from vast deposits in Lake Pontchartrain. Dredging for clamshell, however, was recently banned in the lake due to adverse ecological impacts. Alternative cultch materials were considered in light of the uncertain availability and the escalating cost of clamshell.

Several alternatives to clamshell have and are being investigated. Butler (1955) tested Plexiglas, frosted glass, and cement board, whereas Shaw (1967) examined setting on asbestos-plate collectors. Other materials have included stones, bamboo, tiles, tarred ropes, paper, wood, ceramics, and many plastics. Tiles and plastics with a lime coatings have also been examined (Quayle and Clark 1971). Asbestos-cement plates were used by Kennedy (1980), Hidu et al. (1981) tested polished granite and polished marble, and Mann et al. (1990) examined expanded shale and tire chips. Crushed oyster shells from shucking houses are suitable, but expensive and limited in availability (Chatry et al. 1986). Reef oyster shells were found to be suitable (St. Amant 1959), but the adverse effects of extensive reef dredging limit their use (Bouma 1976) and therefore oyster shell was not considered in this study. Limestone was found to catch about twice as many larvae as clamshell (Chatry et al. 1986), but limestone is 40% more expensive than clamshell by volume (as of May 1990). Coal ash has been investigated, and preliminary results from a Texas study indicate that it should prove to be an acceptable alternative (S. Ray, personal communication).

Oyster larvae will set upon a variety of hard surfaces; however, there appears to be some property associated with a molluscan shell, perhaps calcium carbonate, which seems to enhance a cultch's attractiveness to setting larvae (Hidu et al. 1975). Oyster larvae are induced to initiate settlement behavior upon the detection of bacteria-associated chemicals (Coon et al. 1985). Larvae, during their characteristic crawling behavior across the substrates, respond to factors such as light, texture, and chemical cues which determine the suitability of the substrate. The larvae resume swimming and settle elsewhere if the substrate is unacceptable (Coon et al. 1985). The presence of spat on cultch also seems to stimulate setting (Crisp 1967; Hidu and Haskin 1971; Keck et al. 1971), and there may be some substance secreted by spat which leads to this gregarious induction (Crisp 1967; Hidu 1969).

The purpose of this study was to test several cultch materials for use as alternatives to clam and oyster shell in oyster reef building or planting. Limestone (Tennessee and Mexican), crushed road bed (concrete with some asphalt), and gravel were among the potentially suitable materials. Gypsum met the requirements of being available and inexpensive; its solubility in seawater, however, prevented its use as a substitute for clamshell in the field (Soniat et al. 1991). However, the dissolution rate of gypsum was reduced by mixing it with cement thus making it a potential alternative to clamshell (Haywood and Soniat 1992). Field and laboratory experiments were conducted to test the relative spat catching abilities of these cultch materials.

Materials and Methods

PHYSICAL PROPERTIES OF CULTCH

Physical properties of cultch materials were determined to transform spat per wet liter data to spat per cm^2 and spat per dry liter of cultch. Measured properties included density, surface area, weight, and wet volume per dry liter. One dry liter of cultch was poured into a large graduated cylinder to obtain a wet volume by water displacement. The surface area (cm^2) of a dry liter of cultch was obtained by wrapping aluminum foil around individual rocks.

A gypsum/cement cultch (gypment) was produced by mixing gypsum and cement in a 1:1 weight to weight ratio. Initially, several different mixes of gypsum to cement were made (i.e. 9:1, 8:2, 7:3, 6:4, 5:5) to determine the most suitable mix. Mixtures of <40% cement appeared brittle and a 1:1 mix was chosen for subsequent experiments. The gypsum was obtained from Louisiana Stone Aggregates, Inc. (Gonzales, La.) in sand-sized particles; the Portland cement was purchased locally. The 1:1 mix (w:w) was prepared on site (Grand Terre, La) on 2 May 1991 using a gas powered cement mixer. Several molds were constructed with plywood as a base and molding as borders. The gypment slurry was poured into the molds to a height of about 1.5 cm and allowed to dry for one week. The hardened gypment was then broken into pieces ranging in size from 3 X 4 to 10 X 10 cm.

1990 FIELD EXPERIMENT

Clamshell, concrete, gravel, and limestone were obtained from New Orleans area materials companies and tested for their ability to catch spat. Clamshell was dredged from Lake Pontchartrain, crushed road bed (mostly concrete) was taken from Louisiana highways, gravel was dredged from the Pearl River, and limestone was quarried in the Tennessee valley. Clamshells were whole single valves, ranging in size from 2-5 cm in diameter. Limestone pieces were roughly rectangular in shape with multiple faces, ranging in size from 1x2-3x6 cm. Chunks of crushed concrete ranged in size from 2x2-5x7 cm. Gravel was rectangular to oval, ranging in size from 1x1-3x5 cm. Open, plastic coated wire mesh trays (50 x 50 cm; 1.27 x 1.54 cm mesh) filled with 5 cm of substrate were placed in random (Hollander and Wolf 1973; 40 replicates for each substrate) subplots in a 0.25 hectare experimental pond at Grand Terre, Louisiana. Water from lower Barataria Bay, which served as a source of larvae, was pumped into the pond. Weekly water parameters monitored included salinity (refractometer; Behrens 1965), dissolved oxygen (Azide Winkler modification; American Public Health Association 1985), temperature (mercury thermometer), and flow rate (volume/time). In addition, one test tray per cultch was set up and monitored weekly for spat set. After 12 weeks, the trays were removed, spat were counted, and the volume of material in each tray was measured by displacement. (Spat volume represented no more than 0.16% of total cultch volume.) The number of spat per subplot was converted to spat per liter and spat per cubic yard of material for statistical and comparative purposes. Oyster settlement as a function of substrate was examined using non-parametric, one-way analysis of variance (NPAR1WAY; SAS Institute 1990).

1991 Field Experiment

Clamshell, Mexican limestone, and 1:1 gypment were tested for their ability to catch spat. Forty (40) replicates for each cultch were utilized for a total of 120 plots. Plots were assigned a cultch using a random number generator (Hollander and Wolf 1973) and arranged in a 12 tray by 10 tray grid on the bottom of a 0.25 hectare pond. The trays (50 X 50 X 6 cm) were constructed of plastic coated heavy wire mesh (1.27 x 1.54 cm), and contained cultch material to a height of 3cm. The pond was filled to a depth of 0.6 m with ambient seawater delivered at a rate of 285 *l* min^{-1} for the duration of the experiment. Separate monitoring trays of the three cultches were checked once a week for spat set. Weekly water parameters monitored included salinity (refractometer; Behrens 1965), dissolved oxygen (Azide Winkler modification; American Public Health Association 1985), temperature (mercury thermometer), and flow rate (volume/time). Plankton samples were taken weekly by slowly pulling a plankton net along the length of the pond (60 m) and later observed for oyster larvae. The cultches were in the water from 1 May 1991 to 9 August 1991, at which time the pond was drained and the number of spat per tray counted. The cultch from each tray was poured into a 40 *l* graduated bucket to determine the wet volume of cultch. Oyster settlement as a function of substrate was examined using NPAR1WAY.

1990 Laboratory Experiment

A replication of the 1990 field experiment was conducted at the Texas A&M oyster hatchery (Galveston, Texas) under more controlled conditions and with a greater concentration of larvae. One liter of each cultch was randomly assigned to each of 21 subplots (Hollander and Wolf 1973), and placed in a 1.8 m diameter fiberglass tank and filled to a depth of 0.3 m with seawater. In contrast to the field experiment, there was no spacing between subplots.

Larvae were cultured and set according to methods of Dupuy et al. (1978). Ripe oysters were induced to spawn by elevating the water temperature to 29-30°C. Spawning occurred in separate containers, after which time sperm and eggs were pooled. After one hour, fertilized eggs were counted and stocked (16 eggs ml^{-1}) into a 250 *l* fiberglass tank. The tank was drained every two days; after the first and second drainings, larval concentrations were reduced to 8 larvae ml^{-1} and 4 larvae ml^{-1}, respectively. The larvae were fed Tahitian strain *Isochrysis galbana* at the rate of 1000 cells $larvae^{-1}$ day^{-1}. Larvae reached the eyed-stage after about 10 days. Eyed larvae were held in refrigerated moist mesh bags to insure vitality prior to setting. Approximately 400,000 larvae were introduced into the setting tank.

Live spat were counted after 2 weeks and data were converted to spat per cm^2 of cultch for comparison. Oyster settlement as a function of substrate was examined using non-parametric, one-way analysis of variance (NPAR1WAY).

1991 Laboratory Experiment

Replication of the 1991 field experiment was performed at the LUMCON wet laboratory in Cocodrie, La., using hatchery reared larvae (Gulf Shellfish Farms of Louisiana). Cultches were randomly placed (Hollander and Wolf 1973) in four 40 X 36 cm plastic trays that were divided into 15 sections each for a total of 60 subplots (20 for each cultch). The bottoms of the trays were lined with plastic screening and the plots were separated by 1 cm x 2 cm wooden molding. The trays were placed in a 2 m diameter circular tank 9 cm off the bottom. Ambient (2 ppt, 26.8°C) and high salinity (32 ppt, 26.8°C) seawater were each pumped in at a rate of 6.0 *l* min^{-1} to a height of 15cm and circulated through the tank; the salinity was maintained at about 15 ppt. Approximately 422,000 larvae were placed in the tank in a ready-to-set eyed stage. The experiment was conducted from 17 July 1991 to 24 July 1991, at which time the

Table 1. Physical measurements of clamshell, Tennessee limestone, gravel, concrete (roadbed) and gypsum used in field and laboratory experiments. (Data from Soniat et al. 1991 and Haywood and Soniat 1992.)

	Clam.	TL	Grav.	Conc.	Gyps.	ML	Gypm.
Liquid volume of one dry liter of material (ml)	385.0	512.9	562.1	489.3	436.7	499.0	426.0
Weight of one dry liter of material (kg)	0.69	1.30	1.67	0.93	1.03	2.18	1.89
Surface area of one dry liter of material (cm^2)	2671	2036	2310	1434	1235	2645	1813

Clam.=Clamshell; TL=Tennessee Limestone; Grav.=Gravel; Conc.=Concrete; Gyps.=Gysum; ML=Mexican Limestone; Gypm.=Gypment.

spat were counted. The wet volume of each subplot was obtained by the method described above for the field experiment and converted to dry volume to yield spat per dry liter of cultch. Oyster settlement as a function of cultch was analyzed using NPAR1WAY.

SOLUBILITY EXPERIMENTS

Solubility experiments on gypment were conducted from 7 May 1991 to 24 July 1991 at the LUMCON Lab. Thirty rocks each were placed in a static tank and in a flow tank. The tanks were 3 m long by 0.6 m wide by 0.3 m deep into which ambient seawater was pumped. The static tank was filled to a depth of 9 cm and the water was changed once every two weeks, whereas water was delivered to the flowing tank at a rate of 7.5 *l* min^{-1}. Initial and final weights were compared using a nonparametric analysis of variance (NPAR1WAY) to determine if a significant loss of material occurred.

FLUME EXPERIMENT

An experiment was performed to determine if the gypsum or cement component of the gypment attracted the oyster larvae. Three cultches were tested: the original gypment composed of a 1:1 (w:w) cement:gypsum mix, a pure cement cultch, and a 1:1 (w:w) cement:sand mix (sandment). The cultches were mixed in plastic containers and poured into each subplot.

Cultches were randomly assigned to 21 subplots (7 each) using a random number generator (Hollander and Wolf 1973). Each subplot was 2.85 cm^2 and was constructed by drilling into a plexiglass sheet that fit flush into a flume at the University of New Orleans. The flume contained 95*l* of 16 ppt synthetic seawater (Instant Ocean) circulating at a rate of 1.14 m min^{-1}. Salinity and temperature were maintained at 16 ppt and 22°C. Approximately 5,000 hatchery reared larvae (Gulf Shellfish Farms of Louisiana) were introduced into the system and allowed to set for 24 hrs. The Plexiglas sheet was removed and spat were counted using a stereomicroscope. Temperature, salinity, and flow rate were measured daily. The experiment was conducted from 24 June 1992 to 27 June 1992.

Results

PHYSICAL PROPERTIES OF CULTCH

Results from physical tests on cultch indicate that clamshell (0.69 kg dry $liter^{-1}$) was the lightest cultch while Mexican limestone (2.18 kg dry $liter^{-1}$) was the heaviest. Gypsum (1434 cm^2 dry $liter^{-1}$) had the least surface area per dry liter of cultch while clamshell (2671 cm^2 dry $liter^{-1}$) had the greatest (Table 1).

Table 2. Oyster set on clamshell, Tennessee limestone, gravel, and concrete in a 1990 field experiment as recorded in August 1990. (Data from Soniat et al. 1991.)

	Clamshell	Limestone	Gravel	Concrete
Mean number of spat per cm^2 of cultch	0.08	0.20	0.02	0.20
Range	0-0.24	0-0.77	0-0.24	0-0.47
C.V.	0.859	0.989	2.492	0.588
Mean number of spat per dry liter of cultch	0.22	0.41	0.05	0.29
Range	0-0.64	0-1.56	0-0.56	0-0.68
C.V.	0.835	0.982	2.304	0.584

1990 FIELD EXPERIMENT

Water temperature in the Grand Terre pond ranged from 26.6° to 32.8°C (May to August, 1990) with a mean of 30.1°C. Water flow ranged from 0 to 208 *l* min^{-1}, whereas salinity ranged from 12 to 17 ppt with a mean value of about 15 ppt. Dissolved oxygen levels ranged from 5.8 to 10.0 ppm. Organisms other than oysters which became sequentially attached to cultch materials included green algae, mussels, barnacles, and bryozoans. There appeared to be more fouling on the concrete and limestone, with minimal fouling on the gravel.

The means (and ranges) of spat per liter were 0.22 (0-0.64) for clamshell, 0.41 (0-1.56) for limestone, 0.29 (0-0.68) for concrete, and 0.05 (0-0.56) for gravel (Table 2). Analysis of variance of spat per liter of cultch data ($P<0.05$) shows that all possible two-way comparisons of cultches were significantly different, except clamshell versus concrete and concrete versus limestone. Limestone had a significantly greater ability to attract spat than did clamshell or gravel. Gravel was found to be significantly less apt to attract spat than each of the other cultches.

1991 FIELD EXPERIMENT

Water temperature in the pond ranged from 22.8 to 32.8°C (mean=29.2°C ±3.0), whereas mean salinity was 11.2ppt ±4.2 with a range of 4 to 17ppt. Dissolved oxygen values varied from 5.5 to 8.3 ppm with a mean of 6.3 ppm ±1.0 and were, on average, 87% of satura-

Table 3. Oyster set on gypment (gypsum and cement), Mexican limestone, or clamshell in a 1991 field experiment. (Data from Haywood and Soniat 1992.)

	Gypment	Limestone	Clamshell
Mean number of spat per cm^2 of cultch	0.93	0.63	0.39
Range	0.34-1.82	0.19-1.70	0.07-0.86
Standard Deviation	0.37	0.31	0.20
Mean number of spat per dry liter of cultch	1.69	1.66	1.04
Range	0.61-3.30	0.50-4.49	0.19-2.31
Standard Deviation	0.67	0.81	0.54

Table 4. Oyster set on clamshell, Tennessee limestone, gravel, and concrete in a 1990 laboratory experiment. (Data from Soniat et al. 1991.)

	Clamshell	Limestone	Gravel	Concrete
Mean number of spat per cm^2 of cultch	0.42	0.45	0.06	0.31
Ranges	0.27-0.82	0.16-0.77	0.01-0.15	0.16-0.58
C.V.	0.311	0.416	0.616	0.358
Mean number of spat per dry liter of cultch	1,114.4	915.9	137.2	461.6
Ranges	724.5-2,178.8	323.0-1,565.5	29.7-350.0	227.2-843.8
C.V.	0.311	0.416	0.617	0.358

tion. The rate of water flow into the pond was 285 l min^{-1} and water depth was maintained at 0.6 m.

Based on spat per liter of cultch, clamshell (mean=1.04, range=0.19-2.31, S.D.=0.54) attracted significantly ($P<0.05$) fewer spat than did limestone (mean=1.66, range=0.50-4.49, S.D.=0.81) or gypment (mean= 1.69, range=0.61-3.30, S.D.=0.67), which were not significantly different from each other. When data are expressed as spat per cm^2 of cultch, clamshell (mean=0.39, range=0.07-0.86, S.D.=0.20) attracted significantly ($P<0.05$) fewer spat than did gypment or limestone, and limestone (mean=0.63, range=0.19-1.70, S.D.= 0.31) attracted a significantly ($P<0.05$) fewer spat per cm^2 than did gypment (mean=0.93, range= 0.34-1.82, S.D.=0.37) (Table 3). Spat were not removed in the determination of wet volume of cultch. (The error due to including spat volume with cultch volume was 0.80% at most.)

1990 LABORATORY EXPERIMENT

Hatchery water temperature was 29.5°C, whereas salinity was 15 ppt. The means (and ranges) of spat per liter for clamshell, limestone, concrete, and gravel were 1114 (725-2179), 916 (323-1566), 462 (227-844), and 137 (30-350), respectively (Table 4). Analysis of variance of spat per liter of cultch ($P<0.05$) for the laboratory experiment shows that there was no significant difference in spatfall between clamshell and limestone. All other possible two-way comparisons were found to be significantly different

Table 5. Oyster set on gypment (gypsum and cement), Mexican limestone, and clamshell from a 1991 laboratory experiment. (Data from Haywood and Soniat 1992.)

	Gypment	Limestone	Clamshell
Mean number of spat per cm^2 of cultch	0.28	0.18	0.18
Range	0.13-0.48	0.07-0.38	0.04-0.46
Standard Deviation	0.09	0.10	0.13
Mean number of spat per dry liter of cultch	498.75	482.13	466.32
Range	239.75-863.54	176.87-1,017.45	104.05-1,230.77
Standard Deviation	155.52	272.86	339.56

Table 6. Oyster spat set per subplot in the flume experiments for gypment (gypsum and cement), sandment (sand and cement), and cement. (Data from Haywood and Soniat 1992.)

	Gypment	Sandment	Cement
Mean number of spat per subplot	21.19	9.90	7.52
Range	4 - 48	2 - 23	1 - 21
Standard Deviation	10.30	4.98	5.32

with limestone and clamshell being significantly greater in spat attracting ability than concrete and gravel.

1991 Laboratory Experiment

Spat per liter data show no significant differences between clamshell (mean=466.3, range=104.1-1230.8, S.D.=339.6), limestone (mean=482.13, range=176.87-1017.45, S.D.=272.86), or gypment (mean=498.75, range=239.75-863.54, S.D.=155.52). When transformed to spat per cm^2, gypment (mean=0.28, range=0.13-0.48, S.D.=0.09) attracted significantly ($P<0.05$) more spat than limestone (mean=0.18, range=0.07-0.38, S.D.=0.10) or clamshell (mean=0.18, range =0.04-0.46, S.D.=0.13). Limestone and clamshell were not significantly different from each other (Table 5).

Solubility Experiments

Seawater salinity ranged from 2 ppt to 8 ppt with a mean and standard deviation of 3.6 ppt ± 2.15; temperature ranged from 23.8°C to 27.4°C with a mean of 26.3°C ± 1.36. No significant difference was found between the initial and final weights of gypment in either the static or flow systems.

Flume Experiment

Spat per subplot data were analyzed using non-parametric ANOVA. Gypment (mean=21.19, range= 4-48, S.D.=10.30) attracted significantly ($P<0.05$) more spat per subplot than did sandment (mean=9.90, range=2-23, S.D.=4.98) or cement (mean=7.52, range=1-21, S.D.=5.32) which were not significantly different from each other (Table 6).

Discussion

Spat set data were analyzed in units of spat per dry liter and spat per square centimeter of cultch. Volume was used since it is easily measured and of practical significance, whereas an area measurement was needed to insure that differences between cultches were not simply due to differences in surface area. In the flume experiment, the manufactured cultches were identical in size and shape and thus data are reported as spat per subplot.

Results from both field and laboratory experiments confirm reports by Chatry et al. (1986) that limestone is a biologically suitable cultch for oysters. A 1.0:1.9 ratio of oyster spat set per liter on clamshell vs. limestone in the 1990 field experiment corresponds closely with the 1.0:2.1 ratio observed by Chatry et al. (1986). Clamshell attracted more spat than roadbed, is lighter and thus is a superior cultch. Furthermore, crushed roadbed is a heavy heterogeneous material of inconsistent quality and may contain hydrocarbon and other pollutants. Gravel attracted relatively few spat in 1990 field and hatchery experiments, indicating that it is not a biologically acceptable alternative. Limestone should prove to be an economically feasible, biologically acceptable, and environmentally benign alternative to clamshell as cultch for oysters. Crushed roadbed and gravel are not viable alternatives.

Both 1991 field and laboratory results suggest that gypment performed as well as or better than clamshell and limestone in attracting spat. Mexican Limestone also performed well by attracting at least as many spat per liter or per cm^2 as did clamshell. The greatest difference among cultches for 1991 tests was found in the field experiment. The spat used in the laboratory experiment were reared in a hatchery and purchased at a ready-to-set stage. When placed in the tank at the laboratory they possibly had less time to be selective in their cultch choice. Therefore, this could have resulted in less variation in spat set numbers. In contrast, larvae used in the field experiment were pumped in from lower Barataria Bay and thus were at natural concentrations. Variation in spat set numbers here was much more evident, perhaps because they had a greater amount of time to be selective.

Despite the low spat set numbers from in the field experiment, significant differences were observed. The poor set is attributable to the excessively low salinity which likely caused a reduction in spawning activity (Butler 1949). Cumulative rainfall was two times higher than the annual norm at the termination of the experiment. The low set is not attributable to low dissolved oxygen. Oxygen concentrations were about 87% of saturation and taken in the morning hours when values are characteristically lower due to the absence of photosynthesis during the night.

Louisiana has a surplus of gypsum to the extent that it is a solid waste problem. The rapid dissolution of raw gypsum makes it impractical for use as cultch. However, we have demonstrated that it can be stabilized with cement and it is as good as or better than clamshell at producing spat. A 1:1 mix of gypsum and cement was used although lesser amounts of cement should be more economical and equally effective. A 6:4 mix of gypsum to cement should prove successful yet a 7:3 mix appeared to be excessively brittle. The flume experiment suggests that it is the gypsum component, and not the cement which is most attractive to the larvae.

It is not known if the larvae are induced to settle in response to the chemical composition of the substrate, substrate texture, or chemicals associated with bacteria on the substrate. Gravel, because its chemical composition is similar to sand, may be interpreted by setting larvae as an unfavorable substrate, or its smooth surface may also be unfavorable (Ray, personal communication). Colonization by bacteria may be important in conditioning the substrate for the subsequent settlement of various invertebrates (Crisp 1967). Minimal setting of other invertebrates on gravel corresponded with minimal setting of oyster larvae. Temporal relationships of other invertebrates attaching to the other cultch materials were similar to those found by previous studies (Shaw 1967; Kennedy 1980). The success of both calcium sulphate (gypsum) and calcium carbonate (limestone) in attracting spat indicates that it is probably the calcium and not necessarily calcium carbonate, that is the important component of a superior cultch.

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Dredged Material as a Substrate for Fisheries Habitat Establishment in Coastal Waters

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Abstract

In a continuing search for environmentally acceptable options for placement of dredged material, US Army Corps of Engineers (USACE) field offices have only recently begun to examine open-water beneficial use applications. Although a comparatively long record of intertidal and upland beneficial uses of dredged material (e.g., marsh creation, emergent "spoil" banks) has been accumulated, open-water options have been given considerably less consideration. This discrepancy can be attributed to several factors, including generally negative perceptions associated with open-water disposal on the part of resource agencies, and perhaps a predisposition for more visible forms of habitat creation on the part of dredging project planners. A trend for diminished availability of upland disposal sites, combined with rising costs for transporting dredged material to deep-water sites, justifies a closer look at inshore open-water alternatives.

Demonstration projects involving the use of dredged material to provide substrate for the establishment of fisheries habitat have been conducted in Maryland waters of Chesapeake Bay (Figure 1). Sponsored by the U.S. Army Engineer Baltimore District, and in coordination with a number of state and federal agencies, dredged material was placed at two sites in 1987 with the objective of testing the feasibility of creating seagrass bed and oyster reef habitat. These habitat types have suffered declines on a wide scale within Chesapeake Bay. Both projects were identified within the framework of a Memorandum of Agreement between the USACE and the National Marine Fisheries Service (NMFS) on the topic of habitat creation and restoration (Pullen and Thayer 1989; Thayer et al. 1989). Since the physical completion of the dredging and disposal operations in 1987, personnel from the Beaufort Laboratory of the NMFS and the US Army Engineer Waterways Experiment Station have monitored the project sites with respect to their viability as fisheries habitat.

The conceptual approaches and preliminary findings for these projects have been reported previously (Earhart et al. 1988; Pullen and Thayer 1989; Thayer et al. 1989). This paper will briefly summarize these concepts and findings, and present the results of completed monitoring efforts at both sites.

