



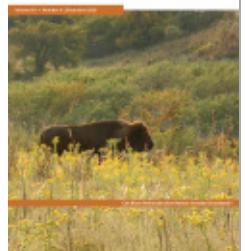
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# Species Interactions Critical to Restoration Success in an Urban Living Shoreline

Shannon Cooper, Mary Alldred, Beryl Kahn, Thomas Whaley, Amanda Flores, Anais Cardenas, Jason Smith, J. Stephen Gosnell and Chester B. Zarnoch

## ABSTRACT

Nature-based methods for shoreline erosion control, often referred to as living shorelines, can help maximize local ecosystem services in urban areas where they may otherwise be lost. Living shorelines that incorporate salt marshes and oyster reefs have been shown to improve water quality by removing excess nutrients and protecting coasts from storm surges, but adaptive and continual management is essential. Positive and negative species interactions may influence the success of these shoreline projects. Here we synthesize the results of a multi-year study of the Sherman Creek Living Shoreline in New York City, NY. We conducted studies of shoreline habitat types pre- (2019) and post- restoration (2020), following a mussel-addition experiment (2021), and following the implementation of enhanced goose-exclusion techniques (2023). In each year, we collected sediment cores from shoreline habitat types (mudflat, rip-rap, existing marsh, new marsh) and performed continuous-flow incubations to quantify dissolved gas and nutrient fluxes, with the goal of comparing rates of nitrogen removal among habitat types. We also assessed above- and below-ground biomass and sediment characteristics of each habitat. Though sediment organic content in the existing marsh was more than double that of any other habitat type, we found similar rates of nitrogen removal via denitrification in the existing and newly restored marsh. Adding mussels to the marsh plants increased rates of nitrogen removal by 50%. Post goose-exclusion, we saw plant growth like that of the existing marsh, showing that managing species interactions can have a positive effect on the benefits provided by living shorelines.

**Keywords:** coastal restoration, denitrification, *Geukensia demissa*, salt marsh, *Spartina alterniflora*

Nature-based infrastructure in the form of living shorelines is an alternative to typical gray infrastructure that utilizes marsh vegetation, fill, and offshore structures to restore ecosystem services and enhance shoreline resiliency (Davis et al. 2015). Living shorelines may combine characteristics of natural and engineered shorelines to maintain ecosystems in areas where they may otherwise be lost (Smith et al. 2018). When properly designed, they can attenuate wave energy and provide coastal buffers that reduce volume and velocity of surface water runoff with

marsh vegetation, and maintain natural coastal processes (O'Donnell 2017). Additional benefits provided by living shorelines include the creation or protection of shoreline access, as well as nesting and foraging areas for migratory shorebirds, turtles, and mollusks (O'Donnell 2017). The development of these living shorelines has become an increasingly common approach to maintaining coastal processes and protecting urban communities from the consequences of climate change (Baker and Gittman 2025).

In New York City and other urban coastal environments, surface waters are impacted by wastewater inputs and combined sewer overflows (CSOs). These large inputs of anthropogenic nitrogen contribute to poor water quality, exacerbating eutrophication and harming living resources (Wigand et al. 2014, Zhu et al. 2019). Excess nitrogen can be removed from ecosystems through a natural process called denitrification, where sediment microbes convert reactive forms of nitrogen into inert nitrogen gas (McClain et al. 2003). Habitats included in living shorelines have been shown to support denitrification, which could help mitigate eutrophication (Onorevole et al. 2018, Schoell et al. 2023); however, there is conflicting evidence on whether this important ecosystem service increases as a living shoreline

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## Restoration Recap

- Sherman Creek is a public park with 2 ha (5 acres) of living shoreline in Manhattan, New York City, NY, USA. Due to its urban context, vandalism, herbivory, and predation are common and need to be adaptively managed to create a sustainable living shoreline.
- When herbivores were excluded with robust fencing, the living shoreline experienced plant growth, and provided nitrogen-removal services, equivalent to those in a reference marsh.

- Restoration of ribbed mussels was ultimately unsuccessful due to vandalism and predation by raccoons. If successful, mussel addition could enhance nitrogen removal rates by 50%.
- We recommend that managers consider both abiotic and biotic site-specific challenges when developing a living shoreline restoration plan.
- Pre-restoration surveys may be needed to identify potential challenges from herbivore and predator populations and enact protective measures to avoid setbacks.

ages. Long-term monitoring is needed to resolve this issue and to contribute to adaptive management of the project.

Marsh vegetation in living shorelines such as *Spartina alterniflora* (smooth cordgrass) influences denitrification rates by facilitating O<sub>2</sub> diffusion into sediments through aerenchyma (Cartaxana and Lloyd 1999, Maricle and Lee 2002, Sousa et al. 2012), and promoting coupled nitrification-denitrification in otherwise anoxic sediments. *Spartina alterniflora* is a flowering terrestrial grass with roots that extend horizontally in a rhizome system, enhancing diffusion across the sediment-water interface. The oxic micro-zones surrounding the plant's rhizosphere transport oxygen into the sediment anoxic zone, promoting coupled nitrification-denitrification at the oxic/anoxic interface. *Spartina alterniflora* also positively influences denitrification by releasing organic carbon from root exudates and decomposing root tissue, which provides energy for microbes. When marsh vegetation is lost, there is a corresponding loss in sediment denitrification capacity (Hinshaw et al. 2017).

The introduction of *Geukensia demissa* (Atlantic ribbed mussels) to living shorelines can positively influence the environmental conditions required for denitrification (Zhu et al. 2019). *Spartina alterniflora* and *G. demissa* engage in a facultative mutualism. *Spartina alterniflora* facilitates mussel populations by providing structure and habitat, and the mussels help to stabilize the root structures of *S. alterniflora* by attaching to its substrate with byssal threads (Bertness 1984, Altieri et al. 2007, Whaley and Alldred 2023). Through suspension feeding, the mussel transfers particulate organic matter from the water column to the sediment via biodeposits, fertilizing plant growth and providing an energy source for denitrifying microbes (Bilkovic et al. 2017).

The use of living shorelines to stabilize degraded urban coasts has increased over the last few decades, yet factors leading to the long-term success or failure of these structures remain poorly described (Callaway 2005). Often, living shoreline projects are built and left to develop on their own with the assumption that nature will take over

and finish the job. Unfortunately, when initial restoration plans do not work as intended, lack of monitoring and subsequent intervention can result in a degraded shoreline. Thus, the application of adaptive management practices is essential, and long-term monitoring should be adequately funded in these projects (Baker and Gittman 2025). While restoration efforts target physical conditions of the system, the role of biological factors such as species interactions in restoration success is often neglected (Jobe et al. 2022). The level of isolation of urban marshes within the landscape can concentrate the abundance of wildlife, making the marshes especially vulnerable to the impacts of herbivory and predation (Jobe et al. 2022), yet these species interactions can be overlooked in restoration plans. Moreover, essential microbial processes like denitrification are rarely quantified in restored systems (Whaley and Alldred 2023). This information gap poses a serious challenge for managers who increasingly want to reestablish ecosystem function as a goal of restoration.

