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Can Oyster Restoration Reverse Cultural Eutrophication in Chesapeake Bay?

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ABSTRACT: We investigated the hypothesis that effects of cultural eutrophication can be reversed through natural resource restoration via addition of an oyster module to a predictive eutrophication model. We explored the potential effects of native oyster restoration on dissolved oxygen (DO), chlorophyll, light attenuation, and submerged aquatic vegetation (SAV) in eutrophic Chesapeake Bay. A tenfold increase in existing oyster biomass is projected to reduce system-wide summer surface chlorophyll by approximately 1 mg m^{-3}, increase summer-average deep-water DO by 0.25 g m^{-3}, add 2100 kg C (20%) to summer SAV biomass, and remove 30,000 kg d^{-1} nitrogen through enhanced denitrification. The influence of oyster restoration on deep extensive pelagic waters is limited. Oyster restoration is recommended as a supplement to nutrient load reduction, not as a substitute.

Introduction

Eutrophication of coastal waters is a problem of global significance (NRC 2000; Smith et al. 2006). Reduction of anthropogenic nutrient loads is the commonly prescribed remedy for the eutrophication problem (e.g., NRC 2001). Human population growth, cost, and technological limits to controlling diffuse nutrient sources render reductions in nutrient loading difficult to attain. Recent work indicates the deleterious effects of anthropogenic nutrient loads are amplified by concurrent destruction or depletion of natural resources. Loss of submersed macrophyte beds eliminates associated particle trapping (Ward et al. 1984; Rybicki et al. 1997) and sediment denitrification (Caffrey and Kemp 1990, 1992). Loss of tidal marshes eliminates nutrient trapping (Merrill and Cornwell 2000) and denitrification (Stevenson et al. 2002) that occurs in these systems. Harvesting of piscivorous predators reduces zooplankton populations and enhances phytoplankton through the trophic cascade (Schindler 2006). The association between resource depletion and eutrophication leads to the hypothesis that eutrophication can be reversed through resource restoration, as well as via nutrient load reductions.

The Chesapeake Bay is an extensive estuarine system located on the east coast of the United States and in a state of cultural eutrophication characterized by bottom-water hypoxia, diminished submerged aquatic vegetation (SAV), and diminished fisheries harvests (Flemer et al. 1983). During the 19th century, saline waters of the bay and tributaries supported abundant native oysters, *Crassostrea virginica* (Newell 1988; Kirby and Miller 2005). Since then, the oyster population has declined steadily to a few percent of its previous value. Causes of the decline include overfishing (Jordan and Coakley 2004), disease (Andrews 1965, 1988), and habitat destruction (Rothschild et al. 1994; Kirby and Miller 2005). A link between decimation of the oyster population and deteriorating water quality was proposed by Newell (1988) who suggested an increase in the oyster population could significantly improve water quality by removing large quantities of particulate carbon. We investigate here the hypothesis that a tenfold increase in the native oyster population, specified in a call for management action (USEPA 2000), will lead to eutrophication abatement in Chesapeake Bay. The call for a tenfold increase is based on an assessment of restoration feasibility rather than attainment of specific benefits. Evaluation of the nature and magnitude of beneficial effects is the prime motivation for this study. We also investigate, as a limiting extreme, effects of restoring oyster biomass to 19th century levels although restoration of this magnitude is unlikely due to habitat destruction (Rothschild et al. 1994; Kirby and Miller 2005) and other irreversible alterations in the system.

Implementation of system-wide restoration is an impractical means to test our hypothesis. Effects must be extrapolated from laboratory-scale experiments (Newell et al. 2002; Porter et al. 2004), transferred from systems that have experienced a bivalve resurgence (Cohen et al. 1984; Caraco et al. 2006), or estimated through a mathematical model (Gerritsen et al. 1994; Newell and Koch

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2004). Our approach employs a predictive model, the results of which are compared to experimental and in situ observations. The bay system encompasses a variety of environments ranging from shallow enclosed embayments to an extensive open-water main stem. Restoration effects are examined in bay segments, which exhibit a range of geometry and environmental conditions, as well as system-wide.

The Study System

Chesapeake Bay extends 300 km from the Susquehanna River, at the head, to the Atlantic Ocean, at the mouth. Mean depth is 8 m although a deep trench with depths to 50 m runs up the center. The Susquehanna provides the majority of freshwater flow (ca. 64%) and nutrient loading (Boynton et al. 1995). Virtually all remaining runoff and loads originate in several western tributaries. The bay and major tributaries are classic examples of partially-mixed estuaries (Pritchard 1967). Onset of hypoxia (dissolved oxygen < 2 g m^{-3}) occurs in late May and persists, at depths > 10 m, until mid-September when surface cooling and autumn winds mix surface water to the bottom of the bay (Officer et al. 1984). The severity and duration of the hypoxia are sufficient to cause near total faunal depletion within the hypoxic zone (Holland et al. 1977).

Methods

The Oyster Model

The most significant properties to be modeled are the spatial and temporal distribution of filtering capacity and the fate of filtered materials. Multiple approaches to this representation are possible. Our approach models oysters from a mass-balance perspective. Oysters are quantified as the organic carbon incorporated in soft tissue per unit area. Carbonaceous biomass is computed as a function of food availability, respiration, and mortality. Environmental effects on life processes are considered so that filtering capacity is consistent with environmental conditions. Significant barriers to restoration, including disease and reef destruction, are not considered. Our work addresses the question ''What if oysters are restored?'' The feasibility of restoration is a different issue, to be addressed after the benefits of restoration are established.

The essential processes of the model are filtration, ingestion, assimilation, respiration, and mortality. Oysters filter particulate matter, including carbon, nitrogen, phosphorus, silica, and inorganic solids, from the water column. The amount of carbon filtered may exceed the oyster's ingestion capacity. In that case, the excess of filtration over ingestion is deposited in the sediments as pseudofeces. A portion of the carbon ingested is refractory or otherwise unavailable for nutrition. The unassimilated fraction is deposited in the sediments as feces. Biomass accumulation (or diminishment) is determined by the difference between carbon assimilated and lost through respiration and mortality. Respiration losses remove dissolved oxygen (DO) from the water column. Mortality losses are deposited to the sediments as particulate carbon. Nitrogen and phosphorus constitute a constant fraction of oyster biomass. Particulate nitrogen and phosphorus, filtered from the water column, are subject to ingestion and assimilation. Assimilated nutrients that are not accumulated in biomass or lost to the sediments through mortality are excreted to the water column in dissolved inorganic form. All filtered particulate silica is deposited to the sediments along with a fixed fraction (10%) of filtered inorganic solids. Remaining solids are considered to be resuspended and are released to the water column.

The mass-balance equation for oyster biomass is:

$$\frac{dO}{dt} = \alpha \times Fr \times POC \times IF(1 - RF) \times O - BM \times O - \beta \times O \quad (1)$$

where O = oyster biomass (g C m^{-2}), α = assimilation efficiency ($0 < \alpha < 1$), Fr = filtration rate (m^3 g^{-1} oyster C d^{-1}), POC = particulate organic carbon in overlying water (g m^{-3}), IF = fraction ingested ($0 < IF < 1$), RF = respiratory fraction ($0 < RF < 1$), BM = basal metabolic rate (d^{-1}), β = specific mortality rate (d^{-1}), and t = time (d).

