Estuaries and Coasts
https://doi.org/10.1007/s12237-021-01023-z

Biotic Recovery Following Ice-Rafting in a Salt Marsh

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Received: 27 July 2021 / Revised: 22 October 2021 / Accepted: 27 October 2021

Abstract
Salt marshes provide critical ecosystem services and functions including habitat provision and coastal community protection from storms. Chronic disturbances (e.g., anthropogenic inputs, climate change) and episodic disturbances (e.g., storms, oil spills) can affect the species composition and abundances of salt marsh biota, thus influencing ecosystem function and service provision. One such disturbance typical of the northeastern USA is annual nor'easter storms which deposit ice-rafted sediments on the salt marsh surface. In the winter of 2018, however, the extratropical cyclone, winter storm Grayson, deposited sediments equivalent to 15 years of accumulation on portions of the Great Marsh in Ipswich, Massachusetts, USA, potentially causing historic impacts. The recovery of the plant and invertebrate communities were evaluated 3 months, 6 months, and 18 months post ice-rafting from winter storm Grayson. We hypothesized sediment deposits would smother underlying plants, surface-dwelling invertebrates (i.e., epifauna), and surface-feeding infauna, such as polychaetes, although we expected little to no impact to subsurface-feeding infauna, such as oligochaetes. As predicted, plant, epifauna, and surface-feeding infauna were all impacted initially by sediment deposition, with lower abundances in deposits than in references, whereas subsurface-feeding infauna were unaffected. Despite historic volumes of sediment deposited by winter storm Grayson, we saw full recovery of the biotic community within 18 months. Sediment deposits had a maximum thickness of 6.5 cm and were patchily distributed throughout the marsh, and quick revegetation and invertebrate recolonization may ultimately have been from nearby, undisturbed areas. The fast recovery of the biotic community suggests minimal impacts to ecosystem services and functions and indicates an overarching resilience of the salt marsh to natural disturbances such as nor'easters.

Keywords *Spartina alterniflora* · *Spartina patens* · *Distichlis spicata* · *Manayunkia aestuarina* · *Orchestia grillus* · *Melampus bidentatus* · Thin-layer deposition

Introduction

We rely on coastal salt marshes for nutrient cycling (de Groot et al. 2012), carbon storage (McLeod et al. 2011; Bulseco et al. 2019; Smith and Kirwan 2021), shoreline protection (Gedan et al. 2009), food production (Jänes et al. 2020), and many other services (Friess et al. 2020; Whitfield et al. 2020). In some cases, chronic disturbances, such as anthropogenic activities and climate change, can lead to salt marsh loss (McLeod et al. 2011), with episodic disturbances (e.g., storms, oil spills) exacerbating these effects. Further, these episodic disturbances can also alter the species composition, abundances, and health of salt marsh biota (e.g., plants, invertebrates) (Ellison et al. 2005; Hill et al. 2020). Not all disturbances result in salt marsh loss, however. Thus, it is important to evaluate the effects of individual disturbance events to understand how they may influence ecosystem function and overall salt marsh resilience.

Ice-rafting (Fig. 1A, B), the physical movement of frozen sediments from intertidal mudflats to adjacent salt marshes during storm events, is a well-documented disturbance in the salt marshes of New England, USA (composed of the northeast Atlantic states: Connecticut, Massachusetts, Rhode Island, New Hampshire, Vermont, Maine) (Hardwick-Witman 1985; Wood et al. 1989; Ewanchuk and Bertness 2003; Argow et al. 2011; FitzGerald et al. 2020; Moore et al. 2021). Ice-rafting from winter storms occurs annually in this region, and it can have both positive and negative impacts on the salt marsh. Ice-rafting

Communicated by R. Scott Warren

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Published online: 11 November 2021

Fig. 1 **A** Ice-raft-containing sediments are deposited onto the high marsh habitat in the Great Marsh, Ipswich, MA, USA (photo: unknown). **B** Sediment deposit in May of 2018 (photo: S. Wittyngham). **C** Sediment deposit in May of 2018 with 0.0625 m^2 quadrat (photo: S. Wittyngham)

has been cited as one mechanism potentially driving pond or panne formation (Redfield 1972; Burns 2021), leading to decreased plant cover and marsh stability. Ice-rafting, however, also serves as an important secondary source of sediment to New England salt marshes (Wood et al. 1989; Argow et al. 2011; FitzGerald et al. 2020), which are surrounded by estuaries with historically low sediment supply (Hopkinson et al. 2018; Coleman et al. 2020; Langston et al. 2020). For instance, in the winter of 2018, New England experienced a historic extratropical cyclone, winter storm Grayson, which brought storm surges of ~ 1 m (FitzGerald et al. 2020; Moore et al. 2021). Paired with extremely high tides, ice-rafting from Grayson patchily deposited sediments equal to 15 years of accumulation and covered a spatial area of ~ 56.6 ha, approximately 1% of the Great Marsh in Ipswich, Massachusetts, USA (FitzGerald et al. 2020).

Global climate change is expected to increase the frequency and duration of winter storms like Grayson and thus the impacts of associated ice-rafting (FitzGerald et al. 2020). Although much is known about the volume (Wood et al. 1989; Argow et al. 2011; FitzGerald et al. 2020) and composition (Moore et al. 2021) of ice-rafted sediments in New England, only two studies have focused on ice-rafting impacts to the plant community (Hardwick-Witman 1985; Moore et al. 2021), and no studies, to our knowledge, have examined the combined recovery of salt marsh plant and invertebrate communities following disturbance from an ice-rafting event. Understanding invertebrate community recovery can inform us about both salt marsh food webs (Levin and Talley 2000) and the status of the salt marsh, as many invertebrate species serve as indicators of environmental health and water quality (Johnson et al. 2007). Thus, in this study, our overarching objective was to evaluate the recovery of the plant and invertebrate communities in a New England salt marsh 18 months post ice-rafting from winter storm Grayson.

