Marsh Plants Enhance Coastal Marsh Resilience by Changing Sediment Oxygen and Sulfide Concentrations in an Urban, Eutrophic Estuary

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Abstract

Despite considerable efforts to restore coastal wetlands, the ecological mechanisms contributing to the success or failure of restoration are rarely assessed. Accumulation of hydrogen sulfide in sediments may accelerate rates of marsh loss in eutrophic estuaries and is likely driven by complex feedbacks between wetland plant growth and microbial redox reactions. We used a chronosequence of restored marshes in urbanized and eutrophic Jamaica Bay (New York City, USA) to assess how sediment redox conditions change among seasons and over the lifetime of restored marshes. We also compared a stable extant marsh to one that has deteriorated over the past 50 years. We collected seasonal sediment cores from each marsh, and used a motorized microprofiling system to measure the vertical distribution of oxygen and sulfide. We fit a logistic function to each profile to estimate (1) maximum concentrations, (2) rates of increase/decline, and (3) depths of maximum increase/decline. We quantified sediment density, porosity, organic content, and belowground plant biomass, and estimated differences in daily tidal inundation among sites using water-level loggers. We found that minimum oxygen and maximum sulfide concentrations occur during summer. Sulfide concentrations were highest in sites that experienced the longest daily tidal inundation, including the degraded extant marsh and the oldest restored marsh. Spatial patterns in oxygen and sulfide were related to belowground plant biomass, supporting our hypothesis that root growth increases sediment oxygen and partially alleviates sulfide stress. Our data support the growing body of evidence that belowground plant growth may enhance the resilience of marshes to sea-level rise by increasing marsh elevation and facilitating oxygen diffusion into marsh sediments.

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Introduction

Human use and development of coastal areas has resulted in the loss of over 50% of historic wetland area, with much higher rates of loss in urban areas (Zedler and Kercher 2005; Gedan et al. 2009; Kingsford et al. 2016). Successfully conserving and restoring coastal wetlands and the many services they provide to human populations (Zedler 2003; NOAA 2019), despite future losses to accelerating rates of sea-level rise (IPCC 2014), will be vital to the future health and economic well-being of coastal communities. Effective management of coastal areas will depend, in large part, on resolving uncertainties surrounding interactions between sea-level rise and the growth and function of coastal marshes. A substantial body of literature has addressed the mechanisms contributing to coastal marsh inundation and loss due to sea-level rise. These mechanisms are extremely complex and involve dynamic feedbacks among plant growth, microbial processes, and sediment redox conditions. In order to keep pace with

sea-level rise, marshes must accumulate sufficient allochthonous sediment or produce sufficient autochthonous organic matter such that the marsh platform grows vertically faster than sea levels (e.g., Redfield 1972; Warren and Niering 1993; Morris et al. 2002, 2016; Rooth et al. 2003). Several mechanisms may hinder marsh growth. Any land development that decreases sedimentation rates (i.e., damming, shoreline hardening, or watershed reforestation) may decrease sediment delivery to coastal marshes and thus their vertical accretion rates (Mudd 2011; Kirwan and Guntenspergen 2012; Weston 2014; Anisfeld et al. 2016). Likewise, erosion may remove sediment from marshes and decrease marsh elevation. Erosion increases with high-intensity storm surges, which may increase in frequency as a result of climate change or offshore dredging activities (Ashton et al. 2008; Nicholls and Cazenave 2010; IPCC 2014). Marshes experiencing coastal subsidence due to natural (e.g., peat compaction or crustal processes) or human activities (e.g., fluid extraction) are at a greater risk of loss, as marshes must grow vertically to keep pace with simultaneous rates of sea-level rise and subsidence (Donnelly 1998; Morton et al. 2002; Morton et al. 2005; Törnqvist et al. 2008; Nicholls and Cazenave 2010). In contrast, marshes with a higher initial height are at less risk due to "elevation capital," or an initial buffer against losses due to sea-level rise (Watson et al. 2017; Cahoon et al. 2019).

The greatest uncertainties in projections of future marsh loss pertain to the responses of marsh vegetation and microbial processes to increasing inundation, particularly when coupled to concurrent stressors such as eutrophication or sulfide accumulation. Marshes that grow primarily by organic-matter accumulation are particularly subject to these mechanisms because plant production and rates of microbial decomposition both respond to the availability of oxygen, which decreases with increasing duration of tidal inundation (Nyman et al. 1995; DeLaune and Pezeshki 2003). Nutrient addition can accelerate rates of marsh loss by decreasing the growth of belowground plant biomass, leaving sediments at greater risk of loss due to erosion (Darby and Turner 2008; Turner 2011; Deegan et al. 2012; Wigand et al. 2014; Alldred et al. 2016). Nutrient addition can also increase rates of microbial decomposition, reducing organic matter accumulation and oxygen availability (Wigand et al. 2009), and eventually leading to the formation of harmful byproducts of anaerobic respiration such as hydrogen sulfide (H_2S) that reduce the growth of vegetation (Howarth 1984; Koch et al. 1990). Indeed, the accumulation of H_2S to toxic concentrations, as a result of prolonged flooding and anoxia, has been recognized as a tipping point beyond which a stable marsh rapidly converts to a mudflat (Kolker 2005; Fagherazzi et al. 2006).

Marsh plants often play a role in accumulating and stabilizing marsh sediments and engineering sediment conditions to resist H_2S toxicity (Silliman et al. 2019). Plant stems attenuate wave energy and reduce the erosional forces that

destabilize and remove marsh sediments (Leonard and Luther 1995; Maximiliano-Cordova et al. 2019). Plant roots stabilize marsh sediments (Gedan et al. 2011; Silliman et al. 2019) and contribute to organic matter accumulation (DeLaune and Pezeshki 2003; Nyman et al. 2006; Marani et al. 2010). Belowground growth of plant roots and rhizomes also introduce oxygen to anoxic marsh sediments (Howes et al. 1981) and reduce sediment density, which increases sediment porosity and facilitates diffusion of oxygen into sediments (Davey et al. 2011). As a result of all of these mechanisms, the loss of aboveground and/or belowground plant growth (i.e., due to prolonged inundation), may result in a catastrophic shift in coastal systems from accretion to erosion, leading to marsh collapse (Marani et al. 2010; Marani et al. 2013; Silliman et al. 2019). Management actions, such as sediment addition or reconstruction of a higher elevation marsh, may be able to reverse this shift and return the marsh ecosystem to a stable state (DeLaune et al. 1990; Rafferty et al. 2011). However, the mechanisms contributing to marsh stability or loss have rarely been examined for constructed coastal wetlands.

