

REPLY COMMENT

Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: Reply to Newell et al. (2007)

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ABSTRACT: Recently published models, which allow for spatial and temporal matching of oyster and phytoplankton populations in mainstream Chesapeake Bay, support the conclusion of Pomeroy et al. (2006; Mar Ecol Prog Ser 325:301–309) that oysters cannot, and could not, control the spring blooms that are the ultimate cause of summer hypoxia. We enlarge upon our earlier exposition of how top-down and bottom-up processes interact in Chesapeake Bay to permit the occurrence of phytoplankton blooms in spring, but not in summer.

KEY WORDS: Oyster · Hypoxia · Filter-feeders · Phytoplankton blooms

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INTRODUCTION

Newell (1988) proposed that oysters controlled spring phytoplankton blooms and thus prevented or reduced summer hypoxia in Chesapeake Bay in the pre-1800s. He further postulated that restoration of an oyster population was a means to reduce hypoxia. This hypothesis has been widely accepted as fact and is often cited as such (e. g. in Jackson et al. 2001, which has been cited 600 times). After 2 centuries of over-exploitation and the introduction of devastating oyster diseases in the 1950s, replacement of the depleted native population with a disease-resistant oyster species is frequently advocated and is assumed by some scientists, the public, and policy makers to be a substitute for remediation of the anthropogenic eutrophication of the Chesapeake catchment area, which has led to intense spring phytoplankton blooms and summer hypoxia. Pomeroy et al. (2006) showed that key

assumptions in Newell's (1988) calculations are incorrect, and we re-affirm that recent and more detailed research, including several model simulations (Gerritsen et al. 1994, Cerco & Noel 2007, Fulford et al. 2007), reach the same conclusion regarding the potential impact of a larger oyster population.

OYSTER FILTRATION AND SPATIAL SEPARATION

Pomeroy et al. (2006) identified 2 errors in Newell's (1988) calculation of pre-industrial oyster filtration capacity: (1) the inherent but unstated assumption that oysters were in constant contact with all phytoplankton, and (2) a maximum, and inappropriate, summer filtration rate; this led him to conclude that oysters were potentially able to filter phytoplankton cells quickly enough to prevent the spring phytoplankton bloom from occurring. Three published modeling efforts, starting with Gerrit-

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sen et al. (1994), have concluded that oysters could not control phytoplankton blooms because of spatial separation of the core spring bloom in the main stem from oyster reefs at the margins and in the river mouths. In fact, Cerco & Noel (2005, Chapter 4, p. 2.), based on their spatially detailed Chesapeake model, stated, 'Nitrogen removal via oyster restoration can be a valuable supplement to alternate methods of nutrient control, but is no substitute for conventional nutrient controls.' Fulford et al. (2007; p. 57) stated: 'the bulk of present-day oyster biomass is in tributaries, while the bulk of phytoplankton is in the main-stem Chesapeake Bay.'

In Pomeroy et al. (2006), Fig. 1, reproduced in Newell et al. (2007) as part of their Fig. 1, illustrates the spatial separation. We showed the position of a bloom, taken from the literature; this is one of many possible locations, depending on wind and tidal currents, but it illustrates the limits of oysters to control the bloom. One side of the bloom was at the margin of the main stem and in contact with oyster reefs that were filtering and potentially limiting it, but it extended to the center of the Bay, where its doubling rate could not be constrained by benthic filter-feeders. Blooms may occur anywhere, but it is in the main-stem Bay that they grow uncontrolled in early spring. We really do not need a mathematical model to tell us that, but all extant Chesapeake Bay models support this assertion. The spatial separation was the same before harvesting began as it is today. The models also tell us that restoration of the oysters will have positive effects on water clarity in the river mouths and tributaries, where oysters formerly were abundant. This will in turn promote restoration of the sea grass beds that have been severely depleted by phytoplankton-related turbidity. These are indeed positive outcomes as would be the replenishment of a commercially harvestable oyster crop in the shallow areas of the Bay—a goal we hope can be obtained. Nonetheless, it will still be necessary to control summer hypoxia.

