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INFLUENCE OF EASTERN OYSTERS ON NITROGEN AND PHOSPHORUS REGENERATION IN CHESAPEAKE BAY, USA

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Abstract: Suspension-feeding bivalves couple pelagic and benthic processes because they consume seston from the water column, and their biodeposits (feces and pseudofeces) settle on the sediment surface. Abundant stocks of bivalves can exert grazer control on phytoplankton; in the process, nitrogen and phosphorus are regenerated to the water column as excreta and via microbial decomposition of their biodeposits. Bivalve biodeposition, however, enhances net ecosystem losses of N and P via sediment burial and bacterially mediated, coupled nitrification-denitrification. Bivalve feeding also reduces turbidity and thereby increases light available for microphytobenthos. Although microphytobenthos may compete with nitrifying bacteria for N, potentially reducing coupled nitrification-denitrification, they retain N and P within sediments, further reducing net regeneration to the water column.

Keywords: benthic-pelagic coupling, bivalves, Chesapeake Bay, nitrogen, denitrification, nutrient burial, oyster, phosphorus

INTRODUCTION

Many estuaries and coastal water bodies worldwide are anthropogenically enriched with Nitrogen (N) and Phosphorus (P). These fertilizing elements emanate from point sources (e.g., sewage treatment plant effluent), non-point sources (e.g., agricultural run-off and septic-tank discharge), and atmospheric deposition. These anthropogenically enhanced sources of N and P cause fundamental changes in the magnitude and distribution of phytoplankton biomass and primary production (Fisher et al. 1988, Malone 1992, Conley 1999), and the resulting enhanced phytoplankton production and blooms of both toxic and nontoxic microalgae frequently have deleterious effects on the structure and function of coastal ecosystems (Cloern 2001). In some locations, such as Chesapeake Bay and Long Island Sound, USA, microbial decomposition of the excess phytoplankton biomass supported by nutrient enrichment causes bottom water and sediments to become anoxic during warmer months (Boicourt 1992).

In shallow eutrophic water bodies, consumption of phytoplankton by abundant stocks of bivalve suspension-feeders directly reduces the amount of

particulate organic matter (POM) available to be remineralized by pelagic consumers and bacterioplankton (Cloern 1982, Officer et al. 1982). Hence, observed phytoplankton concentrations are not only the result of anthropogenic nutrient inputs - the so called "bottom-up" influence - but also are affected by changes in the abundance of grazer organisms that exert "top-down" control (Newell 1988, Dame 1996, Strayer et al. 1999, Newell 2004).

Newell (1988) postulated that present-day high phytoplankton biomass in Chesapeake Bay is caused, in part, by the reduction of "top-down" grazing control. In particular, there has been a large decline in the abundance of suspension-feeding eastern oysters, *Crassostrea virginica*, superimposed on the well-recognized effects of nutrient enrichment stimulating phytoplankton production (Kemp and Boynton 1992, Cloern 2001, Harding et al. 2002). Intensive harvesting of oysters in the 19th century led to a severe decline in oyster stocks and their reef habitat (Kennedy and Breisch 1981, Rothschild et al. 1994). This loss of material, in combination with shell becoming covered in sediment from erosion and resuspension (Smith et al. 2001), led to a steady decline in the clean shell necessary for oyster larval settlement. In addition, since the 1950's, two major parasitic diseases, MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*), exacerbated the harvest-related decline in oysters in Chesapeake Bay (Ford and Tripp 1996). Newell (1988) estimated that eastern oyster populations in the early 19th Century filtered 80% of the < 9 m water volume in Chesapeake Bay per day during summertime; the precipitous decline in oysters, however, reduced this to < 1% filtration of the shallows per day by 1988. This collapse of the eastern oyster population in Chesapeake Bay has also occurred in other estuaries (e.g., Delaware Bay and Long Island Sound) along the Atlantic coast of North America (Mackenzie 1996). This suggests that these other estuaries have also lost the benthic-pelagic coupling function once provided by abundant stocks of eastern oysters.

Bivalve suspension-feeders serve an important biogeochemical role in coastal ecosystems because N and P from the water column are transferred to the sediments in their biodeposits. Many investigators have focused on the nutrient regeneration aspects of bivalve grazing (Prins and Smaal 1990, Asmus and Asmus 1991, Yamamuro and Koike 1993, Pietros and Rice 2003); here we emphasize the importance of bivalve biodeposition in enhancing the processes leading to nutrient burial and denitrification (Fig. 1, Newell et al. 2002, Newell 2004). For simplicity in Fig. 1 we only include processes related to bivalve feeding, and ignore gravitational settling of senescent phytoplankton, etc. If all of the phytoplankton N and P that is removed from the water column by suspension-feeding bivalves is regenerated either in excreta (urine) or microbially regenerated from bivalve biodeposits, then bivalve populations simply serve to recycle N and P ($T = R$ in Fig. 1). Under these conditions, recycling of N and P by bivalves maintains primary production at a maximum level determined by inputs (I) less physical losses

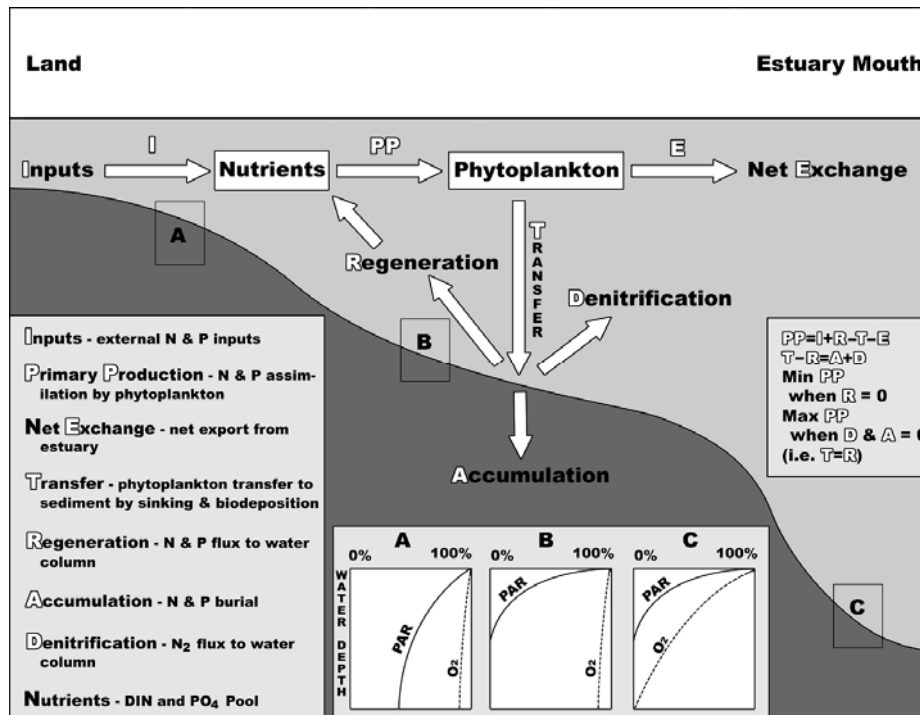


Fig. 1. Conceptual diagram of how phytoplankton production (PP) in the Choptank River estuary is supported by inputs (I) and sediment regeneration (R) of N and P. The amount of N and P flushed from the estuary, buried in the accumulating sediments, and denitrified controls the maximum phytoplankton biomass supported. Illustrated in the three boxes for locations A, B, and C are how the percentage of surface photosynthetically active radiation (PAR) and degree of oxygen saturation varies with water column depth from the shallows flanks (< 2 m) of the estuary (A), to slightly deeper areas (2 to 8 m) that form the majority of the estuary bottom (B), to deep water sites (C) located in the deepest (> 8 m) main channel of the estuary.

(net Exchange in Fig. 1). To the extent that N and P from biodeposits either accumulate in sediments ($A > 0$ in Fig. 1), are denitrified ($D > 0$ in Fig. 1), or are trapped by microphytobenthos (Fig. 2A), then bivalve feeding enhances nutrient loss from the ecosystem ($R < T$). Due to this removal mechanism within the sediments, phytoplankton production is set at a level lower than that determined by the nutrient inputs from the watershed, airshed, and exchanges with the next downstream ecosystem. In addition to altering nutrient regeneration processes, bivalve grazing, by removing phytoplankton and inorganic particles from the water column, can reduce turbidity. The resulting increased light penetration (Fig. 1 Box A) can potentially enhance the area of sediments with sufficient light intensity to support photosynthesis of benthic plants (Newell and Koch 2004). Other deeper or more turbid areas may either have insufficient light (Fig. 1 Box B) or insufficient light and low dissolved oxygen (Fig. 1 Box C).