Urban, eutrophic estuaries are subject to multiple stressors that contribute to marsh loss. For example, extensive shoreline development has reduced sediment inputs to Jamaica Bay in New York City (NYC), USA, such that sediment exported from the bay greatly exceeds inputs of new sediments (Peteet et al. 2018), and offshore dredging has increased the depth of the bay and increased the energy of waves and storm surges, leading to increased erosion (Swanson et al. 2016). As a result, any increases in marsh elevation in Jamaica Bay result primarily from belowground organic matter production or seston deposition, similar to many marshes throughout New England (Bricker-Urso et al. 1989; Roman et al. 2000; Weston 2014; Carey et al. 2017). Sewage effluent from combined sewage overflows and other non-point sources of nutrient pollution have resulted in chronic eutrophication (Swanson et al. 2016; Watson et al. 2018), with corresponding changes in marsh plant production and organic matter accumulation (Wigand et al. 2014). Moreover, newly constructed marsh islands experience sediment subsidence following their initial construction (Messaros et al. 2010). Due to the combined effect of all of these stressors, Jamaica Bay has lost over 92% of its historic wetland area over the past century (Hartig et al. 2002). These losses, and the corresponding losses in ecosystem services, have generated significant investment in marsh restoration through sediment addition and replanting of marsh vegetation (Rafferty et al. 2011). However, the long-term outlook for constructed marshes in Jamaica Bay and other urban estuaries is uncertain.

In this study, we made use of a chronosequence of constructed wetland islands, as well as a deteriorating and a stable extant island, in Jamaica Bay to determine which mechanisms contribute most strongly to the stability of natural and restored

coastal marshes. We used a comparative approach to answer the following questions:

1. Do sediment oxygen and sulfide concentrations differ between a stable and unstable extant marsh in an urban estuary?
2. How do sediment oxygen and sulfide concentrations develop over time in constructed marshes?
3. Is the period of daily tidal inundation related to the accumulation of sulfide in marsh sediments?
4. Is belowground plant biomass related to sediment oxygen and sulfide dynamics?

We expected that the trajectory of development within the constructed marshes would follow one of two potential pathways, with the deteriorating and stable extant marshes representing the endpoints of these pathways. With sufficient elevation capital, marsh plants may be able to accumulate sufficient organic material for the marsh platform to keep pace with sea-level rise (Fig. 1). In this scenario, plant growth would remain sufficient to oxidize sediments during periods of inundation and anoxia, keeping H_2S concentrations low and allowing plant growth to continue and organic matter to accumulate. If elevation capital is not sufficient, or if subsidence of marsh sediments contributes to increasing periods of inundation, then plant-mediated oxidation may become insufficient to compensate for prolonged periods of anoxia, allowing H_2S to accumulate to toxic levels. In this scenario, plant growth would decrease, marsh root biomass would

deteriorate, and the marsh platform would undergo rapid transition to a mudflat (Fig. 1).

Methods

Site Description

We made use of a chronosequence of restored marsh islands in Jamaica Bay to assess how sediment redox conditions, specifically oxygen and sulfide depth profiles, change among seasons and over the lifetime of young restored marshes. A 0.8-ha area of marsh island at Big Egg marsh was restored in 2003 using a swing-ladder dredge that sprayed sediment from the adjacent mudflats onto the marsh surface to increase the surface elevation (Frame 2006). Yellow Bar, Elders West, and Elders East consisted of 16–18 ha restorations in which nearby and imported sediment slurry was placed on the site and graded to the desired elevation (Messaros et al. 2012). Sites were planted with *Spartina alterniflora* using a variety of methods including plugs, hummock relocations, and seedings (Rafferty et al. 2011). We also examined two extant marshes in the Bay: JoCo, which has remained relatively stable in extent over the past 50 years, and Black Bank, which has deteriorated significantly both in extent and in sediment stability over the past 50 years (Wigand et al. 2014). Together, these extant marshes provide positive and negative controls, respectively, against which to compare sediment dynamics in restored marsh islands. The hydrology of Jamaica Bay results in well-mixed

Fig. 1 Hypothesized outcomes for marshes experiencing sea-level rise in an urban, eutrophic estuary
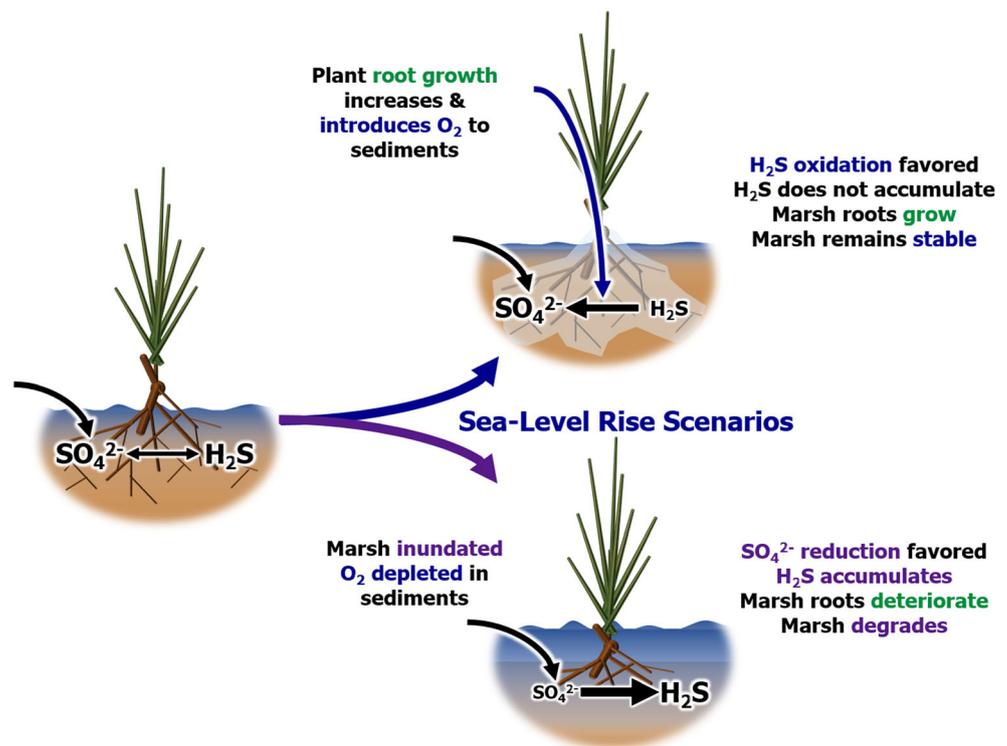
and homogeneous surface water conditions within the Bay, such that all marsh islands experienced similar temperature and water chemistry conditions throughout the course of our surveys.

