

## **An ecosystem approach for oyster restoration and management**

E. W. North, D. M. King, J. Xu, R. R. Hood, R. I. E. Newell, K. T. Paynter,  
M. L. Kellogg, M. K. Liddel, and D. F. Boesch

In addition to supporting a harvest, the eastern oyster (*Crassostrea virginica*) in Chesapeake Bay provides ecosystem services such as removing seston, enhancing water clarity and creating benthic habitat. Our objective was to create a flexible ecosystem-based decision-making tool to support oyster restoration and management. This Oyster Restoration Optimization model (ORO) incorporates predictions from three-dimensional water quality (NPDZ with oyster filtration) and larval transport models; calculates size- and salinity-dependent growth, mortality, and fecundity of oysters; and incorporates economic costs of restoration efforts. An optimization approach is used to identify the most suitable locations for oyster population restoration that maximize one or more benefits such as reduction in seston, increase in light penetration, spawning stock enhancement, and harvest, subject to cost constraints and other limitations. The iterative solution technique incorporates and estimates uncertainty such as that caused by climate variability. Preliminary results indicate that the restoration of oysters in three sub-systems of the Chesapeake Bay would maximize different suites of benefits due to interactions between salinity gradients, salinity-dependent growth and mortality rates of oysters, the residence time of water in the sub-systems, and the relationship between size of oysters and the number of bushels harvested. The strengths and constraints of the ORO model as applied to ecosystem-based fisheries management are discussed.

**Key words:** Eastern oyster, modeling, optimization, ecosystem-based management

### **Contact Information:**

*E. W. North (contact author), R. R. Hood, R. I. E. Newell: University of Maryland Center for Environmental Science Horn Point Laboratory, P.O. Box 775, Cambridge, MD 21613, USA [e-mails: enorth@hpl.umces.edu, rhood@hpl.umces.edu, newell@hpl.umces.edu].*

*J. Xu: Coast Survey Development Laboratory, Office of Coast Survey, National Oceanic and Atmospheric Administration, 1315 East-West highway, SSMC3, N/CS13, Silver Spring, MD 20910, USA [email: jiangtao.xu@noaa.gov]*

*K. T. Paynter, M. L. Kellogg, M. K. Liddel, University of Maryland Center for Environmental Science and Department of Biology, College Park, Maryland 20742 [e-mails: paynter@umd.edu, mlisakellogg@gmail.com, liddel@umd.edu]*

*D. F. Boesch, University of Maryland Center for Environmental Science, Cambridge, MD 21613, USA [e-mail: boesch@umces.edu]*

## I. INTRODUCTION

We developed an integrative quantitative tool, the Oyster Restoration Optimization (ORO) model, for the practical implementation of an ecosystem approach to fisheries restoration and management. “An ecosystem approach to management is management that is adaptive, specified geographically, takes into account ecosystem knowledge and uncertainties, considers multiple external influences, and strives to balance diverse social objectives” (NOAA 2005). Our ORO model links ecosystem characteristics (hydrodynamics, phytoplankton growth, oyster filtration, oyster population dynamics) with social objectives (water quality, harvest, spawning stock sanctuaries, cost control) in an optimization framework that provides spatially-explicit information to support oyster restoration and management decisions in Chesapeake Bay.

Water circulation patterns and changes in salinity (0 to ~28) from the head of Chesapeake Bay to the mouth of the estuary strongly influence the population dynamics of the native eastern oyster *Crassostrea virginica*. Chesapeake Bay is a large (~300 km long), partially mixed estuary with a persistent halocline and predominantly two-layer circulation patterns driven primarily by river inflow (Pritchard 1952, Wang 1979). River inflow influences salinity distributions, which in turn affect the distribution of oysters: adults are generally found in salinities > 5 throughout the Chesapeake Bay and tributaries (Kennedy 1991). Salinity influences growth (Shumway 1996), disease mortality of adults (Calvo et al. 2001) and larval mortality (Davis and Calabrese 1964). In addition to river flow, the Chesapeake mainstem and tributaries are influenced by tides (0.3 – 0.9 m tidal amplitude, Schubel and Pritchard 1987, Zhong and Li 2006) and by winds that act both locally and remotely (Boicourt 1992, Zhong et al. *submitted*). These circulation patterns alter the residence time of water in sub-estuaries (North et al. *in prep*) and the transport and dispersal of oyster larvae (North et al. *in review*).

