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Donna Marie Bilkovic
Virginia Institute of Marine Science, donnab@vims.edu

Molly Mitchell
Virginia Institute of Marine Science, molly@vims.edu

Robert E. Isdell
Virginia Institute of Marine Science, risdell@vims.edu

Matthew Schliep
Virginia Institute of Marine Science

Ashley R. Smyth
Virginia Institute of Marine Science

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Mutualism between ribbed mussels and cordgrass enhances salt marsh nitrogen removal

Donna Marie Bilkovic,† Molly M. Mitchell, Robert E. Isdell, Matthew Schliep, and Ashley R. Smyth[1]

Virginia Institute of Marine Science, College of William & Mary, P.O. Box 1346, Gloucester Point, Virginia 23062 USA

Abstract. Salt marsh ecosystems have declined globally and are increasingly threatened by erosion, sea level rise, and urban development. These highly productive, physically demanding ecosystems are populated by core species groups that often have strong trophic interactions with implications for ecosystem function and service provision. Positive interactions occur between ribbed mussels (*Geukensia demissa*) and cordgrass (*Spartina alterniflora*). Mussels transfer particulate nitrogen from the water column to the marsh sediments, which stimulates cordgrass growth, and cordgrass provides predator and/or heat stress refuge for mussels. Here, we test mussel facilitation of two functions in salt marshes that relate to N removal: microbial denitrification and water filtration. Microcosm experiments revealed that the highest rates of N_2 production and nitrification occurred when mussels were present with marsh vegetation, suggesting that mussels enhanced coupling of the nitrification–denitrification. Surveys spanning the York River Estuary, Chesapeake Bay, showed that the highest densities of mussels occurred in the first meter for all marsh types with mainstem fringing (1207 $\pm$ 265 mussels/m^2) being the most densely populated. The mussel population was estimated to be ~197 million animals with a water filtration potential of 90–135 million L/hr. Erosion simulation models demonstrated that suitable marsh habitat for ribbed mussels along the York River Estuary would be reduced by 11.8% after 50 years. This reduction in mussel habitat resulted in a projected 15% reduction in ribbed mussel abundance and filtration capacity. Denitrification potential was reduced in conjunction with projected marsh loss (35,536 m^2) by 205 g N/hr, a 16% reduction. Because of the predominant occurrence of ribbed mussels at the marsh seaward edge and because the highest proportional loss will occur for fringing marshes (20%), shoreline management practices that restore or create fringing marsh may help offset these projected losses.

Key words: biogeochemistry; denitrification; ecosystem functions; fringing marsh; *Geukensia demissa;* nitrogen; ribbed mussels; salt marsh; *Spartina;* wetland.

[1] Present address: Kansas Biological Survey, University of Kansas, 2101 Constant Avenue, Lawrence, Kansas 66047 USA.
† **E-mail:** donnab@vims.edu

INTRODUCTION

Humans rely on ecosystems to provide a range of services fundamental to their well-being (Costanza et al. 1997). Global declines in estuarine and coastal ecosystems (marsh, seagrass, oyster reefs) have been linked to significant loss of viable fisheries, nursery habitat provision, and water filtration services provided by suspension feeders (Barbier et al. 2011). The latter is critical to maintain water quality and is a management goal with significant societal investment. Salt marshes have long been recognized to provide numerous ecosystem services, but their position at the land–water interface places them at high risk from multiple stressors including erosion, sea level rise, and development (Kennish 2001). Significant global declines in salt marshes have occurred over

the past century (Kennish 2001), a trend that is not likely to be reversed. Growing coastal populations (Small and Nicholls 2003) and rising seas (e.g., Boon and Mitchell 2015) will likely lead to increased shoreline armoring and subsequent loss of wetland habitats and ecosystem function (e.g., Bilkovic and Roggero 2008, Peterson and Lowe 2009 and references within, Bulleri and Chapman 2010, Dugan et al. 2011, Dethier et al. 2016).

Ribbed mussels (*Geukensia demissa*) and cordgrass (*Spartina alterniflora*) have a mutualistic relationship which can enhance multiple ecosystem functions (Angelini et al. 2015). Ribbed mussels remove large amounts of particulate organic material comprising algae, detritus, and bacteria (Gosner 1971) from overlying waters through filtration and consumption. A portion of this material is transferred to the sediments as biodeposits, where it can fuel microbial processes, including denitrification. Additionally, by actively manipulating their habitat, mussels help to stabilize the marsh. Specifically, mussels tend to aggregate around cordgrass stems (Nielsen and Franz 1995), stimulate marsh plant root and rhizome growth with biodeposits, and bind sediment, which increases marsh height, stabilizes the marsh, and reduces erosion (Bertness 1984). In turn, high-density clumps of marsh plants serve as predator and/or heat stress refuge for mussels. Because ribbed mussels are the predominant intertidal bivalve species (Kuenzler 1961) found throughout salt and brackish marsh systems along the Atlantic Coast and into the Gulf of Mexico, and have a high filtration capacity, they are capable of mediating ecosystem services at local and broader estuary scales. Human and climate change-induced salt marsh loss places ribbed mussel ecosystem service provision at risk even before it is fully quantified. Accordingly, a better understanding of their facilitation of marsh function can inform the prioritization of wetland mitigation, conservation, and restoration efforts, with the intent of maintaining and enhancing ecosystem services.

Filtration rates of suspension feeders vary depending on factors such as the species, size of the individual, velocity of the water, and water temperature (Rice 2001, Comeau et al. 2008). In addition, for bivalves in the intertidal zone, filtration is restricted to periods of submergence. Filtration rates of *G. demissa* can be similar to those of the eastern oyster (*Crassostrea virginica*) and

higher than many other bivalves (including *Brachidontes exustus*, *Spisula solidissima*, and *Mercenaria mercenaria*) (Riisgard 1988). Ribbed mussels and oysters preferentially selected the same algae species under controlled experimental conditions (Espinosa et al. 2008). However, *G. demissa* are able to retain particles of a smaller size, such as small-sized bacteria, compared to *C. virginica* and *Mytilus edulis* (Wright et al. 1982). Bacteria in free suspension have been shown to contribute 25.8% to the metabolic carbon requirements of marsh mussels (Langdon and Newell 1990) and may be important contributors to the carbon and nitrogen budgets of mussels. Other food sources for ribbed mussels include microzooplankton (Langdon and Newell 1990, Lonsdale et al. 2009), *Spartina* (plant) detritus (Peterson et al. 1985, Kreeger et al. 1988, Langdon and Newell 1990), microphytobenthos, phytoplankton, and protists (Kemp et al. 1990, Newell and Krambeck 1995, Kreeger and Newell 1996). Particle retention efficiency of ribbed mussels is also high with 100% retention of 4- to 5-μm or larger particles and about 70% retention of 2-μm particles. In comparison, oysters retain 100% of 4- to 5-μm or larger particles and about 50% of 2-μm particles (Riisgard 1988). In general, the filtration capacity, which reflects filtration rate and particle retention efficiency, of ribbed mussels is relatively high among marine bivalves.