Field Methods

We collected three intact sediment cores (7 cm diameter, ~ 10–20 cm deep) from each marsh location during the winter, spring, summer, and autumn. Yellow Bar and Elders East were sampled in August 2015 (in situ temperature 26 °C), October 2015 (20 °C), January 2016 (4.5 °C), and May 2016 (15.5 °C). Elders West, Big Egg, JoCo, and Black Bank were sampled in August 2016 (26 °C), October 2016 (18 °C), early March 2017 (5.5 °C), and May 2017 (18 °C). Winter sampling was later in 2017 relative to 2016 due to prolonged ice cover in the Bay that made field sampling infeasible until early March. Sediment cores were collected from the edges of the marsh islands between mid and high tide when sediment surfaces were fully inundated. Care was taken to minimize disturbance to aboveground and belowground plant materials, which consisted exclusively of *Spartina alterniflora*, during extraction and transport of sediment cores. Cores were transported to the Aquatic Research and Environmental Assessment Center at Brooklyn College CUNY and maintained in site-collected water on a 16–8 h light-dark cycle. Site water was maintained at field-collected temperatures using an aquarium chiller to minimize within-season temperature variation during microprofile data collection. All O_2 measurements were performed within 36 h of initial core extraction, and all H_2S measurements were performed within 72 h of initial extraction.

To estimate differences in tidal inundation among sites, we deployed HOBO® water level loggers (Onset®, Model: U20-001-01-Ti, Bourne, MA, USA) at the creek edge of each marsh island in autumn 2016 (Brin et al. 2010). The location of the loggers corresponded to the same elevation at which we collected sediment cores for determination of sediment O_2 and H_2S. Loggers were deployed in stilling wells and took measurements every 15 min for at least one complete lunar phase cycle at each site. The amount of time the marsh was inundated was determined for each day, and a mean daily inundation rate (h day^{-1}) was calculated for each site for the deployment period.

Laboratory Methods

We measured the vertical distribution of O_2 and H_2S in sediment cores using a motorized microprofiling system (Unisense A/S, Aarhus, Denmark). Measurements began 2.0 mm above the sediment-water interface and proceeded downward at fixed depth intervals ranging from 0.3 to 2.0 mm, depending on the required resolution and total depth among sites and seasons. Two analytical replicates were performed for each core using duplicate microsensors, resulting in a total of four analytical replicates per core. When larger total depth intervals were needed, or when microsensor tips broke or malfunctioned during data collection, larger intervals were used to complete analysis of replicate cores. O_2 measurements were collected using an OX-50 microsensor (Revsbech 1989), and H_2S measurements were collected using an H$_2$S-50 sensor, which has been demonstrated to work well in highly reduced sediment conditions (Jeroschewski et al. 1996). The microsensors were allowed to equilibrate for ~ 24 h and were calibrated according to the manufacturer's instructions.

After O_2 and H_2S profile measurements were completed, we disassembled cores to characterize sediment and plant material. Surface sediments (< 3 cm below the sediment-water interface) were homogenized and subsampled to determine bulk density and porosity after drying at 70 °C for at least 24 h, total organic content after ashing at 500 °C for at least 5 h, and carbon and nitrogen content using a Perkin-Elmer 2400 Series II Elemental Analyzer (PerkinElmer Inc., Shelton, CT, USA) operating in CHN mode following acidification and redrying to remove carbonates (Nieuwenhuize et al. 1994). Belowground plant biomass, including all living and dead coarse roots and rhizomes, was collected using a 60 mL syringe corer inserted to the maximum rooting depth for the area sampled. Belowground material was wet sieved on a 1 mm mesh to separate root material from sediments, dried, and weighed to determine total belowground biomass.

Analytical Methods

All analyses were performed in R version 3.6.1 (R Core Team 2012). Our data are publicly available (Alldred et al. 2019), and all code used for model fitting and data analysis is available in supplementary material (Online Resource 1). The model fitting procedure was facilitated by using the dplyr (Wickham et al. 2019), tidyr (Wickham and Henry 2019), and purrr (Henry and Wickham 2019) R packages. Each replicate profile was fit to a logistic function using the nls.multstart package (Padfield and Matheson 2018):

$$[X] = \frac{[X]_{max}}{1 + e^{r(D-D_{0.5})}} \tag{1}$$

where [X] refers to the concentrations of O_2 or H_2S, $[X]_{max}$ refers to the maximum concentration of O_2 or H_2S in the profile, r refers to the intrinsic rate of consumption of O_2 and production of H_2S with depth, D refers to depth, and $D_{0.5}$ refers to the depth of maximum consumption/production rates.

We estimated three parameters from the logistic fits: (1) maximum concentrations of solute, (2) the rate at which the solute was consumed (O_2) or produced (H_2S) with depth, and (3) the depth at which production or consumption was

maximized (Fig. 2). This method allowed us to compare these parameters among sites and seasons regardless of the spatial resolution at which the data were collected. Parameters were only retained for statistically significant ($p < 0.05$) logistic fits. Because this filter often resulted in an unbalanced number of replicates among cores, a nested analysis was not practical; instead, parameters were averaged among analytical replicates for each core prior to statistical analysis, resulting in three replicate estimates per site per season. We tested for differences in O_2 and H_2S profile parameters among seasons and sites using a linear model including main effects and interactions between season and site variables. Values for JoCo marsh and during the winter season were included as intercepts in the model because they represent average conditions for a stable reference marsh during the time of year when biological activity is minimal. We tested the ability of belowground plant characteristics and tidal inundation to explain variation in maximum H_2S and the depth of maximum O_2 consumption and H_2S accumulation among sites and seasons using linear regression; separate regressions were performed for each season.

Results

Daily tidal inundation varied from 3.38 h day^{-1} at Yellow Bar, the youngest restored marsh, to 9.4 h day^{-1} at Big Egg, the oldest restored marsh (Table 1). JoCo, the stable extant marsh experienced a mean daily tidal inundation of 4.17 h day^{-1}, while Black Bank, the degraded extant marsh was inundated an average of 8.95 h day^{-1} (Table 1). Sediment characteristics were relatively similar among restored marshes, with mean bulk densities of ~1.2 g cm^{-3}, sediment porosities ranging from 42 to 47%, and organic contents ranging from 0.9 to 1.5% (Table 1). The two extant marshes, Black Bank and JoCo, differed with respect to sediment characteristics. Sediments at JoCo had a mean bulk density of 0.2 g cm^{-3}, a mean porosity of 91% and mean organic content of 36% (Table 1). In contrast, sediments at Black Bank had a mean bulk density of 0.9 g cm^{-3}, a mean porosity of 60%, and a mean organic content of 7.6% (Table 1). The organic content, porosity, and bulk density of marsh sediments were all strongly correlated (Pearson $r > 0.90$, $p < 0.0001$, $n = 72$). Additionally, all sediment variables were significantly, but less strongly, correlated with belowground plant biomass (Pearson $r = 0.53$–0.56, $p < 0.0001$, $n = 72$). Belowground plant biomass ranged from 331 to 473 g m^{-2} in the restored marshes to 503 g m^{-2} at Black Bank and 990 g m^{-2} at JoCo (Table 1).