Dredged Material as a Substrate for Seagrass Bed Creation

The Baltimore District conducts a large number of small to moderate volume maintenance dredging projects. At Twitch Cove, located along the eastern shore of Smith Island, MD, about 24,000 yd^3 of dredged material were placed to shoal the bottom depth and provide suitable substrate for establishment of a seagrass bed. The seagrass, in turn, would hopefully serve as nursery habitat for juvenile fishes and as a shedding area for blue crabs. The Twitch Cove site was selected because of its proximity to the navigation channel to be dredged, and the absence of submerged aquatic vegetation. Much of the Smith Island shoreline supported mixed stands of eelgrass (*Zostera marina*) and widgeon grass (*Ruppia maritima*). It was hypothesized that the absence of seagrass at the Twitch Cove site was due to deeper than optimal water depths, which resulted in insufficient available light under the prevailing turbid water conditions. By raising the bottom with dredged material, conditions were intended to be brought within appropriate light levels for the seagrasses.

Planting units (PUs) of eelgrass were obtained from a donor site and transplanted to Twitch Cove in a process that was completed in October 1987. PUs consisted of approximately 15 eelgrass shoots fastened to an 8-inch L-shaped wire anchor and implanted according to a methodology described by Fonseca et al. (1982). About 3 acres of bottom were planted with a transplant spacing of 2 ft on center. This required approximately 32,670 eelgrass PUs.

One major concern associated with the project was the stability of dredged material as a substrate upon which the eelgrass could become established. The Twitch Cove shoreline section of Smith Island was an exposed site periodically subject to wind/wave action, particularly during winter storms. The requirement that maintenance dredging material (in this case 60 percent silt, 40 percent sand) be placed in a shallow setting created the possibility that much of the overburden would be dispersed from the site. To address this concern, the District contracted the deployment of Longard tubes to form a barrier to dissipate wave forces. Longard tubes are elongate double-walled fabric capsules that are filled with sediment to form rigid tubes. Three tubes, each with a diameter of about 3.5 ft and length of 330 ft, were placed end-to-end along the bayside perimeter of the site within several weeks following the disposal operation.

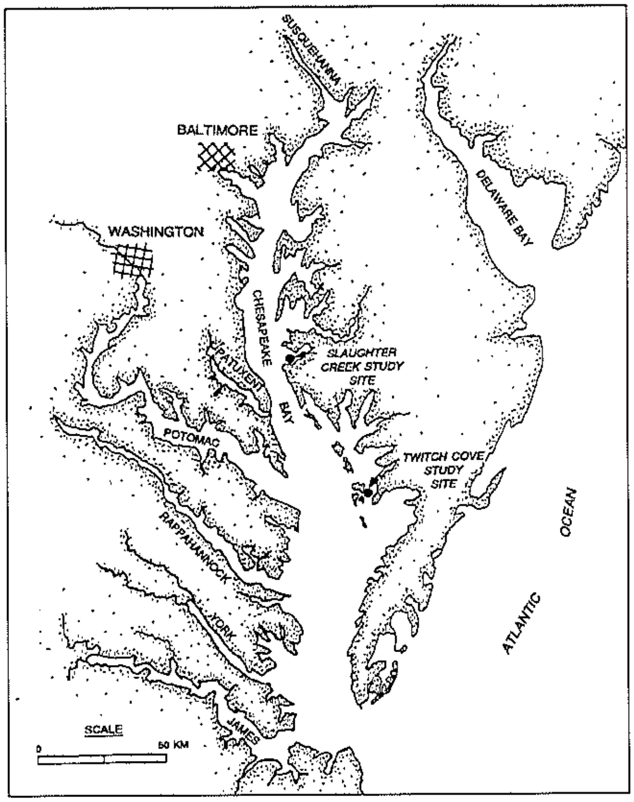

Figure 1. Locations of the study site in the Chesapeake Bay.

Non-quantitative surveys of the transplant site by the transplant contractor during the following summer (June 1988) indicated that PU survival through the winter had been relatively high (approximately 85 percent) in the northern three quarters of the plot, and low (approximately 10 percent) in the remainder. To obtain a quantitative measure of seagrass survival at the site, NMFS personnel conducted surveys in July 1988, June 1989, and June 1990. A systematic point-dot grid survey technique was used. A 140 m X 90 m grid was erected over the transplant plot with moveable lines to assist divers in the survey. Lines were run at 10 m intervals to create a grid with a total of 150 intersection points. Seagrass PUs were examined within a 1 m^2 quadrat at each point in the grid. Presence/absence of PUs or other seagrasses was recorded. In addition, each quadrat was subdivided into 16 equal 0.25 m X 0.25 m subsections. These subsections were used to estimate plant coverage at each point (i.e. the number of subsections with seagrass expressed as a percentage).

In July 1988, the NMFS survey yielded 33 eelgrass contacts at the 150 grid points (Figure 2). Extrapolation of the 150 m^2 sampled area to the 12,541.5 m^2 total transplant plot gives an estimate of 2,822 m^2 (22 percent) site coverage after one year. This represents roughly 0.69 acres of seagrass habitat. At those grid points at which eelgrass was encountered, 36.4 percent of the quadrat subsections contained eelgrass shoots. In theory, had a similar survey been conducted soon after the transplantation process had been completed, the entire site would have shown a 25 percent coverage. This assumes that each 1 m^2 quadrat would have contained four PUs, the maximum number that could be enclosed based on 2-foot planting centers. Therefore, the survey data indicate that a substantial portion of the initial transplants had been lost within the first year, but also that the PUs in the central portion of the plot had undergone some detectable growth. Field personnel noted that a number of the PUs had coalesced such that individual PUs could not be differentiated. In fact, spread of rhizomes from these PUs precluded direct counts of surviving PUs and necessitated the point-dot sampling strategy.

The site was visited again in June 1989. The survey was performed in a manner identical to that of the previous year. A total of 31 eelgrass contacts was obtained (Figure 3), which equates

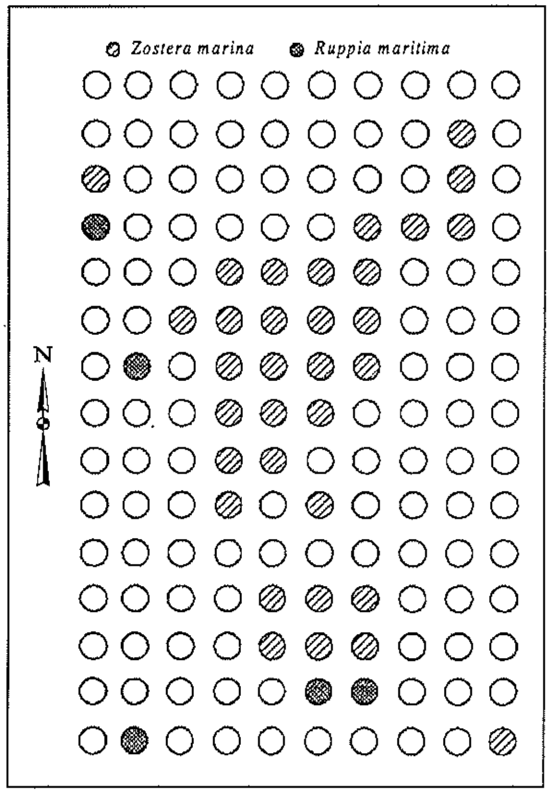

***Figure 2.** Sampling grid (on 10m centers) at Twitch Cove seagrass transplant site during 1988. Open circles represent sampling points at which no seafrass was detected within a 1-meter² quadrat. Occurrences of transplanted* Zostera marina *and naturally recruited* Ruppia maritima *are indicated.*

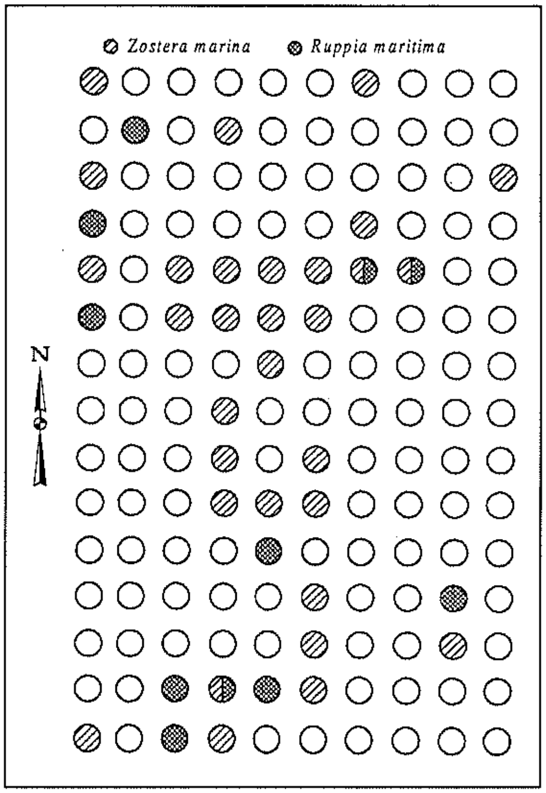

***Figure 3.** Sampling grid (on 10m centers) at Twitch Cove seagrass transplant site during 1989. Open circles represent sampling points at which no seafrass was detected within a 1-meter² quadrat. Occurrences of transplanted* Zostera marina *and naturally recruited* Ruppia maritima *are indicated.*

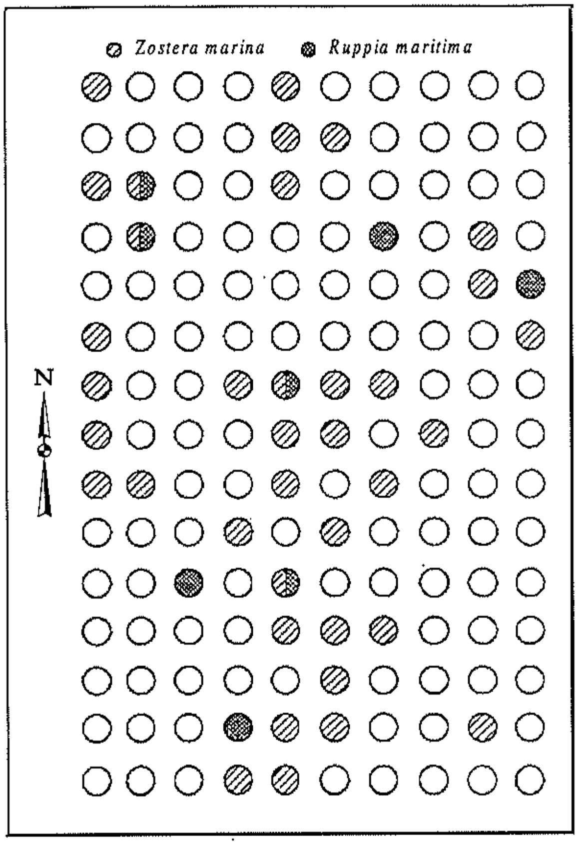

Figure 4. Sampling grid (on 10m centers) at Twitch Cove seagrass transplant site during 1990. Open circles represent sampling points at which no seafrass was detected within a 1-meter² quadrat. Occurrences of transplanted Zostera marina *and naturally recruited* Ruppia maritima *are indicated.*

to 2,650.5 m^2 of seagrass habitat within the original plot (20.6 percent occurrence within the site). The change in this parameter between 1988 and 1989 was not statistically significant. Based on the areal dispersion of quadrats in which eelgrass shoots occurred, a pattern of survival generally confined to the central portion of the plot persisted. In terms of small-scale coverage, however, the percentage of quadrat subsections with eelgrass shoots at grid with eelgrass had diminished to 25 percent. This coverage was approximately equal to that provided by the original planting.

A final survey was conducted at the site in June 1990. This survey yielded 37 seagrass contacts (Figure 4), which equates to 3,137.6 m^2 of seagrass habitat within the original plot (24.7 percent occurrence within the site). Small-scale coverage, however, declined further to 21.1 percent. The differences between the 1989 and 1990 survey results, both with respect to the observed increase in overall seagrass coverage and decrease in small-scale coverage, may be attributable to inherent sampling variability rather than actual trends.

Several factors may account for the observed reduction in small-scale coverage between 1988 and 1990. For example, the 1989 spring-early summer period was characterized by low salinities and high river discharges. These conditions may have contributed to generally higher ambient turbidities at the study site and resulted in lower growth rates or even some degree of mortality. Alternatively, some unknown deficiency in substrate quality provided by the dredged material cannot be ruled out at this time. However, the results are encouraging in several respects. The overall survival of eelgrass in the central portion of the plot for two years after transplanting somewhat negates the fear that storms would rapidly eradicate plants from the site, either by direct damage or by transporting the dredged material away from the site. With the passage of time the overburden can be expected to consolidate and further stabilize. The fact that survival was largely limited to the center of the plot may reflect a response of the PUs to adequate elevation of the pre-existing bottom only in that area. In fact, the volume of dredged material placed at the site (approximately 24,400 yd^3) may have been insufficient to optimally raise the bottom. The distribution of surviving seagrass may also reflect the limits of stable substrate within the site, perhaps defined by the degree of protection from erosion derived from the presence of the Longard tubes.

An additional note of encouragement for the Twitch Cove project is found in the recruitment of *Ruppia maritima* to the transplant site. As seen in Figures 2-4, widgeon grass was detected in 5 quadrat samples in 1988, 11 quadrats in 1989, and 8 quadrats in 1990. In the long term, widgeon grass may become the dominant seagrass at the site or achieve some balance with eelgrass resembling the mixed nature of seagrass beds in surrounding areas.

Dredged Material as a Substrate for Oyster Reef Creation

At Slaughter Creek (Figure 5), which is situated in Dorchester County, MD, approximately 14,000 yd^3 of dredged material was placed in an area historically known to have been a productive oyster bar, but which no longer provided substrate suitable for settlement of oyster spat. The dredged material (60 percent fine sand and 40 percent silt) was deposited to form a 2.1-acre mound with a designed overburden thickness of approximately 3 ft (90 cm). Following disposal, 2,256 yd^3 of oyster shell cultch was barged to the site and washed off the barges by means of high-pressure water hoses. A designed 8-inch (20 cm) thick cap of cultch over the dredged material was intended to provide substrate for the attachment of naturally recruited oyster spat. The capping operation was completed in June 1987.

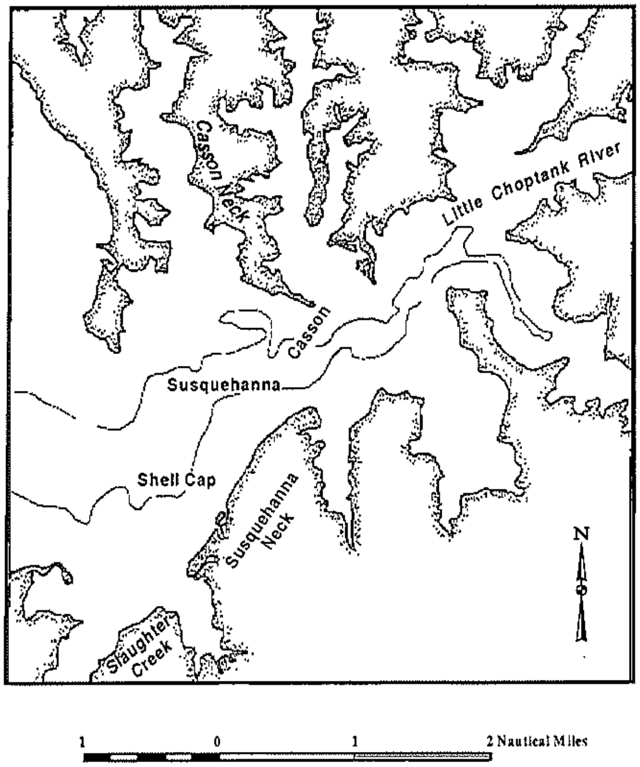

Figure 5. Locations of the Slaughter Creek shell cap experimental oyster bar site and the Susquehanna and Casson natural oyster bar sites. The 10-ft. depth contour is given.

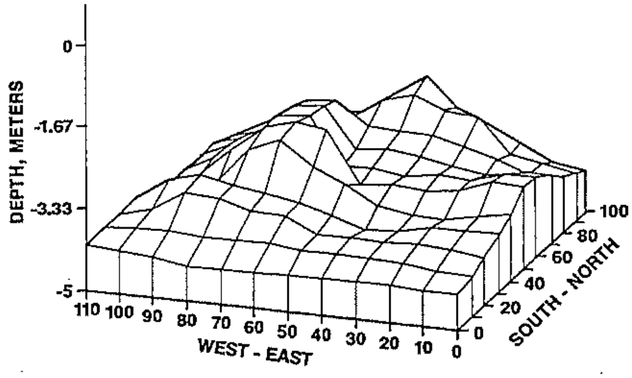

Figure 6. Post-construction bathymetry at the Slaughter Creek experimental oyster bar as determined by a point survey on 10m centers in 1998.

As was the case at Twitch Cove, long-term stability of the dredged material was a major concern for the success of the Slaughter Creek project. In the absence of prior studies of this type, the amount of subsidence of oyster cultch into the maintenance material was unpredictable. Too much subsidence or the prevalence of silty sediment on the surface of the cap might effectively remove the substrate from use by settling oysters. A side-scan sonar survey of the site was performed in 1987 to evaluate the coverage of the shell cap. Survey results indicated that the cultch layer was relatively complete, but that the central portion of the mound had received a thinner layer than the perimeter areas. As part of the Slaughter Creek project monitoring efforts, NMFS personnel mapped the overall bathymetry of the site (Figure 6) and measured cultch thickness at randomly selected points. These measurements, taken in 1988 and 1989, indicated that the shell cap had maintained its integrity over that span of time. If subsidence of the shell cap into the dredged material overburden is occurring, the rate of subsidence is apparently not rapid.

In November 1987, the Maryland Department of Natural Resources conducted a survey of spat settlement at Slaughter Creek and other oyster bars in the vicinity. Slaughter Creek yielded a count of 62 spat per bushel, which fell within the 39 to 341 spat per bushel range measured at the natural bars (Glenn Earhart, USACOE, pers. comm.). Density of newly

Table 1. Summary data for spat and oyster size and survival at the Slaughter Creek experimental shell cap and Casson and Susquehanna natural oyster bar sites in 1988, 1989, and 1990. Cultch size measured as height (umbo to lip) in mm of unfragmented shell samples from each site.

	Slaughter Creek Experimental Site			Casson Natural Bar			Susquehanna Natural Bar		
	1988	1989	1990	1988	1989	1990	1988	1989	1990
No. Shells in Sample	632	1244	1112	443	410	220	435	334	551
Mean Cultch Size (mm)	47.2	44.8	48.7	67.5	65.1	70.5	79.2	72.6	83.8
Total Cultch Weight (kg)	6.500	11.930	15.303	9.983	15.708	4.900	12.567	10.50	12.466
No. Spat in Sample	41	1	178	52	4	23	60	1	61
Mean Spat Size (mm)	16.5	16.9	14.4	15.1	16.5	15.6	14.5	5.6	16.0
Spat/100 Shells	6.71	0.09	16.0	11.34	0.86	10.46	13.70	0.27	11.07
Spat/kg Cultch	8.00	0.08	11.63	5.2	0.25	4.69	4.78	0.10	4.89
No. Sub-market Oysters in Sample	29	81	88	28	52	11	16	22	17
Mean Sub-market Oyster Size (mm)	37.8	41.7	53.3	46.6	57.2	55.	53.1	49.2	47.7
Sub-market Oysters/100 Shells	5.97	6.58	7.91	6.0	12.72	5.00	3.65	6.51	3.08
Sub-market Oysters/kg Cultch	4.46	6.79	5.75	2.8	3.31	2.24	1.27	2.09	1.36
No. Market Oysters in Sample	----	----	2	12	2	2	6	10	3
Mean Market Oyster Size (mm)	----	----	89.2	87.8	86.4	85.6	90.9	87.9	80.4
Market Oysters/100 Shells	----	----	0.18	2.79	6.6	0.90	1.50	2.88	0.55
Market Oysters/kg Cultc	----	----	0.13	1.20	1.78	0.41	0.48	0.95	0.24

settled spat is known to vary greatly on an annual basis and among sites in the same general area. Krantz and Meritt (1977) reported that counts of spat per bushel of natural shell cultch ranged from 0.6 to 72 in the Maryland portion of Chesapeake Bay. A "typical" count was estimated to be 60 spat per bushel. Numerous studies have established the wide degree of natural variation in spat counts (e.g., Andrews 1949, 1955; Loosanoff and Nomejko 1951; Carriker 1959; Webster and Shaw 1968; Kennedy 1980). These references listed counts within the range from 0.35 to 500 spat per bushel of shell.

To quantitatively assess the extent of spat settlement at Slaughter Creek as compared to two other oyster bars (Casson and Susquehanna) in the vicinity, NMFS personnel visited the site in November 1988, October 1989, and late September 1990. A grid was constructed in a manner similar to that described above for Twitch Cove. The Slaughter Creek grid consisted of 121 intersection points based on 10 m line spacings. Ten sample stations were then randomly selected from the 121 possible sampling points. Divers retrieved samples of surface shells in labeled bags and maintained them on ice for later analyses. At Casson and Susquehanna bars a 50-m weighted line was placed along the bottom. Ten distances were selected at random along the line, as were perpendicular distances of up to 5 m either left or right from the line. Samples of surface shells were then collected at the ten random locations. In the laboratory all live oysters were counted and measured. Spat were defined as all oysters less than 25 mm from umbo to lip. Juvenile or sub-market size oysters were counted as all oysters equal to or greater than 25 mm and less than 76 mm, and market size oysters were those equal to or larger than 76 mm.

Data on cultch characteristics and spat and oyster survival are summarized in Table 1 and Figures 7-9. Cultch size, measured as the height (umbo to lip) of unfragmented shells, was significantly smaller at the experimental capping site than at the two natural bars. Mean cultch size was approximately 20 mm smaller at Slaughter Creek than at Casson natural bar, and 30 mm smaller than at Susquehanna natural bar. This difference in mean cultch shell size, however, did not appear to deter attachment of spat. Although counts of spat per 100 cultch shells were lower for the Slaughter Creek samples, the significant cultch size differential represented a smaller available surface area for potential attachment of spat. Spat counts per standardized weight of cultch may be a more accurate measure of available surface area. In terms of spat per kg of surface cultch, the experimental shell cap yielded comparatively higher spat densities than either natural bar in 1988 and 1990, and comparable densities in 1989 (Figure 7).

A similar pattern for occurrence of sub-market oysters was observed, in which counts based on samples of 100 shells indicated relatively equal densities across sites and years (with the exceptionally high count for Casson in 1989). If the surface area effect is taken into account, however, the standardized counts based on sub-market oysters per kg of cultch suggest that the comparatively high spat densities at the experimental site were maintained as sub-market size was reached (Figure 8).

Samples taken at the experimental site contained no oysters of market size (i.e. >75 mm) in either 1988 or 1989, whereas counts at the natural bars ranged between 0.48 and 1.78 per kg of cultch. The absence of market oysters at Slaughter Creek during these surveys probably reflected an insufficient passage of time for growth between the natural spat set in 1987 and sampling in October 1989 (Figure 9). Times of oyster spawning and larval settlement vary among locations. In Chesapeake Bay, Beaven

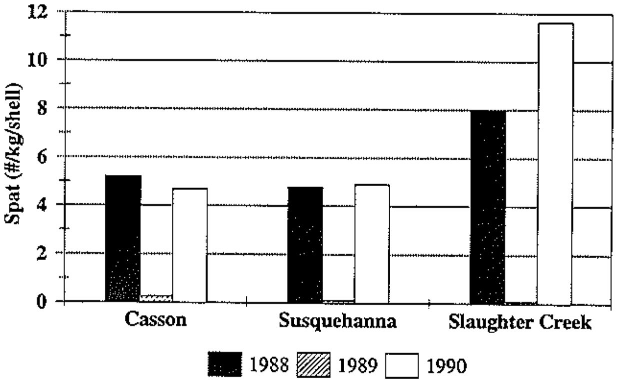

Figure 7. Comparative densities of live oyster spat at the Casson and Susquehanna natural bars and Slaughter Creek experimental site in 1988, 1989, and 1990.

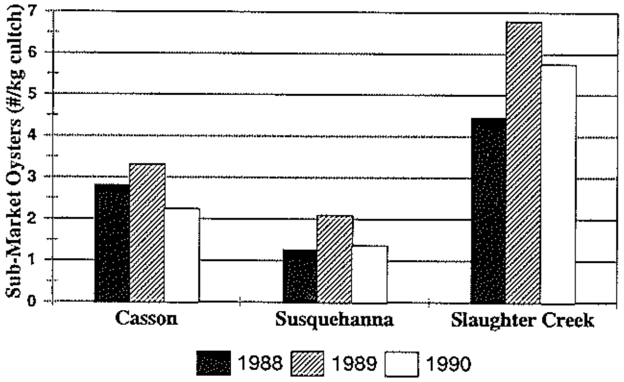

Figure 8. Comparative densities of juvenile oysters at the Casson and Susquehanna natural bars and Slaughter Creek experimental site in 1988, 1989, and 1990.