We hypothesized ice-rafted deposits would smother underlying salt marsh plants, surface-dwelling invertebrates (i.e., epifauna), and surface-feeding infauna, such as polychaetes, leading to declines in their densities. In contrast, we hypothesized little to no impact to subsurface-feeding infauna, such as oligochaetes. Further, we expected changes in species composition for plant and infauna communities. Sediment deposits increased elevation in small spatial areas, potentially allowing less flood-tolerant plant species such as *Salicornia europaea* and *Atriplex patula* to gain a foothold in parts of the marsh platform where they may otherwise not be able to survive. Ice-rafted sediments originate from intertidal mudflats, potentially displacing species closely associated with mudflats such as the polychaete, *Streblospio benedicti*, similar to the findings of MacFarlane et al. (2013). Ultimately, full recovery of the biotic community may be a combination of sediment deposit thickness (Moore et al. 2021), time since the ice-rafting event (Moore et al. 2021), and whether there was disturbance to the belowground peat layer (e.g., ice scour) (Ewanchuk and Bertness 2003; Sharp and Angelini 2016). Thus, we expected larger, thicker sediment deposits to lead to slower biotic recovery over time.

Methods

Study Site and Sampling Design

This study was conducted at the Plum Island Ecosystems (PIE) Long-Term Ecological Research (LTER) site in Ipswich, Massachusetts, USA (Fig. 2). We sampled at the salt marsh surrounding Sweeney Creek (42.720818° N, −70.8493415° W), a part of the Great Marsh, the largest and most extensively studied salt marsh in New

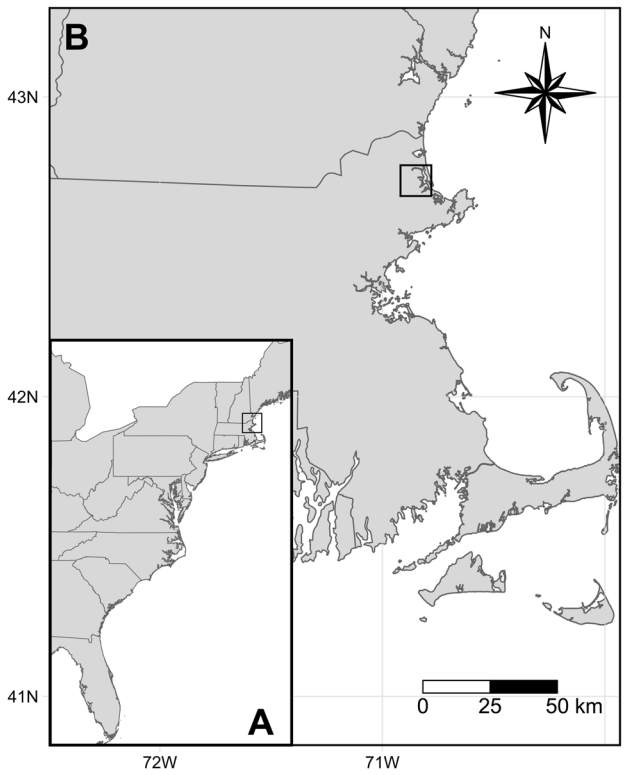

Fig. 2 **A** Inset map of the Atlantic coast of the USA. Black box indicates study area shown in panel **B**. **B** Enlarged map of Eastern Massachusetts, USA. Black box encloses the study area of Sweeney Creek located within the Great Marsh

England (FitzGerald et al. 2021). The Great Marsh and thus Sweeney Creek are characterized by extensive high marsh areas (above the mean high-water line) with low relief (< 30 cm; FitzGerald et al. 2021). These high marsh areas are infrequently flooded and underwater only 4% of the time with mixed plant communities dominated by *Spartina patens* and *Distichlis spicata* interspersed with stunted *Spartina alterniflora*, *Limonium carolinianum*, *Salicornia europaea*, and *Atriplex patula* (Johnson et al. 2016). The high marsh is fringed by less-extensive low marsh areas (below the mean high-water line) made up of monotypic stands of tall-form *S. alterniflora* (Johnson et al. 2016; FitzGerald et al. 2021).

Our study focused specifically on the high marsh. The infauna (sediment-dwelling invertebrates) of this area is dominated by both polychaetes, with *Manayunkia aestuarina* as the primary polychaete, and oligochaetes, primarily in the family Enchytraeidae (Johnson et al. 2007; Johnson and Fleeger 2009). The epifauna (mobile, surface-dwelling invertebrates) are numerically dominated by the coffee bean snail, *Melampus bidentatus*, the amphipod, *Orchestia grillus*, and the isopod, *Littorophiloscia vittata*, with other arthropods such as spiders and insects comprising the rest of the community (Johnson 2011; Johnson and Heard 2017).

