

**Key Points:**

- Through suspension feeding and biodeposition, mussels augment sedimentation of organic matter (OM) produced inside and outside of salt marshes
- OM accumulation in sediments and aboveground storage increases with increasing mussel density
- Mussels bolster the capacity of salt marshes to counteract coastal eutrophication and provide blue carbon services

**Supporting Information:**

Supporting Information may be found in the online version of this article.

**Correspondence to:**

S. L. Williams,  
[sydney.williams@ufl.edu](mailto:sydney.williams@ufl.edu)

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**Author Contributions:**

**Conceptualization:** Sydney L. Williams, Jamie L. Rogers, Hallie S. Fischman, Elise S. Morrison, Christine Angelini  
**Data curation:** Sydney L. Williams, Jamie L. Rogers, Hallie S. Fischman  
**Formal analysis:** Sydney L. Williams  
**Funding acquisition:** Sydney L. Williams, Christine Angelini  
**Investigation:** Sydney L. Williams, Jamie L. Rogers, Hallie S. Fischman  
**Methodology:** Sydney L. Williams, Jamie L. Rogers, Hallie S. Fischman, Elise S. Morrison, Christine Angelini  
**Project Administration:** Sydney L. Williams  
**Resources:** Sydney L. Williams, Jamie L. Rogers, Hallie S. Fischman, Elise S. Morrison, Christine Angelini

## The Role of a Faunal Engineer, *Geukensia demissa*, in Modifying Carbon and Nitrogen Regulation Services in Salt Marshes

Sydney L. Williams<sup>1</sup> , Jamie L. Rogers<sup>2</sup> , Hallie S. Fischman<sup>1</sup> , Elise S. Morrison<sup>1</sup> , and Christine Angelini<sup>1</sup>

<sup>1</sup>Engineering School for Sustainable Infrastructure and Environment, University of Florida, Gainesville, FL, USA, <sup>2</sup>School of Fisheries, Aquaculture & Aquatic Sciences, Auburn University, Auburn, AL, USA

**Abstract** Interest in leveraging suspension feeders, such as marine bivalves, to exert top-down control on organic matter (OM) loading in estuaries is gaining momentum. Not only can these faunal engineers alleviate the consequences of nutrient pollution, but they may also bolster the critical blue carbon services provided by coastal ecosystems—a potential dual, mitigating effect on cultural eutrophication and climate change. Ribbed mussels, *Geukensia demissa*, offer a useful model for assessing faunally driven carbon (C) and nitrogen (N) processes in these systems and their relationships with faunal density. Combining bulk geochemical analyses with Bayesian stable isotope mixing model frameworks (MixSIAR), we quantified the effect of mussels on the source and amount of organic C and N deposited to the benthic floor (i.e., sedimentation), accumulated in surface sediments, and stored in aboveground *Spartina alterniflora* in Georgia salt marshes. Relative to areas without mussels, mussel presence shifted the source of deposited and accumulated OM to a more allochthonous makeup; amplified the amount of deposited, but not accumulated, allochthonous and autochthonous OM; and enhanced aboveground storage of C and N. Both sources of OM accumulated in sediments as well as standing stocks of C and N were highly and positively correlated with local mussel density (ind. m<sup>-2</sup>) but unrelated to neighboring mussel density (ind. ~25 m<sup>-2</sup>) in adjacent, non-mussel areas. This work provides new evidence that suspension feeders, through their faunal engineering activities, can interact powerfully and synergistically with primary producers to enhance the blue carbon services of marshes and counteract coastal eutrophication.

**Plain Language Summary** Coastal ecosystems regulate carbon and nitrogen generated both inside and outside of their physical extents—important ecosystem services that can help combat the consequences of pollution and climate change. Suspension-feeding animals living in these ecosystems, like mussels, may enhance this regulation by feeding on algae suspended in the overlying tidewater and depositing their waste to the habitat bottom. There, these deposits can accumulate in sediments or be taken up by plants. We studied how ribbed mussel presence and density influence carbon and nitrogen regulation processes in Georgia, USA salt marshes. By comparing deposits in marsh areas with and without mussel aggregations with elemental and stable isotope analyses, we found that mussels amplify the reclamation and import of marsh-derived and marine-derived carbon and nitrogen, respectively. We took a similar approach to sediment and found that concentrations of both sources of carbon and nitrogen increase as mussel density increases within their aggregations. Finally, we found that mussel presence and density boosted cordgrass biomass and, in turn, carbon and nitrogen storage. Mussel populations are disproportionately augmenting the role of salt marshes in regulating carbon and nitrogen pollution and should be incorporated into coastal management decisions related to these challenges.

### 1. Introduction

Despite the well-documented and significant capacity of vegetated coastal ecosystems (VCEs) to trap and retain carbon and nutrients, organic matter (OM) input increasingly threatens their integrity (Malone & Newton, 2020). Although commonly produced outside of VCEs, high OM concentrations (e.g., OM derived from algal blooms) are often caused by anthropogenic discharges of nitrogen (N) (i.e., cultural eutrophication) and can trigger highly turbid states, deoxygenation, and submerged aquatic vegetation loss within these systems (Bricker et al., 2008). This domino effect of biophysical responses can extend to degrade the health and economic welfare of coastal communities (Court et al., 2021; Medina et al., 2022). Among coastal and water resource managers, interest in

**Supervision:** Elise S. Morrison, Christine Angelini

**Visualization:** Sydney L. Williams, Hallie S. Fischman, Christine Angelini

**Writing – original draft:** Sydney L. Williams, Christine Angelini

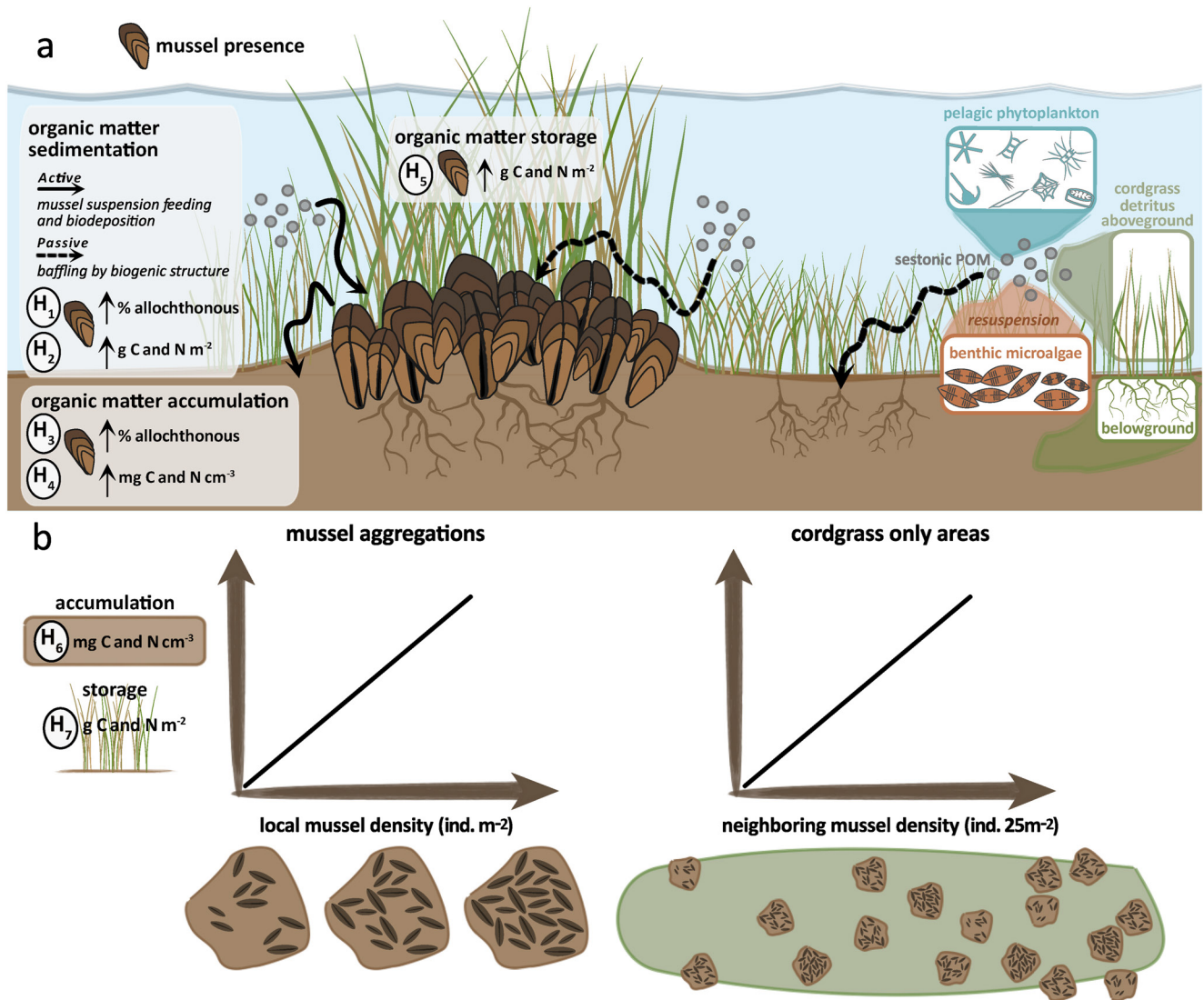
**Writing – review & editing:** Sydney L. Williams, Hallie S. Fischman, Elise S. Morrison, Christine Angelini

leveraging suspension feeders, such as marine bivalves and sponges, to exert top-down control on OM loading in estuaries is gaining momentum. However, not only can this faunal engineering alleviate the consequences of nutrient pollution, but it may also bolster the critical, highly valued carbon (C) sequestration services provided by VCEs. For example, a decade-long restoration effort in Shinnecock Bay, NY to revitalize the bay's collapsed hard clam (*Mercenaria mercenaria*) population resulted in significant and synergistic effects on C-fixing primary producers, namely the removal of harmful brown tide alga followed by an increase in the extent of native seagrass beds (Gobler et al., 2022). This potential dual effect of suspension feeders in mitigating both cultural eutrophication and climate change has received little attention. Thus, as investments in suspension feeders continually grow to address coastal management challenges, their role in both C and N regulation requires deeper investigation.

Prior to this recently ignited interest in suspension feeders, the role of dominant primary producers (e.g., seagrass, *Spartina spp.*, mangroves) in C and N sequestration received significant and well-justified attention. In addition to storing these elements in their living tissue, coastal macrophytes promote C and N sedimentation and accumulation in coastal sediments by baffling water flow, trapping sestonic particles, and suppressing resuspension (Gacia et al., 2002; Loomis & Craft, 2010; Middelburg et al., 1996). Source tracking with stable isotopes has further shown that a significant proportion of sediment OM in VCEs is imported from adjacent systems, highlighting their capacity to remove externally produced (i.e., allochthonous) algal material from the water column (Middelburg et al., 2004; Zhou et al., 2006). An extensive body of research on macrophyte-driven C and N sequestration has thus solidified our understanding of these systems' imperative, global function in mitigating cultural eutrophication and climate change (Duarte et al., 2005).

Through both active and passive mechanisms, suspension feeders also can drive C and N processes in estuaries. Active benthic-pelagic coupling by these animals involves the removal of C-fixing and N-rich algae from the water column via grazing and subsequent biodeposition of this material (Gili & Coma, 1998). Further, many species within this functional guild form epibenthic reefs or beds—structures that passively alter boundary layer flows and, in turn, act as sedimentation sinks for particulate material (Bouma et al., 2007; Lim et al., 2020; Nikora et al., 2002). When associated with coastal macrophytes, suspension feeders also can stimulate their primary production and, in turn, enhance C and N standing stocks in above- and below-ground macrophyte tissues by reducing water column turbidity and increasing light availability to the benthos; and concentrating bioavailable nutrients for macrophyte uptake and growth (Bertness, 1984; Peterson & Heck, 2001). Thus, suspension feeders—particularly those that build biogenic structures, have high biodeposition rates, and occur in close association with macrophytes—may act as major conduits for C and N input and retention in VCEs. To trace the influence of these fauna to source-specific (i.e., autochthonous vs. allochthonous) sediment deposition, accumulation (i.e., burial in sediments), and storage (i.e., macrophyte production) of organic C and N, elemental and stable isotope analyses of suspension feeder biodeposition and the sediment and macrophytes directly related to them, are needed. However, such tools have been largely applied to the soft tissues of these animals to resolve their diets (Bouillon et al., 2008; Dang et al., 2009; Kon et al., 2015; Sullivan & Moncreiff, 1990; Vafeiadou et al., 2013) or as indication of nutrient enrichment (Bannon & Roman, 2008; Marchais et al., 2013; McKinney et al., 2001; Pruell et al., 2006; Watanabe et al., 2009). Filling this knowledge gap is essential for informing when and where projects with suspension feeders may be most effective in augmenting the mitigation services of VCEs.