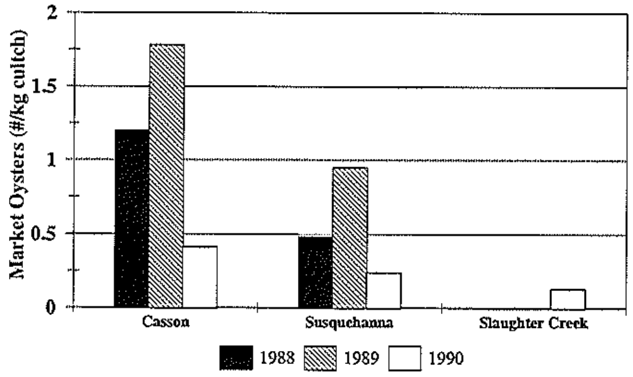

Figure 9. Comparative densities of adult (legal harvest size >3 inches) oysters at the Casson and Susquehanna natural bars and Slaughter Creek experimental site in 1988, 1989, and 1990.

(1955) found that spawning occurred from May to September, whereas setting occurred from May to October with a two-week peak, usually in July. Andrews (1951) noted that peak setting in open-bay bars may occur in July, August, or September. Therefore creation of the shell cap at Slaughter Creek should have occurred early enough in 1987 to be exposed to natural recruitment that year. The 1988 spat counts and size estimates support the contention that initial colonization of the experimental site occurred in 1987.

Growth rates appear to offer a reasonable explanation for observed oyster size classes within the samples. According to Carter (1986), oysters in Maryland waters become legally harvestable at three inches (76 mm) height, when they are about three years old. Stanley and Sellers (1986) reported that the minimum marketable size of 90 mm is reached in two to five years in mid-Atlantic oyster populations. Although absolute sample size was small (2 market oysters within the 1990 Slaughter Creek sample), the numbers of market oysters among the three sites did not differ statistically. Survival beyond the sub-market stage at Slaughter Creek appears to track with rates observed at the natural bars sampled.

Natural spat mortality is generally high. For example, Webster and Shaw (1968) determined that survival through the first season ranged from 1 to 27 percent in bars of the Choptank River, Maryland. In the James River, Virginia, Andrews (1949) measured survival at 4.5 percent after one season. However, mortality decreases substantially after the first year of growth. Subsequent monitoring of the Slaughter Creek site might be expected to reveal the attainment of market size by those sub-market oysters observed during the second and third year surveys. Mortality due to factors such as MSX or Dermo disease infections, water quality conditions, or substrate characteristics appeared to effect oyster populations equally at all three sites.

Conclusions

Demonstration projects were undertaken in Chesapeake Bay to examine the feasibility of establishing seagrass and oyster reef habitat on dredged material substrate. Based on the results of three years of monitoring, each project can be rated as a qualified success. As can be expected with demonstration projects, much was learned retrospectively. At Twitch Cove, it is possible that the dredged material overburden raised the existing bottom only marginally within the zone of ambient light requirements of the transplanted eelgrass. The observed distribution of surviving eelgrass transplants at the site suggests that a correlation may exist between percent survival and water depth and/or substrate stability. A recommendation that attention be given to ensuring adequate lift of the bottom in future projects could be handled by coordinating post-disposal bathymetry surveys with transplanting contractors. In this manner, effort would be focused on placing planting units only on appropriate sections of the dredged material overburden. At Twitch Cove, maintenance material from the next dredging cycle could potentially be used to correct problem areas of the initial transplanting effort. Additional study should be directed at the relationships between dredged material characteristics and small-scale sediment transport processes within the transplanted seagrass bed. In addition to the depth factor, sediment erosion/accretion and nutrient availability are likely to be important determinants of transplant success.

Concerns that dredged material overburdens would be too unstable at shallow water sites to support viable fisheries habitat seem unfounded based on the results of these studies. With adequate precautions, such as the deployment of Longard tubes to dissipate wave energies, dredged material can be used to shoal water depths for a variety of purposes. Based on experience gained at Slaughter Creek, concerns that the oyster shell cap would subside into the "soft" dredged material overburden also appear to be unsubstantiated. The Slaughter Creek site project will provide an opportunity to monitor the persistence of an intact shell cap over a dredged material overburden on a long-term basis.

Although the short-term limitation of sampling methodology employed at Slaughter Creek leaves room for speculation in interpretation of the monitoring data, spat settlement and survival, and growth and survival through submarket size categories at the experimental site are encouraging. Further monitoring is required to document continued growth of oysters into harvestable size categories at Slaughter Creek. At Twitch Cove, it would be reasonable to pursue attempts at creating a healthy seagrass bed. The next dredging cycle would provide an opportunity to incorporate information gained from monitoring efforts to date. For example, switching from eelgrass to widgeon grass as a transplant species deserves consideration. Once a seagrass bed has been established at the site, follow-up monitoring on use of the created habitat by juvenile fishes and crabs will be required. Comprehensive documentation of progressive development of each demonstration site into viable fisheries habitat can only be obtained through long-term studies.

With appropriate consideration given to key factors governing the probability of successful habitat creation (e.g., site selection, dredged material sediment characteristics, designed and achieved overburden thicknesses, seagrass transplant species selection), the outlook for beneficial use projects of the type described herein is positive. Cooperative efforts with input from the cumulative expertise represented by all interested federal and state agencies and parties should continue so that where practicable, dredged material can be used to achieve true resource benefits.

Acknowledgments

Appreciation is extended to Glenn Earhart of the U.S. Army Engineer Baltimore District, who conceived and implemented the beneficial use demonstration projects described herein, and to Bob Blama, who has assisted the progress of these studies to completion. Thanks are also due to Dr. Gordon Thayer and Mark Fonseca of the National Marine Fisheries Service Beaufort Laboratory, who led the monitoring activities at both field sites.

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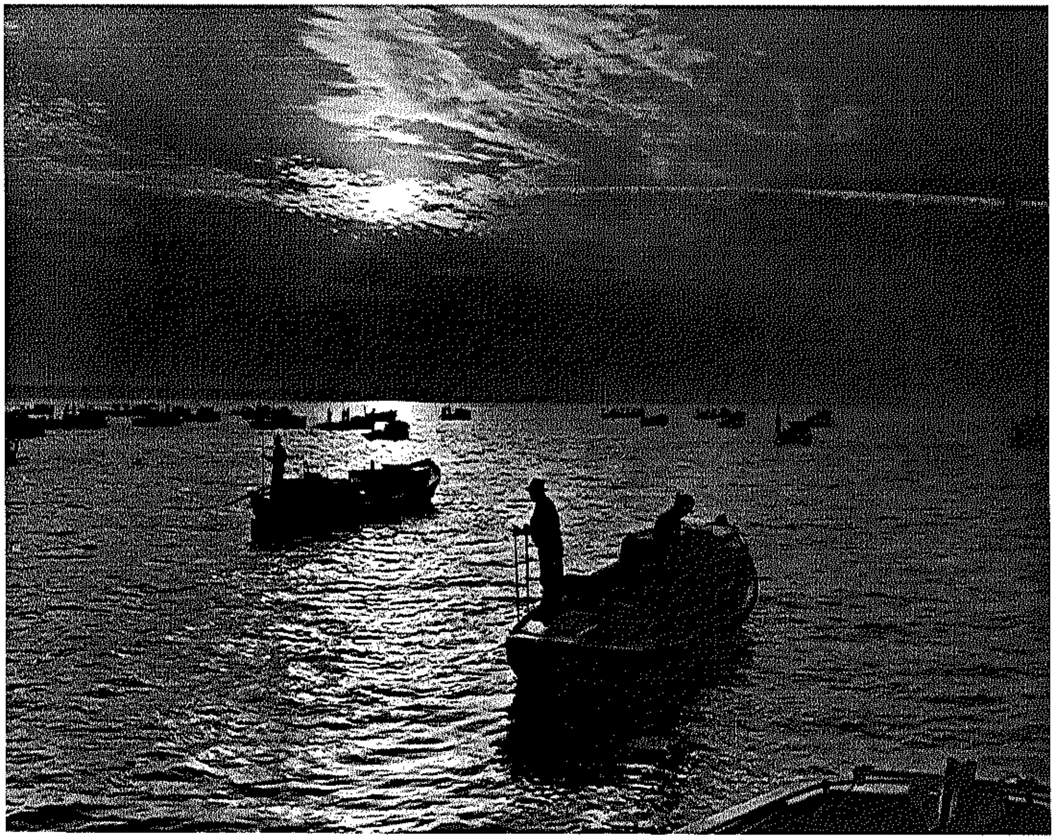
Part V

Management Options And Economic Considerations



Managing Around Oyster Diseases in Maryland and Maryland Oyster Roundtable Strategies

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Abstract

In response to declines in harvest and the widespread distribution of *Perkinsus marinus* (Dermo) the state of Maryland has engaged in the movement of oyster seed from moderate to low salinity areas. In 1993 an "Oyster Roundtable" was convened to develop recommendations for reviving oyster populations in the Maryland portion of Chesapeake Bay. Action items were developed concerning five general issues of oyster production and/or ecology: 1) management of diseases affecting oyster populations, 2) habitat and water quality, 3) production/management of the fishery, 4) institutional barriers, 5) funding. The concept of Oyster Recovery Areas (ORAs) was established. A review of the individual elements of the plan indicates that further consideration needs to be given to balancing issues related to spread of disease and persistence of reefs in low salinity areas.

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[1] This article represents the author's interpretation of the Maryland Oyster Roundtable Action Plan and does not represent the views or interpretations of the group as a whole or any of its members except KTP.

Introduction

Perkinsus marinus (Dermo) has been detected in all Maryland oyster bars surveyed in the last few years. The Department of Natural Resources Fisheries Division predicts that most of the one-year old oysters in the Maryland portion of the Bay will die during their second summer - just before reaching market size - from *Perkinsus marinus* infections. In order to prevent the total collapse of the fishery, the State initiated a seed movement program which transplants one year old oysters from moderate salinity areas, where they will be more likely to succumb to infections, to more brackish waters where a greater percentage will survive to market size and be harvested (Christmas and Jordan, 1988, Abbe, 1988, Krantz, 1992, Smith and Jordan, 1993). This program is responsible for most of the current production in the State.

A review of the literature, especially the work of Andrews and Ray (1988), reveals that specific management strategies dealing with *Perkinsus* have been developed and employed in many areas. Some strategies have been relatively successful, others have not, and success has been variable from region to region. The first and foremost recommended management practice is to utilize disease-free stocks. While the definition of "disease-free" remains controversial, the concept is clear: seed oysters with undetectable *P. marinus* infections are much more productive than oysters with even very light infections. Also recommended in the literature is the early harvest of infected beds followed by fallowing for a year to limit mortality and distribution of the disease in subsequent plantings. Finally, intensive monitoring of beds for disease is required to allow for specific management practices, such as early harvest, to be initiated at the appropriate times in the disease process.

The State seed transplantation program in Maryland is not based on the recommendations summarized above but rather on the observations that seed oysters infected with *P. marinus* survive much better in low salinity areas (<10ppt, Ragone and Burreson, 1990). The political realities of the management community require the State to provide harvestable oysters to maintain the public oyster industry. However, the practice, which usually transplants large amounts of diseased seed, brings many parastites into regions where they may not normally occur through natural transmission. In addition, this large-scale transfer is probably inadvertantly selecting for low salinity tolerant protozoans; indeed, low salinity tolerant *P. marinus* cultures have been produced in the laboratory. These strains have a much higher survival rate in low salinity than parasites raised at higher salinities (Burreson et al., 1994) . It is not yet known whether these low salinity parasites are as virulent as the higher salinity protozoans, but it would certainly seem wise to avoid accelerating the low salinity selection process.

Some intensive oyster culture ventures in Maryland have attempted to put the management recommendations of Andrews and Ray (1988) into practice (Paynter et al., 1992). The production of seed in the hatchery followed by nursery culture in low salinity areas has produced hundreds of thousands of seed oysters which have no detectable infections. Most of these oysters are annually transferred to higher salinities during their second year and reach market size before they succumb to *P. marinus* infections. Therefore, it would seem that previously established management strategies may be productive in Maryland's portion of Chesapeake Bay.

In 1993 the State of Maryland convened a group of 40 individuals who represented many groups concerned about the decline of the oyster resource in the Maryland portion of Chesapeake Bay. The members of this "roundtable" group consisted of fishermen, aquaculturists, environmentalists, legislators, academic scientists, and senior staff from the Maryland Departments of Natural Resources, Agriculture, Environment, and Governor's office. The goal of this roundtable was to develop sound, broadly-supported recommendations for reviving oyster populations in the Bay. Specific objectives were developed by the Roundtable to guide ensuing discussions and recommended actions. They included maximizing and enhancing the ecological benefits of oyster populations in the Bay, maximizing and enhancing the economic benefits derived from harvesting the public and private oyster grounds, and maximizing the ability of government to respond effectively to the magnitude of the problem. It was agreed that all recommendations of the Roundtable be made by concensus, therefore all action items had to be supported unanimously.

The Roundtable developed action items concerning five general issues of oyster production or ecology: 1) diseases affecting oyster populations, 2) habitat and water quality, 3) production/management, 4) institutional barriers, 5) funding. We also developed the concept of Oyster Recovery Areas (ORAs). These ORAs will be regions of the Bay in which shellfish harvesting and planting are restricted and carefully controlled. Within these areas two zones will be established: Zones A and B. Within Zone A all shellfish harvesting will be prohibited and only seed which has zero prevalence of *H. nelsoni* (MSX) and *P. marinus* (Dermo) will be allowed to be planted. In Zone B harvesting will be allowed but, as in Zone A, only parasite-free seed will be allowed to be planted. A Zone C was also defined but contained no restrictions on harvest or seed planting.

The strategies involved in developing these ORAs were varied but drawn from a few fundamental principles. The academic scientists argued strongly that the annual transplantation of *Perkinsus* infected seed into the upper tributaries of the Bay by the State repletion program was detrimental to the long-term recovery of oyster populations. In addition, environmental interests expressed the need for establishing oyster reef sanctuaries for both broodstock and ecological benefits. There was also significant interest in providing the opportunity for interested parties (aquaculturists and fishermen) to experiment with various forms of intensive oyster culture. Finally, there was an acute need for set-aside areas where research could be conducted without the uncontrolled influence of private and state activities including harvesting and seed planting. The establishment of the ORAs served many of these strategies and will be used as a vehicle for further resource rehabilitation and research.

The establishment of permanent or semi-permanent oyster reef communities must incorporate sensible disease management practices including such destructive methods as total harvest to remove protozoan infestations. Only using sound scientifically-based management practices can the Chesapeake Bay oyster population be reestablished and maintained.

Current Management

Current oyster management practices in Maryland are essentially directed towards the fishery rather than the resource. While the cull laws and gear restrictions which protect the size and number of oysters harvested, the bulk of the management activity has been dedicated to seed transplantation to augment the number of naturally occurring oysters in low salinity, low disease areas. Since the regions in Maryland's portion of the Chesapeake Bay which usually have heavy recruitment (ie. a good spatfall) are typically areas where Dermo prevalence and intensity is high, left alone most of each year's spatfall will succumb to the disease before attaining market size (Andrews, 1988). However, if the recruits are moved to lower salinities following their first winter, a much higher percentage of them reach market size. This seed transplanting or "repletion" program is generally thought to provide the bulk of each year's harvest.

While the repletion program has clearly contributed to the annual harvest and maintained, to some degree, the waterman's way of life, there may be several important drawbacks to the program. First and foremost, the current program, under which hundreds of thousands of seed oysters infected with dermo are moved to lower salinity areas sometimes many miles away, clearly transports millions of protozoans into low salinity areas where they would not normally have drifted or been carried after their hosts succumbed. Unfortunately, unlike MSX which is apparently killed by low salinity (Haskin and Ford, 1990; Ford, 1992), Dermo is not and can in fact continue to proliferate wihtin it's host even a low salinity (Ragone-Calvo and Burreson, 1994). Although the parasite does indeed remain within the oyster at low salinity, it's physiological impact on the host is apparently reduced allowing the oyster to reach market size and be harvested (Ragone and Burreson, 1990; Paynter and Burreson, 1991; Smith and Jordan, 1993).

As long as the bulk of the oysters transplanted remained alive and were removed by harvest, there would be no net contribution to the parasite burden in these areas. However, survival of these seed oysters to market size has been estimated at less than 50% (C. Judy, Maryland DNR, personal communication) indicating that a significant number of parasites are released into the ecosystem where they can infect other organisms. Furthermore, these infections would not be limited to oysters but would occur in other bivalves as well including *Macoma baltica* and the soft clam, *Mya arenaria* . Even if infections in other bivalves are not pathogenic, they represent a potentially large reservior of parasites which will serve to maintain infections in the local oyster populations.

Clearly, the transportation of large numbers of parasites into low salinity areas is not a productive activity. The value of the increased production of harvestable oysters should be weighed against the potential detrimental effects on the oyster populations in the long-term. Unfortunately, laboratory studies indicate that the parasite which causes dermo can regulate it's cell volume (O'Farrell, 1995). This means that it can control the effects of salinity change and could suggest that the parasite may become more virulent in lower salinities given enough time and selective pressure. A parasite which is more virulent in lower salinity waters would be devastating to the current industry in Maryland since the industry depends upon the survival of infected oysters in low salinity.

Growth and virulence data in floating tray studies suggest that production of seed in low salinity areas can result in relatively large oyster (1.5 to 2.5 inches) free from dermo infection (Paynter and Burreson, 1992; Paynter et al., 1992). When these seed are moved into higher salinity areas, their growth increases greatly and they can reach well beyond market size before MSX or Dermo kill them. Unfortunately, natural spatfall is rare in low salinity areas and in order to produce significant quantities of seed in low salinity areas, naturally caught seed would have to be relayed much earlier, probably within 8 to 10 weeks after settlement, to remove the seed before it became infected. This may not be feasible due to large mortalities in the young spat caused by transportation and handling. However, the concept has not yet been tested.

In summary, State activities associated with management of oysters in Maryland is focused on producing market size oysters for watermen to harvest. This involves the transportation of spat from southern regions of the Chesapeake where disease prevalences are high to northern, lower salinity areas where the spat will survive to market size. There is currently little State support for intensive ostraculture and many laws and regulations suppress it's development.

Maryland Oyster Roundtable Action Plan

The Maryland Oyster Roundtable (MOR) Action Plan outlines a variety of recommended actions that should aid in the rehabilitation of the oyster populations. The action items will be reviewed and discussed in the order that they are presented in the MOR Action Plan document.

I. DISEASES

1) Monitor prevalence and intensity of MSX and Dermo in the Bay.

This action recomends a continuation of the annual disease survey conducted in October by the Maryland Department of Natural Resources (DNR) but also suggests that it continue on an enhanced level which will provide more information about disease intensities, prevalences, oyster sizes, and additional data analyses. The Cooperative Oxford Laboratory in Oxford, Maryland, has already begun this process by integrating the data with a computer-based geographic information system (GIS) which will allow greater access to not only the oyster disease data, but to relevant water quality data as well (Smith and Jordan, 1993).

2) **DNR management programs should minimize the possibility of spreading MSX and Dermo through the repletion program.**

Analysis of the seed transplanted from southern Maryland waters to low salinity upper Chesapeake Bay waters has shown that the oysters are typically infected with Dermo and many times with MSX as well. Infections of MSX are not considered to be a problem since MSX infections disappear in oysters transferred to salinities less than 10 ppt (Haskin and Ford, 1990; Ford, 1992) . However, Dermo has spread rapidly into the low salinity regions of the Bay in the last 10 years and recent laboratory investigations have shown that the protozoan which causes Dermo is quite capable of adapting to low salinities (Goggin et al., 1990; Ragone-Calvo, et al, 1994; O'Farrell, 1995). This makes *Perkinsus* a much more dangerous protozoan in terms of potential increases in low salnity oyster mortalities.

In order slow the rapid intensification of Dermo in low salinity areas, any management techniques which would serve to lower the prevalence and intensity of Dermo infections in the transferred seed would be valuable. Currently, the seed is moved in the Spring after the year it set which means that the seed is usually around 25 mm long and has likely acquired *Perkinsus* infections during the previous Fall. If the seed could be effectively moved prior to infection, then the State could accomplish it's goals of enhancing oyster productivity without adding to the parasite burden in low salinity areas.

3) **DNR and the University of Maryland, in conjunction with other regional especially neighboring State and Federal agancies, should implement a coordinated, multi-year, stabily funded, goal-oriented research program aimed at specific methods to identify, understand, prevent and control MSX and Dermo and other potential pathogens.**

This recommendation has obvious value in that it will provide information necessary for improving the survival and viability of the oysters in Chesapeake Bay. It will also enable managers to make better decisions with regard to the management of infected populations. The major thrust of this action item was to illustrate the need for stabily-funded, long-term research programs as compared to annually renewed, highly competitive, uncoordinated programs.

4) **Establish criteria and rationale for certifying oysters, including seed oysters, as having zero prevalence and intensity of MSX and Dermo (as well as any other pathogen which is found to significantly impact the oyster) at the time of planting as determined by current technology.**

This action item was established to enable a program of seed "certification" so that projects and programs in which "disease-free" seed are required will have a consistent benchmark and the State can establish an official measure of disease-free quality.

5) **Conduct an environmental impact assessment of the introduction of non-native species of oysters as a contingency.**

Recent proposals to introduce *Crassostrea gigas* into Chesapeake Bay have sparked much controversy regarding the importation of exotic species and the dangers inherent to those introductions (Burreson et al., 1990). The members of the Roundtable recognized the value of determining the resistance (or lack thereof) of other oyster species to MSX and Dermo and how well those species might perform in Chesapeake Bay (Allen, 1993). In light of the potential benfits of a resistant oyster to both the industry and ecology of the Bay, this action item was proposed to determine the potential impacts of non-native oyster introduction.

II. HABITAT/WATER QUALITY

1) **Conduct a phased program to evaluate and implement projects to restore physical oyster habitat.**

There was general agreement that significant destruction of areas once conducive to oyster settlement and growth has occurred over the last several decades (see Hargis and Haven, 1988). It was agreed that a program should be initiated which would evaluate historic areas of oyster habitat, determine which areas have become unproductive, investigate the reasons for the failure of the area to remain productive and develop a plan or plans which will lead to the rehabilitation of the area to a productive oyster bar. These activities may include large scale construction and seeding programs, restriction of harvesting, and careful monitoring to determine the productivity of the area after rehabilitation. We do not know what will be the most productive methods and strategies to employ for rehabilitating oyster bars and therefore expect to test a variety of approaches.

2) **Ensure that Bay water quality is maintained at levels necessary to support healthy oyster populations.**

There was concern among the Roundtable members that degradation in water quality, especially in terms of sedimentation, is having a significant negative impact on the oyster population. This action item was included not only to acknowledge those concerns but also to make certain that the oyster recovery plan was as comprehensive as possible and that all of the important aspects of Chesapeake Bay ecology which might influence oysters were included in the ensuing research and management projects. Although there is little evidence in the scientific literature to support it (Chu and Hale, 1994), there is a also some fear that chemical pollution has injured the oyster population and the Roundtable sought to stimulate research in this area as well.

III. INCREASE PRODUCTION/MANAGEMENT

1) **Increase the hatchery production of oyster larvae and seed oysters**

Hatchery production of seed oysters and other bivalves has played an important role in the recovery of the major oyster producing areas in the world. The Pacific Northwest of the US, the Northeastern US and France have all employed large-scale hatchery production to augment natural production or to replace it altogether. There was general agreement, although certainly not a concensus, that hatcheries could and should play an important role in the rehabilitation of Chesapeake Bay oyster communities. In light of these beliefs, it was recommended that the University of Maryland hatchery at the Horn Point Laboratory and the State hatchery at

Piney Point be improved to increase larval and seed production at both facilities. These hatcheries will produce seed for rehabilitation and reconstruction efforts and provide a relatively low-cost seed for aquaculture ventures. The regional lack of high quality seed is considered one of the main constraints to the developement of private ostraculture in Maryland.

2) **Prepare a comprehensive analysis of past and current oyster culture techniques and managment approaches. Utilize existing expertise and experience in the National Marine Fisheries Service and elsewhere.**

As previously mentioned, several regions have experienced a complete collapse of the oyster industry. The Pacific Northwest, the Northeast, and France have all seen their oyster industries decline to essentially zero during this century. All have thriving industries at this date due to the changes in the industry that the collapses imposed. All three industries shifted from hunting/ gathering/management techniques of natural production to more intensive large-scale farming activities where standard agricultural practices are utilized to maximize production and minimize problems including disease and predation. Having once been the single largest oyster producing area in the world, the Chesapeake Bay community can learn from the experience of the other areas which have recovered (Kennedy, 1989; Kennedy and Breisch, 1983). Therefore, it was recommended that a comprehensive analysis be conducted which will distill the most practical and productive activities that could be tested in the Chesapeake Bay.