In May of 2018, we selected twenty individual ice-rafted sediment deposits (hereafter "deposit") in the high marsh surrounding Sweeney Creek (Fig. 2). All deposits were at least 7 m apart from one another and varied in distance from the creekbank. At each deposit, we measured the total perimeter, as well as length and width at the widest points. The thickness of the deposit was measured at four locations and averaged per deposit. We used a paired design for the plant, infauna, and epifauna communities in which one sample was taken within the deposit (at least 0.25 m from deposit edge; $n = 20$) and one sample was taken outside of the deposit to serve as a reference (at least 0.5 m from deposit edge; $n = 20$). Deposits were sampled in May 2018 (3 months post deposition event), August 2018 (6 months post deposition event), and August 2019 (18 months post deposition event). One deposit sampled in May and August 2018 was inaccessible in August 2019; thus, it was not included in any analyses.

Plants

For our initial sampling in May 2018, we randomly placed one 0.0625 m^2 quadrat within the deposit (Fig. 1C) and one within the reference. For each quadrat in deposits, all plant species were identified, and the number of stems was counted per species. For each quadrat in references, only plant species were identified, as stems were too dense to be counted. Similarly, in August 2018 and 2019, we randomly placed one 0.0625 m^2 quadrat within the deposit and one in the reference. However, due to high stem densities and homogeneity of plant cover, we were unable to count stems while in the field. Instead, we removed all plant material from each quadrat by cutting it at the sediment surface using a serrated knife. Plant material was then placed in a resealable bag and frozen for later processing. In the lab, all plant samples were sorted by species and then by live vs. dead tissue. All live, intact stems were then counted by species. All plant material was then dried for 7 days at 60 °C and dry mass was recorded.

All statistical analyses were conducted in R version 1.3.1093 (R Core Team 2020). Due to the opportunistic nature of the plant sampling in May 2018 (e.g., stem densities were only recorded within deposits, not in references), these data were not included in statistical models and are only presented visually. For plant data collected in August 2018 and August 2019, a two-way, repeated measures ANOVA was used to assess the effects of disturbance (deposit vs. reference) and sampling date on total plant biomass. A second, two-way ANOVA tested the effect of deposit thickness and size on total plant biomass within deposits. For both models, additive and interactive effects were tested, and biomass data were square root transformed to meet the assumption of homoscedasticity. For stem counts

within quadrats, two separate, two-way, repeated measures ANOVAs with negative binomial distributions were used to assess (1) the effects of disturbance (deposit vs. reference) and sampling date on total plant stem density and (2) the effects of deposition thickness and size on total plant stem density within deposits.

Infauna

To assess infauna communities, one sediment core (5 cm depth, 6.6 cm diameter) was taken within deposits and one in references in May 2018, August 2018, and August 2019. Cores were preserved in 5% formalin for later processing. In the lab, infauna cores were passed through a 1-mm sieve stacked on top of a 500-µm sieve and stained with Rose Bengal. All samples were sorted under a microscope, and organisms were identified to the lowest possible taxonomic group.

The same collection methods were used for infauna samples in May 2018, August 2018, and August 2019; therefore, all data were analyzed together. As metrics of infauna alpha diversity, we calculated species richness and Hill numbers (i.e., the effective number of species; Jost 2006) using the R package "vegan" version 2.5–6 (Oksanen et al. 2019). Two-way, repeated measures ANOVAs were used to assess the effects of disturbance (deposit vs. reference) and sampling date on diversity indices and total abundance. When applicable, interaction effects were explored further using contrasts created with the "emmeans" package in R (version 1.5.2–1; Lenth et al. 2020). Because multiple hypothesis tests were performed on the same dataset, we corrected our p values for multiple comparisons using the false discovery rate (FDR) adjustment method (function p.adjust in R package "stats").

We assessed changes in infauna community composition (1) visually using non-metric multidimensional scaling (NMDS; Field et al. 1982) ordination plots and (2) statistically using permutational multivariate ANOVA (perMANOVA; Anderson 2001). First, we created three NMDS plots using Bray–Curtis dissimilarity matrices to visualize any differences in community composition within deposits and references across sampling dates (May 2018, August 2018, and August 2019). The quality of NMDS fits were assessed based on their stress values. NMDS fits with lower stress values (e.g., < 0.1) more accurately represent the infauna community composition than those with higher stress values (e.g., > 0.2). Data for these NMDS plots were transformed to produce the best fit (i.e., lowest stress value). Data from May 2018 were log transformed, and data from August 2018 and August 2019 were Hellinger transformed (i.e., species-specific sample abundances were divided by the total species abundance and then its square root was calculated). One reference infauna sample from August 2019 was removed from the NMDS because it only included one taxon (Dolichopodidae) and thus negatively impacted the NMDS fit (i.e., the stress was substantially higher for the NMDS when including this sample).

Second, when applicable, we used one-way perMANOVA tests (function adonis in R package "vegan") to statistically assess whether infauna community compositions differed between deposits and references. perMANOVA tests were only performed when the assumption of homogeneity of multivariate dispersion (i.e., variance) was met, a key assumption of this test. If this assumption is met, it would indicate that sampling locations within deposits were not more or less similar to each other than those within references (i.e., the beta diversity did not differ between deposits and references) (Anderson and Walsh 2013). If this assumption is not met, we would conclude that sampling locations within deposits or references were more dissimilar to each other than sampling locations within the other. Thus, we used a permutation test (function betadisper in R package "vegan"; Anderson et al. 2006) to assess the assumption of multivariate dispersion between deposits and references during each sampling date (i.e., we performed three permutation tests corresponding to the three sampling dates, May 2018, August 2018, and August 2019), and then performed perMANOVA on the data which met this assumption.