Ribbed mussels, *Geukensia demissa*, (hereafter, “mussels”) offer a useful model for assessing faunally driven C and N processes in VCEs. Ranging from St. Lawrence Bay (Canada) to southern Florida (USA), mussels are sessile suspension feeders that graze on a wide array of particle types, including pelagic and benthic algae, detrital vegetation, and bacteria (Kreeger & Newell, 2001; Langdon & Newell, 1989). In the southeastern US where this study is focused, mussels typically form dense, clumped aggregations on intertidal salt marsh platforms in association with the dominant primary producer, smooth cordgrass (*Spartina alterniflora*; hereafter “cordgrass” (Crotty & Angelini, 2020). Mussel aggregations, which are embedded in the mud around cordgrass stems, cover 0.2%–1.1% of marsh platforms in this region and locally enhance cordgrass production (Angelini et al., 2015; Stiven & Gardner, 1992). Additionally, mussels actively facilitate high rates of sediment deposition. Crotty et al. (2023) found that mussels transfer 2.8 to 10.7-times more material onto a Georgia salt marsh during summer neap, summer spring, and winter spring tides via biodeposition when compared to passive sedimentation in areas where mussels were absent. By enhancing rugosity of the marsh bottom, these biogenic features also may passively influence particulate transport processes at the sediment-water interface (Butman et al., 1994; Nikora et al., 2002; Widdows et al., 1998). Mussels are thus important biogeochemical couplers of the water column and the marsh bottom, facilitating the exchange of C and N in these ecosystems (Bilkovic et al., 2017; Dame



**Figure 1.** Conceptual diagram illustrating C and N processes and hypotheses addressed in this study. Pelagic phytoplankton (aqua), resuspended benthic microalgae (red), and aboveground cordgrass detritus (light green) exist in the water column when tidal water floods over a salt marsh (a). Sestonic particulate organic matter can be transported to the marsh surface via both active and passive sedimentation (a). Additionally, the study's hypotheses ( $H_1$  through  $H_7$ ) regarding mussel presence (a) and density effects (b) on organic C and N sedimentation ( $\text{g m}^{-2}$ ), accumulation ( $\text{mg cm}^{-3}$ ), and aboveground storage ( $\text{g m}^{-2}$ ) on mussel aggregations and cordgrass only areas are depicted. Some symbols here and below are courtesy of the Integration and Application Network ([ian.umces.edu/symbols/](http://ian.umces.edu/symbols/)), University of Maryland Center for Environmental Studies.

et al., 2002; Kuenzler, 1961). Further, mussel density, both within individual aggregations at the patch scale and across populations of aggregations at the landscape scale, likely modulates the effect of these organisms on C and N processes (Bertness, 1984; Crotty et al., 2023; Moody & Kreeger, 2020; Smith & Frey, 1985). Despite the key, multifaceted importance of these abundant and productive bivalves, the fate of mussel biodeposition as it relates to source-specific sedimentation, accumulation, and storage of C and N—and how mussel density affects these pathways—in salt marshes has not been explored.

Combining bulk geochemical analyses with Bayesian stable isotope mixing model frameworks (MixSIAR), we model source contributions to sestonic particulate organic matter (POM) and then quantify the effect of mussels on the source (i.e., proportion of autochthonous and allochthonous sources) and amount of organic C and N in material related to sediment deposition, accumulation, and storage processes (Figure 1a). Specifically, we analyze material transported from the water column to the marsh surface (i.e., sedimentation), accumulated in the first 5 cm of the sediment layer, and stored in cordgrass tissue to test process-specific hypotheses. First, we hypothesize

that mussels augment OM coupling at the sediment-water interface and, in turn, shift the assemblage of deposited material towards a more allochthonous makeup (%) ( $H_1$ ). Then, we hypothesize that, due to high mussel biodeposition rates, mussels increase the amount of allochthonous and autochthonous organic C and N ( $\text{g m}^{-2}$ ) transported to the salt marsh surface ( $H_2$ ). Our next hypotheses assert that mussel-driven sedimentation accumulates in surface sediments, whereby mussel presence shifts the assemblage of OM towards a more allochthonous makeup ( $H_3$ ) and increases the sediment concentration of allochthonous and autochthonous organic C and N ( $\text{mg cm}^{-3}$ ) ( $H_4$ ). We also hypothesize that organic C and N standing stocks ( $\text{g m}^{-2}$ ) in aboveground cordgrass are enhanced with mussel presence ( $H_5$ ). Lastly, we consider the effects of mussel density on accumulation and storage (Figure 1b), hypothesizing that with increasing local (within aggregation,  $\text{ind. m}^{-2}$ ) and neighboring mussel density around cordgrass only areas ( $\text{ind. } \sim 25 \text{ m}^{-2}$ ), the concentration of allochthonous and autochthonous organic C and N in sediments increases ( $H_6$ ) as does the organic C and N storage in aboveground cordgrass ( $H_7$ ). Overall, this work provides new evidence that suspension feeders, through their faunal engineering activities, bolster the capacity of VCEs to regulate C and N, demonstrating that suspension feeding bivalves interact synergistically with primary producers to counteract coastal eutrophication and enhance the blue carbon services of salt marshes.

## 2. Methods

### 2.1. Field Sites

Studies were conducted on the platforms of two salt marshes on the coast of Georgia, USA: Old Teakettle Creek (31.451999,  $-81.317059$ ), and Dean Creek (Sapelo Island, 31.390296,  $-81.273586$ ) (Figure S1 in Supporting Information S1). Marsh platforms in this region are characterized by intertidal creeks that stem from larger main channels. Both sites flood and drain semidiurnally via Doboy Sound and are tidally inundated for  $\sim 6$  hr per day. Doboy Sound receives fresh- and saltwater input from the Altamaha River and Atlantic Ocean, respectively. In estuarine systems, seston concentrations and characteristics vary across tidal, lunar, and annual cycles. Elevated POM and chlorophyll *a* concentrations are observed in spring and summer months and during spring, as opposed to neap, tides (Berg & Newell, 1986; Cadee, 1982; Toro et al., 1999). These temporal patterns in seston availability are reflected in mussel biodeposition rates, which peak during summer spring tides in our study region (Crotty et al., 2023). To assess these more active periods of mussel biodeposition, we collected samples during Summer 2019 and 2020 and, when applicable, during spring tides. Each study took place at one of the two sites. The motivation for site selection and experimental design is reported in Supporting Information S1.

### 2.2. Mussel Effects on Organic Matter Sedimentation

#### 2.2.1. Sample Collection at Dean Creek

Using a filter paper method adapted from Reed (1989), we captured seston transported to the marsh surface via separate processes: (a) active and passive sedimentation by mussels through biodeposition and baffling and (b) passive sedimentation through either background settling or baffling by cordgrass (Figure 1a). Specifically, we staked ashed and pre-weighed filter papers (Whatman glass microfiber filters, Grade GF/F, diameter 90 mm; hereafter “benthic filters”) with 1.5 mm steel wire on mussel aggregations (i.e., within interstitial spaces between mussels) and cordgrass only areas ( $n = 21$  per area type) naturally occurring between 0 and 20 m from the platform’s creek head during low tide. Cordgrass only areas were located at least 1 m away from any mussel aggregation. Benthic filters then captured transported material during a spring, daytime high tide (+1.64 m MSL; Rockdedundy NOAA Tide Station). At three time intervals during the same high tide, sestonic POM was collected in 1 L grab samples 10 cm below the surface by kayak at eight locations across the marsh platform ( $n = 24$ ). Benthic filters were retrieved at low tide 6 hr after deployment. Both benthic and sestonic samples were transported on ice to the lab. A small subset of benthic filter papers was incorrectly staked onto mussel aggregations ( $n = 5$ ) and either floated away during tidal inundation or failed to collect mussel sedimentation as a result. These samples were removed from the data set prior to further processing and analyses. POM samples were immediately vacuum filtered through two ashed 25 mm GF/F filters (Whatman glass microfiber filters, Grade GF/F, diameter 25 mm; hereafter “pelagic filters”). Benthic and pelagic filters were stored at  $-20^\circ\text{C}$  until further processing.

#### 2.2.2. Bulk Geochemistry

We freeze-dried and measured benthic and pelagic filter dry weights. Then, we selected a random subsample of benthic filters, ground them to a fine powder, and weighed subsets of each sample into one silver ( $n = 8$  per area type) and one tin ( $n = 12$  per area type) capsule (Costech)—the former were fumigation acidified according to

Harris et al. (2001) and analyzed for percent weight total organic C (%TOC) and  $\delta^{13}\text{C}$  while the latter were analyzed for percent weight total N (%TN) and  $\delta^{15}\text{N}$ . All elemental and stable isotope analyses described here and below were conducted at the University of Florida's Stable Isotope Laboratory, using a Carlo Erba 1500 CN elemental analyzer coupled to a Thermo Electron DeltaV Advantage isotope ratio mass spectrometer (Carlo Erba/ThermoFisher Scientific™, Waltham, MA, USA). Stable isotope ratios are reported in standard delta ( $\delta$ ) notation relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric  $\text{N}_2$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. We evaluated the conditional effect of area type on dry weight, %TOC, and %TN with Bayesian generalized multivariate models; all multivariate models described here and below were built, run, and assessed using Stan (Stan Development Team, 2023) and R (v. 4.3.1, R Core Team, 2023) with the R packages brms (v. 2.19.0, Bürkner, 2017, 2018, 2021), CmdStanR (v. 0.6.0, Gabry et al., 2023), bayesplot (v. 1.10.0, Gabry & Mahr, 2022), and posterior (v. 1.4.1, Bürkner et al., 2023). For all models related to bulk geochemistry described here and below, model formulas are summarized (i.e., response distributions and link functions) in Table S2 in Supporting Information S1. We multiplied dry weight by %TOC and %TN to calculate the amount of organic C and N (g) captured by the benthic filters and then extrapolated these values to estimate sediment deposition per square meter of mussel aggregation and cordgrass only areal coverage ( $\text{g m}^{-2}$ ) across the marsh platform during a single, spring high tide (see Crotty et al. (2023) for similar methods of extrapolation). Pelagic filter duplicates were analyzed for either  $\delta^{13}\text{C}$ , after acidification, or  $\delta^{15}\text{N}$ . These values were later incorporated into isotope mixing models described below.

### 2.2.3. Organic Matter Source Tracking

To address our first hypothesis that mussels augment OM coupling at the sediment-water interface and, in turn, shift the assemblage of sedimentation material toward a more allochthonous source ( $H_1$ ), we modeled OM source contributions to benthic and pelagic filters. Specifically, we created and executed two Bayesian mixing model frameworks by incorporating  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from benthic filters, with area type defined as a random effect, and pelagic filters. All isotope mixing models described here and below were built, run, and assessed using JAGS (v. 4.3.1, Plummer, 2017) and the R packages MixSIAR (v. 3.1.12, Stock et al., 2018) and rjags (v. 4.14, Plummer, 2023). Informed by prior estuarine food web studies, we considered three endmembers as candidate OM sources: (a) aboveground cordgrass detritus; (b) benthic microalgae; and (c) pelagic phytoplankton (Haines & Montague, 1979; Peterson & Howarth, 1987). As C and N concentrations vary widely across these sources, we incorporated concentration dependence into our model frameworks with source-specific C:N ratios (Phillips & Koch, 2002; Phillips et al., 2014). All source data were gathered from previous studies on the southeastern U.S. Atlantic coast, most of which were conducted on or adjacent to Sapelo Island, Georgia, USA. Summary statistics of  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and C:N data for candidate sources and additional detail regarding source data are reported in the supporting information (Table S1 in Supporting Information S1). Although isotopic discrimination occurs during mussel fecal production, source-specific, fecal discrimination factors (DFs) have not been quantified for marine bivalves, nor for invertebrates more broadly. Thus, we input DFs of 0‰ for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . To account for variation in food availability and assimilation across mussel aggregations and individuals, we defined error as “process  $\times$  residual” in our model frameworks (Stock & Semmens, 2016). Finally, priors were defined as “generalist,” which assumes that all source proportions are equal before model execution (Stock et al., 2018).

We calculated the proportion of autochthonous and allochthonous sources in benthic filter OM by summing the source proportions of aboveground cordgrass detritus and benthic microalgae of each MixSIAR model solution into the autochthonous group while pelagic phytoplankton source proportions represented the allochthonous group. Since this approach utilizes each individual solution, it preserves the covariation structure among source proportions (Phillips et al., 2005). To test our hypothesis that mussel presence increases sedimentation of autochthonous and allochthonous organic C and N ( $H_2$ ), we multiplied individual autochthonous and allochthonous source proportions by each extrapolated organic C and N value ( $\text{g m}^{-2}$ ), calculated the median and standard deviation for each sample, and measured the effect of area type on these medians using Bayesian generalized multivariate models. Standard deviations were used to account for measurement noise in the models. For all models evaluating extrapolated C and N metrics described here and below, formulas are summarized in Table S5 in Supporting Information S1.

## 2.3. Mussel Effects on Organic Matter Accumulation in Sediments

### 2.3.1. Mussel Manipulation at Old Teakettle Creek

In summer 2017, we performed a mussel manipulation whereby all mussels from one area ( $\sim 1,000 \text{ m}^2$ ) were excavated and transplanted to another, directly adjacent area of similar size. Excavated mussels remained in the

same clusters when transplanted into marsh areas at least 1 m away from any existing aggregations. A third, adjacent area of marsh was left undisturbed, representing natural mussel cover along an otherwise artificial, landscape-scale gradient of mussel aggregation density.

### 2.3.2. Mussel Survey and Sample Collection

In summer 2020—three years after the landscape-scale mussel manipulation—we randomly selected mussel aggregations and cordgrass only areas ( $n = 40$  per area type) across the gradient of mussel cover created by the manipulation (i.e., excavated, transplanted, and undisturbed). Selected areas were located between 0 and 20 m from the platforms' tidal creek heads and cordgrass only areas were located at least 1 m away from any mussel aggregation. We measured local mussel density in each aggregation by counting all surficial mussels within a  $0.5 \times 0.5$  m quadrat (individuals  $0.25 \text{ m}^{-2}$ ). We also measured neighboring mussel density by counting all mussels residing within a 3 m radius from the center of each cordgrass only area, which ranged from 0 to 600 individuals  $9\pi \text{ m}^{-2}$  (Figure 1b). We then composited three sediment samples from each aggregation and cordgrass only area ( $n = 40$  composites per area type) by pushing away the biodeposit layer (for mussel aggregations only), collecting a sediment core with a cut-off 60 mL syringe (2.5 cm diameter  $\times$  5 cm depth), recording each composite's total fresh volume, and then placing the samples on ice.