3) **Maintain and adapt the current state repletion program.**

As mentioned earlier, there was significant concern among many of the members that the repletion program, in it's current form, continues to augment and exacerbate the disease problems in low and moderate salinity areas. Large numbers of infected oyster seed are transplanted annually from southern, higher salinity, high disease prevalent areas like Tangier Sound to low salinity regions in the upper Bay. In the low salinity areas the disease persists but does not intensify as rapidly. As a result, many more oysters reach market size than would if they were left in higher salinities. This practice was apparently borne out of a program which was dealing primarily with MSX. However, in contrast to MSX infections which are eliminated entirely when oysters are tranferred to low salininty, Dermo infection persist. Recent investigations have shown that the protozoan which causes Dermo, *Perkinsus marinus*, is capable of surviving very low salinities and that protozoans grown at low salinities tolerate even lower salinites much better than those from higher salinities (Ragone-Calvo, et al. 1994). Additionally, the protozoan also has the ability to regulate cell volume (O'Farrell, 1995). This means that continued inoculation of low salinity areas might result in a more virulent low salinity protozoan.

Regardless of the parasite transmission concerns, however, there was considerable support for the maintenance of the repletion program since it is thought to produce the bulk of the oysters harvested annually and watermen depend on additional income resulting from their participation in repletion activities.

4) **Provide fresh shell to be used by the state hatchery and for community groups for ecological enhancement.**

As mentioned previously habitat for oysters, clean shell, is thought to be greatly reduced in the Bay. Fresh shell is required for a variety of enhancement/rehabilitation efforts. It must be used to produce spat from the hatchery for planting on reconstructed bars. It is needed to build up areas which have sunken into mud or to place in areas where recruitment needs to be improved. This action item provides for the State to furnish fresh shell to the appropriate groups and communities which require it for such rehabilitation purposes.

5) **Evaluate the potential advantages and disadvantages of a "slot limit" with a minimum size of 2.5" and a maximum size of 4".**

To date there is little evidence that oyster populations in any region of the US have developed any resistance to Dermo. One hypothesis regarding the lack of this "natural selection" is that annual harvesting removes most of the resistant animals leaving the least resistant to contribute the most to the next years recruitment. If resistance can be developed in *C. virginica* a "slot limit" which would protect those resistant oysters from harvest might allow them to contribute more substantially to subsequent spawns and perhaps accelerate natural selection of resistant or tolerant populations. Populations of oysters resistant to MSX have been developed by Rutgers University (Ford and Haskin, 1987)

6) **Strengthen assessment of oyster stocks.**

The assessment of oyster stocks has recently been in question. Maryland officials claim that recent studies show that oyster abundance is relatively similar to abundances of 50 years ago (Homer and Jensen, 1995). There remains considerable skepticism regarding the interpretation of these results. They suggest that oyster abundance is not reduced but that the smaller oysters die from disease before they reach market size. Their contention is that disease is the primary cause of the reduction in the oyster harvest, not problems associated with recruitment or habitat. This action item calls for further analysis of natural stocks and oyster populations in the Maryland portion of the Bay.

7) **Encourage innovation by private industry by offering grants for the development of restoration, culture and production techniques.**

The State of Maryland has been notoriously hostile to the concept of private oyster culture in Chesapeake Bay (see Kennedy and Breisch, 1983, for review). Although some 2,500 acres of leased bottom are available for private oyster cultivation, they are largely held by families or communities which do not actively pursue oyster cultivation or are in poor growing areas. This action item is an attempt to stimulate the private sector rather than suppress it.

IV. INSTITUTIONAL BARRIERS

1) **DNR should establish a pilot permitting program for oyster aquaculture demonstration projects.**

As mentioned above, the Roundtable sought to breakdown the barriers to aquaculture within the State. A pilot permitting program would allow individuals to legally attempt oyster culture and allow the State to learn how to best permit and control the developing industry.

2) **DNR should establish an aquaculture permit clearinghouse service for applicants.**

This action item was intended to remove many of the hurdles and barriers which currently confront anyone wishes to grow oysters in Maryland. These impediments seem small when a company is first starting up but can be critical if the appropriate permits are held up or not awarded. Costs resulting from permit delays can be very high.

3) **Define acreage available for leasing oyster bottom.**

Additional acreage needs to be set aside for leasing to private growers. Most of the current acreage is in poor growing areas and/or long held by families or communities who do not want to give them up. Further, many of the leased areas are in places which make them unprotectable. In order for private culture to succeed, the State must cooperate in providing access to growing areas that are practical, protectable, and in areas that are conducive to oyster culture. These kinds of areas often conflict with the interests of watermen who want to harvest clams in the areas. Many former oyster bars which are now unproductive and have been silted over are dredged for soft-shelled clams by the watermen.

4) **Compliance/enforcement and aquaculture projects**

Again, the State has never supported aquaculture in a fundamental way. This action item states that aquaculture should be given a fair chance and that respect of leased bottom, culture trays and other aspects of oyster culture should be strongly enforced.

V. RESEARCH

1) **DNR and the University of Maryland, in conjunction with other State and Federal agencies, academic institutions and private research organizations, should initiate a multi-year, stably funded, goal-oriented research program on topics which will lead to the ability to detect, prevent and control MSX and Dermo.**

This action item was drawn up to encompass the scientific needs of the oyster rehabilitation effort. It emphasizes the needs of the research community to have a multi-year, stable set of funds from which to work. It also states that the research should be directed for the most part at the diseases which affect the Chesapeake populations. Finally, it strongly states that the State and other agencies, such as the University of Maryland, work together toward a common goal.

VI. Oyster Recovery Areas

One of the initial Roundtable discussions centered around the concept of quarantine areas where both harvesting and planting would be highly regulated. Following the recommendations of Andrews and Ray (1988) large areas should be cleaned of disease-laden oysters, allowed to fallow for at least one year and then planted with uninfected stocks. These practices would be impossible in a public area where harvesting and planting were occurring annually. Furthermore, any aquaculture ventures would be seriously impeded by planting of infected seed within the vicinity of the cultured stocks and therefore a hindrance to any capital investment in moderate-scale oyster culture. In an effort to facilitate aquacultural experimentation and test the concept of establishing relatively dermo-free areas by planting only hatchery or uninfected natural seed, oyster recovery areas were developed.

Oyster recovery areas, or ORAs, were established with specific regulations and restrictions applicable within them. Three zones were established. Zone A was the most regulated zone where most, if not all, shellfishing (clams and oysters) was prohibited and planting of MSX- or Dermo-infected oyster seed was prohibited. In zone B shellfishing was allowed but planting of infected seed was prohibited. Zone C carried no restrictions beyond the standard state regulations but was established for possible future modification. The primary objective of these ORAs was to secure areas where moderate-scale aquaculture and rehabilitation pilot programs could be established.

Since Zone A areas within each ORA are strictly off limits to harvest, scientists, aquacultural entrepreneurs and environment groups could conduct a variety of studies including: the determination of how to efficiently produce oysters on a commercial scale, how to create or rebuild an oyster bar, how the benthic community might change with the establishment of a densely populated oyster bar or whether or not oysters from a hatchery become as quickly infected by *Perkinsus* as natural seed when they are planted on the bottom. Finally, in Zone A sanctuaries might be established to promote greater local recruitment in low salinity areas and be protected from rampant harvest. Oyster recovery areas were initially established in the Choptank, Chester Magothy, Nanticoke, Patuxent and Severn Rivers and are expected to be established in most subestuaries in Maryland. The Maryland Department of Natural Resources can provide an accurate description of the ORAs currently established and the geographical designations of the zones within them.

VII. Oyster Recovery Partnership

The action plan also called for the establishment of a non-profit co-venture between all interested parties that would facilitate oyster recovery efforts, to implement many of the actions called for in the plan and to be a focal point for the programs established by the action plan. This partnership has been formed and is active in the pursuit of funding, participation, and cooperation in a variety of recovery projects.

Summary

A vast amount of knowledge and experience exists in the historic record regarding oysters in Chesapeake Bay.

The Chesapeake Bay and it's numerous salt-water tributaries contain prolific and valuable oyster beds.... The legislatures of Maryland and Virginia have, at every session for many years, revised and re-revised the laws upon this subject for their respective states; but have always been content to work in the dark, knowing nothing practically, and never seeing the value of obtaining full information upon so important an industry.

-E. Ingersoll, 1881

We have wasted our inheritance by improvidence and mismanagement and blind confidence; but even if our beds had held their own and were to-day as valuable as they were fifty years ago, this would be no just ground for satisfaction, in this age of progress, to a generation which has seen all other resources developed and improved.

-W. K. Brooks, 1891

In spite of the fact that less than half of the potential producing bottoms, one-half of those formerly productive, are now producing and only one-fifth as many oysters are now being produced, there has never been a single constructive forward looking attempt to rehabilitate the Bay. It has been conservation, and not altogether successful conservation as statistics show, and conservation only that seemed to dominate the policies of those in charge. Thus aiming at conservation and falling short of the mark has meant destruction of the oyster industry. Rehabilitation, alone, not conservation, can save the situation.

-Reginald V. Truitt, 1925

The common thread in these quotations of well-respected biologists is that knowledge of the biology and ecology of the resource should be utilized to develop an intelligent management plan and, furthermore, that active *production* of oysters and oyster bars is more logical than intense removal of naturally occurring oysters and bars.

The Maryland Oyster Roundtable sought to incorporate the lessons and advice of the past, the theories and data of the present, and innovative approaches in the management not only of the fishery but also of the oyster resource in the Maryland portion of Chesapeake Bay. The Roundtable started by seeking to maintain the level of the present fishery and to begin to conduct research to determine the most productive and valuable ways to augment and facilitate the recovery of this ecologically important natural resource.

While oyster reef production or construction is thought to be an important and appropriate way to restore the natural resource, diseases in the Chesapeake Bay oyster population complicate the concept. However, agricultural management practices have been developed which help control and sometimes eliminate diseases from domesticated stocks. The same concepts can and should be applied to aquatic species. For instance, the issue of virluence and it's relationship to salinity needs to be considered when oyster reef construction or rehabilitation is planned. If an oyster reef is considered to be a long-term investment in benthic habitat production, then the survivorship of the planted oysters must be taken into account. If oyster reefs are planned in an area where disease pressure is high, then most oysters will likely die during the second year after planting. Unless the organization(s) planting the reef intend to reseed the reef every three to four years, the reef would have to be located in an area where annual natural recruitment was high. Similarly, in areas where disease pressure is very low, oysters may grow for many years but not have any appreciable recruitment, so additional seeding would need to be planned after a certain number of years depending on mortality rates in the area.

In general, following the recommended practices of Andrews and Ray (1988) will be a good starting point for reef rehabilitation. However, serious thought should be given to the appropriate management of the reef. For example, if and when it becomes infected, should the managers remove the infected animals to minimize the spread to new recruits? If so, how should the reef be harvested? If large organizations join together to create large tracts of oyster bar, what retrictions and regulations should be imposed? Should they be required to use disease-free seed? Should they be required to open the tracts for harvest when the oysters are market size or when they become infected? Will it be productive to create non-harvested reefs to enhance "natural selection" for disease-resistant animals? In general, these are the kinds of hard questions that need to be discussed when considering actively building oyster reefs.

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Chapter 23

Chesapeake Oyster Reefs, Their Importance, Destruction and Guidelines for Restoring Them

by

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Abstract

The eastern oyster, *Crassostrea virginica* (Gmelin), can live any place in coastal marine and estuarine waters of the North American east coast offering suitable setting and survival opportunities. It occurs singly or in small clumps scattered widely but thrives best in colonial aggregations which, like those of tropical corals, are truly reefs. The massive self-renewing oyster reefs ("whole banks and beds") reported by early Chesapeake observers have yielded much. Without readily accessible oyster reefs the first English colonists of Jamestown might have starved. Without them the rich oyster industries of later years could never have developed. But oyster reefs benefitted the oysters that built and maintained them as well as the humans using them.

The oyster reefs of the Chesapeake region, including those on Seaside, developed during some 7,000-6,000 years of Bay evolution during the current (Holocene) Epoch. Until about 200 years ago reef oyster populations were able to maintain themselves and their reef habitats and withstand the inroads of biological enemies, other natural hazards and increasing harvests. By the late 1800s, Chesapeake public market oyster harvests had peaked and total market harvests and the oyster populations which provided them were in decline.

Continued overharvesting had done more than reduce harvestable populations. It had reduced broodstock fecundity and the genetic qualities of the various Chesapeake subpopulations as well. Further, it had diminished natural shell replacement due to excessive removal of shell-producing oysters and their shells, causing reef destruction. Additionally, removal of shells for landfill, road building, construction, chemical production, soil conditioning and poultry grit hastened that destruction. The synergistic cycle of population reduction and habitat destruction accelerated. Today many formerly-productive reefs are mere remnants (or totally obliterated—even eliminated) and Chesapeake *public* (aided or unaided) market oyster production is far less than one percent of its maximum.

If the trend of decline of self-sustaining natural oyster production is to be reversed, public oyster reefs must be restored. Proven guidelines exist. Such factors as location, geometry and materials have been naturally tested over time. The features which developed during the millennia of successful natural oyster reef evolutionary trial-and-error should be employed in well-planned reef-restoration activities. Where improvement is possible it should be done.

An effective reef restoration program will benefit not only the oyster resource, the public owners, the industry and consumers but the Bay's ecology and finfishermen as well. Active oyster reefs harbor many

epifaunal and infaunal organisms, increasing overall estuarine productivity and diversity. Further, they attract finfishes and other browsers and predators. Sportfishing charts identify many formerly-productive oyster reefs as fishing spots. This is no accident! More importantly, better utilization of H. L. Mencken's immense "protein factory" and restoration of such filtering and cleansing capabilities of reef oyster populations and their associates as may occur will benefit all Chesapeake citizens and others region- and nation-wide.

Introduction

Review of numerous reports on details of oyster production by earlier students of oyster ecology and the oyster industry of the Chesapeake Region, and elsewhere (i.e. Winslow 1881, 1882 and 1884; Baylor 1894, Stevenson 1894, Moore 1910, Loosanoff 1932, Marshall 1954), and the recent studies and conclusions of DeAlteris (1988), Hargis and Haven (1988a and b), Hargis and Haven (1995), Newell (1988) and Rothschild et al. (1994), has resulted in our recent realization of the great importance of viable reefs to the past and future natural production of oysters. These and other studies show that brood-stock reduction and impairment of genetic quality by over a century of adverse selection and destruction of the preferred natural habitat of *C. virginica*, the reefs, have been the primary, long-term factors in the tremendous decline in the natural, self-renewing production and harvest of market and seed oysters in the Chesapeake system.

As a consequence, Hargis and Haven (unpublished reports) have urged in several public forums since early 1991 the rebuilding, or replacement, of oyster reefs as a measure in restoring the population levels and viability of *C. virginica* and the industry dependent thereon on the public or natural oyster grounds. We again recommend this restorative action. Doing so, whether by passive (simple recuperative closure) or active (actual replenishment by shells and/or seed, plus significant recuperative closure) restoration or by new construction (also aided by closure), will require careful planning, site selection and design. Below we develop and support these conclusions and offer some guidelines for restoration.

Brief History of Oyster Reefs in the Chesapeake

When English settlers reached the Chesapeake in 1607 they found hundreds of massive, medium-sized and small upthrusting (most common in the Bay, itself) and fringing (most common in the lagoons and embayments of the Eastern Shore) oyster reefs. The heights or crests of many ebbed dry, or nearly so, at low water (Wharton 1957). Harvesting oysters required little effort. One had only to wade, pole, paddle, row or sail to the nearest exposed reef and hand-pick, rake or shovel a sack full, canoe full or boatload.

As time passed and demand and harvests increased, reef elevation and extent diminished and rake and tong handles (tongs are really opposed rakes, operating in scissor-like fashion) had to be lengthened. The harvesting efficiencies, effective depth range and, incidentally, destructive capabilities of tongs were increased with the introduction of mechanically—and later hydraulically, operated patent tongs (Haven et al. 1978).

Dredges (or their lesser relatives, scrapes), which enabled the taking of more oysters more efficiently than with rakes or tongs—and from deeper-lying populations, were brought into service. Reef elevation declined ever more rapidly as live oysters (with their shells) and associated empty shells were removed by tongs and dredges. Then, dredge and patent tong cables and hand tong handles were elongated even further. Removal of living oysters and shells increased and the cycle intensified.

Oyster reefs declined still further in height, base dimensions, volume and surface area. Though the base extent of each was undoubtedly increased for a time as the uppermost or outermost shells and surviving oysters were dragged onto the surrounding bottom by dredges or knocked over onto or deposited there by tongers (as indicated by Winslow 1891, Stevenson 1894, Moore 1910), it, too, eventually shrank as further harvesting and shell removal, over-sedimentation and sinking occurred and that temporary harvest-related advantage was lost. The process continued throughout each harvest year, decade after decade over two centuries or so.

In early times there were no closed seasons and sailing dredge boats remained over the reefs until their holds and decks were filled. Often buy-boats or "runners" emptied the dredge boats while the latter were still over the oyster beds enabling uninterrupted dredging and reduction of populations, and reefs, proceeded relentlessly. Continuous harvesting by tongs (ordinary and patent) did the same, only more slowly (per tong or per tong boat).

Besides taking living oysters for food markets, harvesters have removed shells from the reefs for direct use or transformation into shell by-products. In Colonial times crushed shells were employed in mortar, which often included recognizable shell fragments. Many shells were used to "sweeten" the soil and build walkways. Later huge numbers of whole shells, some with meats still in them, were employed in landfills and in the building of roads, alleys and walkways. For example, much of the city of Crisfield, Maryland was built on shell-filled wetlands and many, probably most, cities, towns and counties of tidewater Maryland and Virginia had oyster shell road beds, roadways and alleys. Shells were also used as ballast for railroad track construction. The total used for these purposes is unknown—probably unknowable.

We are somewhat better informed about the quantities used as ground- or burnt-lime or ground into poultry grit in recent times. Large-scale demand for these shell by-products had developed in the 1800s. By the early 1900's factories producing them had sprung up all around the coasts of the United States. In 1921 the U.S. Bureau of Fisheries reported 54 shell-processing plants nationwide. Of them the majority (29 or 53.7%) were in the Chesapeake Bay region; 18 in Maryland and 11 in Virginia (U.S. Department of Commerce Report for 1922). The Department of Commerce began reporting details of production of oyster shell byproducts in the United States in 1920. It, or the Department of Interior continued to do so until around 1945. Though production of shell byproducts had begun long before 1920 and continued after 1945, reporting of annual production *state-by-state* began in 1920 and continued, with at least one interruption, until 1943. Despite certain variations in the details they contained one can derive useful information from these reports. Briefly, from 1920 to 1944 the two Chesapeake Bay states are reported to have produced over 2,770,000 *tons* of shell byproducts. Of them at least 1,555,000 tons were in the form of poultry grit, with at least 1,215,000 tons as ground and/or burnt lime (Reports of the U.S. Department of Commerce for 1921 through 1939: Reports of the U.S. Department of Interior for 1939 through 1945). We have no ready conversion factors to allow determination of the *number of bushels* of whole shell required in preparing the tonnage of each type of by-product. Obviously, it was great—greater for the fine-grained lime products than for the much coarser grit.

Even after the flattening of reefs occurred, either through removals of live oysters for use as seed, "soup" or market oysters or through incidental and purposeful shell removal, the remaining shells have not escaped use. Large-scale mining activities employing heavy dredging equipment have taken shells from recent reef foundations as well as from remaining older sub-bottom reef deposits since World War II. For example, ancient and recent reef strata were mined by a commercial shell-dredging company (Radcliffe Materials, Inc.) in the lower James River estuary downriver of the current seed beds in the 1960's with the Virginia Marine Resource Commission (VMRC) receiving 1/3 of the harvest as the public's share of the shell (Haven et al. 1978, DeAlteris 1988). During 6 years (1963 through 1968) this activity produced a total of about 39 million bu of so-called "extinct" or "ancient reef" oyster shells. This large-scale commercial mining of shells in Virginia was halted by VMRC, with the urging and concurrence of the Virginia Institute of Marine Science (VIMS), when the mining company requested use of more accessible and more recent shell deposits.

In Maryland, buried reef shell has been commercially mined for about 30 years by Langenfelder and Son, Inc. for landfill, lime manufacture and other commercial uses and to be sold as cultch for Maryland's Oyster Repletion Program. Virginia has purchased Langenfelder-produced shells for the same purpose from time to time as have other states and private parties. According to sources within the Maryland Department of Natural Resources some 5 to 7 million bushels were mined annually. Thus, a total of as many as 150 to 200 million bushels of shells, or more, have been taken to date. Mining of shells from "ancient" and recent oyster reef deposits continues in Maryland, apparently at about the same rate. In both states (especially Virginia) many shells, originally from oysters set and grown on public bottoms and all nurtured by primary and secondary productivity of public waters, have been employed by private planters to firm their leased (private) grounds for subsequent planting of seed oysters.

The total number of shells taken from the reefs and bottoms of the Chesapeake system and employed for the various uses described above will never be known. All shells applied to uses other than *public* reef repletion programs were (and are) essentially removed from any possibility of employment in efforts at replenishment of *natural* reefs by state management agencies. All shells originating from public reefs and disposed of elsewhere contributed to destruction of those reefs and reef-fields!

Realization of possible problems associated with oyster (and shell) harvesting and reef destruction, and their possible ecological and economic significance developed during the late 18th or early 19th century, albeit slowly and fitfully. Dredging was banned early on (1811—Va. and 1820—Md.) but later restored by both states. For most of this century dredging of market and seed oysters has been banned from Virginia's public reefs (Hargis and Haven 1995). Eventually efforts were made by both Chesapeake states to reduce the rate of shell removal, small oyster removal and destruction and reef reduction through requiring the culling of market-oyster catches on the grounds whence they came (Ingersoll 1881, Stevenson 1894, Yates 1913, Kennedy and Breisch 1983). Unfortunately, *in situ* culling was avoided wherever possible by many, probably most, harvesters, and public management agencies were largely unable to effectively enforce cull laws and regulations. Even closures or gear restrictions were often violated.

In 1924, Maryland began a program of reef replenishment, or repletion, by planting shell on the diminishing natural oyster beds. Virginia's public reef shell-planting program began in 1928. Later, both states planted seed on public reefs as well, though shell plantings have always predominated (Haven et al. 1978). These efforts at public reef rehabilitation (for considered carefully that is what they really were, though true rehabilitation was rarely accomplished—probably never) failed to halt the long-term decline of reefs and their living populations. The reason they failed is simple. Instead of being closed to harvest after replenishment (either with shell or seed, or both) for sufficient time to allow restorative or even recuperative rebuilding of their oyster populations or of the reef structure, itself, the "repleted" beds were quickly opened. Without known exceptions, they were rapidly harvested. Repleted public oyster grounds came to be operated (essentially) as "put-and-take" fisheries in both Chesapeake states. Since monies developed from non-industry sources, including state General Funds, were often employed, the repletion programs (shell and/or seed planting) have been, in large measure, public subsidies to harvesters. Ultimately, these reef-improvement efforts were not enough and in some cases, accelerated by sedimentation, predation, disease and effects of toxicants (all of which must be factored into management decisions and allocations), production on the public grounds plummeted, due—primarily—to continued habitat destruction and population reduction. Additionally, many natural public reefs were allowed to be reduced without regular replenishment efforts. Neither state could afford to attempt to maintain all of its dwindling or already barren public reefs!

That oyster reefs have been overharvested and mined away (reduced in height, volume and surface area volume) can be documented not only by records of reduced harvests of market and seed oysters from the Chesapeake's many once very productive public reefs and reef fields, but by other reliable means. Already mentioned are early reports that many reefs reached upward into the intertidal zone in Colonial times (Wharton 1957 and others).

Though well over half century of harvesting had already destroyed many, some reefs continued emergent in the market and seed oyster areas of the James River into Civil War times. As late as 1871-73, soundings made by the U.S. Coast Survey (USCS 1872 & 1874) showed a number of reefs breaking the surface at mean low water. Some were extensive. For example, the emergent portion of Long Shoal Reef in the James River seed area near Point of Shoals Light was over a mile-and-a half long (USCS 1872 and 1874). (See Hargis, Chapter 1, this volume.) Certain of these emergent reefs persisted into the 20th century.

Marshall (1954) surveyed elevations of several oyster reefs in the lower James River and compared his depth data with those shown on older hydrographic charts. After allowing for changes in sea level he reported a loss in elevation of about 30 cm (12 in.) in about 90 years. This finding of declining reef height was reinforced by Hargis (1966) who confirmed reef height reductions and other geomorphological changes by harvesters after a large-scale VIMS study of the James estuary. Later, DeAlteris (1988), comparing old and recent hydrographic charts, estimated an elevation reduction of 1.2 to 1.8 m (4 to 6 ft.) at Wreck Shoal in the James River seed area (upriver from the market oyster area that Marshall had studied) over the 130 years preceding his field work. Unquestionably the reefs in the James River have been severely reduced by harvesting and shell mining.

