

COMMENT

Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: Comment on Pomeroy et al. (2006)

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ABSTRACT: Pomeroy et al. (2006) proposed that temporal and spatial mismatches between eastern oyster filtration and phytoplankton abundance will preclude restored stocks of eastern oysters from reducing the severity of hypoxia in the deep channel of central Chesapeake Bay. We refute this contention by presenting arguments, data, and model results, overlooked by these authors. Our analysis indicates that oyster populations living on extensive reefs along the flanks of the mainstem Bay could substantially reduce summer phytoplankton growth and particulate organic carbon deposition to deep waters of the central channel. Because hypoxia in these deep waters is maintained through microbial decomposition of organic carbon generated by summer phytoplankton production, we conclude that reduced carbon fluxes to the deep channel associated with greatly increased oyster grazing could reduce the severity of hypoxia.

KEY WORDS: Algal blooms · Biodeposition · *Crassostrea virginica* · Chesapeake Bay · Hypoxia · Oyster · Restoration · Suspension-feeder · Water quality

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INTRODUCTION

Pomeroy et al. (2006) present arguments aimed at refuting the hypothesis that the extirpation of once highly abundant eastern oysters *Crassostrea virginica* has removed their role as dominant grazers of phytoplankton in Chesapeake Bay, USA (Newell 1988). Newell's hypothesis implies that reduced consumption of phytoplankton by oysters has exacerbated the effects of anthropogenic nutrient enrichment on phytoplankton production, and of associated eutrophication

effects during the last half-century (Kemp et al. 2005, Newell et al. 2005). The principal lines of reasoning advanced by Pomeroy et al. (2006) relate to purported temporal and spatial mismatches between potential oyster filtration and phytoplankton abundance. This argument suggests that, whereas oyster grazing is confined to the estuary's summer season and its shallow waters, phytoplankton abundance peaks in spring and in the Bay's deeper open waters. Although the focus of their argument is confined to the potential impact of oysters on summer hypoxia, it is important to note that

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recent studies have emphasized a much broader range of influences that oysters and other bivalves may exert on ecosystem processes in shallow estuaries (reviewed by Dame 1996, Coen et al. 2007, this volume). Losses of bivalve populations result in (1) degradation of habitat for diverse sessile and mobile animals (e.g. Coen et al. 1999), (2) increased turbidity that reduces abundance of seagrasses and benthic microalgae (e.g. Newell & Koch 2004), and (3) reduced rates of denitrification and nutrient burial (e.g. Newell et al. 2005).

SPRING AND SUMMER BLOOMS SUSTAIN HYPOXIA

The central premise in the 'temporal mismatch' argument of Pomeroy et al. (2006) is their presumption that bottom-water hypoxia in the mesohaline part of the Bay during summer is both initiated and maintained by microbial respiration of particulate organic carbon (POC) deposited from the spring phytoplankton bloom. This reasoning fails to recognize that, although substantial ungrazed POC from the spring bloom does enter the sub-pycnocline waters of the central channel to fuel the spring decline in bottom-water O_2 , this organic matter input is insufficient to sustain the benthic and bottom-water respiration rates that maintain hypoxia throughout the summer (Kemp et al. 1992, 1999, Hagy 2002, Hagy et al. 2005). The observed summer sub-pycnocline respiration rates in this region require additional organic carbon inputs that are provided by high summer rates of net plankton community production in overlying surface waters and in adjacent littoral regions (Smith & Kemp 1995, Kemp et al. 1997).