Filtration rate is represented as a maximum rate that is modified by temperature, suspended solids, salinity, and DO:

$$Fr = f(T) \times f(TSS) \times f(S) \times f(DO) \times Fr\max \quad (2)$$

where $f(T)$ = effect of temperature on filtration rate ($0 < f(T) < 1$), $f(TSS)$ = effect of suspended solids on filtration rate ($0 < f(TSS) < 1$), $f(S)$ = effect of salinity on filtration rate ($0 < f(S) < 1$), $f(DO)$ = effect of DO on filtration rate ($0 < f(DO) < 1$), and $Fr\max$ = maximum filtration rate (m^3 g^{-1} oyster C d^{-1}).

Filtration rate was based primarily on measures (Jordan 1987) conducted in a laboratory flume maintained at conditions in the Choptank River, a mesohaline Chesapeake Bay tributary that supports a population of native oysters. These were supplemented with laboratory measures conducted on oysters removed from the same system (Newell and Koch 2004). Jordan reported a weight-specific biodeposition rate that represents a minimum value for filtration since material incorporated into bio-

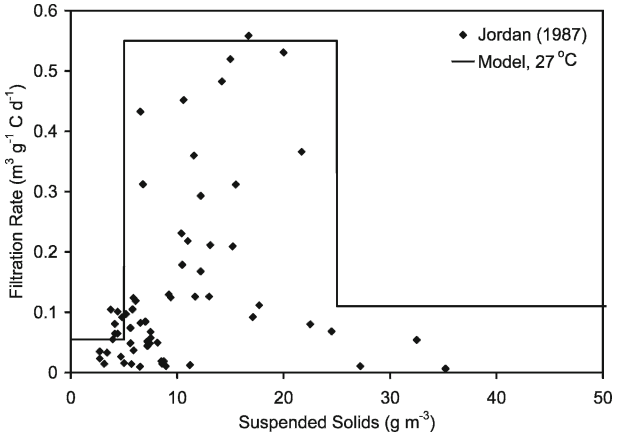

Fig. 1. Observed and modeled effect of suspended solids concentration on filtration rate.

mass is not deposited. Filtration rate was derived:

$$Fr = {}^{WBR}/_{TSS} \tag{3}$$

where WBR = weight-specific biodeposition rate (mg g^{-1} dry oyster weight [DW] h^{-1}), and TSS = total suspended solids concentration (mg l^{-1}). Filtration rate was converted from l g^{-1} DW h^{-1} to model units based on a carbon to DW ratio of 0.5, characteristic of marine organic matter (Anderson 1995; Hedges et al. 2002).

The observed rates indicate a strong dependence of filtration on temperature although the range of filtration rates observed at any temperature indicates the influence of other factors as well. The maximum filtration rate and temperature dependence are represented by a curve drawn across the highest filtration rates at any temperature:

$$Fr = Fr\max \times e^{-Ktg(T - Topt)^2} \tag{4}$$

where Ktg = effect of temperature on filtration ($°C^{-2}$), T = temperature (°C), and $Topt$ = temperature for optimal filtration (°C).

Effects of suspended solids on filtration rate are illustrated by recasting Jordan's data (Fig. 1). Filtration rate is depressed when solids range below 5 gm m^{-3} and above 25 gm m^{-3}, relative to filtration rate when solids are between these two levels. We attribute the depressed filtration to different influences. At high solid concentrations, filtration rate decreases to minimize the removal of inert material from the water column. Filtration rate is diminished at low solid concentrations to minimize the physiological expense of filtration when particulate organic matter is not available. Suspended solid effects are modeled as a multiplier applied to the base filtration rate, obtained through visual fit to Jordan's data and supplemented with Loosanoff and Tommers' (1948) results.

Experiments indicate filtration rate is diminished at 7.5‰ salinity and ceases at 3‰ (Loosanoff 1953). We described these effects with a functional form:

$$f(S) = 0.5(1 + \tanh(S - KHsoy)) \tag{5}$$

where S = salinity (‰), and $KHsoy$ = salinity at which filtration rate is halved (7.5‰).

Two forms of respiration are considered: active respiration, associated with acquiring and assimilating food, and passive respiration (or basal metabolism). Active respiration is considered to be a constant fraction of assimilated food. Basal metabolism is represented as a constant fraction of biomass, modified by ambient temperature:

$$BM = BMr \times e^{KTbmr(T - Tr)} \tag{6}$$

where BM = basal metabolism (d^{-1}), BMr = basal metabolism at reference temperature (d^{-1}), Tr = reference temperature (°C), and $KTbmr$ = a constant that relates metabolism to temperature ($°C^{-1}$).

The model formulation incorporates DO effects on filtration and mortality. Within the shallow oyster beds, DO seldom enters the range (< 2 g m^{-3}) in which these effects are significant. Mortality from all other sources, primarily disease and harvest, is represented by a spatially uniform and temporally constant first-order term. Magnitude of the term is specified to produce various system-wide population levels with the model. A summary of model parameters is presented in Table 1.

The Chesapeake Bay Environmental Model Package

The oyster model was incorporated into the Chesapeake Bay Environmental Model Package (CBEMP), a mass-balance based model system that has been extensively employed to examine eutrophication issues in Chesapeake Bay. Applications include examination of the benefits of a proposed 40% reduction in nutrient loads (Cerco 1995), development of management plans for major western tributaries (Cerco and Meyers 2000), and development of the most recent set of nutrient and solid load allocations in the bay (Cerco and Noel 2004). Three models are at the heart of the CBEMP. Distributed flows and loads from the watershed are computed with a highly-modified version of the HSPF (Hydrologic Simulation Program – FORTRAN) model (Bicknell et al. 1996). Flows are entered into the CH3D-WES Computational Hydrodynamics in Three Dimensions – Waterways Experiment Station hydrodynamic model (Johnson et al. 1993) that computes three-dimensional intratidal transport. Computed loads and transport are

TABLE 1. Parameters for oyster model.

Parameter	Definition	Value Units	Source
*Fm*ax	Maximum filtration rate	0.55 $m^3 g^{-1}$ oyster C d^{-1}	Jordan 1987, Newell and Koch 2004
Topt	Optimum temperature for filtration	27°C	Jordan 1987
Ktg	Constant that controls temperature effect on filtration	0.015$°C^{-2}$	Jordan 1987
KHsoy	Salinity at which filtration rate is halved	7.5‰	Loosanoff 1953
BMR	Base metabolism at 20°C	0.008 d^{-1}	Winter 1978
KTbmr	Constant that controls temperature dependence of metabolism	0.069$°C^{-1}$	Shumway and Koehn 1982
Tr	Reference temperature for specification of metabolism	20°C	
RF	Respiratory fraction	0.1 $0 < RF < 1$	Boucher and Boucher-Rodoni 1988, Dame et al. 1992
α	Assimilation efficiency	0.75[a] $0 < \alpha < 1$	Tenore and Dunstan 1973
β	Specific mortality rate	0.015 d^{-1}	Evaluated to obtain a tenfold biomass increase

[a] For phytoplankton and labile organic matter. Zero otherwise.

entered into the CE-QUAL-ICM (Corps of Engineers Water Quality Integrated Compartment Model) eutrophication model (Cerco and Cole 1993) that computes algal biomass, nutrient cycling, and DO, as well as numerous additional constituents and processes. The eutrophication model incorporates a predictive sediment diagenesis component (DiToro 2001), SAV component (Cerco and Moore 2001), and subtidal benthic algal component (Cerco and Seitzinger 1997).

The hydrodynamic and eutrophication models operate on a grid of 13,000 cells. The grid contains 2,900 surface cells (4 km^2) and employs nonorthogonal curvilinear coordinates in the horizontal plane. Z coordinates are used in the vertical direction, which is up to 19 layers deep. Depth of the surface cells is 2.1 m at mean tide and varies as a function of tide, wind, and other forcing functions. Depth of subsurface cells is fixed at 1.5 m. Ten years, 1985–1994, are simulated continuously using time steps of 5 min (hydrodynamic model) and 15 min (eutrophication model). The 10-yr sequences are looped, with output from one providing input to the next, until repeatable computations are obtained, indicating equilibration with forcing functions and computed oyster populations.