It is well documented that there have been severe economic

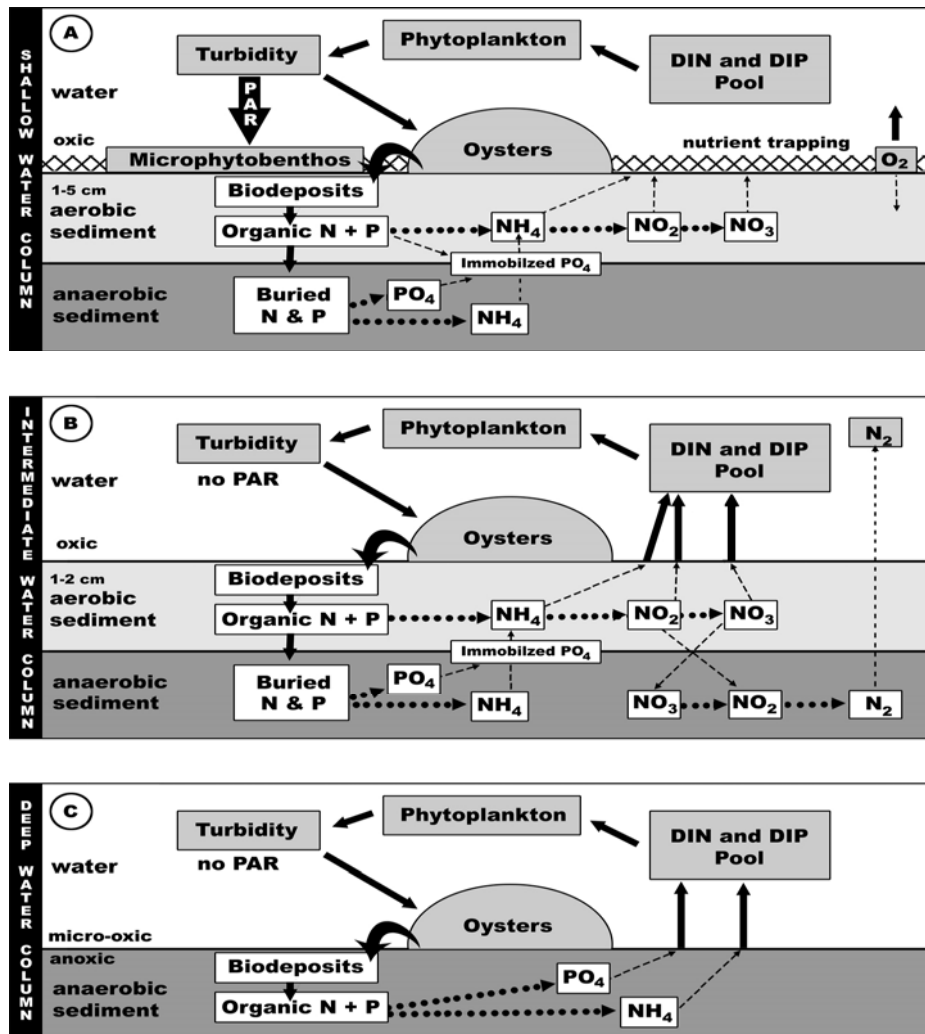


Fig. 2. Role of eastern oysters in removing phytoplankton from the water column and transferring undigested particulate material as biodeposits to the sediment surface. Illustrated are benthic-pelagic scenarios for three locations (Boxes A, B, and C; Fig. 1) with different levels of photosynthetically active radiation (PAR) and dissolved oxygen concentrations. From surficial aerobic sediments (middle panel; Location B) N and P are released to the water column. The microbially mediated process of nitrification in the aerobic surface sediments, coupled to denitrification within the underlying anaerobic sediments, causes N to be lost from biodeposits as N₂ gas. N not regenerated is buried in accumulating sediments and P is immobilized in the aerobic sediments. In contrast, little nutrient regeneration into the water column takes place in locations with sufficient light to support active microphytobenthos that absorb regenerated N and P at the sediment surface (upper panel; Location A). Coupled nitrification-denitrification is also reduced because the microphytobenthos out-compete bacteria for NO₂⁻, NO₃⁻, and NH₄⁺. In locations where the sediments are anoxic (lower panel; Location C) nitrification is inhibited and all N and P is regenerated from the sediments as NH₄⁺ and PO₄³⁻. Some burial of N occurs but P sorption is precluded. Solid lines indicate transfer of materials; dashed lines indicate diffusion of materials; dotted lines indicate microbially mediated reactions.

consequences to the fishing communities in Chesapeake Bay (Kennedy and Breisch 1981, Rothschild et al. 1994) stemming from the decline in eastern oyster harvests from the peak of ~60,000 metric tons wet tissue weight annually in the late 19th Century to ~ 300 metric tons in 2002 (National Marine Fisheries Service; www.st.nmfs.gov). Less easy to assess are the adverse ecological consequences and the economic costs to coastal ecosystems of essentially the complete loss of eastern oysters. Ecological effects associated with eastern oyster populations can be divided into 1) the influence of their suspension-feeding activity on water quality, and 2) the role of the physical oyster reef structure itself in providing habitat for other organisms. We focus here on the primary effects associated with oyster populations filtering particles from the water column and transferring material to the sediment surface. We do not consider the secondary effects of oyster reefs providing habitat for many invertebrate and vertebrate species (Coen et al. 1999).

The objective of this paper is to review available data to determine whether suspension-feeding bivalves are simply rapidly regenerating nutrients, thereby maintaining phytoplankton production at levels set by inputs; alternatively, if by enhancing denitrification and burial, can bivalve feeding be considered a “sink” for N and P? We then apply this information to estimate the possible effects of stocks of sub-tidal eastern oysters on the watershed-level nitrogen and phosphorus budgets for the Choptank River, a mesohaline tributary of Chesapeake Bay, USA.

EASTERN OYSTER FEEDING AND PARTICLE REMOVAL

Crassostrea virginica is an active suspension-feeder that exhibits a complex feeding response when exposed to seasonal variations of temperature and seston concentration (reviewed by Newell and Langdon 1996). Captured particles are sorted, and the less nutritious ones or those in excess of gut capacity are immediately rejected as pseudofeces (Newell and Jordan 1983, Ward et al. 1994, Newell and Langdon 1996). Nutritious particles are ingested and subject to extracellular and intracellular digestion and the remains are defecated within ~ 24 h (Langdon and Newell 1996). The number of captured particles that can be ingested by bivalves is dependent on gut residence time and gut volume, which is a function of body size (Bayne et al. 1984). Once maximum ingestion rates are attained, any further increase in seston concentration results in increasing amounts of material being rejected as pseudofeces (Haven and Morales-Alamo 1966, Newell and Jordan 1983). Thus, at low seston concentrations eastern oyster pseudofeces are composed primarily of inorganic material, but as seston concentrations increase the proportion of POM in their pseudofeces also increases.

Eastern oysters maintain high clearance rates even when the volume of particles captured on their gills exceed their limited gut capacity. Under such circumstances excess particles are rejected as pseudofeces prior to

ingestion. By maximizing the number of particles captured and subjected to efficient pre-ingestive selection, eastern oysters maximize their ingestion of nutritious particles (Ward et al. 1994, Newell and Langdon 1996). Today, throughout the majority of the eastern oyster's range, anthropogenic nutrient enrichment has increased phytoplankton biomass; consequently, once the oyster's nutritional needs are satisfied, even phytoplankton cells are rejected in pseudofeces, in addition to less nutritious detrital and silt particles. This response of eastern oysters to increasing seston concentrations is quite different from other suspension-feeding bivalves, such as infaunal cockles and clams, which mainly regulate their ingestion rates by constraining their clearance rates rather than rejecting excess particles as pseudofeces (Hawkins et al. 1998, Grizzle et al. 2001). Consequently, the species of bivalves that can exert the greatest influence on benthic-pelagic coupling are those, such as oysters and mussels, which maintain high clearance rates and reject relatively large amounts of POM as pseudofeces.

