Research Article

Comparison of Vegetation Community Diversity, Biomass, and Sediment Properties among Constructed and Reference Salt Marshes at Deer Island, Mississippi, U.S.A.

Nikolas R. Murphy[1], Patrick Biber[2]

1. Gulf Coast Research Laboratory, University of Southern Mississippi, United States; 2. University of Southern Mississippi, United States

Beneficial Use (BU) of dredge sediments has been used in coastal salt marsh restoration to renourish areas with excessive edge erosion and marsh platform subsidence. Restoration of these degraded salt marshes can include the construction of new marsh habitats at appropriate elevations for vegetation establishment. However, little is known about how these newly constructed vegetative communities develop and function over time. Two such projects were constructed with BU sediments at Deer Island, Mississippi, USA, in 2004 and 2015. They were planted with native vegetation in anticipation that they would recover in *Juncus roemerianus* (Black needlerush) dominated salt marshes. The two constructed sites were compared to an adjacent reference salt marsh using metrics that included vascular plant diversity, standing stock biomass, and sediment composition. Sampling over six seasons from spring 2017 to fall 2019 demonstrated the establishment of new vegetation resulting in a diverse floristic community. The two constructed sites were found to have higher species richness and plant diversity than the natural reference marsh. However, the two constructed sites had significantly lower below-ground biomass and sediment organic content (SOC) compared to the natural reference site. Soil bulk density, SOC, and grain size of the sediments at the two BU sites were also dissimilar to the natural marsh reference. All metrics evaluated indicated the two BU restorations were not yet identical to the reference salt marsh, even after more than a decade of ecosystem recovery, and that *J. roemerianus* had failed to establish as expected.

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Introduction

Loss of coastal marshes from anthropogenic impacts is widespread due to altered sediment supply and hydrology, coastal development, and more recently, climate change, and accelerated sea level rise (Turner 1990, 1997; Herbert et al. 2016; Wu et al. 2017, 2020). Salt marshes in the U.S. are expected to be reduced by 20-45% by the end of the 21st century. In the northern Gulf of Mexico (GoM) marsh loss is extensive, with more than 13 ha being lost per day (Stedman and Dahl 2008; Engle 2011; Kirwan and Megonigal 2013). To offset these losses, the construction of coastal marshes is promoted as a preferred management action (Craft 2016). Restoration in the northern GoM has included new construction of previously lost marsh platforms using upland fill or dredged sediments and the construction of islands, hummocks, or cheniers (a type of beach ridge) to form a localized sediment source for future marsh accretion.

Beneficial Use of dredged material (BU) is the practice of repurposing sediment from maintenance dredging projects that is used to augment marsh habitat elevation or create new habitat along eroding marsh edges (Streever 2000; Gailani et al. 2019; Suedel et al. 2021). In many projects, the dredged sediments are fine silt and clay with substantial water content, necessitating the construction of a containing berm or levee at the receiving location (Earhart and Garbish 1983). Sediment placement is initially higher than the desired final elevation due to anticipated compaction and dewatering of the BU material over time (Gaffney et al. 2005; Zentar et al. 2011). Additional topographic shaping and construction of tidal exchange channels, allowing for organismal access to the interior of the project site, can be conducted after dewatering and compaction are completed. Examples of recent BU projects for salt marsh restoration in the northern GoM include 30 ha at Deer Island, 220 ha at Round Island, MS (Roth et al. 2012; Lang 2012; Ramseur 2020), and the creation of over 800 ha of new marsh in West Bay, LA (Suedel et al. 2021), using the principles of the US Army Corps of Engineers Engineering with Nature® (EWN) program (Bridges et al. 2021). Depending on the desired habitat, these BU projects were either planted with target vegetation or allowed to naturally colonize.

To ensure appropriate revegetation of the newly constructed habitat, factors that should be considered include elevation, planting density and material, and physical and chemical sediment characteristics (Mitsch and Wilson 1996; Zedler and Callaway 1999, 2002; Herbert et al. 2016). Many salt marsh distribution studies have highlighted the role of elevation in wetland zonation and restoration success (Woerner and Hackney 1997; Bockelmann et al. 2002; Silvestri et al. 2005). As salt marsh plant species often have wide physico-chemical tolerances, the drivers of salt marsh vegetation success usually relate to topographic heterogeneity and hydroperiod (Stagg and Mendelssohn 2010, 2011; Mossman et al. 2012). Physical sediment characteristics such as texture, porosity, and bulk density can influence rhizobacteria and plant root growth (Mendelssohn and Morris 2002; Mavrodi et al. 2018). These factors combined to influence the speed at which vegetation diversity and standing stock biomass change post-construction (Craft et al. 2002, 2003; Herbert et al. 2016; Ebbets et al. 2019). Restoration success is, therefore, intertwined with the succession of plant species and substrate changes until the desired endpoint is approached, typically referenced to nearby natural marshes (Luken 1990; Mossman et al. 2012). Plant community diversity in restored marshes is usually expected to become similar to that of nearby reference marshes; however, this does not always occur (Zedler and Callaway 1999, 2000). Vegetation diversity and percent cover are often used as indicators of a restored site's similarity to reference conditions. However, the inclusion of other indicators (e.g., standing stock biomass, sediment properties) can aid in a more thorough assessment of a restored site's ecological functions over time (Petchey and Gaston 2006; Almeida et al. 2016; Taddeo and Dronova 2018).

Coastal restoration in salt marshes in Texas, Louisiana, and along much of the Atlantic coast of the United States (Webb and Newling 1984; LaSalle et al. 1991; Taniguchi 1996) has generally targeted *Sporobolus alterniflorus* (Loisel) P.M. Peterson & Saarela (syn. *Spartina alterniflora* - smooth cordgrass) dominated salt marshes. Restoration projects that assess vegetation diversity and standing stock biomass trends in *Spartina*-dominated marshes have, therefore, been extensively studied (Woodhouse 1979; Webb and Newling 1984; Zedler and Callaway 2000, 2004). However, reports from restored *Juncus roemerianus* Scheele (black needlerush) dominated marshes, in particular in the northern GoM are limited, and thus there are fewer assessments of marsh restoration success with this species (Sparks et al. 2013, 2015; Constantin et al. 2019; Martin et al. 2021). *Juncus roemerianus*, recognizable by its characteristic grayish-green to black hues, is a salt-tolerant rush that covers large areas in coastal salt and brackish tidal marshes in Mississippi (MS) and Alabama (AL). The leaf blades are stem-like, long, stiff, and round with very sharp needle-like points (Eleuterius 1973; Eleuterius and Eleuterius 1979). This species is a space competitor and generally dominates percent cover to the exclusion of most other marsh species; as such, many *Juncus*-dominated marshes have low vegetation diversity (Eleuterius and Eleuterius 1979; Kruczynski 1982; Pennings et al. 2005). Furthermore, this species tends to be slower growing than *S. alterniflorus* and may take longer to establish after substantial disturbance or marsh construction (Ramsey et al. 2002). The Deer Island project is one of the few BU projects available for assessment of marsh construction with repurposed dredged material where the desired salt marsh vegetation is *Juncus romerianus*, as opposed to the more commonly researched S. alterniflorus, dominated marshes.

The goal of this study was to document the condition of the salt marsh at two BU sites constructed at different times and compare them to an adjacent natural reference marsh, co-located on Deer Island, MS, USA. The aim was to determine whether the BU construction resulted in the formation of a *Juncus*-dominated marsh, as per the project goals, with these objectives:

1. Analyze site elevation data to determine if post-construction changes resulted in marsh-appropriate conditions suitable for marsh plant community development.
2. Assess the role of planted vegetation versus natural recruitment by comparing vegetation diversity and cover among the sites.
3. Determine differences between the two constructed sites and natural marsh reference community by comparing above- and below-ground vegetation biomass.
4. Measure sediment characteristics to better understand differences among sites that may influence successful plant establishment and growth.

Materials and Methods

Study sites

This study took place during 2017-2019 on two constructed sites of differing ages and a natural reference marsh on Deer Island, MS. The Deer Island Multi-Year Restoration (DIMR) 1 and DIMR2 projects were constructed in 2004 and 2015, respectively, on the northeastern shore of Deer Island (Figure 1). The constructed sites, DIMR1 and DIMR2, are adjacent to each other and joined by a sand containment berm that protects the marsh platforms from edge erosion. Construction involved BU of sediments from the maintenance dredging of navigational channels in the nearby area. The BU sediments were placed adjacent to the existing island shoreline on a shallow subtidal habitat that was a former marsh area, which had been lost after rapid shoreline erosion and retreat. Sediments were tested for pollutants and toxicity prior to reuse; only those meeting state-mandated thresholds were used in construction. At both sites, a low-profile sandy containment berm was constructed and filled with BU sediments pumped in at numerous discharge locations within each containment area to create variation in the finished elevation (Roth et al. 2012; Gerhardt-Smith et al. 2015). Dewatering and settlement of the BU material over time created shallow subtidal areas within each containment berm.