Fits for all microprofiles are available via an interactive online app (Online Resource 2). Of the 1020 parameters extracted from logistic fits of O_2 profiles (Fig. 3), 42 did not result in a significant fit and were discarded from further analysis. Of the 996 parameters extracted from H_2S profiles

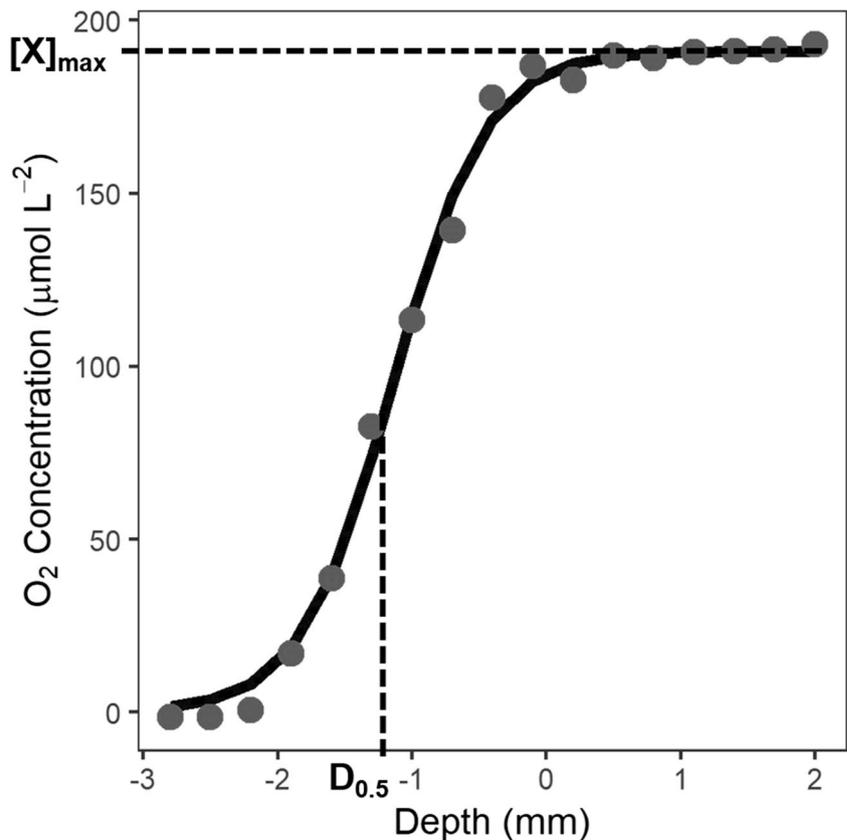**Fig. 2** Representative sediment microprofile, showing logistic fit to the data

Table 1 Characteristics of each marsh site. Values in parentheses indicate standard errors of the mean

Site name	Site status	Coordinates	Tidal inundation (h day^{-1})[a]	Sediment density (g cm^{-3})[b]	Sediment porosity (%)[b]	Sediment organic content (%)[c]	Belowground plant biomass (g m^{-2})[c]
Yellow Bar	Constructed 2012	N 40°36.713′ W 73°50.240′	3.85 (0.27)	1.22 (0.03)	42.1 (1.4)	1.20 (0.20)	330.7 (95.5)
Elders West	Constructed 2010	N 40°37.929′ W 73°51.287′	3.38 (0.26)	1.26 (0.03)	41.8 (0.6)	0.87 (0.09)	440.5 (92.4)
Elders East	Constructed 2006	N 40°38.160′ W 73°50.838′	6.40 (0.20)	1.19 (0.03)	47.0 (1.1)	1.48 (0.19)	455.5 (124.6)
Big Egg	Amended 2003	N 40°35.788′ W 73°49.610′	9.40 (0.24)	1.26 (0.03)	41.7 (0.4)	1.21 (0.45)	473.0 (87.4)
Black Bank	Extant deteriorating	N 40°37.106′ W 73°50.063′	8.95 (0.25)	0.92 (0.09)	59.7 (3.5)	7.65 (3.19)	503.3 (113.4)
JoCo	Extant stable	N 40°36.514′ W 73°47.476′	4.17 (0.33)	0.24 (0.01)	91.3 (0.2)	36.45 (0.71)	989.7 (104.9)

[a] Sample size = 26, 39, 41, 53, 58, and 47 days, respectively

[b] Sample size = 24 site^{-1}

[c] Sample size = 12 site^{-1}

(Fig. 4), we discarded 262 due to lack of significance. Non-significant fits appeared to be more likely during seasons when maximum H_2S concentrations were close to zero, with 40% of the non-significant parameters obtained from fits of winter profiles, 23% from spring profiles, and 23% from autumn profiles. All parameters extracted from logistic fits of O_2 sediment profiles were strongly correlated (Pearson $r = 0.56$–0.62, $p < 0.0001$, $n = 72$). The depth of maximum H_2S production was weakly correlated to the rate of H_2S production (Pearson $r = -0.33$, $n = 62$, $p = 0.0084$), as well as the depth of maximum O_2 consumption (Pearson $r = 0.29$, $n = 68$, $p = 0.0155$) and rate of O_2 consumption with depth (Pearson $r = 0.25$, $p = 0.0435$). Maximum H_2S concentrations were also weakly correlated with the rate of O_2 consumption with depth (Pearson $r = 0.30$, $n = 70$, $p = 0.0119$). To address our research questions, we hereafter focused on maximum H_2S concentration, as well as the depths of maximum O_2 consumption and H_2S accumulation as the response variables of interest, and belowground plant biomass and average daily tidal inundation as the predictor variables of interest.

