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ORIGINAL PAPER

Loss of salt marsh plants impacts ribbed mussel (*Geukensia demissa*) size, density, and influence on sediment nitrogen cycling

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Abstract The mutualism between *Spartina alterniflora* (Smooth Cordgrass) and *Geukensia demissa* (Ribbed Mussels) can increase ecosystem services, including the removal of excess nitrogen via denitrification. However, different responses of these species to sea-level rise and eutrophication can cause mussel beds to persist in areas where cordgrass has been lost to erosion and excessive tidal inundation. The function of these remnant mussel beds, in the absence of cordgrass mutualists, remains unclear. In this study, we sampled an eroding salt marsh in Jamaica Bay (NY, USA) to determine mussel density and size in non-vegetated mussel beds and vegetated marsh. We also collected sediment cores from remnant mussel beds and adjacent mudflats (i.e., former marsh) and performed continuous-flow core incubations to measure benthic nutrient fluxes, sediment oxygen demand, and denitrification. We found that remnant mussel beds were dominated by larger mussels compared to vegetated beds, which suggests less recruitment to remnant beds. In contrast to previous studies, which have found positive effects of mussels on denitrification, we found similar rates in mussel beds and mudflats. Sediment oxygen demand was also higher in remnant mussel beds suggesting that sediments may become more reduced due to mussel respiration. Our study suggests that the presence of mussels does not enhance, and may inhibit, nitrogen removal in eroded marsh sediments.

Keywords Marsh loss · Denitrification · Recruitment · Mutualism · Eutrophication · Mudflat

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Introduction

The structure and function of salt marsh ecosystems rely strongly on the presence of foundation species such as smooth cordgrass, *Spartina alterniflora*, as well as positive and negative species interactions within the marsh community. On the Atlantic coast of North America, ribbed mussels, *Geukensia demissa,* participate in a facultative mutualism with *S. alterniflora* (Bertness 1984). Mussels attach to the marsh surface with strong proteinaceous byssal threads, which increase the structural stability of marsh sediments and help the marsh resist erosion (Isdell et al. 2018; Bertness 1984). By suspension feeding, mussels also reduce stress on the cordgrass by pumping water over the marsh surface, which oxygenates sediments, and by depositing feces and pseudofeces, which promotes growth of the *S. alterniflora* (Bertness 1984). The cordgrass benefits the ribbed mussels by facilitating settlement of planktonic larvae and providing shelter from desiccation and predators such as the blue crab *Callinectes sapidus* (Bertness and Grosholz 1985). Negative species interactions can also influence the growth of *S. alterniflora* and thus the stability of the marsh (Hooijberg et al. 2019).

Marsh plants and ribbed mussels play a critical role in the sediment nitrogen (N) cycle, often modifying the sediment environment in ways that promote removal of N via microbial denitrification. Denitrification is the permanent removal of N from the sediment through the reduction of nitrate (NO_3^-) or nitrite (NO_2^-) into N_2 gas (Groffman et al. 2006). Ribbed mussels transfer N from the water column to the sediment through suspension-feeding and biodeposition (Bilkovic et al. 2017). About half of the N assimilated by the mussels as food is excreted as ammonium (NH_4^+), which is a nutrient used for primary production (Bilkovic et al. 2017) and can act as a fertilizer for marsh plants (Bertness 1984). Ammonium can also be turned into NO_3^- by aerobic microbes through nitrification. This is a particularly important process in salt marshes as *S. alterniflora* release oxygen into the rhizosphere allowing nitrification to occur near anerobic sediment where the NO_3^- can then be converted to N_2 through denitrification thus facilitating coupling between nitrification and denitrification (Koop-Jacobsen and Giblin 2010; Rosenzweig et al. 2018). Denitrification is considered an important ecosystem service in eutrophic systems because it removes reactive N coming from runoff or sewage effluent (Bowen et al. 2020). The NO_3^-, however, could also be transformed back into NH_4^+, a reactive form of N, through a process called dissimilatory nitrate reduction to ammonium (DNRA; Giblin et al. 2013) that can sustain eutrophic conditions and degrade ecosystem heath.

Despite the important role salt marshes can play in removing N, evidence suggests that eutrophic conditions also reduce the stability of marshes and contribute to their erosion (Alldred et al 2017; Deegan et al. 2012; Wigand et al. 2014). In the presence of excess N, salt marsh plants may develop less extensive root systems, producing less belowground organic material, and leaving sediments more vulnerable to erosion. When NO_3^- is used as an electron acceptor by denitrifiers, it also fuels decomposition of organic material, decreasing marsh stability and elevation (Day et al. 2018; Bowen et al. 2020; Watson et al. 2014). Lastly, high N loads can create sediment conditions in the marsh that stimulate DNRA (Koop-Jacobsen and Giblin 2010).