Restoration of *C. virginica* oyster populations in Chesapeake Bay is a high priority goal of regional scientific and management communities (Chesapeake 2000 Agreement, <http://www.chesapeakebay.net/agreement.htm>). Potential benefits include support of a revived commercial fishery, improved water quality through oyster filtration (Newell et al. 2005), and enhanced benthic fauna and fish habitat through reef restoration (Harding and Mann 2001, Rodney and Paynter 2006). Efforts to restore *C. virginica* are on-going in Chesapeake Bay. Although Bay-wide oyster populations are not flourishing and disease-related mortality rates are still high in some areas (NRC 2004), there has been notable success in oyster longevity and reef establishment at some low salinity restoration sites (Rodney and Paynter 2006, Paynter 2001). Expansion of the habitat recovery and juvenile oyster production efforts are limited by financial and a variety of other resources. It is desirable that a more quantitative approach be used to support decisions regarding allocation of limited resources.

The objective of our research program was to create a spatially-explicit flexible ecosystem-based decision-making tool to inform restoration decisions and to identify the tradeoffs associated with these decisions that are related to the ecosystem services of oysters. This paper presents a first ‘proof of concept’ model that links physical, biological and economic optimization models to provide quantitative information about the ecosystem benefits associated with spatial strategies in oyster restoration. We describe here the model formulation and present examples of model predictions to demonstrate the utility of this approach. It should be noted that

this ‘proof of concept’ model is not yet ready for implementation as a management tool. Rather, this describes a path toward a quantitative structure that, with some enhancements, shows promise as a useful technique to support an ecosystem-based approach to oyster restoration and fishery management.

## II. METHODS

The Oyster Restoration Optimization (ORO) model in its current formulation focuses specifically on predicting how the enhancement of natural oyster populations with hatchery-reared juvenile ‘seed’ oysters influences the ecosystem services provided by oysters in specific regions. (An alternate formulation, a determination of how reduction in natural oyster populations by harvest influences ecosystem services, follows directly from this methodology but has not yet been implemented.) The ORO model is a decision support tool that 1) tracks the growth and mortality of hatchery-produced oysters planted at different sites, 2) estimates benefits (e.g., water quality, harvest, spawning stock production), and 3) determines the optimum locations to plant oysters that maximize desired benefits given current constraints. It incorporates predictions from three-dimensional hydrodynamic, water quality (NPDZ with oyster filtration) and larval transport models, calculates size- and salinity-dependent growth, mortality, and fecundity of oysters, and incorporates economic costs of restoration efforts. An optimization approach is used to identify the most suitable locations for oyster population restoration that maximize a weighted sum of potential benefits. The iterative solution technique provided by Palisade’s RISKOptimizer program (<http://www.palisade.com/riskoptimizer/default.asp>), an Excel add-on, allows the incorporation and estimation of uncertainty associated with climate variability and biological variables. We describe the overall ORO model structure and the optimization solution technique, and illustrate how they can be used to identify tradeoffs associated with oyster restoration decisions.

### 1. Model structure

**Domain.** The ORO model incorporates predictions from models with different space and time scales. Physical conditions (salinity, temperature) and ecosystem services related to oyster filtration and spawning stock production are predicted with hydrodynamic, water quality, and larval transport models that have domains that span the entire Chesapeake Bay (Fig. 1) and have time steps on the order of minutes (< 6 min). In specific regions (Fig. 1), the change in abundance and size of seed oysters planted in each region are tracked in annual time increments, from seed oysters (Yr 0) to 5-yr old adults. Fifteen specific regions that span three salinity zones were incorporated into this ‘proof of concept’ version of the model.

**Control Variable.** The ORO model optimizes the number of seed oysters planted in each region. Because restoration managers use a constant target ‘planting density’ of 300 seed oysters  $m^{-2}$  and specify their goals in terms of acres planted, the ORO model expresses the control variable (the variable to be adjusted and optimized) as the number of acres planted ( $A$ ), which is related to number of seed oysters planted ( $N$ ) by:

$$N = A \times 4,047 \frac{m^2}{acre} \times 300 \frac{oysters}{m^2} \quad (\text{equation 1})$$

It should be noted that, while model calculations were conducted in metric units, all input and output quantities are expressed in units most commonly used in oyster restoration and management efforts within the Chesapeake region (e.g., acres of habitat, bushels of oysters).