We compared maximum H_2S values among all sites and seasons using a generalized linear model, using JoCo marsh and the winter as reference conditions. The model explained 60% of the overall variation in H_2S (F = 2.997; $df = 23, 46$; $p = 0.0008$). The only significant terms in this model were interactions between the summer season and the Black Bank ($p = 0.008$) and Big Egg ($p = 0.006$) sites. These significant interaction terms relate to an average increase in H_2S of 808 μmol at Black Bank and 840 μmol at Big Egg during the summer (Fig. 5). We ran a similar linear model to compare the depth of rapid H_2S accumulation among sites and seasons. This model explained 51% of the total variation in H_2S-accumulation depths (F = 1.993; $df = 23, 44$; $p = 0.02$), but the only

significant term was an interaction between the summer season and Yellow Bar marsh ($p = 0.03$), which indicated a shallower depth of H_2S accumulation in Yellow Bar marsh during the summer. The linear model comparing the depth of rapid O_2 consumption among sites and seasons explained 64% of the overall variation (F = 3.715; $df = 23, 48$; $p = 6.2 \times 10^{-5}$). Significant interaction terms indicated shallower depths of rapid O_2 consumption in Yellow Bar marsh during the spring (9.8 mm, $p = 0.007$), summer (14.8 mm, $p = 0.0001$), and autumn (13.5 mm, $p = 0.0003$) (Fig. 5). Significant interactions also indicated shallower depths of O_2 consumption at Elders East in the summer (7.4 mm, $p = 0.04$) and Black Bank in the autumn (13.5 mm, $p = 0.0004$) (Fig. 5). We observed similar patterns in depths of H_2S accumulation and O_2 consumption among sites and seasons (Fig. 5), which was unsurprising given the significant correlation between the two variables (Pearson $r = 0.25$, $p = 0.0435$).

Maximum sediment H_2S concentrations were significantly related to average daily tidal inundation during the spring, summer, and autumn, but not during the winter (Fig. 6). Slopes of these relationships were similar during the spring and autumn, with an increase of approximately 40 μmol of H_2S per hour of daily tidal inundation (Fig. 6). During the summer, we observed a greater increase of 139 μmol of H_2S per hour of daily inundation (Fig. 6). Belowground plant biomass was not significantly related to maximum H_2S concentrations in any season. However, when H_2S concentrations reached their seasonal maximum in summer, the depth at which H_2S accumulated was strongly and significantly related to belowground plant biomass (Fig. 7). Similarly, the depth of O_2 consumption was strongly and significantly related to belowground plant biomass during the summer (Fig. 7).

Fig. 3 All O_2 measurements from sediment cores collected in Jamaica Bay marshes. JoCo and Black Bank represent a stable and a deteriorating extant marsh, respectively. Big Egg, Elders East, Elders West, and Yellow Bar represent a series of marsh restorations, from oldest (14 years) to youngest (3 years)
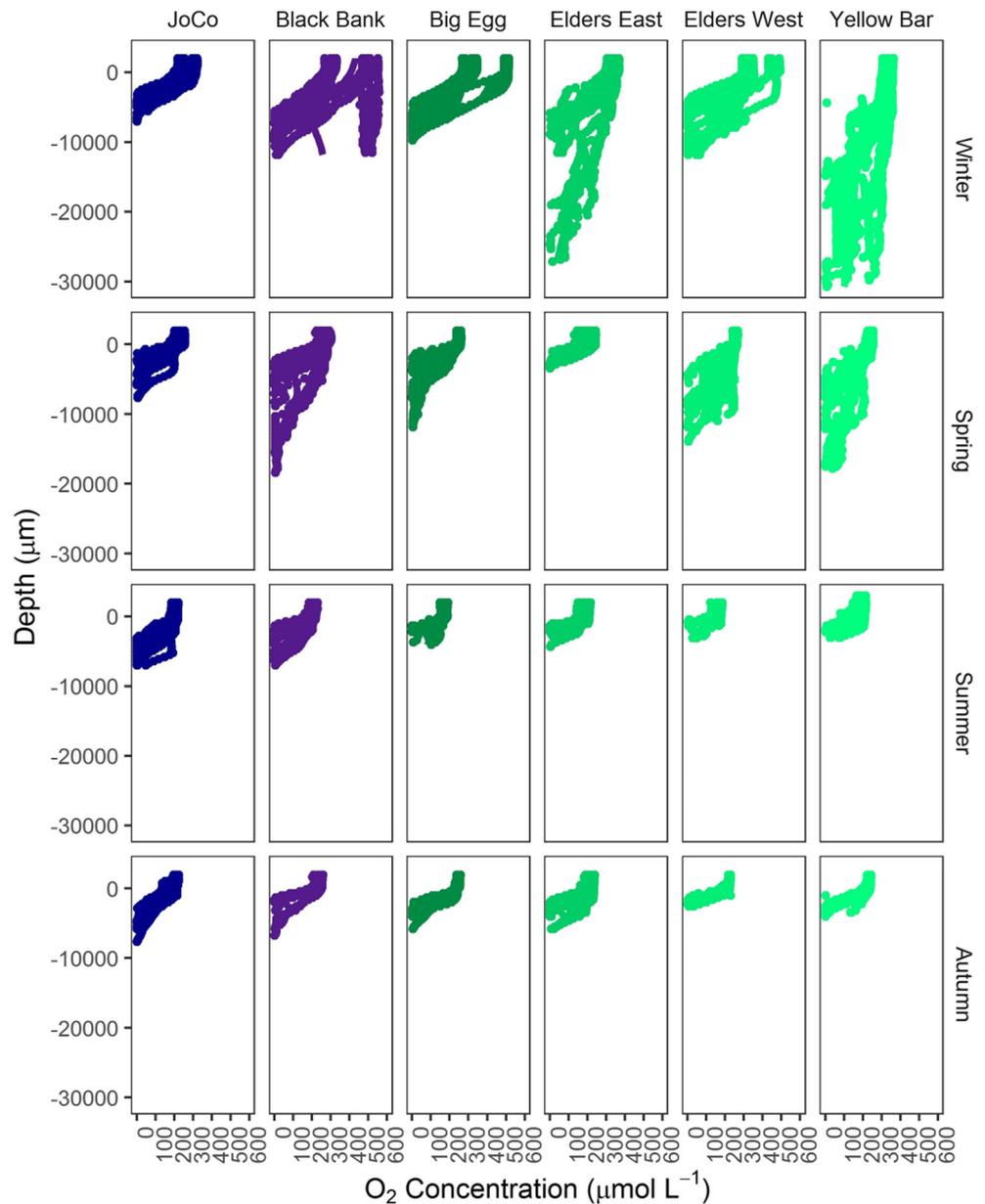
Discussion

Despite the many concurrent stressors that could hinder marsh stability in Jamaica Bay, our results provide strong evidence that marsh stability is possible. Stability appears to be directly related to two factors: the period of time the marsh remains inundated, which is likely related to initial elevation of the marsh, and the amount of belowground plant material, which facilitates diffusion of oxygen deeper into marsh sediments. Moreover, we found strong evidence that reconstruction of lost marsh area can result in marshes that remain relatively free of sulfide accumulation for at least 9 years after initial construction. This analysis is unique in the literature and offers clear lessons for ecosystem managers to improve the capacity

for successful and continued urban marsh growth over many years, despite challenging ecological conditions.