Existing Biomass

Installation of a tenfold oyster biomass increase in the model first required an estimate of existing biomass and location. The existing oyster biomass and distribution in the southern Virginia portion of the bay were obtained from patent tong surveys (Mann unpublished data) conducted in 1998–2002. Samples (4 to 50) were averaged for each model cell (coefficient of variation [CV] = 0.11–1.67). Mean density (g DW m^{-2}) was multiplied by cell area, then summed over all cells to obtain total biomass (kg). Our estimate of Virginia biomass (CV = 0.088) is three times the biomass from an alternate independent estimate (Table 2). In the northern Maryland portion of the bay, habitat was determined from Yates (1911). Biomass was obtained from Jordan et al. (2002). This estimate of Maryland biomass is roughly half the biomass from two other independent estimates (Table 2).

The biomass and distributions obtained indicate distinctly different patterns in the southern and northern portions of the bay. In the southern portion, high densities (mean = 6.2 g DW m^{-2}) are concentrated in limited areas (377 km^2), primarily in the lower James and Rappahannock Rivers. In the northern portion, lower densities (0.43 g DW m^{-2}) are distributed over a wide area (1330 km^2).

Modeled Biomass

Exploratory model runs indicated a tenfold biomass increase in each existing oyster bar was not feasible. Food limitations foiled a tenfold increase in the regions that presently contain the highest oyster densities. Adverse conditions (salinity, solids, DO) prevented a tenfold increase in some regions that presently exhibit low densities. We settled on a strategy in which a uniform bay-wide mortality rate (Table 1) was prescribed that produced the target biomass. Local biomass increases were determined by local conditions. The mortality rate represented combined effects of harvest and disease. Assignment of a zero value reproduced the pre-1870 biomass estimated by Newell (1988).

Intraannual and interannual variations in computed biomass made an exact multiplier of existing oyster biomass impossible to obtain. The 10-yr average modeled biomass for the tenfold increase is 13 times the estimated existing population. Biomass in individual years varies by 50% above and below the mean. Owing to local conditions and existing densities, the southern Virginia portion of

TABLE 2. Estimates of existing and historical oyster biomass.

Source	Maryland (kg C)	Virginia (kg C)	Total (kg C)
Existing, this study	287,000	1,170,000	1,457,000
Existing, Newell 1988	550,000	400,000	950,000
Existing, Uphoff (unpublished data)	570,000[a]		
Tenfold increase, model	14,100,000	4,375,000	18,475,000
19th century, Newell 1988			94,000,000
Historic, model	69,750,000	17,200,000	86,950,000

[a] Year 2000 exploitable biomass based on skipjack catch per unit effort.

the bay receives only a fourfold biomass increase while the northern Maryland portion increases nearly 50 times.

Model Results

Oysters affect the environment on spatial scales ranging from their immediate surroundings outwards to the entire water body. The effects are considered here on three scales. The first is the smallest that can be resolved in the model, the model cell (ca. 10^6 m^2). Since modeled oysters are uniformly distributed within cells, the processes in cells occupied by oysters are comparable to processes in bars containing similar densities of oysters. The second spatial scale is the regional scale (10^8 m^2) represented by Chesapeake Bay Program Segments (CBPS, 1983 definition, USEPA 2004). Program segments are subdivisions of the bay determined by salinity, natural boundaries, and other features. Median area is 1.5×10^8 m^2, of which only a fraction is occupied by oyster bottom. The third scale is system-wide, an area of 1×10^{10} m^2.

We examine here three CBPS that provide a range of geometry (Table 3) and environmental conditions. CB4 is a mainstem bay segment with the greatest volume, surface area, and depth of the selected segments. One significant characteristic of the segment is the regular occurrence of summer bottom-water anoxia. EE2 is an eastern embayment that encompasses the mouth of the Choptank River. Minimum DO concentration in bottom water occasionally falls below 3 g m^{-3} but persistent anoxia does not occur. Segment ET9 is the Big Annemessex River, located on the Maryland eastern shore. The Big Annemessex is the smallest of the three selected segments and minimum DO concentration exceeds 6 g m^{-3}.

Biomass-specific Processes

Effects on the scale of cell size are presented for a cell at a depth of 6.7 m within the lower Choptank River, EE2, representative of the environment from which oysters were drawn for the experiments of Jordan (1987) and Newell and Koch (2004).

Computed biomass-specific filtration rates agree closely with the experiments on which the rates were based as well as with other independent measures and calculations (Table 4). Order of magnitude similarity prevails between modeled and measured respiration and ammonium excretion. An interesting contrast occurs with carbon deposition. The model agrees well with Jordan's measures but departs from other reports. The modeled and measured filtration and respiration measures are comparable across systems because these are primarily functions of oyster physiology. Carbon deposition is influenced by local organic carbon concentration as well as by physiological processes, and can only be compared when local organic carbon concentrations are similar.

Areal-based Effects

Sediment diagenetic processes and fluxes between the bottom sediments, oysters, and water column are examined for a range of oyster densities. The basis for comparison is the 2002 version of the CBEMP (Cerco and Noel 2004), which included no oysters. This is compared to model runs with oysters, conducted at various mortality rates, which produced a range of oyster densities. All values are annual averages across the 10 simulated years.

The introduction of oysters results in biodeposition of carbon to the sediments (Fig. 2). Carbon deposition due to gravitational settling is simultaneously diminished as particulate carbon that pre-

TABLE 3. Geometric characteristics and percent oyster bottom of segments selected for analysis.

Region	Latitude	Longitude	Volume (10^9 m^3)	Area (km^2)	Mean Depth (m)	Percent oyster bottom
CB4, Middle Central Chesapeake Bay	38.69	−76.39	10.8	966	11.2	71
EE2, Lower Choptank River	38.65	−76.25	1.8	334	5.3	100
ET9, Big Annemessex River	38.05	−75.8	0.1	33	2.8	100

TABLE 4. Modeled and observed biomass-specific oyster filtration, respiration, excretion, and deposition.

Property	Rate	Source	Comments
Filtration rate, $m^3\ g^{-1}$ oyster C d^{-1}	0.24	Model	Summer average
	0.22	Jordan 1987	Mean value, T > 20°C
	0.26	Newell and Koch 2004	Average of measures at 20°C and 25°C
	0.027 to 0.33	Epifanio and Ewart 1977	For algal suspensions > 1 g C m^{-3}
	0.27	Riisgard 1988	Calculated for a 2.1 g DW oyster at 27°C to 29°C
Respiration rate, g DO g^{-1} oyster C d^{-1}	0.04	Model	Summer average
	0.03 to 0.06	Boucher and Boucher-Rodini 1988	Spring and summer rates
	0.017	Dame et al. 1992	Annual average
	0.02	Dame 1972	1 g DW oyster at 20°C to 30°C
Ammonium excretion, mg N g^{-1} oyster C d^{-1}	1.43	Model	Summer average
	< 0.1	Hammen et al. 1966	Ammonium plus urea
	2.8 to 3.88	Boucher and Boucher-Rodini 1988	Spring and summer rates, includes urea
	0.8	Srna and Baggaley 1976	1 g DW oyster at 20°C
	4.8 to 7.9	Magni et al. 2000	*Ruditapes* and *Musculista*
Carbon deposition, g C g^{-1} oyster C d^{-1}	0.088	Model	Summer average
	0.099	Jordan 1987	Mean value, T > 20°C
	0.03	Haven and Morales-Alamo 1966	
	0.002 to 0.012	Tenore and Dunstan 1973	Depends on C concentration, range is 0.1 to 0.7 g C m^{-3}

viously settled is instead filtered. Total carbon deposition is diminished by the introduction of oysters indicating that the minimum computed density is sufficient to reduce net production of particulate carbon in the water column. Carbon removal by filtration levels off as oyster densities increase beyond the initial value. We attribute the level filtration to equilibrium between carbon supplied, through transport and production, and carbon removed. As oyster density increases, biodeposition decreases through two processes. The first is reduced flux of dead oyster material to the sediments, brought about by reduced mortality from predation and disease, which promotes the density increases. The second is an increase in the fraction of carbon lost through respiration. Total carbon deposition, through settling and biodeposition, decreases continually in response to increased oyster density.