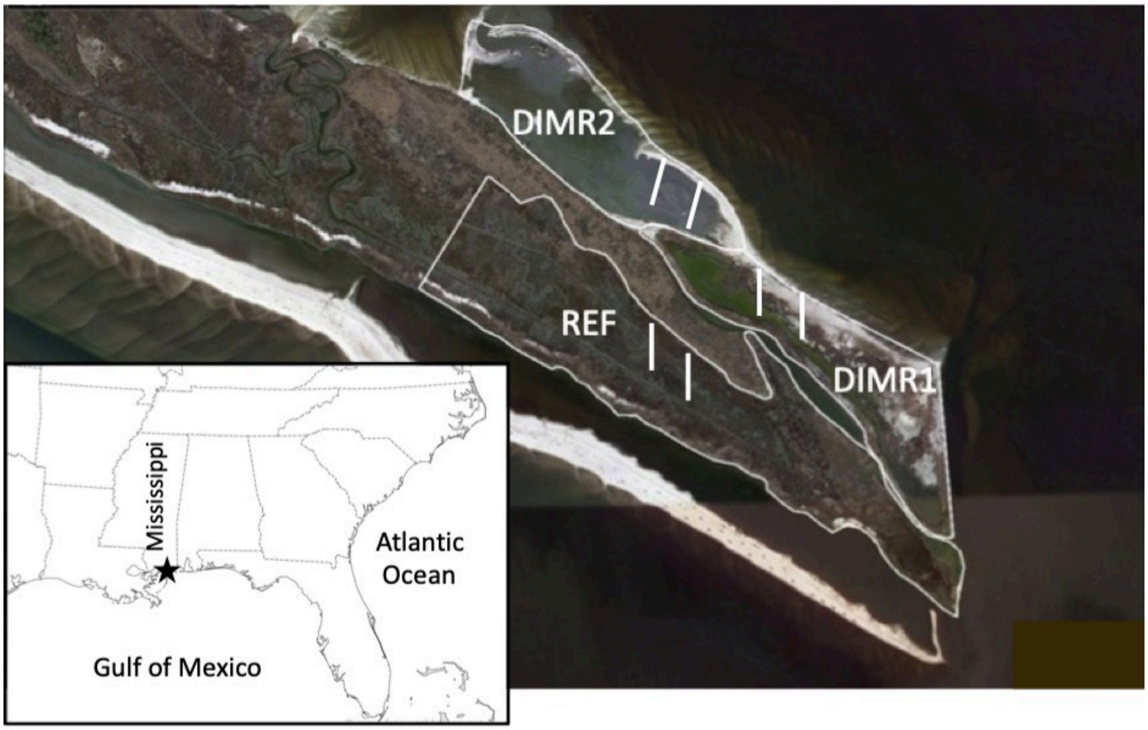

Figure 1. Location of transects sampled on Deer Island, MS, with the two constructed salt marshes of differing ages and a natural reference marsh. Sites are DIMR2 (2+ years old), DIMR1 (10+ years old), and REF is the natural reference site (100+ years old).

The older (10+ year) site, DIMR1, was constructed in 2004 with dredged sediments sourced from a nearby navigational channel and is 18 ha in size (Roth et al. 2012; Gerhardt Smith et al. 2015). This site was first planted in the spring of 2005 with field-harvested *J. roemerianus*, as well as commercially purchased *S. alterniflorus* and *S. patens* within the containment berm; all 46,700 plugs were obtained from local sources. Following extensive berm failure during and after Hurricane Katrina (Aug 2005), a wider containment feature was constructed during 2010-2011 (Lang 2012; Roth et al. 2012). The 10+ yr constructed site has since experienced periodic sediment renourishment and supplemental plantings to address ongoing erosion problems. Further planting of *J. roemerianus, S. alterniflorus*, *Spartina patens* (Aiton) Muhl. (saltmarsh hay), *Panicum amarum* Elliott (bitter panicgrass), and *Uniola paniculata* L. (sea oats) was periodically completed from 2008-2011. The most substantial planting was 23,000

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containers of *J. roemerianus*, *S. alterniflorus,* and dune plants in 2008 (Biber 2011), with natural recruitment of vegetation since.

The younger (2+ year) site, DIMR2, is a 16-ha area constructed from 2015 to 2018 with sediments dredged from multiple nearby sources. The eastern third of the site was planted in the spring of 2016 with commercially purchased *J. roemerianus* and *S. alterniflorus* in the interior high and low marsh zones, respectively. On the exterior, a containment dike, *S. patens*, *P. amarum*, and *U. paniculata* were installed (Biber 2020). All 45,800 plugs were obtained from local sources prior to grow-out in a nursery. Revegetation of the remainder of this site occurred through natural recruitment.

The 100+-year-old natural reference marsh is located approximately 500 m to the south of the two constructed sites and separated from them by an upland dune ridge colonized by *Pinus elliotii* Engem. (slash pine), and a variety of shrubs such as *Serenoa repens* W. Bartram (small saw palmetto) and *Baccharis halimifolia* L. (eastern baccharis). The natural marsh is almost entirely comprised of mixed *J. roemerianus* and *S. alterniflorus*, with occasional interspersed patches of *S. patens* and *Distichlis spicata* (L.) Greene (salt grass). Drainage ditches (0.6-1.2 m deep) are a regular feature cut into the natural marsh platform and are tidally influenced through a creek and inlet to the west of the three sites (Figure 1). Comparison of the natural marsh vegetation and sediment characteristics with similar *Juncus*-dominated marshes in the nearby Grand Bay National Estuarine Research Reserve (Peterson et al. 2007) and other prior studies (Eleuterius and Eleuterius 1979; Wright et al. 2013) corroborate this reference site as representative of natural *Juncus*-dominated marsh habitat in the region.

Elevation, tides, and field sampling

High-precision elevation data (± 2 cm) was collected at 165 randomly placed points throughout the three sites with a Trimble R8 GNSS receiver in April 2017 and August 2018 (Tables 1,2). Positions were corrected through real-time kinematic positioning using the USM Gulf Coast Geospatial Center's Real Time Network (GCGC RTN, rtn.usm.edu). These data were used to create an elevation contour map referenced to the North American Datum of 1983 (NAD 83) and the North American Vertical Datum of 1988 (NAVD88) in ArcGIS (Esri, Redlands, CA).

The diurnal microtidal range in the northern GoM is between 0.3 and 0.6 m with a single high and low tide in a 24-hour time span (diurnal, microtidal). The tidal range in this region is heavily influenced by wind, with more frequent and deeper immersion in summer than winter. The reference site was regularly inundated at high tide, whereas the two constructed sites had limited tidal exchange and were mostly groundwater-fed (Lang 2012) with permanent standing water only in the lower elevations.

Field sampling was conducted in the emergent marsh areas during the spring and fall of 2017, 2018, and 2019 (six seasons total, Table 1). During the initial spring 2017 sampling season, two parallel 100 m long transects were established at each study site approximately 250 m apart and oriented perpendicular to the shoreline (Figure 1). Along each transect, replicate 1m^2 quadrats were sampled for biomass and sediment cores in each of the three marsh zones (low-, mid-, and high marsh). The same starting points were retained across all sampling seasons.

Parameter	Spring 2017	Fall 2017	Spring 2018	Fall 2018	Spring 2019	Fall 2019
Transects	X	X	X	X	X	X
Species coverage	X	X	X	X	X	
Biomass cores	X	X	X	X	X	
Sediment cores		X	X	X	X	
Elevation Points		X		X		

Table 1. Summary of sampling events conducted at each site over the six sampling seasons.

Percent cover and vegetation diversity

Total vegetation percent cover was estimated in each 1 m^2 quadrat (Table 1, Figure 2), and the percent cover of each of the three most abundant species was estimated by a minimum of two personnel experienced in identifying plants that occur in the northern GoM. Finally, all remaining species present in the quadrat were identified to the lowest taxonomic level. For any plants unidentified in the field, one or more voucher specimens were returned to the laboratory for identification using appropriate field guides (Correll and Johnston 1970; Radford et al. 1983; Clewell 1985). Transects were grouped by site to calculate species richness, the Shannon-Wiener Index (H’), and Simpson’s Index (D) of alpha diversity. Bray-Curtis dissimilarity was computed to estimate the beta diversity across the three sites and to calculate ANOSIM and nMDS.

