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RESTORATION POTENTIAL OF SEVERAL NATIVE SPECIES OF BIVALVE MOLLUSCS FOR WATER QUALITY IMPROVEMENT IN MID-ATLANTIC WATERSHEDS

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ABSTRACT Bivalve molluscs provide water quality benefits throughout mid-Atlantic watersheds, such as Chesapeake Bay and the Delaware River basins. Whereas most of the attention has focused on the role of the eastern oyster *Crassostrea virginica*, there are many other bivalve species, in both salt and fresh waters, that provide similar benefits. This review summarizes current knowledge regarding the capacity of diverse mid-Atlantic bivalves to filter particles and potentially enhance water clarity and quality. Species with the greatest clearance rates and population carrying capacity were also considered for their restoration and enhancement potential. Compared with eastern oysters, several additional species of saltwater bivalves and freshwater mussels are reported to filter water at rates that merit restoration attention and have been shown to attain significant population sizes. More work is needed to estimate system-carrying capacity and to eliminate restoration bottlenecks for some species—all bivalve species have constraints on their distribution and abundance. Nevertheless, a diversified, watershed-wide bivalve restoration strategy is likely to be more successful than a monospecific focus because it would address pollutant issues in more diverse places and multiple habitats along the river to estuary continuum.

KEY WORDS: bivalve, restoration, water quality, clearance, filtration

INTRODUCTION

Bivalve molluscs provide water quality benefits throughout coastal watersheds, such as the Chesapeake Bay and Delaware River Basin. Most of the attention on those benefits has focused on the role of the eastern oyster *Crassostrea virginica* (Gmelin, 1791) in estuarine ecosystems (Newell 1988, Pomeroy et al. 2006, Cerco & Noel 2007). There are a number of other bivalve species, however, that might provide similar benefits in other habitat niches that span the salinity gradient, including headwater streams, large rivers, tidal fresh and brackish zones, and saltwater areas. The water quality benefits of these bivalves are poorly understood, compared with those of oysters. The intent of this review is to summarize the knowledge about the filtration ability of bivalves (other than oysters) that live in mid-Atlantic watersheds, such as the Chesapeake and Delaware systems. This review also discusses their conservation status and restoration prospects to assist scientists and coastal resource managers throughout the mid-Atlantic region in planning and prioritizing research and management activities.

The intended audience for this review includes scientists, managers, and restoration practitioners, and, therefore, the prose and depth of referencing vary among sections that are likely to be of greatest interest to different sectors. The imbalanced referencing also reflects variability in the quality and quantity of available information for commercial versus noncommercial, and freshwater versus saltwater species. Much of the available data on the range, physiology, and restoration potential for species other than oysters are not in peer-reviewed literature. To summarize what is known about their potential benefits to water quality, preferred habitat niches, and their restoration promise, this review necessarily considers unpublished data sources and observations from scientists, managers, and restoration practitioners in the mid-Atlantic study area. By contrast, there is a rich published literature on the feeding physiology, restoration, and culture methods of commercially important species [e.g., oysters *Crassostrea virginica*; blue mussels *Mytilus edulis* (Linnaeus, 1758)], and for those species the reader is directed to comprehensive reviews by other authors (Bayne & Newell 1983, Kennedy et al. 1996, Cranford et al. 2011).

Mid-Atlantic bivalves include diverse species that live in saltwater, freshwater tidal, and freshwater nontidal areas, extending from the headwaters to the mouths of coastal bays. Kreeger and Kraeuter (2010) tallied more than 60 species of bivalves in the Delaware River Basin, for example. Generally, the same mid-Atlantic species occur in the Chesapeake Bay as in the Delaware River, with the exception that there are 15 more species of freshwater mussels in the Chesapeake Bay watershed. Some of these species are rare, but many are abundant enough to be considered "ecologically significant" (Kreeger & Kraeuter 2010), meaning that they can reach sufficient population abundance to provide water quality benefits or other ecosystem services (Table 1).

The ability of filter-feeding bivalves to improve water quality has been the subject of intense research and debate for the past 30 y or more (Pomeroy et al. 2006, Newell et al. 2007). Most of the attention on those benefits has focused on the role of the eastern oyster *Crassostrea virginica*, which inhabits subtidal and low intertidal estuarine areas having a salinity of 10–30. Some of the other bivalve species live in niches that can overlap with *C. virginica*, such as the ribbed mussel *Geukensia demissa* (Dillwyn, 1817), which is a predominantly intertidal species. Other species live in areas where oysters are absent, such as freshwater mussels (Table 1). A variety of mussel species live in various niches extending from small headwater streams to tidal fresh zones

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TABLE 1.

Summary of ecosystem services furnished by oysters, ribbed mussels and freshwater mussels categorized according to the Millennium Ecosystem Assessment (adapted from Kreeger & Kraeuter 2010).

Bivalve natural capital		Relative importance scores		
Categories	Ecosystem services	Oysters	Ribbed mussels	Freshwater mussels
Provisioning	Dockside product (e.g., seafood and shells)	√√√	–	√
Regulating	Shoreline and bottom protection (e.g., wave attenuation)	√√√	√√	√
	Shoreline and bottom stabilization (e.g., bed stability)	√√	√√√	√√
Supporting	Structural habitat (e.g., essential fish habitat)	√√√	√√	√√
	Biodiversity (e.g., imperiled species)	–	–	√√√
	Biofiltration (e.g., seston removal)	√√√	√√√	√√√
	Biogeochemistry (e.g., nutrient transformation)	√√	√√	√√
	Trophic (e.g., prey value)	√	√√	√√
Cultural, spiritual historical, human health	Watermen lifestyle, ecotourism	√√		
	Native American heritage (e.g., shells)	√√	–	√√√
	Watershed indicator (e.g., environmental status and trends)	√√√	√√	√√√
	Bio-assessment (e.g., toxicity testing)	√√√	√√	√√√

of estuaries (Ortmann 1911, 1919, Bogan & Ashton 2016). A singular focus on oyster restoration may therefore miss opportunities to enhance ecosystem services in areas of the watershed that oysters do not inhabit.

The concept of restoring (and conserving) populations of bivalves other than oysters for the principal purposes of sustaining and improving water quality has been gaining attention. For example, one of the actions under the 2009 Executive Order 13,508, "Chesapeake Bay Protection and Restoration" was "FW20 White paper: evaluate native bivalve restoration for water quality improvement." Action 1 was stated as follows: "Complete literature review of relevant studies on the ability of tidal and nontidal (freshwater and estuarine) bivalves to enhance water quality. Where the literature review finds gaps, identify topic areas and funding needed to support new studies to evaluate the effect of native bivalves on Bay water quality."

This review was written in response to that action. Although investments in bivalve populations can be considered a new best management practice (BMP) for enhancing water quality, these efforts should not be viewed as a replacement for traditional BMP. Indeed, the water quality benefits of bivalves will scale mainly with their population biomass, which will be constrained by the system's carrying capacity and the success of other measures to promote water and habitat quality.

Bivalves contribute biofiltration services by pumping water across enlarged gills that function both in gas exchange and feeding (Bayne 1976, Bayne & Newell 1983, Newell & Langdon 1996). By filtering water to satisfy their nutritional demands, suspension-feeding (a.k.a. filter-feeding) bivalves indiscriminately remove vast quantities of microscopic particles such as phytoplankton, detritus, and suspended sediments, which collectively comprise the seston (Langdon & Newell 1996, Kreeger & Newell 2000, Cranford et al. 2011). Captured particles are then sorted so that the more nutritious particles are selected for ingestion into the mouth (Ward 1996, Ward & Shumway 2004). The term "suspension-feeding" more accurately reflects the physiological trapping of microparticulate matter on mucous-lined structures, rather than the term "filter-feeding" which suggests sieving. To be understandable to the widest audience, however, this review hereafter uses "filter-feeding" because this term is more commonly understood.

In areas where the bivalve population is dense relative to the residence time of the water mass, bivalve filter feeding can result in a direct improvement in water clarity and light penetration (Cloern 1982, Sousa et al. 2009, Cerco & Noel 2010). The actual effects of filter feeding on water quality depend on the volumes of water filtered by the combined population biomass of the bivalves, the temperature which regulates physiological activity, and the concentration and composition of particles in the water. Population biomass density (*e.g.*, kilograms of dry tissue mass per hectare) is therefore a useful metric for gauging the ecological impacts of bivalve assemblages *in situ*. Population biomass density combines the numerical abundance (per hectare) and body size (per animal); therefore, smaller bivalves can still have a large impact on water quality if they achieve sufficient densities. Water clarity depends on concentrations of total suspended solids, and areas with a greater biomass density of bivalves will have greater potential for enhancing water clarity than areas with lower population biomass. Reductions in specific pollutants, such as particulate forms of nutrients and pathogens, depend on biomass density of the bivalve population and the composition of the pollutants in the seston. Nutrients and pollutants can be adsorbed to particle surfaces such as clays and silts or they can be bound within particles such as algae, bacteria, and detritus. In areas where a robust population of bivalves is exposed to seston enriched in nutrients, pollutants, or pathogens, the potential water quality benefits will be greater than in areas having fewer, smaller sized animals or unenriched seston.

This review focuses on the capacity of mid-Atlantic bivalves to filter seston from the water column. The net water quality effects of bivalve filter-feeding *in situ* also depend on the eventual fate and form of filtered matter. Some components of the filtered particles are incorporated into the tissues and shells of the bivalves, some are added to the sediments in biodeposits, and some are transformed from particulate to dissolved forms (remineralization). Excreted products can then be used by other biota, such as nitrogen uptake by denitrifying bacteria (Fig. 1). The net effects of bivalve filter feeding should therefore consider the proportion of filtered material that gets removed, sequestered, and/or recycled in various forms, and the time lag needed for physiological and biogeochemical transformations (Dame

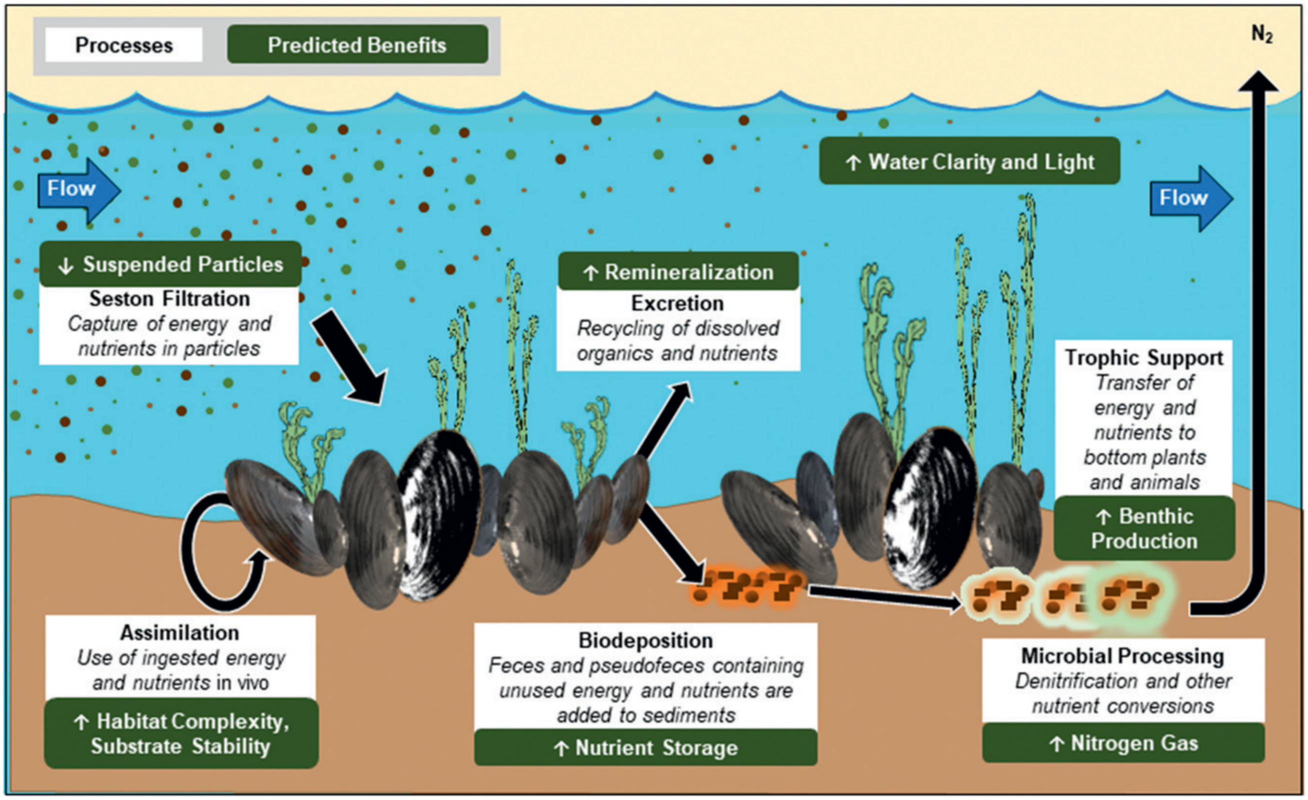

Figure 1. Ecological processes mediated by bivalve suspension feeders that could affect water quality and benthic communities, especially in areas where bivalve population biomass is robust relative to water volumes and hydrologic residence time.

1996, Newell et al. 2005, 2007, Dumbauld et al. 2009). Because biodeposited material can fuel benthic organisms or enter the microbial loop, energy and nutrient cycling mediated by bivalves can also enhance food web efficiencies and decomposition processes, which in turn affects habitat quality for other organisms (Coen et al. 2007, Vaughn et al. 2008, Atkinson et al. 2013). Some filtered biodeposits, and eventually the shells of the bivalves, can get buried. These complex biogeochemical conversions, which are portrayed in Figure 1, can therefore result in losses (e.g., via burial and denitrification) or recycling (*e.g.*, via particle resuspension and nutrient rerelease) of nutrients and some other pollutants.

The literature is replete with examples showing how increases/decreases in bivalve abundance have been associated with improved/degraded water quality, respectively. Bivalve-mediated biofiltration services thus merit the increasing management and restoration interest. As a first step in understanding the prospects of a multispecies restoration approach, this review compares the actual water filtration and restoration prospects of mid-Atlantic bivalves (other than oysters), including species that span the salinity gradient in Chesapeake and Delaware river basins. More analyses and study will be needed to examine other factors that can modulate the water quality outcomes in natural systems.

GOALS

This review has three goals:

1. To evaluate whether native bivalves other than *Crassostrea virginica* provide similar water filtration services in the mid-Atlantic region.
2. To identify species that have had or could potentially have sufficiently high clearance rates (CR) and population abundance for use in restoration projects aimed at improving water quality, potentially diversifying places and habitats for shellfish restoration.
3. To summarize factors that limit natural populations or restoration of each promising species and recommend next steps for research and restoration testing.

Oyster restoration can and should continue to be investigated as a tactic for water quality remediation in the portion of the system where they are sustainable. Oyster restoration is challenging as a tool to improve water quality, however, because of very limited shell substrate, high cost, disease susceptibility, salinity constraints, and fluctuations in natural recruitment. Diversification of target species may provide new opportunities to achieve greater outcomes for water quality, while also providing tangential benefits to aquatic ecosystems and coastal communities. Restoration of freshwater mussels in nontidal waterways, for example, could potentially intercept pollutants before they reach the tidal estuary, and restoration of noncommercial saltwater species could potentially help to remediate pollution within the tidal estuary.

Stocks of noncommercial species are not monitored, and more surveys are needed to assess the status and trends of noncommercial bivalves. Best scientific judgment suggests that most native bivalve species are presently far below their historic abundance, however. For example, freshwater mussels are the most imperiled of all animals in North America (about 75% of 300 native species). Of the 28 native freshwater mussel species in the Chesapeake Bay, only one, *Elliptio complanata* (Lightfoot, 1786), is considered stable by the States of Pennsylvania, Maryland, and Virginia (Watson, VA Department of Game and Inland Fisheries, personal communication; Welte, PA Fish and Boat Commission, personal communication; Ashton, MD Department of Natural Resources, personal communication). The distribution and abundance of that species, however, are greatly reduced compared with historic reports.

Among estuarine species, the ribbed mussel *Geukensia demissa* does not appear to be as reduced as other bivalves; however, it is increasingly threatened by the loss of its preferred habitat, intertidal marshes (Kreeger et al. 2010, 2011, PDE 2012). Another estuarine bivalve, the softshell *Mya arenaria* (Linnaeus, 1758), once had a commercial harvest in the Chesapeake Bay, but their numbers have fallen so much that recent Chesapeake harvests average less than 1% by weight of the peak harvest in 1969, with no harvest reported in several recent years (NMFS 2012).

Considering the reduced current population abundances for most if not all native bivalves, significant potential exists to improve water quality, from headwater streams to lower estuary areas, by alleviating reproduction bottlenecks and improving the system's carrying capacity, similar to efforts to restore oyster stocks because they historically filtered more of the water than presently (Newell 1988).

Of course, this focus on filtration capacity and water quality benefits is oversimplified. As noted earlier, the actual net effects of bivalve populations on water quality depend on complex hydrodynamic, biogeochemical, and ecological interactions. A separate review (and more study) is needed on the ecological fate of filtered matter and implications for water quality. Populations of bivalves are also naturally patchy, and the water quality benefits depend in part on the degree to which they interact with water bodies. The physiological rate functions of bivalves also vary with organismal health and seasonal and ontogenetic changes in nutritional status, which are governed by the interplay between shifting nutritional demands and available food quantity and quality. Water quality improvement via filtration is only one of many services provided by bivalves (Table 1). More research and analysis will be needed to improve the understanding of potential outcomes from nonoyster bivalve restoration investments. Recommendations for next steps are provided at the end of this review.

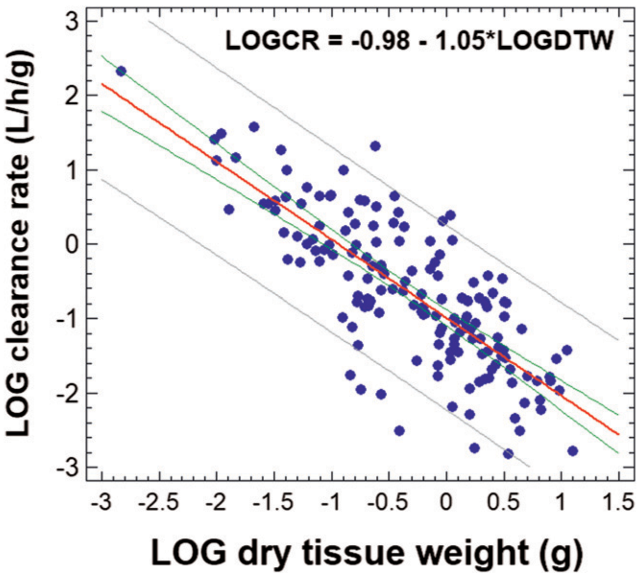

Figure 2. Relationship between CR and DTW for 155 individuals of three species of freshwater mussels living in streams of eastern Oregon (Kreeger et al. 2011). The red line represents the modeled relationship (linear regression $R^2 = 61.3\%$) and the outer lines depict 95% prediction limits for new observations.

BIVALVE FILTRATION

Definitions

The volume of water cleared of particles per unit time is referred to as the ''clearance rate'' (CR), whereas the biomass of particles (i.e., ''seston'') that is removed over unit time is referred to as the ''filtration rate'' (Cranford et al. 2011). The filtration rate (mg seston per unit time) can be calculated by multiplying the CR (volume of water per unit time) by the particle load (mg seston per volume of water). Filtration rate is more relevant to ecological impacts, but it is much harder to measure. Most bivalve ''filtration'' studies therefore measure CR. Hence, comparative assessments in this review were constrained to CR data because there are fewer published studies of actual filtration rates.

Measuring Comparable CR

Clearance rates are inversely and nonlinearly proportional to body size, on a weight-specific basis (Fig. 2). To facilitate comparisons among studies and taxa, it is therefore important to normalize measured rates to body size. There are numerous methods for measuring bivalve CR at the individual and population level, and these are not reviewed here. At least four different ways are reported frequently in the literature: rates per individual, and weight-specific rates using three different measures of body (or tissue) weight. The three different measures of tissue weight are (1) dry tissue weight (DTW), (2) ash-free dry tissue weight (AFDW), and (3) grams of tissue carbon (g C). Dry tissue weights are determined by dissecting tissues from the shell and drying them to constant weight at 60°C. Tissue weight is the preferred metric because shells vary widely in weight among species, and shell mass is generally inconsequential for routine maintenance metabolism. Ash-free DTW are preferred over DTW because the organic portion is expected to scale more tightly with metabolic activity than the inorganic fraction; however, this determination requires an added step of combusting the dried tissue matter and assessing the weight loss on ignition. Typically, in healthy animals, the values for DTW and AFDW are within 15% of each other. Because the carbon content (g C) is generally about 50% of tissue organic weight (or AFDW), rates reported per gram carbon will generally be twice the rates reported per gram of ash-free dry tissue and more than twice the rates reported per gram of dry tissue. Either DTW or AFDW is preferred for interspecific standardization of CR, whereas carbon units are more useful for constructing energy and carbon budgets.