The same has happened elsewhere in the Bay. Bailey (1941), who studied oysters of the York River for the Virginia Fisheries Laboratory (predecessor of the Virginia Institute of Marine Science), wrote:

> *"Oysters have in the course of their long evolutionary period evolved as reef animals.... Prior to 1880 good oyster rocks (bottoms) were common in the York River. They were the results of generation after generation of oyster shells settling on top of the previous crop, until finally the "oyster bars" were exposed at low tide. Those the results of natural conditions, but not for long."*
>
> *"By 1900 the oystermen had tonged up most of the oysters and had failed to return any appreciable amount of the shells. They sold the shells as well as the meats. The shells were ground and sold as chicken grit or burned into lime."*
>
> *"No better proof of this lowering or even total removal of the oyster rocks can be presented than the examination and comparison of a York River Coast and Geodetic Chart of 1858 with a recent one.*[1] *"Bare at low water" is the notation on the 1858 chart at Pages Rock Lighthouse. Today the reading at the same spot shows a depth of three feet and the bottom is soft mud."*

Clearly, destruction of Chesapeake oyster reefs has resulted from oyster harvesting and shell mining activities. Equally clearly, reef

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[1] In 1858 the organization was officially titled the U. S. Coast Survey. It did not become the U.S. Coast and Geodetic Survey until the late 1870s or early 1880s.

destruction in the Chesapeake system has resulted in reduction of self-renewing oyster populations and in declining market oyster production among other adverse effects!

Location of Oyster Reefs in Virginia - Their Sizes, Shapes and Associated Bottom Types

We are most familiar with and have access to considerable information on the reefs of the lower Chesapeake, especially those of the James River which, of those in Virginia's waters, have been studied most. Consequently, we emphasize them here; however, the same principles, results and conclusions derived from study of the James can be applied to oyster reefs throughout the Chesapeake!

The James estuary is similar in essential geomorphological and hydrological features to Maryland's upper Bay northward of the mouth of the Patuxent River as well as to the estuary of the Potomac River. The estuarine areas of all three systems are affected significantly by freshwater inflow from extensive piedmont and montane watersheds. (Annually, the Susquehanna River normally contributes about 49% of all riverine freshwater entering the Bay, the Potomac about 18% and the James about 16%, or about 83% all together—Figure 1. Obviously, all of the rest of the rivers and creeks around the Bay contribute relatively little freshwater—about 17% of average annual inflow.) The normal freshwater inflow patterns of the upper Bay and of the Potomac and James estuaries and their effects on the hydrographic and ecological aspects of those systems are similar. The same is true of their hydrographic and ecological responses to abnormal precipitation in their upper watersheds. Hence, their freshets and salinity advances and retreats and other freshwater-inflow-affected dynamics are similar. Historically, all three of these mesohaline estuarine areas have produced many market (and seed) oysters on extensive reefs and reef fields. Undoubtedly, common favorable ecological factors have contributed to their successes. Today natural market oyster production in all three is markedly reduced to less than one percent of former maxima (Hargis and Haven, 1995).

Some of the Bay's "natural", or public, oyster reefs were first investigated systematically by Lt. Francis Winslow USN, then working for the U.S. Coast and Geodetic Survey. Winslow (1882) examined reefs in both Maryland and Virginia and did the earliest such work in the James River. Winslow's surveys, especially those of Tangier and Pocomoke Sounds, established reef contours and provided some population-relevant information.

The locations of Virginia's natural oyster reefs were identified in 1892-93 by Lt. John Bowen Baylor, USN, also with the Coast and Geodetic Survey. This survey identified and plotted the borders of areas within which oysters and oyster reefs had occurred historically according to the collective memories of the participating watermen, many of whom were Commissioners (Baylor 1894). Unfortunately, it did not carefully examine the condition of the reefs within these areas or establish the size (i.e. height, basal area, slope, or surface area) of the then-surviving reefs or the nature of the bottoms around them (Haven et al. 1981). It is reported that the Baylor boundaries included at least 391 known, named reefs and large areas of unproductive bottom. The official public oyster grounds of Virginia were legally established in 1892 by Acts of Assembly. Actual legal boundaries were based on Baylor's survey results. They have been resurveyed since 1894 and occasionally augmented by General Assembly action. At present, some 243,000 acres are *officially* designated as public grounds (also called Baylor grounds) in Virginia. About 199,000 acres are within the Chesapeake system. Some 43,000 to 44,000 are on Seaside of the Eastern Shore (Figure 2).

Surveys conducted during the years 1906-1912 established the numbers, boundaries and names of the public grounds in each oyster-producing county of Maryland, see Yates 1913.

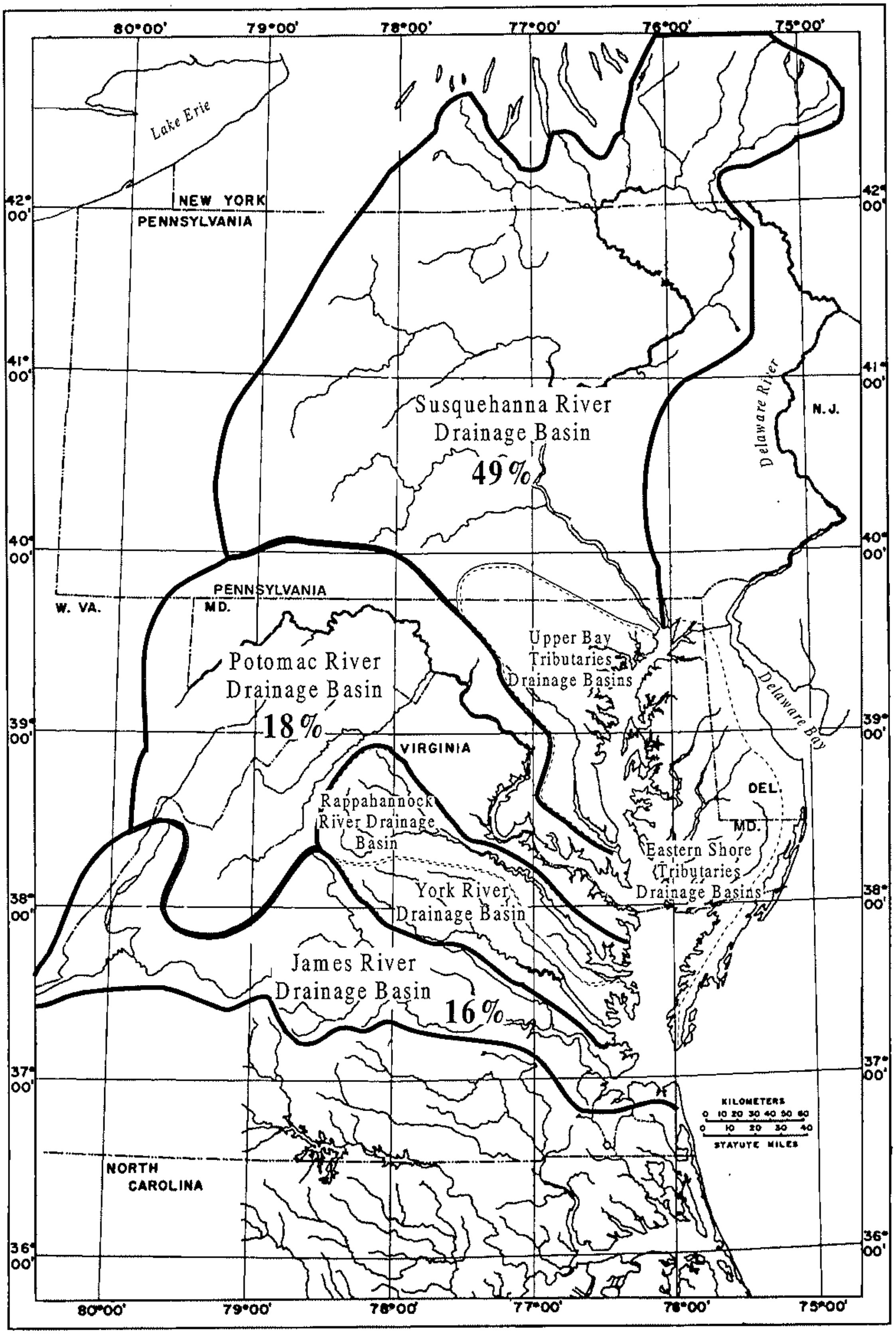

Figure 1 *. The Chesapeake Bay Drainage System Showing the Average Annual Freshwater Inflows of the Three Major Drainage Basins . The Susquehanna, Potomac, and James Drainage Basins, comprising most of the overall drainage area and contributing most of the Bay's riverine freshwater, are clearly identified.*

In all, this extensive survey covered 741 named reefs in 11 counties bordering Maryland's Chesapeake. Most occurred in the areas which Stevenson had outlined in 1894 (Figure 3). But, Yate's surveys involved more than areal outlines. They actually determined availability of oysters and bottom types as well as the areas and locations of the reefs. The surveys of Yates were used to establish the official (legislatively established) public oyster beds of Maryland.

It is known that the natural oyster reefs in both states had been extensively reduced by harvesting activities long before either of these two official surveys (i.e. Baylor, 1894; Yates, 1913) was conducted (Ingersoll 1881, Stevenson 1894, Hargis and Haven 1995).

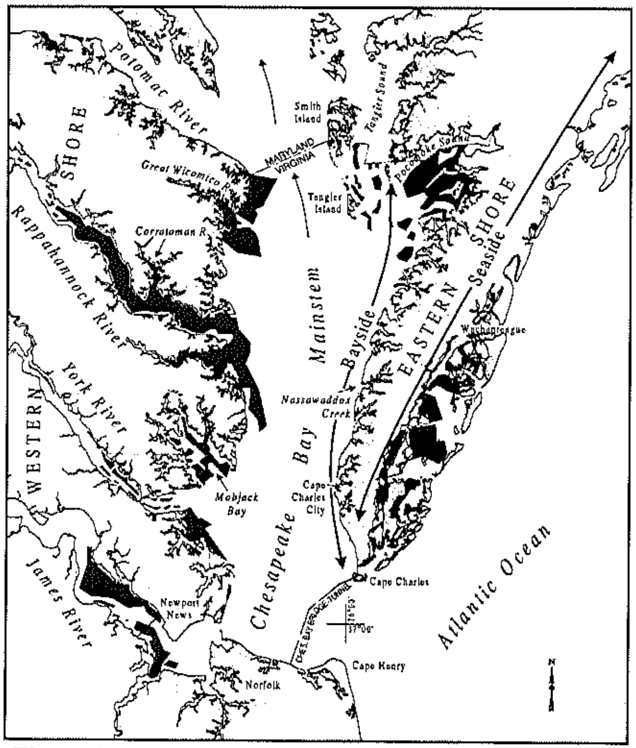

Figure 2. The Public Oyster Grounds of Virginia. Black areas outline and contain the natural (public or"Baylor") oyster reefs and reef fields of Virginia at the time of the Baylor Surveys of 1892 and 1893 as modified by later official additions. (Modified from Haven et al, 1978)

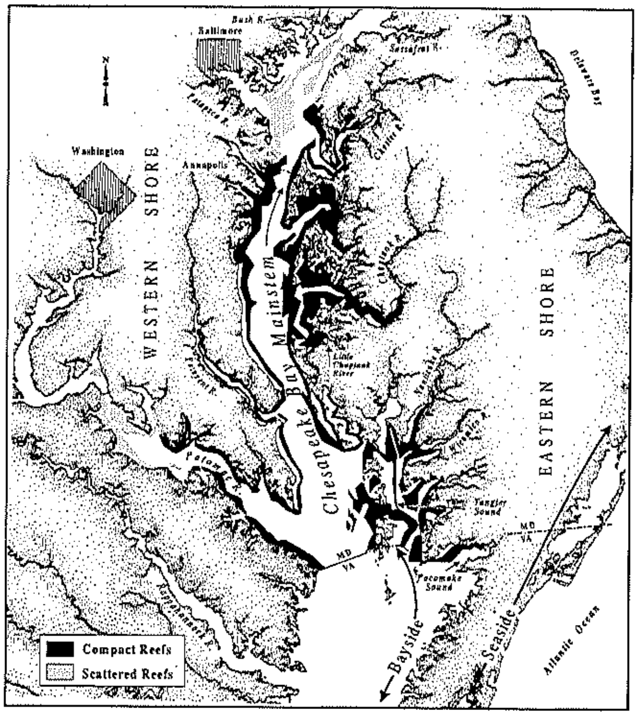

***Figure 3.** General Distribution of Oyster Reefs and Reef Fields in Maryland's Chesapeake Bay System, early 1890s. (Modified from Stevenson, 1894)*

The Structure and Special Ecological Features of An Oyster Reef

No one, to our knowledge has "dissected" an *unharvested*, upthrusting natural Chesapeake oyster reef to determine its detailed structure. However, De Alteris (1988) examined the structure and age of the once-important Wreck Shoal reef in 1986 and 1987. Unfortunately, by then Wreck Shoal had been largely destroyed.

It is possible to make some inferences from early charts and descriptions such as those prepared by the U.S. Coast Survey for the James estuary in 1871, '72, and '73 (USCS 1872 and 1874). (See Hargis 1998, Chapter 1, this volume.) As well, past field observations in the Chesapeake, and reports therefrom provide some information about reef morphology (Winslow, 1882, Stevenson 1894, Moore 1910, Loosanoff 1932, Haven et al. 1981, Haven and Whitcomb 1983 and 1989, DeAlteris 1988, and Whitcomb and Haven 1987).

We have attempted a diagrammatic "reconstruction" of an idealized unharvested reef in Figure 4. Consisting of two main above-bottom components, the "core" and the "veneer", the entire reef rests on a foundation of shells, shell fragments, and other persistent materials embedded in a matrix of sand-mud or silt. The core consists of depositional materials such as shell, shell fragments, sand, silt or clays in various proportions. The veneer consists mostly of living oysters, shells of recently-dead oysters, biological associates and persistent depositional materials. This whole structure rests typically on old shoreline and adjacent upland features existing prior to Holocene sea level flooding in the particular section of the estuary in which the reef was developed (Hargis, Chapter 1, this volume).

The masses of shell in the underlying core of an "undisturbed" successful living reef kept growing vertically and horizontally by accretion as successive generations of oysters set, grew, reproduced and died, leaving their shells behind. Eventually these shells were themselves overlain by new ones deposited as the oysters in the veneer died and by living oysters as the reef grew upward and outward. Of course, many individuals of each age group died of various causes, including disease undoubtedly (all animals and plants harbor parasites and have diseases), before maturing but enough survived to perpetuate themselves and contribute to growing populations and reefs. Or so it went until excessive seed and market oyster harvesting and shell mining upset the progression.

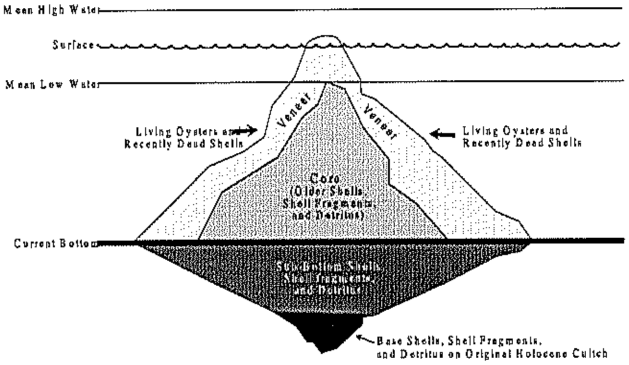

Figure 4. *Diagram of an "Upthrusting" Chesapeake Oyster Reef, the Oyster's (a communal animal) "Favored" Habitat. (Details of the early post-Wisconsinan, "original Holocene Cultch" Base are hypothetical. To our knowledge, no one has carefully "dissected" the sub-bottom portion of an upthrusting reef.)*

The interstices between shells and shell fragments provide places where sediment particles and reef wastes from upper levels may be sequestered even though the residence time therein of some of this material may be more or less temporary. Undoubtedly some is transferred, transformed, and even consumed by biological and chemical processes in the interim. A certain residue probably remains sequestered as long as the core remains undisturbed. Particulate material dropping away from reef "heights" can also settle onto the adjacent estuary bottom or be swept away from the reef by currents. Thereby, portions of the exposed outer surfaces of the veneer of the reefs, themselves, remain relatively clean of particulates. At the same time increasing reef elevation, bolstered by the shell being continually added to the core, and by new spatfall and growth in the veneer keeps the living oysters away from the bottom (the sediment-water interface) even though the surrounding sediment layer and associated nephalic layer may, themselves, thicken. Consequently, stresses exerted on living reef oysters by proximity to the bottom (bottom effects) are lessened and survival enhanced. Further, infective materials released by living, moribund or dead animals are more likely to drop or be carried away from other oysters living on the heights (or in the upper layers) of the reef's veneer than they would on a flat bed, or even on a low, bottom-hugging "lump".

The reef topography also increases the overall surface area significantly (as intestinal rugae and villi do in the guts of in higher vertebrates) available to setting and growing oysters. Consequently, chances of successful setting on suitably clean, exposed surfaces are improved.

Hidu (1969) and others have shown that the presence of living oysters enhances spatfall. The presence of living oysters in the veneer should, therefore, improve setting.

While general patterns of estuarine salinity are dominated by fluvial freshwater input and salty water intrusions from down- estuary and/or the nearby ocean, it is highly likely that significant local rainfall events and temperature changes affect the oysters on the crests and upper elevations of the reefs. Most probably there are (or were) vertical differences in salinity and temperature related to local weather phenomena as well as normal estuarine stratification on the upthrusting reefs of the Chesapeake. Likely, these micro-environmental variations are (or were) sufficient to affect survival of the oysters. This possibility deserves further scientific attention.

Upthrusting reefs also interdict and modify surrounding currents. Undoubtedly a large group of upthrusting oyster reefs (hereafter called a reef field) exerts considerable influence upon local current patterns and other hydrographic and geological features (Hargis, Chapter 1, this volume).

Taken together, paleontological, archaeological, historical, geological and ecological evidence shows that oysters set, survive and grow better on elevated reefs with substantial "cores" of oyster shells and "cinders", and other suitable substrate, and healthy "veneers" of living oysters than on beds near or on the bottom. Spatfall is better, growth is faster, predation effects are lower and disease-related effects reduced. Oysters lying flat on the bottom or partially submerged in the bottom do not fare nearly as well. Relative successes of "off-bottom culture" efforts employing man-made structures to maintain the living oysters off of the bottom in disease- and predation-prone areas confirm this.

Oyster reefs benefit other biota as well. Hundreds of micro-organism and small macro-organism species colonize them using oyster shell surfaces and interstices and wastes and those of other reef-associated invertebrates for support, shelter and sustenance. The oyster reef biocoenose (Moebius 1883) includes organisms of many life styles and food web levels. Attached and infaunal sessile plants and animals abound as does associated nekton. In the Chesapeake several finfishes (oyster toadfish, skilletfish, gobies, blennies and others) are among the regular inhabitants and the whole reef attracts many other grazers, browsers and predators. Though this aspect is generally ignored, it is highly likely that the oyster-reef biocoenose was the most prominent one in the Chesapeake system!

On reefs which have been heavily worked (overworked) live oysters mixed with shell and shell fragments and some organic matter and inorganic sand, silt or clays form a flat, hard crust up to 15 to 46 cm (6-18 in.) thick on the less-solid estuary floor. Typically a mixture of oyster shell and shell fragments ("cinder") embedded in a stiff matrix of sand-mud and silt lies below (Table 1). These latter substances (*i.e.* sand, silt or clay) may often form 50% of the total mix, and sometimes more (Haven *et al.* 1981, DeAlteris 1988). Oyster reefs usually extend below the surface sediment as shown in the Gulf of Mexico by Bouma (1976) and in the Chesapeake Bay by DeAlteris (1988) and by Nichols, Johnson and Peebles (1991). In the Wreck Shoal area of the James River the foundations of extant oyster reefs may extend into the bottom 6 m (19.7 ft) or more. Still older buried shell reefs associated with the changes in sea level during earlier interglacial oceanic transgressions may lie beneath the foundation layers of some recent reefs.

In summary, it is evident that reefs, nature's off-bottom culture "devices", have been important to the survival and natural renewal of *C. virginica*. If they were not, oyster populations would not have survived and produced so well on the many reefs that they "built" during the evolution of the current (Holocene) Chesapeake. Without those reefs and their accumulated populations the valuable public oyster fisheries of the Bay states would never have developed. Wherever natural reefs have been destroyed by natural forces or human activities (or both) along the Atlantic or Gulf coasts, economically significant *natural (unaided)* production of oysters has declined—even disappeared. Overall estuarine productivity has been reduced and finfish have declined as well.

TABLE 1. Subenvironment sediment sample made in the vicinity of Wreck Shoals, James River, Va. (Means and standard deviations) (From De Alteris 1988)

	Hard-Rock		Sand-Shell		Mud-Shell	
Parameter	Mean	S.D.	Mean	S.D.	Mean	S.D.
Water Depth (ft)	11.9	0.9	11.9	0.6	17.0	1.8
(m)	3.6		3.6		5.2	
Volume of Exposed Cultch (qt)	5.0	2.8	2.0	1.2	2.5	1.4
(l)	4.7		1.9		2.3	
Total Number of Live Oysters	74.4	22.8	90.9	30.8	24.9	12.7
Volume of Live Oysters (qt)	5.3	1.4	4.9	1.2	3.1	1.3
(1)	5.0		4.6		2.9	
Number of Oyster Boxes[1]	8.3	4.5	6.5	3.6	4.4	3.1
Sediment, Percent Gravel[1]	39.4	6.2	34.0	7.4	8.1	8.7
Sediment, Percent Sand	38.0	6.1	41.6	7.2	25.5	6.2
Sediment, Percent Silt-Clay	22.5	5.0	23.8	5.4	66.5	7.9

[1] Gravel consisted mostly of shell fragments.

Decline in Chesapeake Oyster Populations Related to Overharvesting and Concomitant Reef Destruction and Vice-Versa

Hargis and Haven (1995) established that both Maryland and Virginia natural (or public) oyster populations have been overharvested over the last 150 years or more. Many others, including Ingersoll 1881, Winslow 1882, Brooks 1891 and 1905, Stevenson 1894, Baylor 1894, Moore 1910, Yates 1913, Loosanoff 1932, Bailey 1941, Kennedy and Breisch 1983 and Rothschild et al. 1994, have concluded likewise. The relationship between harvesting effort and the Chesapeake oyster population decline is simple and direct. When more living adult (or any other sought-after age- or size-class) animals are removed from any population than nature (aided or unaided) can replace, overharvesting is taking place and the demise of the overall (or target) population (economically or even ecologically) is inevitable as long as the process continues. When any population's genetic strength is reduced by continuous adverse selection, their ability to survive environmental adversity, including disease, is weakened. When the essential habitat is destroyed in the process the population decline occurs faster and the likelihood of its self-restoration is seriously diminished. These are immutable and implacable "laws of nature". Their violation endangers the economic utility of those natural resources and may ultimately destroy the resource as well. Human wishes, political solutions (compromises), harvesting goals and management plans which are not consistent with these natural laws *are irrelevant and doomed to failure*! The question becomes not whether the resource will decline and the fishery will fail—but merely when.

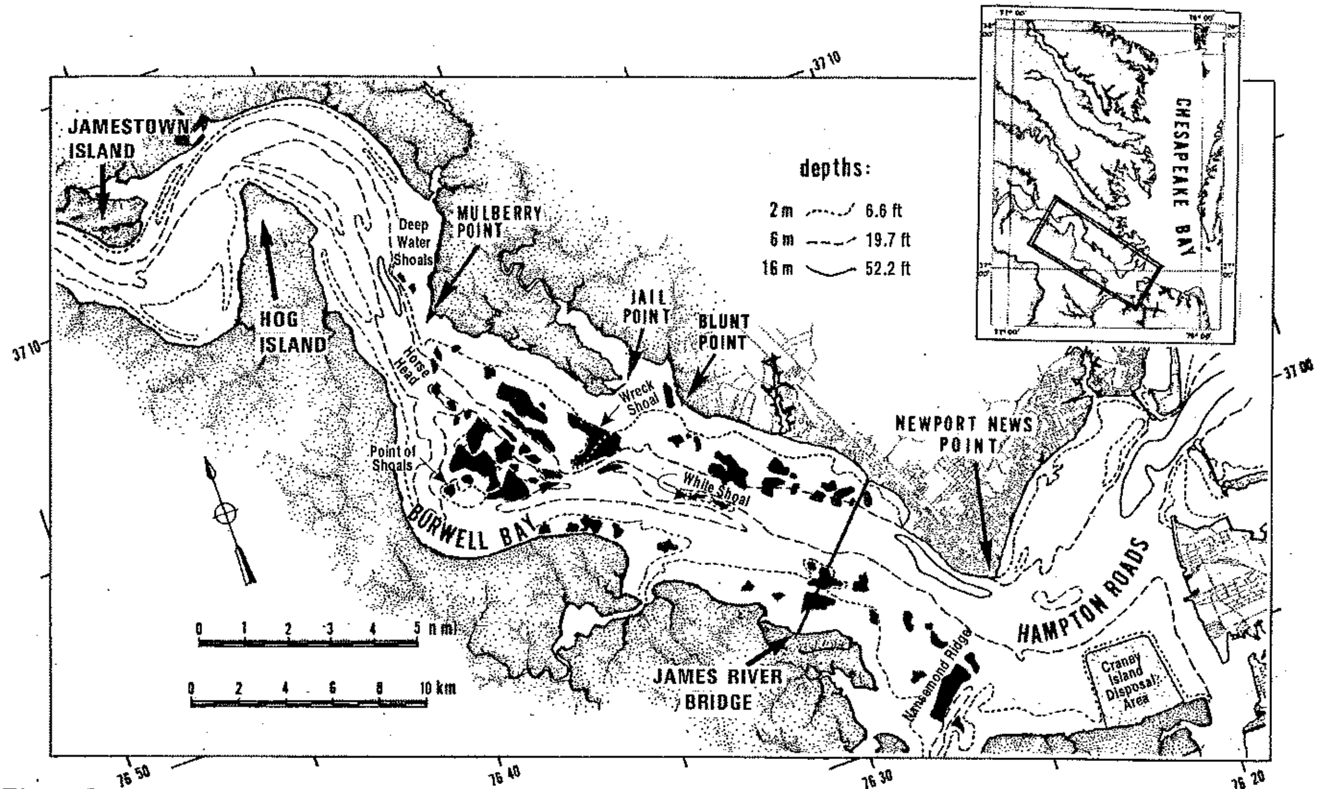

Figure 5. *James River Estuary Chart Showing General Bathymetry, Location of Public Seed Oyster Beds and Named Features Referred to in Text. Inset shows location of James relative to Chesapeake Bay.*

The "first" rule of responsible renewable-resource management is: The essential habitat must be preserved. The "second" is: the essential survival-related features of the target populations must be preserved. The "third" is: harvests must be limited to available "surpluses". Determination of "available surpluses" must consider all applicable negative ecological factors such as diseases, predators, adverse water quality, poor spawning and poor setting years, etc! The surplus available for harvesting in any harvest period is that which remains after these and other adverse factors have been considered: That and no more! Because of the natural uncertainties involved in the quantitative affects of thees processes, the approach to determining "available surpluses" must be conservative!