Ribbed mussels transfer particulate nitrogen (N) from the water column to the marsh sediments through filtration. About half of the nitrogen from filtered suspended particles is ingested by the mussel and about half of the ingested nitrogen is excreted as ammonium (NH_4^+; Jordan and Valiela 1982), a form of nitrogen that is used for primary production. Through biodeposition, the mussels can "fertilize" marsh plants and have been shown to stimulate the growth of cordgrass (Bertness 1984). Alternatively, mussel presence may enhance sediment microbial processes. For example, nitrification, the microbial oxidization of ammonium to nitrite and then nitrate, both bioavailable forms of N, may be enhanced in the presence of mussels because of the increased ammonium availability associated with excretion and mineralization of biodeposits. Further, under anaerobic conditions, the produced nitrate can be reduced to gaseous nitrogen, dinitrogen (N_2), and nitrous oxide (N_2O), during denitrification, a

microbial process that is an important N removal mechanism in coastal systems (Fig. 1). Complete denitrification leads to N_2, an inert form of nitrogen only available for primary production by nitrogen fixation. In contrast, incomplete denitrification to N_2O contributes to harmful greenhouse gases. Mussels facilitate sediment nitrogen cycling by transferring and concentrating nitrogen and carbon from tidal water to the marsh sediment through feeding and byssal thread production and decomposition (Bertness 1984). The organic matter and nitrogen transferred by mussels then become available for microbial metabolism. Mussel feeding activity and bioturbation may also oxygenate the sediments, which could enhance rates of coupled nitrification–denitrification as has been shown for other macrofauna including mollusks (Laverock et al. 2011). In this sense, mussels are mediators of the removal and recycling of nitrogen from aquatic ecosystems, although the magnitude of their contribution is yet uncertain. However, efforts to understand the movement of nitrogen through marine ecosystems have revealed habitat-specific differences in denitrification with higher rates found in the structured habitats of oyster reefs and marshes compared to intertidal and subtidal flats (Piehler and Smyth 2011).

To investigate the potential for ribbed mussel, *G. demissa*, facilitation of nitrogen cycling and thus water quality enhancement, we characterized *G. demissa* contribution to two functions in salt marshes that relate to N removal: microbial denitrification and water filtration. We conducted a continuous flow microcosm experiment to determine the influence of *G. demissa* on nitrogen processes in salt marshes. We used extensive population surveys and literature-derived filtration rates to estimate total contribution to water processing rates within a sub-estuary of the Chesapeake Bay. Our experiment was designed to investigate the effects of the individual species (cordgrass, mussel) as well as their combined effects on nitrogen cycling. To examine the implications of ongoing wetlands loss from erosion for ribbed mussel-mediated denitrification and water filtration, we modeled future (50 years from now) marsh extent and ribbed mussel abundance and distribution along the York River. Understanding the current and projected future capacity for mussels to process water and nutrients can inform marsh creation and conservation efforts, and
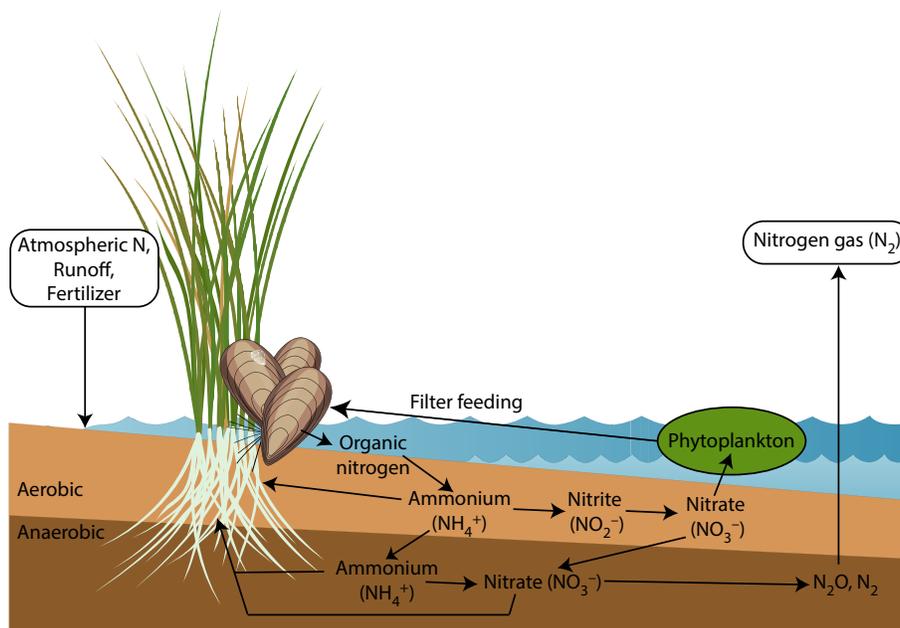

Fig. 1. Conceptualization of the role of ribbed mussel in mediating the marsh nitrogen cycle. Some symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/), University of Maryland Center for Environmental Studies.

deepen our comprehension of the mutualistic relationship between ribbed mussel and cordgrass originally explored by Bertness (1984).

MATERIALS AND METHODS

Study area

This study was conducted in the York River Estuary, Virginia, one of five major tributary systems in Chesapeake Bay and generally representative of conditions encountered throughout the Bay and similar estuaries (Reay and Moore 2009). The York River Estuary is a brackish system approximately 64 km long and begins at the confluence of the Mattaponi and Pamunkey rivers (Fig. 2). It possesses a wide range of salinities from approximately 20 ppt near the mouth of the river, to 0 ppt several kilometers upriver of the
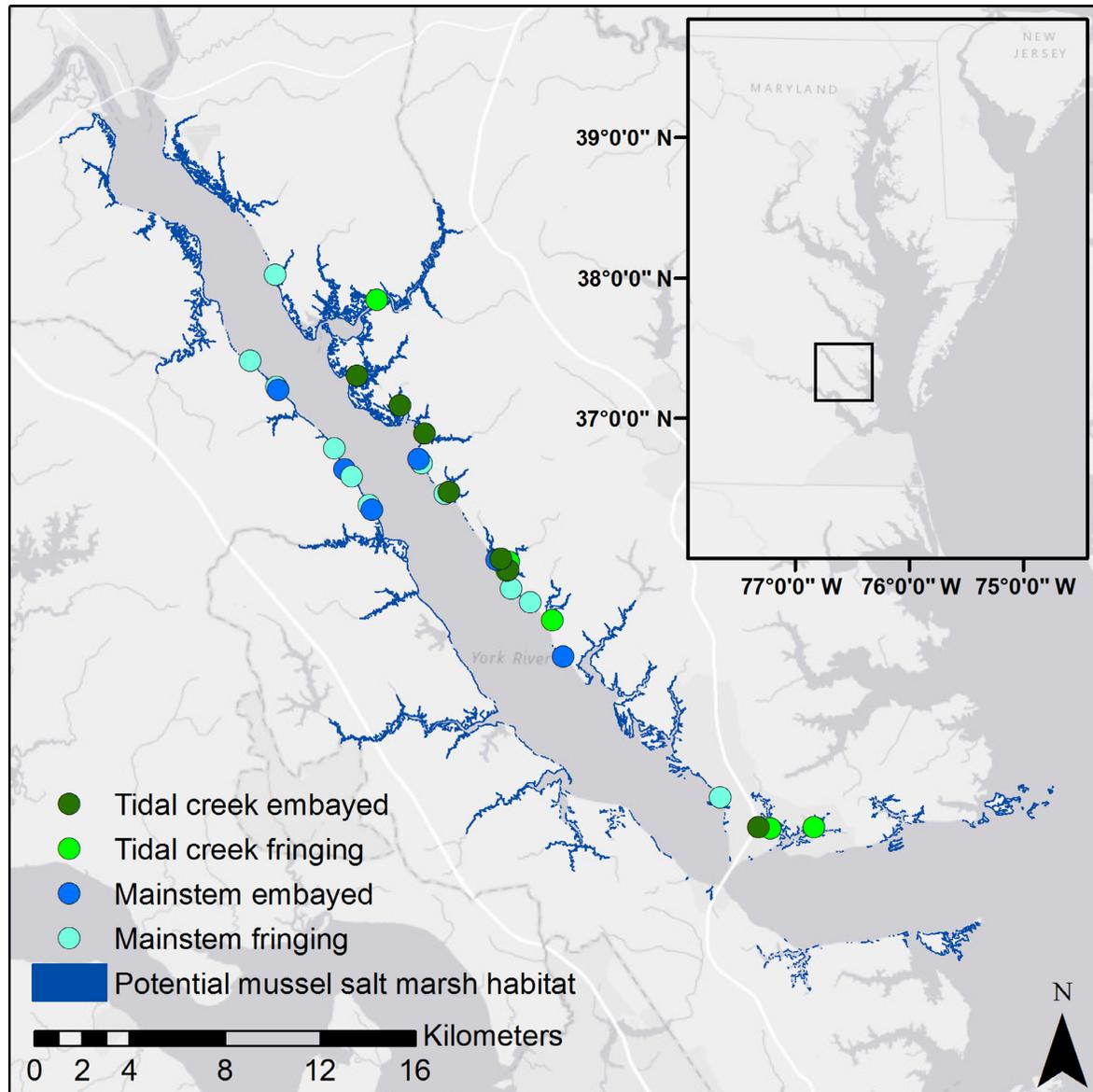