**Benefits.** Most ecosystem benefits of oysters in each region are characterized using measures (e.g., seston reduction, increased sub-surface irradiance, spawning stock production) that are known to be leading indicators of ecosystem benefits (e.g., water quality, increased production of seagrass, oyster population increase). Harvest is the only model output that is assumed to be a direct benefit measure. All benefit measures are based on the number and size of oysters in each region during each year after planting, and are calculated by incorporating physical and biological characteristics of the planting region. Year- and region-specific benefits are summed to determine the total cumulative benefit ( $B$ ):

$$B = \sum_{i=1,15} \sum_{y=1,5} b_{i,y} \quad (\text{equation 2})$$

where  $b$  = benefit,  $i$  = region, and  $y$  = year. The following benefits were calculated in ORO:

- $R_{local}$  = Seston reduction in the region ( $\text{mg l}^{-1}$ )
- $R_{remote}$  = Seston reduction near the mainstem Bay ( $\text{mg l}^{-1}$ )
- $L$  = Increased sub-surface irradiance in the region at 2 m depth, a critical depth for seagrass growth ( $\text{watt m}^2$ )
- $S$  = spawning stock production (number of larvae produced that survive to spawn)
- $H$  = Harvest (number of bushels, the volumetric quantity of trade in the commercial fishery, roughly  $0.046 \text{ m}^3$ )

Although not included in this version of the ORO model, the benefit of enhanced secondary production related to reef community formation and associated increase in biomass of piscivorous fish (i.e., recreational fisheries) is under development.

All benefits calculated in the ORO model rely on predictions from a hydrodynamic model (for salinity and temperature) and a juvenile/adult demographic model (for size and abundance of planted oysters). Changes in seston concentrations ( $R_{local}$ ,  $R_{remote}$ ) and consequent subsurface irradiance ( $L$ ) induced by oyster filtration are calculated with a coupled hydrodynamic-water quality model with an oyster filtration and biodeposition sub-model. The benefit of spawning stock production ( $S$ ) is calculated using information from the demographic model, fecundity estimates, and a larval transport model. The harvest benefit ( $H$ ) is calculated as a simple proportion of the abundance of planted oysters once their average size is greater than the legal minimum length.

**Constraints.** The ORO model predicts the optimum spatial allocation of seed oysters that maximizes a weighted sum of benefits subject to a set of specific constraints. The major constraints that are used in the model are 1) the maximum number of seed oysters cannot exceed hatchery-raised seed oyster production capacities, and 2) the costs of restoration (e.g., seed oysters, site preparation and transport costs) cannot exceed the funds available. In addition, the model solution is constrained by the amount of available oyster habitat in each region. Model solutions that violate these constraints are rejected. The model then searches the range of feasible model solutions for those that maximize the weighted sum of benefits.

## 2. Optimization solution technique

The ORO model can be used to maximize a single benefit or to maximize a group of benefits. The solution technique involves maximizing the mean of the predicted Total Benefits (TB), where:

$$TB = w_1 \sum_{i=1,15} \sum_{y=1,5} R_{local\ i,y} + w_2 \sum_{i=1,15} \sum_{y=1,5} R_{remote\ i,y} + w_3 \sum_{i=1,15} \sum_{y=1,5} L_{i,y} + w_4 \sum_{i=1,15} \sum_{y=1,5} S_{i,y} + w_5 \sum_{i=1,15} \sum_{y=1,5} H_{i,y}$$

and  $w$  = weighting factors (subscripts are defined as in equation 2). In the case of maximizing a single benefit,  $w = a/M$  where  $a$  is a user-defined selectivity parameter ( $a = 1$  for the benefit of choice and  $a = 0$  for the remaining benefits), and  $M$  is an estimate of the maximum possible benefit that could result if all available habitat was planted.  $M$  converts the benefit to a unitless quantity and reduces the orders-of-magnitude difference between benefits (e.g., 0.96 mg l<sup>-1</sup> seston reduction vs  $3 \times 10^7$  offspring produced). When maximizing a combination of benefits, then  $w = ac/W$ . In this case,  $a$  is set to the appropriate proportion (e.g., for equal weighting,  $a = 0.2$  for all benefits) and a scaling factor ( $c$ ) is used to ensure that the benefits are additive. The scaling factors are estimated with model runs that maximize each individual benefit separately and is calculated as  $c_k = TB_{max}/TB_k$  where  $TB_{max}$  is the highest TB from all runs, and  $TB_k$  is the TB for each individual benefit  $k$ .