### 2.3.3. Bulk Geochemistry

We oven-dried the sediment samples at  $60^\circ\text{C}$  until they reached a constant weight and then ground them to a fine powder. We then randomly selected a subsample of sediment ( $n = 20$  per area type), measured their dry bulk density ( $\text{g cm}^{-3}$ ), and weighed subsets of each sample into one silver and one tin capsule—the former samples were fumigation acidified and analyzed for %TOC and  $\delta^{13}\text{C}$  while the latter samples were analyzed for %TN and  $\delta^{15}\text{N}$ . Measurements indicated that one sediment sample, collected from a cordgrass only area, had exceptionally high dry bulk density and we therefore removed this outlier from the data set prior to statistical analyses. We evaluated the conditional effects of area type and mussel density on dry bulk density, %TOC, and %TN with Bayesian generalized multivariate models. Model frameworks evaluating local and neighboring mussel density effects incorporated response data of sediments collected from mussel aggregations and cordgrass only areas, respectively. We then multiplied each sample's dry bulk density by their %TOC and %TN to calculate the concentration of organic C and N ( $\text{mg cm}^{-3}$ ) in surface sediments.

### 2.3.4. Organic Matter Source Tracking

To test our hypothesis that mussel presence shifts the assemblage of accumulated OM (top 5 cm) toward a more allochthonous makeup ( $H_3$ ), we estimated OM source contributions using a concentration weighted, MixSIAR model frameworks. These frameworks incorporated surface sediment  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  with area type defined as a random effect. We considered three end members as candidate sources: (a) belowground cordgrass detritus; (b) benthic microalgae; and (c) pelagic phytoplankton (Table S1 in Supporting Information S1). Similar to the sedimentation frameworks, we defined DFs, errors, and priors as 0‰, “residual  $\times$  process,” and “generalist,” respectively. We calculated the proportion of allochthonous and autochthonous sources in sediments by summing the source proportions of belowground cordgrass detritus and benthic microalgae of each MixSIAR model solution into the autochthonous group while pelagic phytoplankton source proportions represented the allochthonous group. To test our hypothesis that mussel presence increases the accumulation of autochthonous and allochthonous organic C and N in surface sediments ( $H_4$ ), we multiplied individual proportions of both sources by each concentration of organic C and N ( $\text{mg cm}^{-3}$ ), calculated the median and standard deviation for each sample, and measured the effect of area type on these medians using Bayesian generalized multivariate models. Standard deviations were used to account for measurement noise in the models.

MixSIAR can also account for continuous covariates (Francis et al., 2011); however, the package does not fit different slope terms to each random effect level (i.e., area type). Therefore, we modeled the effect of local and neighboring mussel density on sediment OM source contributions in mussel aggregations and cordgrass only areas, respectively, using separate frameworks (i.e., no random effect of area type). We then summed source proportions from each Markov Chain Monte Carlo (MCMC) draw into autochthonous and allochthonous groups, multiplied individual autochthonous and allochthonous source proportions by extrapolated organic C and N value ( $\text{mg cm}^{-3}$ ) for each sediment sample, and calculated the median and standard deviation for each sample. To test our hypothesis that the concentration of allochthonous and autochthonous organic C and N in surface sediments increases with increasing mussel density ( $H_6$ ), we measured the effect of local and neighboring mussel density on

medians of mussel aggregations and cordgrass only sediments, respectively, using Bayesian regression models. Standard deviations were used to account for measurement noise in the models.

## 2.4. Mussel Effects on Organic Matter Storage in Cordgrass

### 2.4.1. Sample Collection at Old Teakettle Creek

In the summer of 2020, we collected leaf clips from the same mussel aggregation and cordgrass only areas in the accumulation study (see “*Mussel effects on OM accumulation in sediments above*”) by clipping the newest, fully emerged leaf from three plants and compositing them ( $n = 40$  composites per area type). We then extracted sediment cores (10 cm diameter  $\times$  70 cm depth) and harvested all aboveground biomass (AGB) that fell within the circumference of the corer face ( $n = 40$  per area type). We immediately placed AGB and sediment cores on ice until we rinsed them with freshwater and separated live above- and belowground biomass (BGB) from dead plant material. We then oven-dried the live AGB and BGB at 60°C until they reached constant weight and measured their dry tissue weight.

### 2.4.2. Bulk Geochemistry

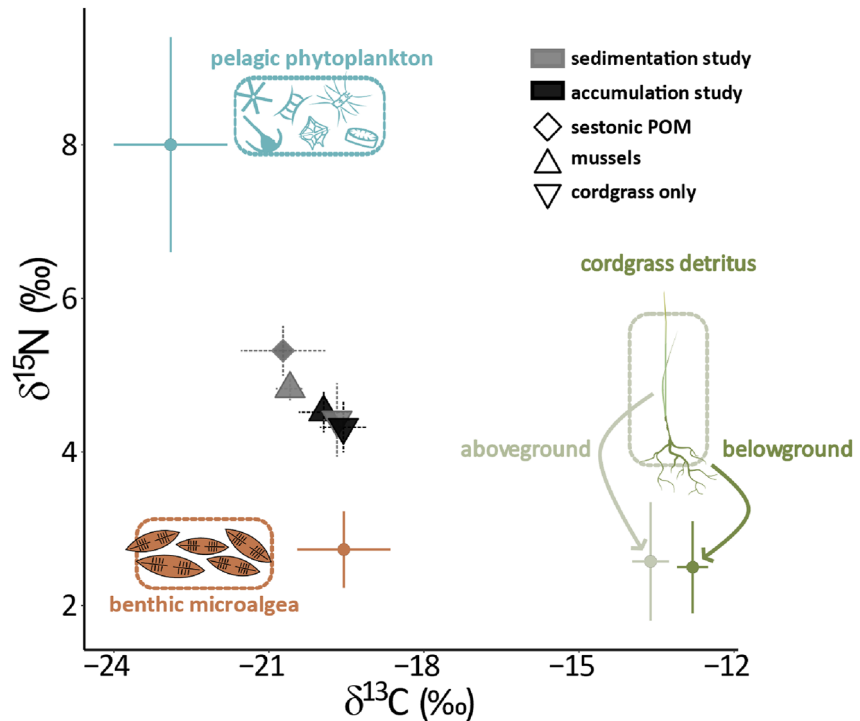
We rinsed the leaf clips with deionized water, dried them at 60°C until they reached constant weight, and ground them to a fine powder. We then randomly selected a subsample of leaf clips ( $n = 20$  per area type) and weighed subsets of each sample into one silver and one tin capsule—the former samples were fumigation acidified and analyzed for %TOC while the latter samples were analyzed for %TN. Cores were not assessed by elemental analyzer because of analytical costs. We evaluated the conditional effects of area type and mussel density on AGB, BGB, %TOC, and %TN with Bayesian multivariate models, with biomass and geochemical response variables built into separate frameworks. Model frameworks evaluating local and neighboring mussel density effects included core and leaf clip data collected from mussel aggregations and cordgrass only areas, respectively. For each area included in the leaf clip subsample, we multiplied the area's AGB dry weight by its leaf clip %TOC and %TN and then extrapolated these values to estimate aboveground storage of organic C and N per square meter of mussel aggregation and cordgrass only areal coverage ( $\text{g m}^{-2}$ ) across the marsh platform. To address our hypotheses that mussel presence enhances organic C and N storage ( $\text{g m}^{-2}$ ) in aboveground cordgrass ( $H_5$ ) and that C and N storage increases with increasing mussel density ( $H_7$ ), we measured the effect of area type, local mussel density, and neighboring density on these extrapolated values in separate Bayesian multivariate model frameworks like those described just above (i.e., AGB, BGB, %TOC, and %TN).

## 3. Results

### 3.1. Mussel Effects on Organic Matter Sedimentation

Here and below, conditional effects of area type on bulk geochemistry are presented as estimated median posterior of differences between mussel aggregations and cordgrass only area results from each MCMC draw (i.e., coefficients) with 90% credible intervals (CIs) and are summarized in Table S2 in Supporting Information S1. Meanwhile, estimated median values from all model outputs are presented with 95% CIs. Estimated median dry weights of material captured by benthic filter papers increased from 0.29 g (0.24, 0.37) in cordgrass only areas to 1.32 g (1.06, 1.74) on mussel aggregations (Figure S2a in Supporting Information S1), revealing an 130% enhancement in sedimentation of water column particulate by mussels on their localized aggregations (coefficient = 1.51 [1.24, 1.78]). While the median %TOC values of the material captured on the filter papers did not differ measurably (0.22 [−0.01, 0.45]) between mussel aggregation (3.61% [3.42, 3.83]) and cordgrass only areas (3.40% [3.19, 3.59]) (Figure S2b in Supporting Information S1), mussel presence substantially increased median %TN values in deposited material from 0.31% (0.27, 0.35) on cordgrass only areas to 0.39% (0.34, 0.43) on their aggregations by a difference of 0.08% [0.02, 0.13] (Figure S2c in Supporting Information S1).

Stable isotope analyses and isospace plot visualization demonstrated that pelagic and benthic filter signatures fell within the source polygon and in the same region along  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  environmental ranges (Figure 2; Table S3 in Supporting Information S1). Sestonic POM  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures ( $-20.73\text{‰} \pm 0.82\text{‰}$  and  $5.31\text{‰} \pm 0.33\text{‰}$ , respectively) were more similar to material deposited onto mussel aggregations ( $-20.59\text{‰} \pm 0.27\text{‰}$  and  $4.82\text{‰} \pm 0.15\text{‰}$ ) than onto cordgrass only areas ( $-19.68\text{‰} \pm 0.26\text{‰}$  and  $4.42\text{‰} \pm 0.48\text{‰}$ ), an observation corroborated by model summary statistics (global mean (%) [95% CI]) (Figures 3a–3c; Table S4 in Supporting

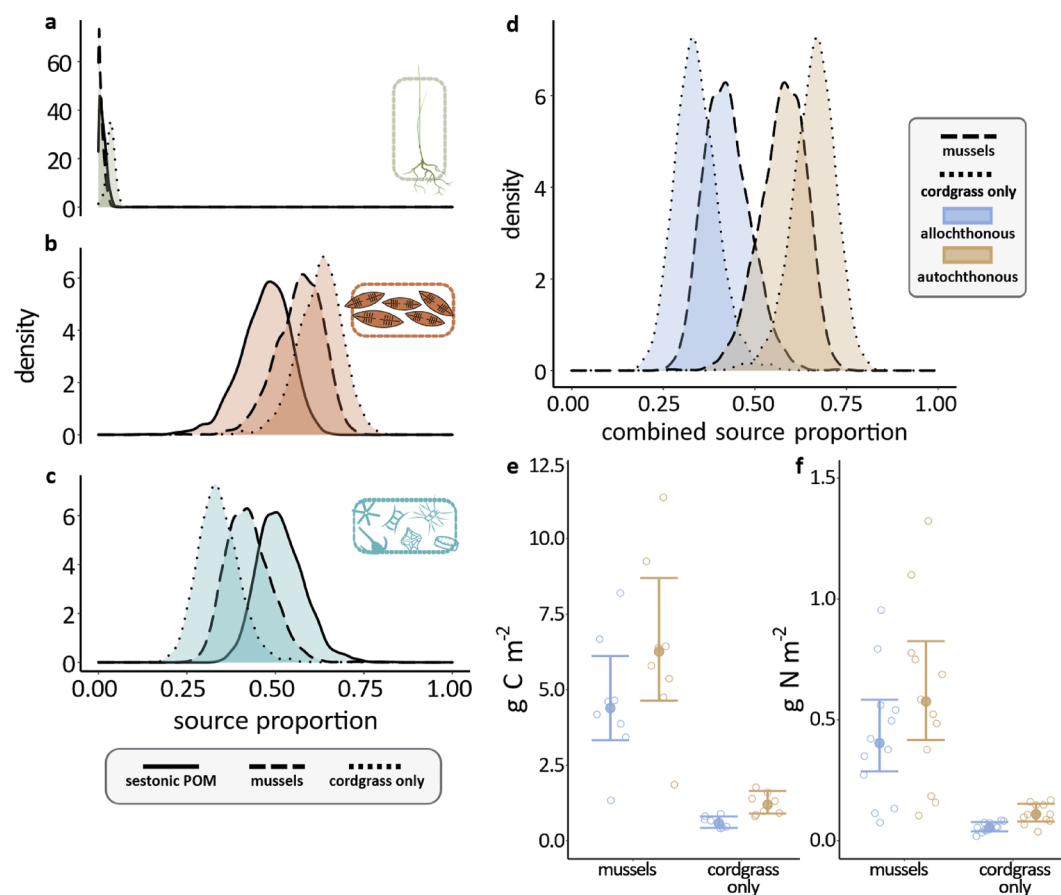


**Figure 2.** Stable isotope signatures for source and mixture data. Isospace plot shows  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures (mean  $\pm$  SE) of sestonic particulate organic matter and benthic filters collected during the Dean Creek sedimentation study (gray); sediments collected underneath mussel aggregations and cordgrass only areas during the Old Teakettle Creek accumulation study (black); and source data from previous literature.