As marshes erode and are exposed to greater periods of inundation, sediment conditions become less conducive to plant growth and survival (Watson et al. 2017; Cahoon et al. 2019). The loss of vegetation can result in remnant mussel beds that were once living among *S. alterniflora* without the benefits of the mutualism. Since ribbed mussel recruitment is partially attributed to their attraction to conspecific adults (Nielsen and Franz 1995), the loss of vegetation can be problematic for future larvae that recruit to these suboptimal habitats (Watt et al. 2011). Such a scenario may constitute an ecological trap, or an ecological cue that causes an organism to colonize unsuitable habitat (Schlaepfer et al. 2002). Ribbed mussels that recruit to degrading salt marshes due to the presence of conspecifics may not persist over the long term in the absence of their *S. alterniflora* mutualist.

It is also unclear whether mussels in a degraded, unvegetated marsh (hereafter referred to as remnant mussel beds), provide the same ecological benefits that mussel populations typically provide. For example, studies have shown the mutualism between ribbed mussels and *S. alterniflora* results in higher rates of denitrification when compared to areas with only *S. alterniflora* (Bilkovic et al. 2017; Zhu et al. 2019; Rossi et al. 2022). Studies are needed to determine if mussels would have similar positive effects on N removal in eroded marsh sediments without *S. alterniflora*.

Jamaica Bay (NY, USA) is a highly eutrophic ecosystem (Hoellein and Zarnoch 2014; Wallace and Gobler 2015) that has historically lost salt marshes to coastal urban development and continues to experience loss due to changes in bathymetry, sea-level rise, and N loading (Hartig et al. 2004; Wigand et al. 2014; Campbell et al. 2017). The erosion of the marsh edge and loss of elevation have resulted in the conversion of marsh to mudflats. In many marsh locations, ribbed mussels have persisted on the mudflats (Fig. 1). Watt et al. (2011) found remnant mussel beds to persist after the loss of vegetation in degraded salt marshes in Nova Scotia. However, to date no other studies have documented this phenomenon, and little is known about ecological processes within remnant mussel beds.

In this study, we performed field surveys of mussel size distributions and conducted continuous-flow sediment core incubations to measure benthic nutrient and gas fluxes at a degraded marsh site with remnant mussel beds in Jamaica Bay. We hypothesized that remnant mussel beds would have a different size structure than adjacent marshes with the intact mussel-cordgrass mutualism. Specifically, we expected to observe fewer small mussels in the remnant beds due to a lack of recruitment. A previous study in Jamaica Bay found the interaction between ribbed mussels and *S. alterniflora* resulted in denitrification rates twice as high as areas with *S. alterniflora* alone (Zhu et al. 2019). In this study, we aimed to determine how remnant mussel beds impacted N cycling in eroded marsh sediments in Jamaica Bay. We expected the remnant mussel beds would continue to support higher rates of denitrification than adjacent mudflats, even in the absence of their *S. alterniflora* mutualist, due to mussel feeding and excretion stimulating sediment denitrification as found in other bivalves (Ayvazian et al. 2021).

Materials and methods

Study area and field sampling

Jamaica Bay is an urban estuary located on the southwestern end of Long Island, New York. It is bordered by the boroughs of Brooklyn and Queens with a highly impervious watershed (Rosenzweig et al. 2018). The freshwater flow largely (~90%)

Fig. 1 **a** Living mussel beds persisting on mudflats adjacent to the eroding marsh platform at JoCo marsh in Jamaica Bay. **b** Mussels embedded in the mudflat sediments

comes from four wastewater treatment plants that release effluent into the bay (Benotti et al. 2007). N associated with this effluent, as well as from other sources (i.e., combined sewer overflows, atmospheric deposition), contribute to the highly eutrophic status of Jamaica Bay (Wallace and Gobler 2014; Hoellein and Zarnoch 2014). Ribbed mussel populations in Jamaica Bay occur at densities up to 10,000 m^{-2} particularly at the marsh edge (Nielson and Franz 1995), which is much higher than other mid-Atlantic (Bilkovic et al. 2017) or southern New England estuaries (Bertness and Gosholz 1985). The greater densities of mussels in Jamaica Bay may be due to the high primary productivity in this system supporting secondary production (Chintala et al. 2006). The water temperature and nutrients in Jamaica Bay have wide seasonal variation as is typical in mid-Atlantic estuaries. The salinity is less variable, compared to other estuaries, due to limited freshwater inputs which is a result of the highly developed watershed (Zarnoch and Schreibman 2012; Hoellein and Zarnoch 2014; Wallace and Gobler 2015).