An optimization approach is used to identify the most suitable locations for seed oyster placement that maximize one or more benefits. The iterative solution technique is provided by Palisade's RISKOptimizer program using the 'budget' solving method. For each ORO model run, simulations are conducted until convergence criteria are met (solution changes less than 0.01% in last 100 simulations). For each simulation, the benefits related to a certain spatial allocation of planted oysters are calculated. Within each simulation, 100 iterations of the model are calculated with salinity and mortality rates that vary based on random numbers drawn from a normal distribution. This iterative solution technique incorporates and estimates uncertainty caused by climate variability and mortality rates. For each simulation, all iterations that do not meet constraints are excluded and the mean Total Benefit (TB) score and standard deviation of acceptable iterations is calculated. Multiple simulations are conducted with an optimization algorithm (a genetic algorithm with mutation rate = 0.7 and crossover rate = 0.2) to restrict the parameter space that is searched (i.e., a limited combination of acres planted is tested by the model). The model conducts hundreds of simulations until the convergence criteria are met and keeps track of mean Total Benefit and its standard deviation for all possible solutions. The solution with the highest mean Total Benefit contains the optimum spatial allocation of seed oysters and an estimate of the associated benefits that could accrue. The solution differs from run to run depending on the weights that are assigned to various benefit measures. Solutions can differ markedly when the model is optimized for only one benefit measure. These differences provide a quantitative basis for assessing tradeoffs related to restoration goals and the strategies needed to achieve them.

## III. EXAMPLE PREDICTIONS

To explore the behavior and capabilities of the model, model runs were conducted with four of the five benefits optimized individually ( $w = 1$  for the benefit of choice and  $w = 0$  for all

other benefits). Coefficients of Variation of Total Benefits from model runs indicated greatest variability in model predictions related to spawning stock production ( $R_{local} = 17.0\%$ ,  $R_{remote} = 5.3\%$ ,  $S = 78.4\%$ ,  $H = 21.0\%$ ). The variability in spawning stock production calculations likely is related to the salinity-dependent larval and adult mortality rates and suggests that climate variability will have a bigger impact on this benefit than on the other benefits of oyster restoration.

The ORO model predicts that the optimum spatial allocation of acres of seed oysters would differ depending upon the benefit that is maximized (Fig. 2). Although all model solutions allocate oysters in multiple regions and multiple systems, the Choptank River system is predicted to be the optimum location to plant oysters in order to maximize seston reduction (local and remote) and spawning stock production. The water residence time and oyster filtration capacity in the Choptank River are high (North et al. *in prep*) and likely contribute to the ability of planted oysters to reduce seston concentrations compared to the other systems. Also, spawning production likely is maximized in the Choptank because salinities in this region provide a balance between adult disease mortality (highest in salinities  $> 15$ ) and larval salinity-dependent mortality (which is 100% at salinities  $< 12$  based on Lough 1975). In comparison with the Choptank River, the Chester River is the optimum place for maximizing harvest, most likely due to low salinities in this region that result in low mortality of adults due to diseases. Although growth is slower in these low salinity waters, the low disease mortality allows more oysters to grow to a larger size and the nonlinear relationship between size of oysters and number of oysters in a bushel results in enhanced harvest.

The ORO model provides quantitative information about the trade-offs associated with maximizing individual benefits (Fig. 3). For example, all optimization configurations result in harvest of  $>20,000$  bushels, but optimizing for harvest is predicted to result in  $>13,000$  more bushels harvested than the other configurations (Fig. 3D). Some model configurations do not result in benefits that are substantially different from the configuration designed to optimize that single benefit. For example, when local reduction in seston is optimized, spawning stock production is nearly the same as when spawning stock production is optimized (Fig. 3C). In contrast, some optimization configurations result in notably lower benefits than the configuration designed to optimize that benefit alone (compare ‘Spawn’ and ‘Harvest’ with other model configurations in Fig. 8A,B,C). The difference between optimizing for harvest and for spawning stock production benefits is notable: optimizing for harvest results in a large reduction in the number of offspring produced compared to other optimization configurations (Fig. 3C).

Additional model runs (not presented here) with different starting spatial arrangements of seed oysters indicate that model results are sensitive to initial conditions. The same model configuration with different initial conditions result in different spatial allocations of seed oysters within each system (Chester, Choptank, Tangier). In addition, the model predictions show a strong dependency on the maximum amount of seed oysters initially allocated to any one region in the model.

## IV. DISCUSSION

The ‘proof of concept’ Oyster Restoration Optimization model demonstrates that ecosystem characteristics (hydrodynamics, phytoplankton growth, oyster filtration, oyster population dynamics) and social objectives (water quality, harvest, spawning stock sanctuaries, economic considerations) can be linked in an optimization framework that deals explicitly with risks, employs measures of costs and several categories of benefits, and provides spatially-explicit information to support oyster restoration and management decisions in Chesapeake Bay. The model incorporates environmental variability and provides information about where to place seed oysters in order to maximize a given benefit or group of benefits. In addition, it provides a quantitative estimate of the consequences of restoration decisions by calculating the benefits associated with different spatial arrangements of seed oysters. Importantly, it provides quantitative predictions (such as size-specific abundance on planted bars and bushels of oysters harvested) in specific regions that could be validated with field observations.