Increasing oyster densities are accompanied by corresponding increases in respiration (Fig. 3) and decreases in diagenetic sediment oxygen consumption. The increased respiration is more than offset by decreased sediment oxygen consumption so that total oxygen consumption decreases as oyster density increases.

The model considers nitrogen, phosphorus, and silica. We limit discussion to nitrogen since this nutrient is the most significant influence on algal production when temperature-dependent oyster filtration is greatest (Fisher et al. 1992; Malone et al. 1996). Fluxes of particulate nitrogen reproduce the pattern established for carbon. The introduc-

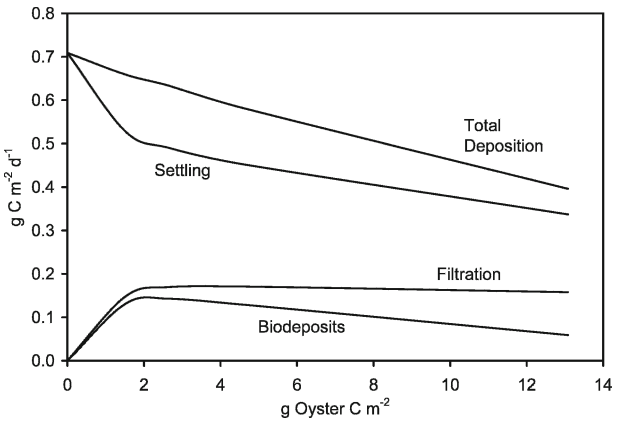

Fig. 2. Modeled effects of enhanced oyster density on sediment-water particulate organic carbon fluxes. Effects are annual averages quantified for a unit area of oyster bottom in the lower Choptank River, segment EE2 (Table 3).

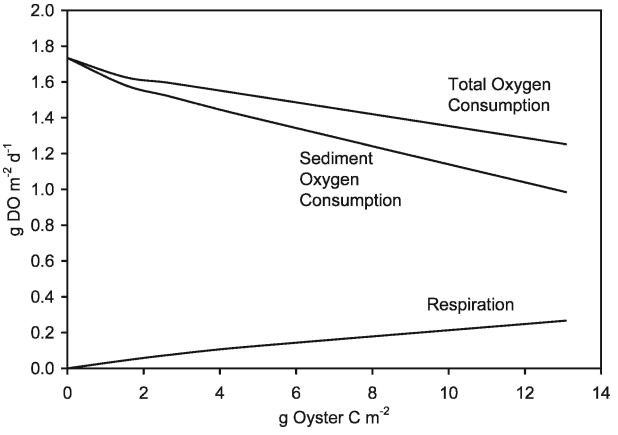

Fig. 3. Modeled effects of enhanced oyster density on dissolved oxygen consumption at the sediment-water interface. Effects are annual averages quantified for a unit area of oyster bottom in the lower Choptank River, segment EE2 (Table 3).

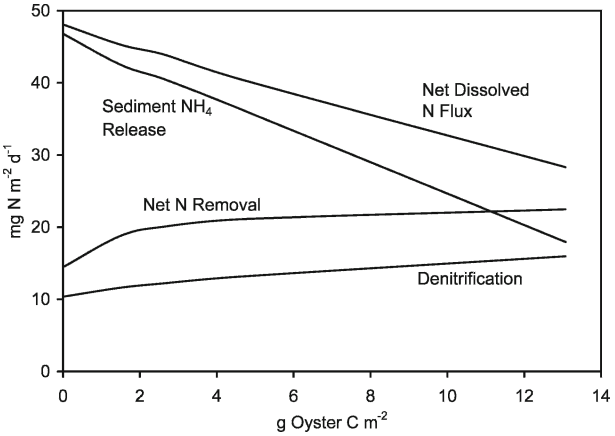

Fig. 4. Modeled effects of enhanced oyster density on sediment-water nitrogen fluxes. Effects are annual averages quantified for a unit area of oyster bottom in the lower Choptank River, segment EE2 (Table 3).

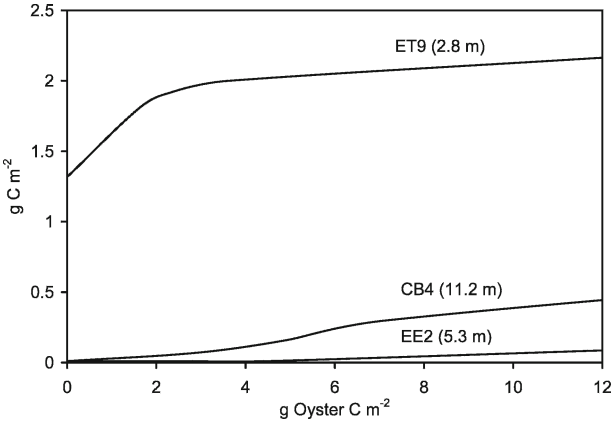

Fig. 5. Modeled effects of enhanced oyster density on density of benthic microalgae in three bay segments of different depths. Effects are annual averages quantified for a unit area of oyster bottom.

tion of oysters produces biodeposits to the sediments. Further increases in oyster density result in decreased biodeposition and settling. Biodeposition is influenced by the same processes that affect carbon: diminished mortality and increased respirational fraction. Settling decreases because formation of particulate nitrogen in the water column, through algal activity, is diminished by oyster predation. The introduction of oysters diminishes the release of diagenetically-produced sediment ammonium (Fig. 4). Diminished release is partially offset by excretion from oysters but the net effect of oysters is reduced net release to the water column, especially at highest densities. Two processes contribute to the reduction in diagenetic ammonium release. The role of reduced nitrogen deposition is obvious. Enhanced sediment nitrification to nitrate is also apparent, as evidenced by enhanced sediment denitrification of nitrate to nitrogen gas. Denitrification is also enhanced by the flux of nitrate from the water column into the sediments; nitrate no longer used in algal production diffuses into the sediments instead. The net effect of oysters on total nitrogen is removal from the water column via enhanced denitrification.

Benthic Algae

Experimental results indicate clearance of solids from the water column by oysters can enhance the activity of benthic microalgae, thereby altering sediment-water nutrient exchange and sediment diagenetic processes (Newell et al. 2002; Porter et al. 2004). Selected cells within the three CBPS indicate the influence of modeled oysters on benthic algae depends on local conditions, notably depth. Benthic algae are nonexistent in the CB4 (3.7 m depth) and EE2 (6.7 m depth) cells in the absence of oysters (Fig. 5). The shallow ET9 cell (2.1 m depth) supports viable benthic algae at zero oyster density. Density of benthic algae increases in all cells concurrent with oyster density as oysters clear the water column of suspended solids. Only the ET9 cell sustains algal density we calculate as sufficient to influence nutrient exchange at the sediment-water interface. The effect of the benthic algae is to diminish sediment oxygen consumption and ammonium release, during periods of illumination, relative to comparable sediments with no benthic algae (Cerco and Seitzinger 1997).