One of the more important effects of bivalve feeding is the repackaging of small seston particles into large aggregates. Particles in eastern oyster feces are tightly bound in a mucoid matrix and voided as pelleted strings that can be as long as several millimeters. Pseudofeces are less tightly bound in mucus and may be subject to some disaggregation when voided from the oyster. As a consequence of the aggregation of both feces and pseudofeces, biodeposits have a faster sinking velocity that is up to 40 times that of non-aggregated particles (Kautsky and Evans 1987, Widdows et al. 1998). Even though epibenthic bivalves, such as eastern oysters live on reefs relatively close to the sediment surface, their biodeposits may be widely distributed by wave action or tidal currents before final deposition (Haven and Morales-Alamo 1968, Dame et al. 1991a, Silvert and Cromey 2001). Biodeposits can only settle where the friction velocity (u^*), which is a function of current velocity and bed roughness, is below a critical velocity required to suspend particles of that particular mass. If biodeposits become fragmented into smaller particles, they will sink more slowly and are resuspended at lower friction velocities (Sanford and Chang 1997). Oyster shells and reefs add appreciably to bed roughness and hence increase friction velocity (Wildish and Kristmanson 1997), thereby enhancing the transport of biodeposits to sediments away from the reef structure. In locations and at times where u^* is below the critical velocity, biodeposits undergo a consolidation process and gradually become incorporated into the sediments (Haven and Morales-Alamo 1966, 1968, Kaspar et al. 1985, Jaramillo et al. 1992, Widdows et al. 1998). Once consolidated into the sediments, a much greater bottom shear stress is required to resuspend the cohesive material (Sanford and Chang 1997). Despite the clearly recognized importance of bivalve biodeposition in benthic pelagic coupling (Fig. 1), exactly how much of the material is transferred to the sediment surface, how much is resuspended, and how much accumulates in the surficial sediment remains poorly characterized. Further research is required to quantify biodeposit

sinking rates and physical conditions leading to their resuspension before we can fully quantify the contribution of bivalves to benthic-pelagic coupling.

EASTERN OYSTER DIGESTION

Bivalves digest and assimilate N from different sources of POM with efficiencies from ~ 20 to 90%. These efficiencies also vary seasonally (Bayne and Newell 1983, Kreeger and Newell 2001), leading to substantial amounts of undigested particulate organic nitrogen (PON) being transferred to the sediment surface in feces in addition to the PON rejected in pseudofeces. Newell and Jordan (1983) reported that eastern oysters feeding on natural seston at concentrations of 5 to 20 mg L⁻¹ assimilated ~ 50% of the PON filtered, and the remainder was voided as biodeposits.

For eastern oysters feeding during summer months on natural seston in the mesohaline Chesapeake Bay, Jordan (1987) found that biodeposits contained ~ 2 to 3 times as much C, N, and P per unit weight as particles settling-out naturally from the water column (Table 1). In numerous studies of sediments near large aggregations of bivalves, an increase in sediment N content has been confirmed (Tenore et al. 1982, Kaspar et al. 1985, Kautsky and Evans 1987, Deslous-Paoli et al. 1992, Hatcher et al. 1994). Therefore, oyster populations remove substantial amounts of planktonic N and P from the water column and enrich the underlying sediment.

The N and P absorbed by bivalves from the ingested food undergo internal metabolic processing. The majority is used for tissue growth, and some is excreted in urine (Bayne and Hawkins 1992). Magni et al. (2000) reviewed the extensive literature on weight specific N excretion for 11 species of bivalve mollusc, and average ammonium excretion rates were ~ 6.0 μmol NH₄⁺ g⁻¹ DW h⁻¹, (DW = dry tissue weight), in agreement with data for

Table 1. Comparison of mean (SE; n = 20 to 25) concentrations (mg g⁻¹) of carbon, nitrogen, and phosphorus in dry eastern oyster biodeposits and in natural seston that settled from the water. Biodeposits were collected by holding oysters in the Choptank River for 2 to 14 d in May, June, July, August, and November 1983 and in May, June, and July 1984. Seston material that settled from the water due to gravity was collected concurrently in an apparatus identical to that used to hold oysters and collect their biodeposits. Data from Jordan (1987).

	Biodeposits	Seston Material
Carbon (mg C g ⁻¹)	34.8 ± 3.15	14.6 ± 1.19
Nitrogen (mg N g ⁻¹)	4.8 ± 0.44	2.1 ± 1.19
Phosphorus (mg P g ⁻¹)	0.58 ± 0.09	0.32 ± 0.03
C:N:P ratio (molar)	154:18:1	117:14:1

Crassostrea virginica (Srna and Baggaley 1976). In comparison to the extensive literature on N excretion by bivalves, the rate of P excretion has received little attention. Magni et al. (2000) directly measured P excretion in different size classes of *Ruditapes philippinarum* and *Musculista senhousia*, and their average measured rates were 1.9 and 1.4 $\mu\text{mol PO}_4 \text{ g}^{-1} \text{ DW h}^{-1}$, respectively. Magni et al. (2000) only found literature data for rates of P excretion in 3 other species of bivalves; when combined with their data, these indicate average excretion rates of $\sim 1.2 \mu\text{mol P g}^{-1} \text{ DW h}^{-1}$.

OYSTERS AS AGENTS OF BENTHIC-PELAGIC COUPLING

Natural sediments have well-developed microbial communities inhabiting distinct zones of oxygen content (Fig. 2; Henriksen and Kemp 1988). Therefore, bivalve biodeposits that settle on sediments with an oxic surface layer are subject to initial decomposition by aerobic bacteria (Fig. 2B). Organic materials are oxidized to CO_2 , PO_4^{3-} , and NH_4^+ , and other aerobic bacteria further oxidize NH_4^+ to NO_2^- and NO_3^- . Some of the NO_2^- and NO_3^- diffuses down into underlying anaerobic sediments, and some diffuses out of the sediment and enters the water-column nutrient pool. In the underlying anaerobic sediments, denitrifying bacteria use the oxidized forms of N as terminal electron acceptors, reducing the NO_2^- and NO_3^- to N_2 gas (Henriksen and Kemp 1988, Seitzinger 1988, Risgaard-Petersen et al. 1994). Absent N-fixation, N_2 is unavailable to plants and passes to the atmosphere. Denitrification can only occur where there is a close juxtaposition between oxygenated sediments that support nitrifying bacteria and anaerobic sediments that support denitrifying bacteria (Kristensen 1988). Bacterial degradation of particulate organic N and P from bivalve biodeposits that settle to anoxic sediments is solely via anaerobic pathways (Fig. 2C). Because the initial nitrification step is precluded, all regenerated N remains as NH_4^+ , and there is negligible sorption of PO_4^{3-} to iron complexes (Krom and Berner 1981). The microbial communities associated with sediments are a crucial element mediating nutrient regeneration processes from biodeposits. Consequently, studies of nutrient regeneration from bivalve communities held in conditions without underlying sediments containing a well-developed microbial community are missing a crucial biological element. For instance, rates of N and P regeneration from oyster biodeposits incubated in small chambers (Jordan 1987) and from eastern oysters maintained in MERL mesocosms without sediments (Pietros and Rice 2003), should not be extrapolated to actual effects of bivalves on coastal ecosystems, where nutrient regeneration processes are considerably more complex.

Rates of net N flux from natural bivalve communities (direct excretion by the animals plus regeneration from biodeposits in the sediments) can be substantial, ranging from ~ 1 to $5 \text{ mmol N m}^{-2} \text{ h}^{-1}$ (Dame et al. 1989, 1991a, Asmus and Asmus 1991, Magni et al. 2000), with rates being greater

in summer than in winter months (Dame et al. 1992). Dame et al. (1989) estimated that a South Carolina coastal intertidal eastern oyster reef transferred in biodeposits $\sim 189 \text{ g N m}^{-2} \text{ y}^{-1}$ from the water to the sediments, with the majority subsequently being regenerated as NH_4^+ ($125 \text{ g N m}^{-2} \text{ y}^{-1}$). The difference between these two values, about 33% of the net N removal, represents N incorporated either into biomass of reef fauna and flora, denitrified, or buried in the sediments. The nitrogen released from bivalve populations comes not only from ingested phytoplankton but also non-phytoplankton material, such as N-rich bacteria and flagellates (Asmus and Asmus 1991), and these heterotrophic organisms are readily captured by bivalves (Bayne and Hawkins 1992, Kreeger and Newell 2001).

