Status Report on Oyster Restoration in Chesapeake Bay

Testimony to House of Representatives Subcommittee
on Fisheries Conservation, Wildlife and Oceans

December 13, 2004

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Chairman Gilchrest posed four questions in his request that I testify before the subcommittee:

1) *What is the ecological role of oysters in the Bay?*
2) *What is the status of native oyster populations in the Bay and what are the controlling factors on oyster populations?*
3) *Have oyster restoration efforts been successful?*
4) *What would be the ecological consequences of introducing non-native oysters to the Bay?*

My testimony is organized under each of these questions.

1) *What is the ecological role of oysters in the Bay?*

The economic significance of the eastern oyster harvest in Chesapeake Bay has long been recognized. What has only become widely appreciated in recent years is the importance of the oyster in the ecological functioning of Chesapeake Bay. Because the major declines in oyster stocks happened over 100 years ago, and there have been other changes in the watershed associated with increasing urbanization, higher nutrient inputs, and atmospheric deposition, direct evidence for the oyster's ecological role is difficult to obtain. But over the last 15 years a substantial body of scientific literature has been published that supports the concept that oysters were once a keystone species within the Chesapeake Bay ecosystem. Many of the scientific studies that support the ecological importance oysters are listed in an attachment to this testimony. Key points from these studies are summarized below.

Historically, oysters were important in maintaining water quality by removing algae and silt from suspension and enhancing rates of nitrogen and phosphorus removal. The effects of abundant oyster stocks on water quality, nutrient dynamics and Chesapeake Bay food webs have been elucidated though experiments and a variety of independently-developed mathematical simulation models (publications listed in the attachment). Though these models differ in their approaches and assumptions, they consistently predict substantial ecological impacts of increased oyster biomass, including reduced phytoplankton biomass, increased water clarity, improvements in bottom oxygen concentrations and expansion of seagrass beds. These models have revealed that even a 10-fold increase in oyster biomass over present levels (which is still well below historical levels of a century ago) would result in significant improvements in each of these environmental parameters. One study indicates that expansion of intensive, off-bottom oyster aquaculture could substantially reduce phytoplankton biomass and thus improve water quality in Chesapeake Bay.

One means of expressing the ecological importance of oysters is to estimate the relative economic value of harvesting oysters compared to leaving them in the Bay to provide ecological services. Roger Newell and colleagues from the University of Maryland have calculated that the value of nitrogen and phosphorus removal by the currently depleted oyster stocks in the middle to upper Choptank River is approximately $315,000 per year. While this is less than the estimated $1.5 million dockside harvest value of these oysters, if left in the river, these oysters would continue to generate nutrient reduction benefits throughout their life span, which in this region of the estuary where disease is generally not an issue would likely be 10+ years in the absence of harvesting. Over a 10 year period, the ecosystem value of the current Choptank River oyster stocks increases to $3.1 million, or over twice their harvest value. This analysis does not include the economic value of the hard reef substrate as habitat for many other animals species that have value for commercial and recreational fisheries.

It is now well established that the hard bottom substrate formed by natural oyster reefs does provide valuable habitat for many species of invertebrates and fish (see list of appended scientific studies). Oyster reefs provide nesting sites for ecologically important demersal fish species, they provide refuge for juvenile blue crabs that may be comparable to that provided by seagrass beds and they enhance biodiversity. By providing refuge and by facilitating the transfer of excess phytoplankton production to higher trophic levels, oysters can increase the production of ecologically- and economically-important finfish species within Chesapeake Bay.

In summary, a considerable body of research has established that oyster populations can have far-reaching ecological effects and it is clear that at historical abundances, they were extremely important components of the Chesapeake Bay ecosystem, affecting water quality, biodiversity and fish production.

2) *What is the status of native oyster populations in the Bay and what are the controlling factors?*

Bay-wide oyster populations have continued to decline in recent years despite restoration efforts. These declines are reflected in fisheries landings which have fallen to record lows in both Virginia and Maryland. During the latest season for which there are complete data, the 2003 – 2004 harvest season, landings were 55,840 and 18,714 bushels in Maryland and Virginia, respectively. Fishery independent estimates of bay-wide oyster populations reveal an increase in total numbers of oysters in 2002 (the latest year for which bay-wide estimates are available) to an estimated 4.8 billion, but this was accompanied by a decrease in total biomass of oysters. These numbers reflect both increased recruitment of oysters in some parts of Virginia and high drought-related disease mortality of older oysters. (See http://www.vims.edu/mollusc/cbope/basin.htm for more complete details of these estimates.) This decline continues to be driven by mortality caused by disease, low recruitment, poor water quality, harmful algal blooms, poor substrate quality and harvest.