Although the ORO model has promise to be a useful tool to support oyster restoration efforts in Chesapeake Bay, its current implementation has restrictive limitations. The resolution of the hydrodynamic and water quality models likely are too low to capture important hydrodynamic features in the Chesapeake sub-tributaries that could have a strong influence on water residence time and the oyster filtration capacity. In addition, the modeled larval salinity-dependent mortality rate (Lough 1975) was based on mortality experiments with Long Island Sound oysters acclimated to higher salinities than those found in the regions of this model (Davis and Calabrese 1964). Because it is likely that larvae produced by oysters in lower salinity waters in Chesapeake Bay are more tolerant of lower salinities (Davis 1958, Donald Merritt pers. comm.), the apparent conflict between optimizing spawning stock and harvest benefits could be exaggerated in the current ORO model predictions.

The next steps for ORO model enhancement include implementing it with higher resolution hydrodynamic and water quality models, adding salinity-dependent larval mortality rates for Chesapeake oysters (laboratory experiments are needed), transferring the model into a compiled computer language (e.g., C++ or Fortran) to allow more modeling flexibility, and conducting model-data validation studies of the juvenile/adult demographic model. The preset risk-based algorithms, spreadsheet format, and embedded graphics makes Paliside Corporation's RISKOptimizer an excellent software package for the initial development of this complex and integrated model. However, because the integrated biophysical models are more complex than those usually employed with this software, the speed of the model runs in RISKOptimizer (0.75 – 5 hrs for one run) would be restrictive for restoration scenarios that incorporate the higher resolution numerical models and additional regions (>100) that are needed to support on-the-ground restoration decisions. In addition, we found the sensitivity of RISKOptimizer solutions to initial conditions limited our confidence that the model was converging on globally optimal solutions. At this time, therefore, we believe the need for speed and a more complete parameter search space would be better met by transferring the model to a compiled program language.

Although the ORO model is in the early stages of development, and is specifically designed for restoration of oysters in Chesapeake Bay, the framework is transferable to other systems and can be adapted to support other aspects of ecosystem-based fisheries management.

For oysters, ecosystem consequences of fisheries management decisions could be assessed by changing fishing mortality or the minimum legal size of harvested oysters within ORO. Also, the model could be implemented to predict how ecosystem benefits are affected by both increasing and decreasing present-day abundances of oysters through restoration and harvest. This would allow a better understanding of how spatial differences in fishing mortality influence the ecosystem benefits of oysters. The optimization modeling framework could also be applied to high-biomass filter-feeding finfish that may influence ecosystem dynamics, although fish migrations make model implementation a more challenging, but not insurmountable, task. In any of these applications, the model could be expanded to assess the cost, risks, and potential benefits of achieving specific population abundance goals by either increasing restoration spending, or by placing more restrictions on harvesting, or both.

## **V. ACKNOWLEDGEMENTS**

We thank Thomas Maslin, Thomas Wazniak, Javier Ordóñez, Mark Luckenbach, Donald Merritt, Chris Judy, and Victor Kennedy for their assistance and insights. This research was funded by the Keith Campbell Foundation for the Environment.