Patterns of O_2 and H_2S in marsh sediments at JoCo were consistent with our predictions for a marsh that is successfully keeping pace with sea-level rise, while conditions at Black Bank were consistent with our predictions for a deteriorating marsh (Fig. 1). Sediments at JoCo remained relatively free of H_2S throughout the year, whereas sediments at Black Bank experienced average maximum H_2S concentrations of 856 μM within the root zone of *Spartina alterniflora* during the summer (Fig. 5). Previous work has shown that H_2S significantly inhibits ammonium uptake and photosynthetic capacity of *Spartina alterniflora* at concentrations as low as 150 μM and completely inhibits ammonium uptake at

Fig. 4 All H$_2$S measurements from sediment cores collected in Jamaica Bay marshes. JoCo and Black Bank represent a stable and a deteriorating extant marsh, respectively. Big Egg, Elders East, Elders West, and Yellow Bar represent a series of marsh restorations, from oldest (14 years) to youngest (3 years)
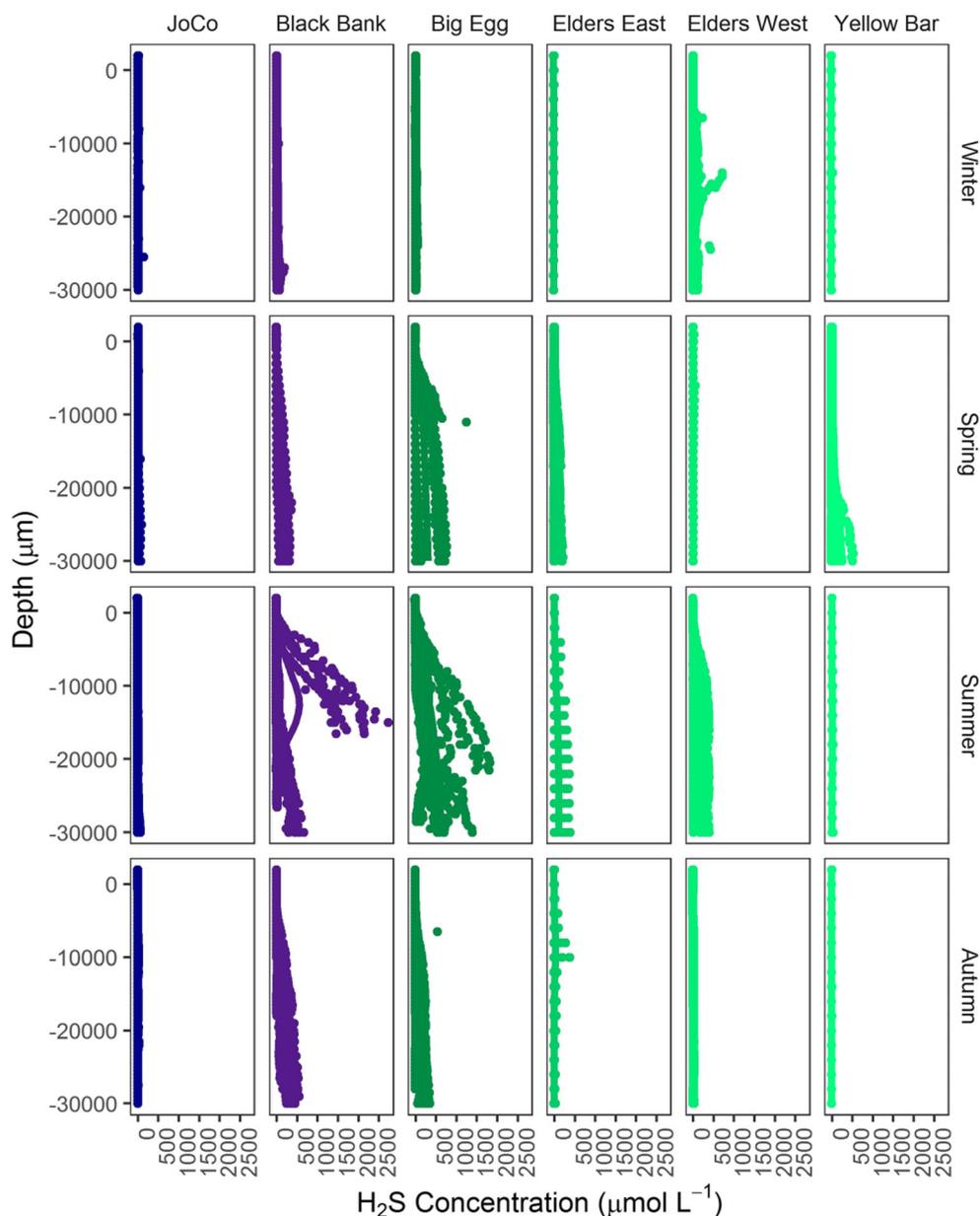

concentrations of 2000 μM (Bradley and Morris 1990), although at least one study has indicated broader tolerances for H$_2$S in *Spartina alterniflora* relative to other salt marsh plants (Chambers et al. 1998). Regardless, plants at Black Bank are very likely suffering from sulfide toxicity during the summer. The difference in sulfide accumulation between JoCo and Black Bank was directly related to the average period of daily tidal inundation that the two marshes experience (Fig. 6). Whereas JoCo is typically inundated for only 4.17 h day^{-1}, Black Bank is inundated for an average of 9.40 h day^{-1} (Table 1), isolating its sediments from exchange with the atmosphere nearly 40% of the time. During summer months, when water temperatures and respiration rates of plants and microbes are maximized, this amount of inundation

likely sustains near-permanent anoxia, resulting in anaerobic microbial respiration and significant production of H$_2$S in marsh sediments. Marshes such as JoCo that are inundated for shorter periods of time likely also experience enhanced O$_2$ exchange with the atmosphere and shorter periods of anaerobic respiration and H$_2$S production. These results are consistent with previous work indicating that elevation capital is critical to the long-term stability of coastal marshes (Watson et al. 2017; Cahoon et al. 2019).

Among the restored marshes, the three youngest marshes—Yellow Bar, Elders West, and Elders East—also maintained relatively low H$_2$S concentrations in sediments throughout the year (Fig. 5), consistent with our predictions for stable marshes keeping pace with sea-level rise (Fig. 1).