Diet composition (quantity and quality) is another factor that can affect CR. From an organismal perspective, the bivalve needs to balance its seasonally changing physiological demands from a natural seston diet that can vary widely in composition. Many bivalves can compensate for reductions in food quantity and quality, and thereby maintain energy intake, by altering CR, ingestion rate, sorting efficiency, or absorption efficiency

(Iglesias et al. 1992, Navarro & Iglesias 1993, Hawkins et al. 1996). Bivalves differ, however, in their abilities to regulate these responses (Hawkins et al. 1990, Navarro & Iglesias 1993). When a bivalve is presented with a change in diet quantity or quality, such as by a switch from low-quality natural seston to a richer optimal laboratory diet, it will typically ''react'' to the change in very different ways depending on an animal's diet history and nutritional status (e.g., stored reserves for energy, protein, lipids, or other essential compounds). Generally, CR determined with optimal laboratory diets will be greater than with seston, leading to overestimated CR for *in situ* conditions.

Measuring Bivalve Density and Biomass

Clearance rates are typically determined at the organismal level, but for assessing ecosystem services, these rates need to be related to the population density and biomass *in situ* to calculate a population-wide clearance or filtration rate for a geographic area. Some survey techniques are tailored for hard bottoms, some for soft bottoms, and some can be used on both—from oyster dredge to ponar grab to benthic sled. Survey techniques also can be very different between marine and freshwater systems. The physical apparatus or method used to collect bivalves depends on the question, and a detailed analysis of the pros and cons of each survey method is beyond the scope of this article. Regardless of how bivalves are collected, quantitative, statistically robust sampling methods are preferred to capture diversity, abundance, biomass, and demographics within the community. Quantitative population data are essential for estimating overall ecological function and ecosystem services.

In freshwater (nontidal) systems, biologists generally use SCUBA or snorkeling techniques to hand collect freshwater mussels buried in bottom sediments. In large freshwater rivers, brailing—as was used in the 1890s by the pearl-button industry—and SCUBA are often used. Most trained mussel surveyors follow the methods described by Strayer and Smith (2003). Their guide includes various survey techniques and sampling methodologies for estimating diversity within the community and estimating abundance at the species level and community level. Smith (2006) also recommended a unique sampling design for detecting rare species; and Dryver et al. (2012) recently provided useful designs for sampling communities with ''hot spots'' of information (*i.e.*, cluster sampling).

In marine systems, bivalve sampling is generally performed with an oyster dredge, oyster tongs (either hand tongs or power-assisted patent tongs), or a ponar grab on soft bottom. For example, the Chesapeake Bay Benthic Survey (Versar, Inc. 2016) used a ponar grab on soft bottom. Fishery-independent oyster sampling in Chesapeake Bay is performed with two methods: an oyster dredge in Maryland, supplemented by patent tongs at some sites, and patent tongs in Virginia (VIMS 2015). The Chesapeake Bay Program (CBP) (NMFS 2012) provides a thorough assessment of oyster restoration in the Chesapeake Bay along with evaluation of restoration techniques and sampling methods and sampling designs. In Delaware Bay, where most areas are managed for harvest, oyster stocks are routinely monitored using dredges via a partnership among industry, state, and academic organizations.

SPECIES INVENTORY

The Chesapeake and Delaware drainages include extensive freshwater tidal areas; therefore, nontidal portions are fresh water and tidal (estuarine) portions include the full salinity spectrum from fresh to salt water. This species inventory is summarized separately between saltwater (and brackish) versus freshwater species. This is not an exhaustive list of all bivalve species within the region; rather, this review focuses on species for which data on CR were available, or species that have the potential to reach comparatively high population biomass. Published CR, habitat, and salinity preferences for native and nonnative bivalves in the Chesapeake and Delaware Bay drainages are summarized in Table 2. Salinity can vary among years, depending on climate. In general, salinity tends to be highest in the fall in Chesapeake Bay (Versar, Inc. 2016).

Information on CR is more prevalent for saltwater and brackish bivalves than for freshwater mussels. One reason fewer studies have been undertaken with freshwater bivalves is that they are not as commercially valued as saltwater bivalves, which have been the focus of intense study by marine biologists and commercial growers for more than 100 y. Published CR data were obtained for just two species of freshwater mussels native to Chesapeake Bay and Delaware River watersheds—the eastern elliptio *Elliptio complanata* and the paper pondshell *Utterbackia imbecillis* (Say, 1829) (Table 2). There are several other species of freshwater mussels, however, that attain high abundances within the Chesapeake and Delaware watersheds, and these might represent excellent restoration targets for water quality enhancement. Because CR for freshwater mussels found in Europe and in the Mississippi drainage are more prevalent, a comprehensive list of known CR for freshwater mussels is furnished to help assess the benefits of restoring them (Table 3).

As noted earlier, data comparability is limited because many published works report CR per animal ($L\ h^{-1}$) and others report weight-specific CR (often as $L\ h^{-1}\ g^{-1}$ DTW). To adjust for diverse units in the literature, allometric normalization of CR was approximated where possible to convert to units of tissue biomass (no shell) rather than per animal or per overall mass (tissue plus shell). Where rates were reported per individual, or where only an allometric equation was provided, a simple weight adjustment was used for each species. Where rates were reported per individual, this rate per gram was converted by dividing it by a value for DTW or AFDW for that species, and determined in one of two ways:

1. Weight of a clam or mussel of the same length as the ones used to make the water clearance measurements–used for *Dreissena polymorpha* (Pallas, 1771) (Reeders & Bij de Vaate 1990) and *Mytilopsis leucophaeata* (Conrad, 1831) or
2. Mean weight of all the individuals of that species collected by the Chesapeake Bay Benthic Survey (Versar, Inc. 2011) or similar survey–used for *Corbicula* sp. (Kramer & Hübner 2000), *Macoma balthica* (Linnaeus, 1758) (Absil et al. 1996), and *Geukensia demissa* (Kreeger & Newell 2001, using Delaware Bay weights).

Where only an allometric equation was given, with the CR depending on DTW, that weight was assumed to be 1 g, and therefore the resulting rate was the coefficient. This was done for softshell (Riisgard & Seerup 2004; $F = 4.76\ W^{0.71}$) and three

TABLE 2.

Reported habitat preference, salinity, and CR for native and introduced bivalves found in Chesapeake and Delaware watersheds that are likely to filter the most water based on relative population biomass and organismal filtration rates.

Species	Salinity, literature	Salinity, measured	Max length (cm)	Bottom type	Native to area?	Clearance rates ($l\ h^{-1}\ g^{-1}$ of DTW, unless listed as AFDW)		Issues
						Laboratory diets	Natural diets	
Crassostrea virginica	7–30*,†	10.8–18.9‡	14*	Hard	Yes	11.5§, 9.6¶	6.8‖, 6.4**	Disease, shell supply, predation, and poaching
Geukensia demissa	10–30†	5.7–16.9‡	10‖	Both	Yes	6.8††, 6.2‡‡	5.1§§	Recruitment on restoration surfaces limited (trials in Bronx river on rafts and in Delaware Bay on living shorelines)
Ischadium recurvum	5–30*,†	7.8–15.8‡	6¶¶	Hard	Yes	Max 4.3–4.6‖‖	–	Little research and no larvae raised in hatcheries
Macoma balthica	5–30†	6.8–18.4‡	3.8‖	Soft	Yes	0.45–1.33 AFDW***	0.4 AFDW†††	Can switch to deposit feeding
Mercenaria mercenaria	15–30†	15.5–28.0‡	10†	Soft	Yes	1.24‖, 1.52 AFDW‡‡‡	0.5**	High salinity only
Mya arenaria	5–30†	9.5–20.1‡	10‖	Soft	Yes	Max 3.5§§§, 4.76 AFDW¶¶¶	–	Dieback started 1992 in Chesapeake Bay
Mytilopsis leucophaeata	0–10†††, 0–26‖‖‖	2.9–13.6‡	2.2****	Hard	Yes	1.96****, 2.37‡‡‡‡	–	Boom-bust cycles and rarely common where native
Rangia cuneata	0.5–10†	0.4–11.5‡	5†	Soft	No	–	2.06§§§§	May not be native
Tagelus plebeius	10–30†	13.5–23.7‡	9‖	Soft	Yes	–	No rates found	Dieback in Chesapeake Bay started in 1994
Corbicula sp.	Not included	Not included	5‖	Soft: silt, sand, and pebbles	No	2.9 AFDW¶¶¶¶	0.1–1.2 AFDW‖‖‖‖	Nonnative in the United States
Dreissena polymorpha	Not included	Not included	2.4‡‡‡‡‡‡	Hard: Pebble and cobble	No	8.3†††††† 2.70 AFDW‡‡‡‡‡, 6.2; 8.6††††††	16.2 AFDW§§§§§, 1.43 AFDW*****, 13.98 AFDW¶¶¶¶¶	Invasive in United States
Elliptio complanata (see Table 3 for details)	Not included	Not included	12‖	Both: Silt, sand, pebble, and cobble	Yes	0.337††††, 0.048‖‖‖‖‖	3.4******	Larval hosts (fish) may be limiting in some areas
Utterbackia imbecilis	Not included	Not included	–	Both: Silt, sand, pebble, and cobble	Yes	0.036††††††	–	Larval hosts (fish) may be limiting in some areas
Other freshwater mussels not native to Chesapeake or Delaware watersheds	Not included	Not included	–	Both: Silt, sand, pebble, and cobble	Yes	–	0.0012–2.75 (see Table 3)	Larval hosts (fish) may be limiting in some areas

* Tarnowski (2010, 2011). † White (1989). ‡ Versar, Inc. (2016) (CBP benthic data survey base). § Cerco and Noel (2007). ¶ Newell et al. (2005) (maximum monthly value).
‖ Lippson and Lippson (1984). ** Newell and Koch (2004). †† Kuenzler (1961) (mean rate). ‡‡ Riisgard (1988) (assuming 1 g weight). §§ Kreeger and Newell (2001) (using 1.11 g DTW).
¶¶ Lipcius and Burke (2006). ‖‖ Gedan et al. (2014). *** Absil et al. (1996) (mean AFDW of 0.0035 g). ††† Hummel (1985) (cited in Cugier et al. 2010). ‡‡‡ Echevarria et al. (2012).
§§§ Bacon et al. (1998). ¶¶¶ Riisgard and Seerup (2004) (assuming 1 g weight). ‖‖‖ Verween et al. (2010). **** Rajagopal et al. (2005a) (calculated weight for a 20 mm mussel).
†††† Paterson (1984). ‡‡‡‡ Rajagopal et al. (2005b). §§§§ Wong et al. (2010). ¶¶¶¶ Kramer and Hübner (2000) (mean AFDW of 0.047 g). ‖‖‖‖ Cheng (2015).
***** Reeders and Bij de Vaate (1990) (using calculated AFDW). ‡‡‡‡‡ Rajagopal et al. (2003). §§§§§ Fanslow et al. (1995) (mean rate). ¶¶¶¶¶ Roditi et al. (1996) (using estimated weight).
‖‖‖‖‖ Leff et al. (1990) (interpreted from graph for 25°C). ****** Kreeger and Gatenby (unpublished). †††††† Silverman et al. (1997, 1995). ‡‡‡‡‡‡ Walton (1996).
§§§§§§ Baker and Levinton (2003) (report 125 mL h^{-1} for a 15 mg^{-1} DTW animal). ¶¶¶¶¶¶ Where only an allometric equation was given, with the CR depending on DTW, that weight was assumed to be 1 g, so the resulting rate was the coefficient. This was done for *M. arenaria* (Riisgard & Seerup 2004, $F = 4.76\ W^{0.71}$), and three bivalves with rates reported by Riisgard (1988): *C. virginica* ($F = 6.79\ W^{0.73}$), *G. demissa* ($F = 6.15\ W^{0.83}$), and *M. mercenaria* ($F = 1.24\ W^{0.80}$). ‖‖‖‖‖‖ Three studies reported *D. polymorpha* filtration rates on a "per mussel" rather than a weight-specific basis (Reeders & Bij de Vaate 1990, Roditi et al. 1996, Rajagopal et al. 2003). In all three cases, these "per mussel" rates were converted to weight-specific filtration rates by (1) calculating the mean weight of the mussels used to measure the filtration rates from their reported mean length and the length–weight equation, and (2) using that weight in the equation to calculate a weight–specific filtration rate from that study.
******* The maximum CR of *M. leucophaeata* (at the optimum temperature, 20°C–28°C) reported by Rajagopal et al. (2005a) was 0.055 L $ind^{-1}\ h^{-1}$ (per mussel) for the largest size class they tested (20 mm long). Tissue weights were not given, and none could be found for a mussel of that size to convert this rate to a weight basis. A published length–AFDW relationship for *D. polymorpha* (Reeders & Bij de Vaate 1990) was applied to *M. leucophaeata*. Using that equation, the AFDW of a 20-mm *M. leucophaeata* would be 0.028 g, yielding a CR based on that weight of 1.96 L $h^{-1}\ g^{-1}$ AFDW.

TABLE 3.

Comparison of CR measured for freshwater mussels. Italicized CR data were estimated from reported data for either L h^{-1} and L h^{-1} g^{-1} DTW when one of the metrics was not reported in the referenced study.

Species	Food type	Ration	CR (L h^{-1})	CR (L h^{-1} g^{-1} DTW)	Mussel size (g DTW or cm shell length)	Reference
Actinonaias ligamentina	Seston	7.02 mg L^{-1}, 1.2 × 10^4 cells mL^{-1}	1.53	*0.288*	5.31 g	Gatenby & Kreeger (unpublished)
	Green and diatom algae	89.7 mg C L^{-1}	nd	0.0032	24.5 cm	Spooner & Vaughn (2008)*
Amblema plicata	Green and diatom algae	89.7 mg C L^{-1}	nd	0.0014	20.3 cm	Spooner & Vaughn (2008)*
	Typhus (cattail detritus)	1.0 × 10^5 cells mL^{-1}	1.0	0.50	1.0 g DTW (198–364 g wet tissue + shell)	Baker & Levinton (2003)†
Anodonta anatina	*Chlorella vulgaris*	1.2 × 10^4 cells mL^{-1}	2.6–2.9	*0.83–0.92*	3.141 g	Kryger & Riisgard (1988)
	Seston	8–19 mg L^{-1}	*0.59–2.2*	0.17–0.62	3.5 g	Pusch et al. (2001)
Anodonta californiensis	Seston	0.8–7.4 mg L^{-1}	0.8	0.9† 1.1‡	0.58 g (0.19–1.9 g, 3.4–8.6 cm)	Kreeger (unpublished)
Cyclonaias tuberculata	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.77*	*1.15*	0.67 g	Silverman et al. (1995, 1997)
Elliptio complanata	2–5 μm beads, lake water	1 × 10^3 cells mL^{-1}	nd	0.337	6–7 cm	Paterson (1984)§
	2 μm beads, 45 μm filtered stream water	No data	0.0109	0.048	4.4 g	Leff et al. (1990)*
	Algae	2 × 10^3 cells mL^{-1}	3.1	nd	7.5–9.5 cm	Gatenby & Kreeger (unpublished)
		<2 × 10^3 cells mL^{-1}	1.9	nd	7.5–9.5 cm	Gatenby & Kreeger (unpublished)
	Seston	2 × 10^4 cells mL^{-1}	2.6	nd	7.5–9.5 cm	Gatenby & Kreeger (unpublished)
		ca. 2.4 mg L^{-1}	–	3.4	7.5–9.5 cm	Gatenby & Kreeger (unpublished)
Elliptio dilatata	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.496*	*0.460*	1.08 g	Silverman et al. (1995, 1997)
	Seston	7.02 mg L^{-1}, 1.2 × 10^4 cells mL^{-1}	1.12	*0.580*	1.93 g	Gatenby & Kreeger (unpublished)
Fusconaia flava	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.358*	*0.299*	1.195 g	Silverman et al. (1995, 1997)
	Green and diatom algae	89.7 mg C L^{-1}	nd	0.0035	7.6 cm	Spooner & Vaughn (2008)*
Gonidea sp.	Seston	0.8–7.4 mg L^{-1}	0.50	0.31† 0.40‡	1.13 g (0.4–2.5 g; 4.3–8.2 cm)	Kreeger (unpublished)
Lampsilis cardium	Green and diatom algae	89.7 mg C L^{-1}	nd	0.0047	14.0 cm	Spooner & Vaughn (2008)*
Lampsilis ovata	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.418*	*0.354*	1.18 g	Silverman et al. (1995, 1997)
Lampsilis siliquoidea	*Chlamydomonas* sp.	2.5 mm^3 l^{-1}	*1.50*	1.45	1.5–2.1 g	Vanderploeg et al. (1995)
Lasmigona costata	Seston	7.02 mg L^{-1}, 1.2 × 10^4 cells mL^{-1}	1.10	*0.375*	2.93 g	Gatenby & Kreeger (unpublished)
Ligumia subrostrata	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.122*	*0.061*	0.1.997 g	Silverman et al. (1995, 1997)
Margaratifera falcata	Seston	0.8–7.4 mg L^{-1}	0.5	0.45† 0.52‡	1.06 g (0.32–2.99 g, 3.7–9.3 cm)	Kreeger (unpublished)
Margaritifera margaratifera	*Crucigenia tetrapedia* (green alga)	1.0 × 10^5 cells mL^{-1}	5.5	2.75	2.0 g DTW	Baker & Levinton (2003)¶
Megalonaias nervosa	Green and diatom algae	89.7 mg C L^{-1}	nd	0.0012	40.6 ± 3.1 cm	Spooner & Vaughn (2008)*
Obliquaria reflexa	Green and diatom algae	89.7 mg C L^{-1}	nd	0.004	4.5 ± 0.25 cm	Spooner & Vaughn (2008)*
Ptychobranchus fasciolaris	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.904*	*0.484*	1.870 g	Silverman et al. (1995, 1997)
Pyganadon grandis	*Microcystis* (bluegreen)	1.0 × 10^5 cells mL^{-1}	1.50	0.75	2.0 g DTW	Baker & Levinton (2003)¶
Quadrula pustulosa	Green and diatom algae	89.7 mg C L^{-1}	nd	0.005	5.7 ± 0.39 cm	Spooner & Vaughn (2008)*
Toxolasma texasensis	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.017*	*0.038*	0.454 g	Silverman et al. (1995, 1997)
Truncilla truncata	Green and diatom algae	89.7 mg C L^{-1}	nd	0.0076	4.3 ± 0.19 cm	Spooner & Vaughn (2008)*
Unio crassus	*Chlorella vulgaris*	1.2 × 10^4 cells mL^{-1}	3.3–4.1	*1.2–1.5*	2.676 g	Kryger & Riisgard (1988)
Unio pictorum	*Chlorella vulgaris*	1.2 × 10^4 cells mL^{-1}	3.2–4.6	*1.1–1.5*	3.017 g	Kryger & Riisgard (1988)
Unio tumidus	*Chlorella vulgaris*	1.2 × 10^4 cells mL^{-1}	2.1–2.4	*0.88*	2.424 g	Kryger & Riisgard (1988)
	Seston	8–19 mg L^{-1}	*0.38–1.45*	0.150–0.581	2.5 g	Pusch et al. (2001)
Utterbackia imbecilis	Bacteria (*Escherichia coli*)	1–2 × 10^7 cells mL^{-1}	*0.043*	*0.036*	1.203 g	Silverman et al. (1995, 1997)
Villosa iris	*Neochloris oleoabundans*	5.0 × 10^4 cells mL^{-1}	*0.053*	0.181	0.29 g	Gatenby (2000)
		1.5 × 10^5 cells mL^{-1}	*0.042*	0.143	0.29 g	Gatenby (2000)
		5.0 × 10^5 cells mL^{-1}	*0.016*	0.056	0.29 g, 5 cm	Gatenby (2000)
Villosa lienosa	Bacteria	1–2 × 10^7 cells mL^{-1}	*0.360*	*0.394*	0.913 g	Silverman et al. (1995, 1997)

seston = naturally occurring suspended material, including algae; reported as milligrams per liter, cells of algae per milliliter, or both.
nd = no data.
ca = approximately.
cells mL^{-1} = cells of algae per milliliter.
mg C L^{-1} = milligrams of carbon per liter, in the algae used.
* = Clearance rates of mussels acclimated to 25°C were reported in bar graphs (as L h^{-1} g^{-1} DTW). Clearance rate values were approximated based on unit scales in the graphs. Clearance rates as L h^{-1} were not determined from reported data.
† = Annual CR was derived from pooled seasonal CR data.
‡ = Summer CR, where data were reported seasonally.
§ = Paterson (1984) reported length (cm) but did not report actual DTW, thus the CR in L h^{-1} was not calculated.
¶ = Clearance rates of mussels were reported in bar graphs as L h^{-1} standard animal^{-1} (2 g DTW). Here, their CR were approximated for animals having 1 g DTW.

bivalves with rates reported by Riisgard (1988): *Crassostrea virginica* ($F = 6.79\ W^{0.73}$), *G. demissa* ($F = 6.15\ W^{0.83}$), and *Mercenaria mercenaria* (Linnaeus, 1758) ($F = 1.24\ W^{0.80}$).

In future studies, physiological processing rates should be standardized to a typical standard-sized animal for a given species using allometric relationships and yielding clearance or filtration rates per gram of dry tissue mass (Kreeger et al. 2013). It will be important to consider relative body size of adults for different species because of typical allometric scaling. Smaller (and younger) bivalves have greater weight-specific rates of filtration (and metabolism), and so an adult clam of approximately 1–2 cm should have a higher filtration rate per gram of body weight than an adult of approximately 6–10 cm, whereas the absolute rate per animal would be lower in the smaller clam. Generally, the preferred standard-sized animal is the geometric mean dry tissue weight of a representative population. Not only do weight-adjusted rate data facilitate comparisons but also they are essential for enabling modelers to combine the rate data with population-level biomass and demographic size estimates (as g dry tissue per unit size class and area of bottom) to calculate population-level filtration rates. In quantitative surveys of natural populations for assessing bulk filtration services (or other ecosystem services), it is therefore important to measure the overall biomass of tissues and size class demographics rather than just the numerical abundance of bivalves.