## VI. LITERATURE CITED

- Boicourt, W. C. 1992. Influences of circulation processes on dissolved oxygen in the Chesapeake Bay. In: Smith, D. E., M. Leffler, G. Mackiernan (eds) Oxygen dynamics in the Chesapeake Bay: a synthesis of recent research. Maryland Sea Grant Publication, College Park, MD, p 7-59.
- Calvo, G. W., M. W. Luckenbach, S. K. Allen, Jr., and E. M. Burreson. 2001. A comparative field study of *Crassostrea ariakensis* (Fujita 1913) and *Crassostrea virginica* (Gmelin 1791) in relation to salinity in Virginia. *Journal of Shellfish Research* 20(1): 221-229.
- Davis, H. C. 1958. Survival and growth of clam and oyster larvae at different salinities. *Biological Bulletin* 114(3): 296-307.
- Davis, H. C., and A. Calabrese. 1964. Combined effects of temperature and salinity on development of eggs and growth of larvae of *M. mercenaria* and *C. virginica*. *Fishery Bulletin* 63(3): 643- 655.
- Harding, J. M., and R. Mann. 2001. Oyster reefs as fish habitat: Opportunistic use of restored reefs by transient fishes. *Journal of Shellfish Research* 20(3): 951-959.
- Kennedy, V. S. 1991. Eastern oyster *Crassostrea virginica*. In: Funderburk, S. L., S. J. Jordan, J. A. Mihursky, D. Riley (eds.) Habitat Requirements for Chesapeake Bay Living Resources. Chesapeake Bay Program, Annapolis, MD, p 3.1-3.20.
- Lough, R. G. 1975. A reevaluation of the combined effects of temperature and salinity on survival and growth of bivalve larvae using response surface techniques. *Fishery Bulletin* 73:86-94.
- National Research Council (NRC), Committee on Nonnative Oysters in the Chesapeake Bay. 2004. Non-native oysters in the Chesapeake Bay. The National Academies Press, Washington D.C. 326 p.
- Newell, R. I. E., T. R. Fisher, R. R. Holyoke, and J. C. Cornwell. 2005. Influence of eastern oysters on nitrogen and phosphorus regeneration in Chesapeake Bay, USA. In: Dame, R., and S. Olenin (eds.) The Comparative Roles of Suspension Feeders in Ecosystems. Vol. 47 NATO Science Series: IV - Earth and Environmental Sciences. Springer, Netherlands, p. 93-120.
- NOAA (National Oceanic and Atmospheric Administration). 2005. New priorities for the 21st century: NOAA's strategic plan. NOAA, Washington, D.C.
- North, E. W., Z. Schlag, R. R. Hood, M. Li, L. Zhong, T. Gross, and V. S. Kennedy. *in review*. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Marine Ecology Progress Series*.
- North, E., J. Xu, R. R. Hood, R. I. E. Newell, D. F. Boesch, M. W. Luckenbach, K. T. Paynter. *in prep*. Quantifying the ability of eastern oysters to filter the waters of Chesapeake Bay.

- Paynter, K. T. 2001. Chesapeake Bay Oyster Recovery Project Comprehensive Monitoring Report 1998-2000, to the US Army Corps of Engineers Baltimore District and Maryland Department of Natural Resources, March 22, 2001. 48 p.
- Pritchard, D. W. 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. *Journal of Marine Research* 11:106-123.
- Rodney, W. S., and K. T. Paynter. 2006. Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *Journal of Experimental Marine Biology and Ecology* 335:39–51.
- Schubel, J. R., and D. W. Pritchard. 1987. A brief physical description of the Chesapeake Bay. In: Majumdar, S. K., and L. W. Hall, Jr., and H. M. Adams (eds) *Contaminant Problems and Management of Living Chesapeake Bay Resources*. The Pennsylvania Academy of Science, Easton, PA, p 1-32.
- Shumway, S. E. 1996. Natural environmental factors. In: Kennedy, V. S., R. I. E. Newell, and A. E. Eble, eds. *The Eastern Oyster: Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland. 734 pp.
- Wang, D-P. 1979. Subtidal sea level variations in the Chesapeake Bay and relations to atmospheric forcing. *Journal of Physical Oceanography* 9:413-421.
- Zhong, L., and M. Li. 2006. Tidal energy fluxes and dissipation in the Chesapeake Bay. *Continental Shelf Research* 26: 752-770.
- Zhong, L., M. Li, and M. G. G. Foreman. *submitted*. Resonance and sea level variability in Chesapeake Bay. *Continental Shelf Research*