Fig. 2. Ribbed mussel sampling sites along the York River Estuary, Virginia. Potential mussel–marsh habitat area was estimated on the basis of suitable mussel habitat and observed mussel distribution patterns (salt marsh habitat within 4 m of the marsh–estuary interface and with salinity >8).

confluence. Annual salinity distribution is correlated with freshwater river discharge (Sisson et al. 1997). Mean tidal range near the mouth of the York River is 0.7 m and increases to 1.1 m in the upper tidal freshwater reaches of the Mattaponi River. The estuary supports a wide range of habitats, from freshwater swamps to tidal freshwater marshes to salt marshes, and the watershed is dominated by forested (61%) and agricultural (19%) land use (Reay 2009).

Mussel effects on nitrogen cycling in marshes

Continuous flow microcosm (10 cm diameter and 35 cm height) experiments were used to determine nitrogen fluxes (Smyth et al. 2013) for treatments with and without ribbed mussels. Nine intact sediment cores (10 cm deep) were collected during low tide on 7 July 2014 from a *Spartina alterniflora* marsh on Whittaker Creek in Gloucester Point, VA (37.333580° N, 76.436667° W). The experimental design consisted of four treatments with three replicates each: (1) mussels only, (2) mussels + sediment, (3) mussels + marsh vegetation (*S. alterniflora*) + sediment, and (4) marsh vegetation + sediment. The mussel-only treatment consisted of one large mussel (mean DW [SD]: 0.75 ± 0.06 g) in each replicate and the other treatments with mussels consisted of three live mussels (mean DW [SD] per core: 1.6 ± 0.6 g) in each replicate, with one exception, a mussel + sediment replicate was found post-experiment to have only one live mussel (0.9 g). Unfiltered York River water (18 ppt) was used as replacement water and held in a reservoir for the continuous flow incubations. Microcosms were incubated in an environmental chamber at 26°C, the same temperature as the collection site, under dark conditions to prevent bubble formation that would interfere with dissolved gas measurements. Each microcosm was capped with a gas and water-tight top, which had an inflow and outflow port. Water from the reservoir was pulled through the microcosms at a flow rate of 2 mL/min. Two lines, which flowed directly from the reservoir into sample vials (bypass lines), were used to test the quality of water being pumped into the microcosm. The microcosms were pre-incubated for approximately 18 h to reach steady state. Incubations then lasted for an additional 24 h. Three 15 mL samples of water were collected from each microcosm's outflow line and the bypass lines at 18, 20,

22, and 24 h, preserved with 200 μL of 50% $ZnCl_2$, and stored underwater, below the collection temperature prior to analysis for dissolved gases. Dissolved N_2, Ar, and O_2 concentrations were measured using a Blazers Prisma QME 200 quadrupole mass spectrometer (MIMS; Kana et al. 1994). Water samples (25 mL) for dissolved inorganic nitrogen (DIN) analysis were also collected and immediately filtered through 0.45-μm Whatman polyethersulfone filter and frozen until analysis. Filtrate was analyzed with a Lachat Quick-Chem 8000 (Lachat Instruments, Milwaukee, Wisconsin, USA) automated ion analyzer for combined nitrate and nitrite (NO_x), and ammonium (NH_4^+).

Fluxes of N_2, NH_4^+, and NO_x were calculated following methodology described in Smyth et al. (2013), and based on the difference between concentrations leaving and entering the microcosm, flow rate, and surface area of the microcosm. A positive flux represents production in excess of consumption, and a negative flux is demand in excess of consumption within the microcosm. N_2 and O_2 fluxes were calculated using the ratio with Ar (Kana et al. 1994, Ensign et al. 2008). With this technique, a net positive N_2 flux indicates denitrification dominates, while a net negative N_2 flux indicates nitrogen fixation dominates. Denitrification efficiency, the percent of the total benthic DIN efflux into the water column that is N_2, describes the portion of nitrogen that is remineralized relative to removal through denitrification. Denitrification efficiency was calculated using the following equation (Eyre and Ferguson 2002):

$$N - N_2 \text{ flux}/(N - DIN + N - N_2 \text{ flux}) * 100 \quad (1)$$

An efficiency greater than 50% indicates that more mineralized nitrogen is being removed through denitrification than recycled (nitrogen sink); however, if the efficiency is less than 50%, nitrogen recycled back to the water column is greater than nitrogen removal (nitrogen source). Mass balance equations were used to estimate the proportion of denitrification that was coupled to nitrate production from nitrification as: $DNF_c = DNF_t + x$, where DNF_c is coupled nitrification–denitrification, DNF_t is the total net positive N_2 flux, and x is the measured nitrate flux. Only positive nitrate fluxes and positive N_2 fluxes were used in the calculation (Gonzalez

et al. 2013). We used one-way ANOVA with Tukey's honestly significant difference procedure to examine differences in fluxes, calculated nitrification rates, percent of denitrification that is coupled to nitrification, and denitrification efficiency among all treatments (JMP v.11.2.0). Percent of denitrification coupled to nitrification was arcsine-transformed prior to statistical analysis to normalize data.