Information S1). Pelagic phytoplankton dominated the OM in the overlying tidal water (52% [0.402, 0.662]) and served as the secondary source for samples from mussel aggregations (42% [0.315, 0.560]) and, of lesser proportion, samples from cordgrass only areas (34% [0.236, 0.467]). Benthic microalgae made up slightly less than half of the sestonic POM (47% [0.316, 0.591]), while it served as the primary contributor to OM deposited onto mussel aggregations (57% [0.424, 0.680]) and cordgrass only areas (63%, [0.492, 0.740]). Meanwhile, aboveground cordgrass detritus had a minor contribution across sample types, making up 1% in sestonic POM [0.001, 0.036] and samples from mussel aggregations [0, 0.028] and 4% [0.01, 0.059] in samples from cordgrass only areas. Other studies in Georgia salt marshes have measured similarly low contributions of cordgrass detritus to seston (Haines, 1977; Haines & Montague, 1979; Sherr, 1982). As mixing model results for sedimentation on mussel aggregations closely aligned with source contributions in seston, these findings suggest that mussel suspension feeding and biodeposition augment OM coupling at the sediment-water interface and thereby enhance the contribution of externally produced pelagic phytoplankton in deposited material ( $H_1$ ) (Figure 3d).

Mussels enhanced the input of both allochthonous and autochthonous organic C and N ( $\text{g m}^{-2}$ ) onto the salt marsh platform in areas relative to cordgrass only areas ( $H_2$ ). Here and below, conditional effects of area type on extrapolate C and N sedimentation, accumulation, and storage metrics are presented as estimated median posterior of differences between mussel aggregations and cordgrass only area results from each MCMC draw with 90% CIs and are summarized in Table S5 in Supporting Information S1. Estimated median values of externally derived OM fractions in sedimentation material jumped nearly 8-fold because of mussel suspension-feeding and biodeposition (organic C coefficient = 2.02 [1.65, 2.40]; organic N coefficient = 2.01[1.64, 2.41]), which increased from  $0.62 \text{ g C m}^{-2}$  (0.60, 0.64) to  $4.67 \text{ g C m}^{-2}$  (4.66, 4.69) (Figure 3e) and from  $0.05 \text{ g N m}^{-2}$  (0.04, 0.07) to  $0.40 \text{ g N m}^{-2}$  (0.29, 0.58) (Figure 3f). Greater amounts of autochthonous OM were transported to the marsh platform in both area types, with mussel presence driving a 5-fold increase in both C (coefficient = 1.65 [1.29, 2.02]) and N (coefficient = 1.65 [1.27, 2.03]) when compared to sedimentation on cordgrass only areas. Autochthonous organic C (Figure 3e) increased from  $1.20 \text{ g m}^{-2}$  (1.17, 1.22) to  $6.34 \text{ g m}^{-2}$  (6.32, 6.37) and autochthonous N (Figure 3f) increased from  $0.11 \text{ g m}^{-2}$  (0.08, 0.16) to  $0.58 \text{ g m}^{-2}$  (0.42, 0.82).



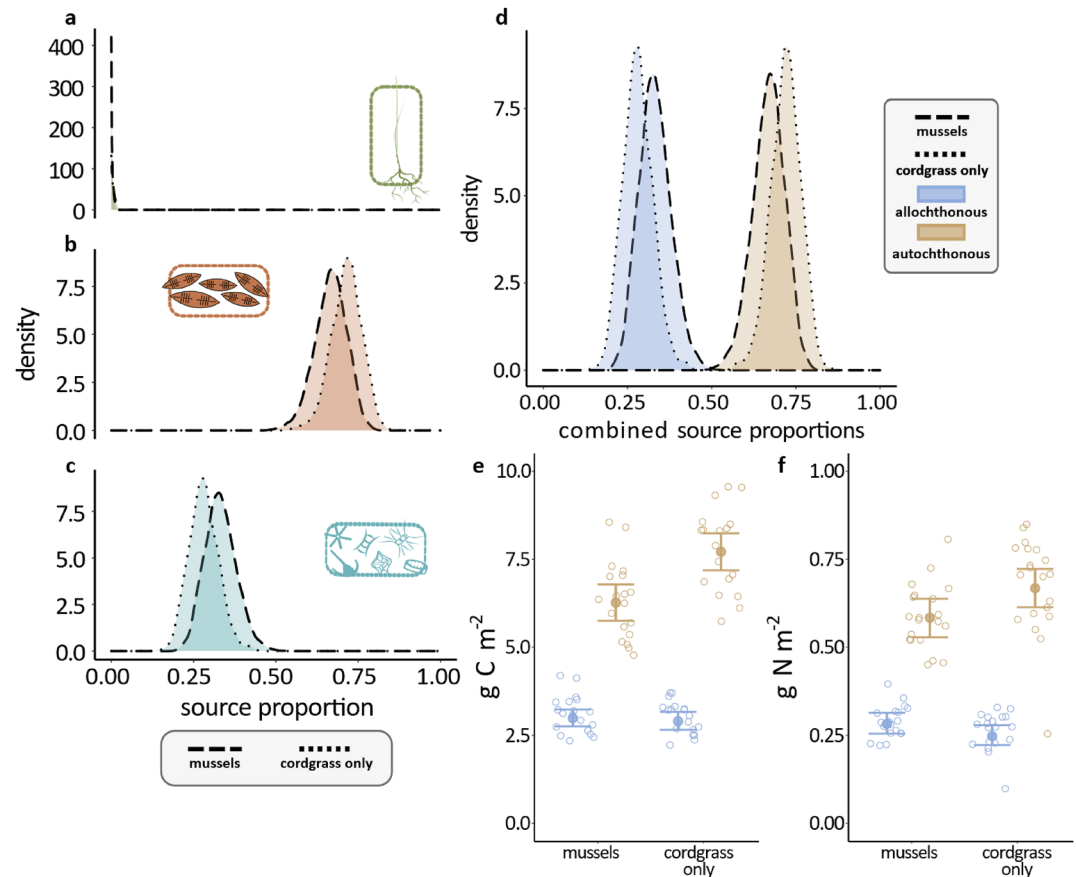


**Figure 3.** MixSIAR model results from sedimentation study. Original distributions of source proportions for (a) aboveground cordgrass detritus, (b) benthic microalgae, and (c) pelagic phytoplankton are presented for sestonic particulate organic matter (solid line) as well as mussel (dashed line) and cordgrass only (dotted line) sedimentation samples. Summations of original source proportions of organic matter captured by benthic filters are presented for allochthonous (light blue) and autochthonous (brown) groups (d). Conditional effects plots show estimated median values (filled points) of allochthonous and autochthonous (e) organic C and (f) N deposited per square meter of mussel aggregation and cordgrass only areal coverage ( $\text{g m}^{-2}$ ) with 95% credible intervals (error bars) and raw data (open points).

### 3.2. Mussel Effects on Organic Matter Accumulation in Sediment

Mussel presence did not influence sediment dry bulk density (coefficient =  $-0.02$  [ $-0.04, 0.008$ ]), %TOC ( $-0.23$  [ $-0.48, 0.02$ ]), or %TN ( $0.001$  [ $-0.01, 0.01$ ]) in accumulated sediment (Figures S3a–S3c in Supporting Information S1). Here and below, effects of mussel density on bulk geochemistry are presented as median estimates of slope coefficients from each MCMC draw with 90% CIs (Table S2 in Supporting Information S1) and Bayesian  $R^2$  values. Although we measured a marginally positive linear relationship between dry bulk density of sediments underneath mussel aggregations and local mussel density (Figure S3d in Supporting Information S1;  $0.0003$  [ $0.00008, 0.00045$ ] Bayesian  $R^2 = 0.28$ ), all other bulk sediment geochemistry metrics were found to be unrelated to local and neighboring density as 90% CIs of model estimates included zero (Figures S3d–S3f in Supporting Information S1).

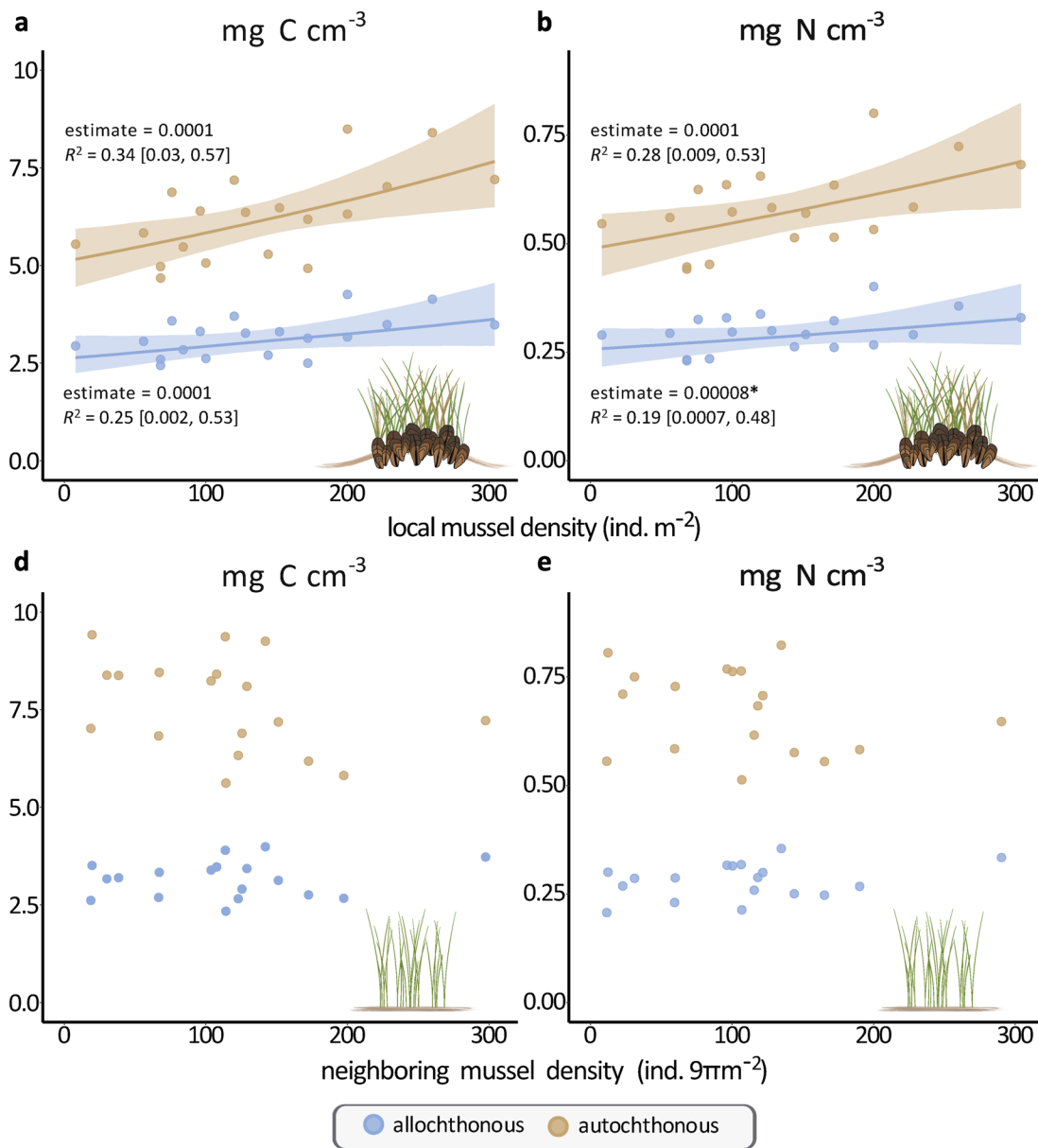
Stable isotope analyses and isospace plot visualization demonstrated that sediment  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures fell within the source polygon (Figure 2; Table S3 in Supporting Information S1). Mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures in sediment underneath mussel aggregations were  $-19.94\text{‰} \pm 0.48\text{‰}$  and  $4.52\text{‰} \pm 0.26\text{‰}$  while those in cordgrass only areas were  $-19.55\text{‰} \pm 0.45\text{‰}$  and  $4.32\text{‰} \pm 0.33\text{‰}$ , respectively. Summary statistics (global mean (%), [95% CI]) from MixSIAR accumulation models showed similar trends to those from sedimentation models (Figures 4a–4c; Table S4 in Supporting Information S1). Benthic microalgae were the major OM source between the two area types, making up 66.6% [ $0.563, 0.753$ ] in mussel sediments and 71.4% [ $0.616, 0.798$ ] in cordgrass



**Figure 4.** MixSIAR model outputs from accumulation study. Original distributions of source proportions for (a) belowground cordgrass detritus, (b) benthic microalgae, and (c) pelagic phytoplankton are presented for sediments collected from both area types. Summations of original source proportions are presented for allochthonous (light blue) and autochthonous (brown) groups (d). Conditional effects plots show estimated median values (filled points) of allochthonous and autochthonous (e) organic C and (f) N sediment concentrations ( $\text{mg cm}^{-3}$ ) with 95% credible intervals (error bars) and raw data (open points).

only sediments. Serving as the secondary contributor, pelagic phytoplankton made up 33.1% [0.247, 0.431] and 28.1% [0.199, 0.373] of sediment OM underneath mussel aggregations and in cordgrass only areas, respectively. Of negligible prevalence, belowground cordgrass detritus contributed no more than 1% to OM fractions in sediment samples from both area types (mussel: [0, 0.012], cordgrass only: [0, 0.018]). Thus, allochthonous sources increased in surface sediments where mussels were present ( $H_3$ ) (Figure 4d), suggesting that the effect of mussels on organic C and N sedimentation (i.e., higher contributions of externally derived OM) in salt marshes persists into accumulation processes.