Field sampling was performed at Black Bank marsh, which is in the center of Jamaica Bay (Fig. 2) and has many of the characteristics of a deteriorating marsh including a fragmented and eroding marsh platform (Hartig et al. 2002; Wigand et al. 2014), reduced belowground structure (e.g., roots, rhizomes), and elevated sediment hydrogen sulfide levels and tidal inundation (Alldred et al. 2020). We established a transect parallel to the seaward marsh edge and sampled three hummocks with live *S. alterniflora* and ribbed mussels as well as three remnant mussel beds (no living *S. alterniflora*). Each sampling site was > 2 m from the nearest neighboring site. In the

Fig. 2 The left panel shows Jamaica Bay in relation to the greater NY/NJ metropolitan area. The right panel shows the sampling location within Black Bank marsh

sites with hummocks, we placed a 0.25 m^2 quadrat on the hummock and harvested all aboveground plant material. The plant material was cleaned, stems counted to determine density (No. m^{-2}) and then dried at 60 °C to calculate aboveground biomass (g m^{-2}). After the plants were removed, we placed a 0.0625 m^2 quadrat on the marsh hummock and removed all mussels and sediment within the quadrat down to a depth where mussels were no longer present (~ 12 cm). A smaller quadrat was used for mussel sampling to minimize disturbance to the marsh. Other studies have used a similar sized quadrat to measure mussel density in Jamaica Bay and found that it was appropriate to describe spatial patterns in density across a marsh (Nielsen and Franz 1995; Franz 2001). Mussels and sediment were kept at 4 °C and transferred to the laboratory where they were carefully washed through a sieve with 2 mm mesh. All mussels were counted to calculate density (No. m^{-2}) and measured with calipers to determine total length (mm). Lastly, we used a real-time kinematic GPS system (Trimble R8s GNSS) with vertical accuracy of < 2 cm to measure surface elevation at the six sampling locations at Black Bank marsh.

Continuous-flow sediment core incubations

Sediment cores (7.6 cm × 30 cm) were collected from Black Bank marsh on 24 November 2019. Four cores were collected from the remnant mussel beds and four cores were collected from the adjacent mudflat with no mussels. Both the mudflat and remnant mussel beds were in eroded marshes with dead belowground plant biomass (see below) but no live aboveground biomass. Each core from the remnant mussel beds was selected to include three live mussels, and the cores from the mudflat had none. Seawater was collected in ~ 20 L carboys from the site for use in core incubations. The cores were held overnight in a 20L tank submerged in aerated site water that was maintained at the temperature of Jamaica Bay at the time of collection (12 °C). Although seasonal measurements would be most helpful in understanding benthic nutrient flux dynamics, this study is limited to fall measurements only.

The cores were prepared for continuous-flow core incubations following Gardner and McCarthy (2009). Cores were fitted with gas-tight lids, volume adjusted to ~ 230 mL, and site water was passed through the cores at a rate of 1.5 mL min^{-1}. Site water was maintained at room temperature (16 °C), which was higher than ambient Jamaica Bay at time of collection. The salinity of site water was 27 ppt. The cores were allowed to equilibrate to the continuous-flow system for 24 h before the first sampling was performed, and the second sample was taken at 6 h after the first sample. Cores were held under dark conditions to prevent photosynthesis from occurring in the cores. For each sampling, we collected seawater samples directly from the inflow carboy and from the outflow for each of the cores. Triplicate samples for water chemistry were filtered with a 0.2 µm nylon syringe filter (Thermo Scientific, Rockwood, Tennessee, USA) into 20 mL scintillation vials and stored frozen at − 20 °C. Samples for dissolved gas analyses were collected in triplicate in 12 mL exetainer sample vials (Labco Ltd., Lampeter, United Kingdom). Water from the carboy was collected with a 60 mL syringe with attached tubing and transferred to the exetainer vials. Water from the core outflows was allowed to flow directly into the exetainer vials. For both inflow and outflow samples, the tubing was placed at the bottom of the vial and the vial was allowed to fill and overflow for at least three volumes. The sample vials were then treated with 200 µL of 50% zinc chloride, capped with no air bubbles, and then stored underwater at 4 °C until analysis.

Dissolved nutrients were measured on a Seal AQ2 + discrete analyzer (Seal Analytical Inc., Mequon, Wisconsin, USA). Soluble reactive phosphorous (SRP) was determined using the antimonyl tartrate method (Murphy and Riley 1962). Nitrate + nitrite (NO_x^-) and nitrite (NO_2^-) was measured using the sulfanilamide method with and without cadmium reduction, respectively (APHA 1998). Ammonium (NH_4^+) was measured with the phenol-hypochlorite assay (Solorzano 1969). Mean concentrations of dissolved nutrients in the inflow carboy were similar for each sampling and were 40.6 and 46.5 µmol N L^{-1}, respectively for NO_x^- and NH_4^+ while the SRP was 6 µmol P L^{-1}. The dissolved gases ($^{28}N_2$, $^{32}O_2$, ^{40}Ar) were measured with membrane inlet mass spectrometry (MIMS; Bay Instruments, Easton, MD, USA; Kana et al. 1994). An artificial seawater (27 ppt) standard was maintained at a constant temperature (16 °C) and was equilibrated to atmospheric gases by low-speed stirring. Standard was sampled throughout the measurements to correct for instrument drift. Fluxes (μmol element m^{-2} h^{-1}) of gases and nutrients were calculated by subtracting the outflow concentration from the inflow concentration and accounting for the core surface area and flow rate. Negative fluxes indicated net sediment uptake of the nutrient or gas while positive fluxes indicated a release of the nutrient or gas to the water column. Since denitrification and nitrogen fixation can occur simultaneously, negative net N_2 fluxes suggested nitrogen fixation was the dominant process and when net N_2 fluxes were positive denitrification was the dominant process. Core incubations did not include a water only control (Jackson et al. 2018) thus represent combined water and sediment fluxes.