Epifauna

Epifauna were collected in August 2018 and 2019 by randomly placing a separate 0.0625 m^2 quadrat in deposits and in references. At each quadrat, vegetation was removed with a serrated knife, and all epifauna visible to the naked eye were hand-collected. Samples were then frozen for later processing. In the lab, epifauna were thawed, separated, and identified to the lowest taxonomic group. Samples had low species richness; therefore, diversity indices were not calculated. A two-way, repeated measures ANOVA was used to assess the effects of disturbance (deposit vs. reference) and sampling date on total abundance.

Results

Sediment deposits greatly varied in size, with an average length of 3.02 m (range: 0.7–8.9 m), width of 2.75 m (range: 1.1–6.6 m), and perimeter of 10.21 m (range: 5.1–21.9 m). The average thickness of all deposits measured was 2.74 cm (range: 0.5–6.5 cm). Although we only measured sediment thickness 3 months after deposition (May 2018), after 6 months (August 2018), deposits could not be visually distinguished from the surrounding marsh and there was no obvious change in elevation, indicating sediment deposits did not erode nor compact, similar to the findings of Moore et al. (2021).

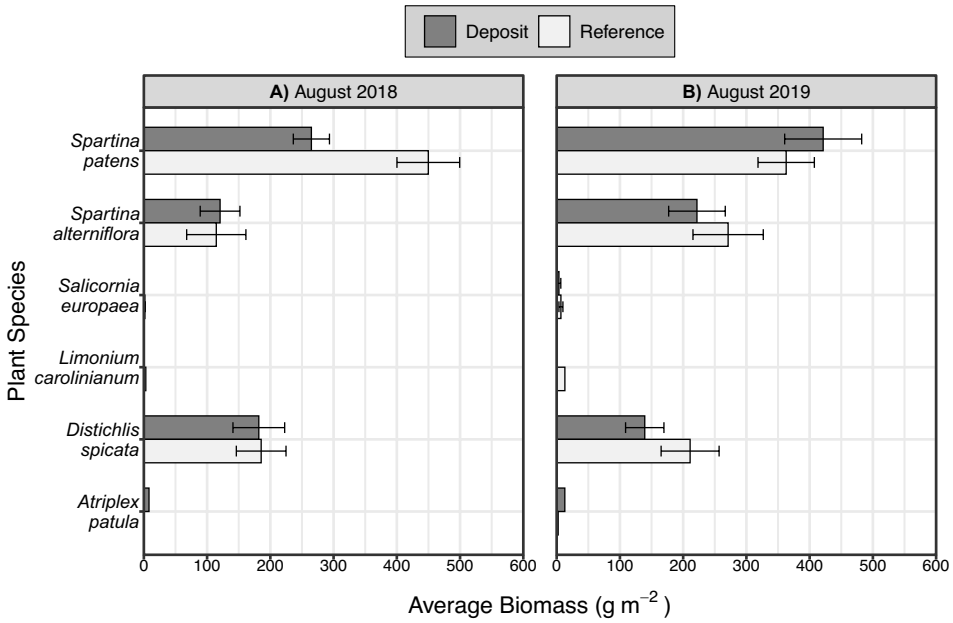

Fig. 3 Average aboveground biomass per plant species in grams per square meter collected from within deposits (dark gray bars) and references (light gray bars) in **A** August 2018 and **B** August 2019. Error bars represent standard error

Plants

There were no interaction effects between sampling date and disturbance (deposit vs. reference) for any of the models; therefore, we proceeded with additive models only. Total plant biomass did not vary between deposits and references ($p = 0.204$; Fig. 3) or sampling dates ($p = 0.472$; Fig. 3A, B). Total plant stem density in references was 13% higher than in deposits ($p = 0.099$; Fig. 4) and this did not vary between sampling dates ($p = 0.280$; Fig. 4A–C). Further, deposit thickness and perimeter did not influence total plant biomass ($p = 0.879$, $p = 0.522$, respectively) or total stem density ($p = 0.812$, $p = 0.340$, respectively). It is also important to note that there was no effect of individual deposits on plant biomass ($p = 0.212$) or stem density ($p = 0.629$), indicating that any potential differences in the sediment composition of deposits (e.g., grain size, shell content, organic content) did not influence the plant community.

In May 2018, the most abundant species within deposits were *D. spicata*, *S. patens*, and stunted *S. alterniflora*, with