Our research contributes to the ongoing adaptive management of restored salt marshes by quantifying microbial nutrient removal and developing effective methods for excluding nuisance herbivores in the Sherman Creek Park Living Shoreline Project. The Sherman Creek Living Shoreline is an erosion control and wetland restoration project designed and implemented by New York Restoration Project (NYRP) in consultation with the New York City Department of Parks and Recreation (NYC DPR), New York State Department of Environmental Conservation (NYS DEC), and NYS Department of Transportation. Here we report the results of four years of research, monitoring, and adaptive management, including plant and sediment surveys and continuous-flow core incubations to estimate nitrogen-removal services. The primary goals of our analysis were to 1) document the effectiveness of adaptive-management actions in restoring vegetation and nitrogen-removal services to the marsh over a five-year period, with a focus on herbivore exclusion, and 2) determine whether the addition of ribbed mussels may enhance vegetation recovery and nitrogen-removal services.

## Methods

### Study Site and Restoration History

The Sherman Creek Living Shoreline Project was implemented on the shore of the Swindler Cove section of Sherman Creek Park along the Harlem River in Manhattan Borough of New York City ( $40^{\circ}51'26.3412''$ ,  $-73^{\circ}55'17.5218''$ ). In 1998, a reclamation project was implemented at Swindler Cove to create a tidal inlet from the Harlem River (Smith 2023). Approximately  $2,700\text{ m}^2$  (over  $30,000\text{ ft}^2$ ) of marsh vegetation was planted as a wetland restitution in 2001, and Swindler Cove opened to the public in 2003. Post-installation monitoring performed by Young Environmental, LLC initially documented robust marsh growth (Smith 2023). By 2003, the restitution plantings of *S. alterniflora* were in decline, particularly those in areas directly adjacent to the waterfront, which were weakened by strong wave action and herbivory by resident Canada geese (*Branta canadensis*). By October 2003, 80% of the marsh vegetation had been lost, with the only remaining area hereafter referred to as the existing marsh. The existing marsh area was protected from waves, currents, and goose predation by a pedestrian bridge and surrounding upland vegetation, with only a narrow channel for tidal exchange.

In 2017, NYRP installed wetland protection measures (under NYSDEC permit # 2-6201-00405/00005) at a remnant marsh that predated the 2001 restitution planting, which had been rapidly eroding since 2010 (Smith 2023). As of 2017 over 50% of this remnant marsh present during park construction (2003) was lost. The wetland protection project consisted of two rows of coir logs and a row of bagged oyster shells. Monitoring documented initial positive results followed by rapid deterioration and eventual return to pre-restoration conditions; however, neither marsh extent nor accretion/erosion was quantified. By 2019 wave energy and currents led to failure of the coir logs, and goose predation led to almost complete loss of vegetation in the shoreline-adjacent low marsh, with a resumption of shoreline erosion.

The Sherman Creek Living Shoreline was installed in the summer of 2020 (Supplementary Materials, Figures S1, S2). It was designed to address the high-energy conditions on site and enhance the resilience of the shoreline to increasing stresses driven by climate change (Smith 2023). It encompassed both the remnant marsh and the marsh restitution area, which were protected from incoming waves with the installation of Oyster Castle® block breakwaters, also referred to as “oyster castles.” Coconut-fiber mats ( $5.6\text{ m}^2$  in size) were placed on site to stabilize sediments for plantings in the high-marsh (27 mats totaling  $150.5\text{ m}^2$ ) and low-marsh (58 mats totaling  $323\text{ m}^2$ ) areas. The low marsh was planted with 5 cm plugs of *S. alterniflora* at a density of 30 plugs per mat, and the high marsh was planted with 5 cm plugs with a mixture of *Distichlis spicata*,

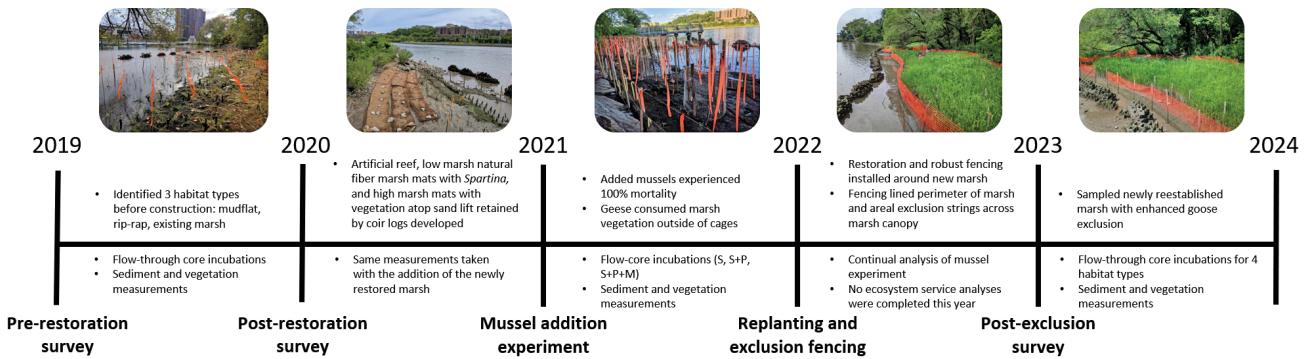
*Schoenoplectus rubustus*, *Solidago sempervirens*, and *Spartina patens*. A protective fence was installed around the planted areas consisting of wooden stakes and nylon string (Supplementary Materials, Figure S3). Our measurements focused on the low-marsh habitat due to its importance to future shoreline stability and nitrogen-removal processes and due to the many challenges associated with successfully restoring this habitat.

Post-installation, the herbivory fence failed, and the low marsh planting was almost completely uprooted by geese. Efforts to deter geese with the addition of brightly colored flagging tape suspended above the fences likewise failed. An experimental installation of ribbed mussels in 2021 failed due to intense predation by raccoons. We attempted a variety of methods to exclude raccoons including constructing cages of chicken wire and placing mussels in oyster cages and zip-tying them to the substrate. Racoons burrowed under and disassembled cages to reach mussels, and oyster bags were cut open and mussels removed. In the spring of 2022, the low-marsh area was replanted and a more robust construction fence was installed, with aerial string extending over the top of the planted areas to exclude geese (Supplementary Materials, Figure S3). Given the construction of the fencing, it is unlikely that other herbivores such as insects, snails, or crabs were excluded.

### Sampling Procedure

In 2019, we collected data from three habitat types before the construction of the restored living shoreline (Figure 1). These included a mudflat, rip-rap (intertidal rocks), and an existing low marsh (Figure 2). A map showing the relative locations of the habitats is available in Supplementary Materials (Figure S1). The mudflat and rip-rap were existing habitats that were to be partially replaced with constructed marsh, while the existing low marsh was to serve as a reference for comparisons to the constructed marsh. The existing marsh is an area located behind the pedestrian bridge that has remained intact since the initial restitution planting in 2001. Four intact sediment cores were collected from each of the three habitats ( $n = 12$ ) on 23 September 2019. Prior to core extraction, we placed  $0.25\text{ m}^2$  plots at each sampling location and measured stem density, diameter using digital calipers, and height using a tape measure. Aboveground biomass in the plot was harvested and frozen at  $-20^{\circ}\text{C}$  until analysis.