TEMPERATURE AND THE FILTER-FEEDING GUILD

Our review demonstrated that Newell's (1988) calculation of filtration impact applied a summer oyster filtration rate that would not occur during the spring bloom when water is cooler and filtration slower. To illustrate our point, we repeated his simple calculation (but did not 'adopt' his flawed assumptions) using a more appropriate temperature to show that oysters would have required about 30 d to accomplish what Newell had calculated would take 2 to 3 d—using his incorrect assumption of full contact of bloom and oysters. Newell et al. (2007) suggest applying instead a time-varying temperature. This factor has already

been incorporated into Chesapeake Bay models (Cerco & Noel 2005, Fulford et al. 2007) that are said by their authors, consistent with our assertion, to show that oysters cannot control the spring bloom. Time-varying temperature is also shown graphically, along with oyster filtration rate (a relative proxy for filtration by all filter-feeders), in Pomeroy et al. (2006: Fig. 2). Were it not for high summer clearance rates by pelagic organisms, from microzooplankton to menhaden, plus the extant filter-feeding benthos, we would see a summer phytoplankton bloom in the present.

As Newell et al. (2007) note, summer feeding activity leads to fallout of fecal material that further contributes to summer hypoxia. Cerco & Noel (2005) pointed out that counter-current flow in the stratified main stem concentrates particulate matter from most of the Bay in the mid-estuary main stem seaward of the salt wedge. This secondary concentration of summer fallout increases summer hypoxia in the central main stem. While some of the summer ammonium regeneration that supports high summer primary production and the resultant fecal pellets may derive from years past (see N-loading in Fig. 3 of Pomeroy et al. 2006), Boynton et al. (1995) attribute essentially all ammonium regeneration to the spring bloom of the same year. The magnitude of summer hypoxia is correlated to the magnitude of the spring bloom (Boesch et al. 2001). If Boynton et al. (1995) are correct, then the size of the spring bloom must largely determine the amount of fallout of fecal material and its contribution to hypoxia in the subsequent summer. Fecal deposition during summer is not an independent phenomenon, as Newell et al. (2007) suggest.

TOP-DOWN AND BOTTOM-UP INTERACTIONS

A basic issue underlying our debate is how natural ecosystems and communities of organisms are regulated, and the Chesapeake Bay data provide an example of alternating control by top-down predator-prey processes, primarily in summer, and bottom-up nutrient-driven processes, primarily in spring. Newell's (1988) hypothesis argues for top-down control in spring by oysters. D'Elia et al. (2003) advocate a bottom-up cause for spring blooms and summer hypoxia by anthropogenic eutrophication in the catchment area, as do the Chesapeake Bay models. Our Fig. 2 (Pomeroy et al. 2006) shows how top-down and bottom-up processes alternate in the Bay. Chlorophyll reaches its annual peak in April, at the time of the bottom-up, nutrient-initiated spring bloom. With nutrient depletion, and perhaps also with rising temperature and increasing total filtration rates of all filter-feeders, chlorophyll falls nearly to winter concentrations in June. Gerritsen et al.

(1994) emphasized, and we re-emphasized, the importance of other filter-feeders, which have a total filtration capacity similar to that of oysters in the pre-colonial era. The importance of these ecological equivalents to oysters cannot be overlooked. Although the spring bloom terminates by May, primary production continues to rise steadily, fueled by recycled ammonium (a function of temperature), and peaks in August. Nevertheless, chlorophyll concentrations remain moderate throughout the summer because the clearance rate of *all* filter-feeders has a summer maximum, thus controlling the potential summer bloom. Much of this summer top-down effect is probably pelagic, producing fallout of fecal pellets that does indeed contribute to summer hypoxia — as Newell et al. (2007) point out and we failed to emphasize in Pomeroy et al. (2006). But the amount of fecal fallout during summer is determined by the magnitude of the preceding spring bloom, a bottom-up-controlled process.

How will Chesapeake Bay change if oyster populations are restored — with the Chinese oyster *C. arakiensis* — to abundance levels as they existed in 1800? Water clarity will likely improve in shallow areas, and seagrasses will probably return to many areas they formerly occupied. The high-standing oyster reefs of pre-colonial times cannot rebuild themselves as long as oyster dredging continues. The Chesapeake Bay model (Cercó & Noel 2005) predicts that some increase in dissolved oxygen will occur, but spring blooms will continue to be large, and summer hypoxia will continue to be a problem until eutrophication from the catchment area and atmosphere is reduced. This is not because the system is in a new stable state, as Newell et al. (2007) speculate, but because of a persistent need to control bottom-up eutrophication. Because Newell's oyster restoration hypothesis enjoys the favor of Chesapeake Bay managers, this is not just a point of academic interest; it is a significant public policy concern. As we stated in our original review, there may be good reasons to restore an oyster population in Chesapeake Bay (e.g. Coen et al. 2007, this volume), but preventing hypoxia in the main stem is not one of them.

Editorial responsibility: Howard Browman (Associate Editor-in-Chief), Storebø, Norway

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*Submitted: May 15, 2007; Accepted: May 17, 2007
Proofs received from author(s): June 29, 2007*