Mussel abundance and distribution

We conducted mussel surveys at 20 *S. alterniflora*-dominated marshes on the York River within ribbed mussel salinity preferences (~8–30 ppt) during the summer (June–July 2013; Fig. 2). Marshes were categorized as fringing (narrow bands of cordgrass along the shoreline) or embayed/extensive (wider meadow marshes in embayments; henceforth extensive) and 10 marshes were randomly selected from each category. We extracted tidal marsh information (extent and type) from a recent tidal marsh inventory (2009) developed using the high-resolution basemap imagery and field surveys (Mitchell et al. 2011). Marshes were further distinguished as being positioned on the mainstem of the York River ($n = 13$) or within primary tidal creeks of the York River ($n = 7$). We determined mussel recruit (<15 mm) and adult density within 0.25-m^2 quadrats along six replicate transects placed at 5-m intervals along the shore. Transects ran perpendicular to the shore from the edge of the marsh to the high marsh habitat. Because mussel density varies with tidal elevation (Bertness 1984), we placed four quadrats along each transect at 1-m intervals from the marsh–estuary edge representing distances of 0–1, 1–2, 2–3, and 3–4 m (preliminary sampling showed that the vast majority (>99%) of mussels are found within 4 m). We collected a representative subsample of mussels ($n = 10$) from two quadrats in two transects in each marsh (40 animals in total) to document the size and biomass distribution of the population. Each mussel was then measured (L × W × H, digital calipers, 0.1 mm), shucked to dry tissue and shell separately (60°C for 48 h), and ashed (550°C for 4 h) to determine ash-free dry matter (AFDM). We estimated a bivalve condition index (CI) based on shell weight (Crosby and Gale 1990) for each animal (Eq. 2).

$$CI = \left(\frac{\text{dry soft tissue wt (g)} \times 1000}{\text{internal shell cavity capacity (g)}} \right) \quad (2)$$

Within each quadrat, we counted marsh plant stems and determined the mean tallest height of five stems for each species present. We used a hand-held YSI sonde to record dissolved oxygen, salinity, conductivity, pH, turbidity, water temperature, and chlorophyll *a* in the waters near the marsh edge at each transect, ~0.3 m above the bottom.

We calculated mussel abundance for each marsh within each 1-m interval from the marsh edge and then estimated the average abundance per interval for each marsh type: mainstem fringing, mainstem extensive, tidal creek fringing, and tidal creek extensive. We calculated the potential total area of marsh habitat per each 1-m interval available to mussels along the York River (constrained by areas with salinity >8, and within 4 m of the marsh–estuary edge) using wetlands spatial data (CCRM-VIMS Tidal Marsh Inventory 2013) in ArcGIS 10.1. We then estimated the total water processing rate (L/h) for mussels in the York River using mean density of mussels per hectare based on marsh type, total hectares of available suitable marsh habitat, previously estimated ribbed mussel clearance rates from June to October (1.6–2.4 L·h^{-1}·g·DW^{-1}, Galimany et al. 2013), and the average dry weight biomass of mussels.

We used generalized linear models to assess the main effect of marsh type, and covariate factors of distance from marsh edge, and *S. alterniflora* stem density on the abundance of ribbed mussels. We examined adult and new recruit (<15 mm) mussels separately. We applied a log-linear Poisson regression model and post hoc pairwise multiple comparisons of factors using the packages "GLM" and "phia" in R (R Development Core Team 2011). If a covariate had a significant effect on mussel density, linear regression analyses were used to determine the percent of variation in mussel density that the covariate explained (R^2 value). We compared condition indices among marsh types using the Kruskal-Wallis rank sum test followed by the Mann-Whitney U test for multiple comparisons. We determined the relationship between total mussel (shell and tissue) dry weight (g) and shell volume (L × W × H mm) with linear regression analyses (JMP 10.0.2).

We estimated the potential loss of marsh habitat due to erosion over the next 50 years by spatially adjusting the leading edge of marshes inland by the current erosion rates (m/yr; VIMS Shoreline Studies Program 2012, Chesapeake Bay EPR (1937–2009) Shoreline Change, http://web.vims.edu/physical/research/shoreline/GISData/Flexviewer/SSP_for_web/; Rodríguez-Calderón 2014) multiplied by 50 years. The subset of the marshes previously identified as having the potential for sea level rise-driven inland migration (i.e., no barriers to migration such as shoreline armoring, low elevation) by Bilkovic et al. (2009) were adjusted inland. Potential mussel habitat was identified as the first 4 m of the projected future marsh extent from the wetted edge, and was divided into four 1-m intervals and grouped by marsh type. We calculated the future mussel mean (95% CI) abundance (number/m^2) and biomass (g/m^2) as measured in the field study for each marsh type and distance interval × the area of marsh in each of those categories. We made the assumption that competition for space is limiting abundance and growth in the crowded, high-density, leading marsh edge (Stiven and Kuenzler 1979) and that given a smaller area of available future habitat mussels would not increase their densities.

Percent change in future mussel water processing potential was then calculated the same way as described above, with future mussel abundance and biomass substituted for the present estimates. Percent change in denitrification potential was derived using estimates of mean N$_2$ fluxes for the whole ecosystem treatment (mussels + marsh + sediment; 410.9 ± 146.1 N$_2$ flux (μmol N·m^{-2}·hr^{-1})) and projected loss of marsh area (m^2) from erosion. We calculated the change in denitrification (μmol N/hr) that might occur with a change in the first 2 m of mainstem marsh area where mussel densities were the most abundant and similar or more dense than experimental conditions ($\bar{x}$ = 423 mussels/m^2 in the whole ecosystem treatment compared to natural densities (mainstem extensive, 408 mussels/m^2; mainstem fringing, 789 mussels/m^2).

RESULTS

Mussel effects on nitrogen cycling in marshes

All treatments had a net positive N$_2$ flux, indicating net denitrification. Mean net denitrification rates (±SE) were significantly higher (410.9 ± 146.1 μmol N·m^{-2}·h^{-1}) in the "whole ecosystem" treatment which included mussels + vegetation + sediment than in the treatment with ribbed mussels alone (58.2 ± 17.9 μmol N·m^{-2}·h^{-1}; one-way ANOVA, $F_{3,8}$ = 7.45, $P < 0.05$; Fig. 3). The marsh vegetation + sediment and mussel + sediment treatments had intermediate net denitrification (208.4 ± 44.2 and 251.3 ± 79.9 μmol N·m^{-2}·h^{-1}, respectively), which were not significantly different from each other or the other treatments (α = 0.05).

There was an uptake of NO$_x$ for the marsh vegetation + sediment and mussel + sediment treatments, but efflux in the whole ecosystem
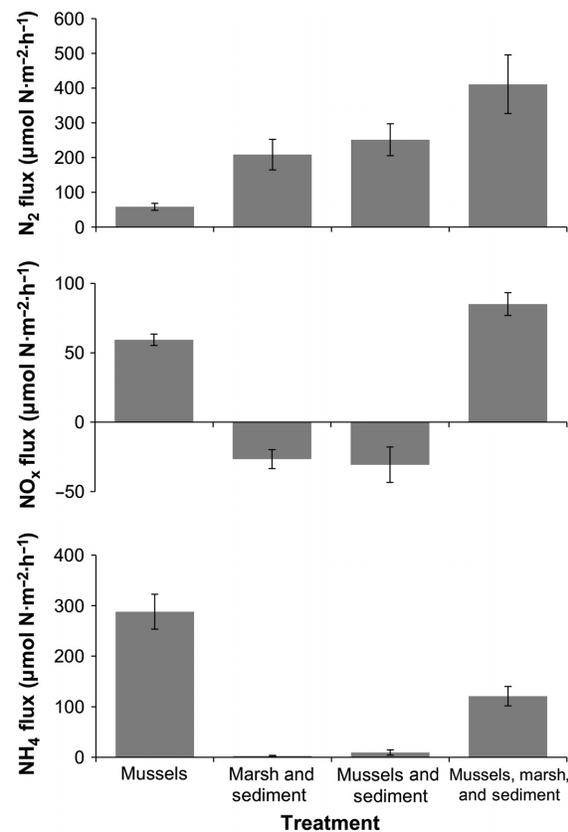