Responsibility for Preservation and Restoration of Public Oyster Populations and Their Habitats

Oysters of the Chesapeake and their natural habitats belong to all of the people of Virginia. They are truly part of the common wealth as former Governor Harry F. Byrd wrote in 1928 (Hargis and Haven 1995). As with other "common-property" resources their effective management is a responsibility and function of government. Regulation of their use and condition is, therefore, not an unjustified or unreasonable imposition by government upon private rights of harvesters and other users but a necessity to preserve the common-property resource and its future social and economic benefits. Public managers may allow socioeconomic use but must also preserve the people's (and posterity's) long-term socioeconomic interests in the resource. Where they do not do so the interests of the present and future owners are damaged, and the public managers are derelict. Prevention of abuse of common property resources should be the state's ultimate management goal: Where abuse has already occurred, restoration of that resource must be a priority!

As state governments undertake to restore natural oyster production on the *public* oyster grounds of the Chesapeake they must restore the oyster's "favored" habitats - the reefs. In doing so they would do well to emulate nature's reefs as closely as possible, including height and other dimensional features. Nature has been "experimenting" with *C. virginica* and its reefs along the western North Atlantic coast for some 18 million years or more under all of the varied ecological, geological, meteorological conditions that have transpired, through interglacial and glacial periods and in both estuarine and marine environments. On such reefs, under pressures of competition, predation and disease, *C. virginica* has survived for millennia.

Scientists talk much of experimentation, and there is room for reef experiments for special purposes. But "nature" has already accomplished the basic experimentation on reefs as suitable natural habitats for *C. virginica.* We can, and should, make use of her efforts and results!

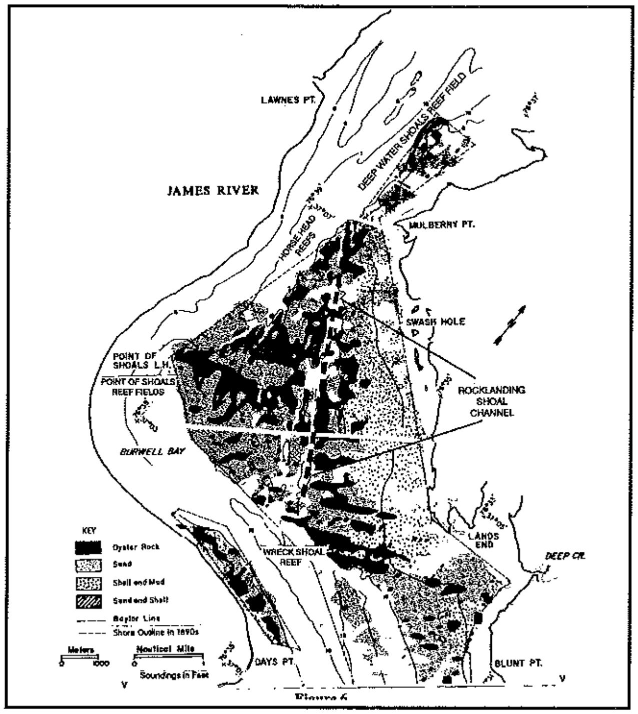

Figure 6. *Distribution and Base Outlines of Oyster Reefs and Reef Fields in Upper Reaches of the Estuarine Portion of the James River in the Early 1980s. Area shown encompasses all of the James River "seed oyster area" as identified by Moore (1910). The bottom types existing in the 1980s are identified -- see key to symbols. (Modified from Haven and Whitcomb, 1983).*

The remainder of our paper is directed at technical aspects relevant to the Chesapeake oyster reefs and their oyster populations.

Ecological Conditions Under Which Oyster Reefs Originate and Survive

Large oyster populations, as exemplified by living oyster reefs, develop and persist only where and when ecological conditions are favorable. For example, large (economically significant) oyster populations occur naturally in locations where biogeological and hydrographic features favor them. Such features include:

1. Salinity range from about 5‰ to full-strength or undiluted seawater—32-35‰. Within this salinity range, areas experiencing salinities averaging between (5‰ to 20‰) are probably most suitable for oyster survival. In contrast, many common oyster predators , such as the oyster drilling snails, *Urosalpinx cinerea* and *Eupleura caudata*,and parasites [including *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX)] do best in salinities averaging higher than 15‰. On the other end of the salinity spectrum frequent and prolonged freshwater conditions (0.5-5.0‰) mitigate against accumulation of living oysters and development of significant reefs. Frequent exposure to prolonged freshets increases mortality, depending on water temperatures, and results in (relatively) more rapid rates of reef shell deposition and build-up, but at the same time populations of living oysters are generally smaller and their growth (including shell growth) is slower. This is illustrated by oyster reefs in the James seed area (i.e. Wreck Shoal and above—Figures 5 and 6) where

oysters become fewer and reefs fewer and smaller (relative to age) as one progresses upriver to the area around the Horsehead Reefs and especially around and above Mulberry Point, *i.e.* the Deepwater Shoals area. The same would apply to the lower salinity reaches of the Potomac and the upper Chesapeake and its tributaries. Low salinity, or upper estuarine areas are not good candidates for "commercial" (as opposed to experimental) reef restoration.

2. Depth range from mid-intertidal to about 8 m (26.2 ft), sometimes more, but mostly between 2.5-5.5 m (8.2-18 ft);
3. Oxygen levels of from about 20% saturation to saturation. Mature, healthy oysters are able to close-up and survive under low oxygen conditions as they can in very low salinity water, but only for relatively short periods of time. Prolonged anoxia leads to the development of H_2S in the water which is quickly lethal;
4. A relatively sheltered area, protected against excessive wave action yet appropriately exposed to water movements which permit and/or facilitate setting, feeding, cleansing and reproduction;
5. Levels of natural predation low enough to permit accumulation of sexually mature oysters of an appropriate sexual mix of mature oysters;
6. Levels of mortality (related to disease and other natural or man-made causes) low enough to permit survival, adaptation and accumulation of favorable genetically transmissible characteristics;
7. Levels of competition from other filter-feeders low enough to permit the same as in 6.
8. Production of viable larvae in numbers sufficient to maintain the endemic oyster populations and the reef habitat, and meet the demands of environmental pressures, including adverse ecological factors such as sedimentation, diseases, competitors and predators, including man.
9. A hydrographic circulation pattern which retains, preferably gathers as well, maturing oyster larvae in the vicinity of the reef or reef field and, optimally, carries oyster larvae from nearby and distant oyster populations to that reef during the season of active setting;
10. Current patterns and velocities sufficient to prevent or reduce the rate of accumulation of fine sand, mud and/or silt, on developing reefs and of infective materials (particles), feces, and pseudofeces or other organic materials on or around the living oysters, and;
11. Sufficient elevation to provide the advantages of height and vertical differences in distribution of water of varying salinity.

Surveys Relevant to Reef Rehabilitation Activities

Moore (1910), using surveying gear, a chain-drag and oyster tongs, delineated the actual outlines and acreage of oyster reefs in the James River. He also established the outlines and acreage of various bottom types and the density of oysters (in terms of economically harvestable quantities available) on the four types of bottom he identified. Unfortunately, reef elevations and contours were not reported.

The first truly comprehensive investigation of Virginia's public oyster bottoms was made during the period from 1978 to 1981 by Dexter S. Haven and his colleagues of VIMS. This three and a half year study employed electronic positioning gear (Hastings Raydist©) and a recording fathometer to establish depth contours, plus a sonic bottom drag to locate and outline reefs (in 2 dimensions, 3 with the fathometer) and to secure data on bottom types. Standardized patent tong samples were used to estimate oyster and shell density and further identify bottom constituents. The data were used to prepare a series of charts and tables presenting basal outlines of existing oyster reefs, acreages of various types of bottoms, estimates of living oysters and shells, setting potentials, and occurrences of diseases and predators. Most of the study was published in an extensive series of reports (Haven et al. 1978, Haven et al. 1981, Haven and Whitcomb 1983 and 1989 and Whitcomb and Haven 1987).

These documents, particularly Haven et al. 1981, provide information relative to reef location, condition and other data needed to plan and conduct reef restoration programs in Virginia. Almost all tributary and Bay bottoms and those of the lagoons and embayments of the Seaside of the Eastern Shore were sampled and described. Until data even more accurate and comprehensive are available the results of Haven et al. (1981) *must* be employed to provide the basis for such work in Virginia and *should not be ignored*! Their conscientious use in developing reef rehabilitation programs is vital!

Specifically, these charts and tables showed:

1. Areas of thick, hard bottom with living oysters and shells;
2. Bottoms less firm than those mentioned above (1) but with a firm crust of live oysters and shell fragments ("cinder") in a matrix consisting largely of sandy sediments;
3. The same as (2) but with a firm matrix of dense sand, silt and clay;
4. Sandy bottoms containing few to no oysters or shells;
5. Mud bottoms containing few to no oysters or shell, and,
6. Buried shell 6-12 inches below the bottom, *i.e.* overlain by sand-mud or other sedimentary material.

A study in 1985 in the James River seed area utilizing patent tongs confirmed the validity of the designation of bottom types by Haven et al. 1981 and their location in a small section of the Wreck Shoal area (DeAlteris, 1988). It also showed that sand or silt-clay may form over 50% of the substrate matrix even on active or producing Hard Rock (Reef) bottoms, i.e. those which continue to produce oysters despite having been severely reduced by harvesting and being merely "bumps" on the bottom (Table 1).

Haven and his colleagues (1981) evaluated about 203,405 acres of the state's approximately 243,000 acres of public (Baylor) bottoms, including both Seaside and Bayside of the Eastern Shore (Figure 2). They showed that in the James River (Figures 5, 6, and 7), which encompassed about 25,152 acres of all public bottoms, a lesser but still substantial acreage (16,245 acres or 64.6%, i.e. 1 to 3, below) of it was suitable for growing oysters. These can be categorized as follows:

1. Hard Oyster Rock, generally with live oyster and some profile;	4,310 acres
2. Shell-Oysters - Mud;	7,487 acres
3. Shell-Oysters - Sand;	4,448 acres
4, Sand - few or no oysters;	1,540 acres
5. Buried shell;	420 acres
6. Soft Mud or Channel Areas	6,947 acres
	25,152 acres

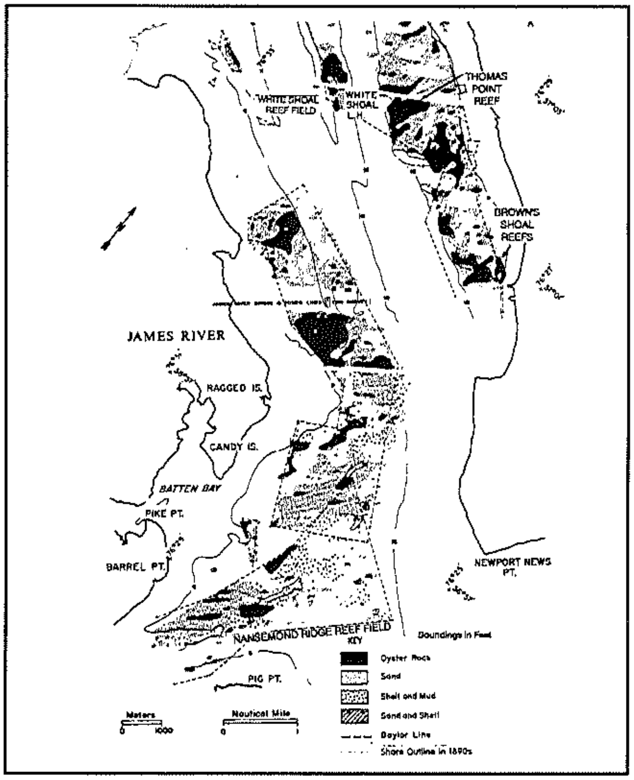

Figure 7. Distribution and Base Outlines of Oyster Reefs and Reef Fields in Lower Reaches of the Estuarine Portion of the James River above Newport News Point in the Early 1980s. Area shown encompasses most of the James River "market oyster area" as identified by Moore (1910). The bottom types present in the 1980s are identified -- see key to symbols. (Modified from Haven and Whitcomb, 1983).

Unfortunately only a small amount (about 3,000-4,000 acres) continues to produce appreciable quantities of seed and very few (5,178 Va. bu. in 1993-94) market oysters. In the James River seed area market oysters were defined as those at least 2 1/2 inches in shell length in 1986-87. In early 1994 it was restored to 3". In the James River seed area size limits mean very little in terms of population protection and conservation because oysters called "seed" can be any size. Additionally, for many years small individuals from the "market" oyster area of the James were harvested for use in the making of oyster soup. Such oysters were called "soups." Soup oysters could be any size but buyers preferred small ones. With such variations in the sizes allowed to be harvested, it is obvious that size limits actually meant very little in the James!

If the primary objective of reef rehabilitation or rebuilding activity is to increase *natural production* (self-reproducing populations) of oysters and restore reef structure as quickly and effectively as possible, *as it should be*, the reefs in the Hard Oyster Rock category (No. 1 above) should receive the most effort. Even if expense is a concern, rehabilitating this category of reef should receive more (and more effective) management efforts since they are in the best condition to rehabilitate themselves with or without addition of shell or seed (more rapidly with both, clearly), but—given adequate respite from harvesting pressures. The implications of this last condition are obvious: To rehabilitate active or inactive reefs most quickly, harvesting pressures must be reduced severely—preferably eliminated, for a significant period of time! Rehabilitation of reefs without closing them and leaving them closed until they achieve significant rebuilding will be wasteful. Even after rebuilding is accomplished and production reefs are opened, harvest levels must be strictly controlled!

Categories 2 or 3 reefs are older depleted ones and are good candidates for reef rebuilding efforts as well. Reefs of these three categories (1, 2 and 3) are sufficiently numerous and extensive that "barren" bottoms need not be considered—except for special purposes. Further, category 1, 2 and 3 reefs are sufficiently widespread to provide suitable "platforms" for rebuilding efforts in every part of Virginia's Bay and its tributaries where oysters once flourished. The same is probably true of Maryland's waters except where shell mining has removed too much sub-bottom shell.

Sizes and Shapes of Oyster Reefs in the James River

As stated above, the survey by Haven et al. (1981) determined size, bottom types and water depths of Virginia's Baylor bottoms. All surveyed were charted and the charts deposited in the VIMS library. Those occurring in the James River above Newport News Point are shown in Figures 5, 6 and 7.

The Hard Oyster Rock areas (reefs) shown in black in those figures are most often irregular in shape. Many are elongated, presumably on sites of old elevated river bank or river bed topography or along prevailing bottom currents, or along the long axis of the river. Many are situated at right angles to the long axis of the river (i.e. to the prevailing bottom tidal currents). The long axes of many are arranged across-river, perhaps reflecting the water mass movements driven by the west to east, wind-driven cross-river currents occurring during the setting season and/or topographic features of the bottom. (Obviously, both the location and orientation of cultch and the prevailing currents have affected the locations and shapes of the reefs.) Some were a mile (6.4 km) or more in length and 1,000 feet (305 m), or more, wide. [The crests of a large number of them are known to have breached the water's surface at mean low water: Some in the not so distant past (Hargis, Chapter 1, this volume.)] Many, however, are much smaller and are often called "lumps" by watermen.

The Haven et al. (1981) study measured the area of discrete Hard Rock Reefs surviving in the James River (Table 2) and elsewhere in

Table 2. Location, Acreage and Percent Total of Hard Oyster Rock (Reef) Areas (Category 1) in the James River by Sections

A. Deep Water Shoals to Mulberry Point — Total - 37.7 acres	
1. 0 to 20 acres	100.0 %
B. Mulberry Point to Point of Shoals — Total 1750.2 acres	
1. <20 acres	4.6 %
2. 20.1 - 100 acres	10.8 %
3. >100 acres	84.6 %
C. Point of Shoals to White Shoals — Total 1355.9 acres	
1. <20 acres	27.1 %
2. 20.1 - 10 acres	30.5 %
3. >100 acres	42.4 %
D. White Shoals to Fishing Point — Total 1031.4 acres	
1. <20 acres	10.9 %
2. 20.1 - 100 acres	17.6 %
3. >100 acres	71.5 %
E. Fishing Point to Nansemond Ridge — Total 135.1 acres	
1. <20 acres	44.6
2. 20.1 - 100 acres	55.4

Virginia's tidal waters at the time of the surveys. These data showed about 4,310 acres of Hard Oyster Reefs in the entire James estuary, i.e. above and below Wreck Shoal. These areas were locations where more extensive reefs existed prior to being subjected to intensive exploitation. Areas classed as Shell-Oyster Sand and Shell-Oyster-Mud were reefs which are gradually being covered with sediments after having been harvested and mined away.

The Vertical Elevation of "Hard Rock" Bottoms in the James River

Fathometer traces of bottom depths were made during the study of Haven et al. (1981). Significantly, these traces showed that most of the "tops" of the hard reef areas in the upper James around Burwell Bay were at least 0.6 m (2 ft) below the water surface at MLW. Further downriver in the important Wreck Shoal area the tops of most reef areas were about 2.4 m (7.9 ft) below MLW. A few areas of reef still showed the classic "peak" or emergent ridge formation as presented in Figure 4 and in early U. S. Coast Survey (USCS) charts, but most showed gradually sloping configurations with little elevation above the surrounding bottom. No oyster-bearing reef crests breached the surface at any normal low tide. This indicates clearly that the natural oyster reefs in the James River, as elsewhere, have been largely "planed" away by over two centuries of harvest by rake and dredge (very early) and tong.. Few "reefs" with significant elevation remain. Most surviving "reefs" are "footprints" only. Shell-oyster-mud and shell-oyster-sand beds showed no appreciable elevation above the surrounding bottom (Haven and Whitcomb 1983).

Review of the studies of Haven and his associates and others discloses clearly that the condition of the natural oyster reefs of the "former" James River seed area (i.e. Wreck Shoals and upriver) is serious! Very little remains of the numerous upthrusting reefs reported in the early 17th century and surveyed and charted over two centuries years later in 1871, '72 and '73 by the USCS that have yielded seed and market oysters for over 200 years. This finding was surprising! Haven and his colleagues expected to find many reefs with greater elevations in the most productive reef fields of the James River seed area. Considering the poor condition of the oyster reefs of the James, it is no surprise that populations of small seed-sized (and market oyster yields) are so low! Nor is it a surprise that surviving populations and setting are so sparse.

The reefs in the lower James below Wreck Shoal (Figures 5 and 7), shown as a market oyster area in the text and charts of Moore (1910), are in worse shape. In fact, most had been significantly reduced before Moore actually made his survey in 1909.

For the James River oyster reef fields to recover as quickly as possible (or even to survive) it is important that the destruction of the structure of existing reefs be halted and that the reefs, themselves, be augmented and/or restored. The oyster's favored habitat must be restored so that self-renewing populations can be rebuilt and/or assisted to rebuild themselves to near their former levels!

The need for this is obvious. Today most public market oyster production in Virginia comes from the James River "seed beds" as it has in the past. If that is to continue, rebuilding is essential. In the past and today *most private oyster* production originated on the same seed beds, as it does today. For example, in the early and mid-1950s private oyster planters were harvesting as many as 2-3 million bushels of market oysters from their rented grounds annually. In fact, from 1930 on, and probably before, about 80 to 85% of the seed oysters for Virginia's large private market oyster production (which reached levels of as much as 70-80% of the total state market production) *came from the public reefs in the James estuary*. If the reefs around the Burwell Bay seed area continue to be depleted and the reef "footprints" become covered over with sediments their present and future utility as a source of seed will be destroyed. Consequently, the likelihood of recovery of the Virginia's private oyster (*C. virginica*) planting industry to former levels will be reduced severely—probably eliminated. Silt-covered reef remnants can produce few oysters.

Restoration (Enhancement) of Oyster Reefs (In the James) and Their Management

Rebuilding oyster reefs in the James River, or elsewhere in the Chesapeake (or on Seaside), should only be attempted if sound plans and procedures for doing so are fully adopted by the entire decision-making apparatus of the management agency (ies) responsible in both states. Money spent on poorly-planned or "half-hearted" attempts is largely wasted. Furthermore, for most rapid Bay-wide recovery, both states must develop clear plans and procedures for future maintenance. We urged reef restoration in several public forums in 1991! Thereafter we recommended establishment of a system of sanctuary broodstock reefs (SBR) and satellite production reefs (SPR), Figure 8. This recommendation is reiterated—forcefully! Since then some reef restoration has been undertaken in both Maryland and Virginia. The trend is encouraging. A few of these projects appear to be showing some positive results. Unfortunately, many, probably most, will fail because of faulty planning, poor placement, inadequate construction and maintenance and/or ineffective post-construction management. Some watermen in both Bay states continue to resist effective oyster management. In fact, some who oppose reef construction actually serve on committees to select sites and other details of reef construction!

To assist in reef rehabilitation we have prepared a list of factors to be employed as guidelines. The features which a reef rebuilding

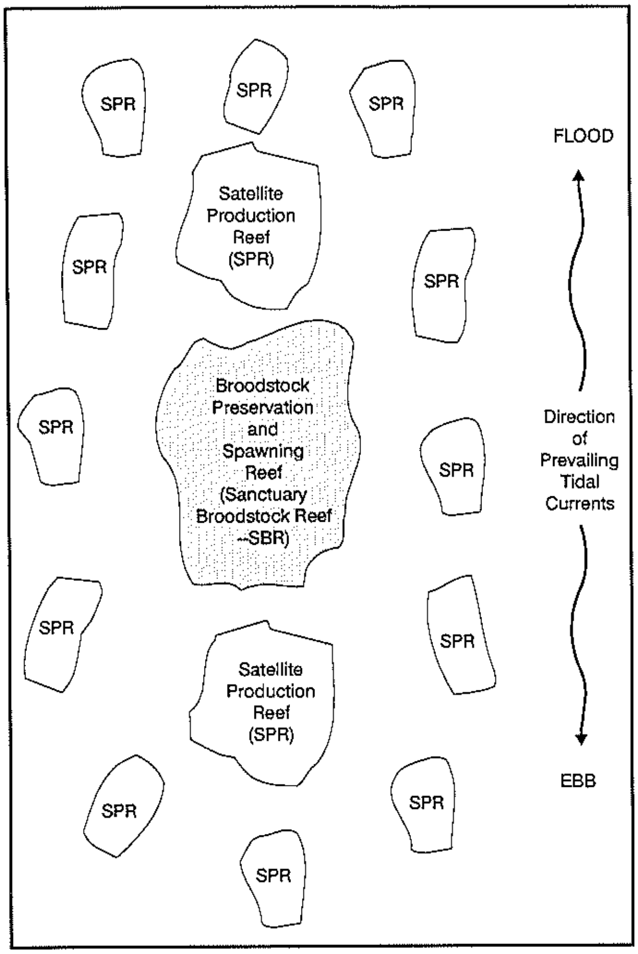

Figure 8. *Diagram of a Two-Tier System of Reef (Reef Field) Restoration Involving Preservation of Broodstock and Spawning Populations and Market or Seed Oyster Production. "[Idealized—Actual configurations may have to differ depending on geomorphological, hydrographic and other important ecological characteristics of the locality in which reefs (or reef fields) are to be restored or built.]*

program designed to produce oysters for harvest should incorporate are:

1) First priority should be given to identification and rapid rebuilding of reefs designated as broodstock sanctuary areas, which we have called Sanctuary Reefs (SR) or Sanctuary Broodstock Reefs (SBR). Harvesting should not be allowed on sanctuary broodstock reefs!
2) These reefs will be the core or central building blocks of our two-tier reef system, or any serious reef rebuilding program. A conceptual design of a combination, or two-tiered reef system is shown in Figure 8. It includes one or, preferably, more sanctuary broodstock reefs (SBR) which must remain closed after establishment and several surrounding satellite oyster production reefs (SPR), reefs which, when restored and ready, can be opened to "controlled" harvesting.