Several years of drought from 1999 through 2002 resulted in the spread of disease into previously low salinity areas, particularly in Maryland, and greatly exacerbated mortality due to disease. While the relationship between disease mortality and salinity is generally considered straightforward—little or no disease mortality below 10 ppt, increasing mortality from 10 – 14 ppt and high mortality above 15 ppt—the story is actually more complex. During this recent drought period, there was good evidence that oysters in some high salinity areas of Virginia were developing resistance to MSX.

Moreover, in the high salinity coastal bays on the seaside of Virginia's Eastern Shore oyster populations remain much healthier than in the Bay. Diseases still cause mortality in the coastal bays, but at lower rates than in the Bay and recruitment of new oysters remains high. Within the Chesapeake Bay, however, disease remains a very significant factor controlling oyster populations and impacting restoration efforts.

The amount of clean oyster shell available for oysters to settle and metamorphose onto has been declining since the overharvesting practices of the 1880's. Harvesting oysters erodes the reef structure, increasing its vulnerablity to siltation associated with sediment resuspension and land runoff. The oyster repletion programs run by the states of Maryland and Virginia, and more recent restoration efforts by the Army Corps of Engineers, have attempted to redress this issue through the planting of oyster shell. However, there is a limited supply of good quality oyster shell available for use in these programs and the mining of "fossil" shell is costly, can have associated environmental consequences and provides substrate of variable quality. It is important to note that hard substrate can be a limiting resource for other species in the Bay (such as barnacles, ribbed mussels, sponges and encrusting organisms) and many of these may compete with oysters for this space on planted shells, especially in the lower Bay. For instance, boring sponges (*Cliona* spp.) in some areas of Virginia cause significant destruction of the shell material that is planted for oyster restoration. Additional research into the effectiveness of alternative settlement substrate material would be valuable in overcoming some of the limitations currently posed by oyster shell availability.

Recruitment of oysters varies both spatially and temporally in Chesapeake Bay. Inter-annual variation in recruitment is very high, but the long-term trend has been decidedly downward. In addition to the limitations posed by the availability of clean substrate, an important factor contributing to the declining recruitment is the reduction in number and density of adult oysters that serve as brood stock for the subsequent generation. The combined results of harvest, disease and other natural mortality has been to reduce adult oyster densities on many of the oyster beds to levels at which not only is total egg production low, but low fertilization success likely further reduces the production of larvae.

Once new recruits settle onto the bottom, mortality rates due to predation can be exceedingly high, reaching as high as 98% in as few as several months in one study. This predation is a natural phenomenon and not the cause of the decline in oyster populations, but it is a very significant factor affecting restoration efforts. It needs to be accounted for in the design of restoration projects and included in projections of potential oyster population growth rates (whether native or non-native oysters are being considered).

It is also clear that water quality can be a factor controlling oyster populations at some locations. Blooms of the harmful algal species *Prorocentrum minimum* or "mahogany tide" during 2000 and 2001 appear to have been responsible for significant mortality of oysters in both Maryland and Virginia. Low dissolved oxygen concentrations have also been associated with the lack of success at some reef restoration sites.

A recent study explored the effects of oyster harvest on the continuing decline in oyster abundances in the Maryland portion of the Bay[1]. The study used both fishery-dependent and fishery-independent data to develop a population dynamics model for oysters and to explore the consequences varying levels of harvest and different management strategies. Results from this study suggest that if oyster harvests in Maryland had been reduced after the disease epizootics associated with the drought in the mid-1980's then oyster stocks would have recovered quite rapidly in some locations, instead of today's continuing declines. Harvests are at all-time lows and the oyster industry in both states is on the verge of collapse, thus discussion of the potential impact of harvest invariable sparks heated debate. But we must recognize that if we are going to ever re-build functional oyster reefs and an oyster population in the Bay, we will have to have some productive areas from which we do not harvest oysters.