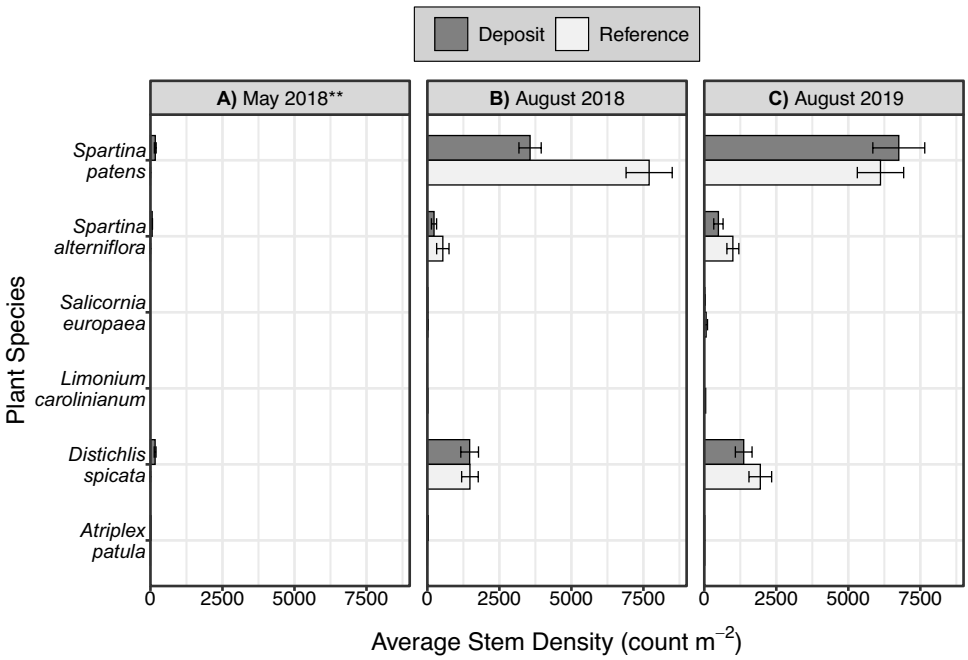

Fig. 4 Average stem density by plant species per meter squared from within deposits (dark gray bars) and references (light gray bars) in **A** May 2018, **B** August 2018, and **C** August 2019. Error bars represent standard error. Double asterisk denotes stem densities in reference habitats were not collected in May 2018

similar densities for all three species (Fig. 4A). These three species remained the most common for both deposits and references in August 2018 and 2019, although their densities differed over time (Fig. 4B, C). Interestingly, *S. patens* quickly outcompeted *D. spicata* and became the dominant species in deposits by August 2018 (Fig. 4B). Similarly, *S. patens* was the most abundant species in references for both August 2018 and 2019 (Fig. 4B, C). Compared to these three species, we saw low densities ($\leq$48 stems/m^2) of *L. carolinianum*, *S. europaea*, and *A. patula* across sampling dates and disturbance (deposit vs. reference) (Fig. 4A–C). Both *L. carolinianum* and *S. europaea* appeared only in August 2018 and August 2019, with *L. carolinianum* found only in references (Fig. 4B, C). By August 2019, there were no differences in stem densities across species or disturbance (deposit vs. reference) (Fig. 4C). Similar species-specific responses were also seen in plant biomass results (Fig. 3).

Infauna

Infauna were grouped into three distinct taxa: annelids, insect larvae, and mites (Fig. 5), although we recognize that some mites and insect larvae may live more often *on* the sediment than *in* the sediment. We also detected some organisms that were not the intended target of sampling; thus, these were not included in statistical analyses and are instead listed in Supplementary Table S1. There was an interaction effect of sampling date and disturbance (deposit vs. reference) on total abundance ($p = 0.033$), species richness ($p = 0.0001$), and Hill numbers ($p = 0.001$). Mean total abundance was 43% higher in references than deposits in May 2018 ($p = 0.255$; Fig. 6A), 45% higher in references than deposits in August 2018 ($p = 0.058$; Fig. 6A), and then 33% higher in deposits than references by August 2019 ($p = 0.099$; Fig. 6A). Average species richness followed a similar pattern, with richness in references 9% higher than deposits in May 2018 ($p = 0.0002$; Fig. 6B) and 32% higher in August 2018 ($p = 0.005$; Fig. 6B). By August 2019, however, species richness was 26% higher in deposits than references ($p = 0.048$; Fig. 6B). In May 2018, Hill numbers were 42% higher in references than in deposits ($p = 0.0005$; Fig. 6C) and 13% higher in August of 2018 ($p = 0.233$; Fig. 6C). By August of 2019, however, Hill numbers were 22% higher in deposits than in references ($p = 0.089$; Fig. 6C).

All NMDS fits were acceptable (stress < 0.16). In May 2018, beta diversity was 31% higher within deposits than in references (i.e., samples within deposits were more dissimilar to each other than those in references; $p = 0.089$, Fig. 7). perMANOVA revealed the infauna community compositions

