AS WE SEE IT

Ecosystem services related to oyster restoration

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ABSTRACT: The importance of restoring filter-feeders, such as the Eastern oyster *Crassostrea virginica*, to mitigate the effects of eutrophication (e.g. in Chesapeake Bay) is currently under debate. The argument that bivalve molluscs alone cannot control phytoplankton blooms and reduce hypoxia oversimplifies a more complex issue, namely that ecosystem engineering species make manifold contributions to ecosystem services. Although further discussion and research leading to a more complete understanding is required, oysters and other molluscs (e.g. mussels) in estuarine ecosystems provide services far beyond the mere top-down control of phytoplankton blooms, such as (1) seston filtration, (2) benthic–pelagic coupling, (3) creation of refugia from predation, (4) creation of feeding habitat for juveniles and adults of mobile species, and for sessile stages of species that attach to molluscan shells, and (5) provision of nesting habitat.

KEY WORDS: *Crassostrea virginica* · Restoration · Chesapeake Bay · Filter-feeders · Water quality · Ecosystem services

INTRODUCTION

Dramatic decreases in eastern oyster *Crassostrea virginica* populations have occurred in many estuaries along the USA Atlantic and Gulf coasts (e.g. Rothschild et al. 1994, Coen & Luckenbach 2000, French McCay et al. 2003, NRC 2004). Although the loss of this valuable fishery species is cause for concern, increasing recognition of the many 'ecosystem services' provided by healthy oyster reefs and by bivalve molluscs in general has led to a broader appeal for restoration of oyster reefs and other bivalve-dominated habitats (see ASMFC 2007). One of these ecosystem services, the grazing of phytoplankton populations, was the focus of a recent review (Pomeroy et al. 2006), which concluded that filtration by *C. virginica* in Chesapeake Bay, either at historical densities or at current restoration target densities, is insufficient for top-down control of the spring phytoplankton bloom and for reduction of...
summer hypoxia on a bay-wide scale. This central premise in Pomeroy et al. (2006) is the subject of a Comment by Newell et al. (2007, this volume) and is indirectly addressed by Cerco & Noel (2007) in a recent modeling paper.

Our aim here is to address arguments that advocates of oyster restoration have advanced to the effect that enhancing oyster populations 'is an easy solution for controlling phytoplankton blooms'. We also seek to clarify the positions that researchers in this field have advanced as the rationale for oyster restoration, vis-à-vis localized effects of oyster filtration that are sometimes overlooked or misinterpreted (e.g. Lenihan & Peterson 1998, Coen et al. 1999, Coen & Luckenbach 2000, Grabowski & Peterson 2007).

ECOSYSTEM SERVICES PROVIDED BY OYSTERS

We take issue with 2 of the points highlighted recently by Pomeroy et al. (2006), who state that (1) native oyster restoration or (2) the introduction of an exotic (non-native) oyster species have been widely advocated in the scientific literature as solutions to eutrophication in Chesapeake Bay. In reviewing the goals and success criteria for native oyster reef restoration, Coen & Luckenbach (2000) and others (reviewed in ASMFC 2007, Coen et al. 2007, Grabowski & Peterson 2007) expressly noted that the system-level effects of oyster filtration have been poorly quantified, especially as they might relate to any specific restoration project (but see Nelson et al. 2004, Newell 2004, Grizzle et al. 2006). The goals and success criteria emphasized by Coen & Luckenbach (2000)—and elaborated upon subsequently by Luckenbach et al. (2005), Coen et al. (2007) and S. P. Powers et al. (unpubl.)—have focused, among others, on the development of: (1) sustainable oyster populations; (2) enhanced species diversity; (3) trophic complexity; and (4) localized material fluxes to the benthos. Similarly, Grabowski & Peterson (2007) point out that although effects of oyster restoration on water quality in large water bodies are difficult to quantify, localized effects of oyster filtration (e.g. reduced turbidity) have been observed and, together with other ecosystem services (e.g. Meyer et al. 1997, Allen et al. 2003, French McCay et al. 2003, Peterson et al. 2003) provided by oyster reefs, constitute a strong case for restoration.

We are aware of only one peer-reviewed paper that expressly advocated the introduction of Crassostrea ariakensis to Chesapeake Bay for the purpose of improving water quality (Gottlieb & Schweighofer 1996). In advocating the consideration of introducing Crassostrea gigas to Chesapeake Bay for fisheries restoration, Mann et al. (1991) mentioned possible water quality benefits, but expressly stated that their commentary was directed towards recovery of a commercial fishery. Ruesink et al. (2005) were cited by Pomeroy et al. (2006) as suggesting that the Ocean Studies Board of the National Research Council recommended the introduction of an exotic species to Chesapeake Bay for controlling phytoplankton blooms; this is inaccurate (cf. NRC 2004). The potential benefits of filtration by oysters as stated in the popular press1 ignore the realities of the scale of restoration required to achieve such benefits, and we concur with Pomeroy et al. (2006) that using this position to support the introduction of an exotic oyster species such as C. ariakensis places the ecosystem at risk.

We welcome the effort to advance more realistic expectations for oyster restoration to policy makers, resource managers and the public, and to dampen the enthusiasm for the introduction of exotic oyster species, which is based on unfounded assumptions (see Newell et al. 2007, Pomeroy et al. 2007, this volume). Nevertheless, by attributing to oyster restoration a goal of system-wide water quality improvement and then proceeding to argue for the futility of that goal, while failing to mention the real and more tractable goals of oyster restoration, critics risk adversely affecting all other oyster restoration efforts in Chesapeake Bay and elsewhere. Specifically, Grabowski & Peterson (2007) have identified 7 categories of ecosystem services provided by oysters: (1) production of oysters; (2) water filtration and concentration of biodeposits (largely as they affect local water quality); (3) provision of habitat for epibenthic fishes (and other vertebrates and invertebrates—see Coen et al. 1999, ASMFC 2007); (4) sequestration of carbon; (5) augmentation of fishery resources in general, (6) stabilization of benthic or intertidal habitat (e.g. marsh); and (7) increase of landscape diversity (see also reviews by Coen et al. 1999, Coen & Luckenbach 2000, ASMFC 2007).