Source-specific OM accumulation models revealed that mussel presence moderately elevated concentrations of externally derived N ( $0.13$  [0.003, 0.257]) but not of C ( $0.03$  [−0.07, 0.13]) in surface sediments. Indeed, while 95% CIs for estimated medians of allochthonous C largely overlapped between the two area types (Figure 4e), those of allochthonous N were more differentiated and increased from  $0.25 \text{ mg N cm}^{-3}$  (0.22, 0.28) in cordgrass only sediments to  $0.28 \text{ mg N cm}^{-3}$  (0.25, 0.31) in sediments underneath mussels (Figure 4f). Conversely, estimated medians of both autochthonous organic C and N sediment concentrations were substantially higher in cordgrass only areas ( $8.06 \text{ mg C cm}^{-3}$  [7.37, 8.84] and  $0.67 \text{ mg N cm}^{-3}$  [0.61, 0.72]) relative to those underneath mussels ( $6.31 \text{ mg C cm}^{-3}$  [5.77, 6.94] and  $0.58 \text{ mg N cm}^{-3}$  [0.53, 0.64]). Thus, we measured negative conditional effects of mussel presence on autochthonous OM accumulation (C coefficient =  $-1.44$  [−2.05, −0.80] and N coefficient =  $-0.08$  [−0.15, −0.02]). By solely indicating a positive effect of mussels on allochthonous N accumulation, our results do not fully support our fourth hypothesis that mussels increase the surface sediment concentrations of both sources of organic C and N ( $H_4$ ).



**Figure 5.** Continuous effects of mussel density on source-specific organic C and N accumulation. Generalized regression models of allochthonous and autochthonous organic C and N sediment concentrations (mg cm<sup>-3</sup>) (a, b) underneath mussel aggregations and in (d, e) cordgrass only areas against local and neighboring mussel density, respectively, are presented. Trend lines, median estimates, and Bayesian R<sup>2</sup> values (95% credible interval [CI]) are shown for meaningful predictors. Shaded areas represent 95% CIs. The asterisked estimate indicates 7.5% of slope estimates from Markov Chain Monte Carlo draws fell below zero.

Positive relationships were also found between local mussel density and allochthonous and autochthonous accumulation pools (Figures 5a and 5b). Here and below, effects of mussel density on extrapolated C and N values are presented as median estimates of slope coefficients from each MCMC draw with 90% CIs (Table S5 in Supporting Information S1) and Bayesian R<sup>2</sup> values. As mussel density increased within their aggregations, concentrations of marsh-derived C and N and marine-derived C increased as log functions with similar slope estimates (coefficient = 0.001; autochthonous C = [0.0005, 0.0006] Bayesian R<sup>2</sup> = 0.34; autochthonous N = [0.0004, 0.0004] Bayesian R<sup>2</sup> = 0.29; allochthonous C = [0.0001, 0.002] Bayesian R<sup>2</sup> = 0.25). Meanwhile, local mussel density as a weaker predictor of allochthonous organic N sediment concentrations relative to the other pools (0.0008 [-0.0001, 0.0018] Bayesian R<sup>2</sup> = 0.19), but with only 7.5% of slope estimates from MCMC draws (*n* = 4,000) falling below zero. In contrast, cordgrass only sediment concentrations were unrelated to neighboring mussel

density (Figures 5c and 5d), suggesting that mussels do not influence the source or concentration of organic C and N accumulating in surrounding marsh areas void of mussels.

### 3.3. Mussel Effects on Organic Matter Storage in Cordgrass

Both aboveground vegetation (ABG) as well as roots and rhizome (BGB) were elevated by approximately 100% among mussel aggregations (ABG = 1.18 [0.95, 1.42] and BGB = 1.02 [0.83, 1.21]), with estimated median values of above- and BGB jumping from 3.46 g (2.86, 4.26) and 2.34 g (2.01, 2.75), respectively, in cordgrass only areas to 11.25 g (9.25, 13.76) and 6.51 g (5.55, 7.72) in mussel aggregations (Figures S4a and S4b in Supporting Information S1). Both biomass fractions increased with increasing local mussel density as log functions along similar slope estimates in mussel aggregations (0.003 [0.001, 0.005]; AGB Bayesian  $R^2 = 0.15$  and BGB Bayesian  $R^2 = 0.21$ ). Conversely, above- and BGB in cordgrass only areas were unrelated to neighboring mussel density (Figures S4c and S4d in Supporting Information S1).

Estimated median values of leaf clip geochemistry indicated that %TOC increased from 39.70 (39.15, 40.20) in cordgrass only areas to 40.70 (40.17, 41.24) in mussel aggregations (Figure S5a in Supporting Information S1; coefficient = 1.00 [0.39, 1.63]). Meanwhile, cordgrass growing with mussel aggregations had lower %TN with estimated medians decreasing from 1.14 (1.07, 1.22) in cordgrass only areas to 0.98 (0.90, 1.06) in mussel aggregations (Figure S5b in Supporting Information S1,  $-0.16 [-0.25, -0.07]$ ). While statistically meaningful, these cordgrass tissue compositional differences are not likely to be ecologically relevant given previous observations of substantial C/N variability (e.g., >200% difference) between north- and southeastern U.S. salt marshes (e.g., Valiela & Teal, 1974) and between nutrient-addition treatments and controls of natural cordgrass stands (e.g., Gallagher, 1975). Plus, %TOC and %TN were found to be unrelated to both local and neighboring mussel density (Figures S5c and S5d in Supporting Information S1).

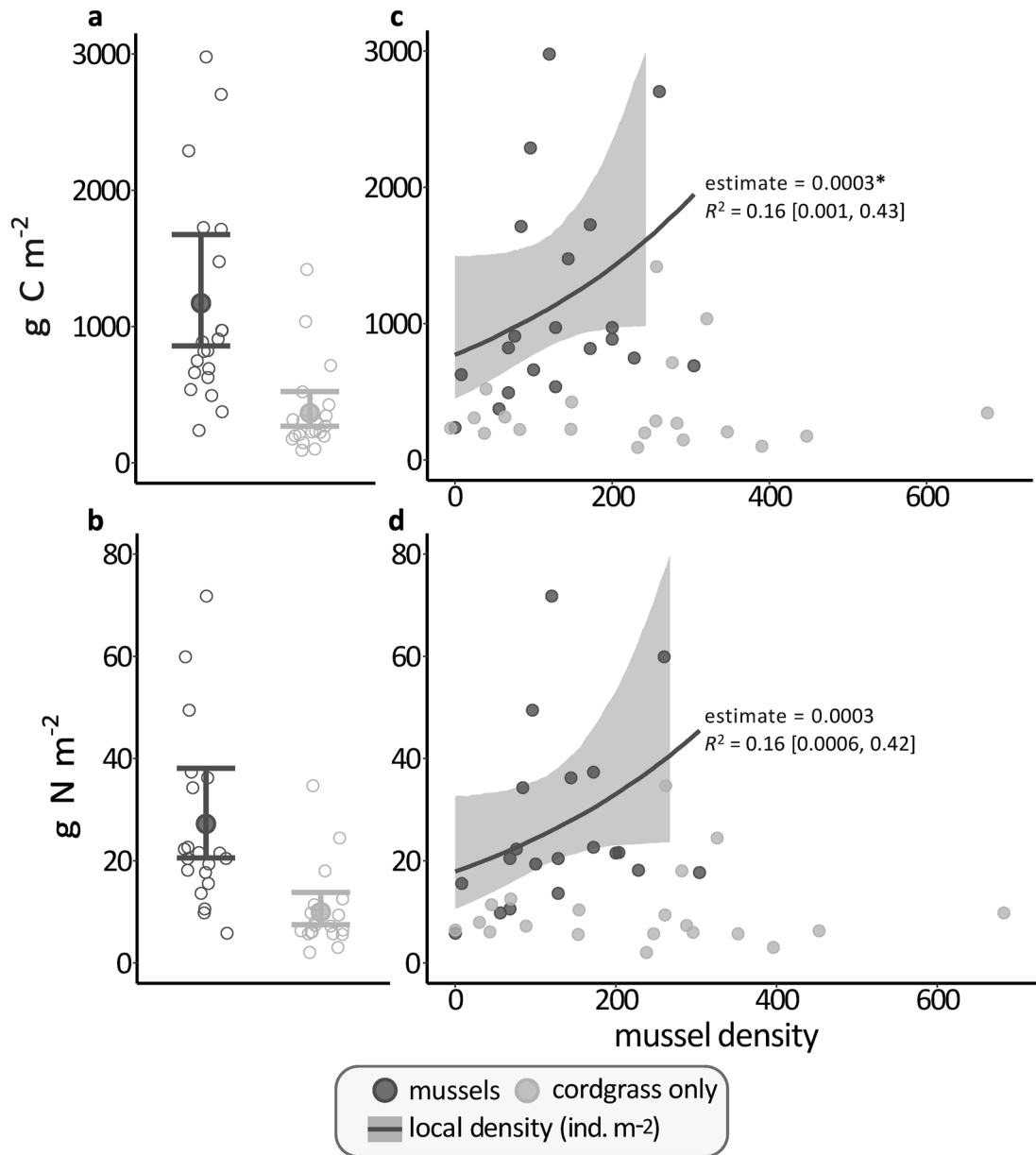
Finally, model results for extrapolated aboveground standing stocks showed that storage of C and N was amplified in mussel aggregations (C coefficient = 1.17 [0.80, 1.53] and N coefficient = 1.00 [0.67, 1.34]) as estimated median values of biomass tripled in vegetation growing with mussel (1,170 g C m<sup>-2</sup> [856.97, 1674.47] and 27.21 g N m<sup>-2</sup> [20.53, 38.07]) relative to vegetation growing in areas void of them (371.37 g C m<sup>-2</sup> [267.72, 523.12] and 9.96 g N m<sup>-2</sup> [7.48, 13.83]) (Figures 6a and 6b). Continuous effects models also revealed an increase in aboveground C and N biomass with increasing local mussel density as a log function, estimating similar slope coefficients and model fits for both C and N (0.003, Bayesian  $R^2 = 0.16$ ) (Figures 6c and 6d). Model uncertainty intervals, however, were marginally negative (C =  $[-0.0001, 0.0061]$ ) or close to zero (N =  $[0.0001, 0.0061]$ )—with 5.6% of slope estimates from MCMC draws of C models ( $n = 4,000$ ) falling below zero—suggesting that the relationships between aboveground C and N storage and local mussel density may not be robust. Meanwhile, these storage metrics in cordgrass only areas were unrelated to neighboring density.

## 4. Discussion

Mussels directly alter sedimentation processes of C-fixing and N-rich algae through a combination of active (i.e., suspension feeding and biodeposition) and passive (i.e., baffling) mechanisms and, in turn, indirectly modulate C and N accumulation and storage in salt marshes. With the objective to better resolve suspension feeders' role in bolstering the capacity of VCEs to regulate externally derived C and N, the study presented here is—to the best of our knowledge—the first OM source tracking analyses conducted on suspension feeder biodeposits and associated sediments. As far as we know, this investigation is also the first of its kind to measure the effect of mussel density on sediment and macrophyte processes (e.g., geochemistry, growth) in adjacent, non-mussel marsh areas—an approach that pushes our understanding regarding the spatial extent of mussel influence beyond their localized aggregations and onto the surrounding salt marsh platforms that support them.

### 4.1. Mussel Effects on Organic Matter Sedimentation

In shallow estuaries worldwide, consistent linkages of sestonic and benthic composition have been well defined, irrespective of estuary-specific features (e.g., nutrient loading) (Carmichael & Valiela, 2005). Across the studies included in Carmichael and Valiela (2005) analyses,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were positively correlated between seston and sediment (top 3 cm) with  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures significantly lower (−) ( $-1.6\text{‰} \pm 0.4\text{‰}$ ) and higher (+) ( $+1.3\text{‰} \pm 0.3\text{‰}$ ) in seston than in sediment, respectively. Our stable isotope analyses of material passively



**Figure 6.** Cordgrass coring and geochemical results. Conditional effects plots show estimated median values (filled points) of (a) organic C and (b) N stored in aboveground cordgrass per square meter of mussel aggregation (dark gray) and cordgrass only (light gray) areal coverage ( $\text{g m}^{-2}$ ) with 95% credible intervals (CIs) (error bars) and raw data (open points). Generalized regression models of these (c) extrapolated C and (d) N values from mussel aggregations and cordgrass only areas against local (dark gray) and neighboring (light gray) density, respectively, are presented. Trend lines, median estimates, and Bayesian  $R^2$  values (95% credible interval [CI]) are shown for meaningful predictors. Shaded areas represent 95% CIs. The asterisked estimate indicates 5.6% of slope estimates from Markov Chain Monte Carlo draws fell below zero.

deposited to cordgrass only areas (i.e., captured by benthic filter papers) at Dean Creek support this paradigm, where mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  differed  $-1.1\text{‰}$  and  $+0.9\text{‰}$  from sestonic POM, respectively. Conversely, this gap in seston and sediment composition diminished on mussel aggregations, where mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of deposited OM differed a mere  $-0.1\text{‰}$  and  $+0.5\text{‰}$  from sestonic POM, respectively. Further, estimations of OM source distributions from our MixSIAR models showed that, across all three candidate sources, sestonic OM were more similar to material deposited on mussel aggregations than in cordgrass only areas. In short, our results quantify amplified benthic-pelagic coupling of OM composition by mussels as they modulate local sedimentation processes ( $H_1$ ).