Fig. 3. Net denitrification (N$_2$ efflux) occurred in all treatments; however, the highest rates were observed in the whole ecosystem treatment that included mussels, marsh vegetation, and marsh sediment possibly because of enhanced coupling of the nitrification–denitrification cycle when ribbed mussels are present in the marsh.

treatment and the treatment with mussels alone. Mean NO_x fluxes ($\pm$SE) were significantly greater in the "whole ecosystem" (85.1 ± 8.2 µmol m$^{-2}\cdot$h^{-1}) and mussels alone (59.4 ± 7.1 µmol m$^{-2}\cdot$h^{-1}) treatments than in the marsh vegetation + sediment (-26.7 ± 6.8 µmol m$^{-2}\cdot$h^{-1}) and mussel + sediment (-30.7 ± 12.8 µmol m$^{-2}\cdot$h^{-1}) treatments ($F_{3,8} = 47.5$, $P < 0.001$). There was an efflux of NH_4^+ from all treatments, although the efflux from marsh vegetation + sediment and mussel + sediment treatments was negligible (Fig. 3). NH_4^+ efflux was highest in the treatment with mussels alone which may be from mineralization of biodeposits and/or direct excretion from the mussel, followed by the whole ecosystem treatment ($F_{3,8} = 44.5$, $P < 0.001$). Net DIN (sum of NH_4 and NO_x) fluxes were generally positive for treatments with mussels (Fig. 3), indicating a net source of inorganic nitrogen to the water column. Two exceptions were observed in the mussels + sediment treatment, when net DIN fluxes were negative (mean: -38.5 ± 8.8 µmol m$^{-2}\cdot$h^{-1}), indicating a net sink of inorganic nitrogen. The nitrification rate was significantly higher for the whole ecosystem treatment compared to all other treatments (one-way ANOVA, $F_{3,8} = 11.1$, $P = 0.003$; Table 1). The mussel-only treatment had a lower denitrification efficiency because of the higher rates of both ammonium and nitrate production (Table 1). Whole ecosystem treatments had intermediate levels of denitrification efficiency (>50%) because of an increase in nitrogen regeneration either directly from the mussels or from mineralization of biodeposits (one-way ANOVA, $F_{3,8} = 92.2$, $P < 0.001$). The proportion of denitrification that was coupled to nitrate production from nitrification was highest for mussel-only and whole ecosystem treatments (one-way ANOVA, $F_{3,8} = 14.0$, $P = 0.002$; Table 1).

Mussel abundance and distribution—
York River Estuary

Mussel abundance was highly variable among marsh types and position; fringing marshes along the mainstem of the estuary possessed the highest average number of animals (adjusted mean: 204 mussels/m^2) followed by mainstem-extensive (122 mussels/m^2) and creek-fringing (21 mussels/m^2) marshes. Ribbed mussels were present at 18 of the 20 marshes, absent in two tidal creek-extensive marshes. When present in tidal creek-extensive marshes, mussels were sparse with only eight total animals observed. Mussel density increased with *S. alterniflora* density ($F_{1, 440} = 143.5$, $P < 0.001$, $R^2 = 0.24$) and decreased with increasing distance into the marsh from the seaward edge ($F_{1, 478} = 74.2$, $P < 0.001$, $R^2 = 0.13$). The highest mean densities occurred in the first meter for all marsh types with mainstem-fringing (1207 ± 265 mussels/m^2) and mainstem-extensive (630 ± 152 mussels/m^2) marshes being the most dense (Table 2). Over 85% of the animals were found in the first 2 m from the marsh edge for every marsh type. Adult and recruit mussels followed similar patterns of distribution among and within marshes (Table 3).

Generally, mussels in mainstem-fringing marshes were the most abundant and in the best condition compared to other marshes. Mussels in mainstem-fringing marshes had significantly higher CI values (113.2 ± 2.6) than those in mainstem-extensive (101.3 ± 2.1) or creek-fringing (103.5 ± 4.1) marshes (Kruskal-Wallis, $P < 0.001$). Condition indices could not be estimated for tidal creek-extensive marshes because of the scarcity of animals. Although they were smaller in number, mussels in tidal creek-fringing marshes had the highest average biomass (0.7 g dry weight of tissue) compared to other marsh types (0.2 g DW) (Kruskal-Wallis, $P < 0.001$). Mussels in fringing marshes within tidal creeks had a broader size

Table 1. Calculated nitrification rates, percent of denitrification that is coupled to nitrification, and denitrification efficiency (the percent benthic efflux that is N_2) for each treatment, mean (SE) for each treatment.

Treatment	Calculated nitrification rate (µmol N$\cdot$m$^{-2}\cdot$hr^{-1})	Percent denitrification coupled to nitrification	Denitrification efficiency
Mussels	117.60 (14.14)[b]	100% (0.00)[a]	14.14% (1.08)[c]
Marsh	181.76 (37.51)[b]	87.36% (0.85)[b]	98.68% (0.71)[a]
Mussels & sediment	220.62 (47.37)[b]	86.79% (6.80)[b]	96.54% (2.18)[a]
Mussels, marsh, & sediment	495.99 (78.35)[a]	100% (0.00)[a]	65.12% (7.81)[b]

Note: Significant ($\alpha < 0.05$) differences among treatments for each estimate are denoted by different superscript letters.

Table 2. Mean mussel density (number of mussels/m^2 [SE]) by marsh type and 1-m increment distances from the marsh edge.

Marsh type	Distance (m) from marsh edge moving landwards			
	0–1	1–2	2–3	3–4
Creek extensive	0	0.3 (0.2)	0	0
Creek fringing	167 (57)	34 (17)	11 (7)	8 (6)
Mainstem extensive	630 (152)	185 (55)	71 (20)	59 (23)
Mainstem fringing and marsh island	1207 (265)	371 (125)	252 (126)	16 (7)

distribution than mainstem marshes (Fig. 4). The overall relationship between mussel dry weight and shell volume (inclusive of all marsh types) was strongly correlated positively ($R^2 = 0.97$, $n = 324$, Eq. 3).

$$DW(g) = 0.44209306 + 0.00021836 \\ (\text{shell volume, mm}^3) \tag{3}$$

We estimated that there is approximately 390 ha of marsh habitat suitable for ribbed mussel occupancy along the York River. The mussel population on the York was estimated to be ~197 million animals (range: 83–313 million, 95% CI; Appendix S1: Table S1). The water filtration potential of mussels on the York River is between 35 and 218 million liters per hour

(mean: 90–135 million L/hr) on the basis of observed biomass and potential clearance rates (Galimany et al. 2013).

Projected mussel abundance and distribution—York River Estuary

Our marsh erosion simulations (Table 4, Fig. 5) indicated that suitable marsh habitat for ribbed mussels along the York River would be reduced by 11.8% from 390 to 343 ha after 50 years of erosion and sea level rise. Of that 11.8% overall change, ~20% of suitable fringing marsh habitat was lost and ~11% of suitable extensive marsh habitat was lost. These losses were fairly similar for marshes occurring in either tidal creeks or along the mainstem estuary (Table 4). This reduction in mussel habitat

Table 3. Analysis of deviance of the effects of marsh type, distance in marsh from seaward edge, *Spartina alterniflora* density (stems/m^2), and the interactions on the abundance (mussels/m^2) of ribbed mussel adults and recruits.