Regional Effects

Three model runs are considered: no oyster restoration, derived from the 2002 version of the model (Cerco and Noel 2004); a tenfold increase in oyster biomass; and historic oyster density. Results are averaged across the entire regional area and across all model years. Our convention for surface concentration is the average over the upper 6.7 m of the water column, roughly the depth of the surface mixed layer in the mid-bay. Bottom DO is represented by all waters below 12.9 m in CB4 and below 6.7 m in EE2. Due to shallow depth, the surface mixed layer coincides with the bottom in ET9.

Water quality standards in Chesapeake Bay are based on DO, chlorophyll, and water clarity (USEPA 2003). The tenfold oyster increase improves summer-average, bottom DO in the mainstem CB4 segment by less than 0.5 g m^{-3} (Fig. 6). Simulation of historic oyster density improves DO by roughly 1 g m^{-3}. Computed surface chlorophyll is reduced by 30% for a tenfold increase in oyster density and is halved when oysters are restored to historic density.

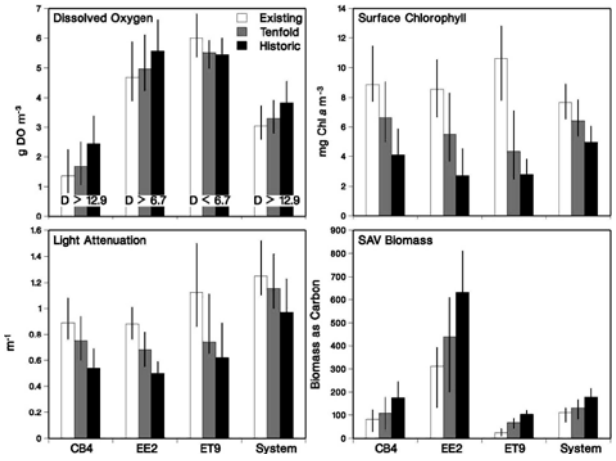

Fig. 6. Effects of oysters on summer-average bottom dissolved oxygen, surface chlorophyll, light attenuation, and submerged aquatic vegetation in three CBPS and for the system (SAV as tonnes C for three CBPS; as 10^2 tonnes for system total). Effects are presented as ten-year means (solid bars) and interannual range (vertical lines).

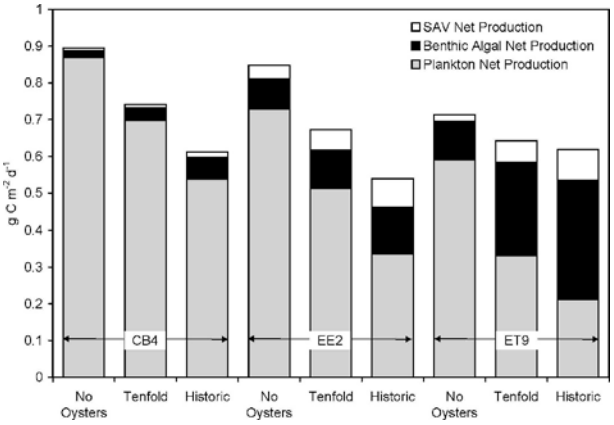

Fig. 7. Effects of oysters on ten-year annual-average net primary production of phytoplankton, benthic microalgae, and submerged aquatic vegetation in three CBPS.

Light attenuation is reduced by roughly 20% for a tenfold increase in oyster density and 40% when oysters are restored to historic density. Improvements in summer-average, bottom, DO at the mouth of the Choptank are consistent with the mainstem segment: less than 0.5 g m^{-3} for a tenfold increase in oyster density and roughly 1 g m^{-3} for restoration to historic density (Fig. 6). Percentage reductions in surface chlorophyll and light attenuation also correspond closely with the adjacent mainstem segment. Computed DO concentration in the eastern shore embayment declines by 0.5 g m^{-3} as a consequence of oyster restoration. The decline in DO reflects diminished production associated with the reductions in summer surface chlorophyll. The tenfold increase in oyster density induces a 60% decrease in summer surface chlorophyll while restoration to historic densities induces a greater then 70% decrease. Light attenuation in this region decreases by a third to nearly a half.

Planktonic versus Benthic Production

Analyses of Chesapeake Bay sediment cores indicate a change from a balanced planktonic and benthic algal community in the presettlement era to a predominantly planktonic community at present (Cooper and Brush 1993). Newell et al. (2002) suggest benthic production in shallow waters may be restored when reduced turbidity induced by bivalve filtration increases light penetration to the benthic microalgal community. Our model results support this suggestion. Under present conditions, net annual primary production is dominated by phytoplankton in all of our regions (Fig. 7). With the tenfold restoration, production in the shallow segment, ET9, is roughly balanced between phytoplankton and the combination of benthic algae and SAV. Under historic conditions, benthic algae become the dominant producers in the shallow segment while the deeper segments remain dominated by phytoplankton. The shallow system also retains a larger fraction of its present production, 87%, through the transition to historical conditions than the other segments, 63% to 69%.

Interannual Variability

Filtration rates are modulated continuously by the influences of salinity and suspended solids. Local variations in these forcing functions, combined with disparate response time scales for oysters and processes influenced by oysters, render the direct effects of environmental influences difficult to discern. In CB4, flow events in three of the simulated years are sufficient to depress salinity into the range (< 10‰) that diminishes filtration rate (Fig. 8). The runoff events that depress salinity in simulated years 9 and 10 are accompanied by suspended solid loads that are sufficiently high to diminish filtration rate as well. Following 4 yr of unlimited growth, oyster density attains its peak in year 5 despite the adverse salinity. The combined effects of low salinity and high suspended solids depress oyster density to the lowest level in the sequence in years 9 and 10.

Computed phytoplankton respond directly and rapidly to computed oyster density (Fig. 8). Chlorophyll removed by oysters in the wet years 9 and 10 is less than half the removal in other years, but SAV response is lagged by one or more years. SAV biomass improvements diminish in the years 9 and 10, concurrent with diminished oyster density. Owing to the looping of 10-yr sequences, the

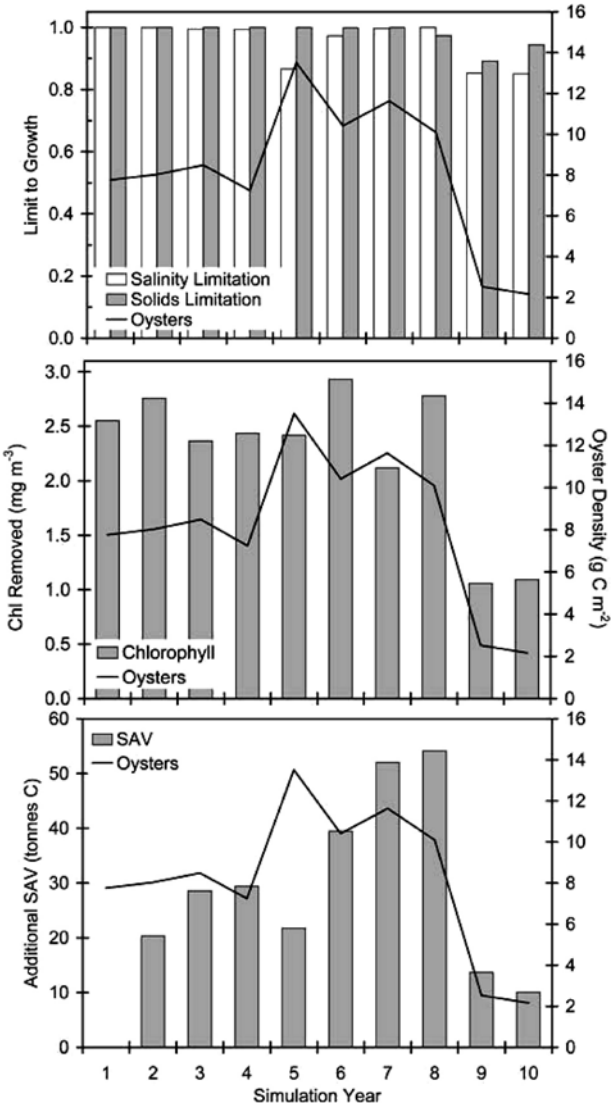

Fig. 8. Interannual variability in: filtration limitations and oyster density; chlorophyll removal and oyster density; and SAV improvements and oyster density. Results are averaged over the oyster growing season (April–November) in segment CB4 (Table 3).