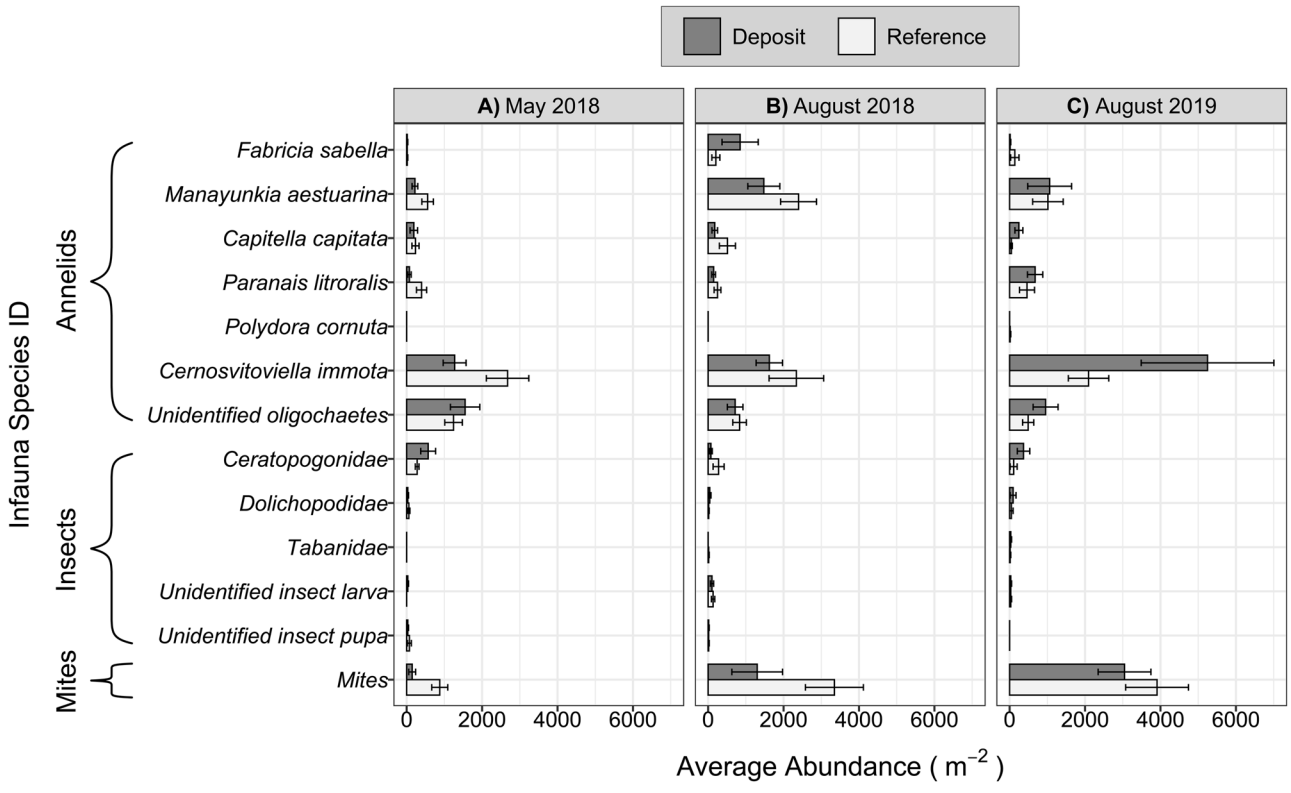

Fig. 5 Mean abundance of infauna (grouped in three distinct taxa: annelids, insects, and mites) per square meter collected within deposits (dark grey bars) and references (light gray bars) in **A** May 2018, **B** August 2018, and **C** August 2019. Error bars represent standard error

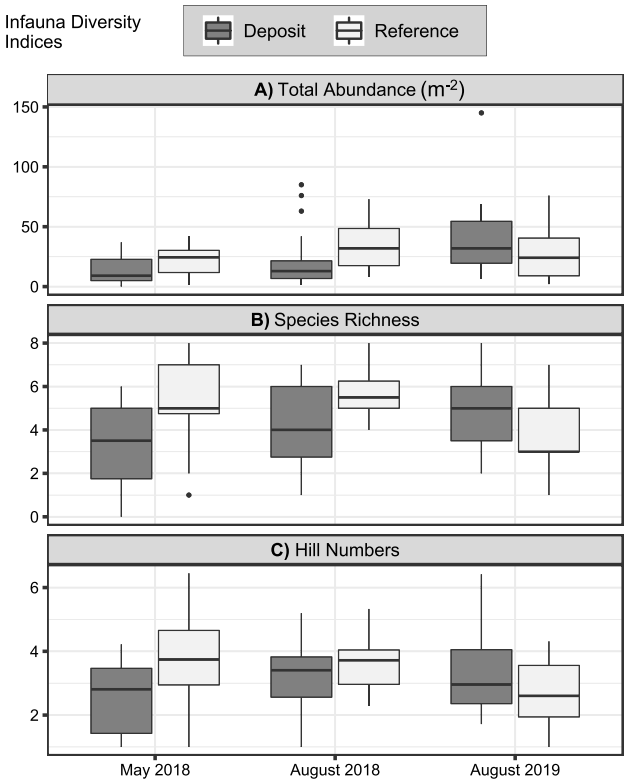

Fig. 6 **A** total abundance per square meter, **B** species richness, and **C** Hill numbers for infauna samples collected within deposits (dark gray boxes) and references (light gray boxes) in May 2018, August 2018, and August 2019

during this period were different between deposits and references ($p = 0.03$). In August 2018, deposits had 34% higher beta diversity than references ($p = 0.010$), indicating that it did not meet the critical assumption of homogeneity of multivariate dispersion. Thus, we were unable to perform perMANOVA on August 2018 data. In August 2019, the beta diversity was similar between deposits and references, with references only 8% higher than deposits ($p = 0.565$). A subsequent perMANOVA test for this period showed the community compositions of deposits and references were similar ($p = 0.196$; Fig. 7).

In May of 2018, oligochaete worms were the most common taxa, with *Cernosvitoviella immota* the dominant species in references, and other unidentified oligochaetes dominant within deposits (Fig. 5A). In August of 2018, mites, *C. immota*, and the polychaete, *Manayunkia aestuarina*, became the most common in both references and deposits (Fig. 5B). By August of 2019, mites and *C. immota* dominated both references and deposits (Fig. 5C).