To better understand the ecology of natural systems, it also is important that future studies of bivalve physiological rate functions attempt to mimic natural conditions, especially ambient temperature and food quantity and quality. Natural seston typically includes particles of diverse sizes and qualities, whereas nutritious laboratory diets have ideal sizes and composition. And natural diets are filtered and processed differently from ideal diets of laboratory-cultured algae, which most published studies have used (Table 2). For example, Kreeger (1993) found that laboratory algae diets were cleared from suspension (and digested) better by tidal mussels than natural seston. Similarly, clearance rates (and digestion efficiencies) by freshwater mussels fed on laboratory algae were higher than those fed on seston in natural river water (C. Gatenby & D. Kreeger, unpublished).

Saltwater Bivalve Species

More than 40 species of brackish and saltwater bivalves live within the Chesapeake and Delaware Estuaries (Kreeger & Kraeuter 2010), but only about 10 species are believed to be abundant enough to warrant consideration for their water quality benefits. Clearance rate data were available for a subset of these species, as described in the following paragraphs and summarized in Table 2. Where information was available, the species descriptions also summarize population distribution data and propagation efforts.

*Eastern Oyster (*Crassostrea virginica*)*

Many researchers have studied CR of eastern oysters (e.g., see reviews by Newell & Langdon 1996, Cranford et al. 2011). For the purposes of this review, four commonly cited and published CR for Chesapeake area oysters are referenced in Table 2, and these ranged from about 6–11 L h^{-1} g^{-1} DTW. These were some of the highest rates in the table, explaining why *Crassostrea virginica* are valued for their ecosystem benefits. The maximum CR for *C. virginica* was derived from Cerco and Noel (2007). The units of the published values were converted (from 0.55 m^3 g^{-1} oyster C day^{-1}) to units of liters and hours, and divided by two because 1 g dry weight was assumed to be equivalent to 0.5 g C. This yielded the rate of 11.5 L h^{-1} g^{-1} DTW in Table 2. It is important to note, however, that the higher rates were derived using laboratory-cultured diets, which are likely not reflective of *in situ* conditions.

Oysters are found in Chesapeake Bay at salinities between 7 and 30, and their distribution is mainly constrained by the presence of hard substrates. The same is true in Delaware Bay, where their salinity range was reported to be 13–30 (Kreeger & Kraeuter 2010). Besides hard substrate, current oyster populations in Chesapeake Bay are limited by a number of factors, primarily habitat loss (mainly from sedimentation and low dissolved oxygen), overutilization, variable recruitment and survival of larvae, predation, disease, and harmful algal blooms (White 1989, Kennedy et al. 1996, Eastern Oyster Biological Review Team 2007). In Delaware Bay, where oyster harvests are carefully managed, oyster populations and productivity are mainly constrained by the lack of hard substrate for recruitment, inconsistent recruitment, disease, predation, and possibly also poor food quality.

There are diverse methods and reasons for restoring oyster populations in systems such as Chesapeake Bay, with varying success (Mann & Powell 2007). Oyster propagation has been practiced successfully for nearly 100 y and multiple hatcheries exist in the Chesapeake and Delaware Bay region to supply the demand for seed for restoration projects. The focus of this review is on species other than oysters, and the reader is directed to other literature for a fuller examination of goals, challenges, and opportunities associated with oyster restoration (Kennedy et al. 1996, Coen et al. 2007, Mann & Powell 2007, Shumway 2011).

Ribbed Mussel (Geukensia demissa)

The ribbed mussel (*Geukensia demissa*) grows up to 10 cm long, lives up to 15 y, and has weight-specific CR ranging from 5.1 to 6.8 L h^{-1} g^{-1} DTW. Kuenzler (1961) reported that its mean CR on laboratory diets was 6.8 L h^{-1} g^{-1} (Table 2) but the article does not say if the tissue weight (g) was ash-free or not (presumably it was not ash-free). Kreeger and Newell (2001) measured seasonal CR for *G. demissa* using natural seston diets and contrasted those among particle types, finding average summer CR of 5.1 L h^{-1} g^{-1} DTW for bulk seston. Ribbed mussels therefore have some of the largest filtration rates of all native bivalves in the Chesapeake and Delaware Bay drainages, just after *Crassostrea virginica* (6.4–11.5 L h^{-1} g^{-1}) (Table 2, Riisgard 1988).

Ribbed mussels are omnivorous, feeding on a wide array of particle types (Kreeger et al. 1988, Kreeger & Newell 2001). This species can filter and digest large-celled benthic algae as well, with assimilation efficiencies greater than 90%. These traits are thought to be adaptations for life in detritus-rich salt marshes (Valiela et al. 1997, Kreeger & Newell 2000), where they live primarily in mutualism with wetland vegetation (Bertness 1984). Of special note, *Geukensia demissa* has an exceptional ability to filter (and digest) free bacteria less than 1 μm in size (Wright et al. 1982, Langdon & Newell 1990, Kreeger & Newell

1996). They even appear to possess their own endogenous cellulases for digesting refractory plant matter (Kreeger & Newell 2001). Filtered bacteria can be assimilated with greater than 80% efficiency (Kreeger & Newell 1996, 2001). The exceptional bacteria filtration and digestion capacity of *G. demissa* could mean that they are especially useful for water quality remediation if they can remove and metabolize bacteria that are pathogenic to people or oysters.

The salinity tolerance of *Geukensia demissa* is slightly broader than that of oysters from 5 to >30 (Lent 1969, Puglisi 2008, Nestlerode & Toman 2009) (Table 2). Lent (1969) reported that mussels can tolerate salinities up to 70 and temperatures up to 56°C at least for limited times, thus demonstrating remarkable hardiness. They are uniquely adapted for intertidal conditions, being able to respire aerobically through air-gaping when the tide is out (Lent 1967), tolerating ice freezing in winter (Kreeger, unpublished), and growing faster intertidally than subtidally (Gillmor 1982, Kreeger et al. 1990). Ribbed mussels can be found intertidally on almost any firm surface. Their primary natural habitat is in salt marshes, where they attach to the rhizomes of marsh plants, particularly smooth cordgrass *Spartina alterniflora* (Loisel). They can live subtidally, but their distribution is generally confined to intertidal areas because of (subtidal) predation from blue crabs (Bertness & Grosholz 1985, Lin 1989). Average densities of *G. demissa* in salt marshes vary with proximity to the edge.

Ribbed mussels sometimes attach to subtidal *Crassostrea virginica*, but in the 5 y of the Maryland fall oyster survey (2005 to 2009), this was rare. They were found on *C. virginica* in only 1% of the oyster bars that were sampled (Tarnowski 2010). Ribbed mussels have also been found by the Chesapeake Bay Benthic Monitoring Program (Versar, Inc. 2016) to occur in soft-bottom habitats in fairly deep water but generally at low abundance (20–1,000 m^{-2}) and low occurrence (1%–3%). These results are not surprising because intertidal salt marshes, where *Geukensia demissa* predominantly inhabits, are not routinely surveyed by the Chesapeake Bay Benthic Monitoring Program. Ribbed mussels have been found as far north as the Elk River and in the mainstem of the upper Chesapeake Bay near Pooles and Hart-Miller islands (both oligohaline), and in the mouth of the Patapsco River (low mesohaline). Anecdotal observations in Delaware Bay suggest that *G. demissa* mainly attaches to vascular plants and wood pilings, rarely occurring as a fouling organism on oyster beds. By contrast, oysters are frequently found colonizing shells of larger ribbed mussels in the low intertidal zone along marsh creeks fringing Delaware Bay.

Kreeger et al. (2011) mapped ribbed mussel distributions using GIS layers for salinity and intertidal marsh edge habitat, and these data were verified with field surveys. Along low marsh edges in the Delaware Estuary, *Geukensia demissa* densities average 147 m^{-2} and 187 g DTW m^{-2}; whereas, high marsh flats contain less than 10 mussels m^{-2} and 5.6 g DTW m^{-2} (Kreeger, unpublished). Despite the much greater area of high marsh compared with low marsh edge, 60% of the numerical abundance and 77% of population biomass of *G. demissa* was in the edge habitat. Summed across both habitats, each hectare of salt marsh was estimated to contain 208,000 mussels (>1 cm shell height) and weigh 205 kg dry tissue. These are consistent with findings of Jordan and Valiela (1982), who reported that *G. demissa* are the functional dominant animal of the salt marsh because they tend to outweigh all other animals combined. Their biodeposits act like fertilizer, helping to sustain high primary productivity in marshes with healthy mussel communities (Jordan & Valiela 1982, Bertness 1984). Moody (2017) examined spatial variability in seston filtration across the marsh platform and among different marshes in New Jersey and Rhode Island, finding that mussels filtered between 93 and 278 kg of particulate nitrogen per hectare per year. The variability partly resulted from differences among marshes in edge erosion, presumably because faster eroding marshes held fewer mussels per unit area.

Populations of *Geukensia demissa* are vulnerable to loss of salt marsh from increased rates of sea level rise and other factors (Kreeger et al. 2010, 2011). This is concerning because this species is estimated to filter more water per year than any other bivalve within the Delaware Estuary drainage basin, ~60 billion L h^{-1}, which is approximately six times greater than *Crassostrea virginica* at current population abundances (Kreeger 2005). The decline in populations of *G. demissa* could also have implications for other water quality aspects (e.g., pathogen removal services) because of the exceptional ability of this species to filter and digest bacteria (Kreeger & Newell 1996, 2000).

Prospects for ribbed mussel projects may be greater in wetland-rich areas. Mid-Atlantic estuaries are experiencing a loss of coastal wetlands, especially salt marshes that provide ribbed mussel habitat. In the Delaware Estuary, for example, the rate of recent coastal wetland loss has been assessed at 0.37 hectares per day (PDE 2012). It is therefore prudent to consider ways to conserve ribbed mussels and their ecosystem services by stemming the rate of loss of their preferred marsh habitat. Bio-based living shorelines represent an example of a restoration approach for conserving and enhancing ribbed mussel populations, while furnishing diverse other ecosystem services related to fish habitat and climate resilience (Kreeger et al. 2011).

Ribbed mussels have been spawned in the laboratory (e.g., Castagna & Kreeger, unpublished), but the process is more difficult than for most of the other bivalves considered in this review because ribbed mussels do not reliably respond to typical thermal and nutritional cues (Kennedy, personal communication). Recently, scientists at Rutgers Haskin Shellfish Research Laboratory spawned and devised rearing protocols for *Geukensia demissa* offspring (Bushek, personal communication). More research is warranted, however, to develop efficient protocols for seed production and to optimize tactics for enhancing ribbed mussel habitat.

Because of their high filtration capacity, ability to filter diverse particles, hardiness, and broad intertidal distribution, *Geukensia demissa* represents an ideal target for restoration projects aimed at enhancing water quality.

Hooked Mussel (Ischadium recurvum)

The hooked or bent mussel *Ischadium recurvum* (Rafinesque, 1820) resembles the ribbed mussel *Geukensia demissa*, but is much smaller, growing to only 4–6 cm long. The hooked mussel has also been little studied. Gedan et al. (2014) delivered laboratory-cultured algal diets to *I. recurvum* from the Chesapeake Bay and found maximum CR of 4.3–4.6 L h^{-1} g^{-1} DTW (Table 2).

This species is restricted to hard substrates where it is often found growing on shells of *Crassostrea virginica*. It was found on 75%–92% of the oyster bars sampled in 2004 to 2009 in the

Maryland fall oyster survey (Tarnowski 2010, 2011). Hooked mussels tend to be more abundant in wet years, such as 2004, which saw the lowest salinity of all survey years (Tarnowski 2011). Preferred salinities in Chesapeake Bay appear to be between 8 and 16 (Table 2). Kraeuter and Kreeger (2010) similarly reported that hooked mussels prefer 8–15 salinity and are ephemerally abundant in the Delaware Estuary.

Lipcius and Burke (2006) documented the density and biomass of *Ischadium recurvum* where they grew with *Crassostrea virginica* on artificial reefs in the York River, estimating maximum mussel density as about 2,750 mussels m^{-2} of reef and mean mussel biomass as 670 g m^{-2} of river bottom in five stacked layers of concrete reef (or 134 g m^{-2} of reef surface). Bahr and Lanier (1981) reported *I. recurvum* density and biomass on intertidal oyster reefs in Georgia, and their mean biomass was 24 g m^{-2}. In Lake Pontchartrain, LA, *I. recurvum* grow on dead *Rangia cuneata* shells on soft bottom, forming small spherical "reefs" about 30 cm in diameter (Poirrier et al. 2009). The maximum lake-wide density of *I. recurvum* averaged 2,284 mussels m^{-2} when salinity in the lake was high (up to 10) during a drought in 2000 to 2001 (Poirrier et al. 2009), very similar to the maximum density reported by Lipcius and Burke (2006) on artificial reefs.

Reported distribution and estimated abundance of *Ischadium recurvum* in the Chesapeake Bay, from the Maryland oyster survey, showed that highest estimated abundances in most years were in two areas—the Chester River near the Corsica River and in the Choptank River near Cambridge (Versar, Inc. 2016). Being a hard-bottom species, *I. recurvum* has rarely been detected in the Chesapeake Bay soft-bottom benthic survey, and a shortage of hard substrate appears to be one of the main limiting factors for this species. The application of hard substrate therefore is a viable option to promote this saltwater species in restoration projects.

Spawning in the laboratory has been performed, raising the larvae to settlement (Chanley 1970). Spawning also may be triggered by sudden drops in salinity (Kennedy 2011a). If *Ischadium recurvum* were to be grown for their biofiltration benefits, it is plausible that they might attach to suspended ropes just as blue mussels (*Mytilus edulis*) that are grown in rope aquaculture (Lesser et al. 1992). Kennedy (2011b) measured the byssal thread strength of a 20-mm–sized *I. recurvum* as 8.7 N, which is similar to values for *M. edulis* (4.9 to 16.7 N). By contrast, recent tests of *Geukensia demissa* in the Bronx River found that their byssal threads could not support their weight when cultured on ropes (Rose, personal communication).

Baltic Macoma (Macoma balthica)

Two published CR were found for *Macoma balthica*, ranging 0.4–1.3 L h^{-1} g^{-1} AFDW (Table 2). This species can also deposit feed using an extendable siphon, but they are thought to use suspension feeding when adequate phytoplankton are available, as is usually the case in the Chesapeake Bay (Gerritsen et al. 1994, Lin & Hines 1994).

The known distribution of *Macoma balthica* is likely governed by physical and chemical factors. It appears to be fairly tolerant of low concentrations of dissolved oxygen (<2 mg L^{-1}) and they can extend their incurrent siphon up in the water column in search of more oxygenated water (Seitz et al. 2003). In the Delaware Estuary, *M. balthica* is considered to be locally abundant at salinities between 10 and 25 (Kreauter & Kreeger 2010). In Chesapeake Bay benthic surveys, *M. balthica* percent occurrence was higher than that of any other species found, typically ranging 25%–45% of samples. The occurrence appears to vary among years, being as high as 75% in 1989 (Versar, Inc. 2016).

This species is an important winter food of diving ducks and other waterfowl (Perry et al. 2007). They are also important food for juvenile blue crabs that migrate from seagrass beds near the mouths of rivers quite a distance upriver to where Baltic macoma can be abundant (Seitz et al. 2005). Considering their abundance and dominance in many benthic communities, *Macoma balthica* should be monitored and sustained for their filtration and ecosystem services. Spawning in the laboratory has been performed (Caddy 1967), but no attempts to raise the resulting larvae are known.

Northern Quahog (Mercenaria mercenaria)

Three published CR were found for *Mercenaria mercenaria* (0.5–1.52 L h^{-1} g^{-1}; Table 2), and these were generally lower than the reported rates for *Crassostrea virginica*. Riisgard (1988) suggested that quahogs might feed at high rates when tested in natural substrates. Newell and Koch (2004), however, reported lower rates by quahogs in sediment than Riisgard (1988) found. Echevarria et al. (2012) reported CR for quahogs not in sediment to be slightly higher, but still low compared with oysters (Table 2). Caution is warranted in comparing rates among studies that used different diets and protocols; however, these generally lower weight-specific CR for *M. mercenaria* suggest that this species may not be as effective as *C. virginica* for improving water quality, on an individual basis. Northern quahogs might be helpful in promoting water quality in different niche habitats not occupied by other species.

Research has shown that large numbers of northern quahogs grown in a small creek (Cherrystone Creek on the Virginia Eastern Shore) can improve water clarity, but the macroalgae that grew on aquaculture nets could have helped to keep predators away from the quahogs, skewing results from natural conditions and possibly leading to lower dissolved oxygen after the algae died (Goldman 2007b). Mesocosm studies using natural seawater from Peconic Bay, Long Island, have shown that *Mercenaria Mercenaria* can exert top-down control on phytoplankton biomass and causes shifts in algal species composition (Cerrato et al. 2004). Culture methods for northern quahogs, sometimes called "hard clams," are well known (Castagna & Kraeuter 1981), and seed of various sizes is commercially available, for example, from BayFarm in New Jersey (BayFarm, Inc. 2013).

Populations of *Mercenaria mercenaria* are still considered to be locally common in areas of Chesapeake and Delaware Bay, where salinities are between 15 and 30 and where suitable soft substrate is available. Populations are believed to have decreased dramatically compared with historic conditions, such as in the Delaware Bay, where a once-vibrant northern quahog fishery ceased to exist in 1974 (Dove & Nyman 1995).

Softshell (Mya arenaria)

Riisgard and Seerup (2004) reported a comparatively high CR of 4.8 L h^{-1} g^{-1} AFDW for *Mya arenaria*, but those rates were for laboratory-cultured diets, and might not reflect conditions *in situ*. Bacon et al. (1998) measured softshell CR using natural seston diets, finding lower rates with a maximum of 3.5 L h^{-1} g^{-1} DTW (Table 2).

Populations of this species might be in decline, and more study is needed to examine their future restoration potential. For example, benthic surveys in Chesapeake Bay reported a sharp drop in percent occurrence from near 20% in 1989 to 0% in 1995, remaining very low after that (Versar, Inc. 2016). Softshells are similarly scarce in Delaware Estuary, although Kraeuter and Kreeger (2010) noted that the deep burrowing behavior of this species prevents it from being sampled by standard grabs and dredge survey gear. For a discussion of limiting factors on softshells, primarily predation by crabs and disease, see Abraham and Dillon (1986) and Dungan et al. (2002). This is a commercial species, and seed of various sizes is available from hatcheries.

Dark Falsemussel (Mytilopsis leucophaeata)

This species is fairly small (length to almost 3 cm) and it is an uncommon inhabitant of low salinity oyster bars (Tarnowski 2011). They can also occur on soft-bottom habitats, as shown by benthic surveys by the CBP. They are uncommon in those surveys as well, having been found in only 1%–13% (mean 3%) of samples by year from 1989 to 2008. The measured salinity ranges for this species (Table 2) are from CBP benthic surveys.

The maximum CR of *Mytilopsis leucophaeata* (at the optimum temperature, 20°C–28°C) reported by Rajagopal et al. (2005a) was 0.055 L ind^{-1} h^{-1} (per mussel) for the largest size class they tested (20 mm long). Their tissue weights were not given, and none could be found for a mussel of that size to convert this rate to a weight basis. Thus, a published length–AFDW relationship for *D. polymorpha* (Reeders & Bij de Vaate 1990) was applied to *M. leucophaeata*. Using that equation, the AFDW of a 20-mm *M. leucophaeata* would be 0.028 g, yielding a CR based on that weight to 1.96 L h^{-1} g^{-1} AFDW (Table 2), very close to the rate for 22 mm zebra mussels reported by Reeders and Bij de Vaate (1990). A similar approach was used to calculate the other CR in the table, from Rajagopal et al. (2003), 1.66 L h^{-1} g^{-1} AFDW, and from Rajagopal et al. (2005b), 2.37 L h^{-1} g^{-1} AFDW. The last and highest rate was for detached mussels, which filtered 42% more than the attached mussels in the same study.

Spawning in the laboratory has been performed, followed by raising the resulting larvae to settlement and beyond, for up to 49 days for one brood (Kennedy 2011a, 2011b). Most larvae had undergone metamorphosis by 9 days.

Populations of *Mytilopsis leucophaeata* appear to be so small and scattered (except during irruptions) that Kennedy (2011a, 2011b) wondered how they persist because fertilization of their gametes seems unlikely. Their tendency to have large and small irruptions (see in the following paragraph) suggests that there may be unknown populations of this species that can produce large numbers of gametes under the right conditions. Where these populations might live, and why they have not been sampled in various surveys, is not known. This sparse and patchy distribution was not mentioned in a review of this species where it was introduced in Europe (Verween et al. 2010) or the Hudson River (Walton 1996), suggesting that the distribution of introduced populations may be more uniform than where this species is native.