This augmented, mussel-driven coupling translated to an increase in the proportion of externally sourced OM (i.e., pelagic phytoplankton) in material transported to the marsh bottom ( $H_1$ ). Previous stable isotope studies

suggest that phytoplankton provide a large proportion of the nutritional requirements for mussels living in south-eastern U.S. salt marshes (Haines & Montague, 1979; Langdon & Newell, 1989; Peterson & Howarth, 1987; Wright et al., 1982). Although larger sized particles (i.e., benthic diatoms and detrital cellulose) are retained on bivalve gills with higher efficiency (Kreeger & Newell, 2001; Riisgård, 1988), mussels selectively capture smaller, perhaps more nutritious, phytoplankton (Kemp et al., 1990). For example, Kemp et al. (1990) estimated that phytoplankton made up 72% of the C removed by mussels in a salt marsh adjacent to Sapelo Island during a summer season. Thus, selective grazing and subsequent biodeposition of externally produced phytoplankton is likely an important driver behind the allochthonous shift in OM assemblage between the two area types. Added physical structure (e.g., higher rugosity) by aggregated mussels may also influence sedimentation processes, as several investigations have emphasized the importance of interactions between bivalve biogenic structures and material deposition to the benthic floor (Butman et al., 1994; Lim et al., 2020; Nikora et al., 2002; Widdows et al., 1998). However, physical sedimentation processes of organic particles in salt marshes driven by faunal structure are not well resolved and our study does not disentangle these effects.

Arguably the most significant finding from our study at Dean Creek was the mussel-amplified sedimentation of organic C and N, particularly that of material produced outside of the salt marsh habitat ( $H_2$ ). Several investigators have observed substantial increases in OM input by suspension feeders (Kamimura & Tsuchiya, 2006; Norkko et al., 2001; Welsh, 2003). For instance, Christensen et al. (2000) measured a 30-fold increase in phytoplankton deposition when the suspension-feeding polychete, *Nereis diversicolor*, was present in non-vegetated, sandy sediments relative to defaunated sediment. Our calculations revealed that, by facilitating over a 7-fold increase in both allochthonous C and N sedimentation, mussels acted as conduits for planktonic biomass to enter the benthic zone that may have otherwise remained sestonic and returned to the marine environment with the ebb tide. We measured a similar boost in recycled, marsh-derived organic biomass on mussel aggregations, largely due to the primary contribution (57%) of resuspended benthic microalgae in mussel biodeposits. Past studies have demonstrated that resuspension of microphytobenthos, facilitated by high current velocities during spring tides or periods of high winds, can contribute to substantial amounts of water column chlorophyll *a* and serve as an important food source for suspension feeders (Currin et al., 1995; Sullivan & Moncreiff, 1990; Zurburg et al., 1994). Thus, mussels are not only driving the import of externally derived algae to the marsh bottom but are also hotspots for the reclamation of internally produced algae, both of which play a critical role in carbon fixation and nutrient uptake in coastal system (Cahoon, 2002; Cloern et al., 2014). By disproportionately supplementing salt marshes with C- and N-rich material via biodeposition, mussels likely magnify subsequent blue carbon and nutrient burial in these ecosystems given that these services in wetlands have been extensively attributed in part to sediment deposition (e.g., Craft et al., 2018; Hupp et al., 2019; Loomis & Craft, 2010; McCarty et al., 2009; Van de Broek et al., 2018).

In addition to potentially enhancing sequestration services in salt marshes, this mode of top-down control may be particularly important during periods of high sediment resuspension when material is more susceptible to exportation and can then contribute to nutrient loading in surrounding estuaries (Corbett, 2010). Conversely, biogeochemical feedbacks directly and indirectly facilitated by mussels may counterbalance their removal of algal seston. Through respiration, excretion, and biodeposit mineralization, mussels can increase concentrations of bioavailable N in the water column and sediments and, in turn, stimulate algal growth (Bilkovic et al., 2017; Murphy et al., 2019). The scope of study presented here does not encompass these fluxes; however, resolving the context-dependent role of mussels, and other suspension feeders, in exerting bottom-up control on algal primary production is an important avenue of research that has largely focused on intensive aquaculture scenarios (Bartoli et al., 2012; Baudinet et al., 1990; Christensen et al., 2000; Murphy et al., 2015) as opposed to natural or restored populations.

#### 4.2. Mussel Effects on Organic Matter Accumulation in Sediments

Across salt marsh, seagrass, and mangrove systems, studies have shown that accumulated C and N in sediments are lower in  $\delta^{13}C$  and higher in  $\delta^{15}N$  than signatures of the system's dominant macrophyte (Boschker et al., 1999; Gacia et al., 2002; J. Middelburg et al., 1996)—a phenomenon attributed to various processes, including trapping of allochthonous OM and input by benthic microalgae. Our accumulation study at Old Teakettle Creek produced stable isotope results consistent with this broadly documented pattern where signatures of sediments collected from both area types more closely reflected those of algal endmembers than of *S. alterniflora*. Interestingly,

isotopic differences between sediment OM and *S. alterniflora* were larger underneath mussel mounds, which translated to a higher allochthonous contribution in mussel-associated, accumulated OM ( $H_3$ ). Initially suggested by Ember et al. (1987) and since supported by others (Butzeck et al., 2015; Friedrichs & Perry, 2001; Hansen et al., 2017; J. J. Middelburg et al., 1997), allochthonous input to soil OM is more significant in salt marsh areas experiencing high rates of sedimentation. Mean sediment accumulation rates measured by (Letzsch & Frey, 1980) on Sapelo Island were highest in the low marsh zone ( $0.9 \text{ cm yr}^{-1}$ ), which experiences the longest inundation period and supports higher density mussel populations, relative to transitional ( $0.45 \text{ cm yr}^{-1}$ ) and high marsh ( $0.1 \text{ cm yr}^{-1}$ ) zones. Amplified sedimentation via mussel suspension feeding and biodeposition, as seen in our Dean Creek study alongside others (Crotty et al., 2023), is likely an important mechanism underpinning the allochthonous shift we measured in accumulated OM, suggesting that the mussel effects we observed at the sediment-water interface (i.e., increased benthic-pelagic coupling and sedimentation) persist into the sediment layer.

Despite this shift in source contribution, our calculations indicated that only allochthonous organic N concentrations were higher in sediments underneath mussel mounds ( $H_4$ ), while autochthonous sediment organic C and N concentrations were higher in cordgrass only areas. Although dry bulk density was statistically equivalent between the two area types, median values were numerically higher in cordgrass only areas and, in turn, drove this difference in calculated autochthonous OM concentrations. Lower dry bulk density values associated with mussel presence was likely an artifact of higher root and rhizome biomass in sediments underneath their aggregations, however, as belowground cordgrass was removed from sediment samples upon collection. Other bivalve systems have been deemed C sinks, including salt marsh-fringing oyster reefs (Fodrie et al., 2017) and restored, green-lipped mussel beds (Sea et al., 2022). These studies analyzed deeper vertical profiles (10–55 cm) underneath shellfish aggregations—depths that would extend beyond the *S. alterniflora* root zone in salt marshes. Thus, this approach may be applied in future work to better resolve the role of mussels in C and N sequestration in salt marsh sediments.

When accounting for the effects of mussel density on accumulation processes, we measured a positive correlation between local density and both allochthonous and autochthonous organic C and N sediment concentrations underneath mussel aggregations ( $H_6$ ). Fodrie et al. (2017) observed that organic C burial was positively correlated with within-reef live oyster (*Crassostrea virginica*) density, attributing this relationship to increasing suspension feeding and baffling by reef structure (i.e., sedimentation) as well as shell production. Thus, we expect that density-dependent sedimentation, which is also positively correlated within mussel aggregations (Crotty et al., 2023), is likely driving the continuous increase in accumulated C and N. Although previous modeling efforts suggest that mussel populations drive sediment deposition and vertical accretion at both creekshed ( $\sim 2,500 \text{ m}^2$ ) and landscape ( $\sim 10,000 \text{ m}^2$ ) scales as their biodeposits are dispersed across the salt marsh platform (Crotty et al., 2023), our study revealed that density-dependent effects on C and N accumulation was not upheld in adjacent, non-mussel areas. One mechanistic explanation for this may be that organic fractions of biodeposits are more readily remineralized locally while mineralogical fractions more effectively redistribute across salt marsh platforms. As far as we know, our results are the first of their kind to address the effect of mussel biodeposits on salt marsh sediment geochemistry beyond their natural aggregations; thus, there remains a paucity of research on the spatial extent of biodeposit dispersal and its landscape-scale effects on salt marsh biogeochemistry (although see this considered for other bivalves species in aquaculture settings in Giles et al. (2009), Labrie et al. (2022), and Pusceddu et al. (2007)).

### 4.3. Mussel Effects on Organic Matter Storage in Cordgrass

Lastly, our findings highlight a strong, positive effect of both mussel presence and density on local organic C and N storage ( $\text{g m}^{-2}$ ) in aboveground cordgrass ( $H_5$  and  $H_7$ )—results largely driven by boosted macrophyte production. Once remineralized, mussel biodeposits act as fertilizer for marsh plants and, in turn, supplement inorganic nutrients available for cordgrass uptake and growth—a mechanism of facilitation that has been previously correlated with mussel presence (Angelini et al., 2015) local mussel density (Bertness, 1984). Indeed, while average standing stocks in our cordgrass only areas aligned with findings from previous surveys of *S. alterniflora*-dominated salt marshes (e.g., Gallagher et al., 1980; Liao et al., 2007), mean N storage in cordgrass growing among mussels ( $26.41 \text{ g N m}^{-2}$ ) was of similar magnitude to that in cordgrass plots ( $18.7 \text{ g N m}^{-2}$ ) treated with high concentrations ( $744 \text{ kg}^{-1} \text{ ha}^{-1} \text{ month}^{-1}$ ) of N fertilizer (Darby & Turner, 2008). Although we

did not conduct elemental analyses on the live roots and rhizomes collected in tandem with stems, we postulate that similar patterns of C and N storage in macrophyte tissue occur underneath the salt marsh surface given that belowground cordgrass biomass too was enhanced in mussel aggregations relative to areas void of mussels and increased with increasing local mussel density (see Derksen-Hooijberg et al. (2018)). Conversely, mussel density around cordgrass only areas did not affect aboveground OM storage ( $H_7$ ), suggesting that biodeposit dispersal does not supplement surrounding, non-mussel areas with enough bioavailable nutrients to elicit a quantifiable response in aboveground macrophyte production/storage. Density-dependent effects of suspension feeding bivalves on associated macrophytes have been found in other VCEs. For example, Booth and Heck (Booth & Heck, 2009) found that seagrass (*Halodule wrightii*) growth rates were highest at intermediate oyster (*Crassostrea virginica*) densities, while sulfide accumulation at maximum oyster densities caused a decrease in shoot density and shoot growth rate; this study and others emphasize the importance of resolving density-dependent interactions in varying environmental contexts (e.g., oligotrophic vs. eutrophic) when considering suspension feeders as a synergistic tool to enhance C and N storage, among other benefits, in coastal macrophytes (Castorani et al., 2015; Zhu et al., 2019).

## 5. Conclusions

Collectively, this work provides compelling evidence that suspension-feeding faunal engineers can interact synergistically with primary producers to elevate the capacity of coastal ecosystems to regulate C and N. Importantly, we emphasize that local, mussel-enhanced sedimentation, accumulation, and aboveground storage processes measured here not only suggest that mussel aggregations are localized hotspots for blue carbon and nitrogen mitigation during the summer but also scale up to variable landscape-wide augmentation depending on mussel coverage (Angelini et al., 2015). More broadly, we set a foundation for future work to explore the nuances of these interactions in differing environmental contexts, scales, and seasons while prompting the need to investigate the effect of suspension feeders on these processes in other VCEs. As the necessity to counteract the impacts of climate change and cultural eutrophication urgently grows, our findings can better inform coastal management decisions related to leveraging mussel populations—either by prioritizing conservation of areas that support high mussel coverage or incorporating mussels into restoration efforts—to enhance the mitigating services of salt marsh ecosystems.

## Data Availability Statement

All figures were created using the R packages ggplot (v. 3.4.2, Wickham, 2016) and ggthemes (v. 4.2.4, Arnold, 2021) and Affinity Designer (<https://affinity.serif.com/en-us/designer/>) while Tables S1–S5 in Supporting Information S1 were created using the R package flextable (v. 0.9.2, Gohel & Skintzos, 2023). Data and corresponding metadata from this paper as well as a comprehensive R Markdown file containing the code for this study can be found at the following Zenodo repository: <https://doi.org/10.5281/zenodo.7842849>.

