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Restoration of the Oyster Resource in Chesapeake Bay: The Role of Oyster Reefs in Population Enhancement, Water Quality Improvement and Support of Diverse Species-Rich Communities

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Restoration of the oyster *Crassostrea virginica* resource to the Chesapeake Bay is a widely supported goal. The role of the oyster in restoration through benthic-pelagic coupling is examined in the context of current and projected watershed management problems, agricultural and urban development with associated nutrient and sediment erosion issues, in the entire Chesapeake Bay watershed. Efforts to date have focused on rebuilding three-dimensional reef structures, often with oyster broodstock enhancement, in predominantly small estuaries with retentive circulation to provide demonstration of increased resultant recruitment. Fishery enhancement activity is then based on local increases in recruitment. Such examples are used to increase public awareness of the success of restoration processes and increase long-term participation in such programs by schools, non profit and civic organizations, and commercial and recreational fishing groups.

The history of the decline of the oyster populations of the Chesapeake Bay has been described many times. The story extends from the pioneering surveys of Baylor,[1] to the commentaries of de Broca,[2] Ingersoll,[3] and Brooks,[4] to later monographs of Hargis and Haven and co-authors,[5-7] to extensive descriptions of disease related losses since 1960, to the summaries of Governor-appointed working panels in both Virginia (in 1994) and more recently in Maryland (1998-1999). There is a groundswell of support for oyster restoration for both ecological purposes, based in the growing realization of the role of the species in benthic-pelagic coupling,[8-10] and fishery restoration. Indeed, these efforts have been celebrated as central to a national effort to restore habitat structure (oyster reefs) as part of both oyster enhancement programs and in support of essential fish habitat restoration.[11] The scientific community, with the support of the political establishments of the Chesapeake Bay states, has been challenged to reverse the long-term trends of decline and effect a ten-fold increase in the Bay population by 2010. The response to this challenge has many components including the need for physical restoration of oyster habitat as described earlier. Such efforts however, need to be sensitive to both environmental limitations and the biology of the target species.

Given the long-term commitment to oyster restoration as an ecological benefit, two immediate questions arise: what form should the restored habitat take, and where should we put it? Oysters are reef-forming organisms; indeed an oyster reef is both a biological feature and a geological feature in estuarine systems. The oyster reefs in the Chesapeake Bay were formed over the past 10 000 years as the bay was inundated by rising sea level. We have increasing evidence to suggest that reefs supported complex communities of invertebrates and associated resident and transient fish populations. Also, we know from numerous historical accounts and formal navigation charts that reefs were intertidal as late as the middle of the nineteenth century. Vertical relief is now markedly absent from most reefs in the Chesapeake Bay; indeed recent calculations based on stock assessment by the author and Dr. James Wesson of the Virginia Marine Resources Commission indicate that shell substrate on most productive oyster bottom in the Virginia portion of the bay is so limited that if it was spread out as a uniform layer it would, in most reef locations, be less than 3 cm thick! Three-dimensional reefs arguably offer many attractive options for restoration — but where do we build them? Fortunately, the comprehensive pre-1900 surveys of Winslow in Maryland and Baylor in Virginia provide superb substrate maps of the former and currently productive oyster regions in the respective states. These maps document the end product of 10 000 years of reef accretion and allow restoration to place newly constructed reefs on the footprints of former natural reefs; however, the choice of location of restoration efforts within the enormous bounds offered by this extensive archive of data is subject to a number of major constrictions.

Oysters in the Chesapeake Bay are currently restricted to relatively low salinity regions by the endemic diseases *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus* (Dermo). This would argue for placement in the upstream sections of rivers. Unfortunately, these regions are also characterized by extreme estuarine conditions of high turbidity. Adult oysters can grow in these locations despite these high suspended inorganic particle loads because they posses highly developed particle sorting capability on the gills and labial palps.[12-15] This allows them to reject the inorganic particles as pseudofeces and maintain ingestion of organic particles; however, these same conditions are perilous for the larval phase of the oyster because they do not have a comparable particle sorting capability.[15] Indeed there are strong arguments to suggest that oyster larval growth and survival in Chesapeake Bay is compromised by the combination of low salinity and high turbidity in that when larvae encounter water column conditions in which available food is essentially diluted by significant quantities of inorganic material they functionally starve, despite an apparently adequate absolute concentration of food, because the relative food concentration is low. Further, larval viability in these high turbidity regions may be compromised by origination from adult populations that reside in suboptimal salinities.[16] The cumulative limitations of origin, turbidity, and food result in larval survival and recruitment being very sensitive to marginal changes in any one of the above environmental variables, with the result that recruitment varies by orders of magnitude on an interannual basis.[17-20]