depressed SAV at the end of year 10 initializes SAV in year 1. The time scale for SAV response is lengthy such that oysters provide no SAV improvement in the first year. SAV biomass improvements attributable to oysters compound almost every subsequent year until the high-flow event at the end of the sequence diminishes oysters and their effects.

Salinity and solids in EE2 are influenced by the same major flow events as CB4. The response of oyster density and oyster-induced effects in EE2 is similar to CB4. The large water volume between ET9 and the Susquehanna River and the relative proximity to the oceanic interface damp the influence of Susquehanna River flow events in ET9. This segment responds to flow events in the local watershed, notably a runoff event that depresses salinity in year 3. This segment demonstrates a pattern of interannual variability that differs from segments upstream.

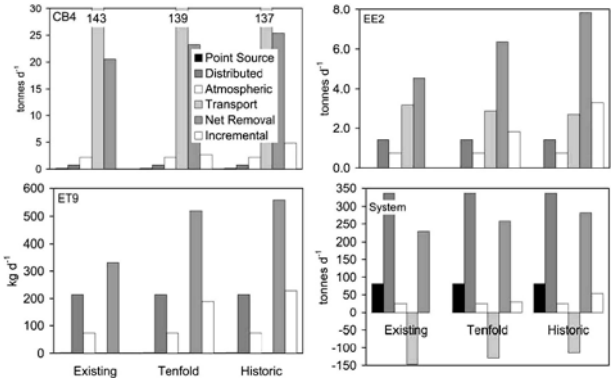

Fig. 9. Effects of oysters on ten-year annual-average nitrogen budgets of three CBPS and system-wide.

Model results indicate that wet years, in which salinity is depressed and solid loads are high, are detrimental to oysters and adversely affect their benefits. The influences of local and remote runoff events and the disparate response scales of oysters and their benefits render direct connections between hydrology and oyster benefits difficult to discern. Benefits are best assessed over a multiyear interval that incorporates a range of wet and dry hydrological sequences.

Regional Budgets

Annual-average nutrient budgets were constructed for each of the regions for the three subject model runs. Terms in the budgets are point source: direct inputs from municipal and industrial facilities, distributed: loads to the region from the adjacent watershed, atmospheric: loads to the water surface, transport: net loads from the upstream region, net removal: accumulation in the bottom sediments plus denitrification, and incremental: increase in net removal due to oysters.

Nitrogen transport down the mainstem of the bay dwarfs all other sources and sinks in CB4 (Fig. 9). In view of the enormity of nitrogen transported relative to the amount removed by oysters, the ability of oyster restoration to affect this segment at all is remarkable. Restoration of oysters increases net nitrogen removal, through denitrification and sediment retention, by 20% to 50% although the reduction in surface total nitrogen concentration is only 10% to 15%. Incremental nitrogen removal by oysters in EE2 is significant relative to other regional sources and sinks. Under the restoration

scenarios, nitrogen removal exceeds the local sources indicating nutrient import from the adjacent mainstem segment. Nitrogen loading and net removal in segment ET9 are closely balanced under existing conditions. As with EE2, enhanced removal via oyster restoration results in nitrogen import from adjacent open waters.

System-wide Effects

The methods, properties examined, and budgeting from the regional analyses are extensible to the entire system, which extends from the fall lines of major tributaries to the mouth of the bay. Since hypoxia is primarily a bottom-water effect, summer-average DO concentration is considered for all portions of the system greater than 12.9 m depth. DO increases by 0.25 g m^{-3} for the tenfold oyster restoration and 0.8 g m^{-3} for restoration to historic levels (Fig. 6). System-wide, summer surface chlorophyll concentration declines by more than 1 mg m^{-3} for a tenfold increase in oyster biomass and 2.5 mg m^{-3} for restoration to historic levels. The chlorophyll reductions contribute to reductions in summer light attenuation of 8% (tenfold increase) to 22% (historic density).

System-wide Budgets

System-wide nutrient budgets can be constructed that parallel the regional budgets (Fig. 9). In this case, transport is the net flux at the mouth of the bay. Negative transport indicates nutrient loss to the ocean; positive transport indicates nutrient import from the ocean. Tenfold oyster restoration removes 30,000 kg d^{-1} total nitrogen from the system. Oysters at historic levels remove 54,000 kg d^{-1}.

Discussion

Bivalve control of phytoplankton has been observed in a variety of systems (Cloern 1982; Cohen et al. 1984; Caraco et al. 2006). The factors favorable to benthic control were described by Officer et al. (1982) and include shallow water and partially enclosed regions with poor hydrodynamic exchange. Our modeled system is consistent with the description. Fractional reductions in chlorophyll concentration, induced by bivalve restoration, are inversely related to regional depth. The greatest fractional reductions in chlorophyll are predicted in ET9 (2.8 m), followed by EE2 (5.3 m) and CB4 (11.2 m).

Diminished DO has been attributed to bivalve respiration in laboratory (Doering et al. 1987) and riverine (Caraco et al. 2000) settings. Bivalve respiration can diminish DO only in the presence of an external carbon source, which is the case for flow-through mesocosms and can apply to riverine systems as well. Otherwise respiration can do no more than consume the oxygen associated with primary production of carbon. Oyster restoration in our modeled system produces enhanced or diminished DO, depending on local conditions. In the shallow environment characterized by ET9, DO declines due to diminished algal production associated with benthic grazing. In deeper, stratified waters DO improvements occur since reduced algal production results in less carbon deposition to benthic sediments. In either case, the DO changes attributable to oyster restoration are likely to be 0.5 g m^{-3} or less.

Improvements in SAV abundance have been attributed to improved water clarity induced by bivalve resurgence (Phelps 1994; Caraco et al. 2006). Our model indicates enhanced SAV abundance is the most significant improvement to be attained through oyster restoration. On a percentage basis, calculated improvements in SAV biomass exceed the improvements in DO and chlorophyll (Fig. 6). In the mainstem CB4 segment and the lower Choptank River, water clarity improvements from oyster restoration produce increases in computed SAV biomass of 33% to more than 100%. In the lower eastern shore embayment, SAV biomass nearly triples for a tenfold increase in oyster density and increases by greater than a factor of four for restoration to historic oyster densities. Computed system-wide SAV biomass increases from 25% to more than 60%. The effectiveness of oysters in SAV restoration is attributed to the close proximity of oysters to the SAV beds. Modification of the local environment is immediately effective versus an attempt to improve bottom-water DO through environmental manipulation on adjacent shoals.