An irruption of *Mytilopsis leucophaeata* occurred in low mesohaline regions of the Chesapeake Bay (especially in the Patapsco and Magothy rivers) in 2003 to 2005 (Carey & Hornor 2005, Goldman 2007a, Bergstrom et al. 2009, Kennedy 2011b). The irruption started during two wet years (2003 to 2004) that followed three dry years and one normal year (USGS 2012), with spawning triggered by a sudden drop in salinity (Kennedy 2011a, 2011b). This normally uncommon inhabitant of low salinity oyster bars became abundant in these and some nearby rivers in the spring and summer of 2004, growing in thick layers on pilings, rocks, ropes, boats, and other hard substrates. Both the frequency of occurrence and estimated abundance of *M. leucophaeata* on oyster bars were slightly higher in 2004 than in 2005 to 2009 (data from oyster surveys in Tarnowski 2011). The fact that the darkfalse mussels were only slightly more common on *Crassostrea virginica* in 2004 suggests that during irruptions, most of the population increase occurs on substrates other than *C. virginica*. In that sense, they resemble an invasive species during an irruption, growing primarily on novel surfaces.

Distribution data for *Mytilopsis leucophaeata* in the Chesapeake Bay are available from the Maryland oyster survey (hard bottom) and from the Chesapeake Bay benthic survey (soft bottom, Versar, Inc. 2016). These surveys indicate that the range of this species is generally confined to upper areas of the Chesapeake Bay. The species has not been reported from the Delaware Estuary. Peak abundance typically has been found in wet years (1996, 2003, and 2004); however, the highest percent occurrence was in a dry year, 1995. The *M. leucophaeata* found in the benthic survey on soft bottom may have been attached to other, larger bivalves, such as *Rangia* shells (Poirrier et al. 2009) or other hard objects. Given its limited distribution and sporadic irruptions, this species is not considered a promising candidate for restoration projects.

Blue Mussel (Mytilus edulis)

Blue mussels usually live attached to hard surfaces in rocky intertidal areas or attached to piers, although the species can also live in deeper ocean waters to 100 m or more (Newell 1989). They occur on the east coast of North America in shallow water as far south as Cape Hatteras, NC; they are prevented from living farther south (in shallow water) by an upper temperature limit of about 27°C. They have been found, however, near Charleston, SC, in deeper, cooler estuaries, tolerating salinity as low as the mesohaline range (5–18) (Newell 1989). In the Chesapeake Bay, they are limited to the cooler, saltier waters near the mouth (Lippson & Lippson 1984). Larvae that settle farther up the bay may grow for a while, but usually die over the summer (Lippson & Lippson 1984). Thus, high summer temperatures and low salinity limit their distribution in Chesapeake Bay. They have been grown in coastal waters in Sweden for nitrogen removal, with mixed results. Similarly, the range of blue mussels has historically been constrained by the lack of suitable hard surfaces at 20–35 salinity in the Delaware Bay (Kreeger & Kraeuter 2010). More recently, warming temperatures are believed to be driving the decline of blue mussel beds in areas of where they once thrived.

As a result of their limited occurrence and dwindling prospects in the mid-Atlantic, they are not considered as a potential restoration target for the region, and hence are not listed in Table 2 or discussed further.

Atlantic Rangia (Rangia cuneata)

Details of the biology and ecology of *Rangia cuneata* (Sowerby, 1832) have been reported by LaSalle and de la Cruz (1982). Wong et al. (2010) reported CR of 2.06 L h^{-1} g^{-1} DTW (Table 2). Published CR from Cerco and Noel (2010) are not included because they were not species-specific and were derived from a generic bivalve equation in Gerritsen et al. (1994). This species is probably nonnative, but it is not generally considered invasive in Chesapeake and Delaware Bays where it has become naturalized. Little is known about its limiting factors in the mid-Atlantic. Regarding propagation potential, *R. cuneata* has been spawned in the laboratory and reared to settlement (Sundberg & Kennedy 1992, 1993).

Atlantic rangia can be very abundant in tidal fresh and oligohaline regions of both the Chesapeake Bay and Delaware Estuary. In the Chesapeake Bay benthic survey (Versar, Inc. 2016), *Rangia cuneata* had the second highest percent occurrence after Baltic macoma *Macoma balthica* and both the density and percent occurrence of Atlantic rangia have varied little by year. Poirrier et al. (2009) reported the maximum density of this species in Lake Ponchartrain, LA (before Hurricane Katrina), as 350 rangia m^{-2} for animals 21 mm or larger, with a maximum biomass of 20–25 g m^{-2}. In the Delaware Estuary, *R. cuneata* is typically found in greatest abundance in freshwater tidal and brackish zones having salinities between 0 and 10 (Kreeger & Kraeuter 2010).

Stout Tagelus (Tagelus plebeius)

No published CR were found for *Tagelus plebeius* (Lightfoot, 1786). One study from South America (Arruda et al. 2003) confirmed that they are suspension feeders. They also reported that this could be the most abundant species in the study area of Brazil. Spawning in the laboratory has been carried out, raising the larvae to settlement (Chanley & Castagna 1971).

Stout tagelus have been found in the Chesapeake Bay benthic survey (Versar, Inc. 2016) at densities of more than 50 m^{-2} up until 1993, but both the abundance and percent occurrence have decreased to incidental status, especially from 1998 onward. Kreeger & Kraeuter (2010) suggested the preferred salinity range is 13–30 for *T. plebeius*, and considered them to be uncommon in the Delaware Estuary.

Freshwater Bivalve Species

There are about 300 species of freshwater mussels in North America, which represents the greatest diversity in the world. More than 70% of these species are in decline nationwide, and they are now considered the most imperiled animals on the continent (Williams et al. 1993, FMCS 2016). Approximately 28 species of native freshwater mussels occur in the Chesapeake watershed, and 13 of these also occur in the Delaware drainage (Bogan & Ashton 2016, PDE 2015, Table 5), and according to State Wildlife Action Plans, most of these are in decline and their distribution reduced.

Nonnative freshwater bivalves that can be abundant and for which clearance data were located are included in the species summaries in the following paragraphs, for review purposes only, as they are not recommended for restoration. These are *Corbicula* sp. and *Dreissena* sp.

Asian Clam (Corbicula sp.)

Asian clams first became abundant in the Potomac River in 1980 and have since spread to many tidal and nontidal tributaries (MBSS 2011, Versar, Inc. 2011). In the Delaware River, *Corbicula fluminae* (Müller, 1774) was first found in the early 1970s near Trenton, NJ, and its rapid spread was documented by Crumb (1977).

The mean CR for *Corbicula* sp. fed an artificial diet was reported to be 2.9 L h^{-1} g^{-1} AFDW (Table 2, Kramer & Hübner 2000). More recently, Cheng (2015) summarized seasonal CR for *Corbicula* fed on natural seston in Delaware River streams, finding these typically fell between 0.8 and 1.2 L h^{-1} g^{-1}, except in one fall experiment where the rates were very low (0.1 L h^{-1} g^{-1}).

According to Versar, Inc. (2016) data for the Chesapeake Bay soft-bottom survey, the percent occurrence of *Corbicula* sp. has been generally low, except in 2004 to 2006 when it rose to near 10%. In the neighboring Delaware Estuary, Asian clams comprised greater than 75% of the benthic biomass between Trenton, NJ, and the Chesapeake and Delaware Canal in DE in a survey during 1992 and 1993 (Environmental Consulting Services, Inc. 1993).

Asian clams are an introduced species not targeted for enhancement; however, it is worth acknowledging that the species is prolific and apparently naturalized in many areas where it does contribute to water quality via seston filtration. For example, some authors (Cohen et al. 1984, Phelps 1994) give *Corbicula* sp. credit for facilitating the resurgence of submerged aquatic vegetation (SAV) in the Potomac River in the mid-1980s by increasing water clarity. Its contribution to water filtration varies with clam population size and seston concentration. For example, Cheng (2015) estimated that Asian clams in the Cooper River, NJ, filtered 5.4 metric tons of total suspended solids (TSS) per year per kilometer, whereas in the similar sized Red Clay Creek, DE, Asian clams filtered only 0.4 tons TSS y^{-1} km^{-1}. Asian clams do not produce byssal threads, and therefore they have not been as problematic for biofouling compared with zebra and quagga mussels (see in the following paragraph). Ecological problems associated with their introduction are largely undocumented.

Zebra and Quagga Mussel (Dreissena polymorpha *and* D. rostriformis bugensis)

McLaughlan and Aldridge (2013) offer a thorough review of the potential for zebra mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensis* Andrusov, 1897) to improve water quality in reservoirs. They also cautioned about risks associated with encouraging an invasive species, even within sites where it has already established. For example, zebra mussels will colonize any hard surface, including native unionid mussels and water control structures where water flows are enhanced. At a 90% efficiency rate, zebra mussels are much more efficient at filtration of small particles than are unionids and Asian clams (Cotner et al. 1995, Silverman et al. 1997).

These species are only included here for comparative purposes of their filtration effects. Their continued expansion represents a serious threat to ecological integrity within the Chesapeake and Delaware drainages, including the viability of native bivalve species. As such, all possible efforts should be taken to neutralize the spread of zebra and quagga mussels.

Several studies of CR exist for zebra mussels, reporting a few of the highest published CR for bivalves. Fanslow et al. (1995) reported the highest weight-specific filtration rate (16.2 L h^{-1} g^{-1}

of DTW) for *Dreissena polymorpha* fed natural seston; the lowest was 1.43 L h^{-1} g^{-1} of DTW from a study by Reeders and Bij de Vaate (1990) (Table 2). Baker and Levinton (2003) estimated CR for a standard 15-mg DTW zebra mussel fed cultured unicellular cyanobacteria, *Microcycstis* sp. at 125 mL·h^{-1}. This rate was scaled up to a standard 1-g DTW bivalve for comparison with other bivalves, bringing this to 8.3 L h^{-1} g^{-1} of DTW (Table 2).

Zebra mussels have had profound effects on the Great Lakes and the Hudson River since they invaded. Shifts in ecosystem dynamics with changes in food web structure and changes in productivity at higher trophic levels have been observed (Baker & Levinton 1999, Madenjian et al. 2005, 2006, Nalepa et al. 2000, 2005, 2006). For example, zebra mussels significantly reduced the biomass of phytoplankton, which increased transparency by 100% in Lake Erie and in Saginaw Bay, Lake Huron (Fahnenstiel et al. 1995, Klerks et al. 1996). The invasion into the Great Lakes also led to significant changes in diversity, distribution, and abundance of both native mussels (Nalepa et al. 1996) and fish species. Indeed, drastic declines in lake trout, alewife, and whitefish populations were attributed to declines in food prey items, due to competition by zebra mussels for planktonic food items (MacIsaac 1996, Madenjian et al. 2005, 2006, Nalepa et al. 2000, 2005, 2006). Changes in habitat occurred over time as a result of changes in visibility. Phytoplankton biomass also declined 85%, following invasion in the Hudson River (Caraco et al. 1997).

Despite control measures, zebra mussels have been gradually spreading down the Susquehanna River from New York, with a few individuals found in Maryland above Conowingo Dam in 2008 and below the dam in 2010 (Chesapeake Bay Journal 2010). In 2011, one zebra mussel was found in the tidal Sassafras River (Chesapeake Bay Journal 2011). Twenty individuals were found attached to the anchors of three navigational buoys located on the Susquehanna Flats in 2012 (T. Wheeler, unpublished). In the Delaware River Basin, zebra mussels have so far been confined to a few locations such as quarries, where divers accidentally introduced them.

No studies were found for clearance or filtration rates by *Dreissena rostriformis bugensis*. As noted for *Rangia cuneata and Corbicula* sp., these Dreissenid mussels are nonnative and highly invasive in U.S. waters, so neither would be used in restoration projects.

Eastern Elliptio **(Elliptio complanata)**

The eastern elliptio is considered to be one of the most common freshwater mussel species of the Atlantic slope (Johnson 1970, Strayer & Jirka 1997). For example, detailed quantitative surveys of four reference beds of freshwater mussels on seven hectares of the tidal Delaware River indicated that five species of mussels native to the Delaware River comprised greater than 99% of the population biomass (Kreeger et al. 2013). The largest and most abundant mussels were *Elliptio complanata*, followed by the alewife floater *Utterbackiana implicata* (Say, 1829). Recent information indicates that CR for *E. complanata* are significantly higher than those published earlier (Paterson 1984, Leff et al. 1990). Summer CR of *E. complanata* have been measured to be 2.6–3.1 L h^{-1} individual^{-1} (Table 3, data from C. Gatenby & D. Kreeger, unpublished), slightly higher for mussels fed laboratory diets than for mussels fed natural seston diets. Summer CR of 3.4 L h^{-1} g^{-1} DTW have also been measured *in situ* for *E. complanata*–fed natural seston from the Brandywine River, PA (C. Gatenby & D. Kreeger, unpublished). This species, *E. complanata*, has been estimated to presently filter more than 9.7 billion liters of water per hour across the basin, on par with the potential volume processed by *Crassostrea virginica* still living in Delaware Bay (Kreeger 2005). Like many other CR studies reviewed here, these estimates for summer CR should not be assumed to be representative throughout the year.

Despite their "common" status, the population size and distribution of the eastern elliptio appears to be dwindling like all freshwater mussel species (PDE 2012, Kreeger & Cheng 2017). Their status is especially grim in systems such as the Brandywine and Susquehanna Rivers where multiple dams block migrations of critical fish hosts such as eels.

The value of these lost tributary mussels is difficult to assess because reference beds for study are now missing from the landscape. In one study of the lower Brandywine River in southeast PA, however, a survey documented that approximately 500,000 *Elliptio complanata* remain in six river miles, whereas historical surveys reported seven species (Ortmann 1919). Nevertheless, this single population was estimated to filter approximately 26 metric tons of dry total suspended solids per year (Kreeger 2005). Indeed, *E. complanata*, are a top restoration target for tidal fresh areas of the Delaware Estuary because they can reach greater than 8 cm in length and achieve densities greater than 25 m^{-2}.

Viable offspring of *Elliptio complanata* have been produced by several research teams and pilot hatchery programs in the Delaware Estuary and Chesapeake Bay, using American eels, *Anguilla rostrata* (Lesueur), brook trout, *Salvelinus fontinalis* (Mitchill), lake trout *Salvelinus namaycush* (Walbaum in Artedi, 1792), mottled sculpin *Cottus bairdi* (Girard), and slimy sculpin *Cottus cognatus* (Richardson) as fish hosts (Lellis et al. 2013, Mair, personal communication, D. Kreeger, unpublished). These results demonstrate promise for restoring this species, however, further research is needed to improve production of *E. complanata* because it is not as easy to culture as other common species (Mair, personal communication).

Restoration of *Elliptio complanata* and other freshwater mussels is possible using various tactics, such as translocations, propagation, and reseeding of historic habitat along with improvements to habitats (e.g., dam removals and substrate stabilization) to sustain the species. Candidate sites can be screened for restoration readiness using sentinel transplants of adults or hatchery seed. Another approach to restoring mussels such as *E. complanata* is to restore their preferred fish host, the American eel (Lellis et al. 2013, Galbraith et al. 2018). The Pennsylvania Fish and Boat Commission conducted an extensive eel stocking program into the 1980s, and many of the streams that received eels support the "best" or "youngest" populations of *E. complanata*. The U.S. Fish and Wildlife Service Maryland Fish and Wildlife Conservation Office is presently working with partners on American eel restoration in the Susquehanna River basin, partly to help restore *E. complanata* (Devers, personal communication).

Alewife Floater **(Utterbackiana implicata)**

The alewife floater is one of the more common freshwater mussel species in many areas of the Atlantic slope. Quantitative surveys of four reference beds of freshwater mussels on 7 ha of tidal Delaware River indicated that *Utterbackiana implicata* was the second most abundant species (after *Elliptio complanata*) (Kreeger et al. 2013). Alewife floaters are also one of the largest sized mussels on the Atlantic slope, often exceeding *E. complanata* in shell length and DTW. The population biomass (and associated ecosystem services) of alewife floaters can therefore exceed that of eastern elliptio despite not being as numerically abundant (Kreeger et al. 2013).

Alewife floaters represent excellent restoration targets because they are one of the easier species to propagate in a hatchery (Mair, personal communication) and they can grow very quickly in suitable conditions. For example, juvenile *Utterbackiana implicata* achieved shell lengths of up to 6 cm in less than 9 mo in recent rearing trials in the Delaware Estuary (D. Kreeger, unpublished).

Tables 2 and 3 do not list *Utterbackiana implicata* because no published data exist for the CR of this species. In hatchery-settings, they have high feeding demands, suggesting high filtration potential *in situ* (Mair, personal communication). Comparative CR data collected during 2016 to 2017 for *U. implicata* and several other mussel species of the Delaware River Basin, suggest that *U. implicata* CR are on par with *Elliptio complanata* during spring, summer, and fall (D. Kreeger, unpublished).

Other Freshwater Mussels

Published information on CR of other mid-Atlantic freshwater mussels besides *Elliptio complanata* is scarce (Table 2). Clearance rates for species found in Europe and other areas of the United States are more prevalent, and these are summarized in Table 3 to represent the typical ranges of rates for this taxonomic group of bivalves. Results from 42 measurements from 12 reports, spanning diverse species and diet types, indicate that measured CR for mussels were extremely variable, from 0.001 to 3.4 L h^{-1} g^{-1} DTW. This variability may have resulted from vastly different body sizes (e.g., see Fig. 2), seasons, diets, and experimental methods rather than from intrinsic differences in filtration capacity by the different species. Because the sizes of experimental mussels in Table 3 varied from 0.6 to 5.3 g DTW and 4–40 cm shell length, reported rates varied considerably if they were not derived using allometric standardization from a range of sizes of experimental animals.

Similarly, bivalve molluscs are poikilothermic and therefore have physiological rates that vary with temperature. Most published studies of bivalve CR (e.g., in Tables 2 and 3) were performed during summer or under standard laboratory temperatures when seasonal rates will be near maximum. Clearance rates in temperate climates such as the mid-Atlantic will be almost nil in winter when temperatures are less than 5°C. For example, a comparison of seasonal CR for three western mussel species showed that rates dropped quickly when water temperatures decreased below 5°C–8°C, and spring and fall CR were typically about 75%–90% of summer rates (D. Kreeger, unpublished).

Clearance rates determined with optimal laboratory diets also are often greater than those with seston. This likely explains the generally higher rates in Tables 2 and 3 for bivalves-fed laboratory diets compared with seston, such as in the case of the *Margaratifera margaritifera* (Hessling, 1859) fed on cultured green algae, yielding a high CR of 2.75 L h^{-1} g^{-1} (Table 3). This is not always the case, however. The lowest CR for freshwater mussels in Table 3 (range 0.0012–0.0076 L h^{-1} g^{-1}) were derived from animals that were fed very high concentrations of cultured algae, which could have supersaturated their gills and led to cessation of feeding. Clearance rates for *Utterbackia imbecillis* (Say, 1829) (0.036 L h^{-1} g^{-1}, Silverman et al. 1997) also appear unusually low for a species that is fast growing and has large gills, but this was likely because they were fed a laboratory-cultured diet of only *Escherichia coli* bacteria, as the investigators were specifically interested in whether freshwater mussels could filter bacteria.

Comparison of CR between Saltwater and Freshwater Bivalves

Freshwater mussels generally grow more slowly and live longer (30–100 y) than their saltwater counterparts (up to 10–15 y) within the mid-Atlantic region. Slower growth rates could be related to poorer food conditions within nontidal river and stream systems compared with eutrophic coastal estuaries, but this has not been well explored. The differences in growth rates may be responsible for the perception that freshwater mussels filter less water than saltwater bivalves such as oysters and marine mussels. Results from Tables 2 and 3 appear to dispel this belief although the rates were highly variable.

Few studies have made interspecific comparisons of natural seston filtration, normalized for the allometric effects of body size and seasonality. To examine differences in CR between freshwater and saltwater bivalves, one of the authors (Kreeger) reviewed data from more than 45 past CR experiments that followed the same methodology, conducted over 30 y with colleagues for a mix of freshwater and saltwater species. This analysis includes CR data for several species of freshwater mussels representing the Atlantic, MS, and Pacific slopes of the United States: *Actinonaias ligamentina* (Lamarck, 1819), *Anodonta californiensis* (Lea, 1852), *Elliptio complanata*, *Elliptio dilatata* (Rafinesque, 1820), *Gonidea angulata* (Lea, 1852), *Lasmigona costata* (Rafinesque, 1820), and *Margatifera falcata* (Gould, 1850). Two saltwater species were represented by the eastern oyster *Crassostrea virginica* and the ribbed mussel *Geukensia demissa*. Data from Cheng (2015) for the introduced species, *Corbicula fluminae*, also were included because they followed the same protocol.

These studies all used a common approach whereby experimental groups of bivalves had diverse body sizes that represented the natural population, were subjected to simulated natural conditions, were fed only natural seston diets, and experiments were conducted at ambient seasonal temperatures throughout the year to discern seasonal variation in core physiological rate functions. Because seasonal temperatures vary considerably among years and locations, CR from different experiments and species were stratified by seasonal temperatures of either greater than 20°C (summer) or 15°C–20°C (spring or fall).

Clearance rates for freshwater and saltwater species of bivalves were not distinctly different (Figs. 3 and 4). At temperatures greater than 20°C (Fig. 3, representing summer), average CR per species ranged from 0.4 to 1.6 L h^{-1} g^{-1} DTW. Rates were not significantly different among species because of high variability of rates among individuals per species, which is typical for physiology studies with bivalves. At temperatures between 15°C and 20°C (Fig. 4, representing late spring and early fall), average CR per species ranged from 0.3 to 1.6 L h^{-1} g^{-1} DTW. Average CR for six bivalve species at temperatures less than 15°C followed a similar pattern, but averaging less than 1 L h^{-1} g^{-1} for all species.