The lack of simple techniques to measure denitrification prior to the development of the membrane inlet mass spectrometric method (Kana et al. 1998, Cornwell et al. 1999, Newell et al. 2002), meant that earlier studies on the ecological role of bivalves in altering patterns of inorganic nutrient regeneration could not measure enhanced N-loss via denitrification (e.g., Jordan 1987, Dame et al. 1989, 1991a, 1992, Asmus and Asmus 1991, Hatcher et al. 1994, Prins and Smaal 1994). Kaspar et al. (1985) used the indirect acetylene block technique to measure denitrification and reported appreciably higher denitrification potential in sediments underlying rope-cultured mussels than in nearby reference sites with similar sediments. More recently, Pelegri and Blackburn (1995), using the ^{15}N isotope pairing technique, observed stimulation of coupled nitrification-denitrification associated with bivalves.

Although bivalves are clearly important mediators of N cycling, their role in P cycling is equivocal. Primary reasons for this ambiguity are the fundamental differences in the chemistry of these two elements and their relative concentration in biodeposits. Not only are biodeposits more enriched in N than P (N:P atomic ratio of 18 in oyster biodeposits compared to 14 in seston; Table 1) but the remineralized N is predominately in the form of NH_4^+ that can readily diffuse out from the sediment. Conversely the balance between binding and release of P from oyster biodeposits is highly dependent on sediment oxygenation and the development of a redox gradient within the sediments (Fig 2B). In estuarine sediments, P fluxes are controlled by interfacial adsorption and desorption processes, often involving oxidized iron and sulfur cycling (Krom and Berner 1981). Iron oxides at the sediment-water interface are a diffusive barrier to P fluxes across the sediment-water interface. Under fully oxygenated conditions most of the P regenerated from biodeposits will be buried in the accumulating sediments. If the depth of the oxygenated zone in the surficial sediments decreases, as it does seasonally in Chesapeake Bay sediments (Fig 2C), the P-adsorbing iron oxide can be reduced to ferrous monosulfides, thereby allowing the release of sedimentary inorganic P (Boynton and Kemp 1985).

Studies on natural bivalve populations indicate that they do not increase P regeneration above background levels (e.g., Dame et al. 1991a) or

increase regeneration only slightly (Asmus and Asmus 1991, Souchu et al. 2001). Similarly, Doering and Oviatt (1986) and Doering et al. (1987) reported no appreciable phosphate fluxes from the sediment in MERL mesocosm tanks containing *Mercenaria mercenaria*, but ammonium fluxes were 60 times higher in tanks containing these clams. Dame et al. (1989) estimated that a South Carolina coastal reef of eastern oysters and associated biota effected a net P transfer to the sediments of $98 \text{ g P m}^{-2} \text{ yr}^{-1}$, presumably either incorporated into fauna and flora or buried in the sediments, with little P release.

Magni et al. (2000) calculated the upward diffusive flux of N (0.2 to $1.5 \text{ mmol NH}_4^+ \text{-N m}^{-2} \text{ d}^{-1}$) and P (0.01 to $0.05 \text{ mmol PO}_4^{3-} \text{-P m}^{-2} \text{ d}^{-1}$) based on pore water nutrient concentrations in sediments collected from within dense natural field populations of the bivalves *Ruditapes philippinarum* and *Musculista senhousia*. At the measured field densities of these two species of bivalve, they estimated direct excretory activity of up to $35.2 \text{ mmol NH}_4^+ \text{-N m}^{-2} \text{ d}^{-1}$ and $5.8 \text{ mmol PO}_4^{3-} \text{-P m}^{-2} \text{ d}^{-1}$, based on laboratory measured excretion rates. The direct excretion of N and P were ~ 23 and 116 times greater, respectively, than sediment regeneration rates. The results from their study may be somewhat atypical, however, in that the rates of P excretion they reported for the smallest size class of *R. philippinarum* that were highly abundant in the field populations were ~ 3 times greater than rates they measured for other size classes.

OYSTERS: PROMOTING OR REDUCING N AND P CYCLING?

Data reviewed above indicates that rates of N release from bivalve excretion and biodeposit regeneration can be substantial although P regeneration appears to be relatively low. Many investigators have surmised, either from these rates of recycling or by direct measurements of higher primary production and phytoplankton biomass in the immediate vicinity of the bivalves, that bivalve feeding activity serves to enhance primary production (e.g., Doering et al. 1986, 1987, Dame and Dankers 1988, Dame and Libes 1993, Dame et al. 1989, 1991b, Prins and Smaal 1990, 1994, Asmus and Asmus 1991, Yamamuro and Koike 1993, Magni et al. 2000, Pietros and Rice 2003). What is ignored in these studies, however, is that bivalves, by virtue of their high clearance rates, filter phytoplankton from large volumes of water. This has the localized effect of focusing nutrients that are then regenerated with a potential increase in the area-specific rates of nutrient recycling. Nonetheless, at the ecosystem level (e.g., estuary or embayment) the maximum phytoplankton standing stock supported by the nutrients regenerated through bivalve populations cannot exceed the level that can be sustained by nutrient inputs from the watershed or from adjoining water bodies (Fig. 1); i.e., regeneration only maintains levels of primary production set by external inputs.

Furthermore, these earlier investigations typically neglect the role that bivalve biodeposition has in enhancing N and P burial and sediment denitrification (Fig. 2B). These processes remove N and P from the water column, thereby reducing phytoplankton biomass and primary production. In situations where bivalves are either at very high population densities or living in locations with low water circulation, biodeposition can stimulate microbial metabolism sufficiently to cause the sediments to become anaerobic (Tenore et al. 1982). In such situations (Fig. 2C), nutrients are regenerated primarily as NH_4^+ and PO_4^{3-} , with little or no loss due to burial and denitrification.

Newell et al. (2002) measured changes in nitrogen fluxes and denitrification in laboratory incubations of sediment cores subject to loading by pelletized phytoplankton cells, an experimental analog for oyster biodeposits. When organics were regenerated under aerobic conditions (Fig. 2B), typical of those associated with oyster habitat, coupled nitrification-denitrification was promoted, resulting in denitrification of $\sim 20\%$ of the added N. In contrast, under anoxic conditions typically found in summer beneath the pycnocline in main-stem Chesapeake Bay (Kemp and Boynton 1992), nitrogen from the added organics was released solely as ammonium (Fig. 2C). Newell et al. (2002) postulated that denitrification of PON remaining in oyster biodeposits may enhance nitrogen removal from estuaries compared to locations without oysters. Furthermore, in aerobic incubations with sufficient light ($\sim 70 \mu\text{mol photons m}^{-2} \text{s}^{-1}$), Newell et al. (2002) found that microphytobenthos absorbed the inorganic nitrogen released from the added organics (Fig. 2A). These results suggest that an ecosystem dominated by benthic rather than planktonic primary production may develop in shallow waters when reduced turbidity associated with bivalve feeding increases light penetration to a level that can sustain benthic microalgal production (Fig. 1A).

In summary, it is well-established that bivalve feeding activity reduces ecosystem levels of phytoplankton biomass. This reduction in biomass and partial regeneration of N and P will tend to make these nutrients less limiting locally to the remaining phytoplankton. This may well alter phytoplankton physiological condition and thereby enhance growth rates, (i.e., production is the product of phytoplankton biomass times cell specific growth rate). This accounts for the observation from many field and mesocosm studies of increasing rates of phytoplankton production in the vicinity of the bivalve consumers (e.g., Prins et al. 1998, Pietros and Rice 2003, reviewed by Dame 1996). We contend, however, that because sediment N and P regeneration are less than 100% efficient due to burial and denitrification (i.e. $T > R$; see Fig. 1), bivalve feeding serves to reduce recycling and ultimately will reduce system-level phytoplankton production and biomass.