3) *Have oyster restoration efforts been successful?*

The answer to this question depends upon our goal(s). If the goal of our restoration effort is to restore the oyster fishery to some historical level in a relatively short period of time, then the answer is a resounding "no". Even if our goal is to stem the decline in oyster fishery landings, then the answer is still "no". But if our goal is to begin the long, arduous process of rebuilding oyster populations, that have been in decline for over a century, with the hope that they might one day provide important ecological benefits and, perhaps, support a more sustainably -managed fishery, then my answer is a mix of "yes", "no" and "maybe". Without a doubt, some individual reef restoration efforts have proven to be complete failures. In some instances shell has been planted at sites that failed to get an adequate recruitment of oysters to even begin the process of building a reef. At others, anoxic bottom waters have killed oysters. In one widely reported case, hatchery-produced brood stock oysters were added to a reef and cownosed rays consumed most of them. Diseases have taken a very large toll on oyster populations at many restoration sites. But again, we need to ask, *What are trying to restore?* It is completely evident that if our restoration goal is to restore oyster harvest, in the short-term, then an episode of mortality from disease that kills 80% of the year class of oysters that is just reaching market size is devastating and represents a failure. But, if we are trying to restore populations over the long-term, 20% survival in this year class may be sufficient. Maybe 10% is sufficient. Unfortunately, we have rarely looked at the situation this way. Absent fishing mortality, we can sustain and grow an oyster population as long as recruitment exceeds natural mortality, even if natural mortality is high. We truly need to employ a much more population dynamics-based approach towards our restoration and management efforts.

I will discuss two specific cases because they highlight some of the potential for success and some of the pitfalls in maintaining a short-term focus. In Maryland, the Oyster Recovery Partnership is coordinating intensive oyster restoration activities in many of the tributaries in the middle and upper Chesapeake Bay. Although these

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[1] Jordan, S. J. and J. M. Coakley. 2004. Long-term projections of eastern oyster populations under various management scenarios. *J. Shellfish Research* 23:63-72.

restoration projects are relatively small in aerial extent (1,000 to 4,000 m^2), oysters in these areas typically have low disease prevalence, high survival and good growth, resulting in oyster densities in excess of 150 oysters > 7 cm in length per sq. meter (more data on these restoration sites are available at www.life.umd.edu/biology/paynterlab). Some of these reefs have been opened to harvest in recent weeks. Although some of the watermen are disappointed in the size of the harvest from these reefs, numbers of large (> 100 cm in length) oysters removed from them has been significant—to the oyster population, if not to the economy. Unfortunately, this approach, which relies upon placing hatchery-produced juvenile oysters onto shelled bars and then later harvesting those oysters, is unlikely to be sufficient to achieve large-scale restoration and support a fishery at the same time. Even the new production-scale hatchery at Horn Point Laboratory, University Maryland Center for Environmental Science, will only be able to produce sufficient larvae to replant about 200 acres of oyster bottom annually, up from the current 30 to 50 acres. With approximately 200,000 acres of historical oyster bars in Maryland[2] it would take 1,000 years at this pace to plant all of these bars with oysters, and that would still not have restored them, because they will have been harvested. To achieve large-scale restoration with native (or non-native) oysters we must establish some permanent sanctuaries in productive areas and permit oyster populations to grow without harvest.

In the Great Wicomico River in Virginia, a collaborative project between the State, the Army Corps of Engineers and the Chesapeake Bay Foundation established a sanctuary reef onto which adult oysters, including over 1 million, hatchery-produced oysters were added as brood stock over a several year period. Consistently higher recruitment of oysters has been observed in this tributary than in nearby ones for the last several years (though cause and effect have not been established) and public and private money has been spent on planting shells in harvest areas of this tributary to catch the enhanced oyster settlement. In 2003, in a move that I believe to have been ill-advised, public money was used to purchase 30 million juvenile (or "seed") oysters from private lease holders in this tributary and move them to Tangier Sound. This highlights several positive aspects of our restoration efforts, including the value of sanctuary reefs and the potential to increase regional recruitment through brood stock enhancement on the sanctuary. The fact that there were 30 million seed oysters in this small tributary constitutes at least an interim success. However, it is my opinion that moving them out of the system was shortsighted and premature. Indeed, a viable restoration strategy will likely require that in time we move oysters from seed-producing areas, like the Great Wicomico River, to those with lower recruitment rates, but we need the persistence to get one system restored before removing oysters from it. Oyster recruitment in the Great Wicomico River was substantially reduced in 2004, following the removal of seed oysters the previous year. Additional brood stock plantings were conducted in 2004 and more are planned for 2005—all positive efforts, but we must resist pressure to harvest oysters that result from spawns of these brood stocks, we must allow a large, multi-year