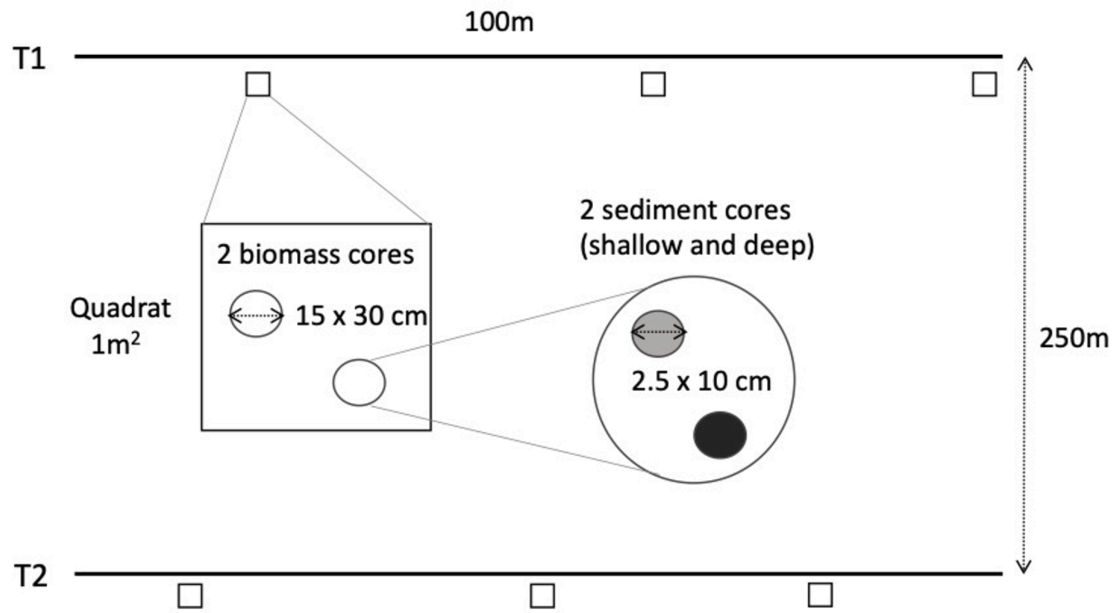

Figure 2. Layout of sampling conducted at each marsh site, transects, and quadrats not to scale. Replicate vegetation cores (15cm dia x 30cm deep) for plant biomass were extracted from each 1m^2 quadrat sampled, along with paired shallow and deep sediment cores (2.5cm dia x 10cm deep) from within each hole after the biomass core was removed.

Vegetation biomass

In each of the 1 m^2 quadrats, two replicate vegetation biomass cores (15 cm diameter x ~30 cm depth) were taken for measurements of canopy and rhizosphere biomass during each of the sampling seasons (Table 1, Figure 2). Care was taken to ensure all above-ground tissues within the diameter of the core were included and that any overhanging vegetation from outside the core was excluded. Vegetative biomass cores were promptly washed to remove sediment and debris from the above-ground material (AGM) and below-ground material (BGM) fractions and returned to the lab on ice. Using shears, the biomass cores were then separated into species-specific tissue fractions consisting of the AGM portion (stems, leaves, and flowering structures) and the BGM portion (roots and rhizomes). The AGM portion was further separated into live (green) and dead (brown) portions. Following separation, tissue fractions were placed in pre-weighed tins and allowed to oven dry at 70^0 C for a minimum of three days to constant weight before the dry mass was recorded.

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Sediment characteristics

After removal of each vegetation biomass core, a 50 cc plastic corer was used to extract paired shallow (5-10 cm within the rhizosphere zone) and deep (20-30 cm, below the rhizosphere zone) sediment core samples (Figure 2). Extracted sediment cores were analyzed for sediment organic content (SOC), bulk density (BD), and grain size. Each 50 cc sediment core was homogenized and separated into two subsamples: 1) a 5 mL subsample used to calculate BD and SOC, and 2) the remainder of the sediment (approx. 40 mL) used for grain size analysis. The two subsamples were both dried at 70° C to constant weight. The first subsample was used to calculate BD and then subjected to loss on ignition at 550° C for 4 h; pre- and post-combustion weights were used to calculate the SOC (LacCore 2013). The second subsample was wet-sieved over No. 10 (=2 mm, coarse), No. 35 (= 0.5 mm, fine sand), and No. 230 (= 0.063 mm, very-fine sand) mesh sieves (Folk and Ward 1957) for grain-size analysis. Following sieving, the dried grain size fractions were weighed, summed, and then subtracted from the pre-sieving mass to determine the silt and clay fraction lost during sieving.

Statistical analyses

All analyses were run in R version 3.5.1 (R Core Team 2018). Vegetation diversity analyses were conducted using the Bray-Curtis distance matrix and ANOSIM. Non-metric multidimensional scaling (nMDS) was performed using 'vegan' package version 2.5.3 (Oksanen et al. 2018) and plotted with 95% CI ellipses around the site centroids.

Separate two-way ANOVAs were performed for sediment BD, SOC, grain size fractions, as well as the vegetation biomass fractions (alive, dead, and below), with sites and sampling seasons as factors. Following any significant ($p < 0.05$) main or interaction effects, Tukey's Honest Significant Difference (HSD) post-hoc tests were performed. Linear regression described the relationship between SOC and BGM across all sites and seasons.

Results

Elevation

The 10+ year constructed site (DIMR1) had the highest mean elevation at 0.76 m NAVD88 and the widest elevation range of 0.80 m (Table 2). The 2+ yr constructed site (DIMR2) was at an average elevation of 0.54 m NAVD88 and had the narrowest range at 0.35 m. The constructed sites were both

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significantly higher than the 100+ yr reference site, which was at an average elevation of 0.27 NAVD88 and had a range of 0.50 m (Table 2, Table S1).

Site	Mean Elevation (NAVD88)	Range (NAVD88)	n
2+ yr constructed	0.54^{b}	0.35	56
10+ yr constructed	0.76^{a}	0.80	55
100+ yr reference	0.27^{c}	0.50	54

Table 2. Mean and range of elevation at two constructed and reference salt marsh sites on Deer Island, MS, measured in meters NAVD88. Superscripts with different letters denote significant ($p < 0.05$) differences calculated from Tukey's HSD.

Vegetation diversity and cover

There were 35 total plant species found across the survey period from spring 2017 to fall 2019 (Table 3). At the time of sampling, the 2+ yr and 10+ yr constructed sites were both comprised of a low elevation *S. alterniflorus*-dominated marsh on the dredged soils and a high marsh zone on the containment berm. Berm vegetation was dominated by the planted *S. patens* and a variety of naturally recruited vegetation such as *D. spicata*, and the two shrubs *B. halimifolia,* and *Sesbania herbacea* (Mill.) McVaugh (bigpod sesbania). The 100+ yr natural marsh was dominated almost exclusively by *S. alterniflorus* and *J. roemerianus*. All sites shared the commonly found salt marsh species *J. roemerianus*, *S. alterniflorus,* and *S. patens*, albeit in different relative abundances (Table 3). The two constructed sites shared species such as the grasses *P. amarum* and *Schizachyrium maritimum* (Chapm.) Nash (gulf bluestem) and a vine *Vigna luteola* (Jacq.) Benth (hairypod cowpea) that were not found in the reference site. *Ruppia maritima* L. (widgeon grass) was found in a submerged portion of both the 2+ and 10+ yr constructed sites. Species unique to the 2+ yr constructed site were *Panicum repens* L., the succulent *Sesuvium portulacastrum* (L.) L. (shoreline seapurslane), and *U. paniculata*. Notable species unique to the 10+ yr constructed site are *B. halimifolia*, and the two herbaceous species *Hydrocotyle bonariensis* Comm. Ex Lam. (largeleaf pennywort), and *Solidago sempervirens* L. (seaside goldenrod). The invasive *Imperata cylindrica* (L.) P. Beauv. (cogon grass) was found at the 10+ yr constructed site, albeit in small amounts (Table 3); both *B. halimifolia* and *H. bonariensis are native species in this region.*

The percent cover sampled in quadrats at the three sites increased over the three-year study, but at different rates. The 2+ yr constructed site showed a steady increase in total percent cover over time, whereas cover at both the 10+ y constructed site and 100+ yr reference marsh remained more consistent. The quadrats from the 2+ yr constructed site increased from 54% in fall 2017 to 86% total cover in fall 2018 (Fig. 3). The quadrats from the 10+ yr constructed site increased from 69% in spring 2018 to 83% in spring 2019. Finally, the quadrats from the 100+ yr reference site increased from 64% in spring 2017 to 75% in spring 2019. The mean coverage increase in the sampling quadrats was 21% per year in the constructed sites compared to only 5.5% in the natural marsh.

The highest species richness recorded was at the 10+ yr constructed site with 21 species, the 2+ yr constructed site had half that many with 12, and at the 100+ yr reference marsh there were only 3 species (Fig. 3, Table 4). Changes in alpha-diversity, (H' and D), were similar to the species richness trends (Table 4). The 10+ yr constructed site was the most diverse (H' = 2.24, D = 0.85), the 2+ yr constructed site had the second highest diversity (H' = 1.62, D = 0.76), and the 100+ yr reference marsh was the least diverse (H' = 1.14, D = 0.67). Both the 2+ yr and 10+ yr constructed sites had higher diversity than the 100+ yr reference site (Table 4), possibly a result of the lower and more homogeneous elevations at the reference site.

Site comparisons showed significant beta-diversity among sites (Table S2). The 10+ yr constructed site and the 100+ yr reference marsh were the most dissimilar with an R statistic of 0.39. The 2+ yr constructed site was most similar to the 10+ yr constructed site (R = 0.11) but was also similar to the reference site (R = 0.21). The centroids and 95% confidence intervals for each site were plotted on the nMDS (k = 2, stress = 0.08) to visualize the differences (Fig. 4). In terms of position on the nMDS plot, the 10+ yr constructed site was more different from the 100+ yr reference marsh than from the 2+ yr constructed site, probably due to the shared higher elevation dune species found only on the containment berm at the two constructed sites.