Fig. 5 Differences in maximum H_2S concentrations, depth of maximum H_2S accumulation, and depth of maximum O_2 depletion among seasons and sites in Jamaica Bay. JoCo and Black Bank represent a stable and a deteriorating extant marsh, respectively. Big Egg, Elders East, Elders West, and Yellow Bar represent a series of marsh restorations, from oldest (14 years) to youngest (3 years)
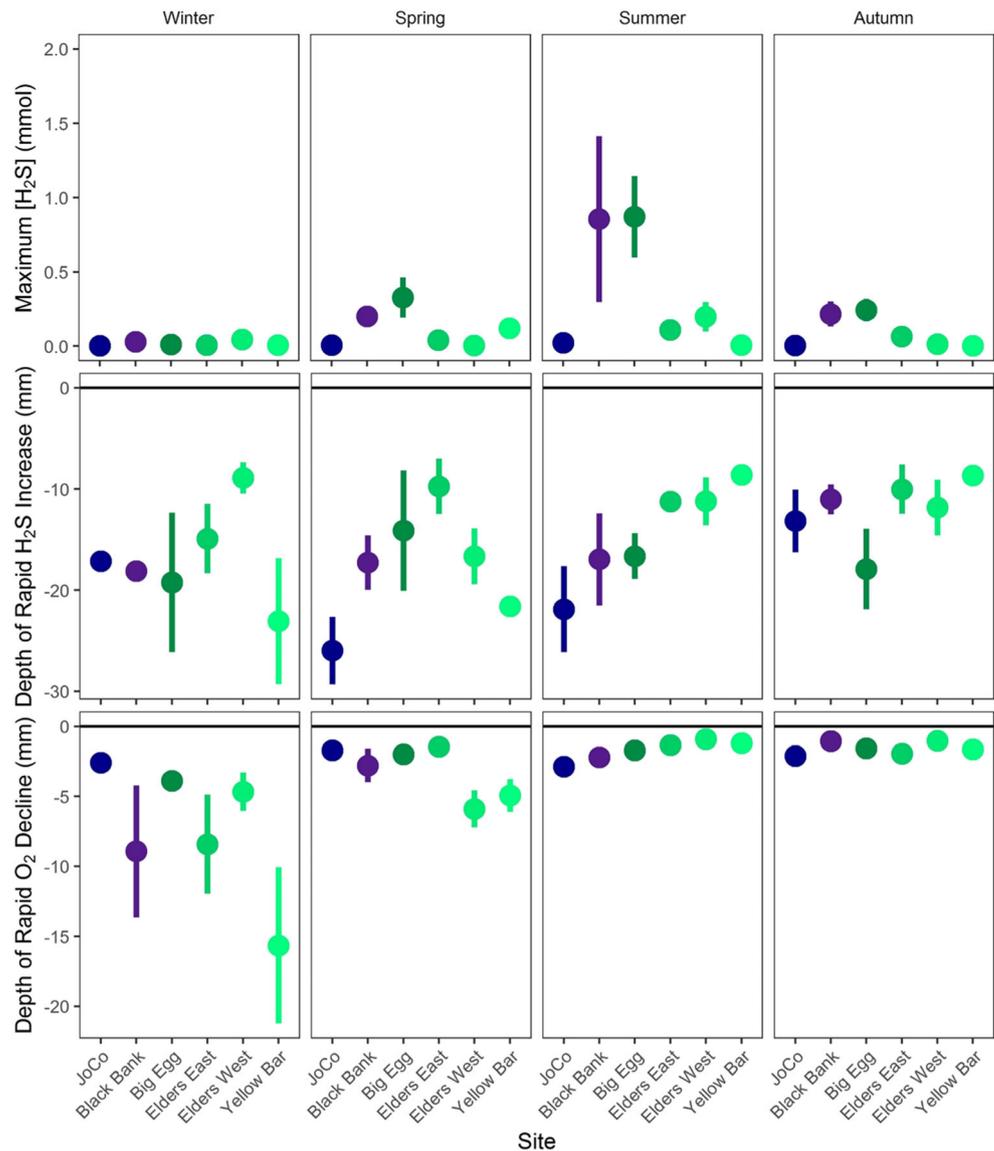
This finding provides strong evidence that increasing the elevation of coastal marshes can successfully restore stable marshes to deteriorated coastal areas. Notably, seasonal H_2S dynamics in the oldest restored marsh, Big Egg, more closely resembled the deteriorating marsh Black Bank, with an average summer H_2S concentration of 891 μM (Fig. 5), well within the range where H_2S toxicity is expected. This result suggests two possible explanations. The first explanation could be that sediment compaction and subsidence of restored marshes after their construction pushes marshes toward the trajectory of a deteriorating marsh (Fig. 1), wherein the decreasing elevation of the marsh causes longer duration of daily inundation, and anoxia and H_2S accumulation to increase to toxic levels. This possibility is supported by increasing duration of inundation with the age of restored marshes (Table 1). However, the second possibility is that the restoration actions at Big Egg marsh were insufficient to create an initial elevation that

would result in a stable marsh, whereas later restoration efforts were successful. As the first restoration in Jamaica Bay, the construction project at Big Egg was much smaller than subsequent restorations, rebuilding only ~0.8 ha of marsh area as opposed to ~16–18 ha, and used sediment amendment from a nearby tidal creek as opposed to large-scale regrading using imported dredged sand (Frame 2006; Messaros et al. 2010; Messaros et al. 2012). Future work should examine changes in marsh elevation and inundation over time in constructed marshes to determine which of these alternatives is true. Monitoring and occasional management of marsh elevation may be necessary to achieve long-term stability in constructed marshes in Jamaica Bay (Stagg and Mendelssohn 2011). However, our initial results indicate that marsh restoration in Jamaica Bay has been successful in establishing a marsh (Elders East) that has remained free of significant H_2S accumulation after a period of 9 years (Table 1, Fig. 5).
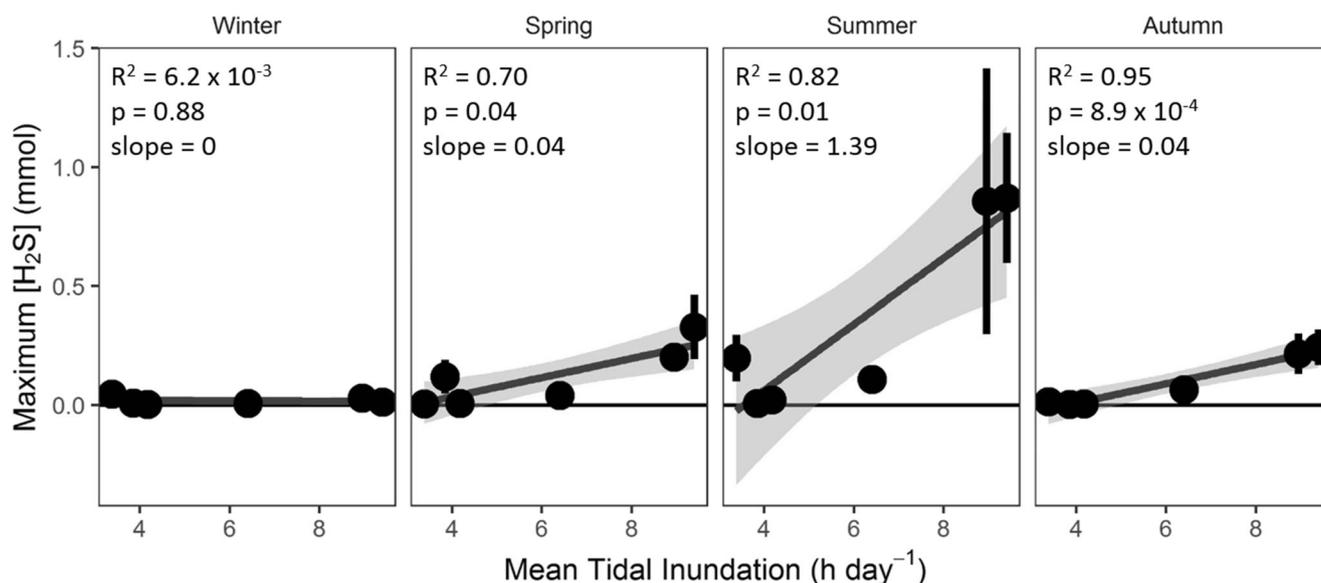
Fig. 6 Season changes in the relationship between mean daily tidal inundation and maximum accumulation of H_2S in sediments of Jamaica Bay marshes