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[2] Smith GF Greenhawk KN Bruce DG Roach EB Jordan SJ 2001 A digital presentation of the Maryland oyster habitat and associated bottom types in the Chesapeake Bay (1974-1983). *J Shellfish Res* 20:192-206.

class population to develop in this tributary and we must accept some disease mortality along the way.

4) *What would be the ecological consequences of introducing non-native oysters to the Bay?*

The truth is that we do not know, and we cannot know with certainty, what all of the ecological consequences would be of an introduction of a non-native species. The best that we can hope to do is to have sufficient knowledge of the biology and ecology of the exotic species to make reasonable predictions about its likely population growth patterns and its interactions with native species. In the case of the oyster currently under consideration, *Crassostrea ariakensis*, we know too little about its basic biology and ecology to make meaningful predictions about how it will grow and survive in the Chesapeake Bay. It has not been well studied in its native environment. In fact, even its identification in those environments is confused and there are apparently multiple species where, until recently, it was thought that there was only one. It has not been widely introduced to other environments, and in one case where it was introduced to the Pacific Northwest of the U.S., it has failed to reproduce and become established. Fortunately, there is a considerable amount of research currently underway and, with continued funding, we will greatly increase our knowledge about this species over the next few years and reduce the uncertainty about the ecological consequences of introducing it to the Chesapeake Bay.

Ecological consequences of a successful introduction of this species to the Chesapeake Bay could be desirable or undesirable; most likely they will be judged after a time to be a mix of the two. Broadly, the potential consequences fall into two categories: (1) the introduction of an associated disease or other pest (which may not depend on the widespread success of the oyster itself) and (2) ecological (and economic) consequences of growth in *Crassostrea ariakensis* populations in the Bay.

The unintentional introduction of a disease-causing pathogen or associated pest species is one of the most undesirable potential consequences of introducing a non-native oyster species. It now appears quite likely that the organism that causes MSX disease, *Haplosporidium nelsoni*, was introduced to the region in the 1950's along with plantings of the Pacific oyster *Crassostrea gigas*[3]. Proper attention to ICES[4] protocols can help ensure against a direct introduction of a new pathogen, but subtler routes exist for a non-native oyster to facilitate an undesired introduction and/or spread of pathogens and pests. For instance, the recent discovery that sterile, triploid *Crassostrea ariakensis* in North Carolina contracted new infections of a previously undescribed protozoan parasite *Bonomia* sp. raises the specter that this oyster could facilitate the spread of a new disease

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[3] Burreson, Eugene M., Nancy A. Stokes and C. S. Friedman. 2000. Increased virulence in an introduced pathogen: Haplosporidium nelsoni (MSX) in the eastern oyster Crassostrea virginica. Journal of Aquatic Animal Health 12:1-8.

[4] International Council for Exploration of the Sea, Code of Practice on Introductions and Transfers of Marine Organisms, 1994.

that might reach the Bay by other mechanisms (e.g., ballast water). This issue, that a non-native oyster might facilitate the introduction and spread of disease, should be very carefully examined prior to an introduction. We really cannot afford to leave any stone unturned in this area. Extreme caution is warranted because, as the case of MSX has revealed, the effects can be devastating. It is important to bear in mind that it was only 12 months ago that this new *Bonamia* species was first detected. Prior to that, we did not expect that it would be an issue.