Model terms	df	Deviance	Residual df	Residual deviance	P(Chi)
Adult mussels—density					
NULL			479	365,179	
Type	3	73,118	476	292,061	<0.001
Distance	1	80,065	475	211,996	<0.001
Spartina	1	11,844	474	200,152	<0.001
Type : Distance	3	198	471	199,955	<0.001
Type : *Spartina*	3	8761	468	191,194	<0.001
Distance : *Spartina*	1	3362	467	187,832	<0.001
Type : Distance:*Spartina*	3	924	464	186,908	<0.001
Recruit-sized mussels—density					
NULL			479	93,074	
Type	3	15,528	476	77,546	<0.001
Distance	1	22,116	475	55,430	<0.001
Spartina	1	5552	474	49,877	<0.001
Type : Distance	3	219	471	49,658	<0.001
Type : *Spartina*	3	3224	468	46,434	<0.001
Distance : *Spartina*	1	23	467	46,411	<0.001
Type : Distance : *Spartina*	3	91	464	46,320	<0.001

Note: Models are fitted sequentially, and a X^2 test is used to test for significance.
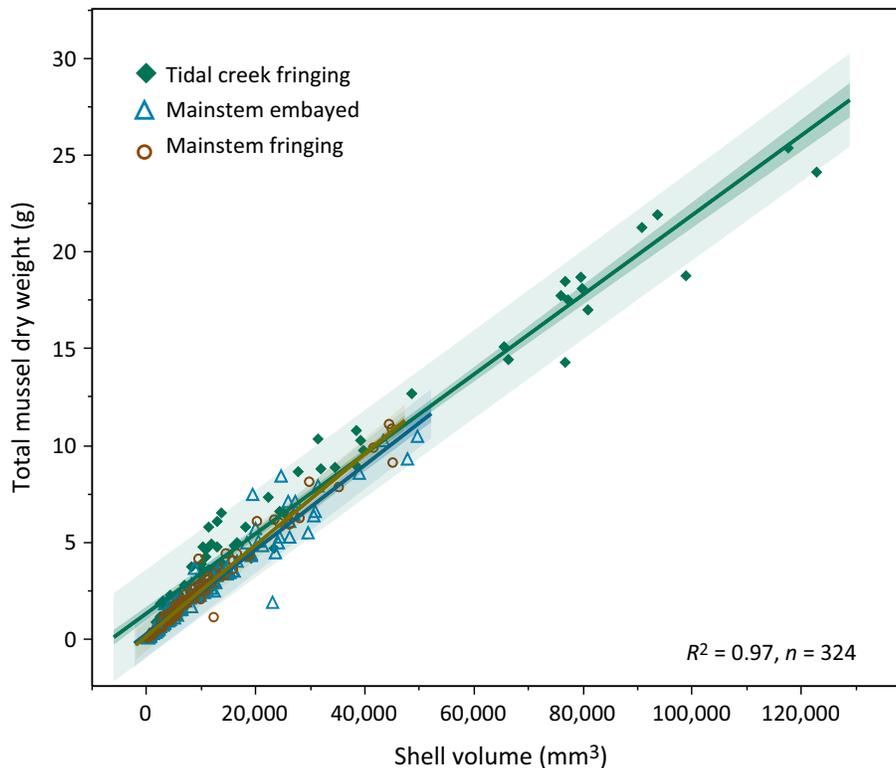
Fig. 4. Relationship between ribbed mussel dry weight and shell volume. Mussels in fringing marshes within tidal creeks had a broader size distribution than mainstem marshes. The overall relationship between mussel dry weight and shell volume (inclusive of all marsh types) was strongly correlated ($R^2 = 0.965$, $n = 324$). Line and confidence of prediction (95% CI) is shown as an expanded shaded area.

resulted in a projected 15% reduction in ribbed mussel abundance from 197 million mussels to 167 million mussels (range: 71–263 million, 95% CI). Future filtration capacity was similarly reduced by 13.9–15.3% (Appendix S1: Table S1) as a result of decreased mussel biomass.

Table 4. Estimated percent change in marsh habitat area from erosion after 50 years by distance from the marsh edge and marsh type.

| Marsh type | Distance (m) from marsh edge | | | | |
	0–1	1–2	2–3	3–4	Total
Tidal creek	−7.2	−12.6	−12.6	−12.5	−11.1
Extensive	−7.0	−11.3	−11.3	−11.5	−10.2
Fringing	−8.3	−25.0	−27.1	−25.5	−20.6
Mainstem estuary	−13.4	−17.7	−18.7	−20.1	−17.4
Extensive	−8.8	−11.4	−11.2	−14.5	−11.4
Fringing	−15.5	−20.7	−22.3	−22.9	−20.2
Total	−7.9	−13.2	−13.3	−13.3	−11.8

Denitrification was reduced in conjunction with projected marsh area loss (35,536 m^2) by 205 g N/hr, a 16% reduction (Table 5).

DISCUSSION

Mussel–Marsh nitrogen dynamics

Interactions between ribbed mussels and cordgrass can have positive effects on water quality and modify nutrient cycling. The increased flux of material from the water column to the sediment as a result of mussel filtration not only cleans the water, but also can stimulate microbial activity. Our results showed the highest rates of denitrification (net N$_2$ production) and nitrification for treatments with marsh vegetation and mussels, suggesting the possibility of enhanced coupling of nitrification–denitrification when ribbed mussels are present in the marsh. This is further supported in mass balance estimates of

Legend

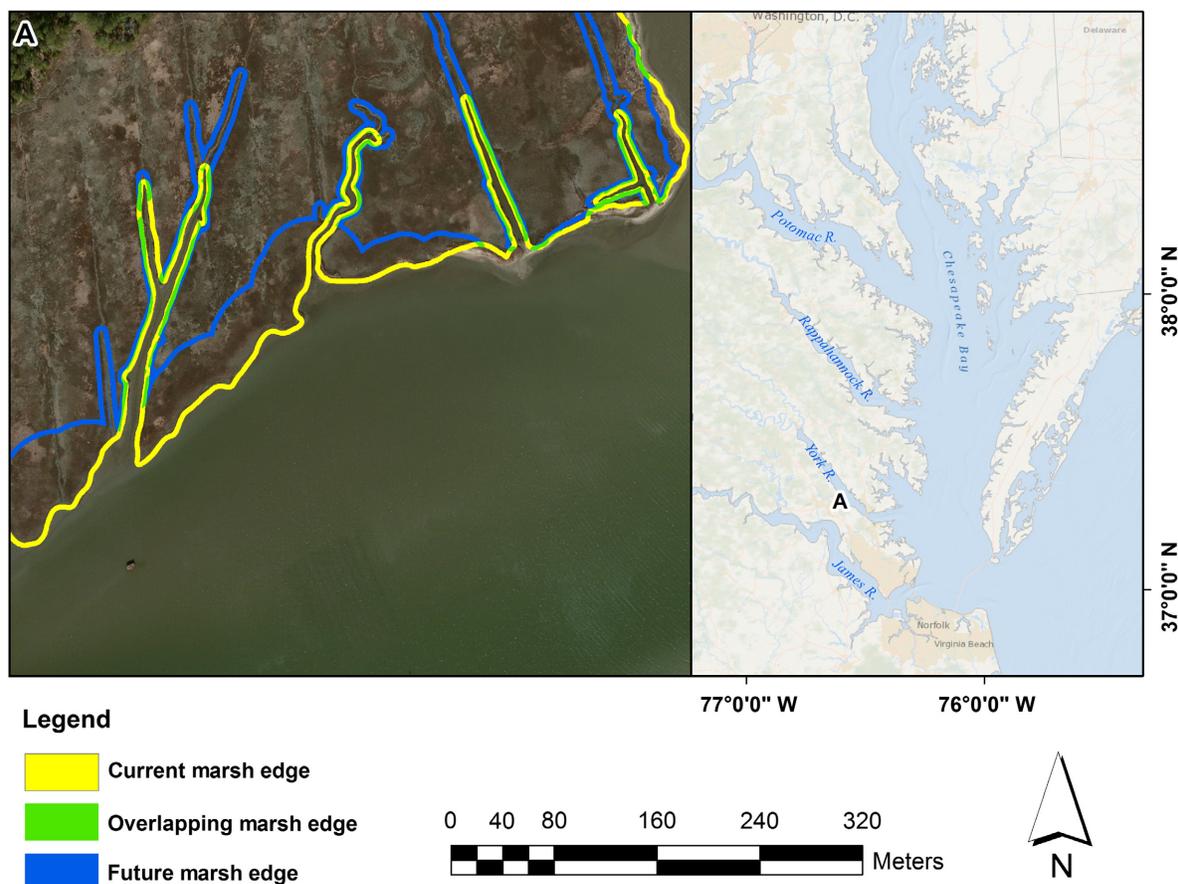|	
🟨	**Current marsh edge**
🟩	**Overlapping marsh edge**
🟦	**Future marsh edge**