In contrast to the spring phytoplankton biomass peak, which is largely dependent on an accumulated nutrient pool associated with spring runoff, the summer production maximum is sustained by rapid nutrient recycling, with each atom of N delivered in spring being potentially recycled 7 times throughout the summer (Malone et al. 1988). Sediment trap studies of the composition and quantity of sinking POC in the mesohaline mid-Bay indicate that particles are composed of mainly intact diatom cells during spring, while a second deposition peak in July consists primarily of zooplankton fecal pellets, diatom chains, and other algal detritus (Kemp & Boynton 1992, Kemp et al. 1999). Rates of POC sinking integrated over the summer are generally similar to or slightly lower than those occurring in spring. This conclusion is further supported by analysis of spring pools of chlorophyll *a* on the sediment surface throughout the Bay (Hagy et al. 2005). This point is key to the question of potential oyster impact on hypoxia, because it means that inputs

of carbon that would support sub-pycnocline O_2 depletion can be regulated through phytoplankton grazing by oysters and other herbivores, whether that grazing occurs in spring or summer.

Like most temperate aquatic animals, the eastern oyster's physiological processes, including water filtration, are highly dependent on ambient water temperatures, with summer rates being substantially higher than those throughout the rest of the year (e.g. Newell & Langdon 1996). Although we acknowledge this general point, which is an important aspect of the argument in Pomeroy et al. (2006), the filtration rate that they used for calculating potential oyster impact on the spring algal bloom should probably be increased 3-fold. Pomeroy et al. (2006) used a value for oyster clearance rate ($0.45 \text{ l h}^{-1} \text{ g}^{-1}$) appropriate for March temperatures, noting that this is when the spring diatom bloom is initiated (Hagy et al. 2005). The spring bloom in the mesohaline Bay generally runs from early March through May, with a peak in April (Harding et al. 2002). Therefore, it would be more appropriate to use a time-varying rate running between ~ 0.5 and $2.0 \text{ l h}^{-1} \text{ g}^{-1}$ (based on mean temperatures and on the relationship given in Newell et al. 2005) to estimate oyster grazing effects on the spring bloom. The important point is that the inherently low grazing rates on algal cells by oysters as well as other benthic and pelagic herbivores allow the spring phytoplankton biomass to accumulate — this is the nature of the spring bloom in coastal systems such as Chesapeake Bay (Malone 1992, Harding et al. 1999, 2002, Kemp et al. 1999); the statement that 'low springtime filtration rates would make it impossible for oysters to control the spring bloom' (Pomeroy et al. 2006, p. 301) is a truism that pertains to all phytoplankton grazers. As indicated above, the most relevant point that counters their argument is the fact that grazing in warmer months by more abundant oysters (as well as by other benthic herbivores) can significantly retard the supply of carbon to the sub-pycnocline, the process that is necessary to maintain summer hypoxia.

OYSTERS ACCESS PHYTOPLANKTON IN SHALLOWER WATER

The central premise of the Pomeroy et al. (2006) 'spatial mismatch' argument is that oysters are confined to the relatively shallow waters that flank the mainstem Bay and dominate its tributary estuaries, while most of the phytoplankton production occurs in waters overlying the deep central mainstem channel. Whereas the first part of this argument is generally true, the second is certainly false. It is important to recognize that more than half of the Bay has mean water depths that are

shallower than the depth of the upper mixed layer (6 to 10 m), which generally coincides with the euphotic depth (e.g. Wofsy 1983, Kemp et al. 1997). This implies that at least half of the vertically well-mixed waters of the Bay are in direct contact with the benthos and with the fauna that occupies these habitats. Furthermore, the charts presented by Pomeroy et al. (2006) to depict historical distribution of oyster bars and their relationship to the current distribution of spring phytoplankton (their Fig. 1) are misleading. Some oyster bars have been omitted, and the 3-dimensional orientation of oyster reefs (Lund 1957, Hargis & Haven 1999, Kennedy & Sanford 1999) has been ignored. Unharvested oyster reefs form structures with a complex vertical relief (Powell et al. 1987, DeAlteris 1988, 1989, Hargis 1999, Hargis & Haven 1999, Smith et al. 2003), which interacts with tidal currents to generate turbulent mixing that enhances particle transfer across the benthic boundary layer (e.g. Wildish & Kristmanson 1997, p. 341).