Sediment characteristics

After completing the continuous-flow sediment core incubations, triplicate sediment samples (5 cm^3) were collected from the top ~ 25 mm of the sediment surface of each core and pooled for analysis. The samples were dried at 60 °C and weighed to determine dry mass and bulk density. One replicate was ashed at 500 °C to determine inorganic mass and % organic content was calculated. The second replicate was treated twice with HCl (Nieuwenhuize et al. 1994) and redried at 60 °C before being measured for % carbon and N on a Perkin Elmer 2400 Series II CHN analyzer (Perkin Elmer Life and Analytical Sciences, Shelton, CT). The third replicate was used to determine sediment % phosphorous using the dry oxidation-acid hydrolysis assay (Aspila et al. 1976) along with colorimetric analysis (Murphy and Riley 1962) as described above. The remaining sediment in each core was placed in a 2 mm mesh sieve and the sediment was washed away leaving only dead belowground plant material (i.e., roots, rhizomes). The belowground material was dried at 60 °C and weighed to determine biomass.

Statistical analyses

Mussel density and elevation were compared between the remnant mussel beds and the hummocks with mussels and live *S. alterniflora* using t-tests. Mussel shell lengths were graphed as histograms to compare the distribution of mussel sizes in these plots. The sediment characteristics, gas fluxes, and nutrient fluxes from the mudflat and remnant mussel beds were compared using t-tests. All data were examined to ensure normality (Shapiro–Wilk) before statistical testing. A p-value of ≤ 0.05 was established for significance, while $p = 0.051–0.099$ were considered marginally significant. Statistical analyses were performed with SigmaPlot 11 (Systat, Inc., Chicago, IL).

Results

Mussel density, size, and cordgrass measurements

Mussel density was greater in the hummock plots (4256 ± 358 m^{-2}) as compared to the remnant mussel beds (2757 ± 584 m^{-2}) although this difference was only marginally significant (t-test; $p = 0.09$). There was also a significant difference (t-test; $p < 0.001$) in elevation between the hummocks (0.128 m ± 0.03; NAV88) and the remnant mussel beds (−0.148 m ± 0.006; NAV88). Mean stem density in the hummock plots was 491 m^{-2} (± 98), mean stem height was 86.3 cm (± 4.7), and aboveground biomass was 1139 g m^{-2} (± 63). In the hummock plots where ribbed mussels and *S. alterniflora* were living together, the mussel shell lengths were normally distributed (Fig. 3a). The remnant marsh plots where the mussels live embedded in mudflat with no living *S. alterniflora* show a skewed distribution towards larger (and older) mussels (Fig. 3b).

Sediment characteristics

Although no aboveground vegetation was present at either sediment core sampling site, the remnant mussel beds and the mudflat locations both had abundant belowground plant biomass, with no statistical difference between the habitats (Table 1). There was, however, a pattern of greater % organic matter, carbon, N, and phosphorus in the remnant mussel sediments (Table 1) although only % organic matter and N were statistically significant (Table 1). There was a marginally significant difference in sediment bulk density with the remnant mussel beds having lower bulk density than the mudflat (Table 1).

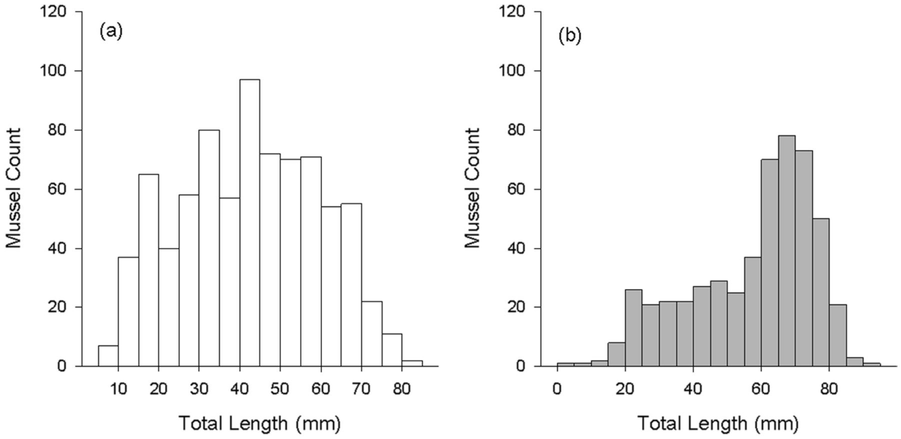

Fig. 3 Distribution of ribbed mussel shell lengths from plots with **a** living cordgrass and ribbed mussels and **b** from plots of ribbed mussels with no living cordgrass

Table 1 Mean (±SE) belowground biomass, sediment characteristics, and elevation from sediment cores collected at Black Bank marsh.