Our model includes multiple mechanisms for nutrient trapping through oyster restoration including enhanced deposition, retention by benthic algae, and denitrification. Laboratory studies (Newell et al. 2002) confirm the enhancement of microphytobenthos and denitrification through oyster restoration, although the mechanism for enhanced denitrification differs from that in our model. In the laboratory, denitrification was fueled through the simulated introduction of oyster fecal mater. Oxidation of this material was accompanied by nitrate reduction. In our model, total carbon deposition to sediments declines as a function of oyster restoration (Fig. 3). It is this diminished deposition, accompanied by diminished oxygen consumption within the bottom sediments, which promotes enhanced denitrification. Oxygen penetrates deeper into the sediments and more ammonium is oxidized to nitrate. This nitrate is subsequently denitrified in anoxic microzones (Jenkins and Kemp 1984). Nitrogen removal is put into

perspective by comparison with other sources, as quantified during the recent nutrient allocation process (Cerco and Noel 2004). The amount of nitrogen removed by a tenfold increase in native oysters, 30,000 kg d^{-1}, is roughly the equivalent of direct nitrogen deposition to the water surface, 25,000 kg d^{-1}, but only 18% of the mean annual nitrogen load from the Susquehanna River, 169,000 kg d^{-1}, the largest flow to the system.

Our model agrees with a wide body of evidence that bivalves can modify their local environment. When bivalves are confined to only a small portion of bottom area, their ability to transform an entire estuarine system is limited. In view of the enormous cost and technological difficulties associated with controlling external loads, DO improvements on the order of tenths of a g m^{-3} and nitrogen removal on the order of 10% of system loading cannot be disparaged. These improvements have economic and ecological values and are to be encouraged. Oyster restoration is no panacea for the host of problems associated with cultural eutrophication. Oyster restoration should be viewed as one of many contributions to remediation of eutrophication in Chesapeake Bay and elsewhere. We recommend that oyster restoration target specific areas with suitable environments and that resulting environmental improvements be viewed on similar, local scales. Oyster restoration is a supplement, not a substitute for reductions in anthropogenic nutrient loads.

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Literature Cited

Anderson, L. 1995. On the hydrogen and oxygen content of marine phytoplankton. *Deep-Sea Research I* 42:1675–1680.

Andrews, J. 1965. Infection experiments in nature with *Dermocystidium marinum* in Chesapeake Bay. *Chesapeake Science* 6:60–67.

Andrews, J. 1988. Epizoology of the disease caused by the oyster pathogen *Perkinsus marinus* and its effect on the oyster industry. *American Fisheries Society Special Publication* 18:47–63.

Bicknell, B., J. Imhoff, J. Kittle, A. Donigian, R. Johanson, and T. Barnwell. 1996. Hydrologic simulation program - FORTRAN user's manual for release 11. U.S. Environmental Protection Agency Environmental Research Laboratory, Athens, Georgia.

Boucher, G. and R. Boucher-Rodoni. 1988. In situ measurement of respiratory metabolism and nitrogen fluxes at the interface of oyster beds. *Marine Ecology Progress Series* 44:229–238.

Boynton, W., J. Garber, R. Summers, and W. Kemp. 1995. Inputs, transformations, and transport of nitrogen and phosphorus in Chesapeake Bay and selected tributaries. *Estuaries* 18:285–314.

Caffrey, J. and W. Kemp. 1990. Nitrogen cycling in the sediments with estuarine populations of *Potamogeton perfoliatis* L. and *Zostera marina* L. *Marine Ecology Progress Series* 66:147–160.

Caffrey, J. and W. Kemp. 1992. Influence of the submersed plant, *Potamogeton perfoliatis* L., on nitrogen cycling in estuarine sediments: Use of ^{15}N techniques. *Limnology and Oceanography* 37:1483–1495.

Caraco, N., J. Cole, S. Findlay, D. Fischer, G. Lampman, M. Pace, and D. Strayer. 2000. Dissolved oxygen declines in the Hudson River associated with the invasion of the zebra mussel (*Dreissena polymorpha*). *Environmental Science and Technology* 34:1204–1210.

Caraco, N., J. Cole, and D. Strayer. 2006. Top-down control from the bottom: Regulation of eutrophication in a large river by benthic grazing. *Limnology and Oceanography* 51:664–670.

Cerco, C. 1995. Response of Chesapeake Bay to nutrient load reductions. *Journal of Environmental Engineering* 121:549–557.

Cerco, C. and T. Cole. 1993. Three-dimensional eutrophication model of Chesapeake Bay. *Journal of Environmental Engineering* 119:1006–1025.

Cerco, C. and M. Meyers. 2000. Tributary refinements to the Chesapeake Bay Model. *Journal of Environmental Engineering* 126: 164–174.

Cerco, C. and K. Moore. 2001. System-wide submerged aquatic vegetation model for Chesapeake Bay. *Estuaries* 24:522–534.

Cerco, C. and S. Seitzinger. 1997. Measured and modeled effects of benthic algae on eutrophication in Indian River-Rehoboth Bay, Delaware. *Estuaries* 20:231–248.

Cloern, J. 1982. Does the benthos control phytoplankton biomass in south San Francisco Bay? *Marine Ecology Progress Series* 9:191–202.

Cohen, R., P. Dresler, E. Phillips, and R. Cory. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. *Limnology and Oceanography* 29:170–180.

Cooper, S. and G. Brush. 1993. A 2,500-year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries* 16:617–626.

Dame, R. 1972. Comparison of various allometric relationships in intertidal and subtidal American oysters. *Fishery Bulletin* 70: 1121–1126.

Dame, R., J. Spurrier, and R. Zingmark. 1992. In situ metabolism of an oyster reef. *Journal of Experimental Marine Ecology and Biology* 164:147–159.

Ditoro, D. 2001. Sediment Flux Modeling. John Wiley and Sons, New York.

Doering, P., J. Kelly, C. Oviatt, and T. Sowers. 1987. Effect of the hard clam *Mercenaria mercenaria* on benthic fluxes of inorganic nutrients and gases. *Marine Biology* 94:377–383.

Epifanio, C. and J. Ewart. 1977. Maximum ration of four algal diets for the oyster *Crassostrea virginica* Gmelin. *Aquaculture* 11: 13–29.

Fisher, T., E. Peele, J. Ammerman, and L. Harding. 1992. Nutrient limitation of phytoplankton in Chesapeake Bay. *Marine Ecology Progress Series* 82:51–63.

Flemer, D., G. Mackiernan, W. Nehlsen, and V. Tippie. 1983. Chesapeake Bay: A profile of environmental change. U.S. Environmental Protection Agency Region III, Philadelphia, Pennsylvania.

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

Hammen, C., H. Miller, and W. Geer. 1966. Nitrogen excretion of *Crassostrea virginica*. *Comparative Biochemistry and Physiology* 17: 1199–2000.

Haven, D. and R. Morales-Alamo. 1966. Aspects of biodeposition by oysters and other invertebrate filter feeders. *Limnology and Oceanography* 11:487–498.

Hedges, J., J. Baldock, Y. Gelinas, C. Lee, M. Peterson, and S. Wakeham. 2002. The biochemical and elemental compositions

of marine plankton: A NRM perspective. *Marine Chemistry* 78: 47–63.

HOLLAND, A., N. MOUNTFORD, AND J. MIHURSKY. 1977. Temporal variation in upper bay mesohaline benthic communities: I. The 9-m mud habitat. *Chesapeake Science* 18:370–378.

JENKINS, M. AND W. KEMP. 1984. The coupling of nitrification and denitrification in two estuarine sediments. *Limnology and Oceanography* 29:609–619.

JOHNSON, B., K. KIM, R. HEATH, B. HSIEH, AND L. BUTLER. 1993. Validation of a three-dimensional hydrodynamic model of Chesapeake Bay. *Journal of Hydraulic Engineering* 199:2–20.