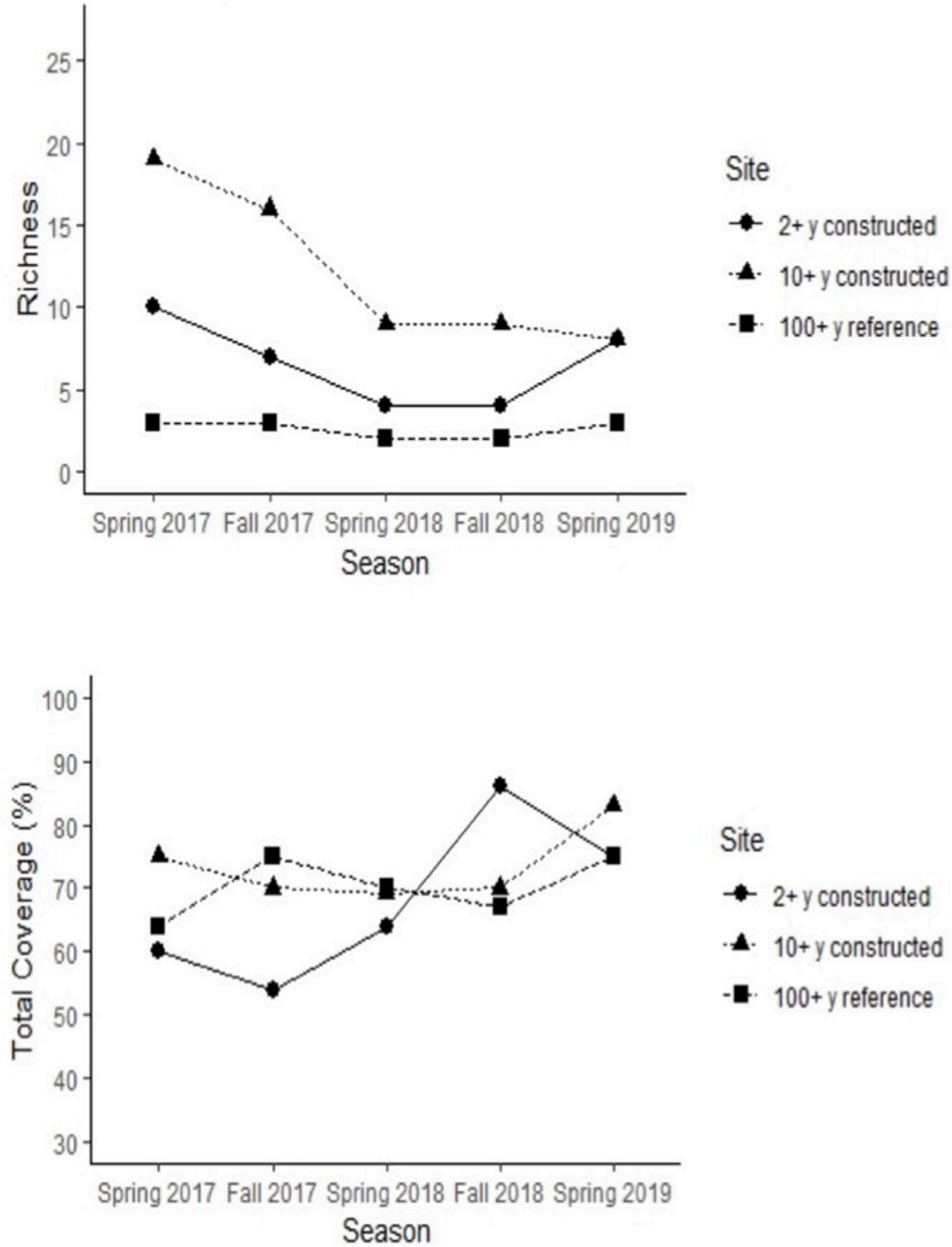

Figure 3. Species richness (upper panel) and total percent coverage (lower panel) of vegetation by season at two constructed marshes of differing ages and a natural reference marsh.

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Species	2+ yr	10+ yr	100+ yr
Andropogon virginicus L.		3	
Baccharis halimifolia L.	<1	2	
Cyperus spp.		1	
Distichlis spicata (L.) Greene	9	8	
Eragrostis secundiflora J. Presl		2	
Eupatorium capillifolium (Lam.) Small		1	
Fimbristylis castanea (Michx.) Vahl		5	
Heterotheca subaxillaris (Lam.) Britton & Rusby			
Hydrocotyle bonariensis Comm. Ex Lam.		1	
Imperata cylindrica (L.) P. Beauv.			
Ipomoea imperati (Vahl) Griseb.		<1	
Iva frutescens L.		2	
Iva imbricata Walter			
Juncus roemerianus Scheele	1	2	36
Limonium carolinianum (Walter) Britton			
Phyla nodiflora (L.) Greene			
Panicum amarum Elliott	5		
Panicum repens L.	<1		
Paspalum distichum L.	6	3	
Physalis angustifolia Nutt.			
Polypremum procumbens L.		<1	

Species	2+ yr	10+ yr	100+ yr
Proserpinaca intermedia Mack.			
Ruppia maritima L.			
Sarcocornia perennis (Mill.) A.J. Scott			
Schizachyrium maritimum (Chapm.) Nash			
Schoenoplectus americanus (Pers.) Volkart ex Schinz & R. Keller	1	1	
Schoenoplectus robustus (Pursh) M.T. Strong			
Sesbania herbacea (Mill.) McVaugh		<1	
Sesuvium portulacastrum (L.) L.	<1	<1	
Solidago sempervirens L.		4	
Spartina patens (Aiton) Muhl.	13	29	1
Sporobolus alterniflorus (Loisel). Peterson & Saarela	63	34	62
Symphyotrichum tenuifolium (L.) G.L. Nesom		1	
Uniola paniculata L.	1		
Vigna luteola (Jacq.) Benth	<1	2	
Total Cover	100	100	100

Table 3. Species list and percent occurrence of salt marsh vegetation observed at two constructed and a natural reference marsh.

Season/Site	Shannon-Wiener (*H'*)	Simpson's (D)	Richness
Spring 2017			
2+ yr constructed	1.47	0.68	10
10+ yr constructed	2.24	0.85	19
100+ yr reference	0.75	0.51	3
Fall 2017			
2+ yr constructed	0.78	0.36	7
10+ yr constructed	1.65	0.69	16
100+ yr reference	0.68	0.48	3
Spring 2018			
2+ yr constructed	0.67	0.33	4
10+ yr constructed	0.97	0.54	9
100+ yr reference	0.55	0.36	2
Fall 2018			
2+ yr constructed	1.37	0.69	4
10+ yr constructed	1.63	0.77	9
100+ yr reference	1.08	0.65	2
Spring 2019			
2+ yr constructed	1.62	0.76	8
10+ yr constructed	1.74	0.78	8
100+ yr reference	1.14	0.67	3

Table 4. Diversity indices and species richness at two constructed and a natural reference marsh across five sampling seasons.

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Vegetation Biomass

Above-ground (live and dead) and below-ground biomass data were obtained from a total of 180 biomass cores across all three sites and five sampling seasons (Fig. 5, Table 5). Live AGM varied significantly among sites but not across seasons (Table S3). Site contrast for live AGM showed that the 2+ yr constructed site was similar to both the 10+ yr constructed site and the 100+ yr reference marsh. The 100+ yr reference site had significantly greater live AGM than the 10+ yr constructed site. There were no significant site or season differences for dead AGM (Table S4), however, there was a significant interaction effect. This could be due to a large increase in dead biomass at the 2+ yr constructed site from spring to fall 2017 (Table 5) that could be attributed to rapid growth, coalescence, and then senescence of *S. alterniflorus* the year after it was planted in 2016. In contrast, BGM showed significant site and season effects (Table S5). The BGM at 2+ yr and 10+ yr constructed sites were similar to each other, but both were significantly less than the 100+ yr reference marsh. The spring 2017 and spring 2018 sampling seasons for BGM were the only pair of sampling seasons that were significantly different (Fig. 5).

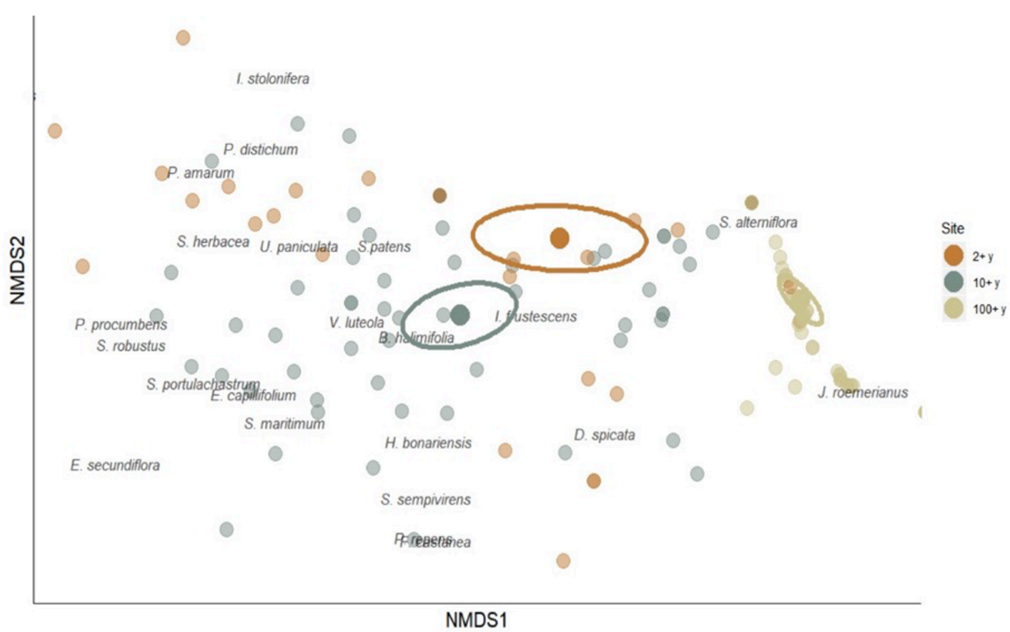

Figure 4. Non-metric multidimensional scaling plot (k = 2, stress = 0.08) of plant species percent cover over all five sampling seasons at two constructed sites and a natural reference site. Larger dots represent site centroids. Ellipses represent 95% confidence intervals.