   It is important to note that only the essential features [*i.e.* one, preferably more, sanctuary (SR) or sanctuary broodstock reefs (SBR), surrounded by several satellite production reefs (SPR) appropriately situated] presented in our conceptual diagram are critical. Where geomorphological or hydrographic conditions around existing or planned reef fields do not lend themselves to the idealized or diagrammatic geometric arrangement shown in Figure 8 an approximation would be satisfactory. Where local current patterns suggest different axial alignment(s) of SBRs and SPRs, some rearrangement would certainly be in order.
3) Reefs designated as satellite oyster production reefs (SPR) must be closed until natural production of oysters has returned. When the satellite production reefs (SPR) are opened to commercial or recreational harvest the quantities available for annual harvest (quotas) should be carefully limited to the ability of those SPR reefs to sustain those harvests and, at the same time, maintain themselves. If prolonged rebuilding of the SPR reefs is intended, annual harvest quotas must be even more restricted. In most instances continual rebuilding of SPRs would be desirable in the long run. In every case, managers should be conservative in setting harvesting quotas. Enough animals should be left on the reef to allow for changes in rates of survival brought about by variations in adverse environmental conditions.

Unfortunately, the fishery management agencies, including legislators whenever they have interfered with rational closure decisions, in both Chesapeake states, and it is they who are ultimately responsible, have consistently avoided (even actively and mistakenly resisted) adoption of management plans which actually limit oyster harvests from public reefs to biologically reasonable levels. Even on reefs being "replenished" at significant public expense, they have not done so! Further, they have never favored actual closure of any producing reefs, even to restore them to formal actual or potential "high" productivity. *This is one of the most significant reasons that state management of the public oyster resource and the fishery that exploits it in both Virginia and Maryland has been ineffective! Biologically reasonable and necessary harvest controls have never been instituted and enforced!*

4) Until truly sound management arrangements and practices can be instituted and enforced, extensive reef rebuilding projects or programs are not to be recommended. Money spent on restoring production reefs which are not appropriately managed will not achieve long-term restoration of public oyster productivity. At best it will be a gift from the state treasury, a subsidy, to public watermen as it has always been—largely. At worst, it will be a waste, as it has most often been. Effective post-repletion, post-reconstruction or post-construction management is the most important aspect of any reef restoration program!

There are valid purposes for reef restoration other than for development of sanctuary reefs or rebuilding or enhancement of commercial, subsistence or recreational harvests of seed and market oysters. These are: 1) Restoration of broodstock levels, and as the oysters mature, of an appropriate sexual mix; 2) Genetic enhancement, i.e. development of desirable characteristics such as disease resistance, rapid-growth or other features by native *C. virginica* by allowing forces of natural selection to act on unharvested, self-reproducing populations of naturally-produced oysters or those from "laboratory-enhanced" populations; 3) Restoration of the filtering, sequestering and transformation capacities of massive oyster populations on revitalized upthrusting oyster reefs, strategically placed as natural pollution reduction measures, and; 4) Restoration of oyster reef-associated communities once so prevalent in the Chesapeake. Oyster reefs are natural fishing reefs (often clearly identified as such on charts intended for use by sportfishermen) which attract and help support desirable finfish. Enhancement of recreational and commercial fin fishing will be a significant bonus of reef restoration. (Actually, efforts, funds and expenditures designed to construct "finfishing" and/or "ecological improvement", or "filtering" reefs, can be adapted to development of sanctuary and even economic production oyster reefs and double- or triple-purpose reefs will result, enhancing ecological and economic benefits and allowing sharing of costs between objectives.) Also, increased water clarity, if such results from the filtering activities of active reef oysters and/or other filter-feeding reef associates, should enhance phytoplankton production and recovery of submerged aquatic vegetation (SAV) in areas influenced by reefs or reef fields and reduce other undesirable effects of excessive sedimentation. Both would be valuable bonuses of oyster reef reconstruction. Yet another benefit of well-situated, properly-designed and constructed oyster reefs would be stabilization of affected lee shores. Further, restoration of reef populations may result in reduction of deleterious micro-organisms by increased filtration of waters in their zones of influence.

Technical Aspects of Reef Rebuilding Which Can Be Recommended

Sufficient information now exists to allow planning for and design of reef restoration activities and pursuit of actual rebuilding or restoration of effective reefs. As we have suggested, all that is required is to emulate nature as closely as possible in the placement and "shaping" of reefs. However, technical aspects pertaining to actual details of reef restoration activities should be examined deliberately to see if nature can be improved upon or, where natural materials such as oyster shell for reef "core" rebuilding are not readily or economically available, to facilitate acquisition and utilization of substitute materials. Further on we will comment in more detail on them and make recommendations. (Also, see the several papers on alternate substrates in this volume).

Ideally, it would be excellent if reef restoration could be undertaken in every tributary or Bay area which formerly held successful and productive reefs. But, doing so would probably cost more than will be available at times when governmental budgets at all levels are apparently constrained. Consequently, priority areas must be chosen. In some measure these can be selected (screened) on the basis of ultimate purpose of the reefs, i.e. ecological restoration, possible pollution reduction and/or economic restoration—or even multipurpose fishing reefs. There may be some geographic areas which favor one or the other (or several) of these objectives. Further, design of reef structure and layout might be varied to achieve one or more of the purposes selected. In many areas of extensive and potentially productive public bottoms one design could serve all functions. Selection of such versatile reef designs should assist in justification, planning, and development of actual reef rehabilitation or rebuilding projects.

To achieve maximum restoration with minimum cost, effort and time we must take our cues from nature in making any site selections. Locations at which nature has been most effective in the past are prime candidates. This can be established from reliable scientific survey data. Early hydrographic charts, including boat sheets, incorporating the results of naval and civilian hydrographic expeditions can be useful. Most valuable will be actual oyster ground surveys reported by Winslow (1882—Md. and Va.), Baylor (1894—VA), Moore (1910—VA), Yates (1913—MD), Haven et al. (1981), Haven and Whitcomb (1983 and 1989) and Whitcomb and Haven 1987—VA) and others. When results of the survey recently conducted by the Maryland Department of Natural Resources (Jordan, personal communication) are finally processed, charted and made available, they should be employed for Maryland waters.

Data from objective and carefully done research and management surveys of both states are of great value and must be employed. Records of such activities as annual oyster ground (reef) surveys, spatfall surveys, disease and survival surveys and other such information are important. (If obtained and treated competently these fishery-independent data, coupled with available ***objective*** survey results, are the most valuable.) Reef rebuilding efforts which fail to incorporate all of the available useful elements of such sources of information should not be pursued. Funding agencies should demand no less.

In Virginia, preselection of sites for reef rebuilding should be based on Haven et al. 1981, and recent data obtained by Mann (personal communication) plus such other relevant site-specific data as are available. Additionally, once a likely reef area or even a specific reef has been identified the site selected should be carefully surveyed employing the most effective positioning and sounding techniques available. Actual probing and positive sampling should be conducted at each site to establish a sound basis for project design and later performance evaluations. Such surveys can be quickly conducted if confined to specific sites and pursued vigorously. Neither design nor construction should be done without this step.

From this discussion it should be apparent that the commonly employed process of selection and design and management by the political committees or pressure groups of "practical" watermen, or their allies, supporters or apologists, should not be utilized! The process *has never worked* in either Maryland or Virginia! It will not work in reef restoration efforts! Experienced, competent watermen can and should be involved (especially informed and responsible ones) but actual selection of sites, design or management *must be controlled* by applicable technical factors and by persons qualified to interpret them objectively and scientifically and not by harvester prejudice and preference. The overall interests of the public and its posterity as well as the users and the resource must be represented fully and fairly. History has clearly shown that management decisions based on political popularity or acceptability to industry or on compromise have been wasteful and fruitless! Management efforts of the past 125+ years *have not* achieved desired goals of restoration and subsequent continuation of self-renewing natural oyster populations and sustained yields! Most have failed completely (Kennedy and Breisch 1983, Hargis and Haven 1995, Rothschild *et al.* 1994)). The long-term interests of the general citizens of both states and their natural oyster resources and the potential productivity thereof *have not been well attended* by state managers!

Concerning possible sources of financing for sustained reef programs, each state has undertaken repletion activities for over a half century. Monies devoted to these state programs can and should be employed in state reef rehabilitation programs. Funds designed for habitat restoration and pollution-control activities can also be applied. Additionally, monies allocated to research and technological development could justifiably be used in reef rebuilding programs. Of major importance are careful follow-up studies of each reconstructed reef. Data, which must be collected annually at least (more often if necessary), should include oyster density, setting experience, growth, condition, disease levels, predator levels and mortality. Details of harvests and other removals are needed. Knowledge of applicable environmental parameters is necessary!

There is room for construction of experimental reefs. Some could even depart somewhat from nature's "tried-and-true" experiments. This is not a new concept. Oyster scientists have talked for decades of using experimental reefs to enhance the introduction and spread of scientifically-developed, disease-resistant or faster-growing broodstocks into estuaries with oyster-producing potential (Ruzecki and Hargis 1989). Were broodstock possessing such desirable genetic features available it could be "seeded", or distributed, to existing, rehabilitated or new reef areas by including it among the oyster shells (and live oysters) of the "veneer" layer. Different geometric configurations can be tried as well.

In Virginia the James River estuary has been the most successful, long-lived and persistent producer of seed, soup and market oysters of any estuary in the Commonwealth. At present, about 3,000-4,000 acres of the former James River "seed" area (or 1.5% to 2.0%) is the last economically significant oyster producer (market and seed oysters) of all 199,000 acres of Virginia's Chesapeake public beds. Its remaining producing reefs should be considered prime candidates as the foundation of reef recovery efforts. Because the public oyster reefs of the James have been so productive of market and seed oysters over the years and have actually been the basis of most market oyster production of private planters, restoration of the area is critical to the recovery of private planting activity using native *C. virginica.*

Based upon these factors we have recommended that reef rehabilitation and enhancement activities in Virginia be pursued in the James River "seed" area on a priority basis! This is not to discourage efforts in other areas such as the Piankatank or Great Wicomico seed areas or in the Rappahannock, which has been so productive of market oysters in the past, but the James should be given highest priority. Political pressures to the contrary should be strongly resisted. *Acquisence to them in the past has* *negated effective management of the public oyster resources of the James!*

Similar areas exist in the estuary of Maryland's Potomac River and its middle Chesapeake and in the lagoons and embayments of the Eastern Shores of both states. A larger area and number of Maryland's historically most-productive public reefs are in generally ecologically favorable situations than those of Virginia. Therefore, restoration of her public reefs should be easier and more economical and more quickly accomplished than those in most areas of Virginia's lower Bay.

Aspects of Reef Rebuilding Which Can be Recommended Today for the James River and Similar Estuarine Reaches of the Potomac and Maryland's Mid Bay on Both the Eastern and Western Shores

1. The most rapid and least costly recovery of reefs can be obtained by employing those Hard Oyster Reefs that retain significant (some) vertical relief and shell volume, have living young and adult oysters upon them and are known to "catch" spat. Simple closure, adequately enforced, is all that is required. The better the shape the selected reef is in [*i.e.* elevation above the bottom, firmness, suitable volume (size) and relief and similar geomorphological as well as favorable hydrographic factors] to begin with, the more rapid the recovery will be. Recovery of such active reefs could be hastened by judicial addition of oyster shell to the core, *i.e.* by "lifting" some of the living veneer off and replacing it after core enhancement, or replacing the displaced veneer by addition of living oysters from elsewhere. [Here we have attempted to separate the Hard Oyster Reefs into those with appreciable living oysters and those without (*i.e.* Hard Oyster Reef footprints).] A light "dusting" of clean oyster shells (*i.e.* 2,000 bu. per acre) over the living veneer of Hard Oyster Reefs each year will enhance set and survival in succeeding years. Of the various restorative techniques offered here and below, this is the best since it causes the least destruction to the oysters already living in the veneer. Closing the reef to harvesting for a period suitable to the intended function and future of that reef must follow shelling!
2. Where "living" producing reefs exist, their productivity can be restored and their recovery to former (or new) conditions and dimensions enhanced by adding new core materials, preferably clean oyster shells, to immediately adjacent hard bottoms, thus extending the basal extent of these reefs. Some of the living oysters in the veneer could be gently transferred to the enhanced "core."
3. On reef rebuilding sites with significant quantities of living oysters (*i.e.* 500 to 1,000 bu per acre) in the "veneer" some of the living oysters could be tonged or gently dredged and moved to other areas or stockpiled overboard nearby for replacement in the veneer of the reef being restored. Thus, possible destruction of living oysters by "smothering" would be reduced or avoided.

   However, great care must be exercised in conducting this phase of the operation to avoid destroying that which is being "saved." Moving of living oysters, which might have to be done twice should this course be decided upon, is usually destructive of the oysters being moved as well as those left behind. Perhaps the best strategy in such a situation is to add only small quantities of shells and/or seed, but to do so each year for a number of years.
4. Where appreciable quantities of living oysters are lacking on existing reefs, reef

rebuilding in the James, and similar areas, should take place on the "footprints" of Hard Oyster Rock as identified in Haven et al. 1981.

5. Some "experimental" reefs should be rebuilt or established anew in waters with depths of 1.8-2.4 m (5.9-7.9 ft) at M.L.W. (or greater if funds permit) and should extend upward into the intertidal. This will permit determination of the differences between setting and survival (and of levels of disease and predation) at one vertical level versus another. Provided, of course, that the experimental reefs are closed and protected and the time and methods of sampling and monitoring are adequate. It is extremely likely that the more-or-less persistent microhydroclimatological differences found at the different depth levels (or heights) of active three-dimensional reefs have been important to the overall past successes of those reefs, and will be to the new or restored reefs.
6. Rebuild some depleted reefs in strategic locations by reshelling to a depth of about 1 foot (30 cm). This will raise the bed slightly above the surrounding bottom and enhance setting and allow comparing results between activities numbers 5 & 6. This technique should be effective in areas of low sedimentation rates and on reefs with low disease and predator levels.
7. Where oyster shells are limited in availability reefs with greater vertical height and volume might be built with "cores" of locally-obtained mollusc shells such as surf clams, ocean scallop or oceanic and estuarine hard clam shells since they are similar in chemical and physical composition to oyster shells. However, cores can also be constructed of shale, small stones or cobbles, crushed rocks, railroad ballast stones, ceramics, ceramic and glass fragments (cullet "dulled," of course) bricks, clean building rubble of appropriate size, large stones, rocks or dolmans or even artificial cultch manufactured from other biologically-neutral materials. Whichever is employed, all should be topped with a veneer of clean oyster shell at least 15 cm (6.0 in.) thick. It is known that setting occurs on shell surfaces several inches or more beneath the outer layer of shells. Survival of spat on "interior" shell is often better than on that right at the surface because blue crabs and other such predators cannot get at them readily. The veneer also can be "seeded" with living oysters taken from similar sites to speed rebuilding. Living oysters apparently encourage setting (Hidu 1969). As indicated above, oysters with desired special genetic features could also be employed in the veneer if available.
8. All reefs (reconstructed, rehabilitated or new) must be closed to harvest and closely monitored.
9. Those restored reefs intended for economic harvests (*i.e.* Satellite Oyster Production Reefs—SPR, see Figure 8) should not be opened for harvest until they are ready, and when they are opened it should be done on an "allowable harvest quota" basis only. When the "allowed" harvest level is reached the reef should be *promptly closed* and allowed or even assisted to recover before harvesting thereon is permitted again.
10. Harvest quotas on SPR reefs can be adjusted to accomplish desirable rates of rebuilding as can further replenishment efforts and closure times. The quota concept could be modified or enhanced by employment of other "limited access" techniques but, whichever is employed, harvests must be restricted to the reef population's replacement and survival capabilities and to plans for eventual reef building.
11. Actual establishment of reefs or reef sites must be carefully done by competent personnel using accurate positioning

equipment. Adequate records of positions, including Loran, Raydist©, or GPS bearings (whichever is employed) and latitude and longitude are necessary.

12. Any SPR harvests permitted should be recorded accurately as to amount and kind taken (*i.e.* markets, soups, seeds, etc.) from *each specific reef* and the manner of and the time required for removal. Accurate and detailed knowledge of harvest location and time and effort devoted to harvests must be acquired in order to allow evaluation of success or failure of each reef and of the reef-rebuilding program.
13. Where harvesting is allowed after a reef is restored and producing, *in situ* culling of shell should be mandatory and strictly enforced. After shucking of market oysters, shells should be returned to the public reef program.
14. The status of all public reefs should be established twice yearly (or more as necessary) by careful fishery-independent surveys especially designed for such monitoring efforts.

Possible Sources of Oyster Shells for Cultch

Because their shapes and surface texture were established by the evolutionary processes of many millennia and are found in nature's successful "experimental" reefs, clean oyster shells (preferably recent; secondarily ancient) are the most desirable of all natural cultch materials for "core" construction or enhancement. Other suitable materials may be substituted in core construction if necessary, but clean oyster shells are by far the best material for reconstruction or enhancement of the veneer. For veneer rehabilitation every effort should be devoted to securing oyster shells. Some dilution by other suitable materials might be employed to "stretch" shell supplies, but *no* dilution is preferable.

Unfortunately, due to their destruction, misuse, misapplication and employment elsewhere (*i.e.* private plantings and previous public repletion efforts) oyster shells are now scarce. To secure oyster shells for reef enhancement or replacement programs may require the location of new sources, recovery of previously-used shells, use of mined "fossil"[2] shell, or in Virginia even by renewed harvesting of shells from extinct reefs (they are already being mined in Maryland). To assist in the reef rehabilitation efforts we have considered several different possible sources of oyster shells and offer the following:

WHERE SHELL MAY BE OBTAINED

1. As late as November 1994 shell could be purchased from Langenfelder and Son, Inc. in Maryland and barged to the James River. Cost for 300,000 or more bushels, delivered to the James River seed area was then about $0.62/bu. Since there are 16.7 bushels per cubic yard, the cost was about $10.35 yd^3, according to Langenfelder personnel. Costs would have been higher for delivery to shallow sites since the cost advantages, economies of scale, of shipping in and planting from large, deep-draft barges are lost when shallow-water planting is required and smaller, shallow-draft barges must be used.
2. Recent and ancient shell deposits exist in Virginia. In the 1950s large volumes of shell were mined by a large suction dredge operated by Radcliffe Materials, Inc. in the lower James River. A study by VIMS in the late 1980s showed some "relict" shell deposits in other areas (Hobbs 1988). There are undoubtedly others. Hobb's study was purposely limited; it could be profitably expanded. It is suggested that the VMRC investi-

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[2] These shells may well be merely "ancient" or old and many probably are. Use of the term fossil is probably inappropriate.

gate the possibility of controlled mining of shell for reef rebuilding in Virginia. Shell could be stockpiled on the Craney Island Disposal Area or some similar site for later use. (Incidentally, no further outward expansion of Craney Island disposal area shouild be conducted without prior removal of sub-bottom shells where they exist.)

3. Shell planted by the VMRC previously in areas currently unproductive might be recovered by VMRC dredge boats (or those of carefully controlled contractors —perhaps even paid cooperating watermen) and used again. Locations where shells have been planted are known to VMRC. Cleansing of such shells prior to planting would be important. One or more such boats could be equipped with rotating "washer" drums to clean the shells. Costs of such an operation should be investigated, and gear developed if cost-effective. One of us (Haven) was involved in the design and construction of relevant equipment in the 1970s. And it is known that others were also. Undoubtedly plans survive. It is entirely possible that such equipment still exists and that it is little used and could be acquired inexpensively.
4. In high set areas depleted beds might be restored by using shell currently buried around the margins of the reef. This shell could be lifted from the sand-mud cover by mechanical revolving steel fingers or tines on the head of a Maryland-type soft clam harvester. Such a machine was developed by VIMS in 1973 to harvest oysters and hard clams (Haven et al. 1979). It could be modified and improved to raise and clean old buried shell to be redeposited on reefs being "shelled".
5. For compelling socioeconomic reasons, sattelite production restoration reefs (SPR) might be located near isolated communities such as Smith Island in Maryland and Virginia and Tangier Island in Virginia early on. The inhabitants of these locations have very few choices in remunerative employment.

Summary and Conclusions

Natural oyster reefs consist of a supportive "core" of "cultch" --oyster shells, and shell fragments in a matrix of sand, clays or silts overlain by a veneer of living oysters and shells of the "recently" dead. The core of dead oyster shells continually renewed by receiving the "mortal remains" of successive populations of live oysters living in and on the "veneer" constitutes the greatest volume by far. The core is the reef's "framework" and provides (undergirds) the basic height and contours of the reef.

It is the veneer of the shells of living oysters and recently dead ones which "welcomes" maturing eyed-larvae, receives spatfall, and provides support for the survivors and shelter from predators. The living oysters on and in this veneer encourage the setting of mature larvae. They also filter particulate matter from the water and thereby clarify and cleanse it. Other benefits to living oysters are provided by the upthrusting reefs. Their elevation enables a sizeable portion of the reef's oyster population to be above the disturbing influences of the estuary's bottom thereby reducing the negative effects of sedimentation and of exposure to their own wastes and those of other infauna and epifauna. Also, it is likely that exposure to infective particles is reduced for those individuals on the upper levels of the reef. Zonational microhydrological effects resulting from three-dimensional aspects of such reefs may also enhance setting, survivability, growth, reproduction and recruitment.

The larger (older) mature living oysters of the reef provide the essential genetic building blocks which, given time and proper management, will lead to improvements in such features as rapid, robust growth, disease resistance, adaptation to other natural and man-made stressors. Further, it is these living oysters of the reef's veneer which provide the most spawn and larvae per individual to the home reef, nearby reefs and others "downstream". Of course, smaller and younger sexually mature and reproductively active oysters supply gametes as well.

Rational restoration of existing reefs (i.e. with appropriate elevation), or rebuilding (on old reef "footprints" now at or sufficiently close to the surface to provide a ready foundation) will restore natural oyster production in Virginia and Maryland—eventually. Restoration or rebuilding should be based upon the locations of currently active or recent reefs (preferably) or old ones (secondarily) to take advantage of nature's past successful experimentations. The former dimensions of the historically-productive reefs should be emulated as closely as possible as should the materials employed.

Actual sites for reef enhancement should be selected by competent oyster biologists, with assistance of other scientific personnel, including estuarine circulation specialists, hydraulic engineers, geologists, toxicologists, and such other specialists as may be necessary. Information from knowledgeable and responsible oyster harvesters should be sought. All available relevant information, including past survey and monitoring data, harvest data, information related to current distribution and abundance of oysters (including reliable input from harvesters) should be employed.

To have a significant reef rehabilitation or reconstruction program the successful "designs" of nature (outcomes of countless evolutionary experimentations) should be fully employed, as emphasized above. But, there is room for consideration of alternate materials and different "designs", and even alternate sites, where such might enhance reef rebuilding or replacement activities or where the new reef to be built will perform some desirable purpose. For example, some sites in disease-endemic areas might be chosen for development of disease resistance in surviving reef populations. Those sites now bearing surviving adults should receive priority (of course, surviving older oysters from such areas could be used to provide "resistant" young on reefs being rebuilt in disease endemic areas.) Other places might be selected to enhance filtering of sediments and pollution control to encourage SAV recovery in a specific site or sites. Still others might be selected to provide fishing reefs readily accessible to numbers of sport fishermen. Also, experimentation with alternate materials in selected sites may be desirable to improve reef planning, construction or performance and/or reduce costs. Further, it is highly likely that deliberately designed reef restoration configurations should be used to modify local hydrodynamic features so as to enhance and speed reef rejuvenation.

If rapid (relatively speaking) repopulation is the primary objective, the initial and basic reef rebuilding effort should be directed at those sites which are known to have received "good" sets in the past (and likely could do so again), and/or which offer the best chances of survival. Preference should be given to those with significant populations of living oysters. Seeding with appropriate broodstock could enhance reef rehabilitation. In the James River seed area (and similar systems elsewhere in the Chesapeake) existing productive reefs *are the best such sites!* Numerous suitable reef areas exist. In the James estuary of Virginia priority should be given to those in the Point of Shoals—Swash region, *i.e.* East and South-East of Mulberry Island (see Figures 4 and 5). The Wreck Shoal area, and/or suitable sites nearby, would probably be prime locations for disease-resistance monitoring and experimentation. (In 1992-93 and 1993-94 both prevalence and intensity of MSX and Dermo disease declined in these two areas as did disease-induced mortality.)

Additional studies or surveys may be necessary, especially those directed at location of new or more economic sources of oyster shell. Other activities should be directed at discovering or developing alternate materials for "core" and the non-living portion of the veneer. Studies on costs and availability are needed.