If confirmed by others, these results suggest two findings that are relevant for guiding potential restoration of bivalves for water quality enhancement in the mid-Atlantic region. First, freshwater mussels are not inferior to saltwater bivalves in regard to their organism-level CR. Indeed, there are some indications that they might even be more effective than their marine counterparts, but there are other possible explanations for the results in Figures 3 and 4. For example, many streams are less food rich than coastal bays, and higher CR may have occurred if the animals were striving to compensate. Further studies are needed.

The second implication of these results is that CR for saltwater species such as oysters and ribbed mussels are lower than reported previously in the literature. This discrepancy might be partly explained by the seasonal timing and diet choices of past studies. For example, CR in Figures 3 and 4 for ribbed mussels were derived under simulated natural conditions (e.g., intertidal feeding periodicity), using natural seston from the Delaware Bay (e.g., high turbidity and low quality), and using a wide spectrum of body sizes for allometric scaling of rates to DTW. Weight-specific CR would have likely been higher if only small mussels and richer diets were used. Further studies are needed, but future studies of ecosystem services should clearly be based on natural diets, natural size class distributions, and ambient seasonal temperatures.

Another unknown is whether the population-level effects of freshwater mussels are similar to those of saltwater bivalves. For example, does grazing pressure by freshwater mussel species affect plankton and periphyton communities, as has been documented for marine species? Marine bivalves exhibit great plasticity in their postfiltration handling of captured material (Ward 1996, Ward et al. 1998a, 1998b, Milke & Ward 2003, Ward & Shumway 2004, Rosa et al. 2013). For example, the ribbed mussel can adjust gill spacing to capture very small bacteria (Wright et al. 1982). Limited data suggest that freshwater mussels also can adjust the spacing of their gill filaments to capture different types and sizes of particles to best match their nutritional demands, potentially altering the trophic cascade within planktonic food chains (Baker & Levinton 2003, D. Kreeger, unpublished). The retention efficiency and fate of the captured seston, therefore, likely vary among species even if CR are similar. This could lead to important interspecific differences in the degree to which filtered matter gets remineralized as dissolved nutrients, or deposited into the sediment.

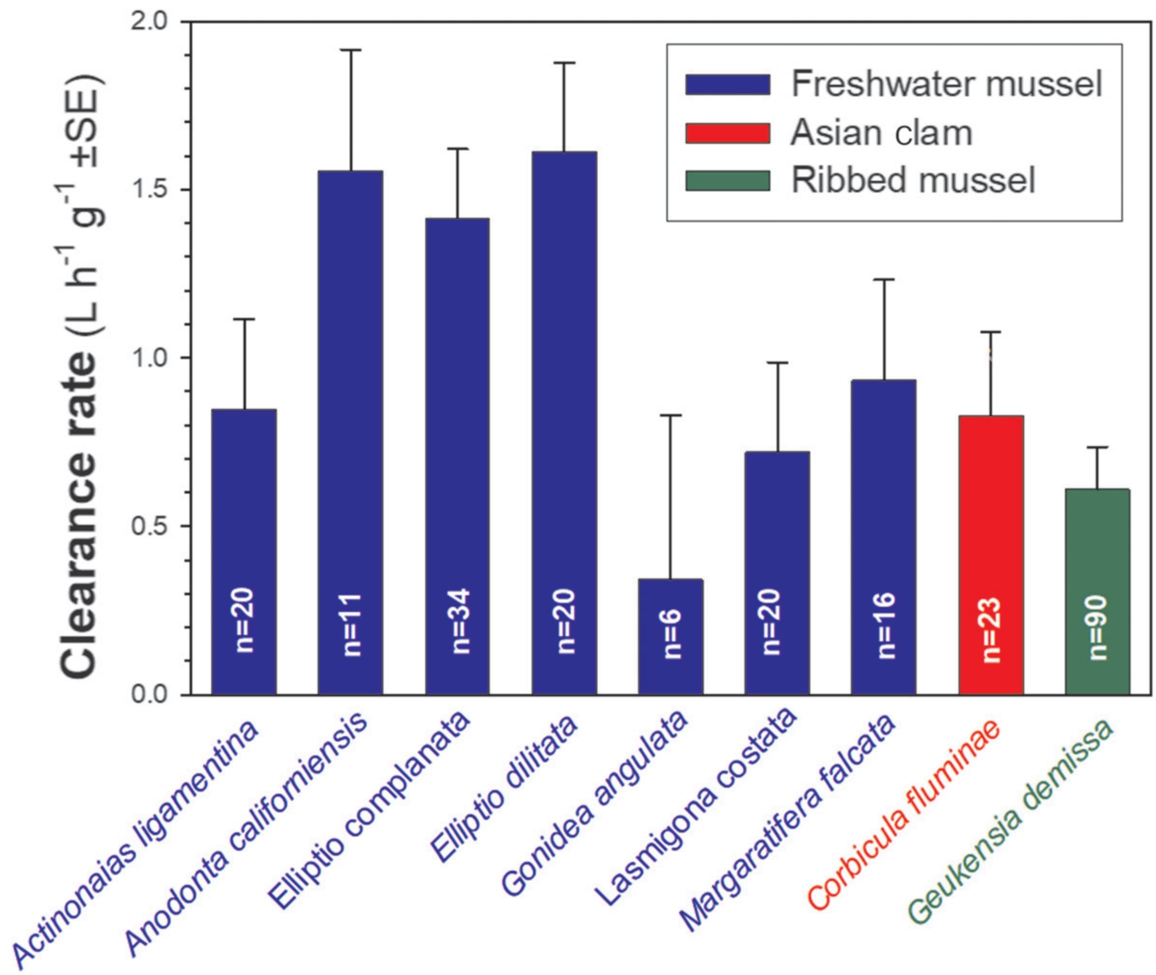

Figure 3. Allometric scaled CR for seven species of freshwater mussels (blue), Asian clams (red), and ribbed mussels (green) assessed using natural seston diets and simulated natural conditions during diverse experiments (1986 to 2014) having ambient temperatures greater than 20°C (Kreeger, unpublished).

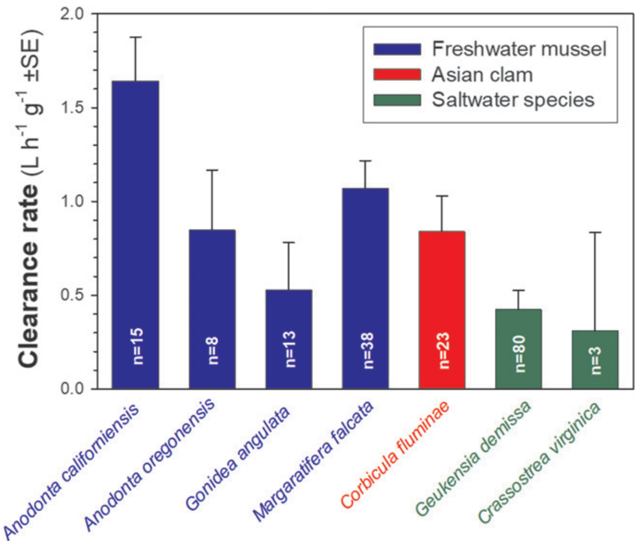

Figure 4. Allometric scaled CR for four species of freshwater mussels (blue), Asian clams (red), and two species of saltwater bivalves (green) assessed using natural seston diets and simulated natural conditions during diverse experiments (1984 to 2014) having ambient temperatures 15°C–20°C (Kreeger, unpublished).

Filtration Effects from Tidal Saltwater Bivalve Species

The Chesapeake Bay is a textbook example of the decline of an estuary from human impacts that resulted in eutrophication. Eutrophication results when excess inputs of nutrients lead to phytoplankton blooms that have two harmful impacts: (1) they cloud the water and contribute to a decline in submerged macrophytes such as wild celery and eelgrass, and (2) they cause low dissolved oxygen after they die and decompose, especially in deeper water in the summer. Insufficient dissolved oxygen can kill fish, shellfish, and other aquatic life. In addition, increased sediment runoff resulting from human actions such as urbanization and some agriculture practices also clouds the water.

The traditional management method to reverse these impacts is ''bottom-up'' rather than ''top-down'' control (Dyer & Letourneau 2003). Bottom-up control involves reducing nutrient and sediment inputs by a variety of methods, such as upgrades to wastewater treatment plants, reducing the use of manure and other fertilizers, controlling sediment runoff using silt fences, and planting cover crops. Clearly, such bottom-up controls are vital for reversing eutrophication; however, top-down controls may also be needed. One example of a top-down control using natural ecosystem services is to augment or restore filter-feeding organisms to control phytoplankton and excess sediment in estuaries. This concept has been proposed or explored for a number of years.

For example, Kuenzler (1961) studied phosphorus budgets of ribbed mussels *Geukensia demissa* in a Georgia salt marsh. He measured their CR to estimate their phosphorus intake, and about 99% of that was taken up in particulate form. Kuenzler stressed the mussel's role in biogeochemical cycling, in contrast to the energy flow theories of Odum and Odum (1953) that dominated ecology at the time:

> *The major effect of the population on the ecosystem was the removal of particulate matter from sea water; the turnover time of the particulate phosphorus in the water was 2.6 days under the supposition that the mussel population was the only agent involved. Mussels are more important as biogeochemical agents than as energy consumers. (Kuenzler 1961)*

Jordan and Valiela (1982) similarly examined the importance of *Geukensia demissa* for biogeochemical cycling of nitrogen in a New England salt marsh. The species was shown to be sufficiently abundant to collectively filter, perhaps more than once, the entire volume of water overlying the marsh per tidal cycle. Much of the material removed from suspension gets deposited as feces and pseudofeces, and mussels were described as important agents for the retention of nitrogen within the marsh. One of the reasons for high nitrogen retention by ribbed mussels is that they are nitrogen-limited in natural marsh habitats for most of the year, whereas carbon stocks supersaturate their energy needs (Kreeger and Newell 2000). Using mesocosms, Bilkovic et al. (2017) found that higher microbial denitrification rates occurred in marsh systems containing ribbed mussels with vascular plants, compared with plants alone, suggesting that pelagic–benthic coupling mediated by ribbed mussels leads to greater net nitrogen removal in salt marshes.

The importance of *Geukensia demissa* for water quality therefore largely hinges on the abundance of healthy marsh acreage. For example, in the Delaware Estuary, which has more than 55,000 hectares of coastal marsh, the combined water clearance by *G. demissa* has been estimated at 60 billion L h^{-1} compared with 10 billion L h^{-1} by *Crassostrea virginica* (Kreeger & Bushek 2008). But the Delaware Estuary is losing 0.37 hectares of salt marsh per day because of erosion (PDE 2012), thus representing an estimated loss of daily biofiltration capacity of more than 400,000 L h^{-1} because of declining *G. demissa* habitat. Similarly, Bilkovic et al. (2017) estimated the water filtration of ribbed mussels in the York River Estuary of Chesapeake Bay to be 90–135 million L h^{-1}, and they also expressed concern that eroding marsh habitat is leading to a loss of water filtration services by *G. demissa*. This scenario demonstrates the importance of conservation to stem continued losses of filtration services, along with discussions of bivalve restoration and habitat restoration.

Cloern (1982) was trying to understand how South San Francisco Bay could have both (1) high nutrient inputs and phytoplankton growth rates and (2) very low chlorophyll concentrations for an estuary with high nutrient inputs, usually less than 5 μg L^{-1} in summer. After concluding that local zooplankton biomass could not consume enough phytoplankton to keep chlorophyll that low, he suggested that three suspension-feeding bivalve species were providing the ''missing'' filtration capacity. He calculated that the known biomass of those bivalves could filter all of the water in South Bay roughly once or twice a day.

Officer et al. (1982) further explored phytoplankton control by filter feeders in estuaries, trying to identify the conditions under which control was most likely. After reexamining the processes in South San Francisco Bay, they discussed two North Carolina estuaries where this control may be occurring. The factor that they identified as making phytoplankton control more likely includes shallow water in partially enclosed regions with poor hydrodynamic exchange. They did not discuss how this control might be exerted in Chesapeake Bay, although parts of that estuary fit that description (Cerco & Noel 2007).

Newell (1988) extended this concept of top-down control by bivalves to Chesapeake Bay, which has the symptoms of eutrophication that seemed to be missing in South San Francisco Bay. He proposed that the standing stocks of *Crassostrea virginica* were once high enough to do what other bivalves were doing now in South San Francisco Bay: controlling phytoplankton populations by filter feeding. He calculated that historic oyster populations could ''potentially'' filter a volume of water equivalent to the entire water column in Chesapeake Bay in the summer in 3–6 days. He also calculated that at their depleted 1988 population levels, *C. virginica* would take almost a year to filter the same amount of water. Both water clearance times (3 days then and 1 y now) are now cited broadly to explain why the health of the Bay has declined.

Newell (1988) did not explore the possibility that other filter feeders in the watershed may have partly assumed the role once filled by *Crassostrea virginica*, other than to mention that two nonnative clams had recently become much more abundant. Both of these species, the Atlantic rangia *Rangia cuneata* and the Asian clam *Corbicula* sp. have much lower salinity tolerances than *C. virginica*, so their ranges, especially for the *Corbicula* sp., have little or no overlap with that of *C. virginica*.

Gerritsen et al. (1994) built on Newell's (1988) study by using a model to calculate what proportion of 1987 to 1989 phytoplankton production in Chesapeake Bay was potentially consumed by populations of benthic filter feeders in those years, including *Crassostrea virginica* and a number of other species. One interesting question the authors asked was whether an increase in oyster populations to near-historic levels could be supported based on the available food. Their model output also led to some surprising recommendations:

> *Model results indicated that existing suspension-feeding bivalves could consume more than 50% of annual primary production in shallow freshwater and oligohaline reaches of the upper Chesapeake Bay and Potomac River. In deep mesohaline portions of the Chesapeake Bay and Potomac River, suspension-feeding bivalves could consume only 10% of primary production. .... Our results suggest that the proposed use of suspension-feeding bivalves to improve water quality of large estuaries will be limited by the depth and width of the estuary, unless the bivalves are suspended in the water column by artificial means.* (Gerritsen et al. 1994)

Cerco and Noel (2007) came to a similar conclusion about the need to have filter feeders in or near most of the water column to improve water quality, based on a modeling study. Their predicted effects of *Crassostrea virginica* on water quality in deeper water were minimal. Cerco and Noel (2010) extended their modeling of Chesapeake Bay filter feeders to include two of the dominant bivalves in tidal fresh and oligohaline reaches (salinity 0–5), *Corbicula* sp. and *Rangia cuneata*, both nonnative in the Chesapeake Bay. They concluded that

> *. . . bivalves may reduce phytoplankton concentrations in oligohaline and tidal fresh waters throughout the system but the most significant effects were noted in the Potomac and Patuxent tributaries. Bivalve impacts were related to hydraulic residence time. (Cerco & Noel 2010)*

The upper mainstem Bay had the highest *Rangia cuneata* biomass, but the upper Potomac had a higher combined bivalve biomass when *R. cuneata* biomass was added. Because the upper mainstem Bay had a much lower residence time than the upper Patuxent, due to higher flow from the Susquehanna River, Potomac and Patuxent rivers had the largest predicted impacts on water quality by filter feeders (Cerco & Noel 2010).

Other studies have shown how introduced nonnative bivalves can increase water clarity and/or reduce phytoplankton by increasing filtration. For example, effects on the San Francisco Bay by introduced clams (Officer et al. 1982, Alpine & Cloern 1992, Thompson 2005), on the Great Lakes and the Hudson River by the introduced zebra mussel *Dreissena polymorpha* (Baker & Levinton 1999, Budd et al. 2001, Caraco et al. 2006, Fahnenstiel et al. 1995, Klerks et al. 1996), and on the Potomac River by *Corbicula* sp. (Cohen et al. 1984, Phelps 1994). Improved water clarity sometimes led to positive increases in submerged aquatic vegetation in the same water bodies; however, negative impacts of introduced zebra mussels also have been well documented (Fahnenstiel et al. 1995).

One study documented the effects of the opposite change, from more to less filtration, namely, the removal of oysters from a eutrophic coastal lagoon in Taiwan (Huang et al. 2008). The lagoon once had very dense oyster aquaculture in racks, but the racks had to be removed when it was designated as a ''National Scenic Area,'' so the study was carried out to document the effects of removal. The lagoon has inner (poorly flushed) and outer (well flushed) regions. After oyster removal, mean light attenuation increased more than 50% and mean concentrations of chlorophyll-*a* and phytoplankton production rate increased 4-fold in the inner region, but all three parameters remained unchanged in the outer region and at the control site. There were also changes in the fish community. After rack removal, lagoon reef fish declined by 23% (probably due to reduced physical structure) and pelagic or planktivorous fish increased by 268%, suggesting that a reverse shift (compared with what usually happens when oysters are added to a lagoon) from periphyton-grazing to phytoplankton-grazing organisms likely occurred in the lagoon after rack removal (Huang et al. 2008).

Several articles mention ''resistance to eutrophication'' and how it can vary among estuaries (Cloern 1982, Carpenter et al. 1985, Cloern 2001, Caraco et al. 2006). This resistance can be physical, for example, when short residence time in flowing waters makes it hard for nutrients to stimulate algae blooms (Caraco et al. 2006), or it can be biological, due to the presence of abundant bivalves (as Cloern 1982, suggested for South San Francisco Bay) or abundant zooplankton (as Carpenter et al. 1985, suggested for lakes as a result of a trophic cascade). Cloern (2001) asked ''Why are some coastal ecosystems highly sensitive to inputs of additional nutrients while others appear to be more resistant (at least to the primary responses)?'' and then described four main ''filters'' (which might be more accurately called buffers or mitigating factors) to which he attributed this resistance, by determining how the ecosystem responds to stressors. The four filters from Cloern (2001) are as follows:

1. Tidal magnitude: macrotidal estuaries such as San Francisco Bay appear to be more resistant to eutrophication than microtidal estuaries such as Chesapeake Bay.
2. Residence time, discussed earlier: shorter residence times seem to confer more resistance because the excess nutrients are mostly exported quickly.
3. Inherent optical properties of water that control the light available to submerged plants, including phytoplankton and rooted SAV: High suspended sediment concentrations,

usually associated with poor water quality, can confer resistance to phytoplankton blooms by shading the plants; which explains some of the resistance of San Francisco Bay compared with Chesapeake Bay. The Delaware Estuary neighboring Chesapeake Bay is also an example of a system that is regarded as largely light shaded by high natural turbidity, perhaps explaining the general lack of harmful phytoplankton blooms there despite some of the highest nutrient loadings in the nation (EPA 2006). Color in the water (such as that from tannins in blackwater estuaries, such as the Nanticoke and Pocomoke rivers in Maryland) can have a similar shading effect (Bortone 2004).

4. Suspension feeders as a biological component of the filter: The dominant taxa tend to be zooplankton in lakes (as discussed in the following paragraph) and benthic suspension feeders (including bivalves) in estuaries.

Three of these four filters (or buffers) were considered in a review of the ecological role of bivalve aquaculture in U.S. West coast estuaries (Dumbauld et al. 2009). The only filter not considered was the inherent optical properties of water. Residence time, along with phytoplankton population growth rates, was seen as a key factor in determining the extent to which bivalves produced measurable effects on water quality (Dumbauld et al. 2009). Site-specific factors may also be important; for example, a mismatch in the timing of phytoplankton blooms and annual peak CR by bivalves can limit the responses of water quality to bivalve biomass. This was seen in the South San Francisco Bay after an introduced clam arrived there, even though the same species had improved water quality in the North San Francisco Bay (Thompson 2005).

A recent mesocosm study by Wall et al. (2011) examined how bivalve filtration (by adult *Crassostrea virginica*, bay scallops *Argopecten irradians* (Lamarck, 1819), and northern quohogs *Mercenaria mercenaria*) could offset the effects of eutrophication, and how that affected the growth of eelgrass *Zostera marina* (Linnaeus, 1753) as well as the growth of juvenile bivalves of those species and one juvenile fish (sheepshead minnow *Cyprinodon variegatus* Lacepède, 1803). The authors found that whereas bivalve filtration had a positive effect on eelgrass (in 1 of 3 experiments), by increasing light penetration, it also had a negative effect on the juveniles of those same bivalve species, as well as the juvenile fish tested (in 2 of 3 experiments). Increased nutrient loading, normally viewed as harmful to estuaries, led to increased growth rates of juvenile bivalves compared with control mesocosms with lower loading rates in 2 of 3 experiments, presumably by increasing the food supply (Wall et al. 2011). In his review of the ecosystem effects of both natural and cultured bivalves, Newell (2004) also noted that extremely high densities of bivalves can cause unintended ecological consequences, such as high biodeposition can cross a tipping point, whereby the positive benefits (e.g., denitrification enhancement) can switch to negative (e.g., high microbial respiration leading to anoxia and inhibition of denitrification).

Filtration Effects from Nontidal and Tidal Freshwater Bivalve Species

Eutrophication occurs in nontidal rivers, streams, lakes, and ponds, as well as in estuaries, and the ability of filter feeders (including freshwater bivalves) to ameliorate its negative effects is beginning to be explored. It is plausible that healthy populations of filter-feeding bivalves in nontidal streams and rivers should be able to help intercept particulate forms of pollution before they enter tidal waters.

Most of the scientific interest in freshwater mussels, and almost all restoration efforts, has been driven by conserving biodiversity. Only in the past 10–15 y has attention begun to focus on the environmental implications of widespread declines in population biomass of native freshwater mussels, regardless of whether species are imperiled or stable.