Site	Alive (g/m^2)	Dead (g/m^2)	Below (g/m^2)
Spring 2017			
2+ yr constructed	696.9 (234.83)^{ab}	487.2 (184.39)^{b}	946.3 (179.24)^{b}
10+ yr constructed	222.0 (80.90)^{b}	622.2 (177.46)^{ab}	1865.9 (493.57)^{b}
100+ yr reference	987.4 (365.76)^{a}	618.4 (104.64)^{ab}	12501.9 (2284.11)^{a}
Fall 2017			
2+ yr constructed	1200.4 (306.16)^{ab}	1470.1 (393.21)^{a}	2562.9(373.02)^{b}
10+ yr constructed	549.4 (350.22)^{b}	451.1 (199.29)^{ab}	2780.7 (804.29)^{b}
100+ yr reference	1080.1 (391.07)^{a}	977.7 (289.18)^{ab}	7793.9 (1235.29)^{a}
Spring 2018			
2+ yr constructed	589.8 (145.51)^{ab}	678.3 (218.35)^{ab}	1023.1 (236.95)^{b}
10+ yr constructed	682.3 (158.98)^{b}	769.1 (126.69)^{ab}	1502.6 (262.67)^{b}
100+ yr reference	660.3 (189.81)^{a}	451.1 (77.59)^{ab}	6535.2 (905.88)^{a}
Fall 2018			
2+ yr constructed	811.0 (122.58)^{ab}	665.6 (116.74)^{ab}	2424.7 (293.3)^{b}
10+ yr constructed	674.6 (144.26)^{b}	494.2 (119.54)^{ab}	3063.0 (820.18)^{b}
100+ yr reference	1095.6 (391.07)^{a}	1010.7 (256.68)^{ab}	8391.2 (1134.06)^{a}
Spring 2019			
2+ yr constructed	923.9 (174.39)^{ab}	1000.2 (192.39)^{ab}	2426.2 (289.40)^{b}
10+ yr constructed	537.5 (118.25)^{b}	477.5 (125.98)^{ab}	1981.7 (446.65)^{b}
100+ yr reference	895.4 (212.85)^{a}	563.5 (190.33)^{ab}	5893.5 (627.85)^{a}

Table 5. Mean (SE) of alive-, dead-, and below-ground biomass at two constructed and a natural reference marsh. Superscripts with different letters within each season denote significant ($p < 0.05$) differences calculated from Tukey's HSD.

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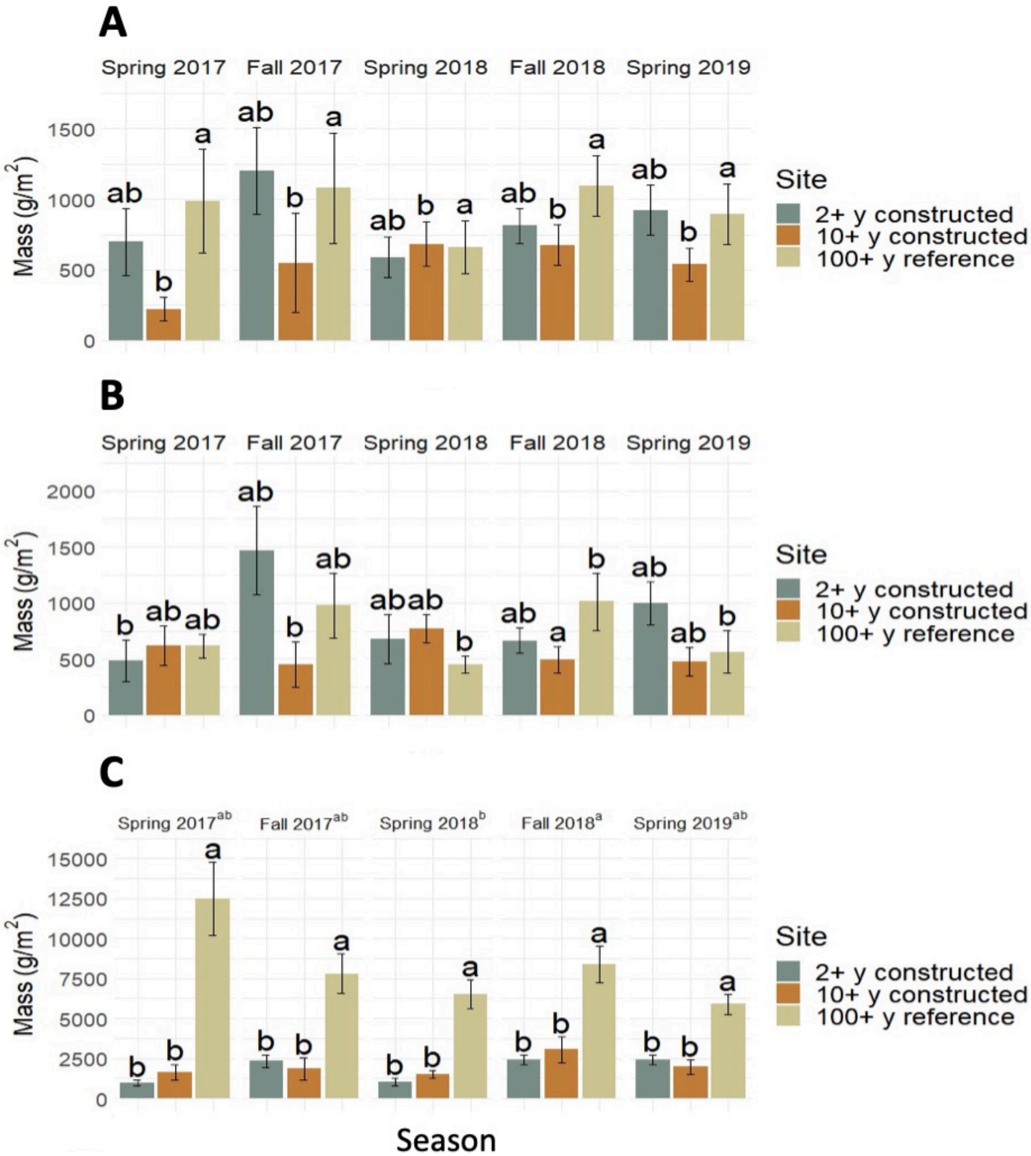

Figure 5. Mean (SE) of (A) alive above-, (B) dead above-, (C) below-ground biomass (g/m^2) of the three biomass fractions in each core at two constructed marshes and a natural reference marsh across five sampling seasons. Letters denote significant ($p < 0.05$) groupings by Tukey's HSD.

	BD (g/cm^3)	SOC (%)	Coarse Sand (%)	Fine Sand (%)	Very Fine Sand (%)	Silt/Clay (%)
Fall 2017						
2+ y constructed	1.20 (0.08)^{a}	2.14 (0.55)^{b}	0.00 (0.00)	3.47 (0.99)	72.88 (10.34)^{a}	23.65 (9.65)^{ab}
10+ y constructed	1.23 (0.09)^{a}	1.50 (0.37)^{c}	3.84 (2.44)	10.00 (3.64)	74.77 (3.14)^{a}	11.39 (4.78)^{b}
100+ y reference	0.82 (0.19)^{b}	10.00 (2.34)^{a}	0.79 (0.79)	1.99 (0.91)	58.42 (9.23)^{b}	38.80 (8.40)^{a}
Spring 2018						
2+ y constructed	1.02 (0.10)^{a}	5.22 (0.94)^{b}	0.00 (0.00)	3.05 (1.12)	52.96 (10.80)^{a}	43.99 (11.18)^{ab}
10+ y constructed	1.12 (0.07)^{a}	1.66 (0.42)^{c}	0.00 (0.00)	3.20 (1.42)	72.87 (11.98)^{a}	23.93 (12.27)^{b}
100+ y reference	0.62 (0.10)^{b}	14.53 (1.99)^{a}	0.00 (0.00)	4.88 (0.98)	37.27 (7.25)^{b}	57.94 (8.19)^{a}
Fall 2018						
2+ y constructed	1.15 (0.15)^{a}	5.29 (1.44)^{b}	0.22 (0.22)	7.58 (3.49)	67.05 (11.47)^{a}	25.15 (9.93)^{ab}
10+ y constructed	1.13 (0.06)^{a}	2.41 (0.54)^{c}	2.14 (1.26)	8.43 (3.92)	72.16 (8.83)^{a}	17.26 (9.07)^{b}
100+ y reference	0.44 (0.06)^{b}	14.83 (1.57)^{a}	1.91 (1.76)	14.29 (4.50)	47.52 (7.32)^{b}	36.29 (6.91)^{a}
Spring 2019						
2+ y constructed	1.21 (0.10)^{a}	4.11 (1.17)^{b}	0.00 (0.00)	3.26 (1.04)	75.29 (6.26)^{a}	21.45 (6.78)^{ab}
10+ y constructed	1.21 (0.15)^{a}	2.32 (0.84)^{c}	0.93 (0.65)	5.22 (1.61)	74.96 (8.56)^{a}	18.89 (7.72)^{b}
100+ y reference	1.09 (0.19)^{b}	11.05 (2.27)^{a}	0.51 (0.51)	12.61 (2.11)	62.89 (4.18)^{b}	23.99 (3.62)^{a}

Table 6. Mean (SE) of sediment bulk density (BD), soil organic content (SOC), and grain size portions in percent. Core samples from two constructed and a reference salt marsh were wet sieved into coarse sand, fine sand, very fine sand, and silt/clay fractions. Superscripts with different letters within each parameter denote significant ($p < 0.05$) differences calculated from Tukey's HSD.