Cores were brought back to the laboratory at Baruch College and continuous-flow incubations were set up according to An et al. (2001) using site-collected water. Site water flowed into each core incubation at a rate of  $1.25\text{ ml min}^{-1}$ , and we collected inflow and outflow samples after 24 hours. Dissolved gas samples were filled from the bottom of the vial and allowed to overflow 3× the vial volume. Samples were then poisoned with  $200\text{ }\mu\text{l }50\%\text{ ZnCl}_2$  and stored submerged in water at  $4^{\circ}\text{C}$  until dissolved gas analysis

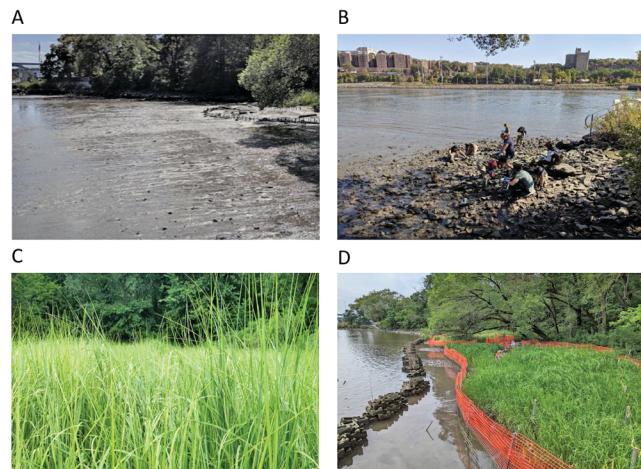


**Figure 1.** Timeline of adaptive management and research activities at the Sherman Creek Living Shoreline Project from 2019–2024.

was completed ( $^{28}\text{N}_2:\text{Ar}, \text{O}_2:\text{Ar}$ ) using MIMS (Kana et al. 1994). Dissolved nutrient samples were filtered with a  $0.2\text{ }\mu\text{m}$  syringe filter and frozen at  $-20^\circ\text{C}$  until analyzed for nitrate + nitrite ( $\text{NO}_x^-$ ), nitrite ( $\text{NO}_2^-$ ), ammonium ( $\text{NH}_4^+$ ), and phosphate ( $\text{PO}_4^{3-}$ ) with a Seal AQ2+ or AQ300 Discrete Analyzer (Seal Analytical USA, Mequon, WI) following USEPA Method 353.2 Rev. 2.0; USEPA Method 353.2 Rev. 2.0; Standard Methods 4500-NH3 G; and USEPA Method 365.1 Rev. 2.0, respectively. We calculated dissolved nutrient fluxes, sediment respiration, and net  $\text{N}_2$  fluxes to compare the rates of nitrogen-removal services provided by each of these habitat types. Positive  $\text{N}_2$  fluxes indicate that denitrification is the dominant process over nitrogen fixation.

Aboveground vegetation was dried at  $70^\circ\text{C}$  for 48 hours and weighed to determine total aboveground biomass. Sediment samples were collected from the upper 2.5 cm of the sediment profile and homogenized. We used one 5 ml subsample from each core to determine soil bulk density, moisture, and porosity after drying at  $70^\circ\text{C}$  for 48 hours and organic content as loss-on-ignition at  $500^\circ\text{C}$  for four hours (Wang et al. 2011). We used a second 5 ml subsample to determine carbon and nitrogen content. For this, samples were dried as described, treated with duplicate aliquots of hydrochloric acid to remove carbonates, weighed into tin capsules ( $\sim 20\text{ mg}$ ), and analyzed using a Perkin Elmer 2400 Series II elemental analyzer operating in CHN mode (Perkin Elmer Life and Analytical Sciences, Shelton, CT) to determine elemental content of carbon and nitrogen as a percentage of sample mass.

After construction in 2020, three intact sediment cores were collected from the same habitat types (mudflat, rip-rap, existing low marsh) but also in the newly restored low marsh ( $n = 12$ ; Figure 2) on 4 October 2020. Similar vegetation characteristics were measured, with the addition of belowground biomass. Continuous-flow incubations were set up as in 2019. In the lab, aboveground biomass was measured following methods in 2019, with the addition of belowground biomass. Belowground root and rhizomes were collected after core incubations (surface area



**Figure 2.** Habitat types sampled for ecosystem services in 2019, 2020, and 2023. (A) mudflats, (B) rip-rap, (C) existing marsh, and (D) restored marsh. The restored marsh photo includes exclusion fencing installed prior to the 2023 sampling and oyster castles.

$0.00397\text{ m}^2$ , inserted to maximum apparent root depth), washed over a 1 mm sieve to remove sediments, dried at  $70^\circ\text{C}$  for 48 hours, and weighed to determine total belowground biomass. Sediment samples were analyzed for sediment bulk density, moisture, porosity, and organic content following the 2019 protocol.

In 2021, we conducted manipulative experiments to examine the effects of adding ribbed mussels to the living shoreline project. We established 10 experimental plots ( $0.25\text{ m}^2$ ) on 7 May 2021 and randomly assigned mussel treatments to five of them. Each mussel plot was planted with 400 mussels ( $1,600\text{ m}^{-2}$ ). Unfortunately, we returned the following week to find 100% mortality of the deployed mussels. We attempted multiple tactics to protect the mussels from predation and apparent vandalism, including shellfish bags and chicken wire cages around the plots, but we had little success. NYRP staff observed raccoons foraging in the shoreline, and tracks around the plots confirmed the presence of raccoons. On 8 September 2021, we added

mussels to the five designated mussel plots and immediately collected a sediment core from each plot that included the mussels, marsh plants, and sediment (M+P+S). We collected another five cores from the caged plots with only plants and sediment (P+S) in each core, and we collected five cores from the unprotected living shoreline where the marsh grasses were consumed and only sediment (S) was present. This allowed us to examine the potential impact each component of the shoreline could have on sediment nitrogen cycling.

Continuous-flow incubations were set up immediately following core collection according to protocol detailed by An et al. (2001). After we collected the 24 h samples described above ( $n = 3$  core $^{-1}$ ), we added  $^{15}\text{N-NO}_3^-$  to the site water inflows to determine the proportion of  $^{15}\text{N}$  that was denitrified (Nielsen 1992). Dissolved gas and nutrients samples were collected at 48 and 72 h ( $n = 3$  core $^{-1}$  sample time $^{-1}$ ) (Bruesewitz et al. 2013, Hoellein et al. 2015). Dissolved nutrient samples were analyzed as in 2019, and gasses ( $^{28}\text{N}_2:\text{Ar}$ ,  $\text{O}_2:\text{Ar}$ ,  $^{29}\text{N}_2$ , and  $^{30}\text{N}_2$ ) with membrane inlet mass spectrometry (MIMS) (Kana et al. 1994). For both 48 and 72 h MIMS, we added a copper column to scrub  $\text{O}_2$  as it has been shown to interfere with labeled  $\text{N}_2$  (Lunstrum and Aoki 2016). After flux measurements, sediment samples were analyzed following 2019 protocols, and belowground biomass was analyzed following 2020 protocols. All data from 2021 mussel experiments, including code used to perform flux calculations, are available as a published dataset (Alldred et al. 2024a).

While cages were not successful in excluding raccoons from mussel treatments, they did successfully deter geese, resulting in the only plant growth in the restored marsh site in 2021. In spring 2022, the restored marsh was replanted with more robust exclusionary fencing, consisting of orange construction fencing along the marsh edge and aerial string suspended over the marsh canopy (Supplementary Materials, Figure S3). No samples were taken from any habitat type in 2022. In summer 2023, we repeated methods from 2019 with the addition of above- and belowground carbon and nitrogen content. For this, aboveground and belowground plant material was subsampled, homogenized using a mortar and pestle, and ~2 mg samples were analyzed using the same protocol as sediment carbon and nitrogen content in 2019 and 2021. All data from 2019, 2020, and 2023 surveys, including code used to perform flux calculations, are available as a published dataset (Alldred et al. 2024b).