JORDAN, S. 1987. Sedimentation and remineralization associated with biodeposition by the American oyster *Crassostrea virginica* (Gmelin). Ph.D. Dissertation. University of Maryland, College Park, Maryland.

JORDAN, S. AND J. COAKLEY. 2004. Long-term projections of eastern oyster populations under various management scenarios. *Journal of Shellfish Research* 23:63–72.

JORDAN, S., K. GREENHAWK, C. MCCOLLOUGH, J. VANISKO, AND M. HOMER. 2002. Oyster biomass, abundance, and harvest in northern Chesapeake Bay: Trends and forecasts. *Journal of Shellfish Research* 21:733–741.

KIRBY, M. AND H. MILLER. 2005. Response of a benthic suspension feeder (*Crassostrea virginica* Gmelin) to three centuries of anthropogenic eutrophication in Chesapeake Bay. *Estuarine Coastal and Shelf Science* 62:679–689.

LOOSANOFF, V. 1953. Behavior of oysters in water of low salinities. *Proceedings of the National Shellfish Association* 43:135–151.

LOOSANOFF, V. AND F. TOMMERS. 1948. Effect of suspended silt and other substances on rate of feeding of oysters. *Science* 107:69–70.

MAGNI, P., S. MONTANI, C. TAKADA, AND H. TSUTSUMI. 2000. Temporal scaling and relevance of bivalve nutrient excretion on a tidal flat of the Seto Inland Sea, Japan. *Marine Ecology Progress Series* 198:139–155.

MALONE, T., D. CONLEY, T. FISHER, P. GLIBERT, AND L. HARDING. 1996. Scales of nutrient-limited phytoplankton productivity in Chesapeake Bay. *Estuaries* 19:371–385.

MERRILL, J. AND J. CORNWELL. 2000. The role of oligohaline marshes in estuarine nutrient cycling, p. 425–441. *In* M. Weinstein and D. Kreeger (eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer, Dordrecht.

NATIONAL RESEARCH COUNCIL (NRC). 2000. Clean Coastal Waters. National Academy Press, Washington, D.C.

NATIONAL RESEARCH COUNCIL (NRC). 2001. Assessing the TMDL Approach to Water Quality Management. National Academy Press, Washington, D.C.

NEWELL, R. I. E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster (*Crassostrea virginica*)? p. 536–546. *In* M. P. Lynch and E. C. Krome (eds.), Understanding the Estuary – Advances in Chesapeake Bay Research, Publication 129, Chesapeake Research Consortium, Baltimore, Maryland.

NEWELL, R. I. E., J. CORNWELL, AND M. OWENS. 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics. *Limnology and Oceanography* 47: 1367–1379.

NEWELL, R. I. E. AND E. KOCH. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793–806.

OFFICER, C., R. BIGGS, J. TAFT, AND L. CRONIN. 1984. Chesapeake Bay anoxia: Origin, development, and significance. *Science* 223: 22–27.

OFFICER, C., T. SMAYDA, AND R. MANN. 1982. Benthic filter feeding: A natural eutrophication control. *Marine Ecology Progress Series* 9: 203–210.

PHELPS, H. 1994. The Asiatic clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River estuary near Washington, D.C. *Estuaries* 17:614–621.

PORTER, E., J. CORNWELL, L. SANFORD, AND R. I. E. NEWELL. 2004. Effect of oysters *Crassostrea virginica* and bottom shear velocity on benthic pelagic coupling and estuarine water quality. *Marine Ecology Progress Series* 271:61–75.

PRITCHARD, D. 1967. Observations of circulation in coastal plain estuaries, p. 37–44. *In* G. Lauff (ed.), Estuaries. American Association for the Advancement of Science, Washington, D.C.

RIISGARD, H. 1988. Efficiency of particle retention and filtration rate in 6 species of northeast American bivalves. *Marine Ecology Progress Series* 45:217–223.

ROTHSCHILD, B., J. AULT, P. GOULLETQUER, AND M. HERAL. 1994. Decline of the Chesapeake Bay oyster population: A century of habitat destruction and overfishing. *Marine Ecology Progress Series* 111:29–39.

RYBICKI, N., H. JENTER, V. CARTER, R. BALTZER, AND M. TURTORA. 1997. Observations of the tidal flux between a submersed aquatic plant stand and the adjacent channel in the Potomac River near Washington, D.C. *Limnology and Oceanography* 42: 307–317.

SCHINDLER, D. 2006. Recent advances in the understanding and management of eutrophication. *Limnology and Oceanography* 51: 356–363.

SHUMWAY, S. AND R. KOEHN. 1982. Oxygen consumption in the American oyster *Crassostrea virginica. Marine Ecology Progress Series* 9:59–68.

SMITH, V., S. JOYE, AND R. HOWARTH. 2006. Eutrophication of freshwater and marine ecosystems. *Limnology and Oceanography* 51:351–355.

SRNA, R. AND A. BAGGALEY. 1976. Rate of excretion of ammonia by the hard clam *Mercenaria mercenaria* and the American oyster *Crassostrea virginica. Marine Biology* 36:251–258.

STEVENSON, J., M. KEARNY, AND E. KOCH. 2002. Impacts of sea-level rise on tidal wetlands and shallow water habitats: A case study from Chesapeake Bay, p. 23–36. *In* N. McGinn (ed.), Fisheries in a Changing Environment. American Fisheries Society Symposium No. 32, Bethesda, Maryland.

TENORE, K. AND W. DUNSTAN. 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. *Marine Biology* 21:190–195.

WARD, L., W. KEMP, AND W. BOYNTON. 1984. The influence of water depth and submerged vascular plants on suspended particulates in a shallow estuarine embayment. *Marine Geology* 59:85–103.

WINTER, J. 1978. A review of the knowledge of suspension-feeding lamellibranchiate bivalves, with special reference to artificial aquaculture systems. *Aquaculture* 13:1–33.

YATES, C. 1911. Survey of the oyster bars by county of the State of Maryland. Department of Commerce and Labor, Coast and Geodetic Survey, Washington, D.C.

SOURCES OF UNPUBLISHED MATERIALS

MANN, R. unpublished data. Virginia Institute of Marine Science, Gloucester Point, Virginia 23062.

UPHOFF, J. unpublished data. Maryland Department of Natural Resources, Fisheries Service, 301 Marine Academy Drive, Stevensville, Maryland 21666.

CERCO, C. AND M. NOEL. 2004. The 2002 Chesapeake Bay eutrophication model. EPA 903-R-04-004. Chesapeake Bay Program Office, U.S. Environmental Protection Agency, Annapolis, Maryland (available at http://www.chesapeakebay.net/modsc.htm).

U.S. ENVIRONMENTAL PROTECTION AGENCY (USEPA). 2000. Chesapeake 2000. U.S. Environmental Protection Agency Region III Chesapeake Bay Program Office. Annapolis, Maryland (available at http://www.chesapeakebay.net/agreement.htm).

U.S. ENVIRONMENTAL PROTECTION AGENCY (USEPA). 2003. Ambient water quality criteria for dissolved oxygen, water clarity and chlorophyll *a* for the Chesapeake Bay and its tidal tributaries. U.S. Environmental Protection Agency Region III Chesapeake

Bay Program Office, EPA 903-R-03-002. Annapolis, Maryland (available at http://www.chesapeakebay.net/baycriteria.htm).
U.S. Environmental Protection Agency (USEPA). 2004. Chesapeake Bay Program analytical segmentation scheme – Revisions, decisions, and rationales 1983–2003. U.S. Environmental Protection Agency Region III Chesapeake Bay Program Office. Annapolis MD. (available at http://www.chesapeakebay.net/segmentscheme.htm)

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