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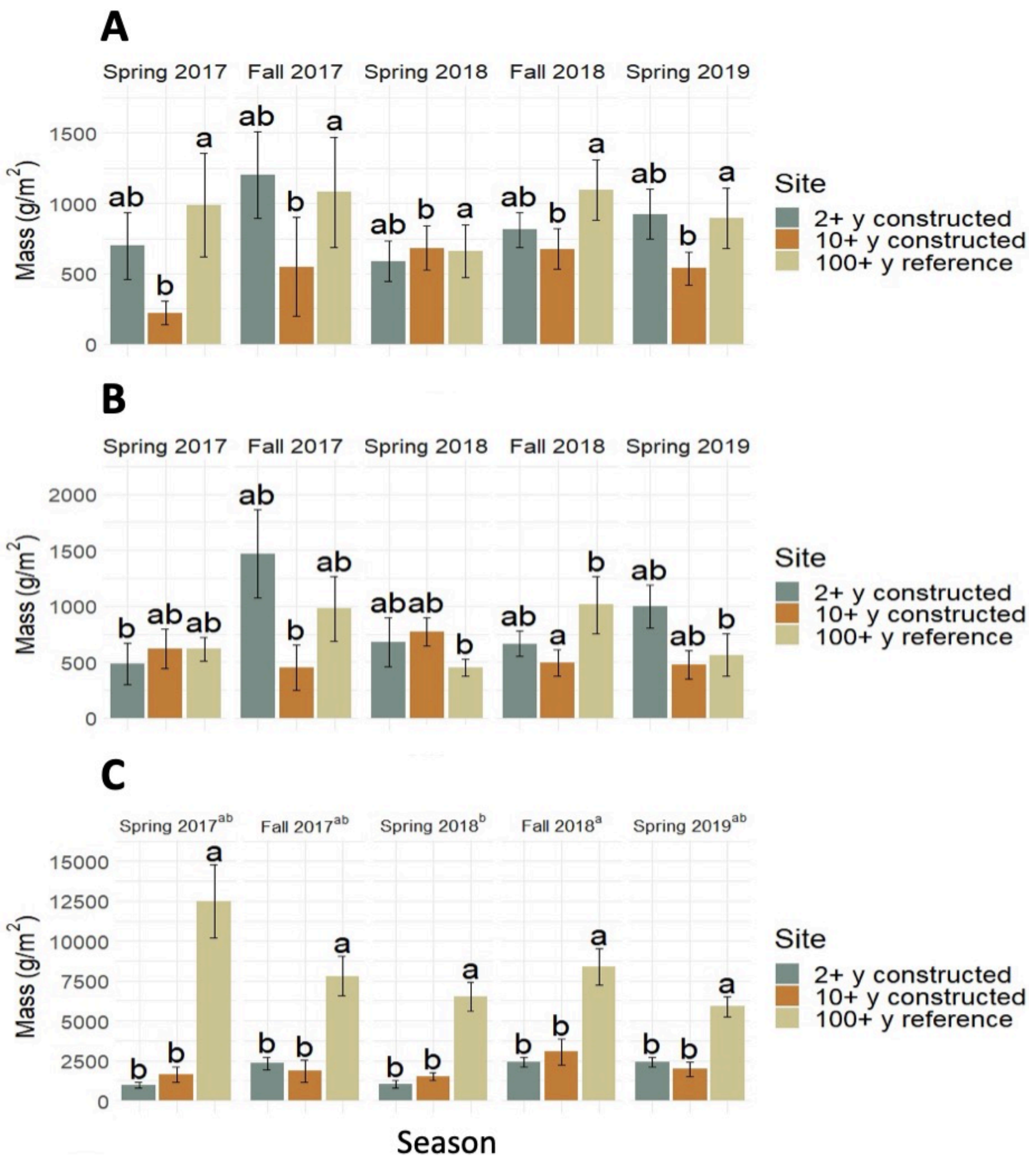

Figure 6. Mean (SE) of sediment parameters (A) BD, and (B) SOC at two constructed marshes and a natural reference marsh across four sampling seasons. Letters denote significant ($p < 0.05$) groupings by Tukey's HSD.

Sediment characteristics

Sediment composition data were obtained from a total of 130 biomass cores (Fig. 6, Table 6). Two-way ANOVA for BD showed significant site and season effects (Table S6). The sediment cores from the 10+

yr constructed site had the highest BD, which was similar to the 2+ yr constructed site (Fig. 6, Table 6). Sediment BD at the 100+ yr reference marsh was significantly lower than at the two constructed sites.

Soil organic content followed an inverse trend to BD, with a significant difference among sites. The reference site had significantly higher SOC than either constructed site (Table S7). The 10+ yr constructed site had the lowest SOC. In the 2+ yr constructed site, SOC increased between sampling seasons from fall 2017 to fall 2018 (Fig. 6, Table 6), possibly in response to the increased vegetation cover since planting in 2016.

There were no significant site or season effects for sediment coarse and fine sand fractions (Tables S8 and S9). Differences among sites in sediment grain size were mostly in the very fine sand and silt/clay portions (Table 6). The constructed sites were similar to each other in both very fine sand and silt/clay fractions, with both having significantly more very fine sand (Table S10) than the reference site. However, the 100+ yr reference site had significantly higher silt/clay (Table S11) than the 10+ yr constructed site, but was similar to the 2+ yr constructed site.

Discussion

Constructed wetlands are becoming commonplace to offset the loss of valuable coastal marshes. Building new coastal salt marshes can help to regain ecosystem functions and services, such as water quality improvement, carbon sequestration, storm surge protection, and wildlife habitat. The success of a marsh creation project can be measured by progress toward goals specifically stated in the management plan associated with the project. However, those goals often lack specificity or a timeline (Zedler and Callaway 2000, 2004). This study measured the different attributes of two marshes constructed with BU material in the northern GoM by comparing ecosystem indicators such as plant species diversity, biomass, and sediment composition to a nearby reference site. Other coordinated studies on the two constructed BU sites included sediment microbiome diversity (Mavrodi et al. 2018), marsh plant community composition and coverage (Murphy 2020), marsh invertebrate and nekton diversity and abundance (Marshall 2021), and resident avifaunal diversity and abundance (Weitzel et al. 2021).

Marsh characteristics such as vegetation coverage, plant species richness, and standing stock biomass can vary with geomorphic position, tidal range, salinity, and soil classification (Adam 1990; Craft et al. 2003) creating additional complexity in determining whether a restoration project is successful. Due to the rarity of long-term monitoring of many restoration projects, there is a shortage of data

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concerning the development of a single site over a time period greater than about fifteen years (Craft et al. 2002, 2003; Suding 2011), especially among marshes that are not dominated by *S. alterniflorus*. Vegetation coverage in restored marshes can develop to reference levels within one year when planted with vegetation or can take up to five years if a site is left to naturally recruit vegetation (Walker et al. 2007; Howard et al. 2020), but this can be regionally variable. Standing stock biomass is often measured for the canopy but frequently neglects the rhizosphere. The canopies of restored *Spartina* marshes are typically comparable to a natural reference site within 2-5 years, whereas root biomass can take more than 15 years (Woodhouse 1979; Webb and Newling 1984; Broome et al. 1988). Development of belowground biomass, which plays a critical role in carbon storage and marsh sustainability (Darby and Turner 2008; Kulawardhana et al. 2015), varies by species as there are species-specific adaptations to abiotic stressors such as salinity and sulfide toxicity (Adam 1990; Bradley and Morris 1990; Mendelssohn and Morris 2002) that are strongly influenced by elevation, tidal flushing, and sediment composition (De La Cruz and Hackney 1977; Morris and Bradley 1999; Windham 2001). Nonetheless, long-term responses in numerous marsh restorations indicate convergence to natural marsh vegetation composition and ecological processes within a few decades (Ebbets et al. 2019; Ledford et al. 2020, 2021; Tatariw et al. 2020).