Variable	Remnant mussels	Mudflat	t-test
BG (g m^{-2})	4541.445 (±507.958)	4797.51 (±718.071)	$p = 0.78$
%OM	11.201 (±0.306)	8.604 (±0.773)	**$p = 0.02$**
%C	10.101 (±0.552)	8.173 (±0.94)	$p = 0.13$
%N	0.753 (±0.055)	0.565 (±0.068)	**$p = 0.08$**
%P	0.12 (±0.006)	0.11 (±0.006)	$p = 0.28$
Bulk Density (g cm^{-3})	0.529 (±0.025)	0.668 (±0.06)	**$p = 0.08$**

BG belowground matter, *OM* organic matter, *C* carbon, *N* nitrogen, *P* phosphorous

Significant p values are in bold. $n = 4$ $habitat^{-1}$

Gas and nutrient fluxes

The remnant ribbed mussels living on a mudflat from an eroded marsh did not enhance denitrification (N_2 flux) as compared to adjacent unvegetated mudflat with no mussels (t-test; $p = 0.22$). The net N_2 fluxes from cores ($n = 4$) taken from the remnant mussel beds were variable with half showing N fixation as the dominant process and the other half showing denitrification as the dominant process (Fig. 4a). The mean of all remnant mussel bed cores (70.4 µmol N m^{-2} h^{-1}) was positive suggesting that across the sampled habitat, more N was being removed rather than fixed. The cores collected from the unvegetated mudflats adjacent to the remnant mussel beds all showed net denitrification (i.e., positive fluxes) with a mean of 220.5 µmol N m^{-2} h^{-1}.

The NH_4^+ and NO_x^- fluxes were similar between the mudflat and remnant mussel beds (t-test; $p > 0.21$). Both habitat types were a source (release) of NH_4^+ to the ecosystem (Fig. 4d) and a sink (uptake) for NO_x^- (Fig. 4b). The SRP fluxes were significantly different between habitat types (t-test; $p = 0.008$) with the remnant mussel beds being a net source of SRP while the mudflats were a sink for SRP (Fig. 4c). The remnant ribbed mussel beds did, as expected, have significantly greater oxygen uptake (t-test; $p < 0.001$), with O_2 consumption rates 3.5 times higher in the cores with mussels (Fig. 5).

Discussion

In this study, the size-structure of mussel populations from remnant mussel beds was dominated by larger, older individuals as compared to populations where mussels and live *S. alterniflora* were co-occurring. Although there were some young individuals in the remnant mussel beds, they were less numerous and may not be able to sustain these remnant mussel beds