INFLUENCE OF BIVALVE FEEDING ON TURBIDITY

Bivalve filtration of suspended particles from the water column reduces turbidity and thereby increases photosynthetically active radiation (PAR) penetration (Box A Fig. 1). Newell and Koch (2004) developed a numerical model to simulate the interaction between wave-induced sediment resuspension, bivalve filtration, and seagrass growth. Their model predicted that the presence of subtidal oysters at 25 g DW m^{-2} (≈ 25 oysters of 7.5 cm shell length) reduced suspended sediment concentrations in shallow waters by nearly an order of magnitude when water temperatures were $\sim 25^\circ\text{C}$ and oyster clearance rates were high, compared to situations where oysters are absent. This reduction in suspended particles produced a significant increase in water clarity and hence the depth to which submerged aquatic plants, such as seagrasses and microphytobenthos (MacIntyre et al. 1996) were predicted to grow. In eutrophic systems where there has been a substantial increase in bivalves through the rapid colonization by a non-native species, there has often been a corresponding increase in abundance of submerged aquatic macrophytes (Cohen et al. 1984, Strayer et al. 1999). In open and well-flushed estuaries, the exchange of suspended particles from adjacent waters means that the localized enhancement of bivalve stocks may not reduce turbidities sufficiently to permit seagrasses to grow. Microphytobenthos, however, require less PAR than seagrasses to sustain positive growth (MacIntyre et al. 1996), and therefore may be able to colonize deeper sediments in the immediate vicinity of an enhanced bivalve population.

Actively growing microphytobenthos can directly intercept much of the inorganic nitrogen regenerated from the sediments by bacterial decomposition, thereby limiting N release to the water column (Fig. 2A; Krom 1991, Rysgaard et al. 1995, Sundbäck et al. 2000, Newell et al. 2002). The actual magnitude of these N fluxes varies depending on the nutrient concentrations in the overlying water, microphytobenthos biomass and species composition, and light conditions. In addition to the role of microphytobenthos in intercepting N regenerated from the sediments, the oxygen produced from their photosynthesis can alter depths of oxygen penetration into the sediments (Fig. 2A). This enhanced oxygen supply can be used by bacteria at the sediment water interface to maintain nitrification (Risgaard-Petersen et al. 1994, Rysgaard et al. 1995, An and Joye 2001). This is important in situations where the POM remaining in bivalve biodeposits stimulates microbial metabolic oxygen demand to levels that exceed the oxygen resupply from the water column. When growth of the microphytobenthos is high, their uptake of NO_3^- competes with the bacteria, resulting in a decline or cessation of denitrification while still preventing nutrient regeneration to the water column (Henriksen and Kemp 1988, Risgaard-Petersen et al. 1994, Rysgaard et al. 1995, An and Joye 2001).

Chesapeake Bay management activities are designed to reduce turbidities, thereby increasing PAR at the sediment surface in order to

enhance seagrass growth. This strategy does not consider that some species of macroalgae (e.g., *Ulva* spp., *Enteromorpha* spp., and *Cladophora* spp.) flourish in locations that have elevated levels of inorganic nutrients and relatively low irradiances (from 18 to 175 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). In shallow and enclosed embayments these nuisance species may out-compete other macroalgae (e.g., Taylor et al. 2001) and often grow so profusely that they restrict water flow and cause sediment hypoxia when they decay (Peckol and Rivers 1995, Rafaelli et al. 1998). In some locations, where bivalve grazing reduces phytoplankton stocks, thereby decreasing inorganic nutrients stored in phytoplankton biomass and increasing PAR at the sediment surface, nuisance macroalgae may become established, rather than a more balanced flora of seagrasses and microphytobenthos.

MODELING OYSTER INFLUENCE ON N AND P REMOVAL

Several modeling studies have been undertaken to evaluate the importance of eastern oysters in the ecology of Chesapeake Bay. Bartleson and Kemp (1990) manipulated an ecosystem model of C and N flow to assess the improvements in water quality associated with a tenfold increase in benthic suspension feeders in water < 10 m deep. This increase in benthic suspension-feeding activity reduced the organic material available to be microbially decomposed in the deep channel, hence leading to a marked increase in bottom oxygen concentrations. Ulanowicz and Tuttle (1992) used an ecosystem model of carbon flow through Chesapeake Bay food webs to explore the trophic consequences of an increase in oyster stocks. Their results suggest that there would be substantial changes in the food web, including lower phytoplankton biomass as a consequence of higher grazing rates by greater oyster stocks. Similarly, predictions from a model that includes the interaction of water flow and bivalve feeding (Gerritsen et al. 1994) suggest substantial reductions in phytoplankton biomass could be achieved by increasing oyster stocks through off-bottom oyster culture.

None of these previous modeling efforts estimated the possible ecological benefits associated with suspension-feeding bivalves altering N and P cycling as a result of removing particles from the water column and transferring undigested remains to the sediment surface. Consequently, because of a lack of quantitative information on these putative benefits it has been difficult to incorporate the value of these ecosystem services in watershed management plans that are attempting to reduce anthropogenic nutrient inputs. We develop here an elementary “spread-sheet” model to assess the influence of eastern oysters on removal of N and P inputs to the Choptank River estuary, a mesohaline Maryland tributary to Chesapeake Bay. We estimated the monthly amount of P buried and N removed due to burial and coupled nitrification-denitrification resulting from the biodeposition activity of adult eastern oysters (shell height 7.6 cm; ~ 1 g DW). These

estimates are applicable to natural oyster reefs where the majority of biomass is in adult oysters. They include neither the reduced levels of N and P removal during the time it takes oysters to grow from juvenile to adult size nor the enhanced levels of N and P removal as oysters grow larger than 7.6 cm.

Monthly environmental data (average water temperature, chlorophyll *a*, and seston concentrations; Table 2) were taken from the EPA Chesapeake Bay monitoring program for station ET5.2 in the Choptank River (www.chesapeakebay.net). Biodeposition rates were estimated from data obtained by Jordan (1987) for eastern oysters held for 4 to 36 h in a flume supplied with flowing (0.8 to 10 cm s⁻¹) Choptank River water at ambient temperatures and seston concentrations over an annual cycle. We calculated the clearance rate of a 1 g DW adult eastern oyster at each monthly water temperature and seston load (Table 2) from Jordan's (1987) data (reproduced as Fig. 15 in Newell and Langdon 1996) by dividing the weight of biodeposits voided per unit time by the seston concentration. This method provides the most accurate possible laboratory estimates of bivalve feeding rates (Cranford 2001). We then calculated the amount of chlorophyll *a* removed from the water column and converted this to N removed using a chlorophyll *a* : Nitrogen ratio of 1 µg chl *a* : 14 µg N (Parsons et al. 1984). We applied an average N assimilation efficiency of 50% derived from physiological data for eastern oysters (Newell and Jordan 1983) to estimate the total amount of undigested PON that was egested as biodeposits by the oysters per month.

We estimated the amount of PON from biodeposits that becomes buried in the sediments by applying a burial rate of 10%, from field data collected in the Choptank River by Boynton et al. (1995), to these monthly biodeposition data (Table 2). We estimated the amount of particulate P transferred to the sediments by applying an average N:P molar ratio of 18:1 (Table 1) to the monthly PON values calculated for oyster biodeposition and then assumed that 90% of P becomes buried in the sediments (Table 2). This 90% value was estimated from the data reviewed above that indicates negligible P release from bivalve biodeposits in aerobic sediments. We used a laboratory derived estimate that 20% of the PON in biodeposits is denitrified (Newell et al. 2002) to calculate the monthly amount of N removed from biodeposits associated with coupled nitrification-denitrification (Table 2). This 20% denitrification value is conservative as it is at the low end of the range calculated from literature data by Seitzinger (1988), who estimated that 20 to 70% of the total N flux from coastal marine sediments is in the form of N₂ gas. Many seasonal and physical factors, such as temperature, sediment porosity, water flow, abundance of bioturbators, and sediment oxygen content, can alter the rate of coupled nitrification-denitrification. The combined nitrogen loss rate of 30% we used in our calculations [burial rate (10%) and denitrification (20%)] is close to the 30% annual loss estimated for

Table 2. Monthly average water temperature ($^{\circ}\text{C}$), seston concentrations (mg L^{-1}), and phytoplankton chlorophyll *a* ($\mu\text{g L}^{-1}$) in the Choptank River (EPA Chesapeake Bay Program monitoring station ET 5.2). Eastern oyster clearance rates ($\text{L h}^{-1}\text{g}^{-1}\text{DW}$) calculated from Jordan (1987) were used to estimate the monthly amount of phytoplankton N filtered from the water column. We then estimated the monthly amounts of N and P biodeposition that were buried ($\text{mg month}^{-1}\text{g}^{-1}\text{DW}$) and N denitrified ($\text{mg month}^{-1}\text{g}^{-1}\text{DW}$). See text for complete details of these calculations.