There has also been a large effort to study the effects of invasive freshwater bivalves (e.g., zebra mussel *Dreissena polymorpha*, quagga *Dreissena rostriformis bugensis*, and Asian clam *Corbicula* sp.) on ecosystem dynamics. Invasive and introduced bivalves in nontidal Chesapeake tributaries include Asian clams and zebra mussels (*D. polymorpha*). These nonnative species can furnish some ecosystem services such as increased visibility and improved water quality through removal of suspended particles and associated nutrients from open water (Cheng 2015), diverting nutrients to bottom sediments. In certain circumstances, however, these services have the potential to disrupt natural ecological relationships and can be inherently unstable. In addition, introduced species can contribute to biofouling problems that can be very costly for water treatment facilities, users of water intake pipes, and the boating industry. See species inventory for more detail on these species.

An emerging literature suggests that native freshwater mussels furnish many of the same filtration benefits and other ecosystem services in fresh tributaries as their marine counterparts (Atkinson et al. 2013, Atkinson & Vaughn 2015, Vaughn 2017). Like saltwater bivalves, mussels filter seston from the water column, potentially decreasing water treatment costs and improving water quality (Newton et al. 2011). Mussel beds can create biogeochemical hotspots via nutrient excretion and storage (Strayer 2014, Atkinson & Vaughn 2015). Mussel-provided nutrients can also alter algal composition, leading to decreasing blue-green algae populations and increasing water quality (Atkinson et al. 2013). Nutrients stored in mussels and shells are retained in the system long term because they are relatively long-lived. Thus, much of the particulate pollutants captured by mussels can be incorporated into the food web rather than being transported downstream (Atkinson et al. 2014). These various benefits scale with mussel population biomass, as discussed earlier for estimates of water clearance and seston removal rates in the Brandywine River and tidal freshwater zone of the Delaware River (Kreeger et al. 2013).

Estuary-wide (Delaware) estimates of mussel filtration capacity are especially notable because the current status of freshwater mussels in the Delaware River Basin is greatly reduced relative to historic conditions (Kreeger & Cheng 2017, PDE 2008, 2012), suggesting that water quality could be enhanced in areas where mussel populations might be restored. Filtration potential estimates require robust information of the relative abundance of freshwater mussels. Such data do not appear to be available for most of the Chesapeake watershed, but it is likely that these animals are well below their habitat's historic carrying capacity (Bogan & Ashton 2016), similar to the situation in the Delaware Estuary watershed. Thus, there is potential to boost water processing by restoring freshwater mussel assemblages in both watersheds.

As with any bivalve species, the actual net water benefits of freshwater mussel beds depend on complex hydrodynamic, biogeochemical, and ecological interactions, and more studies are needed on the interception pathways and fates of filtered matter. For example, water passing over mussel beds can become depleted in small particles and enriched in large particles (D. Kreeger, unpublished), and much of the filtered material can end up in biodeposits in the sediment. Enrichment of sediments with nutrients and organic content, compared with control areas without mussels, potentially fuels production by macroinvertebrates and benthic producers. Indeed, freshwater mussels provide many ecological functions in addition to filtering suspended particles from the water column (Vaughn et al. 2008, Table 1). Interactions among different mussel species living in the same area may also affect processing and ecological fate of suspended material (Spooner & Vaughn 2006, Vaughn et al. 2008).

BIVALVE RESTORATION FOR ECOSYSTEM SERVICES

There are numerous potential opportunities to either conserve or enhance the water quality benefits of bivalves throughout mid-Atlantic coastal watersheds such as the Chesapeake and Delaware Bay drainage basins. These opportunities are discussed in four different parts of the watershed continuum: open waters of the tidal estuary (subtidal salt water), fringing habitats along the tidal estuary (intertidal salt water), freshwater streams and rivers (nontidal fresh water), and tidal freshwater habitats (subtidal fresh water).

As noted earlier, this review omits an extensive discussion of oyster restoration because the intent is to discuss nonoyster species. It is worth noting, however, that oyster restoration for both commercial and ecological purposes has a long history in the mid-Atlantic and continues to be a major focus of natural resource management agencies and environmental programs (*e.g*., CBP and Delaware Estuary Program). Existing oyster restoration programs provide some of the needed infrastructure (e.g., hatcheries) to support restoration of additional noncommercial bivalve species. Extensive published literature and monitoring data from oyster restoration programs can also provide scientific benchmarks for gauging outcomes from nonoyster bivalve restoration. In addition, in some cases (*e.g*., hybrid living shorelines), restoration of oysters can be paired with restoration of noncommercial species such as ribbed mussels. References to oyster restoration are therefore included here where they potentially affect the restoration viability of other species.

Open Waters of Estuaries (Subtidal Saltwater/Brackish)

Marine mussels [*e.g*., *Mytilus edulis* and *Mytilus galloprovincialis* (Lamarck, 1819)] are often grown in aquaculture by suspending them on ropes in the water column, increasing their food availability, as suggested by Gerritsen et al. (1994). In addition to rearing mussels for their direct market value as a human food, mussel aquaculture is increasingly being studied as a tactic to remediate water quality, especially in Europe (Newell 2004, Lindahl et al. 2005, Petersen et al. 2014). Mussel biomass is removed periodically, thereby removing sequestered nutrients and contaminants as a ‘‘bioextraction’’ process. For example, mussel culture on suspended ropes was funded in coastal Sweden for nitrogen removal, at a cost of about US $200,000, which was promoted as a cheaper alternative to upgrading a wastewater treatment plant for the town of Lysekil (Lindahl et al. 2005). Unfortunately, the market for the mussels was not as good as had been projected, so it was not cost-effective to harvest them, and the nitrogen removal that was planned did not occur. As a result, the wastewater treatment plant upgrades were made later (Lindahl, personal communication).

Other bivalves can also be used for bioextraction (Rose et al. 2015). Rhode Island is investigating whether nutrient removal credits might be issued to scallop farmers who routinely harvest product from the estuary (Alves, personal communication). The Long Island Sound Study is exploring ways to incorporate shellfish aquaculture into the Total Maximum Daily Load for Nitrogen that is presently under revision in Long Island Sound (Rose et al. 2015, Rose, personal communication). The Piscataqua Region Estuaries Partnership is investigating the potential use of shellfish aquaculture and restoration for nutrient removal in New Hampshire (Grizzle & Ward 2011).

One group has explored possible ways to enhance populations of bivalves other than *Crassostrea virginica* in low mesohaline estuaries in the Chesapeake Bay. In the West and Rhode rivers, a postdoctoral student at the Smithsonian Environmental Research Center studied the feasibility of using softshell (*Mya arenaria*) seed (salinity range 5–30) bought from hatcheries in New England in 2011. Softshells were grown under nets to provide predator protection, based on modeling done by engineering students at George Mason University. Most of the seed died in summer 2011, however, probably from high water temperatures, and the project switched to oysters instead.

Fringing Waters of Estuaries (Intertidal Saltwater/Brackish)

Blue mussels *Mytilus edulis* are found intertidally in the mid-Atlantic region, but they are too scarce in Chesapeake and Delaware Bays to be considered in this review (see previous text). By contrast, the ribbed mussel *Geukensia demissa* is an abundant intertidal bivalve in salt marshes of the Chesapeake Bay (Lippson & Lippson 1984) and the Delaware Bay (Kreeger & Kraeuter 2010). The conservation and restoration of *G. demissa* appear to have promise for assisting in water quality management and improvement in intertidal areas fringing the Chesapeake Bay, wherever the salinities are within its range, down to about six (Table 2). Kreeger et al. (2011) similarly concluded that *G. demissa* is a high priority species in the marsh-rich Delaware Bay system, and the rapid loss of salt marsh edge where mussels are most abundant has important implications for both water quality management and coastal resilience (Kreeger et al. 2015, Bilkovic et al. 2017). For intertidal areas in Chesapeake and Delaware Bays, oysters and ribbed mussels are therefore considered to be the best candidates for conservation, restoration, and enhancement.

Pilot projects were completed to test the feasibility of culturing *Geukensia demissa* to enhance water quality, such as in the Bronx River, NY (Newell 2011, Newell 2013). The Bronx River project was funded in part through a settlement that resulted from discharges of raw sewage into the Bronx River from local storm sewers. The project attempted to grow *G. demissa* larvae on subtidal aquaculture ropes hanging from a raft that was installed in August 2011, and on intertidal coir logs simultaneously placed in a local salt marsh. No *G. demissa* larvae attached to the ropes, however, and low numbers were observed on coir logs by April 2012. The raft was later removed in December 2012 as a permit condition. The ropes were stocked with mussels from Jamaica Bay, NY, during April 2012 and were harvested in October 2012 (Rose, NOAA, personal communication). Projects to use *G. demissa* for water quality enhancement therefore may need to rely on hatchery-produced mussel seed than on natural recruitment.

Similar efforts have been underway to conserve or enhance *Geukensia demissa* populations for water quality benefits (and erosion control) in the Delaware Bay. For example, the Partnership for the Delaware Estuary and Rutgers University have been incorporating intertidal *G. demissa* (and oysters where permitted) in various types of living shoreline projects since 2008 (Whalen et al. 2012). Similar to the Bronx River studies (see the previous text), obtaining natural recruitment of ribbed mussels on placed settlement surfaces has been a bottleneck to getting high population biomass (Moody et al. 2016). Ribbed mussel spat appear to require interstitial spaces that serve as refugia from predation (J. Moody, unpublished). Living shorelines were, however, found to be successful in stemming erosion of the marsh edge, an important habitat for ribbed mussels. Facing a projected loss of 25%–95% of salt marshes by 2100 (PDE 2012), the ongoing loss of *G. demissa* (from lost habitat) may have important ramifications for the maintenance of water quality in Delaware Bay (Kreeger & Bushek 2008, Kreeger et al. 2011). Efforts to sustain and expand salt marshes therefore represent an indirect but important tactic for sustaining or expanding filtration services provided by *G. demissa* and marsh-associated *Crassostrea virginica* in mid-Atlantic estuaries that have extensive salt marsh habitat.

Streams and Rivers (Nontidal Fresh Water)

With the creation of the Endangered Species Act in 1973 and the listing of 75 freshwater mussel species over subsequent years, the U.S. Fish and Wildlife Service (Service) has been investing in the culture and stocking of freshwater mussels for recovery of endangered species. Research focused on studying the life histories and developing propagation techniques (National Native Mussel Conservation Committee 1998). Advances in understanding the biology and feeding of freshwater mussels (Gatenby et al. 1996, 1997, Henley et al. 2001, Barnhart 2006, Haag 2012, Mair 2013) led to successful captive care and propagation programs at Virginia Tech, the White Sulphur Springs National Fish Hatchery (WSSNFH), Missouri State University, Genoa National Fish Hatchery, Harrison Lake National Fish Hatchery, and North Carolina State University, to name a few (see review in Patterson et al. 2018). The principal motivation has been on rare species recovery. Many in the academic and governmental community are increasingly pressing for preservation and restoration of more ubiquitous species that may not be listed but that supply important ecosystem services and have also experienced dramatic decreases in population distribution and abundance.

Much of the funding for these efforts has come from mitigation sources, especially settlements to repair injuries following environmental disturbances. For example, the WSSNFH worked with the West Virginia Department of Natural Resources and the Ohio River Islands National Wildlife Refuge for 10 y to restore populations of freshwater mussels that were destroyed by a toxic chemical spill that occurred in 1999 in the Ohio River. The spill killed more than 1,000,000 freshwater mussels in a 20-mile reach of river. Adult mussels of several large-sized species were translocated from the Allegheny River (a major tributary to the Ohio River) to help reestablish a mussel bed, and cultured juveniles of both rare and common species were then stocked as well. Ten species from multiple age classes were stocked over 10 y. Annual monitoring of the bed showed continued high survival for both stocked juvenile and adult mussels (Morrison 2012).

In 2007, the Service partnered with the Virginia Department of Game and Inland Fisheries to restore freshwater mussels in Atlantic Slope rivers of Virginia. The cooperative Virginia Fisheries and Aquatic Wildlife Center at the Harrison Lake National Fish Hatchery has raised more than 12 different species, including some endangered. They release between 50,000 to 300,000 mussels annually into Virginia rivers, including the Rappahannock, Appomattox, Mattaoponi, Pamunkey, Meherrin, and Nottoway.

Like marine species, freshwater mussel restoration can occur in various ways, directly via reintroduction, seeding, and stock enhancement (often species-specific), or indirectly by improving the habitat (e.g., dam removals and substrate stabilization) and ecological conditions needed for healthy mussel populations (nonspecific to species), including restoring their host species. In addition, candidate stocking sites can be screened for restoration readiness using sentinel transplants of adults or hatchery seed before investing in a major restoration project when habitat suitability is unknown.

The Partnership for the Delaware Estuary launched a watershed-wide bivalve restoration strategy in 2007 that includes restoration of saltwater species in and along the Delaware Bay along with restoration of native freshwater mussels in tributaries to the the Delaware River (Kreeger 2005, PDE 2013). Their main goal in restoring freshwater mussels is to promote improved water quality. They are surveying and evaluating mussel populations, conducting restoration readiness tests, partnering with others on hatchery propagation and reseeding, species reintroductions, and conducting habitat restoration using living shoreline tactics. They also support extensive education and outreach programs.

Federal and state agencies are working to remove barriers to fish passage, which will enhance mussel reproduction and dispersion. As well, resource agencies are restoring riparian habitat and in-stream channel habitat for fish. If the aforementioned habitat restoration efforts consider mussels in their planning, then fish, mussels, and water quality can be improved in the Chesapeake Bay and Delaware River basins. Stormwater also can be controlled to limit inputs of fine sediments that degrade mussel habitat and to prevent flooding that scours mussels from the bottom.

Tidal Fresh Waters (Subtidal Fresh Water)

The Delaware Estuary has one of the largest freshwater tidal zones in the world, extending about 100 km from the fall line at Trenton, NJ, to near Wilmington, DE (PDE 2012), and many tidal tributaries also have extensive oligohaline reaches. In the Chesapeake Bay, tidal fresh areas are also significant in the upper bay near the mouth of the Susquehanna River and in the upper tidal zone of the James and Potomac watersheds. Freshwater mussels can be very abundant in these areas, especially in the shallow subtidal zone of shorelines that has suitable bottom conditions, as well as in subtidal portions of tidal creeks that drain freshwater tidal wetlands. For example, quantitative surveys in the

Delaware River between Trenton, NJ, and Philadelphia, PA, have found up to 125 mussels per square meter in high-quality reference locations, and, in these areas, mussel beds can even extend into deep channels up to 10 m (Kreeger et al. 2013).

Freshwater tidal areas were some of the most convenient for early settlement, and the result is that they now tend to be urbanized and significantly altered. For example, freshwater tidal waterfronts have been industrialized with bulkheads, riprap, docks, and piers. Channelization and dredging have altered natural hydrodynamics. Tributary mouths contain excessive fine sediments from stormwater. Marine and river-derived debris covers many shoreline and bottom habitats. Hence, the habitat conditions for benthic filter feeders have been significantly degraded in freshwater tidal areas, presenting many opportunities for mussel enhancement via habitat improvement. As an example, new living shoreline designs are being developed that include beds of SAV and freshwater mussels (PDE 2014). These designs are partly based on the co-occurrence of mussels and SAV in tidal freshwater habitats, possibly representing a similar ecological mutualism to that shown between many saltwater bivalves and SAV (Bertness 1984, Peterson & Heck 2001), potentially enhancing nutrient removal rates (Kreeger et al. 2015, Bilkovic et al. 2017). Bivalve restoration in tidal freshwater areas can present unique opportunities to help remediate water quality in urban landscapes closer to sources of pollutants.

BIVALVE SPECIES RECOMMENDED FOR RESTORATION

Bivalve species that hold the greatest promise for delivering potential water quality benefits should be prioritized by comparing both their intrinsic filtration capacity (reviewed in the previous text) and their prospects for enhancement or restoration (summarized here). Consideration of restoration potential should include some understanding of the following additional factors:

- population carrying capacity—how much biomass can be supported by the current or potential habitat?
- spatial footprint and niche separation—where can species be restored in relation to each other?
- hydrodynamics of pollutant exposure—what is the pollutant load in different species niches and how much of it can be intercepted by restored populations?
- viability of restoration tactics—does methodology and infrastructure exist for restocking (e.g., hatcheries) or habitat improvement?
- management constraints—are their policies or other obstacles that could affect permitting and willingness to pay?

Species that are recommended for restoration consideration are listed in the following paragraph based mainly on their physiological capacity and potential population biomass. Saltwater species are recommended first, followed by freshwater species. Where information is readily available, passing reference is made to some of the factors that govern their restoration prospects.

Recommended Saltwater Species for Restoration in mid-Atlantic Watersheds

Four native species of bivalves (other than oysters) were found to occur in estuarine systems and have CR similar to *Crassostrea virginica* (highlighted in Table 4). Three nonnative estuarine bivalves that had high CR were also identified, but these are not considered for restoration projects. It is plausible that the effects of some of the four native estuarine species on water quality could be equal to and possibly greater than those of *C. virginica*, depending on total biomass and other factors. The cumulative effects of restoring multiple species of native bivalves within a range of habitats, exploiting their unique niches, could be significantly greater than any single-species restoration project.

Planning for restoration (see previous text and more in the following paragraph) should include a consideration of what factors are limiting populations now, to assess whether restoration is feasible (if those limitations can be overcome), and if it is feasible, to assist with site selection and increase the chances that restoration will increase populations. For the native estuarine species that are recommended for restoration, information regarding known limiting factors are furnished in Table 4.

The four native estuarine bivalves with CR similar to those of *Crassostrea virginica* are as follows (and see Table 4).

- Ribbed mussels *Geukensia demissa* have been tested in biofiltration pilots (e.g., Bronx River) and living shoreline projects (e.g., Delaware Bay). Ribbed mussels have high tolerance to salinity and temperature extremes, filter diverse particles efficiently, and can be cultured in subtidal and intertidal habitats. Limiting factors include blue crab predation and natural recruitment. They may fare best when cultured in mutualism with vascular plants.
- Hooked mussels *Ischadium recurvum* can reach very high density; however, they have neither been tested for their actual biofiltration potential nor have they been used in restoration projects yet. This species would be suitable for subtidal estuarine restoration. Little is known about the factors that limit their populations, but suitable attachment surfaces are likely to be important.
- Softshell *Mya arenaria* were planned for a pilot biofiltration study in the West River in 2012, but most of the animals died before the study started. This species tolerates a broad salinity spectrum, but could be prone to predation. No information was found regarding factors that could limit their populations.
- Darkfalse mussels *Mytilopsis leucophaeata* were part of a natural experiment in 2004, when hundreds of millions of them appeared in several low mesohaline Chesapeake tributaries. Some of those tributaries had documented improvements in water quality and SAV coverage when they were present, but most of the mussels were gone by 2005. This species might be suitable for subtidal estuarine restoration, but it has not yet been used in restoration projects. Nothing is known about the factors that limit their populations, which naturally oscillate.

Recommended Freshwater Species for Restoration in mid-Atlantic Watersheds

Strategic planning for improving water quality in mid-Atlantic drainages by restoring native freshwater mussels should prioritize species that can attain high population biomass, modify benthic habitats, and filter the most water. To provide a context for judging the species that have the greatest

TABLE 4.

Clearance rates for estuarine bivalve species found in Chesapeake and Delaware bays, arranged in two groups (native and nonnative). Bivalves are listed if they are reported to have maximum CR that are at least 30% of the minimum rate for *Crassostrea virginica*.

Species	CR (L h^{-1} g^{-1} dry tissue)	Salinity range	Main limiting factors	Target habitat
Native species				
Eastern oyster *C. virginica*	6.4–11.5	7–30	Hard substrate, disease, and low recruitment*,†	Subtidal
Ribbed mussel *Geukensia demissa*	5.1–6.8	10–30	Predation, recruitment, and loss of marsh edges‡	Intertidal and subtidal
Hooked mussel *Ischadium recurvum*	4.3–4.6	5–30	Unknown; possibly hard substrate§	Subtidal
Softshell *Mya arenaria*	3.5–4.8	5–30	Disease and crab predation¶	Subtidal
Dark falsemussel *Mytilopsis leucophaeata*	1.7–2.4	0–10	Unknown‖	Subtidal
Nonnative species				
Zebra mussel *Dreissena polymorpha*	2.7–16.2	0–5	–	–
Asian clam *Corbicula* sp.	2.9	0–2	–	–
Atlantic rangia *Rangia cuneata*	2.1	0.5–10	–	–

See Table 2 for literature sources for CR.
* Eastern Oyster Biological Review Team (2007).
† Shumway (1996).
‡ Kreeger et al. (2010).
§ Lipcius and Burke (2006).
¶ Abraham and Dillon (1986), Dungan et al. (2002).
‖ Kennedy (2011a, 2011b).

restoration potential, Table 5 first provides a list of species of freshwater mussels that occur in areas of either the Chesapeake Bay or Delaware Estuary watersheds, with notes on the current state of propagation technology. A subset of these is recommended for restoration in Table 6. The information contained in Tables 5 and 6 was collected through conversations with state malacologists, State Wildlife Action Plans, and professional knowledge of propagation technology. For each species, Table 5 summarizes the mid-Atlantic states in which the species naturally occur, whether the species is in hatchery production, whether hatchery technology is being developed, the potential for producing the species, and an estimated level of investment that will be needed to propagate and stock a species. The latter two metrics are estimated as high, medium, or low. The potential for producing a species incorporated knowledge of life history, expertise among facilities rearing freshwater mussels, and interest level of state and federal partners. High knowledge, high expertise, and high interest equaled high potential for propagation. Medium potential was assigned if interest level by states was medium to low, and either knowledge of life history or expertise was high to medium (e.g., if more research and development is needed). A low potential (for producing a mussel) was assigned if interest was low among state partners, knowledge of the life history was medium to low, and expertise was high to low. Thus, the interest level (willingness to pay) by decision-makers at state and federal levels is balanced with knowledge of the life history and biology of the species by technical professionals. Factors that affected the propagation viability also included whether a species is extremely rare, lack of knowledge on host fish, ability to obtain broodstock and host fish, level of past experience in producing the species, and associated costs to develop new technology where needed. In all cases, these costs assume that the basic hatchery infrastructure is in place. Table 6 lists the subset of species in Table 5 that is recommended for restoration projects.