Fig. 5. Projected change in marsh habitat in the next 50 years was estimated on the basis of current erosion rates. Changes were greatest along the mainstem estuary where erosion rates were highest and barriers to inland migration are extensive.

100% of denitrification being coupled with nitrification when mussels and cordgrass were together. The mechanism for the enhanced rates of denitrification in the whole ecosystem treatments may be due to some combination of the following (1) increased organic nitrogen provided by the mussels, (2) tightly coupled sediment oxygenated–deoxygenated root zones mediated by the plants and mussels increasing nitrification (Jordan and Valiela 1982, Howes et al. 1986, Laverock et al. 2011), and (3) increased availability of labile carbon compounds into the surrounding soil from plant exudes, which have been shown to increase local

Table 5. Change in denitrification potential was determined from estimated future mainstem marsh area loss.

Marsh type	Marsh area loss (m^2)	Denitrification potential loss (%)	Denitrification potential loss (g N·h^{-1})	Annual lost denitrification potential (g N·m^{-2}·yr^{-1})
Mainstem-extensive marshes	−7426	−10.1	−43	−6
Mainstem-fringing marshes	−28,109	−18.1	−162	−23
All mainstem marshes	−35,536	−15.5	−205	−29

Notes: The analysis considered only the first 2 m of the marsh where mussel densities were the most abundant and similar or more dense than experimental conditions ($\bar{x} = 423$ mussels/m^2 in the whole ecosystem treatment compared to natural densities (mainstem extensive: 408 mussels/m^2, mainstem fringing: 789 mussels/m^2). Annual loss in denitrification was conservatively estimated for 7 months of activity, which would be inclusive of the marsh plant growing period.

nitrogenase activity (Boyle and Patriquin 1981) by serving as a carbon source for denitrifiers. The mussels and cordgrass modify the availability resources to the microbial community as well as the physical environment and in turn affect rates of nitrogen cycling processes.

Mussels and marsh plants may have a facultative mutualistic relationship where cordgrass provides particulate nitrogen for mussels to filter and the added ammonium from mussel excretion in a nitrogen-limited marsh may increase cordgrass growth and result in better structural habitat for the mussels (Jordan and Valiela 1982, Bertness 1984). For a New England salt marsh–estuarine ecosystem, Jordan and Valiela (1982) estimated that ribbed mussels filtered 1.8 times the particulate nitrogen exported from the marsh by tidal flushing with slightly more than half of the nitrogen absorbed excreted as ammonium. The position of ribbed mussels at the sediment–water interface likely affords an added benefit of promoting the retention of nitrogen in the marsh for use by cordgrass as opposed to being released in the water column for phytoplankton use, which may lead to nuisance algal blooms or hypoxia events.

The observed patterns in N_2 fluxes suggest that the whole ecosystem has more nitrogen removal than the individual pieces. Partial treatments (mussel + sediment; marsh + sediment) that included sediment both enhanced N_2 relative to the mussel alone. In both cases, there was an increase in the importance of water column nitrate for denitrification, as indicated by a decrease in nitrification. It is likely that denitrification in these treatments is limited by nitrate because there is ample organic carbon available from the primary producers, from the sediment community, and from the mussel biodeposits. The lack of difference in nitrogen fluxes between the mussel + sediment and marsh + sediment treatments suggests that these species individually function similarly in terms of their ability to modify the nitrogen cycle. The whole ecosystem treatment with both species had the highest rate of denitrification. Conditions in this treatment are just right for denitrification where there is plenty of carbon from the marsh, the sediments, and the mussels and there is an ample supply of nitrate due to increased nitrification. However, if the roots increase O_2, the presence of O_2 may limit denitrification, which is an anaerobic process. Overall, having both mutualistic species in a system enhanced the ecosystem service of denitrification.

Dense assemblages of bivalves are major components in the recycling of nutrients in estuaries because of their ability to move material from the water column to the sediment. Intertidal dense mussel beds in two Dutch estuaries had very fast turnover rates for chlorophyll a and ammonium (3 wk or less) that exceeded those rates for individual organisms and were similar to rates observed for intertidal oyster reefs in South Carolina (Dame et al. 1991). The enhanced denitrification in marshes with mussels present combined with the relatively dense ribbed mussel assemblages in York River marshes also suggests that they are a major contributor to N cycling on a system level. Most ribbed mussels tend to settle on aggregates of adult mussels around the stems of *S. alterniflora* (Nielsen and Franz 1995) and can reach densities of 2000–3000 in New England and 10,000 in Jamaica Bay, New York, per m^2 (Kuenzler 1961, Lent 1969, Stiven and Kuenzler 1979, Bertness and Grosholz 1985, Lin 1989, Franz 1997, 2001). Similarly, mussel densities of 3000–4000 were regularly observed along the York River with a few sites reaching 5000–8000 animals/m^2. These observed York River abundances translate to ~56,000 kg of mussel biomass and mean clearance rates of 90–135 million L/hr (using mean filtration estimates from June to October, Galimany et al. 2013). By comparison, the historically low current oyster population on the York River was estimated to be able to filter 109 million L/hr during peak summer months (June–August), an 85% decline in filtration capacity since ~1900 (Zu Ermgassen et al. 2013) and near the mid-range of estimates for ribbed mussel filtering potential. Using the volume of the York River (796,920,000 m^3) and residence time of 11 days, the proportion of the estuary that could be filtered by mussels within its residence time would be ~1.5–2.3%, which is similar to the estimated % volume filtered by present-day oysters on the York (Zu Ermgassen et al. 2013). This assumes that all water is available for filtration, which is not entirely valid owing to potential water access limitations from stratification or spatial positioning in the estuary (Pomeroy et al. 2006). More precisely, only tidal water exposed to the marsh will be available for

filtration by ribbed mussels, but mussels can potentially filter all of the water in the marsh during a tidal cycle (Jordan and Valiela 1982). This in turn will limit export of particulates into the greater estuary, serving to reduce turbidity and enhance water quality. Moreover, ribbed mussels are filtering nearshore and intertidal waters complementing oyster filtration of deeper bottom waters, leading to improved localized water quality in multiple estuarine habitats.