	Water Temp $^{\circ}\text{C}$	Seston (mg L^{-1})	Chl <i>a</i> ($\mu\text{g L}^{-1}$)	Clearance Rate ($\text{L h}^{-1}\text{g}^{-1}\text{DW}$)	monthly nutrient removal g^{-1}DW		
					Mg N denitrified	mg N buried	mg P buried
Jan	3	11.4	5.5	0	0	0	0
Feb	3	14.3	8.7	0	0	0	0
Mar	6	13.2	8.9	0.45	4.08	2.04	2.21
Apr	11	16.7	9.6	0.90	8.69	4.35	4.71
May	17	14.5	12.2	1.72	21.20	10.60	11.50
Jun	23	10.7	12.3	3.74	46.35	23.17	25.13
Jul	27	13.0	15.4	9.62	149.26	74.63	80.92
Aug	27	13.0	16.0	9.62	155.08	77.54	84.08
Sept	25	13.4	11.9	7.46	89.52	44.76	48.53
Oct	19	12.8	7.3	2.34	17.25	8.62	9.35
Nov	11	9.4	6.0	1.38	8.36	4.18	4.53
Dec	6	11.4	5.7	0.44	2.52	1.26	1.37
Annual Total					502.31	251.15	272.34

natural intertidal oyster reefs by Dame et al. (1989). They estimated this loss term from field studies in which they found that the difference between the seasonal average fluxes into an oyster reef (T in Fig. 1) and regeneration (R in Fig.1) was about 33%. Dame et al. (1989) suggested that the difference between these two fluxes was associated with N incorporation into oysters and other organisms, denitrification, and burial in the sediments.

In order to place our estimates of biomass-specific N and P removal into an ecosystem perspective we calculated the size of the eastern oyster population currently present in the upper Choptank River. The total standing stock of oysters > 7.6 cm shell height in Maryland's portion of Chesapeake Bay in 2002 was estimated to be 342×10^6 g DW (Jordan, pers. comm., MD Dept. Natural Resources). Assuming that these oysters are uniformly distributed over the 800 km^2 of oyster habitat in Maryland (Smith et al. 2001), adult 1 g DW oysters are currently at a population density of ~ 0.43 oysters m^{-2} . Because the lower salinities in the upper portion of the Choptank River reduce the virulence of MSX and Dermo epizootics (Ford and Tripp 1996), we assumed that the extant oyster stocks were at a density of 1 oyster m^{-2} . We used acoustic survey data (Smith et al. 2001) on the areal extent of oyster bars to calculate that there are 1,736 ha of oyster bottom in the upper Choptank River. At the current oyster abundance of 1 m^{-2} this area of oyster bottom supports a total of $\sim 17 \times 10^6$ oysters (> 7.6 cm shell length).

We estimated monthly N and P inputs into the drainage basin of the Choptank River with the hydrochemical model, Generalized Watershed

Loading Functions (Table 3). The GWLF model was calibrated with data from the USGS gauging station at Greensboro, MD., that receives inputs from 17% of the land area of the Choptank watershed (Fisher et al. 1998, Lee et al. 2000). Diffuse source inputs of N and P from ungauged areas were modeled using local data on human populations, soils, land-use patterns, atmospheric deposition, and measured waste water treatment plant discharges were added as point sources (Lee et al. 2001).

Inputs from all three source types raise N concentrations in the estuary during winter and spring (Fig. 3) and stimulate phytoplankton production later in the year (Fig. 3) when temperatures are higher (Fisher et al. 1988, 1998, Berndt 1999). Inputs of nutrients from the watershed and airshed are out of phase with the period of maximum phytoplankton biomass. Inputs of DIN were highest in January to May (Table 3) due to high river discharge in these months transporting terrestrial nutrients. High DIN concentrations (predominately NO_3^-) along the length of the estuary at this time of the year (Fig. 3) indicate that nutrients are effectively being stored in the estuary. In contrast to the high delivery of nutrients at low temperatures, in summer nutrients decline because removal processes (e.g., accumulation of N in phytoplankton biomass) exceed inputs (Fig. 3).

We estimated the monthly amounts of N buried and denitrified and P buried by eastern oysters at their current population density of 1 m^{-2} on 1,736 ha of oyster bottom in the upper portion of the Choptank River (Table 3). We then expressed these monthly removal rates associated with 1 oyster m^{-2} as a percentage of monthly inputs (Fig. 4). Seasonal N and P removal associated with biodeposition at current oyster densities were greatest ($\sim 5\%$ and $\sim 34\%$), respectively, from July to September due to highest oyster feeding activity at this time of greatest phytoplankton abundance. We also estimated monthly nutrient removal for oysters at densities of 10 m^{-2} (Fig. 4) that corresponds to the Chesapeake Bay 2000 Agreement oyster restoration goal of a ten fold higher oyster abundance by 2010 (www.chesapeakebay.net). At this modest oyster density of 10 m^{-2} , $\sim 50\%$ and $\sim 350\%$ of the monthly summer N and P inputs, respectively, were estimated to be removed: i.e., P would be removed faster than inputs and half of the N inputs would be removed. Even this oyster restoration goal is possibly a factor of 10 below the ecosystem carrying capacity. Newell (1988) estimated 1988 oyster stocks to be $\sim 1\%$ of historical densities present in Chesapeake Bay prior to commercial exploitation in the 19th Century. Furthermore, adult oyster abundances of 10 m^{-2} ($\equiv 10 \text{ g DW m}^{-2}$) are low for eastern oysters living in natural reefs. For example, Dame (1976) reported that oyster dry tissue biomass on intertidal reefs in North Inlet, South Carolina ranged between 300 to 500 g DW m^{-2} .

Table 3. Total monthly N and P (kg) inputs into the Choptank watershed and airshed estimated by Lee et al. (2001). Values presented are averages for 1980 to 1996. The total amounts (kg month⁻¹) and % of the monthly N and P inputs that are buried and denitrified associated with biodeposition from oysters at a density of 1 g DW m⁻² on 1,736 ha of restorable oyster bottom in the Choptank River were calculated as described in the text.

	Total-N inputs (kg)	Total-P inputs (kg)	Monthly nutrient removal for oysters at a density of 1 g DW m ⁻² on 1,736 ha oyster bottom			
			N (kg)	P (kg)	% N inputs	% P inputs
Jan	281,450	5,245	0	0	0.0	0.0
Feb	261,970	4,837	0	0	0.0	0.0
Mar	312,350	5,351	106	38	0.0	0.7
Apr	292,500	5,338	226	82	0.1	1.5
May	243,930	6,022	552	200	0.2	3.3
Jun	148,250	4,641	1,207	436	0.8	9.4
Jul	75,480	4,059	3,887	1,405	5.1	34.6
Aug	80,810	4,274	4,038	1,460	5.0	34.2
Sep	99,140	4,587	2,331	843	2.4	18.4
Oct	97,940	4,015	449	162	0.5	4.0
Nov	114,500	4,344	218	79	0.2	1.8
Dec	254,270	6,373	66	24	0.0	0.4
Total	2,262,580	59,085	13,080	4,728	0.6	8.0