### **Statistical Analysis**

All analyses were performed in R version 4.4.2 (R Core Team 2024) and are documented in Supplementary Information. We corrected for instrument drift and calculated dissolved gas fluxes using the formula  $f(C_o - C_i)/\alpha$  where  $f$  is the flow rate in L/h,  $C_o$  is the outflow concentration in  $\mu\text{mol}$ ,  $C_i$  is the inflow concentration in  $\mu\text{mol}$ , and  $\alpha$  is

the surface area of the core in  $\text{m}^2$ . All flux calculations are documented in the published metadata for this project (Alldred et al. 2024a, b).

For survey data, we used a two-way ANOVA to test for differences in denitrification rates and sediment respiration among habitat types and sampling years. We used the *emmeans* package (Lenth 2024) to compute contrasts among habitat types within each sampling year, with a significance threshold of  $\alpha = 0.10$  due to the inherent variability of these measurements, and constraints on experimental replication to avoid unnecessary disturbance to the restoration, to reduce the likelihood of a Type II error. We used a three-way ANOVA to test for differences in nutrient fluxes among cover types, sampling years, and dissolved nutrient species ( $\text{NH}_4^+$ ,  $\text{NO}_x^-$ , and  $\text{PO}_4^{3-}$ ). Contrasts were performed as described for gas fluxes. We tested for differences in stem height and stem density between the new and existing marsh sites and among sampling years using two-way ANOVAs with post-hoc contrasts. Stem height and stem density were  $\log_{10}$ -transformed prior to analysis to ensure a normal distribution of model residuals. We compared all vegetation measurements performed in 2023 between the new marsh and the existing marsh using Welch's approximate t-test, which does not assume equal variance between groups.

For mussel experiments, we used a two-way ANOVA to test for differences in denitrification among experimental treatments and isotope-addition treatments (control vs.  $^{15}\text{N-NO}_3^-$ ), with post-hoc contrasts. We used a one-way ANOVA with post-hoc contrasts to test for differences in sediment respiration among experimental treatments. We used a three-way ANOVA to test for differences in nutrient fluxes among experimental treatments, isotope-addition treatments, and nutrient species.

Model residuals were visually inspected to ensure assumptions of normality were met. Residuals of gas-flux and nutrient-flux models for the multi-year survey were normally distributed but showed signs of heteroscedasticity, which is unsurprising given the very large range in measurement values. ANOVA models are robust to violations of the assumption of homoscedasticity for models with equal sample sizes; however, we should note that the heteroscedasticity we observed may result in lower power to detect differences among groups (Sokal and Rohlf 2013). All positive flux values represent net efflux of gas or nutrients, where negative flux values represent a net uptake.

## **Results**

### **Site Characteristics**

Site conditions during discrete sampling differed from 2019 to 2023, with 2019 having the highest water-column salinity and  $\text{NO}_x^-$  concentrations, and 2023 experiencing

the highest water-column temperature (Table 1). Dissolved  $\text{NO}_x^-$  concentrations remained elevated throughout the study period, ranging from 0.38–0.92 mg/L N- $\text{NO}_x^-$ . Sediment organic carbon ranged from ~3–6% for most habitat types, but the existing marsh experienced higher overall organic content ranging ~10–13% (Table 2).

### Gas Fluxes

Net denitrification rates (i.e., positive  $\text{N}_2$  fluxes) differed significantly among habitat types ( $F_{3,29} = 8.34, p < 0.001$ ) and among years of the study ( $F_{2,29} = 18.59, p < 0.001$ ), with no significant interaction between habitat type and year ( $F_{5,29} = 1.23, p = 0.32$ ). We detected significant interannual variability in denitrification rates, with nearly double the rates of denitrification across all treatments in 2019 relative to 2020 and 2023 (Figure 3A). Because the focus of our analysis was to document differences among the habitats, we computed treatment contrasts within each year. We found that all habitat types were different in 2019 (Figure 3A). As expected, denitrification rates were 4-fold higher in the existing marsh compared to the mudflat and 35% higher relative to the rip-rap habitat. In 2020 and 2023 denitrification rates were significantly higher in the new marsh relative to the mudflat but were remarkably similar to rates in the existing marsh habitat (Figure 3A). In 2020, denitrification rates in the new marsh exceeded rates in the mudflat by nearly an order of magnitude; in 2023, the two habitats maintained rates of denitrification similar to those in 2020, but the mudflat was found to be a net source of nitrogen to the atmosphere (Figure 3A). Oxygen demand differed significantly among habitat types ( $F_{3,29} = 14.21, p < 0.001$ ) and sampling years ( $F_{2,29} = 8.38, p = 0.001$ ), with no significant interaction between habitat type and year ( $F_{5,29} = 0.47, p = 0.79$ ). Similar to nitrogen gas fluxes, we detected significant interannual variability, with nearly double the uptake of oxygen in 2019 relative to 2020 and 2023. Net uptake of oxygen was observed for all habitats within all years, with more than double the uptake in the marsh sites compared to the mudflat and rip-rap (Figure 3).

### Nutrient Fluxes

Nutrient fluxes differed significantly among habitat types ( $F_{3,87} = 3.0, p = 0.034$ ) and nutrient species ( $F_{2,87} = 98.51, p < 0.001$ ), with significant interactions between nutrient species and year ( $F_{4,87} = 16.59, p < 0.001$ ) and habitat type

**Table 1. Characteristics of site water collected from the Harlem River at Sherman Creek Park in all sampling years.**

	2019	2020	2021	2023
Salinity (ppt)	18	17	10	8
Temperature (°C)	22	20	23	27
$\text{NO}_x^-$ Concentration (mg/L)	0.92	0.62	0.38	0.51

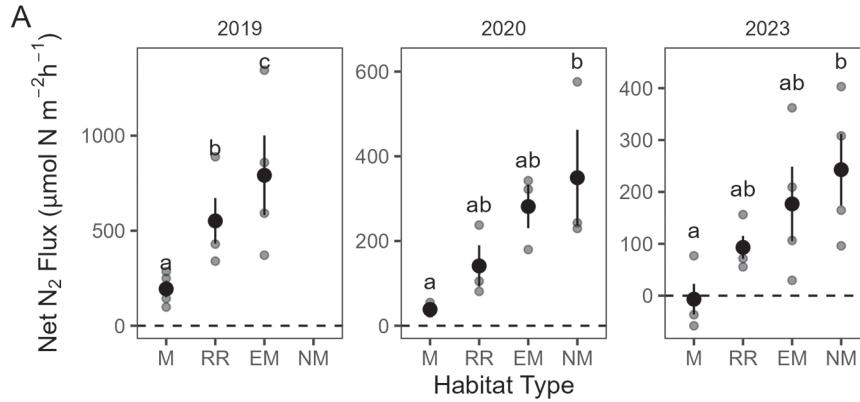
and year ( $F_{5,87} = 2.19, p = 0.061$ ). There were no significant differences among years of the study ( $F_{2,87} = 1.29, p = 0.27$ ), interaction between habitat type and nutrient species ( $F_{6,87} = 1.75, p = 0.11$ ), or between habitat type, nutrient species, and year ( $F_{10,87} = 0.90, p = 0.53$ ). We computed contrasts within each nutrient species and year to examine differences among habitat types, which was the primary focus of our study. We tended to see net efflux of  $\text{NH}_4^+$  from sediments in 2019 and 2020, with nearly ten-fold greater efflux from the mudflat than from the existing marsh in 2019 (Figure 4). In 2023, none of the  $\text{NH}_4^+$  fluxes differed significantly from zero. All habitats served as a sink for  $\text{NO}_x^-$  (nitrate + nitrite) throughout the study period (Figure 4). In 2019, the existing marsh had double the rate of  $\text{NO}_x^-$  uptake relative to the other two habitats. In 2020, the mudflat had a greater net uptake of  $\text{NO}_x^-$  relative to the rip-rap habitat (approximately double), with intermediate uptake rates in the marsh habitats. In 2023, uptake of  $\text{NO}_x^-$  in the new marsh exceeded uptake in the rip-rap habitat three-fold, with intermediate rates in the existing marsh and mudflat. Fluxes of  $\text{PO}_4^{3-}$  (phosphate) were close to zero throughout the study period and did not differ among habitat types (Figure 4).

