Vol. 341: 303–307, 2007 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published July 4

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

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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 impacts on water quality and the provision of habitat (i.e. 'ecosystem services'). Our intent is to clarify our position as restoration scientists on the manifold ecosystem benefits of healthy population densities of filter-feeding bivalves, i.e. to demonstrate the attendant services of oyster restoration 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 *C. gigas* to Chesapeake Bay for the purpose of improving water quality (Gottlieb & Schweighofer 1996). In advocating the consideration of introducing *C. 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 press[1] 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 *Crassostrea 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).

[1]E.g. Zimmerman T: How to revive the Chesapeake Bay: filter it with billions and billions of oysters; US News & World Report, December 29, 1997. Harper S: $2 million approved for oyster revival efforts in Bay; The Virginian-Pilot, January 24, 2007

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 for many declines in 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 seston and overlying phytoplankton communities on both local and larger scales (reviewed in Dame 1996, French McCay et al. 2003, NRC 2004, Cerco & Noel 2007, Grant et al. 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 biomasss in Chesapeake Bay, on 3 spatial scales, and suggest that the enhancement of submerged 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).

Acknowledgements. We thank J. Kraueter, R. Dame, J. Levinton, K. Walters, R. Newell, J. Grabowski, B. Peterson, P. Wilber, and F. Holland for their comments and critiques. A majority of the authors were part of the Oyster Restoration Metrics Working Group supported by Grants from NOAA's South Carolina Sea Grant Consortium (NOAA# NA16RG-

2250) and the South Carolina Department of Natural Resources through its Marine Resources Research Institute. This is Contribution #616 from the Marine Resources Research Institute, South Carolina Department of Natural Resources, Contribution #451 from the Jackson Estuarine Laboratory, University of New Hampshire, and Contribution # 2833 from the Virginia Institute of Marine Science.

LITERATURE CITED

Allen SK Jr, Brumbaugh R, Schulte D (2003) Terraforming Chesapeake Bay. VA Mar Resour Bull 35:2–8

ASMFC (2007) The importance of habitat created by shellfish and shell beds along the Atlantic coast of the U.S. Prepared by Coen LD, Grizzle R, with contributions by Lowery J, Paynter KT Jr. Atlantic States Marine Fisheries Commission, Washington, DC, p 1–116

Beck MW, Heck KL Jr, Able KW, Childers DL and 9 others (2001) The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51:633–641

Breitburg DL (1999) Are three-dimensional structure and healthy oyster populations the keys to an ecologically interesting and important fish community? In: Luckenbach M, Mann R, Wesson J (eds) Oyster reef habitat restoration: a synopsis of approaches. Virginia Institute of Marine Science Press, Williamsburg, Virginia, p 239–250

Cerco CF, Noel MR (2007) Can oyster restoration reverse the cultural eutrophication in Chesapeake Bay? Estuar Coast 30:331–343

Coen LD, Luckenbach MW (2000) Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? Ecol Eng 15:323–343

Coen LD, Bolton-Warberg M (2005) An examination of the impacts of various harvesting/management strategies and boat wakes on oyster bed condition, recovery rates, shoreline erosion and restoration. South Carolina Department of Natural Resources, Marine Recreational Fisheries Stamp Program, Final Report, Charleston, SC

Coen LD, Luckenbach MW, Breitburg DL (1999) The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. In: Benaka LR (ed) Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society, Symp 22, Bethesda, MD, p 438–454

Coen L, Walters K, Wilber D, Hadley N (2007) A South Carolina Sea Grant Report of a 2004 workshop to examine and evaluate oyster restoration metrics to assess ecological function, sustainability and success results and related information. South Carolina Sea Grant, Charleston, SC

Dame R (1996) Ecology of marine bivalves: an ecosystem approach. CRC Marine Science Series, Boca Raton, FL

Fogarty MJ, Murawski SA (1998) Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecol Appl (Suppl 8):S6–S22

French McCay DP, Peterson CH, DeAlteris JT, Catena JR (2003) Restoration that targets function as opposed to structure: replacing lost bivalve production and filtration. Mar Ecol Prog Ser 264:197–212

Glancy TP, Frazer TK, Cichra CE, Lindberg WJ (2003) Comparative patterns of occupancy by decapod crustaceans in seagrass, oyster, and marsh-edge habitats in a northeast Gulf of Mexico estuary. Estuaries 26:1291–1301

Gottlieb SJ, Schweighofer ME (1996) Oysters and the Chesapeake Bay ecosystem: a case for exotic species introduction to improve environmental quality? Estuaries 19:639–650

Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) Ecosystem engineers: concepts, theory and applications. Elsevier-Academic Press, Amsterdam, p 281–298

Grant J, Bugden G, Horne E, Archambault MC, Carreau M (2007) Remote sensing of particle depletion by coastal suspension-feeders. Can J Fish Aquat Sci 64:387–390