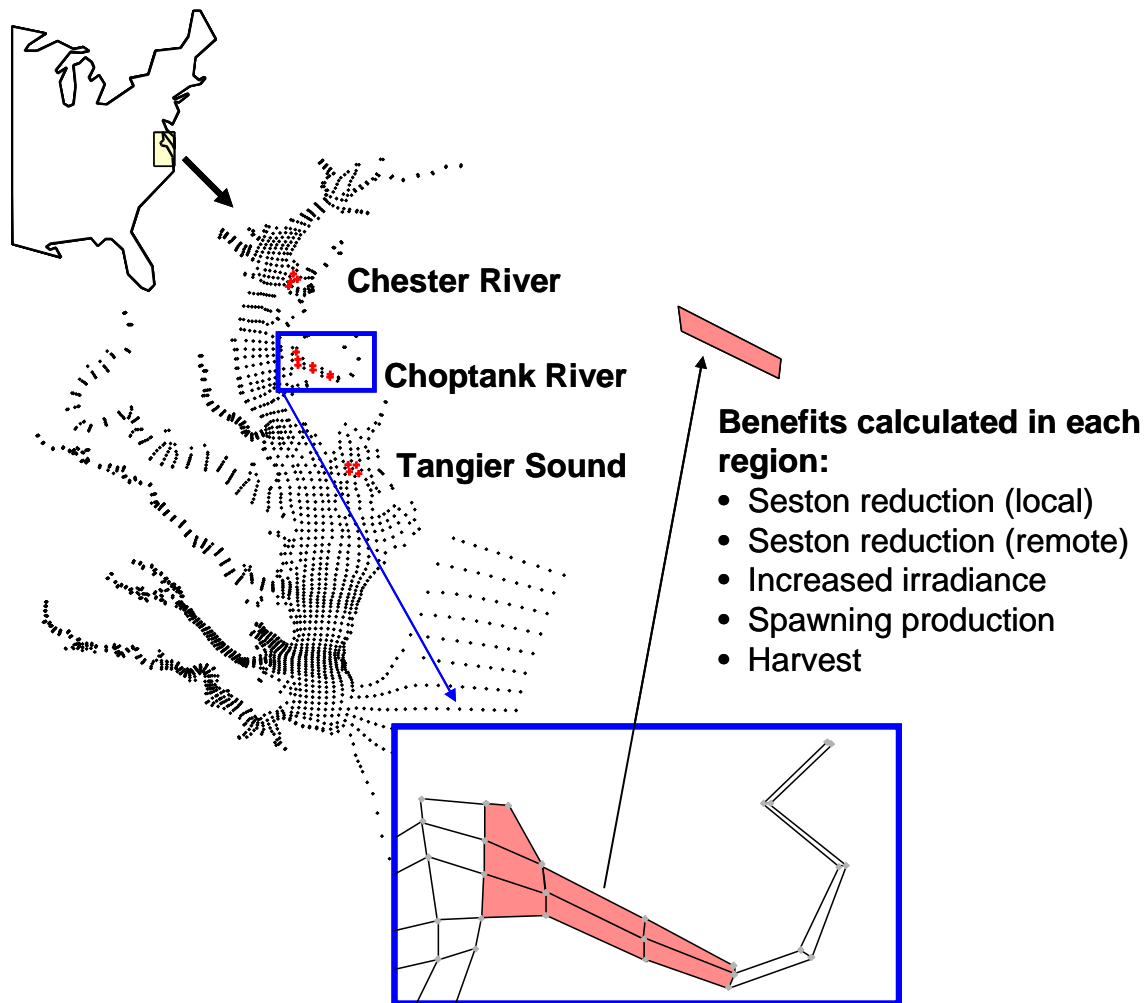


Fig. 1. Location (Chesapeake Bay) and domain of Oyster Restoration Optimization (ORO) model. Chesapeake Bay hydrodynamic and water quality model grid points are indicated by small back circles. Red circles in Tangier Sound and Chester and Choptank Rivers represent regions where the model predicts the influence of enhanced oyster abundances, as do the red boxes in the representation of the model grid cells in the Choptank River (blue box). The ORO model calculates the benefits of enhanced oyster populations in each region and uses an optimization procedure to maximize a certain benefit or combination of benefits.