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## References

- Angelini, C., Van Heide, T. D., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P. M., et al. (2015). Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. *Proceedings of the Royal Society B: Biological Sciences*, 282(1811), 1–9. <https://doi.org/10.1098/rspb.2015.0421>
- Arnold, J. (2021). `ggthemes`: Extra themes, scales and geoms for 'ggplot2'. R package version 4.2.4. Retrieved from <https://CRAN.R-project.org/package=ggthemes>
- Bannon, R. O., & Roman, C. T. (2008). Using stable isotopes to monitor anthropogenic nitrogen inputs to estuaries. *Ecological Applications*, 18(1), 22–30. <https://doi.org/10.1890/06-2006.1>
- Bartoli, M., Naldi, M., Nizzoli, D., Roubaix, V., & Viaroli, P. (2012). Influence of clam farming on macroalgal growth: A microcosm experiment. *Chemistry and Ecology*, 19(2–3), 147–160. <https://doi.org/10.1080/0275754031000119906>
- Baudinet, D., Alliot, E., Berland, B., Grenz, C., Plante-Cuny, M.-R., Plante, R., & Salen-Picard, C. (1990). Incidence of mussel culture on biogeochemical fluxes at the sediment-water interface. *Hydrobiologia*, 207(1), 187–196. <https://doi.org/10.1007/BF00041456>
- Berg, A., & Newell, I. E. (1986). Temporal and spatial variations in the composition of seston available to the suspension feeder *Crassostrea virginica*. *Estuarine, Coastal and Shelf Science*, 23(3), 375–386. [https://doi.org/10.1016/0272-7714\(86\)90034-x](https://doi.org/10.1016/0272-7714(86)90034-x)
- Bertness, M. D. (1984). Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology*, 65(6), 1794–1807. <https://doi.org/10.2307/1937776>
- Bilkovic, D. M., Mitchell, M. M., Isdell, R. E., Schliep, M., & Smyth, A. R. (2017). Mutualism between ribbed mussels and cordgrass enhances salt marsh nitrogen removal. *Ecosphere*, 8(4), e01795. <https://doi.org/10.1002/ecs2.1795>
- Booth, D., & Heck, K. (2009). Effects of the American oyster *Crassostrea virginica* on growth rates of the seagrass *Halodule wrightii*. *Marine Ecology Progress Series*, 389, 117–126. <https://doi.org/10.3354/meps08163>



- Boschker, H. T. S., de Brouwer, J. F. C., & Cappenberg, T. E. (1999). The contribution of macrophyte-derived organic matter to microbial biomass in salt-marsh sediments: Stable carbon isotope analysis of microbial biomarkers. *Limnology & Oceanography*, *44*(2), 309–319. <https://doi.org/10.4319/lo.1999.44.2.0309>
- Bouillon, S., Connolly, R. M., & Lee, S. Y. (2008). Organic matter exchange and cycling in mangrove ecosystems: Recent insights from stable isotope studies. *Journal of Sea Research*, *59*(1), 44–58. <https://doi.org/10.1016/j.seares.2007.05.001>
- Bouma, T. J., van Duren, L. A., Temmerman, S., Claverie, T., Blanco-Garcia, A., Ysebaert, T., & Herman, P. M. J. (2007). Spatial flow and sedimentation patterns within patches of epibenthic structures: Combining field, flume and modelling experiments. *Continental Shelf Research*, *27*(8), 1020–1045. <https://doi.org/10.1016/j.csr.2005.12.019>
- Bricker, S. B., Longstaff, B., Dennison, W., Jones, A., Boicourt, K., Wicks, C., & Woerner, J. (2008). Effects of nutrient enrichment in the nation's estuaries: A decade of change. *Harmful Algae*, *8*(1), 21–32. <https://doi.org/10.1016/j.hal.2008.08.028>
- Bürkner, P. (2017). brms: An R package for Bayesian multilevel models using stan. *Journal of Statistical Software*, *80*(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Bürkner, P. (2018). Advanced Bayesian multilevel modeling with the R package brms. *The R Journal*, *10*(1), 395–411. <https://doi.org/10.32614/RJ-2018-017>
- Bürkner, P. (2021). Bayesian item response modeling in R with brms and stan. *Journal of Statistical Software*, *100*(5), 1–54. <https://doi.org/10.18637/jss.v100.i05>
- Bürkner, P., Gabry, J., Kay, M., & Vehtari, A. (2023). posterior: Tools for working with posterior distributions. R package version 1.4.1. Retrieved from <https://mc-stan.org/posterior/>
- Butman, C. A., Fréchette, M., Geyer, W. R., & Starczak, V. R. (1994). Flume experiments on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer flow. *Limnology & Oceanography*, *39*(7), 1755–1768. <https://doi.org/10.4319/lo.1994.39.7.1755>
- Butzck, C., Eschenbach, A., Gröngroft, A., Hansen, K., Nolte, S., & Jensen, K. (2015). Sediment deposition and accretion rates in tidal marshes are highly variable along estuarine salinity and flooding gradients. *Estuaries and Coasts*, *38*(2), 434–450. <https://doi.org/10.1007/s12237-014-9848-8>
- Cadee, G. (1982). Tidal and seasonal variation in particulate and dissolved organic carbon in the western Dutch Wadden Sea and Marsdiep tidal inlet. *Netherlands Journal of Sea Research*, *15*(2), 228–249. [https://doi.org/10.1016/0077-7579\(82\)90006-0](https://doi.org/10.1016/0077-7579(82)90006-0)
- Cahoon, L. B. (2002). The role of benthic microalgae in neritic ecosystems. In *Oceanography and marine biology, an annual review* (Vol. 37, pp. 55–94). CRC Press.
- Carmichael, R. H., & Valiela, I. (2005). Coupling of near-bottom seston and surface sediment composition: Changes with nutrient enrichment and implications for estuarine food supply and biogeochemical processing. *Limnology & Oceanography*, *50*(1), 97–105. <https://doi.org/10.4319/lo.2005.50.1.0097>
- Castorani, M. C. N., Glud, R. N., Hasler-Sheetal, H., & Holmer, M. (2015). Light indirectly mediates bivalve habitat modification and impacts on seagrass. *Journal of Experimental Marine Biology and Ecology*, *472*, 41–53. <https://doi.org/10.1016/j.jembe.2015.07.001>
- Christensen, B., Vedel, A., & Kristensen, E. (2000). Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes. *Marine Ecology Progress Series*, *192*, 203–217. <https://doi.org/10.3354/meps192203>
- Cloern, J. E., Foster, S. Q., & Kleckner, A. E. (2014). Phytoplankton primary production in the world's estuarine-coastal ecosystems. *Biogeosciences*, *11*(9), 2477–2501. <https://doi.org/10.5194/bg-11-2477-2014>
- Corbett, D. R. (2010). Resuspension and estuarine nutrient cycling: Insights from the Neuse river estuary. *Biogeosciences*, *7*(10), 3289–3300. <https://doi.org/10.5194/bg-7-3289-2010>
- Court, C., Ferreira, J., Ropicki, A., Qiao, X., & Saha, B. (2021). Quantifying the socio-economic impacts of harmful algal blooms in Southwest Florida in 2018.
- Craft, C., Vymazal, J., & Kröpfelová, L. (2018). Carbon sequestration and nutrient accumulation in floodplain and depressional wetlands. *Ecological Engineering*, *114*, 137–145. <https://doi.org/10.1016/j.ecoleng.2017.06.034>
- Crotty, S. M., & Angelini, C. (2020). Geomorphology and species interactions control facilitation cascades in a salt marsh ecosystem. *Current Biology*, *30*(8), 1562–1571. <https://doi.org/10.1016/j.cub.2020.02.031>
- Crotty, S. M., Pinton, D., Canestrelli, A., Fischman, H. S., Ortals, C., Dahl, N. R., et al. (2023). Faunal engineering stimulates landscape-scale accretion in southeastern US salt marshes. *Nature Communications*, *14*(1), 881. <https://doi.org/10.1038/s41467-023-36444-w>
- Curran, C. A., Newell, S. Y., & Paerl, H. W. (1995). The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: Considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series*, *121*, 99–116. <https://doi.org/10.3354/meps121099>
- Dame, R. F., Koepfler, E., & Gregory, L. (2002). Benthic-pelagic coupling in marsh-estuarine ecosystems. In M. P. Weinstein & D. A. Kreeger (Eds.), *Concepts and controversies in tidal marsh ecology* (pp. 369–390). Kluwer Academic Publishers. [https://doi.org/10.1007/0-306-47534-0\\_17](https://doi.org/10.1007/0-306-47534-0_17)
- Dang, C., Sauriau, P. G., Savoye, N., Martinez, P., Millaret, C., Haure, J., et al. (2009). Determination of diet in Manila clams by spatial analysis of stable isotopes. *Marine Ecology Progress Series*, *387*, 167–177. <https://doi.org/10.3354/meps08100>
- Darby, F. A., & Turner, R. E. (2008). Below- and aboveground biomass of *Spartina alterniflora*: Response to nutrient addition in a Louisiana salt marsh. *Estuaries and Coasts*, *31*(2), 326–334. <https://doi.org/10.1007/s12237-008-9037-8>
- Derksen-Hooijberg, M., Angelini, C., Lamers, L. P. M., Borst, A., Smolders, A., Hoogveld, J. R. H., et al. (2018). Mutualistic interactions amplify saltmarsh restoration success. *Journal of Applied Ecology*, *55*(1), 405–414. <https://doi.org/10.1111/1365-2664.12960>
- Duarte, C. M., Middelburg, J. J., & Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, *2*(1), 1–8. <https://doi.org/10.5194/bg-2-1-2005>
- Ember, L. M., Williams, D. F., & Morris, J. T. (1987). Processes that influence carbon isotope variations in salt marsh sediments. *Marine Ecology Progress Series*, *36*(1), 33–42. <https://doi.org/10.3354/meps036033>
- Fodrie, F. J., Rodriguez, A. B., Gittman, R. K., Grabowski, J. H., Lindquist, N. L., Peterson, C. H., et al. (2017). Oyster reefs as carbon sources and sinks. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), 20170891. <https://doi.org/10.1098/rspb.2017.0891>
- Francis, T. B., Schindler, D. E., Holtgrieve, G. W., Larson, E. R., Scheurell, M. D., Semmens, B. X., & Ward, E. J. (2011). Habitat structure determines resource use by zooplankton in temperate lakes. *Ecology Letters*, *14*(14), 364–372. <https://doi.org/10.1111/j.1461-0248.2011.01597.x>
- Friedrichs, C. T., & Perry, J. E. (2001). Tidal salt marsh morphodynamics: A synthesis. *Journal of Coastal Research*, 7–37.
- Gabry, J., Češnovar, R., & Johnson, A. (2023). Cmdstanr: R interface to 'CmdStan'. Retrieved from <https://mc-stan.org/cmdstanr/>, <https://discourse.mc-stan.org>
- Gabry, J., & Mahr, T. (2022). "bayesplot: Plotting for Bayesian models." R package version 1.10.0. Retrieved from <https://mc-stan.org/bayesplot/>
- Gacia, E., Duarte, C. M., & Middelburg, J. J. (2002). Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnology & Oceanography*, *47*(1), 23–32. <https://doi.org/10.4319/lo.2002.47.1.0023>
- Gallagher, J. L. (1975). Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. *American Journal of Botany*, *62*(6), 644–648. <https://doi.org/10.2307/2441945>