### Vegetation

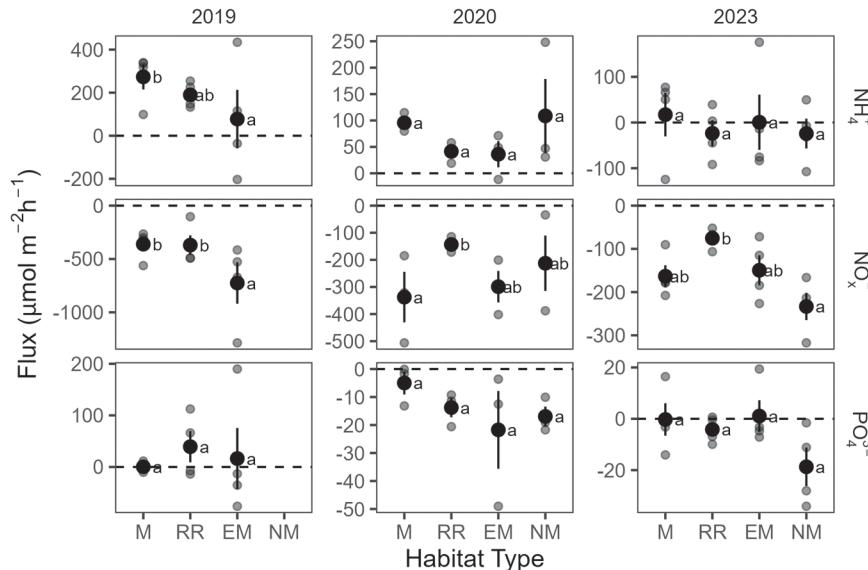
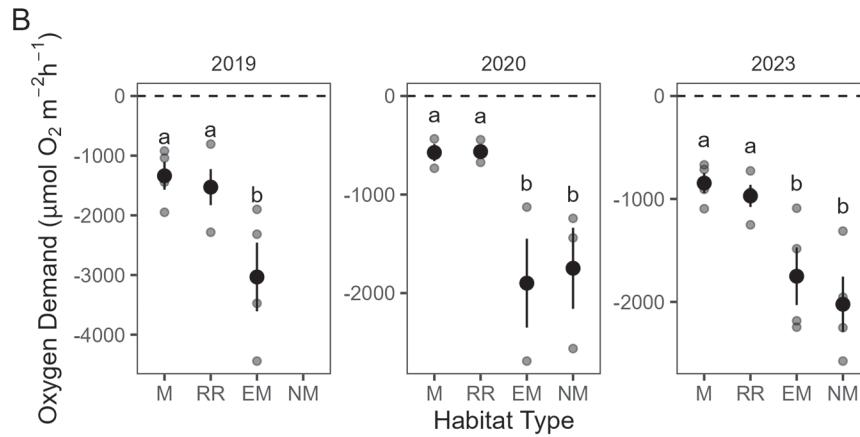
Stem density differed significantly among years ( $F_{3,19} = 15.42, p < 0.001$ ), and between habitat types ( $F_{1,19} = 15.09, p < 0.001$ ), with a significant interaction between habitat type and year ( $F_{1,19} = 15.80, p < 0.001$ ). We observed approximately 10-fold greater stem density in the new marsh in 2023 relative to measurements conducted in 2020 and 2021, while stem density in the existing marsh remained consistent throughout the study period (Figure 5A). Stem height differed significantly between habitat types ( $F_{1,19} = 29.30, p < 0.001$ ) and among years ( $F_{3,19} = 9.56, p < 0.001$ ), with a significant interaction between habitat type and year

**Table 2. Mean sediment organic carbon content (%) in all habitat types at Sherman Creek Living Shoreline. Values in parentheses represent the standard error of the mean.  $n_i = 4, 3, 5, 4$  for sampling years.**

Habitat Type	2019	2020	2021	2023
Mudflat	3.64 (1.13)	6.19 (0.24)	0.92 (0.44)	4.71 (0.35)
Rip-rap	5.83 (2.57)	5.97 (1.28)	—	4.04 (0.34)
Existing Marsh	12.89 (4.43)	10.57 (0.48)	—	9.42 (1.29)
New Marsh	—	3.04 (2.06)	6.32 (3.32)	3.76 (0.68)
Mussel Addition	—	—	4.68 (0.43)	—



**Figure 3.** Fluxes of dissolved (A)  $\text{N}_2$  gas and (B)  $\text{O}_2$  gas across the sediment-water interface among habitat types and survey years. Error bars represent standard error of the mean; lighter circles represent experimental replicates;  $n_i = 4$  in 2019 and 2023,  $n_i = 3$  in 2020. M = mudflat, RR = rip-rap, EM = existing marsh, NM = new marsh. Letters indicate significant post-hoc differences among treatment groups within each panel at  $\alpha = 0.10$ .