Selection of a restoration species should consider its historic range and strive to preserve native genotypes per watershed. Not all of the 28 Atlantic slope species in Table 5 exist outside of the Chesapeake watershed. For example, 13 freshwater mussel species are historically reported in the Delaware River Basin, and only those should be targeted therein. Propagation and restoration efforts for species that are common throughout the region should use source material from within the target watershed from the nearest possible broodstock, and if that is not possible, then appropriate management and heritage agencies should be consulted for guidance.

Freshwater mussel species that merit greatest restoration consideration in tidal freshwater zones of the Chesapeake and Delaware watersheds are the eastern elliptio *Elliptio complanata*, alewife floater *Utterbackiana implicata*, eastern pondmussel *Ligumia nasuta* (Say, 1817), tidewater mucket *Leptodea ochracea* (Say, 1817), and the yellow lampmussel *Lampsilis cariosa* (Say, 1817) (Tables 5 and 6). These species have comparatively high filtration capacity (Kreeger et al. 2013), are relatively common throughout the region (Watson, personal communication), and were historically widespread and abundant. Species such as *L. nasuta* also have high feeding demands in culture (Mair, personal communication), indicating that they may have large filtration rates *in situ*. Both *U. implicata* and *L. nasuta* are easy to culture, however more work is needed to improve hatchery production of *E. complanata* (Mair, personal communication). Additional species might be added to this list in the future as new information is gathered. For example, *Lampsilis radiata* (Gmelin, 1791) is presently being

TABLE 5.

Native freshwater mussels found in parts of Chesapeake and Delaware watersheds, and their potential for propagation. Species in bold font are reported from both watersheds; otherwise, the species is absent from the Delaware watershed.

Species	PA	NY	VA	WV	MD	DE	In production	Developing technology	Potential hatchery production*	Investment†	Facilities capable of production‡	Comments
Alasmidonta heterodon	–	–	x	–	x	x	–	x	High	Med	1,2,3	Technology needs some development; broodstock difficult to find
Alasmidonta marginata	x	x	–	–	–	–	–	–	Low	High	1,2,3	Technology not developed
Alasmidonta undulata§	x	x	x	x	x	–	–	x	Med	Med	1,2,3	Technology needs some development
Alasmidonta varicosa§	x	x	x	x	x	x	x		High	Low	1,2,3	Technology developed; broodstock difficult to find
Anodontoides ferussacianus	x	x	–	–	–	–	–	–	Low	High	1,2,3	Technology not developed
Elliptio angustata	–	–	x	–	–	–	–	–	Low	Med	1,2,3	Technology not developed
Elliptio complanata§	x	x	x	x	x	–	–	x	High	Med	1,2,3,4	Technology needs some development
Elliptio congaraea	–	–	x	–	–	–	–	–	Low	Med	1,2,3	Technology not developed
Elliptio fisheriana	x	–	x	x	x	x	–	x	High	Low	1,2,3	Technology not developed; producing similar species (*E. lanceolata*)
Elliptio icterina	–	–	x	–	–	–	–	–	Med	Med	1,2,3	Technology not developed; producing similar species (*E. lanceolata*)
Elliptio lanceolata§	–	–	x	–	–	–	x	–	High	Low	1,2,3	In production
Elliptio producta	x	–	x	–	x	–	–	–	High	Med	1,2,3	Technology not developed; producing similar species (*E. lanceolata*)
Elliptio roanokensis	x	–	x	–	–	–	–	–	Low	High	1,2	Technology not developed
Fusconaia masoni	–	–	x	–	–	–	–	x	High	Med	1, 2	Technology needs some development; broodstock difficult to find
Lampsilis cardium¶	–	–	x	x	x		x	–	High	Low	1,2,3	In production
Lampsilis cariosa§	x	x	x	x	x	x	x	–	High	Low	1,2,3,4	In production
Lampsilis radiata§	x	x	x	x	x	x	x	–	High	Low	1	In production
Lasmigona compressa	–	x	–	–	–	–	–	–	Low	High	2	Technology not developed
Lasmigona subviridis§	x	x	x	x	x		x	–	High	Low	1,2	Technology needs some development
Leptodea ochracea§	–	–	x	–	x	x	x	–	High	Low	1,2,3,4	In production
Ligumia nasuta§	–	x	x	–	x	x	x	–	High	Low	1,2,3,4	In production
Margaritifera margaritifera	–	x	–	–	–	–	–	–	Med	High	1,2,3	Technology needs some development; broodstock difficult to find
Parvaspina collina§	–	–	–	–	–	–	x	–	High	Low	1	Technology recently developed
Pyganodon cataracta§	x	x	x	x	x	–	x	–	High	Low	1,2,3	In production
Pyganodon grandis	–	x	x	–	–	–	–	x	Med	Med	1,2,3	Technology needs further development
Strophitus undulatus	x	x	x	–	x	x	x	x	Med	Med	1,2,3	Technology needs further development
Utterbackia imbecillis§	–	x	x	x	–	–	–	x	High	Low	1	In production
Utterbackiana implicata§	x	–	x	–	x	x	x	x	High	Low	1,3,4	In production

* Potential hatchery production description: interest level refers to interest by natural resource agencies. high = high interest, high knowledge and expertise; med = medium to low interest, high to medium knowledge, high to medium expertise; and low = low interest, medium to low knowledge, high to low expertise.

† Investment assumptions: (1) infrastructure is in place for hatchery production; (2) costs are estimated for labor (broodstock and host species collection, and hatchery production) and specialty equipment that could be incurred in year one to develop propagation and/or implement production; (3) annual costs would decline as knowledge and capability increased for production of a species, and could be less per species, if multiple species are in production. High = >\$100,000; medium = \$50,000–100,000; low = <\$50,000.

‡ Capability assumptions: (1) expertise available; (2) infrastructure available; (3) proximity to broodstock and host fish; d) strength of partnerships. Example facilities are: (1) Virginia Fisheries and Aquatic Wildlife Center at the Harrison Lake National Fish Hatchery; (2) Aquatic Resource Restoration Center at the White Sulphur Springs National Fish Hatchery; (3) North Carolina State University and North Carolina Wildlife Resource Commission; and (4) Aquatic Research and Restoration Center coordinated by the Partnership for the Delaware Estuary.

§ These species are also listed in Table 6 as species that are recommended for consideration for restoration projects.

¶ *Lampsilis cardium* is not native to Chesapeake watershed, and was likely introduced as result of recreational fish stocking in rivers in the 1980s. This species has become well established in certain tributaries to the Chesapeake Bay. State biologists are not in agreement whether to consider this species for any bivalve restoration effort. The species is included in this table only to provide a comprehensive list of freshwater mussels present in the Chesapeake watershed, and because there is some working knowledge of propagation and ecology of the species.

TABLE 6.

Native species of freshwater mussels found in midAtlantic watersheds that are considered by the authors to be viable candidates for restoration. See Table 5 for comments on the prospects for propagating each species.

Species	Common name	In production	Developing technology	Potential hatchery production	Investment needed	Best use (freshwater or tidal fresh)
Alasmidonta undulata	Triangle floater	x	x	Medium	Medium	FW
Alasmidonta varicosa	Brook floater	x		High	Low	FW
*Elliptio complanata**	Eastern elliptio		x	High	Medium	Both
Elliptio fisheriana	Northern lance	x		High	Low	FW
Elliptio lanceolata†	Yellow lance	x		High	Low	FW
Lampsilis cariosa	Yellow lampmussel	x		High	Low	Both
Lampsilis radiata	Eastern lampmussel	x		High	Low	FW
Lasmigona subviridis	Green floater	x		High	Low	FW
Leptodea ochracea	Tidewater mucket	x		High	Low	TF
Ligumia nasuta	Eastern pondmussel	x		High	Low	Both
Parvaspina collina†	James spinymussel	x		High	Low	FW
Pyganodon cataracta	Eastern floater	x		High	Low	FW
Utterbackia imbecillis	Paper pondshell		x	High	Low	FW
Utterbackiana implicata	Alewife floater	x		High	Low	Both

* Clearance rates have been measured for this species; see Tables 2 and 3.
† Not reported to be native in the Delaware River Basin.

propagated for bioassessment studies and mussel restoration in the Anacostia watershed (Mair & Pinkney, personal communication), but it remains unclear whether they can reach natural abundances that might contribute markedly to water quality.

Interestingly, two of these five species (*Leptodea ochracea* and *Ligumia nasuta*) are listed as rare by states of the Delaware River Basin (Delaware, New Jersey, and Pennsylvania). They were only found living within large populations of the large-bodied common species, *Elliptio complanata* and *Utterbackiana implicata* (Kreeger et al. 2013). Therefore, the viability of restoring species such as *L. ochracea* may hinge on the restoration of more common species. Robust beds of more common species may modify benthic habitat conditions (e.g., sediment stabilization) to make it possible for less common species to become abundant. In the urban areas of the tidal Delaware River, where mussels are found, *U. implicata and E. complanata* are examples of such ''foundational species'' that may underpin robust mussel assemblages. Their apparent tolerance to urban settings suggests that they may be especially good candidates for urban tidal fresh areas that are densely populated and degraded by development and stormwater runoff. Urban shorelines are often heavily altered, and restoring mussel beds to these areas might be best achieved via habitat enhancements (e.g., living shorelines), followed by restoring the foundational mussel species, and then finally the less common species.

In nontidal tributaries, prominent species that are targeted for restoration include the eastern elliptio *Elliptio complanata*, alewife floater *Utterbackiana implicata*, yellow lampmussel *Lampsilis cariosa*, and eastern pondmussel *Ligumia nasuta*, as well as yellow lance *Elliptio lanceolata* (Lea, 1828), eastern floater *Pyganodon cataracta* (Say, 1829), and paper pondshell *Utterbackia imbecillis*. These species are known to be capable of achieving significant densities and population sizes in mid-Atlantic streams. Three of these species, *P. cataracta*, *U. implicata*, and *U. imbecillis*, are fast-growing species with large gills. Additionally, *U. implicata* and *L. nasuta* show high growth rates and survival in culture. They should therefore be very useful in restoration efforts in larger rivers and lentic habitats where they are known to thrive because they have high potential to process large volumes of water sooner after stocking. The eastern elliptio, *E. complanata*, is considered an important restoration species because it was historically ubiquitous, can reach high population biomass, and has been shown to process large volumes of water; however, hatchery propagation of *E. complanata* needs further development.

Based on propagation potential and interest by state agencies (Table 6), the following species of freshwater mussels were also deemed to be of interest in restoration efforts in nontidal freshwater systems of the mid-Atlantic: *Alasmidonta undulata* (Say, 1817), *Alasmidonta varicosa* (Lamarck, 1819), *Lampsilis radiata,* and *Lasmigona subviridis* (Conrad, 1835). Another nontidal species (*Parvaspina collina* Conrad, 1837, the James spinymussel) might be considered in nontidal areas of the James River drainage because an active propagation program is in place with the Virginia Department of Game and Inland Fisheries and the U.S. Fish and Wildlife Service at the Harrison Lake National Fish Hatchery to recover this federally endangered species. Many of the aforementioned species of freshwater mussels are medium to large-sized as adults and therefore would be capable of filtering larger volumes of water (e.g., up to 1 L h^{-1} or more per individual during the growing season). Their relevance for water quality enhancement will therefore depend mainly on the population biomass that can be achieved.

Some of the species in Table 6 do not usually achieve the population biomass (and hence filter as much water) as *Elliptio complanata*, *Pyganodon cataracta*, and *Utterbackiana implicata*, but they may have local significance or be more appropriate for specific ecological niches. For example, the *Alasmidonta* species of freshwater mussels are not very large in size, but they are of special restoration interest in some areas of Chesapeake and Delaware watersheds. They were once abundant throughout eastern West Virginia and Piedmont streams of Maryland, Pennsylvania, and Virginia (Ortmann 1911, 1919, Bogan &

Ashton 2016, Cordeiro & Bowers-Altman 2018, PAFBC 2018). Freshwater mussels as a group historically occupied vast beds in Atlantic Slope rivers with unique species assemblages from the headwaters to the coast. A watershed approach to restoration will ideally target a suite of species for restoring filtration and ecosystem services.

The eastern pearlshell *Margaritifera margaratifera* was not included in Table 6 because little is known about their present distribution and abundance. Furthermore, this species is naturally adapted to coldwater habitats, and its utility for water quality enhancement is likely restricted to the coldest, headwater streams. Propagation methods have been studied for rearing margaritiferids in Europe (Geist 2010, Gum et al. 2011), and these could be adapted to the North American *M. margaratifera*.

Freshwater mussels still occur in many mainstem rivers of the Chesapeake Bay such as the Potomac, Patuxent, Rappahannock, James, Shenandoah, Chester, Choptank, and Susquehanna; however, evidence of them still existing in large numbers is lacking. Similarly, in the Delaware River, a few reference beds still exist showing how abundant mussels can be and likely once were in many other areas. Today though, most areas are devoid of mussels, and even when located, they are usually in low abundance and richness.

As noted earlier, restoration planners should consider environmental factors that may limit the carrying capacity of current populations. These factors are similar for all species of freshwater mussels, and they are briefly described below rather than listing them on Table 5 or 6 (as in Table 4 for subtidal species). Three of the most important constraints of freshwater mussel populations are water quality, habitat quality, and presence of suitable fish hosts for reproduction. Within the Chesapeake and Delaware watersheds, degradation of habitat from urbanization, agriculture, damming, and channelization of rivers have constrained where mussels can live and be abundant. Freshwater mussels tend to favor stable bottoms with low bed transport rates and low episodic scouring events. Flows must be sufficient enough to deliver food and eliminate wastes.

Freshwater mussel viability can also be governed by water quality, which may seem paradoxical to the central thesis that bivalves can enhance water quality. Water quality enhancement occurs within specific pollutant ranges and in the absence of acute toxicants. Certain types of contaminants are toxic to freshwater mussels in low concentrations (e.g., some metals and ammonia). Growth and survival are partly governed by shell calcification processes that depend on an appropriate range of hardness and pH. Toxic pollutant discharges into rivers can reduce populations of freshwater mussels to such low numbers that recruitment can become limited, or the pollutants can impact essential host fish needed for mussel reproduction. Over the past several decades, water quality and management practices have improved in many areas throughout the Atlantic slope and Chesapeake Bay watershed. Some streams and rivers that were too degraded to support mussels may be viable habitats now, as demonstrated in successful pilot reintroductions of mussels that have been monitored for chronic fitness and growth (Gray & Kreeger 2014). Water quality can also be a constraint if insufficient food quality and quantity exist to support a large mussel population; however, few ponds, lakes, streams, and rivers in the mid-Atlantic are oligotrophic.

Finally, dams and other forms of fish passage barriers can short-circuit reproduction by freshwater mussels because each mussel species requires specific sizes and species of fish as hosts for their parasitic larvae (Neves 1993). Successful reproduction and dispersal of mussels depend on these species-specific relationships with fish. The presence of suitable fish hosts is therefore required for recovery of self-sustaining populations of native freshwater mussels. Projects that seek to enhance water quality via mussel restoration could still be completed in areas without fish hosts by propagating and periodically dispersing mussel seed because mussels can live for several decades once reintroduced. This would require a long-term commitment to periodic repeated stocking, and this investment might be warranted if the benefits of the mussel beds are valued higher than the costs.

The pace of dam removal has accelerated in the mid-Atlantic with dwindling support for structures that no longer serve the needs of the community. Thus, suitable habitat is available for populations of freshwater mussels to recolonize in many areas of Chesapeake and Delaware watersheds where mussels once existed. Natural dispersal can be extremely slow, however, because freshwater mussels delay sexual maturity for 4–10 y. Early colonizers remain at risk of a stochastic event that could eliminate a local population entirely. Restoration of freshwater mussels, therefore, will likely be most successful following a population management approach involving propagation and stocking and/or translocation of individuals from dense beds within the watershed to reestablish or boost other populations. Direct release of fish hosts that are infested with mussel larvae is another mussel restoration tactic being used throughout the United States. Even in watersheds that retain fish blockages and have no natural mussel reproduction, as noted above, mussel restoration for water quality enhancement might be justified if there is a long-term commitment to repeated stocking because mussels generally live for 30–50 y and the frequency of augmentation might be low.

For current information on propagation and restoration technology, consult Mair (2013) and Patterson et al. (2018). For stream habitat quality assessments, see the National Fish Habitat Partnership (NFHP) GIS database (with maps) that contains "scores" for most streams/HUCs in the United States (NFHP 2014).

DEVELOPING A BIVALVE RESTORATION STRATEGY AND ESTIMATING ECOSYSTEM SERVICES

A holistic, watershed-wide strategy is recommended for restoring bivalve populations to help maintain and enhance water quality. For the freshwater portion of the watershed, this should support the National Strategy for the Conservation of Native Freshwater Mollusks (FMCS 2016), which highlights the need for additional research on ecosystem services and restoration protocols. Each candidate restoration species has unique habitat requirements and environmental tolerance limits for conditions such as salinity, dissolved oxygen, and substrate. The different niches occupied by the species reviewed here, from headwaters to mouth of the bay, represent opportunities to build a diversified approach to promote water quality along the river to bay continuum. The initial selection of suitable species to target for restoration should therefore consider additional information not fully reviewed here, such as the nexus between current and potential species ranges, the carrying capacity for bivalve populations, and spatial variation in water quality remediation needs.

Ideally, several pieces of scientific information are required to develop a rigorous predictive understanding of the net water quality outcomes from bivalve restoration. These are summarized in the following paragraph. Once a decision is made to restore a particular species, restoration can include measures to directly enhance populations of the bivalves or to enhance the carrying capacity such as via habitat improvements. Direct enhancement requires sources of animals of the target species or the means to propagate them. In areas that are impaired, candidate waters may need to be tested to verify their "restoration readiness" to determine whether they are capable of supporting enhanced populations. The following actions are suggested to help assist with restoration decisions and implement (nonoyster) restoration projects for water quality enhancement:

- Obtain empirical data on weight-specific CR by target species (from this review or new research).
- Appraise the current population abundance, size distribution, and geographic distribution of target species (from census surveys).
- Estimate the current system's carrying capacity for the target species of bivalves, based on the availability of suitable habitat, food resources, and other ecological factors (e.g., fish hosts for freshwater mussels). Consider whether the carrying capacity might change, such as by habitat enhancements that boost populations (e.g., dam removal and living shorelines) or by climate factors that may further undermine populations (e.g., sea level rise and stormwater).
- Compare data on total suspended solid concentrations and associated pollutant levels with the potential bivalve population biomass and species-specific CR in their habitat niches.
- Develop a quantitative understanding of the likely fate of filtered matter in addition to the gross amount filtered, for target species and niches.
- Find sources for target species, or determine propagation methods if no sources are available.
- For impaired waters, use relocation or caging studies to test and rank restoration suitability.
- Start restoration, by propagating and stocking juvenile bivalves, relocating adult bivalves, and/or enhancing habitats in targeted waters.

These actions are described more fully in the following paragraphs.

Obtain Empirical Data on Weight-Specific CR by Target Species

To estimate whether bivalve restoration can help remediate water quality at the ecosystem level, empirical data on weight-specific CR (and filtration rates where available) should be obtained for the target species. In early stages, the target species list should include all reasonable candidates, because it would be easier to drop than to add them later. Getting filtration and CR data requires an understanding of their physiological ecology because physiological processing rates vary among species, body sizes, seasons, and with nutritional and environmental conditions. As discussed in the preceding sections, there are various methods for measuring filtration and CR that can bias or thwart intercomparability of results (*e.g.*, laboratory diets and conditions), For estimating ecosystem services, studies should simulate natural conditions, deliver natural diets, and hold animals at ambient temperatures and conditions that are most reflective of the targeted restoration areas (tidal regime, substrate, etc.). Because filtration and CR vary with age and body size, measurements should be taken for a diverse range of body sizes that best represent the wild population and then the equation for CR be weight-adjusted using allometric relationships for the standard-sized animal.

Appraise Current Population

Estimates of ecosystem services associated with current populations depend on a quantitative appraisal of the current population abundance and size distribution, noting any factors that limit its abundance and distribution. Populations of most noncommercial species are not routinely monitored, and recent survey data can be difficult to obtain. For example, the last comprehensive survey of the distribution of freshwater mussels in Pennsylvania (for which data can be obtained freely) was conducted about 100 y ago (Ortmann 1919). Populations of freshwater mussels are patchy and logistically challenging to assess quantitatively, and their restoration will require a better understanding of the habitat, water and food conditions needed (Strayer 2008). Indeed, it is critical that up to date survey data be readily available via GIS or other means for scientists and managers to develop species management plans and strategies to meet the goals of restoring populations and ecosystems.