Comparison of N_2 fluxes to other bivalve studies

Oysters and mussels are two of the most abundant species in coastal ecosystems, providing water quality benefits due to filtration. Net N_2 fluxes measured in this study fall within the range of N_2 fluxes found in oyster reef ecosystems, which are highly variable based on site and seasonal differences (Kellogg et al. 2014 and references therein). We observed net positive N_2 fluxes for our treatments, indicating that denitrification was occurring in excess of nitrogen fixation. Although each treatment was net denitrifying, the presence of mussels increased denitrification in the salt marsh ecosystem by about 200 μmol N·m^{-2}·hr^{-1}. Net N_2 fluxes from the mussel + marsh treatment were similar to fringing intertidal oyster reefs in North Carolina (Piehler and Smyth 2011). Although denitrification rates were similar, ammonium fluxes were higher in the mussel + marsh treatment, likely due to the presence of mussels inside the chamber which are a direct source of ammonium. In experiments looking at the direct effects of individual oysters on sediment nitrogen cycling, the individual organisms had the highest rate of N_2 production, and this rate was higher than what was observed for the individual mussel; however, when oysters and sediment were combined, N_2 production decreased (Smyth et al. 2013), while for the mussel, the presence of the sediment or marsh grass led to an increase in N_2 production compared to when the mussel was alone. This would suggest that there is an interactive effect between the mussel and sediment microbial community that is absent from the oysters. Differences in particle retention, filtration capacity, and life history between the two bivalves (Riisgard 1988) can contribute to the observed differences as can differences in biofilms or gut microbiomes. While oysters are reef-building mollusks, ribbed mussels form large aggregates integrated into the sediment matrix and anchored to the marsh grass. Biodeposits from ribbed mussels contribute to sediment accumulation and introduction of new material to the sediment surface in the marsh directly (Smith and Frey 1985). For oyster reefs, biodeposit accumulation occurs mostly on the sediment surface and is integrated into deeper sediment over time (Rodriguez et al. 2014). Mussel waste products are likely more accessible to bacteria which reside deeper in the sediment as compared to the oysters, where biodeposits are more likely to settle on the surface. This difference in the quality of organic matter, as well as where and how biodeposits accumulate, could alter sediment nitrogen cycling processes such as denitrification as well as other fluxes such as NO_x and NH_4^+.

Conserving and enhancing cordgrass–mussel mutualism for ecosystem services

The spatial distribution of ribbed mussel populations within a marsh clearly indicates the significance of the immediate marsh edge habitat. The highest densities of mussels were observed within narrow fringing marshes and within the first meter of the marsh. Likely, the availability of food items and accessibility of the habitat during larval settlement periods contributed to the high densities observed in fringing environments. In tidal creek habitats, mussels were fewer in number, but larger in size, which may suggest that predation pressure is lessened in those marsh settings or growth/maturation is delayed due to shorter feeding periods. These patterns are consistent with other research noting although there were less abundant mussels higher on shore, mussel lifespan tends to increase with increasing marsh elevation. Some mussels in the higher tidal zones reach 15 years or older, while mussels on the marsh edge tend to be around 6 or 7 years old (Lutz and Castagna 1980, Brousseau 1982, Bertness and Grosholz 1985, Franz 2001). In addition, contributing to the differences in population structure along an elevation gradient, mussels that are farther inland from the marsh edge tend to grow slower as a result of shorter submergence and feeding time, which can delay maturation an additional year compared to the mussels along the edge of the marsh.

The value of narrow fringing marshes is often overlooked, despite evidence that these marshes are able to perform many of the desired ecosystem services provided by more extensive meadow marshes, including wave attenuation (Knutson et al. 1982, Shepard et al. 2011), fish and invertebrate utilization (Minello et al. 1994, Peterson and Turner 1994, Micheli and Peterson 1999, Currin et al. 2008), sediment trapping (Neubauer et al. 2002), and groundwater nitrate removal (Tobias et al. 2001). This study further supports the value of fringing marsh for water quality enhancement mediated by the dominant marsh bivalve, ribbed mussels. In many settings, fringing marshes are highly vulnerable to erosion and sea level rise because of the presence of barriers to their landward migration such as shoreline armoring and residential or urban infrastructure. The narrow fringing marshes in such a setting will likely be lost first. This study indicated that the highest proportional loss will occur for fringing marshes (20%), while extensive marshes were projected to experience 11% loss. This may result in a potential loss of 15% filtration capacity and 16% denitrification by ribbed mussels in the York River. Our estimates of future marsh loss, and associated ecosystem service loss, are likely conservative because we based erosion rates on historic changes and did not incorporate erosion exacerbated by sea level rise or marsh drowning. The loss of fringing mainstem estuary marshes may also compromise habitat connectivity across the greater seascape. Marshes in connected seascapes may be subsidized by surrounding marsh habitats (e.g., mussel larval source) and ensure the sustainability of mussel populations, while those in highly fragmented seascapes may suffer the effects of isolation. Habitat fragmentation has been linked with shifts in biodiversity, loss of habitat-specific sensitive or functionally important species, and isolation of populations when connectivity is diminished (Kareiva and Wennergren 1995, Fahrig 2003, Thrush et al. 2008), but estuarine systems have been far less studied than in terrestrial systems even though estuaries and coasts have experienced substantial habitat loss and fragmentation (e.g., Lotze et al. 2006). Anticipated significant marsh loss is not limited to the York River Estuary; in Virginia tidal waters of Chesapeake Bay, ~38% of marshes will be unable to migrate because of adjacent developed lands, armored shores, and/or

high bank height and are thus highly susceptible to loss from erosion, sea level rise, and human development (Bilkovic et al. 2009).

Our results suggest that the restoration and conservation of even narrow, fringing marshes inhabited by ribbed mussels have the potential to improve water quality and perhaps alleviate localized eutrophication. This is of particular importance both ecologically and economically. For example, in Chesapeake Bay, a total maximum daily load (TMDL) for key pollutants has been established by the U.S. Environmental Protection Agency to restore clean water. The TMDL requires a 25% reduction in nitrogen, 24% reduction in phosphorus, and 20% reduction in sediment, a costly endeavor to implement (Wainger 2012). Therefore, identifying management activities that will enhance the cost-effectiveness of the TMDL is a high priority.

Ribbed mussels have been described as salt marsh keystone species that enhance multifunctionality (Angelini et al. 2015). The presence of mussel aggregates helps to sustain high levels of multiple marsh functions including decomposition, primary production, water infiltration, and soil accretion. Our results indicate that ribbed mussel–cordgrass mutualism also enhances water quality functions—filtration and denitrification—at the land–water interface, a zone experiencing intense human–natural interactions. Shoreline management strategies should encourage the conservation or creation of marsh habitat that supports ribbed mussel populations. The ecological role mussels and other bivalves may play in mediating eutrophication and providing ecosystem services under varying and changing environmental conditions remains an important area for research.

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Supporting Information

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