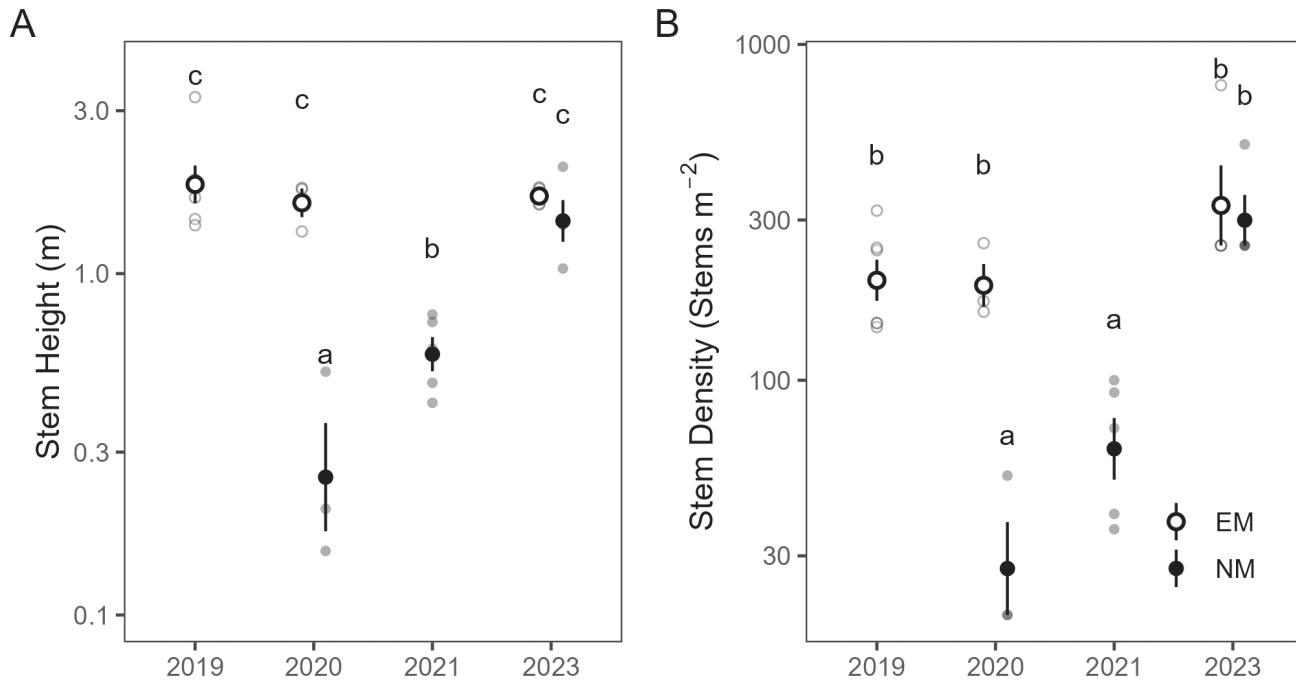
**Figure 4.** Dissolved nutrient fluxes across the sediment-water interface among habitat types and survey years. Error bars represent standard error of the mean; lighter circles represent experimental replicates;  $n_i = 4$  in 2019 and 2023,  $n_i = 3$  in 2020. M = mudflat, RR = rip-rap, EM = existing marsh, NM = new marsh. Letters indicate significant post-hoc differences among treatment groups within each panel at  $\alpha = 0.10$ .

( $F_{1,19} = 24.84, p < 0.001$ ). Stem height remained similar in the existing marsh across all years (Figure 5B). Stem height in the new marsh tripled between 2021 and 2023. By 2023, stem density and height were remarkably similar between the existing and new marsh habitats (Figure 5). This pattern was consistent among nearly all vegetation measurements conducted in 2023 (Table 3); however, we did observe a significant difference in belowground biomass, with nearly

double the amount of belowground biomass in the existing marsh relative to the newly restored marsh.

#### Mussel Experiment Gas Fluxes

Denitrification rates differed significantly among experimental treatments in the mussel-addition experiment ( $F_{2,39} = 11.01, p < 0.001$ ), with no significant differences between control and  $^{15}\text{NO}_3^-$  incubations ( $F_{1,39} = 0.18, p = 0.66$ ), and



**Figure 5.** Variation in (A) stem density and (B) plant height in the existing marsh (EM) and newly restored marsh (NM) in the Sherman Creek Living Shoreline throughout the study period. Error bars represent standard error of the mean; lighter circles represent experimental replicates;  $n_i = 3, 4, 5, 4$ , respectively. Letters indicate significant post-hoc differences among treatment groups within each panel at  $\alpha = 0.10$ .

**Table 3.** Mean characteristics of *Spartina alterniflora* in the existing marsh and newly restored marsh at Sherman Creek Living Shoreline in 2023. Values in parentheses represent the standard error of the mean.  $n_i = 4$ .

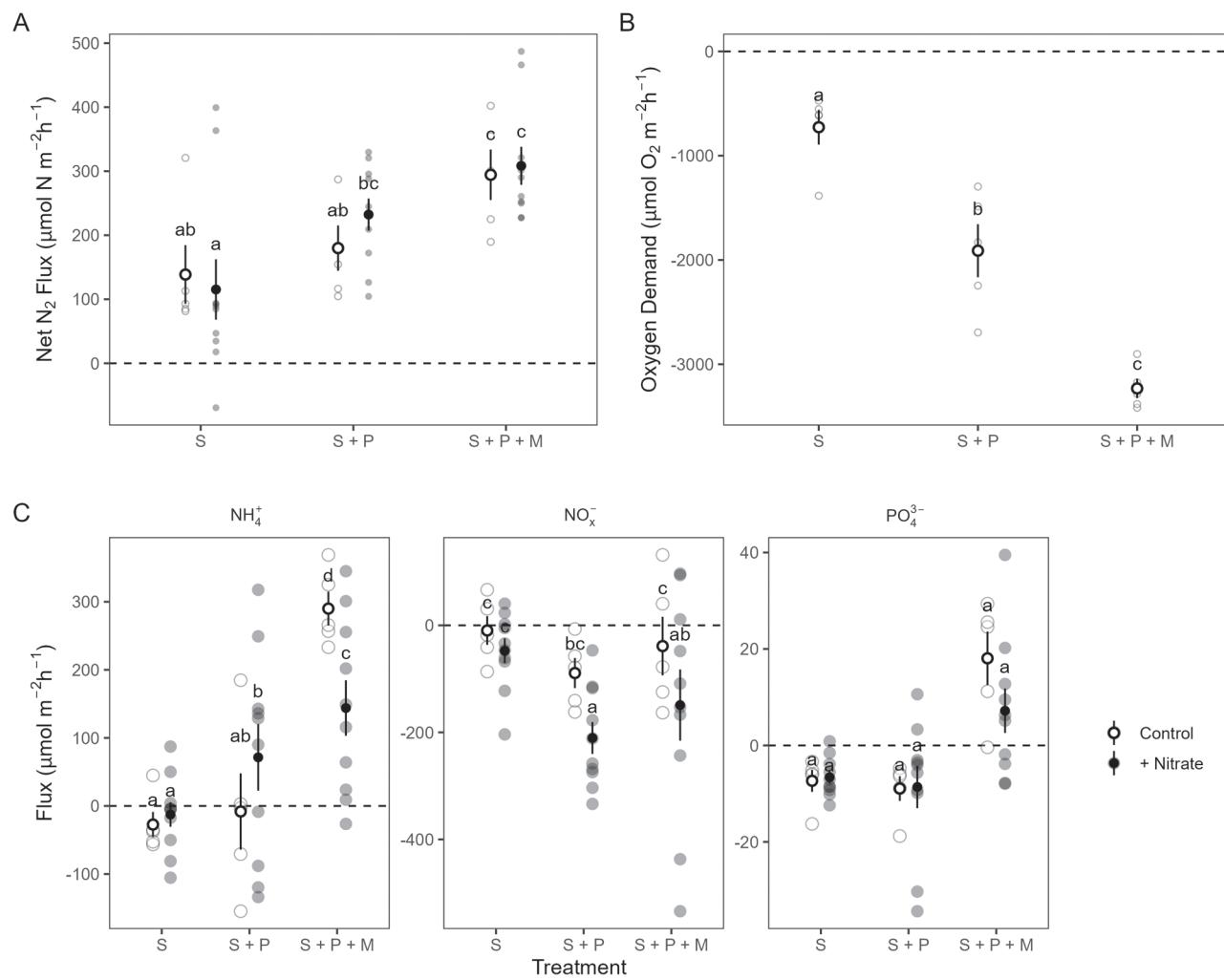
Characteristic	Existing Marsh	New Marsh
Aboveground biomass ( $\text{kg m}^{-2}$ )	3.42 (0.74)	2.24 (0.56)
Belowground biomass ( $\text{kg m}^{-2}$ )*	5.89 (0.95)	3.03 (1.02)
Stem density ( $\text{stems m}^{-2}$ )	377.83 (125.94)	314.86 (62.97)
Stem height (m)	1.69 (0.05)	1.47 (0.21)
Stem diameter (mm)	7.91 (0.97)	7.57 (0.57)
Leaf C (%)	41.68 (0.55)	41.21 (0.54)
Leaf N (%)	1.45 (0.29)	0.92 (0.1)
Leaf C:N	35.54 (11.3)	46.4 (4.49)
Root C (%)	38.06 (1.87)	35.36 (3.56)
Root N (%)	0.76 (0.12)	0.9 (0.38)
Root C:N	53.02 (6.18)	78.24 (43.59)