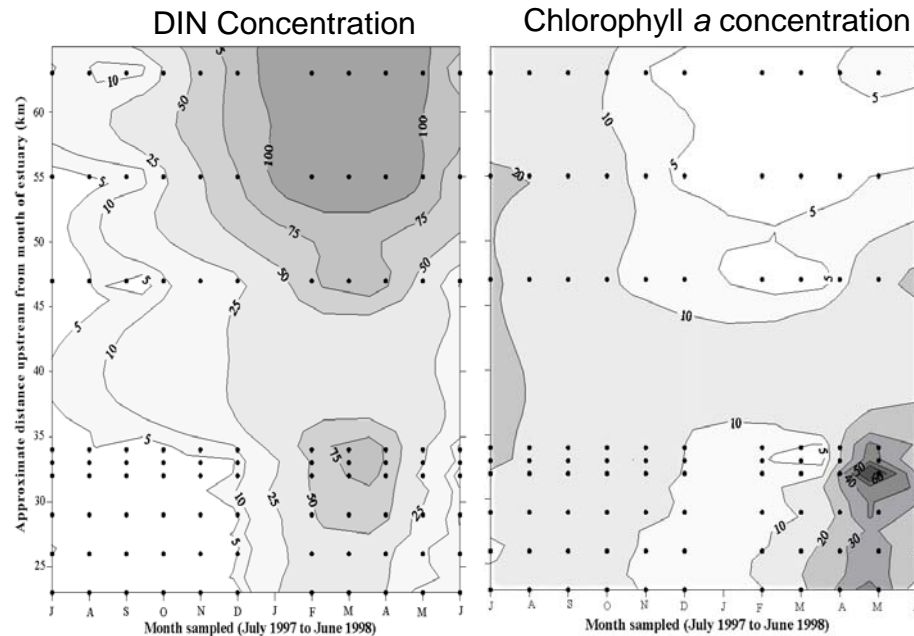


Fig. 3. Temporal and spatial variability in dissolved inorganic nitrogen inputs (μM) and chlorophyll *a* ($\mu\text{g L}^{-1}$) over an annual cycle (July 1997 to June 1998) from the mouth towards the headwaters of the Choptank River Estuary, MD (Berndt 1999).

We summed the monthly amounts of N and P removed for oysters at population densities of 1 and 10 g DW m⁻² on 1,736 ha of oyster bottom and expressed this as a % of total annual N and P inputs to estimate their potential contribution at various abundances (Fig. 4). At their current population density of 1 g DW m⁻², oysters can only remove 0.6 and 8% of annual N and P inputs respectively. Obviously, if oyster stocks are increased tenfold as a consequence of management activities then this will increase to 6% and 80% of N and P inputs, respectively.

The factors that govern N and P removal via bivalve biodeposition are complex and variable; consequently, in our model we have made a number of simplifying assumptions to predict the magnitude of nutrient removal. The magnitude of our estimates are especially sensitive to the phytoplankton chl *a* concentrations (Table 2). Phytoplankton blooms are highly variable spatially and temporally (Fig. 3; Fisher et al. 1988, Harding et al. 2002) and, therefore, our calculations can only be considered an approximation of the magnitude of possible N and P removal associated with eastern oyster feeding. Field studies can be designed to measure the actual N and P fluxes and burial rates in sediment cores collected seasonally from around natural stocks of bivalves. Information on how much of the biodeposits from the bivalve population are incorporated into the sediment is also necessary in order to assess the incremental changes in sediment nutrient regeneration and burial associated with a certain amount of biodeposition. Unfortunately, this is a major technical limitation as we do not currently have a usable method to determine how widely the biodeposits are being distributed across receiving sediments.

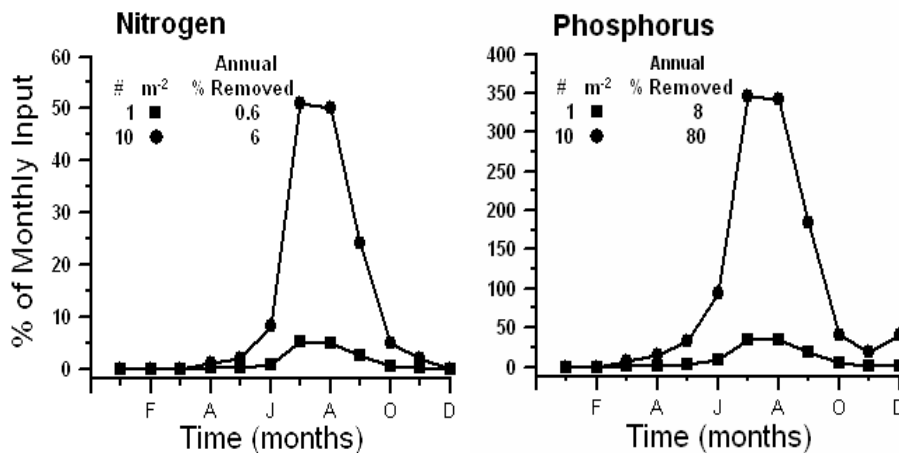


Fig. 4. The monthly amounts of N and P denitrified and buried (Table 3), expressed as % of monthly inputs into the Choptank River MD., associated with eastern oysters at a density of 1 (■) and 10 (●) g DW m⁻² on 1,736 ha of oyster bottom in the Choptank River. The % removal of total annual N and P inputs for oysters at densities of 1 and 10 m⁻² are tabulated.

DISCUSSION

Prevailing eutrophic conditions in Chesapeake Bay are commonly ascribed to anthropogenic nutrient enrichment from the watershed and airshed (D'Elia et al.1992). Undoubtedly this is a major causal factor in stimulating excess primary production that ultimately leads to oxygen deficient bottom waters (Boicourt 1992, Kemp and Boynton 1992). In addition, the demise of the once abundant suspension-feeding eastern oyster has drastically reduced benthic consumption of phytoplankton (Newell 1988), and this has likely caused major disruptions to the Chesapeake Bay food web (Ulanowicz and Tuttle 1992). Today, pelagic metazoan and microbial organisms are the major consumers of phytoplankton (Baird and Ulanowicz 1989), and N and P regenerated by these organisms are released directly back to the water column where they can sustain primary production. In the mesohaline area of Chesapeake Bay, large amounts of phytoplankton that are unconsumed in the upper water column accumulate in the oxygen-poor waters beneath the pycnocline where N and P are regenerated as NH_4^+ and PO_4^{3-} from anaerobic sediments (Kemp and Boynton 1992).

Current management efforts to reduce levels of phytoplankton production in Chesapeake Bay are based on a policy of reducing point and non-point source nutrient inputs (D'Elia et al.1992). While anthropogenic nutrient loadings are indeed the most critical component of curbing excess phytoplankton production, we suggest that the effect of eastern oysters in reducing phytoplankton concentrations and altering patterns of nutrient regeneration may also be crucial to achieving the long-term goal of improving water quality. Our analysis of the interactions between eastern oyster feeding and nutrient inputs to the Choptank estuary indicates that the highest N and P inputs occur at times of lowest benthic-pelagic coupling associated with oyster feeding (winter/spring); whereas times of maximum oyster feeding correspond to times of maximum primary production (Fig. 3; Malone 1992). Despite these apparent imbalances, eastern oysters can exert a direct influence on reducing N and P recycling by enhanced feeding on the accumulated phytoplankton biomass and removing some of this biomass to the sediments. Our proposition that eastern oysters can be extremely important in governing the response of Chesapeake Bay to nutrient enrichment fits the new conceptual model of coastal eutrophication developed by Cloern (2001). Cloern (2001) proposed that coastal systems do not respond either simply or uniformly to nutrient enrichment and that "system-specific attributes act as a filter to modulate the (system) response to enrichment". He suggests that a complete understanding of the biological responses to nutrient enrichment within the physical regime of a particular ecosystem is a prerequisite to developing strategies necessary for ecosystem restoration and rehabilitation. We agree with Cloern's (2001) assessment, and we further suggest that three factors largely determine estuarine response to nutrient inputs: 1) Sufficient water residence time to allow phytoplankton consumption of nutrient inputs

(typically > 30 d), 2) sufficient water clarity (or a sufficiently shallow upper mixed layer; Fisher et al. 2003) to permit net phytoplankton growth, and 3) the presence of active and abundant suspension-feeding bivalves in the shallow waters. The first two factors concern the ability of phytoplankton to intercept the incoming nutrients, whereas the last concerns the interception of phytoplankton by the benthos.