Beyond the disease issue, the remaining ecological (and economic) consequences of an introduction of *Crassostrea ariankensis* will depend largely upon the population growth of this species. If, for any number of reasons, populations of this species do not thrive in the Chesapeake Bay, its impacts, both ecological and economic, are likely to be minor. On the other hand, if the population grows rapidly and expands into many areas of the Bay, it will undoubtedly have broad ecological consequences, and many of them might be desirable. If it forms reefs—and our current knowledge of whether is does or not is incomplete—it will likely provide habitat for many species that were formerly dependent upon native oyster reefs. If its population grows to a large enough size, it will likely affect nutrient cycling and water quality in a manner similar to that historically provided by our native oyster. A large population of this species, if properly managed, might one day support a valuable fishery within the Chesapeake Bay. Of course, it might have consequences that are undesirable, like displacing the native oyster or presenting a biofouling problem. The important point here is that these effects all depend on the growth of the introduced oysters' population to a sufficiently large size—something that will be measured in decades not months or years. Recall from my earlier comments that the current population estimate for the native oyster puts its abundance in the Chesapeake Bay at about 5 billion, which is 100- or even a 1,000-fold too small to provide the ecological and economic benefits that we desire. Earlier in my testimony I reviewed several of the factors that are limiting us in our ability to achieve this increase with native oysters, and disease is only one of those factors. The non-native oyster species appears to be highly resistant to the two diseases that are plaguing our oyster, but starting from a population of zero and getting to 100's of billions or trillions of oysters will require a large effort, a lot of money and a <u>lot</u> of time. It will not be a quick fix to either the Bay's problems or the collapsing industry. Doing the research first to understand the biology of this animal is not just about identifying risks, but also about learning how to take advantage of its potential.

If an introduction is judged to be prudent and successfully implemented, if the population grows over time, and if we avoid a truly catastrophic problem like the introduction of a new pathogen, then decades from now we will likely judge the introduction to have a mix of desirable and undesirable consequences. For instance, the Pacific oyster, *Crassostrea gigas*, was introduced to the west coast of the U.S. during the first half of the 20^{th} Century. It now supports a valuable fishery, provides habitat for commercially important crab species and filters substantial amounts of water, but it has also recently (50 to 75 years after its introduction) begun to invaded marine sanctuaries where it is displacing other species, reducing biodiversity and in some places displacing the native oyster species.

Finally, it is critical that we bear in mind that whatever the consequences of such an introduction, they are likely to be irreversible and far-reaching. If successfully introduced into the Chesapeake Bay, we must assume that this species will spread beyond the confines of the Bay to other coastal ecosystems along the U.S. Atlantic coast. Any decision to introduce this species should be made in this context and with great deliberation.

Acknowledgements:
Assistance in the preparation of portions of this testimony was provided by Dr. Roger Newell (Univ. of Maryland Center for Environmental Science), Mr. Chris Judy (MD Dept. of Natural Resources), Dr. James Wesson (VA Marine Resources Commission) and Drs. Roger Mann and Eugene Burreson (Virginia Institute of Marine Science).

Relevant Scientific Studies

Oyster effects on water quality and nutrient levels

Dame, R.F., 1999. Oyster reefs as components in estuarine nutrient cycling: incidental or controlling? *In:* Luckenbach, M.W., R. Mann and J.A.Wesson (eds.), *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*. Gloucester Point, Virginia: Virginia Institute of Marine Science Press, pp. 267-280.

Dame, R.F., R.G. Zingmark and E. Haskins, 1984. Oyster reefs as processors of estuarine materials. *Journal Experimental Marine Biology and Ecology,* 164, 147-159.

Dame, R.F. and S. Libes, 1993. Oyster reefs and nutrient retention in tidal creeks. *Journal Experimental Marine Biology and Ecology,* 171, 251-258.

Dame, R.F., D. Bushek and T. Prins, 2001. The role of suspension feeders as ecosystem transformers in shallow coastal environments. *In* Reise, K. (Ed), *The Ecology of Sedimentary Coasts*. Berlin: Springer-Verlag, pp. 11-37.

Kemp, W.M., and R.D. Bartleson, 1990 Preliminary ecosystem simulations of estuarine planktonic-benthic interactions: The benthic submodel, in *New Perspectives in the Chesapeake System: A Research and Management Partnership*, pp. 253-264, Chesapeake Research Consortium Publication No.137.

Gerritsen, J.A., A.F. Holland, and D.E. Irvine, Suspension-feeding bivalves and the fate of primary production. An estuarine model applied to Chesapeake Bay, *Estuaries*, *17*, 403-416, 1994.