\* Significant at  $\alpha = 0.10$ , Welch's t-test not assuming equal variance.

no significant interaction between experimental treatment and isotope-addition ( $F_{2,39} = 0.43, p = 0.65$ ). Specifically, rates of denitrification in the sediment + plant + mussel (S+P+M) treatment were double those in the sediment (S) and 50% higher than those in the sediment + plant (S+P) treatments (Figure 6A). Oxygen demand also differed significantly among treatments ( $F_{2,12} = 46.71, p < 0.001$ ), with more than double the net consumption of oxygen in the S+P cores relative to S cores, and even greater net consumption in the S+P+M cores relative to S+P cores (Figure 6B).

### Mussel Experiment Nutrient Fluxes

Nutrient fluxes differed significantly among experimental treatments ( $F_{2,117} = 7.02, p < 0.001$ ), between  $^{15}\text{NO}_3^-$ -addition treatments ( $F_{1,117} = 4.33, p = 0.039$ ) and among nutrient species ( $F_{2,117} = 38.85, p < 0.001$ ). We also found a significant interaction between experimental treatment and nutrient species ( $F_{4,117} = 9.60, p < 0.001$ ) and between isotope-addition treatment and nutrient species ( $F_{2,117} = 2.30, p = 0.1$ ). We observed no significant interaction between experimental treatment and isotope-addition



**Figure 6.** Net flux of (A) dissolved N<sub>2</sub> gas, (B) dissolved O<sub>2</sub> gas, and (C) dissolved inorganic nutrients across the sediment water interface under control and added  $^{15}\text{N}$ -NO<sub>3</sub><sup>-</sup> conditions. Error bars represent standard error of the mean; lighter circles represent experimental replicates;  $n_i = 5$  for control incubations and  $n_i = 10$  for added nitrate incubations. S = sediment only, S + P = sediment with plant, S + P + M = sediment with plant and mussels. Letters indicate significant post-hoc differences among treatment groups within each panel at  $\alpha = 0.10$ .

treatment ( $F_{2,117} = 2.20, p = 0.11$ ), nor among treatment, isotope, and nutrient species ( $F_{4,117} = 1.67, p = 0.15$ ). We observed a net efflux of PO<sub>4</sub><sup>3-</sup> from sediments for the S+P+M experiment in both the control and nitrate-addition incubations, whereas the S and S+P treatments experienced low rates of net PO<sub>4</sub><sup>3-</sup> uptake (Figure 6C). We also observed a net efflux of NH<sub>4</sub><sup>+</sup> in the S+P+M treatment specifically for the control (Figure 6C). We observed no net uptake for NO<sub>x</sub><sup>-</sup> among experimental treatments in control incubations, but we found net uptake of NO<sub>x</sub><sup>-</sup> in the S+P and S+P+M experimental treatments following nitrate additions, showing that the sediment was taking up the added NO<sub>3</sub><sup>-</sup> (Figure 6C).

## Discussion

### Denitrification and Sediment Characteristics

Denitrification is an important microbial process that permanently removes NO<sub>3</sub><sup>-</sup> from the ecosystem. Our measurements in an urban living shoreline were consistent with a similar study conducted at an eroding salt marsh in Martha's Vineyard (MA, USA) that found equivalent denitrification rates in living shorelines relative to reference sites (Schoell et al. 2023). We also found that this functional equivalence in nitrogen removal between living shorelines and reference sites can be achieved within one year. In contrast to a previous chronosequence study (Onorevole et al. 2018), rates of denitrification at Sherman Creek did not increase as the living shoreline aged (e.g., 2020 vs 2023). The Schoell et al. (2023) study similarly did not see an

increase in potential denitrification as the living shoreline aged. These similarities and differences across sites may be due to several site-specific factors including hydrology, physico-chemical conditions, and biotic interactions.

Previous work has demonstrated that an increase in organic content in marsh sediments should translate to greater microbial activity, as well as increased diffusion of water and gasses across the sediment-water interface (Alldred et al. 2020). For example, maximum denitrification enzyme activity was found in the portions of a living shoreline with the highest sediment carbon content (Schoell et al. 2023). While we observed significantly lower carbon content in the new marsh compared to our existing marsh, we observed similar denitrification rates in both 2020 and 2023. Surprisingly, the greater organic content we observed in the existing marsh relative to other habitat types, including the newly restored marsh, did not necessarily translate into greater rates of denitrification. However, our results are not unique. Kleinhuijzen and Mortazavi (2018) concluded that after 21 years of development, sediments of a restored salt marsh in the Gulf of Mexico contained significantly less carbon ( $2.0\% \pm 0.1$ ) than the natural marsh ( $16.4\% \pm 0.5$ ) yet supported similar rates of nitrogen removal.

We infer that the rapid recovery we observed in denitrification rates in the newly restored marsh may be due to the proximity of the living shoreline to CSOs in the Harlem River, which discharge high water column nitrate and dissolved organic carbon, potentially increasing denitrification potential. While organic content was lower in the new marsh compared to the existing marsh, it was high relative to other newly restored marsh projects. A similar 2-year study on a recently constructed *Spartina* marsh recorded anywhere from  $0.11 \pm 0.01$  to  $0.22 \pm 0.04$  sediment % carbon, and from  $0.01 \pm 0.01$  to  $0.03 \pm 0.01$  sediment % nitrogen between the two years (Rezek et al. 2017). In New York City, a study on coastal marsh resilience sampled four restored marsh sites and determined organic content to be between 0.87% and 1.48% (Alldred et al. 2020), far lower than our results in the same region. This relatively high organic content compared to other restoration sites may be attributed to pre-restoration carbon storage in the sediment, or a high input of water-column organics from nearby CSOs. The results from our study suggest that newly restored marshes can support nitrogen removal similar to a ~20-year-old restored marsh after only one year of growth.

Our study noted significant interannual variability in denitrification rates, which was not surprising given the spatial and temporal heterogeneity of conditions that favor denitrification (Alldred et al. 2016, Granville et al. 2021). Specifically, we observed very high water-column nitrate concentrations in 2019, which corresponded to our greatest observed rates of denitrification. We were fortunate to have a stable low-marsh habitat nearby to use as a reference to track relative recovery of the new marsh. In urban restoration, useful references are often not available due to

widespread disturbance of natural habitats. In many cases, the nearest marsh may be many kilometers from the newly restored site and experience very different biotic and abiotic drivers. In such cases, more frequent sampling will likely be needed to account for seasonal and interannual variability. While a greater number of samples would also be helpful in characterizing spatial variation within a site or treatment, care must often be taken to avoid unnecessary disturbance to a site in recovery.