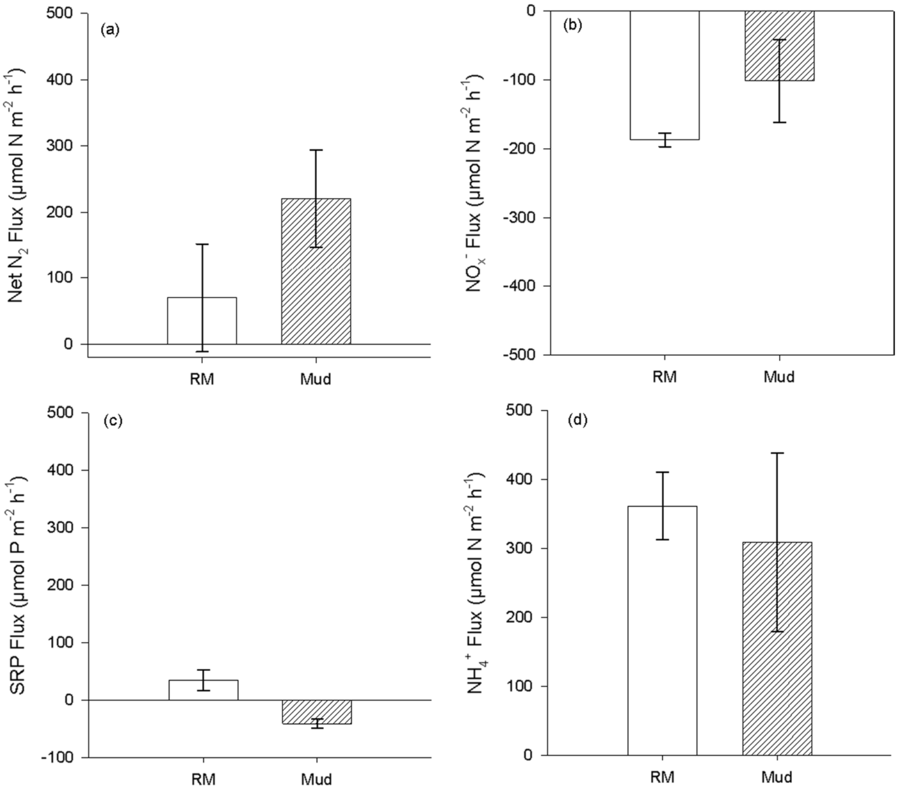

Fig. 4 Nitrogen and phosphorus fluxes from sediment cores collected at Black Bank marsh in plots with remnant ribbed mussel beds (RM) and adjacent mudflats (Mud) with no living cordgrass. **a** Net N_2; **b** NO_x^- = nitrate + nitrite; **c** SRP = soluble reactive phosphorous; **d** NH_4^+ = ammonium. Positive fluxes indicate a release from the sediment to the water column, and negative fluxes indicate sediment uptake from the water column

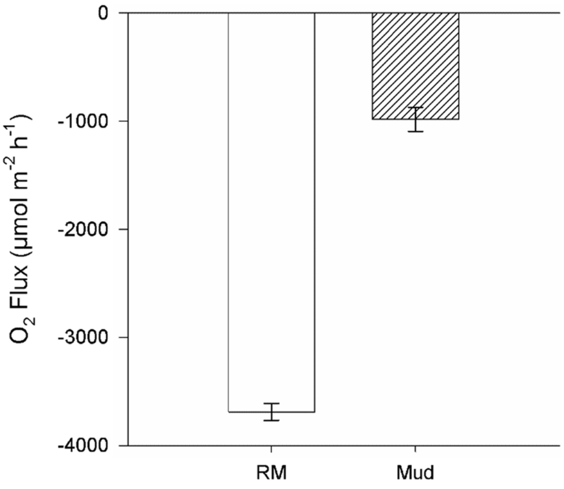

Fig. 5 Oxygen flux from sediment cores collected at Black Bank marsh in plots with remnant ribbed mussel beds (RM) and adjacent mudflats (Mud) with no living cordgrass. Negative fluxes indicate uptake of gases

over a long-time scale. Watt et al. (2011) found that mussel populations in Nova Scotia where vegetation loss has occurred due to marsh drowning also left remnant mussel beds where population size structure was indicative of population decline. Sediment characteristics differed between the remnant mussel beds and the mudflat (i.e., former marsh), which could be due to the biological and physical activity of the mussels or legacy traits of a once vegetated marsh. Organic content and percent N were higher in the remnant mussel beds, which indicates that the mussels create microsites that slows water flow and retains organic material such as biodeposits (Zhu et al. 2019). This may be an important process in allowing for these remnant mussel beds to persist since they are accumulating organic material, which can help maintain or increase elevation (Peteet et al. 2018) rather than the beds getting eroded.

We predicted that the remnant mussel beds would have higher denitrification rates than the mudflat (i.e., former marsh) due to the accumulation of biodeposits and changes in sediment oxygen conditions as found in other bivalves (Ayvazian et al.

2021). The remnant mussel beds, however, had lower rates of denitrification than the adjacent mudflats. Other studies have demonstrated that the mutualism between *S. alterniflora* and *G. demissa* (Bilkovic et al. 2017; Zhu et al. 2019) or *G. granosissima* (Rossi et al. 2022) can enhance denitrification. Therefore it is likely that the loss of *S. alterniflora* reduces the important ecosystem service of enhanced N removal in remnant mussel beds. Hinshaw et al. (2017) identified vegetation as an essential component of N removal processes in the marsh ecosystem as they found that the presence of vegetation resulted in denitrification rates that were four times higher than sediments that have lost vegetation due to erosion. Lastly, our results suggest that sediment conditions during Fall within eutrophic Jamaica Bay can result in remnant mussel beds being a source of N to the ecosystem. Without the presence of *S. alterniflora* in the remnant beds it is likely that this result will be consistent throughout the other seasons.

Ribbed mussel recruitment

The remnant ribbed mussel beds sampled in this study had no living *S. alterniflora*, yet they continued to recruit new individuals to the population, albeit at lesser amounts than nearby hummocks with both mussels and living *S. alterniflora*. This suggests that both *S. alterniflora* and the presence of conspecifics play an important role in ribbed mussel recruitment dynamics. The recruitment of new larvae may be affected by chemical cues associated with adult conspecifics (Nielsen and Franz 1995), which may be enhanced by filtration and deposition of larvae and the biodeposits of existing adults in the mussel bed. Both hummocks with live *S. alterniflora* and remnant mussel beds had fewer recruits than previously reported in Jamaica Bay (Franz 2001), but this may be due to continued loss and fragmentation of marsh as compared to when the previous study was conducted (1991–1999). The low number of recruits to the hummocks and remnant mussel beds were consistent with measurements of ribbed mussel population structure in marshes degraded by sea-level rise in the Gulf of St. Lawrence, Canada (Watt et al. 2011).