Elevation

Salt marsh development is strongly dependent on proper elevation for the successful establishment of vegetation (Stagg and Mendelssohn, 2010, 2011; Mossman et al. 2012). At Deer Island, the elevation and physical sediment characteristics varied significantly between the constructed and reference sites. The 10+ yr constructed site tended to be higher in elevation (0.76 NAVD88) and had higher BD, higher sand content, and lower SOC than either the 2+ yr constructed site (average 0.54 NAVD88) or the 100+ yr reference (0.27 NAVD88) marsh. Salt marsh habitat typically exhibits zonation by elevation, which is influenced by both biotic and abiotic factors (Eleuterius and Eleuterius 1979; Emery et al. 2001; Bockelmann et al. 2002). Zonation in northern GoM salt marshes is marked by three distinct vegetation zones described previously by Eleuterius (1984) and Kruczynski (1982): (1) low marsh at -0.3 – 0.15 m above Mean Sea Level (MSL) elevation zone dominated by the *S. alterniflorus*, (2) mid-marsh at 0.2 – 0.5 m MSL dominated by *J. roemerianus*, and (3) high marsh at greater than 0.5 m MSL dominated by a combination of grasses such as *S. patens* and *D. spicata*, along with other herbaceous and woody plants. Recently, Anderson et al. (2022) provided high-precision elevation corrections with MSL averaging +0.048 m relative to NAVD88 in the study area. Based on the elevation monitoring

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results obtained from the three study sites, the two constructed sites contained elevations that were higher than those most suitable for the establishment of mid-marsh zone *J. roemerianus*. It would be advantageous for future BU projects aimed at creating a *J. roemerianus* marsh habitat to ensure that the site is constructed at low and mid-marsh appropriate elevations, which allows the site to be more frequently tidally inundated.

The construction design of these two BU sites included a sand berm that fully enclosed the periphery to contain the dredged sediments (Roth et al. 2012; Gerhardt-Smith et al. 2015). The lack of channels that could allow regular tidal flushing and provide aquatic organisms access to the interior low-elevation areas capable of supporting marsh vegetation reduces the potential habitat value for aquatic organisms (Baumann et al. 2018; Marshall 2021). A prior study by Lang (2012) documented groundwater flow across the DIMR1 site originating from the natural marsh to the south and percolating to the northeast following the elevation contours of the original seafloor bathymetry prior to site construction. Much of the standing water in the interior of the constructed sites is likely recharged from this groundwater, subsurface hydraulic tidal influence through the coarse sand berm, and rainwater, potentially resulting in lower salinity than would occur with direct tidal inundation. The salt marsh vegetation composition and distribution at the DIMR1 site were potentially influenced by the higher elevations and lower salinity, which has also been observed in other studies (Klijn and Witte 1999; Zedler 2000)

Community composition

Vegetation diversity and species richness increased with elevation across the three sites. The 10+ yr constructed site had the highest mean and widest range in elevation, and in turn, was the most diverse both in terms of species richness (21) and the two diversity indices. The 2+ yr constructed site was intermediate in elevation and had higher species richness (12) and diversity than the 100+ yr reference marsh, which was lowest in elevation and species richness (3). Lang (2012) in an earlier assessment, found higher diversity at the 10+ year BU site (29 species), with *S. alterniflorus, S. patens,* and *D. spicata* the three dominant species encountered soon after replanting occurred in 2008. Plant species diversity has since declined as this constructed site matured and vegetation composition approached that of regionally typical high and mid-marsh habitats (Eleuterius 1973; Eleuterius and Eleuterius 1979).

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Relative abundances of species that were common to all three sites were also different. The abundance of *S. alterniflorus* at the 2+ yr constructed site (63%) was similar to the 100+ y reference marsh (62%), and both were nearly double that in the 10+ yr constructed site (34%). This could be in part because a larger portion of the 2+ yr constructed site and the 100+ yr reference marsh were in the low-marsh zone. *J. roemerianus*, which tends to dominate at mid-marsh elevations, occurred in 36% of the 100+ yr reference marsh quadrats. However, it was effectively absent from the two constructed sites, despite over 18,000 stems planted at the 2+ yr constructed site and over 13,000 stems planted at the 10+ yr constructed site. Possible reasons for the failure of the *J. roemerianus* plantings could include inappropriate planting materials. For instance, plants installed in spring 2005 were field harvested from a donor marsh but did not include adequate BGM for successful reestablishment (Biber, pers.obs.). It is also not clear whether the *J. roemerianus* plants that were commercially purchased had been appropriately acclimated to field conditions (salt hardening) before transplanting. Another reason for the lack of success of the *J. roemerianus* transplants could be that the microbial composition of the dredged sediments was different from the natural site (Mavrodi et al. 2018; Santini et al. 2019) and the appropriate beneficial microbiome had not yet been established in the BU sediments at the time of planting.

Vegetation biomass

The biomass fractions of vegetation in coastal wetlands can serve as indicators for habitat recovery. Craft et al. (2003) approximated marsh biomass responses in *Spartina*-dominated habitats over time by comparing sites of differing ages with similar geomorphic positions, tidal range, salinity, and soil classification to overcome the lack of long-term monitoring data collected from a single site. Craft et al. (2003) found that, in North Carolina restored marshes, above-ground biomass can develop rapidly within the first five years, while root material takes longer to develop, taking up to fifteen years post-construction. Through a meta-analysis of twenty-five restored wetland assessments in the northern GoM, Ebbets et al. (2019) developed a trajectory of above- and below-ground biomass, cover, and soil composition. Ebbets et al. (2019) showed that in the first five years of development, restored marshes tend to have 25% higher AGM than reference sites, and in the first fifteen years, BGM was 44% to 92% lower at restored sites than reference sites. The meta-analysis done by Ebbets et al. (2019), while specific to the northern GoM, is still comprised of entirely *Spartina*-dominated marshes in Texas and Louisiana and lacks data on the *Juncus*-dominated marshes of MS and AL.

In the two constructed sites studied, the AGM and percent cover followed the pattern expected based on previous regional studies (LaSalle 1996; Sparks et al. 2015; Ebbets et al. 2019). The AGM was comparable across all three sites, irrespective of site age. However, the BGM at the two constructed sites was significantly less than that in the adjacent natural reference marsh and was lower than in other studies of constructed sites (Ledford et al. 2020, 2021; Tatariw et al. 2020). The optimal biomass during different stages of establishment in restored *Juncus*-dominated marshes is unknown, as there is a lack of long-term monitoring data on this species. To date, LaSalle (1996) and Sparks et al. (2015) are the only assessments of restored *J. roemerianus* marshes in the region that measured both above- and below-ground biomass. LaSalle (1996) studied an eight-year-old restored *Juncus*-dominated marsh in Pascagoula, MS, and found that AGM at the restored marsh was comparable to the natural reference marsh, while BGM was not. Sparks et al. (2015) showed that above- and below-ground biomass in planted *J. roemerianus* plots were comparable to reference plots after two years in Grand Bay National Estuarine Research Reserve, MS. However, the site examined by Sparks et al. (2015) used transplanted 0.25m^2 sods of field-harvested *J. roemerianus* from a nearby marsh, as opposed to transplanted nursery-raised plugs like at Deer Island. Similarly, recent studies reported from two constructed sites in AL (Ledford et al. 2020, 2021; Tatariw et al. 2020) found the biomass of *J. roemerianus* was not significantly different from an adjacent reference marsh 30+ years after construction.

Sediment composition

The physical sediment characteristics varied significantly between the constructed and reference sites, which could contribute to the differences in below-ground vegetation establishment between the sites. The 10+ yr constructed site was higher in elevation and had a higher portion of sandy sediment than either the 2+ yr constructed site or the 100+ yr reference marsh, suggesting site differences may be more important than age differences. This could be because of sand scour during Hurricane Katrina (Aug 2005), or the additional materials used to augment the eroding sand berm that was installed during 2010/2011 (Roth et al. 2012, Gerhardt-Smith et al. 2015). Finer grain sizes are more beneficial for marsh vegetation as silt and clay particles have a greater ability to retain plant nutrients and organic matter due to high surface area and cation exchange capacity (Jackson et al. 2006). Grain size has been shown to play an important role in the accretion of SOC within salt marsh sediments, as finer sediments tend to accumulate SOC more rapidly (Thomas 2004).

The SOC was comparable between the two constructed sites but was significantly higher at the reference site. SOC may be related to and influence vegetation characteristics, especially BGM development (Gibson et al. 1994, Zedler and Callaway 2002). Linear regression of BGM against SOC (R^2 = 0.78) indicates a strong relationship between these two variables, influenced predominantly by sediment conditions at the natural reference marsh (Fig. 7). The low SOC at the 10+ yr constructed site may be due in part to the coarser sediments used to fill the site. Coarse sediments increase porosity and oxygenation, resulting in more rapid decomposition of organic matter, thereby limiting the SOC pool (Mavrodi et al. 2018; Dutta et al. 2021). A lack of tidal exchange may also be limiting the SOC pool in the two constructed sites, as the burial of SOC within coastal marshes is likely enhanced with more frequent tidal inundation (Cammen 1975; Steinmuller et al. 2019). In other studies, SOC measured in constructed marsh sites tended to become comparable to reference sites after 1-2 decades (Edwards & Proffitt 2003; Craft et al. 2003; Dutta et al. 2021).