### **Effects of Herbivory on *Spartina* Establishment in a Restored Marsh**

Excluding herbivory from a marsh restoration increases the likelihood of success. Consistent with previous studies (Baldwin and Pendleton 2003), we found that limiting grazing pressure by installing exclusion fencing has a positive effect on the establishment and overall productivity of *S. alterniflora*. One year after successfully excluding herbivores from the restored marsh, we observed plant height and density, and nitrogen-removal rates, comparable to the existing marsh site, showing that establishment of a productive marsh can happen quickly if given an opportunity to develop. In the absence of effective exclusion fencing, we observed little growth and development of *S. alterniflora* due to root grubbing and young-plant grazing by geese. Similar studies note that exclusion fencing for geese increased both plant cover and species diversity, creating a distinct plant community compared to an unprotected marsh (Jobe et al. 2022). Conventional wisdom suggests that marsh restoration takes at least five years to develop (Mitsch and Wilson 1996), but our results suggest that with appropriate precautions, ecological functions can recover much faster. Context-specific management practices for restored marshes can have a positive effect on overall success.

Notably, the existing marsh that we used as a reference site for this study has never been devegetated by goose herbivory the way the newly restored marsh sites were until 2022. A number of factors can influence the importance of goose herbivory on the success of newly planted marshes including the status of resident goose populations at the time of planting, ease of access for geese from the shoreline, the presence of canopy cover, and the chemical composition of the seedlings (Buchsbaum et al. 1981, Bergen et al. 2000, NYC Parks 2018). While we cannot establish which of these factors led to lower goose herbivory at the existing marsh that allowed the vegetation to establish and persist, it is likely that the pedestrian bridge isolating the marsh from the shoreline, as well as surrounding forested canopy cover, may have deterred geese from entering the area. Once vegetation has established a rhizome mat, goose herbivory is less likely to result in complete eradication of the marsh and conversion to mudflat as we observed in the shoreline restoration several times. Previous studies have also suggested that geese tend to be attracted to newly planted seedlings,

which tend to be higher in nitrogen content and lower in phenolic acids than mature plants, particularly early in the growing season (Buchsbaum et al. 1981).

The goal of exclusion fencing is to exclude geese from newly planted marshes long enough for the marsh to develop a continuous canopy cover and rhizome mat. We have observed robust marsh growth with a continuous canopy cover for at least three years since the installation of exclusion fencing at Sherman Creek in 2022 (personal obs.). However, we did observe that the one vegetation characteristic in the new marsh that lagged behind that of the existing marsh was total belowground biomass. The decision of when to remove exclusion fencing is a difficult one. Common guidance for New York City suggests 2–3 years, with longer periods in areas subject to high wave energy and herbivore abundance (NYC Parks 2018). However, fences are often unpopular with local stakeholders due to aesthetic concerns and the possibility of trapping species of concern including *Limulus polyphemus* (horseshoe crabs) and *Malaclemys terrapin* (diamondback terrapins) (NYC Parks 2018). Careful monitoring may be necessary to ensure longer term stability of the marsh in areas where resident goose populations are abundant and to avoid negative effects of fencing on species of concern. Longer term monitoring will also be needed to determine whether the benefits of restoration we have observed in this study will continue once the fencing is removed.

### **Lessons Learned from Mussel Addition**

We observed a 100% mortality rate in mussels added to the marsh due to raccoon predation and apparent vandalism. Initial planting of mussels included no fencing and these mussels were planted directly in the coconut fiber substrate alongside plant plugs. Within one week, raccoons consumed all mussels. We then placed mussels into plastic oyster growing cages and attached those cages to the coconut fiber. These cages were either cut open by vandals and mussels were taken, or the cages were removed from the site completely. Finally, we placed wire cages around our plots that consisted of *S. alterniflora* and mussels, but these were also not effective in protecting against raccoons. The raccoons appeared to dig under the bottom of the cages to enter and consume the mussels. While not successful in preventing raccoon predation, we found that plants within the fenced plots were not consumed by geese. Consequently, we were able to pivot the goal of our experiment to measure nitrogen-removal services in a restored marsh with and without goose exclusion in 2021. We included a mussel treatment to estimate the additional short-term effect of mussels on nitrogen removal if we were able to successfully exclude predators. We observed a 50% increase in denitrification with the addition of mussels. This may be due to the mussels creating more anaerobic conditions via respiration and increasing labile organic matter in the form of feces and pseudofeces (Zhu et al. 2019).

This study demonstrated that the presence of mussels and marsh grass can significantly increase rates of N removal in a living shoreline on the Harlem River provided that negative species interactions can be managed, which unfortunately adds to project costs in both materials and time. Other studies on mussel additions to salt marshes parallel ours in that they experience an unexpected degree of predation; however, in the absence of predation, they can increase *S. alterniflora* biomass and overall nutrient cycling (Fischman et al. 2024, Carroll et al. 2024). These efforts illustrate the importance of understanding the predator-prey interactions that can shape urban shorelines. We recommend that future restoration efforts consider the abundance of local shellfish predators, including terrestrial species, in deciding whether mussel addition is likely to be successful.

### **Adaptive Management**

Adaptive management allows us to continue to refine and improve our restoration techniques in ways that lead to more successful outcomes. Small-scale pilot studies can play a significant role in avoiding large-scale failures and developing better management strategies that allow managers to adapt to local challenges. For example, our small-scale mussel-addition experiment, with multiple attempts to exclude predators, was ultimately unsuccessful. However, in successfully excluding geese from our predator cages, we obtained data that supported installation of more robust goose-exclusion fencing. The new fencing led to robust growth and levels of denitrification similar to those in an existing marsh within only one year. We also learned from our difficulties in establishing mussels. Excluding mussel predators remains a significant ongoing challenge in this site relative to similar restorations in New York City (Zhu et al. 2019). To avoid unnecessary costs, future restorations should consider context-specific biotic challenges when planning living shoreline designs in the same way they consider context-specific abiotic constraints such as elevation and potential rates of erosion.

Urban marsh restoration is more likely to be successful when managers understand site-specific conditions. Knowing potential species interactions prior to restoration allows us to anticipate challenges and avoid devoting excess resources in high-predation areas. Pre-restoration surveys and pilot studies are especially important for urban locations, where options for controlling herbivore and predator abundance are more limited. For example, noise-making devices, hunting, and round-ups are often used to control goose populations in agricultural settings, but are less feasible in urban environments (Curtis and Braband 2022). The sound of gunshots, whether real or simulated, is not advisable in densely populated areas, and urban goose populations quickly acclimate to auditory and visual deterrents (Curtis and Braband 2022). Parks also often have strict regulations regarding trapping or hunting of

nuisance species. We also cannot ignore the possibility that control of one nuisance species (e.g., raccoons) could have unintended consequences for the abundance of another nuisance species (e.g., reduction in goose egg predation). Greater awareness of potential species interactions in urban settings could contribute to future restoration success. For example, preliminary studies using camera traps have identified landscape features that may contribute to local abundance of raccoons (Stark et al. 2020, Mowry et al. 2023). These types of studies could provide useful data to inform site-specific restoration goals.

Ultimately, the living shoreline project at Sherman Creek has enhanced net nitrogen storage and removal relative to the pre-existing habitats (i.e., rip-rap and mudflat) and taught us valuable lessons about biotic constraints on urban restoration. Continual monitoring for restored sites similar to Sherman Creek, which face considerable abiotic and biotic pressure, will likely be necessary to ensure they continue to experience the success and provide the benefits we have documented.

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