The physical presence of mussels can also alter hydrodynamics to remove, rearrange, or bring in additional resources that change the suitability of these marshlands (Sara 2006). The differences in sediment characteristics between the remnant mussel beds and the adjacent mudflats supports this idea. However, the presence of vegetation is known to reduce the speed of the water and turbulence, which enhances the process of larval recruitment and deposition into the marshes (Leonard and Croft 2006). In addition, the flow of water in the presence of *S. alterniflora* may allow for more retention of food particles beyond phytoplankton (e.g., benthic microalgae, detritus), consequently allowing for greater recruitment (Bilkovic et al. 2021), as opposed to areas where *S. alterniflora* is absent and food resources are more limited, and thus not a suitable location for larval deposition.

Alternatively, the plots of ribbed mussel without cordgrass may recruit new larvae at similar rates as the hummocks with both mussels and *S. alterniflora*, but these larvae fail to survive due to the absence of protection that the cordgrass provides. *S. alterniflora* provides mussels, especially juveniles, with shade that reduces desiccation and shelters juvenile mussels from predators, which enhances their chances of survival (Bertness 1984). Additional studies are needed to further understand the mechanisms supporting ribbed mussel recruitment, particularly to newly constructed marshes or living shorelines where *S. alterniflora* density is low (Bilkovic et al. 2021).

Gas and nutrient fluxes

The low and variable N_2 fluxes measured from the remnant ribbed mussel cores were surprising since another study (Bilkovic et al. 2017) found significant rates of denitrification (~ 250 μmol N m^{-2} h^{-1}) in core incubations with mussels and marsh sediment (but no plants). This may be due to more reduced sediments in the remnant mussel beds in Jamaica Bay, which favored microbial processes, such as heterotrophic and/or chemotrophic N fixation, rather than denitrification. Fulweiler et al. (2013) found that sulfur and sulfate reducers may mediate sediment N fixation under anoxic conditions in coastal ecosystems. There are several lines of evidence that suggest the co-occurrence of heterotrophic denitrification and N fixation in the remnant mussel beds in this study. The remnant mussel beds were sampled at Black Bank marsh, which is a deteriorating marsh in eutrophic Jamaica Bay (Wigand et al 2014).

Black Bank was found to have high concentrations of hydrogen sulfide in its sediments likely due to low elevation and thus longer tidal inundation periods (Alldred et al. 2020). It is likely that the mudflat and remnant mussel beds sampled in the current study had higher concentrations of sulfide since they had no live *S. alterniflora*, which would oxygenate sediments. As an eroding marsh, refractory carbon sources are likely to be more available for decomposition as compared to a healthy marsh, which is consistent with high C:N and C:P ratios observed in this study. Lower carbon quality may favor sulfate reducing bacteria that mediate N fixation over denitrifiers (Fulweiler et al. 2013). Sediment oxygen demand was much higher in the remnant mussel beds compared to the adjacent mudflat with no mussels. Zhu et al. (2019) hypothesized that mussel respiration may have created sediment anaerobic conditions that favored denitrification, but the site examined in that study was a recently restored marsh with higher elevation and less sediment organic content, where coupled nitrification–denitrification was more likely to be an important contributor to total denitrification rates. The remnant mussel beds and mudflat both likely had high sulfide, but the remnant mussel beds may be more anaerobic, which limits microhabitats for coupled nitrification–denitrification and may explain the lower N_2 fluxes. Sediment oxygen conditions and related benthic nutrient fluxes will vary seasonally, but measurements in this study were performed in fall only. Future studies should examine fluxes from remnant mussel beds across seasons. While the results of this study suggest that sediment conditions in the remnant mussel beds may support co-occurrence of heterotrophic N fixation and denitrification, the potential role of N fixation in these habitats as well as in coastal ecosystems in general needs further investigation. Approaches that integrate measurements of rates, identification of microbes responsible for these processes, and their environmental constraints are needed to advance our understanding of coastal N fixation (Marcarelli et al. 2022).

The ribbed mussels' presence also created an environment that increased SRP fluxes to the water column (Fig. 4c). Cores containing mussels had a significant net positive flux of SRP to the water column, whereas mudflat cores showed a net uptake of phosphorus. Phosphorous is released to the water column under anaerobic conditions in which it becomes unbound to iron (Yoo et al. 2006; Speteri et al. 2008). Under hypoxic conditions, NH_4^+ has been shown to be the greatest output of N (Neubacher et al. 2011). Since remnant mussel beds and mudflats had high NH_4^+ fluxes both likely had anaerobic sediments, yet only the remnant mussel beds had a positive SRP flux. This could be due to mussel respiration (Fig. 5) creating more reduced conditions as suggested by Zhu et al. (2019). The SRP could also be released directly through mussel excretion. Studies on blue mussels, *Mytilus edulis*, have found mussels to be responsible for 31–85% of the total phosphorous flux from a mussel bed (Prins and Smaal 1994).