Although regions of high turbidity have always existed in the Bay sub-estuaries, they were likely much smaller and spatially limited in pre-colonial times. This was when the water sheds were more forested, there was an absence of extensive agriculture, and extensive sea-grass beds and three-dimensional oyster reefs limited the effect of wind fetch on sediment suspension.[21-23] Indeed, the often quoted logs of Captain John Smith in his early voyages on the James River describing how he could see the river bottom beneath his modest trans-oceanic sailing vessel attest to water clarity in the mesohaline zones currently occupied by oyster populations. Turbidity levels are likely to have been exacerbated by the loss of suspension-feeding oysters which may have been crucial in reducing turbidity.[8] Therefore, there is likely to be a negative feedback between the removal of oysters (first overharvesting and now a combination of harvesting and diseases) and turbidity becoming ever less conducive to oyster larval survival. Other cumulative effects (arguably many years or even decades) stem from non-point source runoff of sediment, mostly associated with agricultural practices in the Bay watershed. While the widespread adoption of no-till farming in combination with buffer zones has accelerated amelioration of non-point source issues, there remains a proverbial "long way to go" in eliminating this challenge to resident filter feeders in the recipient waters of the Bay. Both non-point and point-source runoff add nutrients to the Bay ecosystem, and there is a politically stated and strongly supported ongoing effort to reduce nutrient input to the Bay, thereby decreasing associated eutrophication and its ecologically debilitating endpoints (e.g., seasonal hypoxia in deeper waters of the Bay, undesirable algal blooms, and more). Subsumed within these parallel efforts there is need to consider the confounding influences of turbidity and nutrient enrichment. Consider that in the absence of a significant turbidity problem nutrient reduction policies are essential to reduce hypoxia because there is inadequate benthic pelagic coupling to remove the resultant phytoplankton by filter feeding —the oyster populations, once the great benthic-pelagic couplers, are no longer present in sufficient numbers.[8] Ironically, current watershed management practices that emphasize nutrient reduction policies in excess of concomitant sediment load reduction may serve to exacerbate larval survival in receiving waters. In summary, the reef placement issue has obvious limitations—downstream limitations of disease and the upstream limitations of turbidity dictate a clear mid-estuarine region within which efforts should be focused.

Under the guidance of the Shellfish Replenishment Program at the Virginia Marine Resources Commission a reef-based restoration effort was initiated in the Piankatank River in 1993 with construction of a single reef at Palace Bar (site A on Figure 1). This site was chosen because the river is small (thus any effect of restoration would arguably be seen in comparison with background variability), has trap-type retentive circulation that is enhanced by the spit structure at its mouth, and a small tidal range. In addition the watershed is devoid of urban development and has only limited agricultural activity, both of which minimize undesired run-off. Construction is described in Bartol and Mann.[24] No broodstock addition was effected at the site, which has been intensively studied since that time in terms of oyster recruitment and growth,[25] dis-