Pomeroy et al. (2006) illustrated their contention that phytoplankton blooms are spatially separated from eastern oyster habitat along the flanks of Chesapeake Bay. They stated that their illustration (their Fig. 1; re-

produced here in Fig. 1, right panel) is based on an unpublished report by Hood & Boicourt (2005), which should have been cited as Li et al. (2005). Li et al. (2005) developed a biophysical model that they used to predict the location of nitrogen in phytoplankton blooms. The model predicts for a spring period in 1996 that high phytoplankton nitrogen of ~ 15 to 20 mmol N m^{-3} would be broadly distributed across the width of the Bay, reaching both the eastern and western shores along most of the mesohaline portion (Fig. 1). Moreover, extensive aerial surveys of chlorophyll *a* concentrations taken at 1 to 4 wk intervals from 1989 to 2006 (available at: www.cbrsp.org), summarized by Miller & Harding (2007), reveal that phytoplankton blooms in spring and summer tend to be either broadly distributed across the entire Bay or concentrated in the flanks. The diagram created by Pomeroy et al. (2006) does not accurately represent the modeled or field measurements of the spatial distribution of phytoplankton, and instead shows high concentrations of phytoplankton constrained to waters above the deep channel (Fig. 1). Pomeroy et al. (2006) then utilize this to support their argument that there is a high degree of spatial separation between oysters and phytoplankton