The current study demonstrated that eroded marsh sediment, with or without ribbed mussels, was a significant source of NH_4^+ to the water column. In contrast, sediments from a marsh with live *S. alterniflora* typically have low positive fluxes of NH_4^+ and overall are a net sink for N (Bilkovic et al. 2017). The remnant mussel beds and adjacent mudflats had similar NH_4^+ fluxes to the water column. The mudflats, however, had net N_2 fluxes similar to the NH_4^+ flux, while the remnant mussel beds had net N_2 fluxes much lower than the DIN flux. This disparity indicates that the mudflats of an eroded marsh are releasing and removing similar amounts of N, while the remnant mussel beds release more N to the water column and are a net source of N in the ecosystem. Studies on eroding marshes in Chesapeake Bay found the sediment not to be a source of N to the ecosystem and the rates of denitrification were similar to this study's mudflat cores (Cornwell et al. 2022). They did not, however, examine the impact of ribbed mussels on N cycling in those eroding marshes. It is likely that dissimilatory nitrate reduction to ammonium (DNRA), may be favored over denitrification in redox conditions typical of eutrophic eroded marshes and remnant mussel beds, therefore keeping N available in the ecosystem as NH_4^+ (Koop-Jacobsen and Giblin 2010; Giblin et al. 2013). For example, the mudflat had a NO_x^- uptake similar to the net N_2 efflux, however, the remnant mussel bed had a N_2 flux lower than its NO_X^- uptake, suggesting the extra NO_X^- could have been used for DNRA (Vieillard and Fulweiler 2012). A study on clam aquaculture sediments found similar patterns of fluxes of SRP and NH_4^+ as the current study, but they also found higher rates of DNRA in clam aquaculture sediments compared to uncultivated sediments (Murphy et al. 2016). High rates of DNRA have also been found in eutrophic salt marshes (Koop-Jacobsen and Giblin 2010) and tidal creeks (Vieillard and Fulweiler 2012). These studies suggest the presence of bivalves in sediments with high organic carbon, nitrate, and sulfide, like remnant mussel beds on eroded marsh mudflats, can create conditions that reduce denitrification (i.e., inhibiting nitrification) and thus shifts the fate of N from removal to recycling. This result is critical because it suggests that mussels in remnant beds, rather than providing the service of N removal, may exacerbate eutrophic conditions with negative implications for ecosystem health (Murphy et al. 2016; Vieillard and Fulweiler 2012).

The eutrophic condition of urban estuaries could reduce the importance of the mutualism between *S. alterniflora* and the ribbed mussels (Zhu et al. 2019; Whaley and Alldred 2023). Zhu et al. (2019) found no evidence that mussels contributed to the growth or enhancement of *S. alterniflora* in a newly restored marsh in Jamaica Bay. Considering the eutrophic conditions in Jamaica Bay the need for the mutualistic partner, i.e., ribbed mussel, that delivers nitrogen to the sediments was absent. In a meta-analysis, Whaley and Alldred (2023) found that, while this mutualism had the expected positive effects on the growth of both partners in natural salt marshes throughout the species' native range, it had a negative effect on species growth in salt marshes located in urban estuaries. Shantz (2016) found a general pattern among decoupled mutualistic interactions where the phototrophs benefit more than their heterotrophic partners under enriched conditions. This happens in exceptional conditions where the nutritional profile of the heterotroph and the specific enrichment type (i.e., N or phosphorous) impacted the response of the mutualistic relationship. The decoupling of the mussel-*S. alterniflora* mutualism in urban, eutrophic estuaries may have significant impacts on ecosystem structure and functioning. Measurements of sediment N cycling from urban, natural marshes with ribbed mussels and *S. alterniflora* within eutrophic estuaries are needed to compare with measurements taken in less impacted ecosystems (Bilkovic et al. 2017; Rossi et al. 2022). Considering the lower recruitment and higher N recycling in remnant mussel beds managers may want to transplant remnant mussels to newly constructed salt marshes and living shorelines. This could increase denitrification at these sites (Zhu et al. 2019), promote recruitment of other ribbed mussels (Nielsen and Franz 1995), and enhance the resilience of the shoreline (Bilkovic et al. 2021).

Collectively, our results demonstrate that the loss of the salt marsh plant *S. alterniflora* due to marsh drowning and erosion may alter community and ecosystem dynamics within an urban estuary. Loss of its *S. alterniflora* reduced the recruitment and/or the survival of juvenile ribbed mussels. Moreover, remnant ribbed mussel assemblages, in the absence of *S. alterniflora*, did not provide enhanced rates of N removal via denitrification that we would expect based on previous studies of ribbed mussels in the presence of *S. alterniflora*.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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