Epifauna

Epifauna were sorted by three common species, the gastropod, *Melampus bidentatus*, the amphipod, *Orchestia grillus*, and the isopod, *Littorophiloscia vittata*, and one common taxon, spiders (Fig. 8). Any other organisms found in these samples that are inadequately sampled with quadrats were not included in statistical analyses and are displayed in Supplementary Table S2. Mean epifauna abundance was 47% higher in references than in deposits ($p = 0.083$; Fig. 8) and there was no effect of individual deposit ($p = 0.779$) on total abundance. Further, average epifauna abundance was 11% higher in August 2019 than in August 2018 ($p = 0.040$; Fig. 8A, B). In both August 2018 and August 2019, *M. bidentatus* was the numerically dominant species, with higher abundances in references than in deposits (Fig. 8A, B). Abundances of *O. grillus*, *L. vittata*, and spiders increased from August 2018 to August 2019,

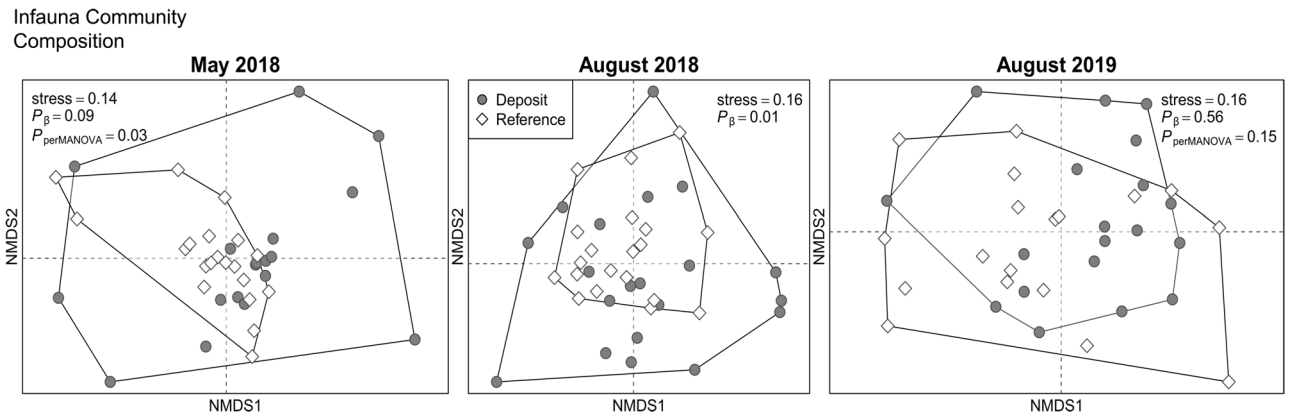

Fig. 7 Non-metric multidimensional scaling (NMDS) ordination plots for infauna community within deposits (filled circles) and references (open diamonds) during May 2018, August 2018, and August 2019. Horizontal and vertical dashed lines denote the *x*- and *y*-axes at zero. Within each panel, the two polygons encompass all sampling locations ($n = 20$ for May 2018 and August 2018; $n = 19$ for August 2019)

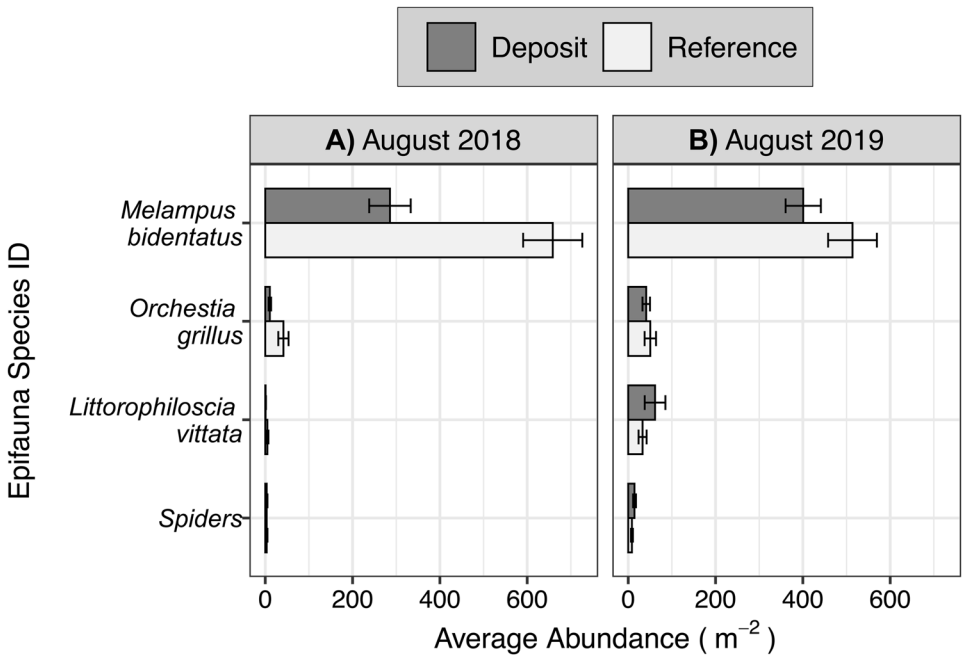

Fig. 8 Average abundance of epifauna per square meter collected within deposits (dark grey bars) and references (light gray bars) in **A** August 2018 and **B** August 2019. Error bars represent standard error

regardless of disturbance (deposit vs. reference) (Fig. 8A, B). The abundance of *O. grillus*, *L. vittata*, and spiders were higher in references in August 2018, but by August 2019, total abundance within deposits were similar to (*O. grillus*), or greater than (*L. vittata* and spiders), those in references (Fig. 8A, B).

Discussion

Although ice-rafted sediment is deposited on salt marshes annually in New England (Wood et al. 1989; Argow et al. 2011), winter storm Grayson was historic in its size and widespread impacts (FitzGerald et al. 2020; Moore et al. 2021). We found that the abundances of some plant and invertebrate species within sediment deposits reached those in references only 6 months (August 2018) after Grayson. By August 2019, approximately 18 months following sediment deposition from winter storm Grayson, there were no differences in plant and invertebrate communities between deposits and references, indicating a full recovery.