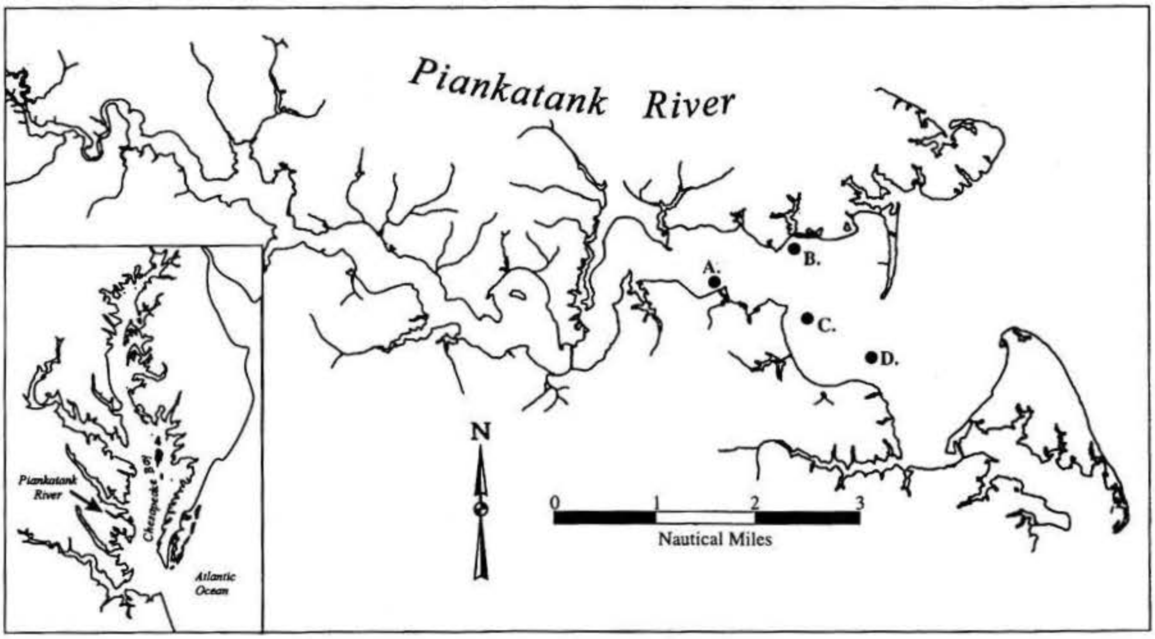

Figure 1. The Piankatank River on the western shore of the Chesapeake Bay. A is the site of the original 1993 reef, with B, C and D being sites of additional reefs constructed from 1997 onwards. Note the small size of the watershed, and the spit on the northern shore of the mouth of the estuary which contributes to retentive circulation of water and entrained larvae.

ease progression in recruited oysters,[26] and development of associated fish and benthic communities.[27,28]

Since 1996 further reefs have been constructed. Within Chesapeake Bay, reefs were added in the Great Wicomico in 1996, and Coan River and Yeocomico River in 1997. Reefs have been constructed in Lynnhaven Bay and at Fisherman's Island at the southern tip of the Eastern Shore in 1995-1996. The Great Wicomico reef was the subject of intense evaluation in the summer of 1997.[29] The Great Wicomico River, although small, was regularly identified as a region of high oyster spatfall prior to the decimation of resident oyster populations by the combined effects of Tropical Storm Agnes in 1972 followed by MSX and *Perkinsus*. The circulation of the river, like that of the Piankatank, served to retain planktonic oyster larvae originating within the river (a factor also influencing the choice of the Coan, Yeocomico and Lynnhaven as reef sites). The lack of resident oysters in the river was confirmed by surveys in late 1995. A chain of unexpected circumstances led to the use of the Great Wicomico reef as a broodstock enhancement site. In late 1996 the Virginia Marine Resources Commission (the regulatory body in Virginia) voted to open the oyster fishery in Pocomoke and Tangier Sounds with a quota not to exceed 2500 bushels (88 100 L) of oysters, to buy back the oysters at US$20/bushel, and transfer them to the Great Wicomico reef. Together with buy-boat transfer charges, this decision approved expenditure in excess of US$50 000, a sum similar to construction cost for the reef itself. The transfer resulted in a resident oyster population with a very high reproductive potential because of the high density of large oysters. Estimated egg production was 4.5 billion eggs per square meter, or about 45 times more than that of oyster populations on the reefs constructed on the Piankatank River, and at least one order of magnitude higher in spawning potential in terms of numbers of eggs produced than any extant reef in the Chesapeake Bay! This analysis provoked the question: "Is the added initial cost of broodstock planting worth it?" The conceptual problem can be answered as follows: If the intent of sanctuaries is to develop actively breeding populations with higher than typical resistance there is good argument for aggregating the few remaining oysters from disease-endemic areas where they are so sparse that fertilization efficiency of freely released eggs is minimal or absent. What about the practical answer? Based on data obtained for summer 1997 observations, I suggest the answer is probably also yes.