Increasing oyster populations in Chesapeake Bay will not be without cost. For a commercially harvested species, such as the eastern oyster, there is an obvious trade-off between harvesting oysters and leaving them on the bottom to provide ecosystem services. One way to compare these divergent uses is to denominate their respective benefits in monetary terms. The dockside harvest value of eastern oysters is ~\$25 per bushel of whole live oysters [a bushel is the customary harvest unit (1 MD bushel \equiv 0.046 m³ \equiv 300 oysters of ~ 7.6 cm shell length)]. At the current assumed oyster abundance of 1 m⁻², the 1,736 ha of oyster bottom in the upper Choptank estuary supports a total of 17.36 x 10⁶ oysters (> 7.6 cm shell length). If this entire stock of oysters were harvested they would yield ~ 57.9 x 10³ Maryland bushels (\equiv 2,663 m⁻³) with a dockside value of ~ \$1.5 million. While consumers may value this harvest at \$1.5 million, it must be noted that its value to harvesters is significantly less. Factoring in costs of harvesting (fuel, labor, and capital), it is likely that the net value to harvesters of harvesting the entire stock of oysters would be less than one half the total dockside value (< \$750,000).

Our simple model indicates that present-day oyster stocks of 1 m⁻² in the upper Choptank River are responsible for burying and denitrifying 13,080 kg N and 4,728 kg P annually (Table 3). The value of this nutrient reduction in dollar terms is the sum of all commercial and non-commercial benefits generated by its impact on water quality. A direct estimate of these benefits is beyond the scope of the present study. However, a much simpler way to estimate a value for these reductions is to determine their opportunity cost. That is, what is the cost of alternative ways of obtaining these same nutrient reductions? To the extent that reductions of any given amount of nutrients by oysters obviate the need to incur those costs, this is their value in terms of nutrient reduction. The EPA Chesapeake Bay Program has recently undertaken a "Use Attainability Analysis" that provides estimates of the cost of reducing nutrient inputs necessary for meeting the water quality goals in the Chesapeake Bay (<http://www.chesapeakebay.net/uaasupport.htm>). The annual Baywide nutrient reduction requirement (relative to year 2000 loads) is 47.17 x 10⁶ kg N and it is estimated that it will cost \$1,138 million annually (operating and amortized capital costs) to achieve this level of N reduction.

Given these available figures, the average cost of removing N from Chesapeake Bay loads is \$24.07 kg⁻¹. This average masks large variations, however, with costs ranging from \$4.6 kg⁻¹ for planting cover crops to \$1,250 kg⁻¹ to implement erosion and sediment controls (www.chesapeakebay.net/eoanalyses.htm). However, under the assumption that reducing nutrient loads

in order to achieve desired water quality outcomes is justified on a cost-benefit basis, this average unit reduction cost provides a useful measure of the nutrient reduction value of oysters.

With respect to the modeled nutrient reduction estimates, the calculated value of the entire stock of oysters in the upper Choptank estuary in removing 13,080 kg N annually is \$314,836. While this is less than the one-time benefit of harvesting these oysters, oysters remaining in the system will continue to generate nutrient reduction benefits over their 10+ y life span. Taking this into account, the ecosystem value of current Choptank River oyster stocks increases to \$3.1 million, or over twice the value of harvesting them. This analysis ignores the economic value of the hard reef substrate as habitat for many other animal species that have value for commercial and recreational fisheries (Coen et al.1999).

It should be noted, however, that some nutrients are removed when oysters are harvested because oyster tissue and shell contains phosphorus (~ 0.8% and ~ 0.1% dry weight respectively) and nitrogen (~ 7% and ~ 0.3% dry weight respectively (Galtsoff 1964, Newell, unpublished data). For a 1 g DW oyster with a shell length of 7.6 cm, the shell weighs ~ 150 g. When this size oyster is harvested 0.52 g N and 0.16 g P are removed in flesh and shell, which is ~ 2/3 of the amounts estimated to be removed annually as a consequence of the oysters normal feeding and deposition processes (Table 2)

Newell (1988) calculated that the eastern oyster stocks that existed in Chesapeake Bay prior to heavy exploitation in the 19th Century required between 23% and 41% of present-day phytoplankton carbon production to sustain their metabolic carbon demands. How is it possible that these oyster stocks required such a large proportion of primary production that is currently sustained by high levels of anthropogenic nutrient enrichment? We speculate that these highly abundant oysters were food limited and slow growing and therefore had high food digestion and assimilation efficiencies. Consequently, denitrification and N and P burial may have been minimal because little POM was voided in their biodeposits. It is likely that excreted NH_4^+ promoted tight N coupling in what used to be an oligotrophic estuary. How did the system change when that tight coupling between phytoplankton production and benthic consumption was changed? Were these changes necessarily linear? It is plausible that phytoplankton biomass in Chesapeake Bay was not appreciably enhanced by the initial loss of eastern oyster grazing until a critical threshold of lower oyster abundance and higher nutrient inputs was reached. After that point the ecosystem switched from one where benthic processes dominated to the current situation where phytoplankton mainly flows through pelagic consumers with substantial nutrient regeneration through the microbial food web (Baird and Ulanowicz 1989).

Ecological theory suggests that when a dominant species in an ecosystem is lost, the vacant niche is filled by another species. What has happened to the niche once occupied by eastern oysters in Chesapeake Bay? Pelagic suspension feeders, such as zooplankton and various planktivorous

fish species may have increased in abundance due to reduced competition for phytoplankton; however, they are not sufficiently abundant to consume all of present-day phytoplankton production (Baird and Ulanowicz 1989). Certainly in some parts of Chesapeake Bay, benthic consumers, such as polychaetes (Thompson and Schaffner 2001) have probably increased to the point that today they are potentially filling part of the ecological niche once occupied by oysters. In the tidal freshwater and oligohaline reaches of some tributaries the asiatic clam *Corbicula fluminea* and the wedge clam, *Rangia cuneata*, can attain extremely high densities (Gerritsen et al. 1994). These authors estimated that > 50% of the annual phytoplankton production in the oligohaline regions is consumed by these abundant benthic suspension feeders. It is in the mesohaline portions of the Bay, however, the region where eastern oysters were once highly abundant Baywide, where no benthic consumer, perhaps with the exception of the tunicate, *Molgula manhattensis*, seems to have filled the niche once occupied by oysters. Yet it is in this mesohaline region of the Bay that nutrient enrichment generates the highest level of primary production (Harding et al. 2002). Consequently, it is this unconsumed autochthonous carbon production from this region that settles to the sediment surface beneath the pycnocline and is responsible for generating bottom water hypoxia and anoxia (Boicourt 1992, Kemp and Boynton 1992). It is this anoxic bottom water that is one of the obvious signs of ecosystem degradation that ongoing management activities are trying to correct.

In summary, eastern oysters, in common with other suspension-feeding bivalves, serve to regenerate large quantities of N to the water column. It is also apparent that bivalve biodeposition can enhance the permanent removal of N and P from the water column via burial and denitrification, thereby reducing the amounts of these two nutrients available to maintain phytoplankton production. The relative balance between nutrient regeneration and permanent removal depends on the amount of biodeposition by the particular species of bivalve and the environmental conditions (Fig. 2).

We suggest that a possible management strategy for improving water quality in Chesapeake Bay is to increase top-down control on phytoplankton through the enhancement of natural eastern oyster populations. This restoration strategy would be most beneficial if it promoted enhancement of bivalves in well-mixed waters because this leads to enhanced nitrogen loss through coupled nitrification-denitrification and the burial of both N and P in the accumulating sediments. In such well-oxygenated locations, the further decomposition of POM-rich biodeposits by both metazoan and microbial decomposers will not lead to the development of hypoxic bottom waters and sediments. Unfortunately, due to ongoing epizootics of Dermo and MSX disease, the long term survival of restored eastern oyster beds in regions of Chesapeake Bay with salinities > 12 must be questioned (Jordan 1995, Ford and Tripp 1996), and hence reliance on these populations to achieve long-term water quality goals is not recommended. Despite the uncertainty about the survival of oysters, we believe that they can still be a useful supplement to

management activities that are centered on controlling nutrient inputs. The use of oysters to help attain water quality goals is important because it offers one of the few opportunities to reduce nutrients once they have entered a receiving body of water.

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