For the plant community, we saw species-specific responses to sediment deposition, with *D. spicata* having similar density and biomass to references only 6 months post deposition (one full growing season; August 2018), with *S. patens* in deposits having equivalent density and slightly higher biomass than references 18 months (2 full growing seasons; August 2019) after the ice-rafting event. *D. spicata* biomass and density, however, slightly declined in deposits between August 2018 and 2019, presumably because it was outcompeted by *S. patens*. Interestingly, by August 2019, stunted *S. alterniflora* within deposits had similar biomass to references, but overall lower stem densities. Contrary to our expectations, and results from a similar study (Moore et al. 2021), neither sediment thickness nor size influenced plant recovery. This suggests plants can fully recover within 2 growing seasons from sediment deposits that are smaller than 21 m in perimeter and less than 6.5 cm thick.

The full recovery of the plant community may be related to the magnitude of the disturbance. Although we expected sediment deposits to potentially stifle the underlying plants, it is important to note we did not see any indication that ice-rafting disturbed the belowground peat layer (i.e., ice scour or gouging), a crucial factor that can determine plant recovery (Ewanchuk and Bertness 2003; Sharp and Angelini 2016). This lack of disturbance to the belowground peat layer may also explain why, in this instance, ice-rafting did not lead to pond formation. Although not explicitly tested, we noted evidence of plant regrowth emerging from underneath the deposit, a process that would not happen if ice scour had occurred, as well as from clonally grown shoots from neighboring plants, both of which can facilitate quick revegetation of sediment deposits (FitzGerald et al. 2020).

Contrary to our expectations, we did not find any displaced infauna species associated with mudflats, such as the polychaete, *Streblospio benedicti*. In May of 2018, however, we did see many shells from the mud snail, *Ilyanassa obsoleta*, within deposits. It is unclear whether these snails were alive when the sediment was deposited, or whether old shells were lifted and transported with the ice raft. As expected, total polychaete densities were lower following sediment deposition, but as time went on, they began rebounding and

were similar to references after 18 months. The dominant species of polychaete was *Manayunkia aestuarina*, a species that feeds at the sediment surface. Its initial low abundance in deposits suggest that sediment deposition smothered this species. *Manayunkia aestuarina* has low dispersal ability and high site fidelity (Light 1969; Bell 1982; Bick 1996); its quick recovery indicates that most of the recruitment likely occurred from within the deposit rather than from the surrounding area.

As expected, oligochaete densities were not initially impacted by sediment deposits. Unexpectedly, however, their densities were 2 times higher, on average, within deposits than in references after 18 months. The oligochaetes found in our samples are predominantly enchytraeids, which are considered later successional animals with low dispersal ability (Talley and Levin 1999). Additionally, oligochaete densities track sediment organic content (Talley and Levin 1999); however, sediment deposits in the Great Marsh are 11% organic, on average, compared to 24% organic within the surrounding high-marsh peat (FitzGerald et al. 2020). Thus, the reason for this increase in oligochaete densities within deposits remains unclear.

Although the gastropod, *M. bidentatus*, was the most abundant species of epifauna present in our samples, their densities in deposits were still lower than references 18 months post ice-rafting. In contrast, the densities of the amphipod, *O. grillus*, the isopod, *L. vittata*, and spiders within deposits were equal to or greater than those in references, indicating a full recovery of these groups. These are mobile animals that live on the sediment surface or in plant canopies (Fell 1982; Johnson 2011; Johnson and Williams 2017); their recovery in the deposits likely reflects adult recruitment from outside of the deposits.

We show following an ice-rafting event, even when associated with a historic storm, both plant and invertebrate communities made a full recovery after only two growing seasons (~ 18 months post sediment deposition). There are two probable mechanisms driving this quick recovery: (1) sediment deposit thickness and (2) the small spatial area impacted by deposition (i.e., patchiness). Sediment deposit thickness can alter marsh elevation and inundation frequency and duration, key determinants of plant growth and recovery (Bertness and Pennings 2000). The sediment deposits in our study had an average thickness of 2.74 cm (range: 0.5 to 6.5 cm), which was thin enough to allow for underlying plants to break through the deposit and regrow, aiding in quick recovery. The plant and invertebrate communities in our study may also have recovered quickly because of the relatively small size and patchiness of the ice-rafted sediment deposits (FitzGerald et al. 2020). This patchiness is different than other disturbances, such as oil spills or hurricanes, which cover large, continuous spatial areas. The ability of plants and invertebrates to recolonize sediment deposits from nearby, undisturbed areas may ultimately be the largest factor driving the fast recovery seen in our study. Overall, we show ice-rafted sediment deposition has strong, localized impacts initially; however, the biotic community can fully recover within 2 years, suggesting salt marsh plants and invertebrates are resilient to ice-rafting. This indicates these nor'easter disturbance events may ultimately cause little to no disruption to the critical ecosystem services and functions provided by salt marshes.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-021-01023-z.

Acknowledgements We thank Sam Kelsey, Erin VanderJeugdt, and Caroline Failon for field help; Tiffany Birge, Catherine Wilhelm, and Leah Scott for laboratory support; Dr. Linda Deegan for helpful discussions; and Dr. Grace Chiu for assistance with statistical analyses. This paper is Contribution 4060 of the Virginia Institute of Marine Science, William & Mary.

Funding This work was funded in part by National Science Foundation grants: 1754259, 1637630, and 1902712, and a Virginia Sea Grant graduate research fellowship #V721500.

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