Past oyster repletion programs, while ineffective at restoring natural oyster populations over the long run, do provide information which will help future reef restoration and maintenance efforts. For example, a Maryland study established that 2,240 Md. bushels of "ancient" oyster shells would cover 1 acre of bottom, about 2.5 cm (1 in) deep and at a cost of $1,388 per acre (at the time of that study). Obviously, future shelling efforts or extensive reef rebuilding or construction efforts would be enhanced by careful evaluation of the various options available and of the cost-benefits thereof.

We conclude that restoration of oyster reefs, the "preferred" habitat of our native oyster (*C. virginica*), on the public oyster grounds of the Chesapeake followed by subsequent effective management (as indicated in detail above) offers *the best hope* for restoration of self-renewing natural oyster populations. (Most likely, other aggregating crassostreid oysters do best in off-bottom situations as well.) *Even in areas where* C. virginica *populations are at a very low level, sufficient potential for such renewal exists as to offer the most likely opportunity for "relatively rapid" restoration of oyster populations in the Bay and on the Eastern Shore, and elsewhere.* Surviving, reproductively-capable native oysters occur in many places in the Bay and its tributaries. These resources should be carefully husbanded and employed in the public reef restoration effort in responsible fashion! To be effective, all reef rebuilding or replenishment efforts must be accompanied by effective closures—closures adequate to the purposes of the restoration program. Upon an effective reef renewal program depends the future of the Chesapeake (*C.virginica*) oyster resource and its ecological functions and economic utility. Should Bay "public" oyster populations be allowed to continue their decline into ecological insignificance and economic oblivion the citizens of both states, and their posterity will suffer. And Virginia and Maryland watermen and their posterity will lose access to yet another economically-productive resource. Soft clam and hard clam populations are much reduced in Maryland and self-renewing, harvestable populations of natural hard clams are destined to drop in Virginia. As well, populations and commercial catches of many edible finfish are down Baywide and Chesapeake blue crab populations appear threatened. Economic disappearance of the oyster will seriously reduce the economic opportunities of Chesapeake watermen. It will also cause the attention of remaining watermen to be focussed even more heavily on blue crabs and hard clams and hasten their economic demise.

As matters now stand, the future of public watermen in the Bay is not bright. All of these self-renewing natural resources of the Chesapeake must be carefully and realistically restored and/or husbanded if watermen and their livelihoods and the character, productivity, ecological stability and diversity of the Chesapeake, itself, are to persist. Both Virginia and Maryland should make strenuous efforts to rehabilitate oyster populations by restoring their "favored" habitat, the self-renewing public reefs.

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Economics of Augmentation of Natural Production Using Remote Setting Techniques

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Abstract

Investment and operating costs of producing oyster seed by remote setting of hatchery-reared larvae were analyzed based on a three-tank setting system operating over a five-month period (May-Sept.). Data were gathered from previous field demonstration projects and interviews with oyster producers. Scenarios were budgeted based on manual labor vs. mechanization, and vessel ownership vs. leasing. Costs per shellbag of seed and potential production of market-size oysters were estimated. The estimates included the purchase of oyster larvae from a hatchery at $100/million. Mechanized cultch handling with vessel ownership constituted the most cost-effective scenario, with setting and nearshore nursery operating costs comprising 64% of the cost of production, 14% in vessel operation, and 5% in labor (cultch handling). Such a scenario could produce 20 mm oyster seed at approximately 20/shell at a cost of $4.92/shellbag, averaging 250 shells/bag. A public entity created for seed production and planting on public oyster reefs is hypothesized.

Introduction

Oyster resources have dwindled in many coastal states of the U.S. for decades. Habitat and water quality degradation, disease, overfishing, and natural disasters are major contributors to the decline (Broutman and Leonard 1988; GSMFC 1991). This decline has impacted the oyster industry, which has historically been a major source of employment in many coastal communities. In some states, natural production no longer can support commercial utilization, either by direct harvest to market or by seed production for transplanting onto oyster leases. The decline has also had an ecological impact on estuaries, since oyster reefs provide a vast water filtration capacity (Galtsoff 1964). The lack of production, therefore, creates serious economic, social, and environmental consequences.

Cultch planting is the historical method of maintaining high productivity on public oyster reefs (Perret et al. 1991). Oyster and clam shells are proven, effective, and widely used cultch materials. Shell planting efforts by state agencies may be hampered by several factors, including lack of or untimely funding support, availability of shell, and the lack of and cost of shell recovery methods (GSMFC 1991). Natural spatfall is affected by many factors, including egg and larval abundance, the timing and location of cultch planting, cultch fouling and burial, the physical environment (e.g., tides and currents, wind direction and strength, food availability, salinity, temperature, etc.), and mortality. Such factors make shell planting a potentially inefficient technique to produce oysters.

Remote setting technology utilizes hatchery-reared oyster larvae. It is a proven and consistent method of producing oysters. The technique was developed for the Pacific oyster (*Crassostrea gigas* [Thunberg]) along the Pacific Northwest (Lund 1972; Budge 1973; Henderson 1983) and successful commercial remote setting methods are well documented (Jones and Jones 1983, 1988). The technology has been transferred to the American oyster (*Crassostrea virginica* [Gmelin]) in the Mid-Atlantic and Gulf regions as well (Gibbons 1988; Bohn 1989; Supan 1991; Supan and Wilson 1993). When remote setting is conducted correctly, it provides a more efficient use of cultch by guaranteeing spat production. Oyster shellbags are typically used as cultch and are placed into the setting tank, receive a set, placed nearshore to allow initial growth (nursery stage), then planted on the waterbottom. This technique can improve oyster production if other factors affecting survival are also taken into account.

Remote setting is typically conducted privately by oyster farmers. Profitability is sensitive to initial investment costs, fixed costs, labor and other operating costs, and the ex-vessel price for market-size oysters (Supan et al. 1994). Yet, remote setting of hatchery-reared larvae has potential for augmenting natural production on public oyster reefs as well. This paper attempts to document the costs of producing oysters by a public entity for improving public oyster grounds.

Methods

This analysis approaches oyster seed production, utilizing remote setting technology, as an activity performed by a public entity to produce 48 acres (19.4 ha) of oyster reef per setting season (5-months). The current absence of public entities using remote setting to survey necessitated the development of a pro forma approach. Information was gathered from previous field demonstration work in Long Lagoon, Louisiana and interviews with oyster farmers in Louisiana and Washington. Prices for construction materials represent an average from three sources (price quotes). Other expenses, such as vessel and labor-related costs, were obtained from records provided by oyster farmers. Management and security costs are not included.

The operation was assumed to have a special source of funding or given priority within the public entity's general budget. Therefore, initial investment costs (necessary equipment [tanks, tank pad, truck]) and operating costs are as-

Table 1. Remote Setting Investment Costs: Three Tank System.

ITEM	UNIT	PRICE ($)	QUANTITY	AMOUNT ($)
Tank pad				
nails	lb	1.00	11	11
timbers	each	3.53	60	212
gravel	cuyd	12.00	42	504
rental (roller)	each	30.00	1	30
total tank pad cost				757
Equipment				
tank	each	383.00	3	1,149
plumbing	each	100.00	1	100
air blower	each	290.00	1	290
water pump	each	135.00	1	135
microscope	each	120.00	1	120
tally counter	each	11.00	2	22
total equipment cost				1,816
Truck				**18,000**
Other Possible Equipment				
shell bagger/washer		9,000.00	1	9,000
pallet jack		500.00	1	500
front-end loader (used)		9,000.00	1	9,000
total other cost				18,500
Vessel (used)		12,000.00	1	12,000
Scenario #1, Tank pad, equipment & truck				20,573
Scenario #2, Tank pad, equipment, truck, & other possible equipment				39,073
Scenario #3, Tank pad, equipment, truck, other possible equipment & vessel				51,073

sumed to be absorbed in the entity's budget. Fixed costs that are associated with private enterprise (e.g., average annual investment, annual depreciation, interest on initial investment and operating funds) are not included in this analyses.

This analysis is based on using a three-tank remote setting system similar to that described by Supan (1991), constructed from wood and fiberglass. The individual tanks are 2.4 x 2.4 x 1.2 m in dimension and will each hold 240 shellbags of oyster shell averaging 250 shells/bag. A "set" consists of filling the tanks with shellbags and filtered seawater, adding approximately 100 larvae/shell to the tanks, covering the tanks, and providing aeration for 48 hrs. The shellbags of fresh spat are unloaded onto pallets (sixteen/pallet) and placed in a nearshore nursery area. It is assumed that nearshore nursery conditions will produce 20 mm ± 8 mm seed in 30 days. Afterward, the pallets and shellbags are removed from the nursery area, the shells with attached seed subsequently removed from the shellbags and planted onto an public waterbottom for grow-out.

Investment and operating costs are included in the analyses. Investment costs include those deemed necessary for constructing a remote setting system (e.g., tank pad, tanks, plumbing, pumps, etc.) and other equipment costs (e.g., truck, cultch handling equipment and vessel) (Table 1). Operating costs are estimated for three different scenarios. Scenario 1 represents the use of necessary equipment (e.g., remote setting system and truck), a leased vessel, and manual labor to make the shellbags, load and unload the tanks, and place and remove the shellbags from the nursery area for planting

Table 2. Operating costs for producing oyster seed using a 3-tank remote settings System. Scenario #1: Unmechanized cultch handling; Leased vessel.

Item	Monthly Average ($)	5-Month Setting Season ($)
Setting and nursery		
electricity	25	125
larvae	7,200	36,000
larval shipping	192	960
shellbags	2,736	13,680
pallets	450	2,250
marking poles	122	612
tank maintenance	10	50
tank covers	9	45
subtotal	10,744	53,722
Labor	3,280	16,400
Groceries	576	2,880
Truck		
fuel & maintenance	100	500
Vessel lease	5,760	28,800
Total estimated cost	20,460	102,302

Table 3. Operating costs for producing oyster seed using a 3-tank remote setting system; Scenario #2: Mechanized cultch handling; Leased vessel.

Item	Monthly Average ($)	5-Month Setting Season ($)
Setting and nursery		
electricity	25	125
larvae	7,200	36,000
larval shipping	192	960
shellbags	2,736	13,680
pallets	450	2,250
marking poles	122	612
tank maintenance	10	50
tank covers	9	45
subtotal	10,744	53,722
Labor	1,000	5,000
Groceries	432	2,160
Truck		
fuel & maintenance	100	500
Front-end loader		
fuel & maintenance	200	1,000
Shell bagger/washer		
maintenance	20	100
electricity	100	500
subtotal	120	600
Vessel lease	5,760	28,800
Total estimated cost	18,356	91,782

Table 4. Operating costs for producing oyster seed using a 3-tank remote setting system. Scenario #3: Mechanized cultch handling; Vessel owned.

Item	Monthly Average ($)	5-Month Setting Season ($)
Setting and nursery	25	125
larvae	7,200	36,000
larval shipping	192	960
shellbags	2,736	13,680
pallets	450	2,250
marking poles	122	612
tank maintenance	10	50
tank covers	9	45
subtotal	10,744	53,722
Labor	1,000	5,000
Groceries	432	2,160
Truck		
fuel & maintenance	100	500
Front-end loader		
fuel & maintenance	200	1,000
Shell bagger/washer		
maintenance	20	100
electricity	100	500
subtotal	120	600
Rope	88	440
Vessel		
fuel & lubricants	400	2,000
storage	126	630
maintenance	600	3,000
subtotal	1,126	5,630
Dock access	360	1,800
Total estimated cost	14,170	70,852

Table 5. Cost per bag of seed for each scenario.

Scenario #1	Scenario #2	Scenario #3
$7.10	$6.37	$4.92

(Table 2). Scenario 2 differs by utilizing mechanized cultch (shellbag) handling (Table 3). Scenario 3 involves the use of an owned vessel with mechanized cultch handling (Table 4). The cost per bag of seed for each scenario is also determined (Table 5).

Production estimates of market-size oysters production (200 oysters/sack) from 5 months of setting effort are provided based on four different seed survival rates (Table 6).

Table 6. Potential production and cost of market-size oysters (200/Sack) based on seed survival.

	Survival			
	25%	**10%**	**5%**	**1%**
Total Sack Production	59,400	23,760	11,800	2,376
Sacks Per Acre (48 Acres)	1,237	495	245	50
Cost Per Sack				
Scenario #1	$1.72	$4.30	$8.66	$43.03
Scenario #2	$1.54	$3.86	$7.77	$38.01
Scenario #3	$1.19	$2.98	$6.00	$29.81

COST ESTIMATES & ASSUMPTIONS

This enterprise budget is based on specific cost estimates and assumptions derived from real and perceived needs. The vessel is assumed to be leased by or purchased for use by the public entity. The vessel lease cost of $600/day (including expenses) was derived from a daily opportunity cost of a typical Louisiana oyster vessel harvesting with two dredges during 1991-92, and is similar to rates paid by the USDA Agricultural Stabilization and Conservation Service's Emergency Conservation Program to oyster vessel contractors during 1993 for debris removal from reefs damaged by Hurricane Andrew. The purchase price and development costs of waterfront property were too difficult to generalize, therefore, vessel storage at a marina and dock access fees were included where applicable (Scenario 3). Dock access fees were calculated from fees assessed on "small" sacks (100 count; half-shell oysters) weighing approximately 40 lbs (18 kg) (same as a 250-shell shellbag) unloaded at a public dock facility in Plaquemine Parish, Louisiana. Each scenario is assumed to produce the same number of spat per shell. The cost estimates include:

1) Tank pad measures 19.5 x 8.5 m, with three 2.1 x 2.4 m raised pads for tank draining, framed with landscape timbers and filled with limestone at $12/yd^3.
2) Tanks are constructed of braced plywood with fiberglass interiors and painted exteriors at $383.00/tank (Supan 1991).
3) Truck is a flat-bed, 1-ton pick-up truck for hauling shellbags, purchased new. Fuel & lube equals $25/week x four wks/mo.
4) Six million larvae/set/tank x three tanks x four sets/mo. at $100/million.
5) Larval shipping at $48/wk x four wks.
6) Shellbags at $0.95/bag x 240 bags/tank x three tanks x four wks (9.5 yd^3 of oyster shell @ $16.50/yd^3 + 1.8 m of mesh material/bag @ $0.16/m x 240).
7) Marking poles (for marking pallets of shellbags while in the nursery area) at 3 m of pipe/pallet x 180 pallets/mo x two months ÷ 6 m/length x $3.40/length.
8) 450 pallets x $5.00 (forty-five/wk x four wks/mo x two months + two extra weeks, lasting one season.
9) Three tank covers at $15.00 each, lasting one season.
10) Vessel leased at $600/day x two days/set x four sets/mo x five months + eight additional days. Includes captain & dock access.

SPECIFIC COST ESTIMATES FOR SCENARIO 1

11) Labor at $0.52/ft^3 of tank space to load, unload tanks, place and remove shellbags from nursery area + $1.00/ shellbag [$0.52 x (3 tanks at 8' x 8' x 4')] + $1 x (240 bags/tank x three tanks x four sets/mo).
12) Groceries at $15/day/man x four men x two vessel-days/wk x four wks x five mos + eight additional days.

SPECIFIC COST ESTIMATES FOR SCENARIOS 2 & 3

13) Front-end loader is purchased used. Fuel and lub. equals $200/mo.
14) Shell bagger/washer is custom made. The two conveyors were purchased used.

15) Labor at \$0.52/ft^3 of tank space to load, unload tanks, place and remove shellbags from nursery area + three man crew/day x \$50/man/day x four days/mo (three man crew makes enough shellbags in four days to use all month).
16) Groceries, etc at \$15/day/man x three men x two vessel-days/wk. x four wks x five mos + eight additional days.

Specific Cost Estimates for Scenario 3

17) Dock Access at \$0.125/shellbag x 2,880 shellbags/mo.
18) Rope at 3.35 m of 9.5 mm (dia.) rope & 1.2 m of 12.7 mm (dia.) rope/pallet; 9.5 mm rope (roll) at \$30.00 x 8 = \$240; 12.7 mm rope (roll) at \$50.00 x 4 = \$200 (guy ropes for mechanized handling of palletized shellbags from the nursery area;
19) Purchased vessel is a 6.1 x 12.2 m self-propelled spudbarge with crane, purchased as used oil field equipment. Fuel & lub., storage, and maintenance costs represent a nine-year average for a 18.3 m oyster vessel, adjusted to a daily, monthly or annual rate. Maintenance includes annual haul-out, paint, solvents, welding, etc. but does not include extraordinary annual costs (new engine, light plant, etc.).

Results

There is a wide range of costs associated with remote setting, depending upon assumptions. Estimated remote setting investment costs are \$20,573 for Scenario 1, \$39,073 for Scenario 2, and \$51,073 for Scenario 3 (Table 1). Seasonal (five-month) operating costs range from \$102,302 for Scenario 1 to \$70,852 for Scenario 3 (Tables 2-4).

The costs associated with producing a shellbag of seed range from \$4.92 for Scenario 3 to \$7.10 for Scenario 1 (Table 5). Mechanized cultch handling reduced the cost per shellbag of seed by 8%. Additional vessel ownership further reduced the total cost by 17%.

Three-hundred shellbags of remote set seed are typically planted per acre by oyster farmers (Wiegardt 1991). Based on our assumptions, it would cost a public entity \$1,476 to \$2,130/acre to seed an oyster reef using remote setting (Table 5).

Discussion

Based on our assumptions and cost estimates, a public entity using remote setting could seed a 48-acre oyster reef for \$70,852 to \$102,302. Mechanized cultch handling and vessel ownership appears to be the most cost-effective scenario. Annual cost of vessel ownership is approximately \$16,052 versus an annual leasing cost of \$28,800. This ownership cost is comparable to the average total daily expense of \$337 for planting “wild” seed (i.e., \$337 x 48 vessel-days = \$16,176) during 1988-90 (Melancon and Condrey 1992).

Production estimates can be used to calculate the return of market-size oysters. The following calculations were used to estimate production based on Pacific Northwest and Louisiana remote setting experiences (Table 6):

- 6 million larvae/tank x 3 tanks/set= 18 million larvae/set;
- 18 million larvae/set, 20% setting rate = 3.6 million spat;
- 3.6 million spat @ 66% survival = 2,376,000 seed;
- 2,376,000 seed x 4 sets/month = 9,504,000 seed/month, and;
- 9,504,000 seed x 5 months = 47,520,000 seed/setting season.

Production would be approximately 59,400 sacks (1.5 bu, ca. 200 oysters/sack) at 25% survival to market-size, 23,760 sacks at 10% survival, 11,800 sacks at 5% survival, and 2,376 sacks at 1% survival, a 4:1, 1.6:1, 0.82:1, and 0.16:1 sack return ratio (Table 6). A 3% return of market-sized oysters from the amount of larvae used in the setting tank(s) is common for commercial remote setting using shellbags and onbottom grow-out; with this production estimate it would equate to 54,000 sacks. An average return of 1.1:1 was estimated by Melancon and Condrey (1992) in their study of Louisiana oyster farming using "wild" seed oysters, with a 0.14:1 return necessary to break even. Yield ratios of 0.4:1 to 1.68:1 (Melancon 1990), 0.89:1 and 1.52:1 (Mackin and Hopkins 1961) and 3:1 to 4:1 (Perret and Chatry 1988) have also been estimated using wild seed, although Dugas (1977) suggests that a reasonable average for using wild seed in Louisiana is 1.21:1.

The accuracy of survival estimates depends mainly on seed size at planting. Nearshore nursery conditions using shellbags in Louisiana routinely produced 20mm ± 8mm seed in 30 days with a 33% mortality due mainly to *Styloccus* sp. predation. Survival to market-size averaged 2.5 oysters/shell within 24 months. Krantz et al. (1984) found that Maryland growing conditions produced a 20 mm seed oyster in 13 weeks with a 10% survival at 1 year with a unit cost of $13.86/1,000, but recommended a 26 week-old seed (40 mm) for planting with a 50% survival at 1 year with a $3.66/1,000 unit cost. With Louisiana production and survival results with a $4.92 cost for a shellbag of 3,375 seed oysters (250 shells/bag x 20 spat/shell with 66% survival during the nursery stage x 22% survival to market-size [2.5/shell]) would have a comparable unit cost at 2 years of $6.78/1,000 at, similar to 20 week old spat planted in Maryland at a unit cost at 1 year of $6.43/1,000 (Krantz et al. 1984). Beside seed size, survival will depend mainly on waterbottom characteristics at the planting site, and exposure to disease and predation during grow-out.

Perhaps the assumption that funding is available to a public entity to utilize remote setting is irrational. This may indeed be a stretch of the imagination, since funding is a major problem in conducting oyster reef management by public agencies (GSMFC 1991). Smaller public entities, such as county or community governmental agencies, commissions or boards may not have suitable budgets for this assumption. A revenue bond may be necessary in order to obtain the investment and operating capital to utilize remote setting and harvesters of this "renewable resource" may be required to pay for the privilege. Principle and interest payments would be included as fixed costs to be factored into total cost analyses, similar to the opportunity cost of financing remote setting by private enterprise (Supan et al. 1994).

This analyses also assumes that liability insurance is provided at no direct cost to the remote setting operation. Handling shellbags is very laborious and shellbags placed in a nearshore nursery stage, though adequately marked, can both expose the public entity to litigation. Risk management is provided at the state and county level, but may be an additional cost for smaller public entities. Insurance would also be an additional fixed cost to be factored into determining the total cost of producing remote-set seed.

This economic analysis of augmenting natural production describes the costs that may be associated using remote setting by a public entity. There may be more, such as principal and interest on revenue bonds, insurance, and/or a salaried biologist to manage and provide surveillance for the operation. There may be less; front-end loaders, vessels and docks may be already owned and/or available, and "voluntary" prison labor may be used (Posadas et al. 1991). Other such direct and indirect cost must be determined on a case by case basis.

Remote setting is fundamentally a low-cost technology for producing seed oysters, as is recommended by Krantz et al. (1984) to suppliment a public fishery. We agree with their recommendation, however, that public entities should also focus on the privatization of oyster production through a progressive leasing program.

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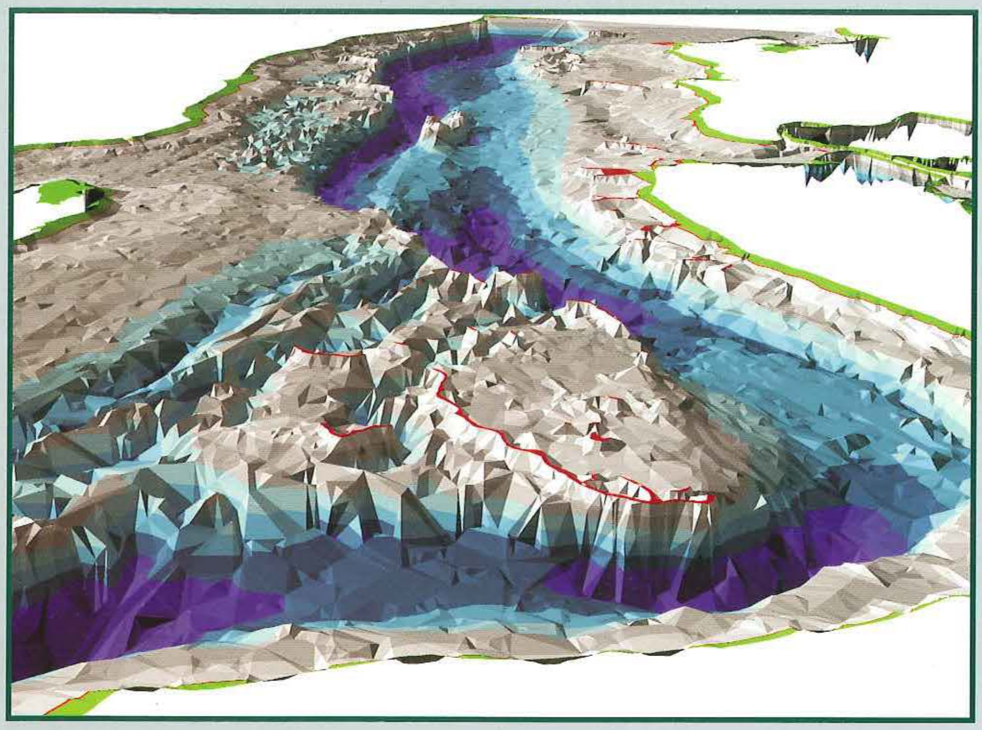

These cover illustrations, three-dimensional images of the bottom topography of the James River oyster reef system in Virginia's lower Chesapeake Bay, were prepared from hydrographic soundings made by the U. S. Coast Survey from 1871-1873. Clearly shown are the prominent oyster reefs and reef fields of the lower James estuary. On the front cover is a view looking upriver from Newport News Point. The image on the back cover represents the massive oyster reefs and reef fields of Burwell ('s) Bay.

These illustrations are from *Bathymetry of the James River Oyster Reef System in 1871-73* by W. J. Hargis, Jr., Helen E. Woods, Sharon Dewing, Marcia R. Berman, Rebecca C. Arenson, and Elizabeth M. Mountz of Virginia Institute of Marine Science, School of Marine Science, College of William and Mary. All images were produced using ArcView© from original nineteenth-century data.

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