Grizzle RE, Adams JR, Walters LJ (2002) Historical changes in intertidal oyster (*Crassostrea virginica*) reefs in a Florida lagoon potentially related to boating activities. J Shellfish Res 21:749–756

Grizzle RE, Greene JK, Luckenbach MW, Coen LD (2006) A new *in situ* method for measuring seston uptake by suspension-feeding bivalve molluscs. J Shellfish Res 25: 643–649

Hosack GR, Dumbauld BR, Ruesink JL, Armstrong DA (2006) Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. Estuar Coast 29:1150–1160

Lenihan HS, Peterson CH (1998) How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. Ecol Appl 8:128–140

Luckenbach MW, Coen LD, Ross PG Jr, Stephen J (2005) Oyster reef habitat restoration: relationships between oyster abundance and community development based on two studies in Virginia and South Carolina. J Coast Res Spec Issue 40:64–78

Mann R, Burreson E, Baker PK (1991) The decline of the Virginia oyster fishery in Chesapeake Bay: considerations for introduction of a non-endemic species, *Crassostrea gigas* (Thunberg). J Shellfish Res 10:379–388

Meyer DL, Townsend EC, Thayer GW (1997) Stabilization and erosion control value of oyster cultch for intertidal marsh. Restor Ecol 5:93–99

NRC (National Research Council) (2004) Non-native oysters in the Chesapeake Bay. National Research Council, National Academies Press, Washington, DC

NRC (National Research Council) (2007) Mitigating shore erosion along sheltered coasts. National Research Council, National Academies Press, Washington, DC

Nelson KA, Leonard LA, Posey MH, Alphin TD, Mallin MA (2004) Using transplanted oyster beds to improve water quality in small tidal creeks: a pilot study. J Exp Mar Biol Ecol 298:347–368

Newell RIE (1988) Ecological changes in Chesapeake Bay: are they the result of overharvesting the eastern oyster (*Crassostrea virginica*)? In: Lynch MP, Krome EC (eds) Understanding the estuary. Advances in Chesapeake Bay research. Chesapeake Research Consortium Publ 129, Gloucester Point, VA, p 536–546

Newell RIE (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve mollusks: a review. J Shellfish Res 23:51–61

Newell RIE, Koch EW (2004) Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries 27:793–806.

Newell RIE, Kemp WM, Hagy JD III, Cerco CA, Testa JM, Boynton WR (2007) Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: Comment on Pomeroy et al. (2006). Mar Ecol Prog Ser 341:293–298

Peterson BJ, Heck KL Jr (1999) The potential for suspension feeding bivalves to increase seagrass productivity. J Exp Mar Biol Ecol 240: 32–52

Peterson BJ, Heck KL Jr (2001a) Positive interactions between suspension-feeding bivalves and seagrass faculta-

tive mutualism. Mar Ecol Prog Ser 213:143–155
Peterson BJ, Heck KL Jr (2001b) An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity. Mar Ecol Prog Ser 218:115–125
Peterson CH, Grabowski JH, Powers SP (2003) Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar Ecol Prog Ser 264:249–264
Piazza BP, Banks PD, La Peyre MK (2005) The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. Restor Ecol 13:499–506
Pomeroy LR, D'Elia CF, Schaffner LC (2006) Limits to top-down control of phytoplankton by oysters in Chesapeake Bay. Mar Ecol Prog Ser 325: 301–309
Pomeroy LR, D'Elia CF, Schaffner LC (2007) Top-down control of phytoplankton by oysters in Chesapeake Bay, USA: Reply to Newell et al (2007). Mar Ecol Prog Ser 341: 299–301
Posey MH, Alphin TD, Powell CM, Townsend E (1999) Oyster reefs as habitat for epibenthic fish and decapods. In: Luckenbach M, Mann R, Wesson J (eds) Oyster reef habitat restoration: a synopsis of approaches. Virginia Institute of Marine Science Press, Williamsburg, VA, p 229–237
Reusch TBH, Chapman ARO, Groger JP (1994) Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina*, but fertilize shoot growth through biodeposition. Mar Ecol Prog Ser 108:265–282
Rothschild BJ, Ault JS, Goulletquer P, Héral M (1994) Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Mar Ecol Prog Ser 111:29–39
Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, Byers JE, Kay MC (2005) Introduction of non-native oysters: ecosystem effects and restoration implications. Annu Rev Ecol Syst 36:643–689
Tolley SG, Volety AK (2005) The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. J Shellfish Res 24:1007–1012
Valentine JF, Heck KL Jr (1993) Mussels in seagrass meadows: their influence on macroinvertebrate abundance, and secondary production in the northern Gulf of Mexico. Mar Ecol Prog Ser 96:63–74
Wall L, Walters L, Sacks P, Grizzle R (2005) Recreational boating activity and its impact on the recruitment and survival of the oyster *Crassostrea virginica* on intertidal reefs in Mosquito Lagoon, FL. J Shellfish Res 24:965–974

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

Submitted: April 19, 2007; Accepted: May 18, 2007
Proofs received from author(s): June 1, 2007