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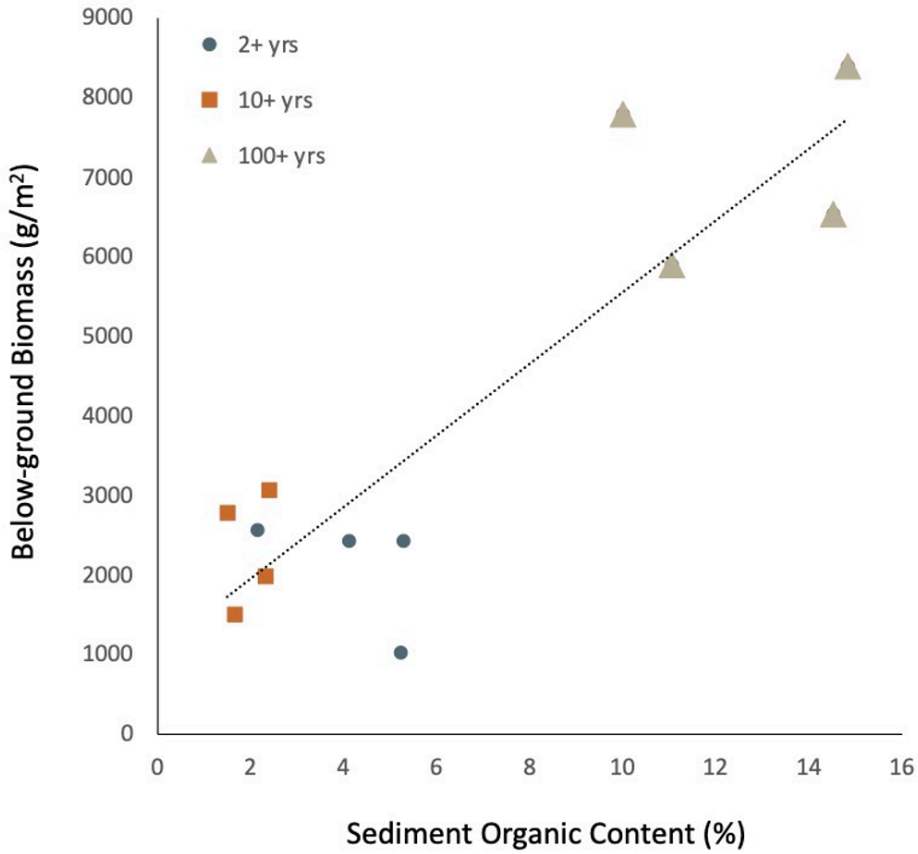

Figure 7. Sediment organic content (SOC) and below-ground biomass (BGM) for the two constructed salt marshes and a natural reference marsh, with linear regression relationship ($y = 450.6x + 1046.1$, $R^2 = 0.78$).

As a corollary to the low SOC in the two constructed sites, the BD at both was significantly higher than in the 100+ y reference marsh. Lower sediment BD has been shown to correlate with increased *S. alterniflorus* BGM (Avnimelech et al. 2001; DeLaune and Pezeshki 1988). However, the relationships between BD and BGM remain underexplored in *Juncus*-dominated marshes, an important data gap as these relationships can vary by species (Jones, 1983; Helliwell et al. 2019). Sediments used in future BU projects should more closely mimic reference site soils in terms of grain size, BD, and SOC. Consideration of appropriate soil characteristics within restoration design and practice may better facilitate the recovery of diverse wetland functions including nutrient cycling (Ledford et al. 2020, 2021) and carbon sequestration (Kulawardhana et al. 2015). In particular, fine-grained sediments with more SOC appear to better mimic reference conditions, and this could be further enhanced where

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lower elevations allow more frequent tidal inundation (Crawford and Stone 2015; Helliwell et al. 2019; Steinmuller et al. 2019). Future studies in restored marshes should examine the relationship between sediment conditions and vegetation biomass, especially focusing on *J. roemerianus*, to evaluate their importance over the long term.

Conclusions

This study provides the first comparative assessment of two BU sites that were planted to create *Juncus*-dominated wetlands indicative of healthy northern GoM salt marshes. The vegetative assessment at the 2+ yr and 10+ yr constructed site has shown mixed success, with *J. roemerianus* remaining mostly absent from the vegetation community. The vegetation diversity of the plant community was higher in the two constructed sites compared to the reference site, probably due in part to the higher elevations present at the two BU sites. Standing stock biomass measurements indicated similar AGM at all three sites, suggesting the constructed sites may already provide suitable above-ground habitats for salt marsh-dependent organisms. However, the BGM at both constructed sites is still far below that of the 100+ yr reference marsh. Sediment composition at the constructed sites was sandier, with higher BD and lower SOC than the reference marsh, suggesting initial sediment composition or hydrogeomorphic processes may be responsible. Finally, SOC correlated strongly with BGM and may provide a proxy for root/rhizome development over time, as this parameter cannot be readily observed during typical monitoring assessments. The future of salt marsh restoration using BU sediments in the northern GoM will require successful colonization of *J. roemerianus*, whether by planting or natural recruitment, as this species is a key component of healthy marshes in this region.

Appendix

Summary ANOVA tables for statistical tests of significant differences among means

Source	*df*	SS	MS	*F*	*p*
Site	2	6.638	3.319	239.4	< 0.001
Residuals	162	2.246	0.014		

Table S1. One-way ANOVA table for mean elevation (NAVD88) by site (n = 3).

Comparisons	Distance (R)	Significance
2+ y to 10+ y	0.11	< 0.001
2+ y to 100+ y	0.21	< 0.001
10 + y to 100 + y	0.39	< 0.001

Table S2. Results of ANOSIM comparison of Bray-Curtis dissimilarity across two constructed and a natural reference marsh.

Source	df	SS	MS	*F*	*p*
Site	2	4.05×10^{6}	2.03×10^{6}	4.07	0.02
Season	4	2.49×10^{6}	6.23×10^{5}	1.25	0.29
Site x Season	8	2.82×10^{6}	3.53×10^{5}	0.71	0.68
Residuals	145	7.21×10^{7}	4.97×10^{5}		

Table S3. Two-way ANOVA table for alive biomass by site (n = 3) and season (n = 5).

Source	**df**	**SS**	**MS**	***F***	***p***
Site	2	2.29×10^6	1.15×10^6	2.62	0.08
Season	4	3.17×10^6	7.92×10^5	1.81	0.13
Site x Season	8	7.18×10^6	8.97×10^5	2.05	0.04
Residuals	145	6.35×10^8	4.38×10^5		

Table S4. Two-way ANOVA table for dead biomass by site (n = 3) and season (n = 5).

Source	**df**	**SS**	**MS**	***F***	***p***
Site	2	1.22×10^9	6.12×10^9	107.02	< 0.0001
Season	4	6.14×10^7	1.53×10^8	2.68	0.03
Site x Season	8	1.91×10^8	2.38×10^8	4.17	0.08
Residuals	145	8.29×10^8	5.72×10^6		

Table S5. Two-way ANOVA table for below-ground biomass by site (n = 3) and season (n = 5).

Source	**df**	**SS**	**MS**	***F***	***p***
Site	2	6.14	3.07	23.88	< 0.001
Season	3	1.15	0.38	2.99	0.03
Site x Season	6	1.08	0.18	1.39	0.22
Residuals	118	15.04	0.13		

Table S6. Two-way ANOVA table for sediment bulk density by site (n = 3) and season (n = 4).

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Source	df	SS	MS	*F*	*p*
Site	2	2801.50	1400.75	79.78	< 0.001
Season	3	161.30	53.77	3.06	0.03
Site x Season	6	84.40	14.07	0.80	0.57
Residuals	118	2054.28	17.56		

Table S7. Two-way ANOVA table for percent sediment organic content by site (n = 3) and season (n = 4)

Source	df	SS	MS	*F*	*p*
Site	2	29.53	14.77	2.80	0.07
Season	3	28.71	9.57	1.82	0.16
Site x Season	6	27.35	4.56	0.86	0.53
Residuals	118	279.50	5.27		

Table S8. Two-way ANOVA table for mean percent of coarse sand per quadrat by site (n = 3) and season (n = 4).

Source	df	SS	MS	*F*	*p*
Site	2	214.60	107.31	3.02	0.06
Season	3	377.20	125.72	3.54	0.02
Site x Season	6	368.60	61.43	1.73	0.13
Residuals	118	1881.40	35.50		

Table S9. Two-way ANOVA table for mean percent of fine sand per quadrat by site (n = 3) and season (n = 4).

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Source	df	SS	MS	*F*	*p*
Site	2	6476.59	3238.29	7.61	< 0.01
Season	3	2569.32	856.44	2.01	0.12
Site x Season	6	1067.47	177.91	0.42	0.86
Residuals	118	22547.82	425.41		

Table S10. Two-way ANOVA table for mean percent of very fine sand per quadrat by site (n = 3) and season (n = 4).

Source	df	SS	MS	*F*	*p*
Site	2	5410.24	2705.12	6.43	< 0.01
Season	3	3974.13	1324.71	3.15	0.03
Site x Season	6	1202.79	200.47	0.48	0.82
Residuals	118	22283.98	420.45		

Table S11. Two-way ANOVA table for mean percent of silt and clay per quadrat by site (n = 3) and season (n = 4).

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