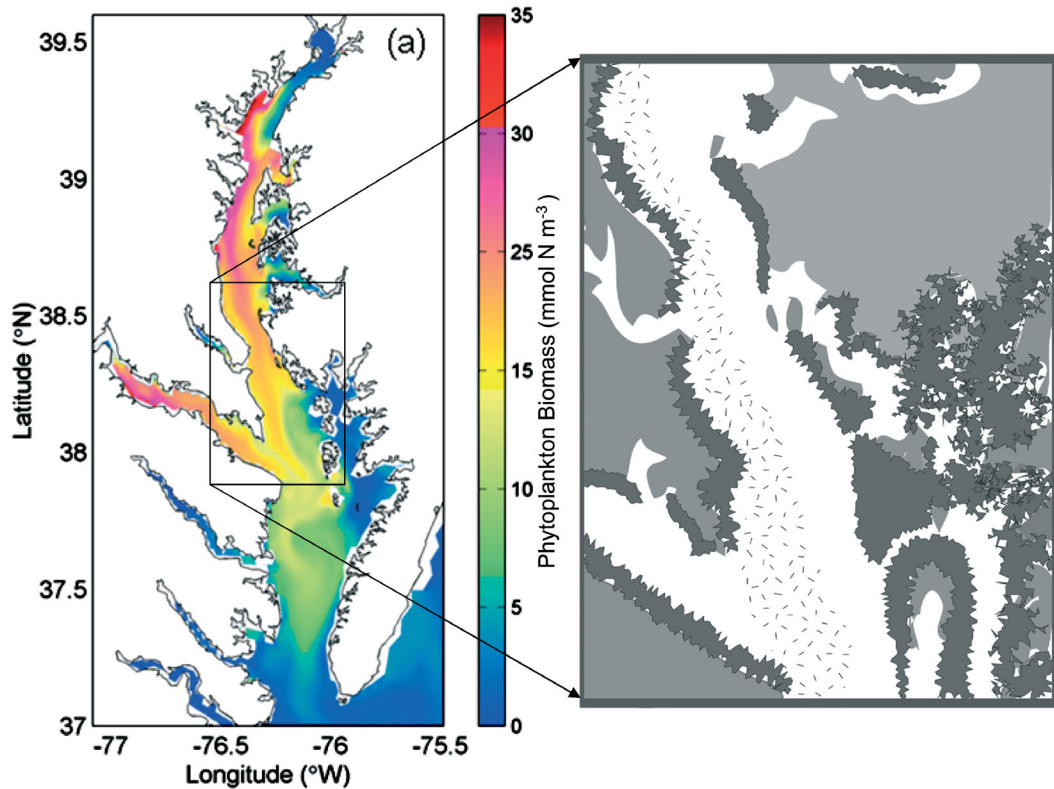


Fig. 1. Left: Output from a biophysical model for Chesapeake Bay that shows the spatial distribution of phytoplankton biomass (modeled as mmol N m^{-3}) during spring 1996 (from Li et al. 2005, their Fig. 18). Right: Fig. 1 from Pomeroy et al. (2006) purported to show 'the active core of a major spring diatom bloom (stippled) in central Chesapeake Bay.' Although Pomeroy et al. (2006) state that this figure is based on the phytoplankton N concentrations shown in the left panel, their diagram does not accurately reproduce the broad distribution of phytoplankton biomass across the width of the Bay

blooms. Based on the aerial surveys of chlorophyll *a* concentrations, we conclude that oyster reefs in the Bay, although generally confined to waters <8 m deep, historically had effective access to a substantial proportion of the estuary's phytoplankton communities and that the complex vertical relief of these reef structures tended to minimize re-filtration, enhancing oyster feeding efficiency. Oysters living in such locations would consume phytoplankton, and undigested organic material in their feces and pseudofeces would be incorporated into the surrounding sediments (Haven & Morales-Alamo 1966, 1968, Newell et al. 2005). In such aerobic locations the remaining organic material is subject to metazoan and bacterial decomposition that does not contribute to the development of hypoxia in the bottom waters of the central channel of the Bay.

LIMITS TO TOP-DOWN CONTROL BY EXTANT BENTHIC SUSPENSION-FEEDERS

Pomeroy et al. (2006) also suggest that the filtration capacity of existing benthic suspension feeding guilds (Thompson & Schaffner 2001, Schaffner & Thompson 2002) is similar to that estimated for historical oyster stocks. Based on this supposition, Pomeroy et al. argue that the inability of these extant benthic grazer communities to regulate phytoplankton and bottom water hypoxia implies that oyster grazing was never important in controlling summer sub-pycnocline hypoxia in the mesohaline part of the Bay. This line of reasoning ignores the fact that benthic filter-feeding invertebrates are not evenly distributed along the Bay's main salinity gradient. Presently, the polyhaline (lower Bay) benthic community contains a diverse guild of suspension-feeders (e.g. Diaz & Schaffner 1990, Thompson & Schaffner 2001), while the upper oligohaline region of the estuary is dominated by dense beds of bivalves (e.g. Gerritsen et al. 1994).

Benthic filtration in both of these regions appears capable of regulating phytoplankton abundance and growth (Gerritsen et al. 1994, Thompson & Schaffner 2001), but in the mesohaline region, where summer hypoxia prevails, benthic filter feeders are currently too sparse to exert significant grazing pressure on phytoplankton (Gerritsen et al. 1994). The eastern oyster is one of the most euryhaline of all indigenous bivalves, growing well at salinities ranging from 5 to 34 (Shumway 1996). Following the extirpation of oysters from the mesohaline Bay during the last century, no other benthic suspension feeding species has succeeded in occupying this niche (Diaz & Schaffner 1990, Newell & Ott 1999). The historically extensive oyster populations in this part of the mesohaline Bay were likely supported by high phytoplankton produc-

tion typical of the chlorophyll maximum zone located just seaward of the estuarine turbidity maximum; the location of this zone varies seasonally and at short time scales, but it is almost always found between latitudes 39° 10' N and 39° 28' N, i.e. in the vicinity of Kent Island, MD (Sanford et al. 2001). Consequently, there is now a regional mismatch between the high biomass of suspension feeders in the oligohaline and polyhaline regions, and the Bay's mesohaline region, where summer phytoplankton growth is high (Harding et al. 2002, Miller & Harding 2007) and bottom water oxygen concentrations are low (Kemp et al. 2005).