Newell, R.I.E. 1988. Ecological Changes in Chesapeake Bay: Are they the result of overharvesting the Eastern oyster (*Crassostrea virginica*)? Pages 536-546 In: M.P.

Lynch and E.C. Krome, (eds.) Understanding the Estuary: Advances in Chesapeake Bay Research. Chesapeake Research Consortium Publication 129 (CBP/TRS 24/88), Gloucester Point, VA.

Newell, R.I.E., T.R. Fisher, R.R. Holyoke, and J.C. Cornwell. 2004. Influence of eastern oysters on N and P regeneration in Chesapeake Bay, USA. In: *The comparative Roles of Suspension Feeders in Ecosystems*. R Dame and S. Olenin (Eds.) NATO Science Series: IV - Earth and Environmental Sciences. Kluwer, Netherlands. In Press.

Newell, R.I.E., and E.W. Koch. 2004. Modeling sea grass density and distribution in response to changes in turbidity stemming from bivalve filtration and sea grass sediment stabilization. Estuaries. 27:793-806.

Newell, R.I.E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. Journal Shellfish Research. 23:51-61

Newell, R.I.E, J.C.Cornwell and M.S.Owens. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: a laboratory study. Limnol. Oceanogr. 47: 1367-1379.

Ulanowicz, R.E. and J.H. Tuttle, The trophic consequences of oyster stock rehabilitation in Chesapeake Bay, Estuaries, 15, 298-306, 1992.

<u>Oyster effects on habitat, biodiversity and fish abundance</u>

Bahr LM (1974) Aspects of the structure and function of the intertidal oyster reef community in Georgia. Ph. D. Dissertation, University of Georgia. 149 pp.

Bahr LM, Lanier WP (1981) The Ecology of intertidal oyster reefs of the South Atlantic Coast: a community profile. U.S. Fish Wildl. Serv. Program FWS/OBS/-81/15, 105 pp.

Breitburg, D. 1999. Are three dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? *In:* Luckenbach, M.W., R. Mann, and J.A.Wesson (eds.), Gloucester Point, Virginia: *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*. Virginia Institute of Marine Science Press, pp. 239-250.

Coen L.D., Luckenbach M.W, and Breitburg D.L., 1999: The role of oyster reefs as essential fish habitat: A review of current knowledge and some new perspectives. *Amer. Fish. Soc. Symp.*, **22**, 438-454.

Dame RF (1979) The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. Proc. Natl. Shellfish. Assoc. 68:6-10.

Dumbauld, B.R., E.P. Visser, D.A. Armstrong, L. Cole-Warner, K.L. Feldman, and B.E. Kauffman. 2000. Use of oyster shell to create habitat for juvenile Dungeness crab in Washington coastal estuaries: Status and prospects. J. Shellfish Res. 18:379-386.

Harding, J.M. and R. Mann, 1999. Fish species richness in relation to restored oyster reefs, Piankatank River, Virginia. *Bulletin Marine Science,* 65, 289-300.

Larsen, P.F. 1974. Quantitative studies of the macrofauna associated with the mesohaline oyster reefs of the James River, Virginia. Ph.D. Dissertation, College of William and Mary, 182 pp.

Lehnert, R.L., and D. M. Allen, 2002. Nekton use of subtidal oyster shell habitats in a Southeastern U.S. estuary. *Estuaries,* 25, 1015-1024.

Lenihan, H.S. and J. H. Grabowski, 1998. Recruitment to and utilization of oyster reef habitat by fishes, shrimps, and blue crabs: an experiment with economic analysis. *Fisheries Resource Grant Report*, *June 1998*, North Carolina Division of Marine Fisheries, Morehead City, NC.

Posy, M.H., T.D. Alphin, C.M. Powell, and E. Townsend, 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. In: Luckenbach, M.W., R. Mann, and J. A.Wesson, (eds.), Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches. Gloucester Point, Virginia: Virginia Institute of Marine Science Press, pp. 229-237.

Wells H.W. 1961. The fauna of oyster beds, with special reference to the salinity factor. Ecological Monographs 31:239-266.

Zimmerman R, T.J. Minello, T. Baumer and M. Castiglione. 1989. Oyster reef as a habitat for estuarine macrofauna. NOAA Technical Memorandum NMFS-SEFC-249