It is notable that, in the donor locations, extant oyster population density is too low to effect reasonable probability of fertilization success and subsequent recruitment. Calculations of estimated fecundity of the resultant Great Wicomico reef population suggest that oyster egg production from this source is within an order of magnitude of total egg production in the Great Wicomico River prior to Tropical Storm Agnes. Field studies in 1997 indicated spawning by reef oysters from July through September, while plankton tows recorded oyster larval concentrations as high of $37\,362 \pm 4380$ m^{-3} on June 23! Such values are orders of magnitude higher than those typically recorded in Virginia subestuaries of the Chesapeake Bay in the past three decades, and strongly endorse a premise of aggregating large oysters to increase fertilization efficiency. Drifter studies suggest strong local retention of larvae, a suggestion reinforced by marked increases in local oyster spatfall on both shellstring collectors and bottom substrate in comparison to years prior to 1997. While disease was evident in the population — *Perkinsus* prevalence increased from 32% in June to 100% in July and intensity increased from June to September — the Great Wicomico effort demonstrates that a choice of location where local circulation promotes larval retention with the combination of reef construction and broodstock enhancement can provide an accelerated method for oyster population restoration. Following the above observation in the Great Wicomico, other reef sites have been added in the Piankatank (Fig. 1, B through D) that are also part of a broodstock enhancement program using large oysters collected from high salinity regions of the Bay where disease pressure remains high. Similar efforts are underway in two small tributaries of the Potomac River (the Coan and Yeocomico), the Elizabeth River, Pungoteague Creek on the Bay side of the Easter Shore of Virginia, and Lynnhaven Bay on the south shore of the Chesapeake Bay mouth. In addition, reefs of various substrate types have been constructed at Fisherman's Island at the southern tip of the Easter Shore of Virginia and are the site of continuing intense study by Mark Luckenbach and collaborators based at the Virginia Institute of Marine Science Wachapreague laboratory.

So we have a promising approach to restoration of oysters in small trap-type estuaries. But, it is important to emphasize that restoration benefits other species in addition to oysters.[27,28,30] Oysters improve water quality by removing a portion of the phytoplankton standing stock, and they provide a structured habitat that may increase production of finfish and decapod crustaceans such as crabs.[31] Extrapolations from laboratory filtration rates,[8,32,33] direct field measurements[34] and models[9] demonstrate the role of oysters as cornerstone organisms whose ability to reduce phytoplankton contributes to reduction of eutrophication in coastal waters.

Inevitably the question arises as to the applicability of these small studies to larger subestuaries in the Chesapeake Bay and to the mid-Atlantic in general. Scale is a daunting issue for restoration, not just in terms of spatial and temporal coverage, but equally so in terms of money and continued public support over extended periods. In Virginia we have recently begun a bold program that addresses the next step in scale. The Virginia Oyster Heritage Program proposes to restore oyster resources in the lower Rappahannock River by employing reef-building techniques previously developed in small subestuaries. A comprehensive survey of the current status of the resident lower Rappahannock oyster stocks in terms of absolute abundance, demographics, and disease status was completed in the fall of 1999. Reef construction began in the spring of 2000 and continues as this manuscript is being written. This is an exciting time and reports of progress with this venture will be the subject of future articles. In examining the issue of scale in context of restoration of oyster populations in the entire Chesapeake Bay some numbers illustrate that this will be a long-term effort. The Chesapeake Bay is 298 km long (185 miles), has a surface area of 8484 km^2 (3277 sq. miles) and has a volume of 71.5×10^9 m^3. The combined watersheds of the subestuaries of the Bay stretch from the Appalachian Mountains in the west to near the Canadian border in the north. The resident population of the watershed is approximately 15 million, but with growth projections as high as another 3 million over the coming 20 years. Whereas 90% of the watershed was forested during early Colonial times that number is nearer 60% today. All of these numbers illustrate pressures upstream, which are concentrated downstream in the regions of restoration effort, often with sufficient geographical removal to have the source of the problem fail to appreciate the impact when it is "not in my back yard." We have a long way to go, but education and citizen involvement are becoming the strongest tools to ensure a long term and successful effort in restoration.

The Virginia oyster restoration effort involves active collaboration of a number of workers, and it is a pleasure to acknowledge the contributions of my colleagues Mark Luckenbach, Juliana Harding, Melissa Southworth, Ian Bartol, James Wesson, Francis O'Beirn, and Janet Nestlerode. Financial support for field efforts have been provided by general funds from the Virginia General Assembly to the Virginia Institute of Marine Science and the Virginia Marine Resources Commission, and grant funds from the National Oceanic and Atmospheric Administration (through the Virginia Department of Environmental Quality) and the Environmental Protection Agency. Partial support to the author during the period of manuscript preparation was provided by National Science Foundation grant *number OCE-9810624. Support to present the manuscript at the session "Interaction between Aquaculture and the Environment" at Aquaculture Canada 2000 was provided by the Aquaculture Association of Canada. The invitation to present the manuscript by convener Prof. Gilles Miron is gratefully acknowledged. This is contribution number 2379 from the Virginia Institute of Marine Science.*

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