SIMULATION MODELS OF THE ECOLOGICAL FUNCTION OF OYSTERS

The preceding discussion illustrates that the question of oyster top-down control of phytoplankton growth in the Bay depends on the correspondence between spatial distributions and temporal sequences of phytoplankton and oysters. The coarse scales of the original illustrative calculations developed by Newell (1988), which were adopted by Pomeroy et al. (2006), are not adequate to address these oyster–phytoplankton interactions. Recently, Cerco & Noel (2005, 2007) extended a coupled biophysical model of the Bay's ecosystem dynamics (Cerco & Cole 1993) to simulate eastern oyster filtration and associated complex ecosystem changes at fine temporal (h) and spatial (1 m vertical \times 1 km horizontal) resolution. They estimated that ecological responses to 10- and 100-fold increases (from present low levels) in oyster abundance would increase summer mean O₂ concentrations beneath the mesohaline Bay pycnocline by ~20 and ~80%, respectively, over today's baseline levels (1.35 mg l⁻¹). Moreover, these modeling scenarios predicted that the area of Bay-bottom where water clarity is sufficient to allow seagrass growth would increase by 20 and 60%, respectively. On a Bay-wide basis, projected bottom-water O₂ improvements from a 100-fold increase in oyster abundance are comparable to improvements associated with mandated reductions in anthropogenic nutrient loading to the Bay (26 vs. 30% respectively), while projected improvements in seagrass biomass exceed those associated with nutrient reductions (60 vs. 38%). Model simulations also indicated that oyster restoration in the shallow and enclosed Bay tributaries will tend to have the greatest impact on improvements in water clarity and seagrass habitat.

The value of strategically siting oyster restoration activities has also been confirmed by other modeling studies. For example, Fulford et al. (2007) developed a spatially-explicit algorithm to estimate oyster removal

of phytoplankton biomass from 36 Bay regions, with oyster feeding rates adjusted for observed seasonal variations in water temperature, O_2 , suspended solids and phytoplankton biomass (3 size classes). Model scenarios indicated that, despite the current negligible impact of oysters on Bay phytoplankton, a 25-fold increase in oyster abundance over present day low levels would remove algal cells in Bay tributaries at annual mean rates that equal or exceed observed specific growth rates for phytoplankton.

CONCLUSIONS

We conclude that, in contradiction to the assertions in Pomeroy et al. (2006), most of the available information supports the hypothesis of Newell (1988) that eastern oysters once provided an important check on phytoplankton production. This suggests that the demise of the oyster has exacerbated the current effects of eutrophication in the Bay. This conclusion leads us to the recommendation that oyster restoration should be an important component of a multi-faceted program to reduce the adverse affects of human development on Chesapeake Bay. The use of oyster restoration in addition to nutrient control is an important element of the overall strategy because it is one of the few possibilities to control ecosystem processes after anthropogenic nutrient inputs have altered the Bay (Newell et al. 2005). Forecasts of how the Bay might respond to increases in oyster abundance must be viewed with caution, however, because the ecosystem may well develop an alternative trophic state, rather than return directly to the original condition (e.g. Dame 2005). Although management plans call for a Bay-wide 10-fold increase in oysters over the low abundances present in 1994 (Chesapeake 2000 Agreement; www.chesapeakebay.net/c2k.htm), ongoing disease epizootics (Ford & Tripp 1996) and relentless harvest pressure continue to promote a general decline of eastern oyster populations throughout the Bay (e.g. Jordan & Coakley 2004). In tributaries of the upper Bay, where oyster diseases are less virulent, there has been modest success in restoring nascent oyster reefs in recent years. By focusing on restoration in small regions, some of the environmental benefits discussed above may begin to be achieved, even if Bay-wide restoration of historic oysters stocks is not immediately achievable. Recognition of the diverse ecosystem benefits provided by oyster populations (see also Coen et al. 2007), is a necessary precursor and stimulus for actions to conserve and rebuild eastern oyster populations, so that they can once again provide beneficial ecosystem services and ultimately, perhaps, support a sustainable fishery.

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