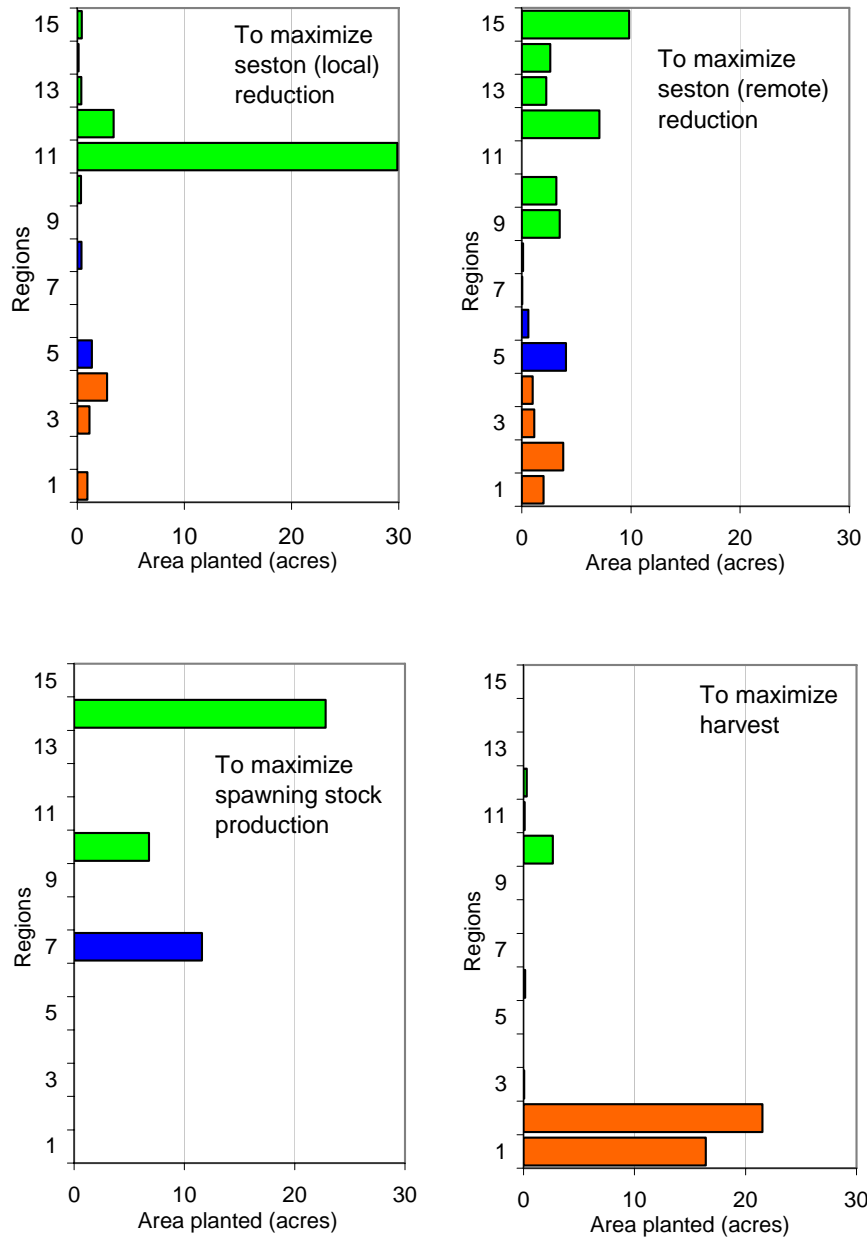


Fig. 2. Example predictions from ORO model runs that maximize a single benefit or all benefits weighted equally. The optimum spatial allocation of acres of seed oysters (x axis) is indicated for each region (y axis) for each model run (indicated in the upper right of each panel). Bars are color coded according to region (orange = Chester River, blue = Tangier Sounds, green = Choptank River).

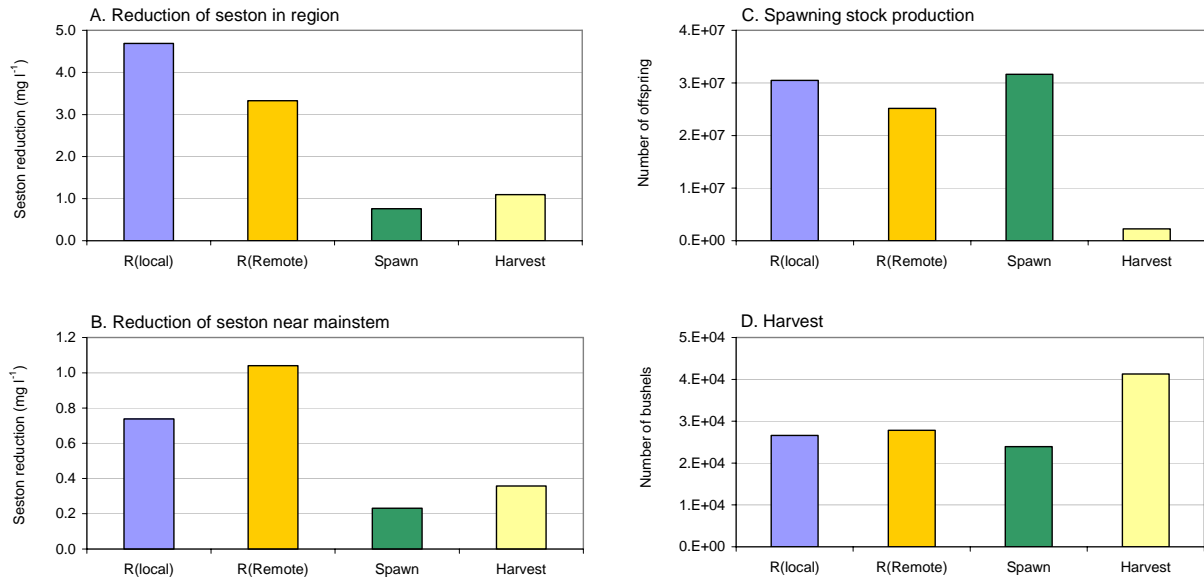


Fig. 3. Predicted A) local seston reduction, B) remote seston reduction, C) spawning stock production, and D) harvest that would accrue given optimization choices of maximizing individual benefits: R(local) = Seston reduction in the region; R(remote) = Seston reduction near the mainstem Bay; Spawning = spawning stock production (number of offspring produced); and Harvest = number of bushels harvested.