In the following section we highlight categories 2, 3, 5, 6 & 7, as summarized in Grabowski & Peterson (2007).

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DISTURBANCE AND RESTORATION

The dramatic decline in oyster abundances in Chesapeake Bay and other estuaries along the Gulf and Atlantic coasts of the USA over the 20th century has led to concomitant reductions in hard substrate habitat in ecosystems dominated by sedimentary habitats (e.g. Rothschild et al. 1994, NRC 2004). Studies comparing invertebrate faunal abundance and diversity between restored and non-restored oyster reefs (e.g. Luckenbach et al. 2005, Rodney & Paynter 2006, L. D. Coen et al. unpubl.), between oyster reefs or reef mimics, and soft bottom habitats (e.g. Posey et al. 1999, Tolley & Volety 2005), and among oyster reefs of varying complexity (e.g. Coen & Luckenbach 2000, Luckenbach et al. 2005), consistently find higher abundances, biomass and species richness on the structurally more complex reef habitats. Densities of decapods and meiofauna on oyster reefs are similar to those in other structured habitats (e.g. Glancy et al. 2003, Hosack et al. 2006).

Abundance, biomass and species richness of finfish species are higher at oyster reefs than in unstructured estuarine habitats (reviewed in Coen et al. 1999, ASMFC 2007). Some of these species (e.g. gobies, blennies and toadfish) are obligate reef residents throughout their post-larval life, while other species are either facultative residents or transient associates (discussed in Breitburg 1999, Coen et al. 1999, ASMFC 2007). Though few studies have yet sought to quantify secondary production attributable to oyster reefs, Peterson et al (2003) estimated that restored oyster reef habitat may yield 0.26 g m\(^{-2}\) yr\(^{-1}\) of fish and large decapod crustacean biomass in southeastern USA estuaries.

Habitat disturbance and/or loss are ranked worldwide as the principal threat to biodiversity, and are also responsible in part in declined fisheries (Fogarty & Murawski 1998, Lenihan & Peterson 1998, Beck et al. 2001, NRC 2007). In the southeastern USA (southern North Carolina, South Carolina, Georgia, parts of Florida) and in Virginia and the Gulf of Mexico, oysters are predominantly intertidal, forming a protective breakwater that retards shoreline (primarily marsh) erosion (e.g. Meyer et al. 1997, Grizzle et al. 2002, Coen & Bolton-Warberg 2005, ASMFC 2007, NRC 2007). In addition to natural erosion, coastal development and boat traffic have accelerated disturbance of oysters and of the fringing saltmarsh, e.g. by increasing wave effects (Grizzle et al. 2002, Coen & Bolton-Warberg 2005, Piazza et al. 2005, Wall et al. 2005, NRC 2007, L. D. Coen et al. unpubl, L. J. Walters et al. unpubl). Oyster restoration can slow down disturbance effects on marshes and fringing oysters, and constitutes an alternative to the hard bulk-heading of shorelines (e.g. Meyer et al. 1997, Coen & Bolton-Warberg 2005, NRC 2007).

There is a need for rigorous establishment and clear articulation of the goals of oyster restoration, especially in the context of large public expenditures, as well as deliberations surrounding the introduction of an exotic species. Our central tenet is that ecological goals of oyster restoration are broader than the top-down control of phytoplankton production on a system-wide basis. The complex interactions between filter-feeders and their environment are not completely understood, but evidence is accumulating that native and introduced bivalves, including those on aquaculture farms, have significant impacts on seagrass and overlying phytoplankton communities on both local and larger scales (reviewed in Dame 1996, French McCay et al. 2003, NRC 2004, Cerco & Noel 2007). For example, Mercenaria mercenaria aquaculture in lower Chesapeake Bay appears to be enhancing seagrass abundance (see Grizzle et al. 2006). In Florida, seagrass beds often harbor dense American horse mussel Modiolus americanus populations (up to 2000 ind. m\(^{-2}\); Valentine & Heck 1993), and the activities of these and other filter-feeders enhance seagrass production further via a positive feedback loop (e.g. Reusch et al. 1994, Peterson & Heck 1999, 2001a,b, C. C. Wall et al. unpubl.). In their recent modeling paper, Cerco & Noel (2007) assess the impact of a 10% increase in oyster biomass in Chesapeake Bay, on 3 spatial scales, and suggest that the enhancement of submersed aquatic vegetation would be the greatest direct beneficiary of oyster restoration through water clarity.

CONCLUSIONS

Although it is difficult to determine empirically the system-wide effects of historical abundances of oysters and of restoration targets (Pomeroy et al. 2006, Newell et al. 2007), localized influence of oyster reefs on water quality has been verified. In situ measurements have demonstrated that oysters reduce the quantity of suspended solids and phytoplankton (chlorophyll a or other proxies) (e.g. Nelson et al. 2004, Grizzle et al. 2006). At the current oyster abundances in Chesapeake Bay, these effects are limited, but significantly enhanced abundances of filter-feeders can significantly improve water quality in shallow, mesohaline regions of estuaries (e.g. Newell & Koch 2004, Cerco & Noel 2007).

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