Our results provide strong support that plant roots facilitate diffusion of O_2 into sediments during the summer (Fig. 7), when O_2 is most limiting and H_2S reaches maximum concentrations (Fig. 5). By allowing O_2 to penetrate deeper into marsh sediments, plant roots also forced the zone of maximum H_2S accumulation to greater depths, providing a refuge for root growth in shallow sediments. This pattern is consistent with our hypothesis that root-mediated aeration promotes a feedback that enhances plant growth and thus marsh stability (Fig. 1). It is also consistent with previous work showing plant roots enhance sediment aeration and allow sufficient accumulation of sediment organic matter to maintain marsh elevation (Gedan et al. 2011; Kirwan and Guntenspergen 2012; Silliman et al. 2019). The strong correlation between

belowground plant biomass and sediment porosity suggests that this effect is driven by enhanced diffusion of O_2 across the sediment-water interface. However, we cannot rule out the possibility of direct O_2 ventilation through stems and rhizomes of marsh plants, which has been observed for many marshes dominated by *Spartina alterniflora* (Teal and Kanwisher 1966; Howes et al. 1981; Arenovski and Howes 1992; Howes and Teal 1994; Lee et al. 1999). We also cannot rule out the possibility of a threshold beyond which increasing tidal inundation will overwhelm the ability of plants to aerate sediments and provide refuge for their roots from H_2S toxicity (Fig. 1). Indeed, the high accumulation of H_2S in Black Bank and Big Egg during the summer may provide evidence that this threshold has been crossed in deteriorating marshes.

Fig. 7 Relationships between belowground plant biomass and the depths of maximum O_2 depletion and H_2S accumulation in marsh sediments of Jamaica Bay during the summer
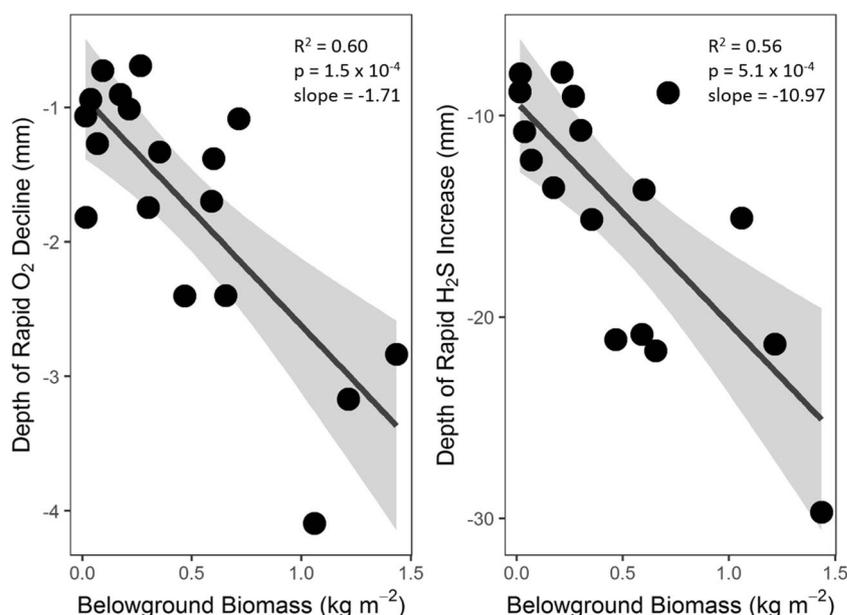
Notably, though we observed less belowground biomass in Black Bank than JoCo, we did not observe an overall trend of decreased belowground biomass in sites with significant H_2S accumulation (Table 1). This finding seems to contradict our hypothesis that high H_2S concentrations stunt root growth and reduce sediment stability in deteriorating marshes (Fig. 1). In fact, the restored marsh with the greatest belowground plant biomass, Big Egg, also experienced the greatest maximum H_2S concentrations in summer (Fig. 5). Several mechanisms could explain this discrepancy. Since we sampled vegetated areas of Big Egg and Black Bank, these areas had not yet reached the tipping point beyond which plant dieback occurs, though they may be in the process of approaching that tipping point. Another explanation is that the plants at Big Egg and Black Bank may be experiencing changes to belowground growth that is not reflected in simple measurements of belowground biomass. Marsh plants can alter their morphology to produce thicker roots and rhizomes and fewer fine roots when exposed to anoxic conditions, allowing them to more efficiently transfer O_2 into sediments (Davey et al. 2011; Wigand et al. 2014). This change in morphology could result in similar total belowground biomass in stable and deteriorating marshes, but with very different consequences for sediment stability.

Overall, our data suggest that belowground plant growth enhances the resilience of extant and restored marshes to sea-level rise and eutrophication by facilitating oxygen diffusion into anoxic marsh sediments. Our results show the long-term success of marsh restoration will likely depend on a variety of factors that influence tidal inundation including initial marsh elevation at the time of construction, compaction and subsidence of added sediments, acceleration in the rate of sea-level rise, and the influence of continuing eutrophication on the accumulation and loss of organic matter. Achieving long-term restoration success within a eutrophic, urban estuary will require continual monitoring and management of marsh elevation, as well as developing a better framework for predicting change in the many abiotic and biotic factors that influence marsh elevation and tidal inundation.

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