The Chesapeake Bay has decades of monitoring data collected by the CBP with fairly complete information on soft-bottom benthos (including bivalves) in deeper tidal waters (Versar, Inc. 2011). Abundance and distribution data are much more limited for bivalves on hard bottom, however, except for annual surveys of oyster habitat. Almost no data exist for bivalves living in shallow water or intertidal marsh edges. Nontidal bivalves are sampled at sites in Maryland by the Maryland Biological Stream Survey (MBSS 2011), but nontidal benthic sampling in other states in the watershed (Delaware, New Jersey, Pennsylvania, Virginia, West Virginia) is more limited. Citizen science survey programs can help to fill data gaps for the distribution of freshwater mussels (PDE 2015). After population demographics are assessed, these data can be paired with allometric and seasonal estimates of bivalve filtration (and other rate functions, see previous text) to obtain first-order mass balance estimates for the water processing potential of current populations.

Model the Movement of Water and Associated Pollutants

The system's carrying capacity for the target species of bivalves should be estimated or modeled where possible. In some cases, carrying capacity can be estimated from data on historic ranges and population abundances, except it is important to consider the trajectory of the system's carrying capacity for the species. Changing conditions may have curtailed or shifted the location and extent of suitable habitats. For example, some streams and rivers may no longer be suitable for freshwater mussels because of degraded water and habitat quality. Some cold-adapted species may shift northward with warming climate. Increasing rates of sea-level rise threaten tidal marshes that are home to intertidal *Geukensia demissa*. To ensure that resources are invested strategically in sustainable places and species, predicted trajectories of climate change and continued watershed development should be considered in developing best possible estimates of future carrying capacity, which is likely to be different from current carrying capacity. In some cases (*e.g.*, freshwater mussels), assisted migration of southern species might be needed to sustain ecological services in the north. In cases where the restoration is designed to improve habitat or food conditions, the enhanced carrying capacity might be estimated by examining bivalve populations at reference sites that already possess the envisioned (improved) conditions.

Development of a GIS database of likely current and future suitable habitat for various bivalve species will provide a first-order framework for considering carrying capacity. This habitat layer can then be tempered by geospatial information on impediments or constraints on natural populations. Examples of potential density-dependent factors to be considered in carrying capacity estimates are disease prevalence (*e.g.*, *Crassostrea virginica*), dams that impede fish hosts, suboptimal water quality, susceptibility to predators, vulnerability to frequent disturbances (*e.g.*, spills), and the presence of toxic levels of contaminants. In addition to ecological carrying capacity, logistical and political considerations should also be weighed. These could include habitat tradeoff concerns by fisheries groups, esthetic concerns by homeowners, and development restriction concerns if protected species are restored.

Estimate Pollutant Load Reduction

The potential water processing by current or restored bivalve populations in target areas can be estimated by comparing the current or potential population biomass of the target species with typical concentrations of particulate pollutants in the areas targeted for restoration. A fuller examination of potential pollutant reduction, via bivalve-mediated particle filtration, should also consider the hydrodynamics and movement of water and associated pollutants through the system in relation to the geospatial distribution of bivalve populations (Dame 1996, Wildish & Kristmanson 1997). Systems that have greater residence times of water over bivalve populations allow more time for water to be filtered (and refiltered), resulting in comparatively higher net pollutant removal efficiency. By contrast, high flows, short residence times, and patchy bivalve populations might limit the interception of pollutants via bivalve filtration. Bivalve restoration in areas that have very low pollutant loads will matter little for the watershed-wide management of those pollutants.

Develop a Quantitative Understanding of the Fate of Filtered Matter

The capture of suspended matter through bivalve filtration is not necessarily a pollutant sink. Some of the filtered matter gets defecated or remineralized (Fig. 1), and within 24 h returns to the system in different forms. Some gets incorporated and used for growth (and reproduction), eventually returning to the system (*e.g.*, when the animal dies). The proportion that gets permanently removed depends on the time lag and definition because even buried shells can be remineralized on geologic time scales.

If anoxia is a consideration, then organic matter in biodeposits can be a concern. Much of the filtered material is of poor nutritional value and will be bound in mucous and rejected as biodeposits (feces and pseudofeces). Biodeposits sink, and bivalve filtration leads to clearer water with enhanced light availability to benefit bottom producers. Biodeposits can get buried, resulting in a net ecological sink; however, as discussed in the background section in the previous text they can also be ingested or degraded by benthic and microbial organisms or be returned to the ecosystem via remineralizers (Newell et al. 2005).

The bivalves themselves also remineralize nutrients by excreting dissolved ammonium and phosphate ions (Fig. 1). In general, for water quality management purposes the key end product to consider is this filtered material that gets quickly returned via excretion of dissolved compounds that can flow back to primary producers. In addition, bivalves feed and digest adaptively, leading to variable physiological processing rates (filtration, absorption, assimilation, respiration, and excretion) with changes in seasonal or ontogenetic nutritional demands and diet composition, leading to varying rates of biodeposition and nutrient excretion. For example, tidal mussels can increase nitrogen assimilation 8-fold and curtail ammonia excretion when protein demands are not being met (Kreeger et al. 1995).

The potential benefits of bivalves to water quality therefore depend partly on pollutant-specific goals of management agencies. Is the goal to have clearer water, lower nutrients, or some other goal? In any of those cases, a quantitative understanding of the fate of filtered matter for targeted species and under natural conditions will clarify expected outcomes and strengthen the restoration project design. Developing a better understanding of the ecological fate of ingested matter under differing conditions would therefore strengthen the understanding of the net environmental benefits of bivalve feeding for water quality. The use of stable isotopic tracers and other new methods may also boost the understanding of how much anthropogenic, allochthonous sources of pollutants can be accumulated in both nontidal and tidal bivalve populations (*e.g.*, for nutrient retention, see Valiela et al. 1997, McKinney et al. 2001, 2002).

Choose Restoration Approach

Bivalve restoration can take many forms. Direct population enhancement can be achieved by reintroducing reproductive adults that can serve as broodstock or seeding with hatchery-propagated juveniles. Juvenile seeding projects are obviously dependent on the availability and capacity of a hatchery with propagation knowledge for the target species. If habitat is the main constraint, existing habitats can be enhanced, such as by increasing settlement surfaces for marine species, stabilizing erosion of existing habitat, or facilitating passage of essential fish hosts for freshwater mussels. There are new tactics being developed continuously; for example, infestation of fish hosts with freshwater mussel larvae and release of only the infested fish.

Restoration success will be enhanced by a science-based understanding of the ecological relationships discussed previously; for example, factors that can guide the strategic selection of species, growing location, and restoration tactic. The restoration of bivalve shellfish for ecosystem services is a new concept, and monitoring and sharing of outcomes are also warranted to facilitate post-restoration analysis and understanding of why any restoration attempts succeeded or failed. For some species, restoration interests might challenge traditional management paradigms. For example, if no suitable source for a target species can be found in the drainage areas, it might be necessary to (re)introduce the species from the nearest possible source; however, the consensus scientific view is that this should be a last resort due to potential genetic (and possibly biosecurity) concerns. Interstate transfer of most native tidal bivalves is allowed with a permit. Interstate and interbasin transfers of freshwater mussel species are strictly regulated. Some transfers are allowed with a permit, and require close collaboration with state and federal agencies, good communication on goals and objectives, and justifiable explanation of projected outcomes.

Gauge Restoration Suitability

Pilot reintroduction studies (*e.g.*, caging studies) may be warranted in places where there is uncertainty of whether a candidate restoration species will survive and prosper. To gauge restoration suitability, caged or tagged bivalves can be introduced into prospective restoration areas and their fitness can be monitored for a period of time relative to control (source) locations. Waters that support the greatest fitness or growth are then prioritized for restoration, thereby strengthening the chances for successful restoration leading to self-sustaining populations. Comparative studies of suitable bottom habitat are also helpful for the same reason. In cases where habitats are enhanced and natural colonization is expected (*e.g.*, living shorelines for saltwater species), *a priori* settlement tests might be warranted to confirm the availability of larvae in the targeted locations.

Bivalve Restoration

There are myriad ways to conserve, restore, and/or enhance bivalve populations, and this review does not attempt to review these tactics. As discussed in the previous text, one approach is to manage and restore the habitat needed by bivalves (and their host fish), including such activities as shell planting for oysters, salt marsh erosion control for *Geukensia demissa*, dam removals, stormwater controls, and restoring riparian zones for freshwater mussels. In cases where new habitat is created or past disturbances are removed, bivalves can be reintroduced through straightforward transplanting, and this is especially important where natural dispersal is impeded. Finally, the technology now exists to propagate almost all native species in hatcheries, providing seed to reintroduce species, expand species ranges, and boost natural populations by stocking juvenile bivalves that are bred and raised in hatcheries, with appropriate genetic conservation protocols. Even in cases where the carrying capacity for a target species might be low (*e.g.*, lack of fish hosts for freshwater mussel reproduction), subsidized restoration (*e.g.*, periodic stocking) might be warranted if the value of the water quality benefits outweighs the restoration costs.

IMPEDIMENTS TO BIVALVE RESTORATION FOR ECOSYSTEM SERVICES

Science Needs

There are a number of reasons why efforts to restore bivalves to enhance ecosystem services are just getting started. Despite the clear evidence that oscillations in bivalve populations can elicit dramatic changes in water quality at the system scale (reviewed in the previous text), there remains some skepticism that the benefits of bivalve restoration will materially address management goals for water quality and outweigh the costs. There also is justifiable concern that large-scale shellfish restoration could have unintended consequences for other species, and habitat trade-offs are a common concern in permitting discussions. Funding for environmental restoration is also getting tighter, and funders are increasingly requesting scientifically rigorous, quantitative predictions for the expected ecosystem benefits. In many cases, the empirical data needed for robust predictive models for noncommercial bivalves simply do not exist yet.

A more comprehensive understanding of the current range, physiological ecology, carrying capacity, and predicted functional benefits of noncommercial bivalves is therefore needed to confirm that such investments are warranted. Funding to fill these knowledge gaps has been nearly impossible to obtain by the research community because these species have not been valued as much as commercial species. Despite more than 100 y of scientific study of bivalves (particularly commercial species), this understanding is not yet mature, particularly for freshwater mussels (FMCS 2016). Most physiological studies have used nonnatural diets and culture systems because the intent was to optimize captive care of imperiled species, promote aquaculture, or augment shellfishery outcomes rather than environmental benefits. Additionally, culture and propagation of freshwater mussels only just began in the late 1990's, and more research is needed to maximize production of species that contribute the most ecosystem services. The field of marine physiological ecology advanced in the 1960s to 1990s, followed by increasing attention to ecosystem-level effects in the 1990s to 2000s. Field experimentation is expensive and large-scale manipulative experiments of bivalve populations are rare. The inconsistency in methods and units due to the varied research purposes further muddies assessments of ecosystem services in natural systems. As a result, much of the essential empirical information on organism-level and ecosystem-level processing of natural seston, and associated pollutants, has yet to be fully discovered.

As a result, a fundamental barrier to the restoration of noncommercial species for water quality enhancement is getting the funding to perform scientific studies that are required to justify the restoration. A question that typically arises is regarding the fate of filtered material. Project implementers, managers and funders typically want to have a quantitative understanding of the mass balance flow of particles and pollutants, often seeking a simple number for each product. Factoring these postcapture processes into calculations of services can quickly become complicated [Bayne & Newell 1983 (*Mytilus edulis*), Kreeger & Newell 2001 (*Geukensia demissa*), Langdon & Newell 1996 (*Crassostrea virginica*), D. Kreeger, unpublished (fresh water mussels)]. Bivalves are extremely adaptable organisms that strive to satisfy changing nutritional demands from an ever-changing diet.

Despite this complexity, predictive models can easily be developed for each target species if sufficient empirical evidence is obtained to parameterize the models. The main variables are season (temperature), population demographics, natural diet quantity, natural diet quality, and general estuary/stream location (salinity zones, etc.). With this information, seasonal and nutritional effects can be captured, thus developing an annual estimate of ecosystem services for a particular species in a general river or estuary location. As with most restoration projects, funding for monitoring of project outcomes is also difficult to secure, but validation of ecosystem service models will be another important need to adaptively manage watershed programs aimed at bivalve restoration for water quality enhancement.

Human Health/Competition with Commercial Aquaculture

Impediments to quantifying bivalve ecosystem services also include usage and management conflicts. In 2010, the State of New Jersey enacted a ban on restoration of commercial (edible) species of shellfish in areas closed to shellfish harvest, forcing some restored oyster reefs to be eradicated. This policy was designed to protect both the public health and the oyster shellfishery by ensuring that no one gets sick from eating tainted animals from restoration sites or from oyster gardening projects. It is plausible that similar public health concerns over elevated bacteria and/or toxin levels might be extended to nontarget species that are raised in restricted waters even though they are not usually harvested or grown for human consumption. The public health concern is that some people will eat almost any shellfish regardless of the species or where they got it, as long as it resembles an edible species. For example, *Rangia cuneata* are eaten in Mexico and other areas and look quite similar to hard clams sold as food, and *Corbicula* sp. have been illegally collected in the Delaware River to be used in cooking. Freshwater mussels are not a typical food source for humans, and we know very little about health risks of consuming them.The main issue to be considered is the limits of responsibility of public health agencies to protect consumers from themselves. Most shellfish restoration for water quality enhancement will be situated in impaired waters with the intent to perform ecosystem services, and none of those animals should be eaten. This is an example of how education and outreach programs can serve a critical role in bivalve restoration, informing the public about the intent and benefits (and potential hazards) of various projects.

Potential conflicts with raising shellfish for food could also occur when the same hatcheries, cultch materials, and/or grow-out facilities are used for bivalves grown primarily for food as those that are grown primarily for ecosystem services. Conflicts can also occur over the habitats being managed for different purposes, such as in coastal bays where oystermen typically oppose projects that could potentially limit the areas open to harvest. There are also potential conflicts if bivalves that are considered a harmful fouling species on *Crassostrea virginica*, such as *Ischadium recurvum*, were cultured for their water quality and habitat benefits. Harmful fouling on *C. virginica* from such bivalve restoration could be minimized by growing out the *I. recurvum* in areas that presently have few *C. virginica* or *I. recurvum* (see in the following paragraph).

In general, the aquaculture of bivalve shellfish is thought to promote water quality in some localized areas where shellfish biomass is high and water exchange is low, helping to offset eutrophication stemming mainly from excess nutrient runoff (Burkholder & Shumway 2011, Coen et al. 2011). Bivalves raised in aquaculture provide interim services while they are growing, and they are usually harvested as soon as this is profitable. This limits how long they can provide ecosystem services. On the other hand, harvested shellfish contain nutrients, and this ‘‘bioextraction’’ via the removal of nutrient-laden animals is seen as a tactic that could be profitable for both growers and management agencies in certain circumstances (Rose et al. 2015). Modeling efforts, such as the Farm Aquaculture Resource Management (FARM) model, can be used to shed light on the complex interactions among resource uptake by bivalve populations, remineralization rates, aquaculture operations and business plans, geospatial planning, and system carrying capacity (Ferreira et al. 2007, 2009, Burkholder & Shumway 2011). As a result, the two goals of natural restoration and aquaculture can be compatible in some situations, for example, if growers are paid to leave their bivalves in the water for another year after they could be harvested to enhance the ecosystem services they provide, such as habitat, filtration, and spat for nearby wild populations.

Some aquaculture experts have argued that only bivalves that are raised in commercial aquaculture (and thus for food) can be raised in enough quantity to provide significant ecological services, so this conflict may be hard to avoid. Most efforts to propagate and raise bivalves are to supply seed for aquaculture or to augment stocks for harvest, and there is a need for more research and facilities to support ‘‘restoration aquaculture’’ of both commercial (edible) and noncommercial species.

Public Perception/Education

Traditional management paradigms and policies at federal, state, and local levels generally fail to recognize the habitat and water quality benefits of restored bivalve populations. There is even less awareness about the risks to water quality of continuing to lose natural stocks. Public interest in noncommercial species is also presently low, but only because of lack of awareness. Once educated about the importance of these animals, the public tends to quickly become interested and supportive. Bivalves offer a wealth of outreach opportunities due to the sessile nature of the animals (*e.g.*, they can be tended in ‘‘gardens’’) and the clear water quality benefits that are conveyed by simple aquarium demonstrations (Fairmount Water Works 2017). In many areas of the United States, outreach and citizen science programs have also been successfully used to thwart poaching of animals from restoration sites.

Funding

Finally, perhaps the most important impediment to advancing bivalve restoration for ecosystem services is the difficulty obtaining funding for projects, including basic physiological and ecological research and pilot projects to monitor outcomes (see also Science Needs in the previous text). Being able to quantify ecosystems services from bivalve restoration is important both to justify the money spent on it and also to calculate any payments that may result from it.

Despite these challenges and impediments, most are solvable and the methods and scientific prowess presently exist in the mid-Atlantic region to quantify bivalve services. Propagation technology is well understood for oysters, clams, tidal mussels, and even freshwater mussels, which grow slowly and have a convoluted life history strategy. The only major hurdle is funding to optimize culture and reintroduction methodologies (*e.g.*, *Geukensia demissa* and freshwater mussels) and to more directly quantify core ecosystem services with ecophysiological and modeling studies. Formation of an interdisciplinary technical workgroup comprised of culture specialists, physiological ecologists, modelers, water quality experts, economists, and hydrodynamics specialists could tackle these needs efficiently.

RECOMMENDATIONS

Some resource managers view the use of top-down controls on nutrients, such as bivalve enhancement, as an admission that traditional source control methods have failed. The authors do not advocate abandoning traditional management methods in favor of a program focused on top-down approaches. Indeed, in most areas, the success of bivalve restoration programs will hinge on the sustained momentum of much broader efforts to protect and restore watersheds, via traditional BMP such as nutrient controls, riparian buffer enhancement, forest and wetland protection, and stormwater management. BMP for bivalve restoration, such as the one being advanced for oysters in Chesapeake Bay (Cornwell et al. 2016), are a plausible *complement* to existing water management programs, providing some level of water quality benefits that can augment other, more accepted BMPs.

The ability of bivalve populations to improve water quality should not be overstated until more evidence is gathered from proof-of-concept, pilot projects. Measureable reductions in particulate pollutants may only be achievable in smaller, closed systems (*e.g.*, ponds or bays with high residence time) that can support high biomass densities of bivalves. Bivalve populations tend to be naturally patchy; therefore, efforts to enhance the total population biomass of a targeted species might yield modest outcomes even if the targeted waters have high carrying capacity (Carmichael et al. 2012). Improving the carrying capacity for bivalves is likely to be a daunting task. Many streams and rivers are altered by dams, lack riparian buffers, and impaired by stormwater runoff. Many estuarine shorelines are degraded by human alterations, and many subtidal estuarine areas are choked by sedimentation. Nevertheless, water quality could be plausibly enhanced by investing in bivalve populations in areas where bottlenecks to carrying capacity can be alleviated.

Besides their plausible benefits to water quality, investments in bivalve populations should promote other ecosystem services, such as the provision of essential fish habitat. Shellfish beds can help to stabilize erosion of stream bottoms and vulnerable marshes. A watershed-wide approach to restoring bivalves could also provide synergistic positive feedbacks because the restoration of freshwater mussel beds in nontidal areas can benefit tidal shellfish through water quality enhancement, whereas restored shellfish reefs and mussel beds in estuaries might aid diadromous fish that later serve as hosts for freshwater mussels.

The current ecosystem management paradigm relies on older restoration methods that can limit the acceptance and funding of bivalve restoration. In some cases, outdated management paradigms (*e.g.*, restoration only to historic conditions or on historic reefs) may also hinder the ability to adapt to the changing climate due to shifting species ranges with temperature and salinity rise. In addition, nutrient trading credits that help fund restoration are usually limited to treatments of wastes before they are discharged into a receiving water body, not after discharge, which often rules out traditional credits for bivalves. It will therefore be necessary for management policies and practices to evolve to best capitalize on restoration that is motivated by enhancement of ecosystem services.

The following recommendations may assist future research and planning efforts aimed at filling information gaps or testing pilot projects associated with bivalve restoration for water quality enhancement.

1. Develop a regional restoration strategy for native bivalve species to augment oyster restoration efforts for water quality remediation.
   - Prioritize ecologically significant, native species with high promise for restoration.
   - Include representative freshwater, brackish, and saltwater species.
   - Select pilot project sites in nontidal, intertidal, and subtidal waters.
   - Coordinate between Chesapeake and Delaware watersheds to enhance outcomes and information sharing.
2. Form a bivalve restoration task force consisting of scientists and managers to prepare and guide implementation of the strategy.
   - A technical subgroup should identify and fill knowledge gaps, provide pilot project specifications, and guide implementation and monitoring of pilot projects
   - A policy subgroup should identify and work to overcome operational impediments, such as permitting, and provide guidance for development of BMP.
   - An outreach subgroup should work to educate the public about the importance of noncommercial bivalves and build awareness for their conservation and restoration.
   - The task force should include representatives from Chesapeake and Delaware river basins (and potentially other mid-Atlantic watersheds), because of shared challenges, opportunities, and Atlantic slope bivalve species.
3. Fund research and development to fill vital knowledge gaps and standardize methods.
   - Deduce current species ranges and potential carrying capacity for target species.
   - Quantify core physiological rate functions for target species and ecological fates of filtered matter under expected natural conditions with common methods.
   - Model potential water quality benefits of target species at pilot project sites.
   - Optimize culture methods for species that contribute the most ecosystem services.
4. Adaptively manage the strategy.
   - Implement and monitor pilot projects.
   - Modify strategy periodically to adjust for lessons learned from monitoring of pilot projects and new scientific literature.
   - Expand implementation, building on the most successful pilot projects.

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