- Gallagher, J. L., Reimold, R. J., Linthurst, R. A., & Pfeiffer, W. J. (1980). Aerial production, mortality, and mineral accumulation-export dynamics in *Spartina alterniflora* and *Juncus roemerianus* plant stands in a Georgia salt marsh. *Ecology*, *61*(2), 303–312. <https://doi.org/10.2307/1935189>
- Giles, H., Broekhuizen, N., Bryan, K. R., & Pilditch, C. A. (2009). Modelling the dispersal of biodeposits from mussel farms: The importance of simulating biodeposit erosion and decay. *Aquaculture*, *291*(3), 168–178. <https://doi.org/10.1016/j.aquaculture.2009.03.010>
- Gili, J.-M., & Coma, R. (1998). Benthic suspension feeders: Their paramount role in littoral marine food webs. *Trends in Ecology & Evolution*, *13*(8), 316–321. [https://doi.org/10.1016/S0169-5347\(98\)01365-2](https://doi.org/10.1016/S0169-5347(98)01365-2)
- Gobler, C. J., Doall, M. H., Peterson, B. J., Young, C. S., DeLaney, F., Wallace, R. B., et al. (2022). Rebuilding a collapsed bivalve population, restoring seagrass meadows, and eradicating harmful algal blooms in a temperate Lagoon using spawner sanctuaries. *Frontiers in Marine Science*, *9*, 911731. <https://doi.org/10.3389/fmars.2022.911731>
- Gohel, D., & Skintzos, P. (2023). `_flextable: Functions for tabular reporting_`. R package version 0.9.2. Retrieved from <https://CRAN.R-project.org/package=flextable>
- Haines, E. B. (1977). The origins of detritus in Georgia salt marsh estuaries. *Oikos*, *29*(2), 254–260. <https://doi.org/10.2307/3543611>
- Haines, E. B., & Montague, C. L. (1979). Food sources of estuarine invertebrates analyzed using  $^{13}\text{C}/^{12}\text{C}$  ratios. *Ecology*, *60*(1), 48–56. <https://doi.org/10.2307/1936467>
- Hansen, K., Butzeck, C., Eschenbach, A., Gröngröft, A., Jensen, K., & Pfeiffer, E.-M. (2017). Factors influencing the organic carbon pools in tidal marsh soils of the Elbe estuary (Germany). *Journal of Soils and Sediments*, *17*(1), 47–60. <https://doi.org/10.1007/s11368-016-1500-8>
- Harris, D., Horwath, W. R., & van Kessel, C. (2001). Acid fumigation of soils to remove carbonates prior to total organic carbon or CARBON-13 isotopic analysis. *Soil Science Society of America Journal*, *65*(6), 1853–1856. <https://doi.org/10.2136/sssaj2001.1853>
- Hupp, C. R., Kroes, D. E., Noe, G. B., Schenk, E. R., & Day, R. H. (2019). Sediment trapping and carbon sequestration in floodplains of the lower Atchafalaya basin, LA: Allochthonous versus autochthonous carbon sources. *Journal of Geophysical Research: Biogeosciences*, *124*(3), 663–677. <https://doi.org/10.1029/2018JG004533>
- Kamimura, S., & Tsuchiya, M. (2006). Effects of opportunistic feeding by the intertidal gastropods *Batillaria zonalis* and *B. flectosiphonata* on material flux on a tidal flat. *Marine Ecology Progress Series*, *318*, 203–211. <https://doi.org/10.3354/meps318203>
- Kemp, P., Newell, S., & Krambeck, C. (1990). Effects of filter-feeding by the ribbed mussel *Geukensia demissa* on the water-column microbiota of a *Spartina alterniflora* saltmarsh. *Marine Ecology Progress Series*, *59*(1), 119–131. <https://doi.org/10.3354/meps059119>
- Kon, K., Tongnunui, P., & Kurokura, H. (2015). Do allochthonous inputs represent an important food resource for benthic macrofaunal communities in tropical estuarine mudflats? *Food Webs*, *2*, 10–17. <https://doi.org/10.1016/j.fooweb.2015.03.001>
- Kreeger, D. A., & Newell, R. I. E. (2001). Seasonal utilization of different seston carbon sources by the ribbed mussel, *Geukensia demissa* (Dillwyn) in a mid-Atlantic salt marsh. *Journal of Experimental Marine Biology and Ecology*, *260*(1), 71–91. [https://doi.org/10.1016/S0022-0981\(01\)00242-8](https://doi.org/10.1016/S0022-0981(01)00242-8)
- Kuenzler, E. J. (1961). Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnology & Oceanography*, *6*(2), 191–204. <https://doi.org/10.4319/lo.1961.6.2.0191>
- Labrie, M. S., Sundermeyer, M. A., & Howes, B. L. (2022). Quantifying the effects of floating oyster aquaculture on nitrogen cycling in a temperate coastal embayment. *Estuaries and Coasts*, *46*(2), 494–511. <https://doi.org/10.1007/s12237-022-01133-2>
- Langdon, C., & Newell, R. (1989). Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*. *Marine Ecology Progress Series*, *58*, 299–310. <https://doi.org/10.3354/meps058299>
- Letzsch, S. W., & Frey, R. W. (1980). Deposition and erosion in a Holocene salt marsh, Sapelo Island, Georgia. *Journal of Sedimentary Petrology*, *50*(2), 529–542. <https://doi.org/10.1306/212f7a45-2b24-11d7-8648000102c1865d>
- Liao, C., Luo, Y., Jiang, L., Zhou, X., Wu, X., Fang, C., et al. (2007). Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze estuary, China. *Ecosystems*, *10*(8), 1351–1361. <https://doi.org/10.1007/s10021-007-9103-2>
- Lim, H. S., Fraser, A., & Knights, A. M. (2020). Spatial arrangement of biogenic reefs alters boundary layer characteristics to increase risk of microplastic bioaccumulation. *Environmental Research Letters*, *15*(6), 064024. <https://doi.org/10.1088/1748-9326/ab83ae>
- Loomis, M. J., & Craft, C. B. (2010). Carbon sequestration and nutrient (nitrogen, phosphorus) accumulation in river-dominated tidal marshes, Georgia, USA. *Soil Science Society of America Journal*, *74*(3), 1028–1036. <https://doi.org/10.2136/sssaj2009.0171>
- Malone, T. C., & Newton, A. (2020). The globalization of cultural eutrophication in the coastal ocean: Causes and consequences. *Frontiers in Marine Science*, *7*, 670. <https://doi.org/10.3389/fmars.2020.00670>
- Marchais, V., Schaal, G., Grall, J., Lorrain, A., Nerot, C., Richard, P., & Chauvaud, L. (2013). Spatial variability of stable isotope ratios in oysters (*Crassostrea gigas*) and primary producers along an estuarine gradient (Bay of Brest, France). *Estuaries and Coasts*, *36*(4), 808–819. <https://doi.org/10.1007/s12237-012-9584-x>
- McCarty, G., Pachepsky, Y., & Ritchie, J. (2009). Impact of sedimentation on wetland carbon sequestration in an agricultural watershed. *Journal of Environmental Quality*, *38*(2), 804–813. <https://doi.org/10.2134/jeq2008.0012>
- McKinney, R. A., Nelson, W. G., Charpentier, M. A., & Wigand, C. (2001). Ribbed mussel nitrogen isotope signatures reflect nitrogen sources in coastal salt marshes. *Ecological Applications*, *11*(1), 203–214. [https://doi.org/10.1890/1051-0761\(2001\)011\[0203:RMNISR\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[0203:RMNISR]2.0.CO;2)
- Medina, M., Kaplan, D., Milbrandt, E. C., Tomasko, D., Huffaker, R., & Angelini, C. (2022). Nitrogen-enriched discharges from a highly managed watershed intensify red tide (*Karenia brevis*) blooms in southwest Florida. *Science of the Total Environment*, *827*, 154149. <https://doi.org/10.1016/j.scitotenv.2022.154149>
- Middelburg, J. J., Nieuwenhuize, J., Lubberts, R. K., & van de Plassche, O. (1997). Organic carbon isotope systematics of coastal marshes. *Estuarine, Coastal and Shelf Science*, *45*(5), 681–687. <https://doi.org/10.1006/ecss.1997.0247>
- Middelburg, J. J., Nieuwenhuize, J., Slim, F., & Ohowa, B. (1996). Sediment biogeochemistry in an East African mangrove forest (Gazi Bay, Kenya). *Biogeochemistry*, *34*(3), 133–155. <https://doi.org/10.1007/BF00000899>
- Middelburg, J. J., Soetaert, K., Herman, P. M. J., Boschker, H. T. S., & Heip, C. H. R. (2004). Burial of nutrient in coastal sediments: The role of primary producers. In S. L. Nielsen, G. T. Banta, & M. F. Pedersen (Eds.), *Estuarine nutrient cycling: The influence of primary producers* (pp. 217–230). Springer Netherlands. [https://doi.org/10.1007/978-1-4020-3021-5\\_8](https://doi.org/10.1007/978-1-4020-3021-5_8)
- Moody, J., & Kreeger, D. (2020). Spatial distribution of ribbed mussel (*Geukensia demissa*) filtration rates across the salt marsh landscape. *Estuaries and Coasts*, *44*(1), 229–241. <https://doi.org/10.1007/s12237-020-00770-9>
- Murphy, A. E., Anderson, I., & Luckenbach, M. (2015). Enhanced nutrient regeneration at commercial hard clam (*Mercentaria mercenaria*) beds and the role of macroalgae. *Marine Ecology Progress Series*, *530*, 135–151. <https://doi.org/10.3354/meps11301>
- Murphy, A. E., Kolkmeier, R., Song, B., Anderson, I. C., & Bowen, J. (2019). Bioreactivity and microbiome of biodeposits from filter-feeding bivalves. *Microbiology of Aquatic Systems*, *77*(77), 343–357. <https://doi.org/10.1007/s00248-018-01312-4>
- Nikora, V., Green, M. O., Thrush, S. F., Hume, T. M., & Goring, D. (2002). Structure of the internal boundary layer over a patch of pinnid bivalves (*Atrina zelandica*) in an estuary. *Journal of Marine Research*, *60*(1), 121–150. <https://doi.org/10.1357/002224002762341276>

- Norkko, A., Hewitt, J. E., Thrush, S. F., & Funnell, T. (2001). Benthic-pelagic coupling and suspension-feeding bivalves: Linking site-specific sediment flux and biodeposition to benthic community structure. *Limnology & Oceanography*, *46*(8), 2067–2072. <https://doi.org/10.4319/lo.2001.46.8.2067>
- Peterson, B. J., & Heck, K. L. (2001). Positive interactions between suspension-feeding bivalves and seagrass — A facultative mutualism. *Marine Ecology Progress Series*, *213*(1985), 143–155. <https://doi.org/10.3354/meps213143>
- Peterson, B. J., & Howarth, R. W. (1987). Sulfur, carbon, and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. *Limnology & Oceanography*, *32*(6), 1195–1213. <https://doi.org/10.4319/lo.1987.32.6.1195>
- Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., et al. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology*, *835*(August), 823–835.
- Phillips, D. L., & Koch, P. L. (2002). Incorporating concentration dependence in stable isotope mixing models. *Oecologia*, *130*(1), 114–125. <https://doi.org/10.1007/s004420100786>
- Phillips, D. L., Newsome, S. D., & Gregg, J. W. (2005). Combining sources in stable isotope mixing models: Alternative methods. *Oecologia*, *144*(4), 520–527. <https://doi.org/10.1007/s00442-004-1816-8>
- Plummer, M. (2017). JAGS version 4.3.1. Retrieved from <https://sourceforge.net/projects/mcmc-jags/>
- Plummer, M. (2023). `_rjags`: Bayesian Graphical Models using MCMC\_ R package version 4-14. Retrieved from <https://CRAN.R-project.org/package=rjags>
- Pruell, R. J., Taplin, B. K., Lake, J. L., & Jayaraman, S. (2006). Nitrogen isotope ratios in estuarine biota collected along a nutrient gradient in Narragansett Bay, Rhode Island, USA. *Marine Pollution Bulletin*, *52*(6), 612–620. <https://doi.org/10.1016/j.marpolbul.2005.10.009>
- Pusceddu, A., Frascetti, S., Mirto, S., Holmer, M., & Danovaro, R. (2007). Effects of intensive mariculture on sediment biochemistry. *Ecological Applications*, *17*(5), 1366–1378. <https://doi.org/10.1890/06-2028.1>
- R Core Team. (2023). `_R`: A language and environment for statistical computing\_ R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Reed, D. J. (1989). Patterns of sediment deposition in subsiding coastal salt marshes, Terrebonne Bay, Louisiana: The role of winter storms. *Estuaries*, *12*(4), 222. <https://doi.org/10.2307/1351901>
- Riisgård, H. U. (1988). Efficiency of particle retention and filtration-rate in 6 species of Northeast American bivalves. *Marine Ecology-Progress Series - MAR ECOL-PROGR SER*, *45*, 217–223. <https://doi.org/10.3354/meps045217>
- Sea, M. A., Hillman, J. R., & Thrush, S. F. (2022). The influence of mussel restoration on coastal carbon cycling. *Global Change Biology*, *28*(17), 5269–5282. <https://doi.org/10.1111/gcb.16287>
- Sherr, E. B. (1982). Carbon isotope composition of organic seston and sediments in a Georgia salt marsh estuary. *Geochimica et Cosmochimica Acta*, *46*(7), 1227–1232. [https://doi.org/10.1016/0016-7037\(82\)90007-2](https://doi.org/10.1016/0016-7037(82)90007-2)
- Smith, J., & Frey, R. (1985). Biodeposition by the ribbed mussel *Geukensia demissa* in a salt marsh, Sapelo Island, Georgia. *SEPM Journal of Sedimentary Research*, *55*, 817–828. <https://doi.org/10.1306/212F880F-2B24-11D7-8648000102C1865D>
- Stan Development Team. (2023). Stan modeling language users guide and reference manual, version 2.32. Retrieved from <https://mc-stan.org>
- Stiven, A. E., & Gardner, S. A. (1992). Population processes in the ribbed mussel *Geukensia demissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: Spatial pattern, predation, growth and mortality. *Journal of Experimental Marine Biology and Ecology*, *160*(1), 81–102. [https://doi.org/10.1016/0022-0981\(92\)90112-n](https://doi.org/10.1016/0022-0981(92)90112-n)
- Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, *6*, 1–27. <https://doi.org/10.7717/peerj.5096>
- Stock, B. C., & Semmens, B. X. (2016). Unifying error structures in commonly used biotracer mixing models. *Statistical Reports*, *97*(10), 2562–2569. <https://doi.org/10.1002/ecy.1517>
- Sullivan, M. J., & Moncreiff, C. A. (1990). Edaphic algae are an important component of salt marsh food-webs: Evidence from multiple stable isotope analyses. *Marine E*, *62*(1), 149–159. <https://doi.org/10.3354/meps062149>
- Toro, J. E., Paredes, P. I., Villagra, D. J., & Senn, C. M. (1999). Seasonal variation in the phytoplanktonic community, seston and environmental variables during a 2-year period and oyster growth at two mariculture sites, southern Chile. *Marine Ecology*, *20*(1), 63–89. <https://doi.org/10.1046/j.1439-0485.1999.00066.x>
- Vafeiadou, A.-M., Materatski, P., Adão, H., De Troch, M., & Moens, T. (2013). Food sources of macrobenthos in an estuarine seagrass habitat (*Zostera noltii*) as revealed by dual stable isotope signatures. *Marine Biology*, *160*(9), 2517–2523. <https://doi.org/10.1007/s00227-013-2238-0>
- Valiela, I., & Teal, J. M. (1974). Nutrient limitation in salt marsh vegetation. *Ecology of Halophytes*, *14*, 547–563.
- Van de Broek, M., Vandendriessche, C., Poppelmonde, D., Merckx, R., Temmerman, S., & Govers, G. (2018). Long-term organic carbon sequestration in tidal marsh sediments is dominated by old-aged allochthonous inputs in a macrotidal estuary. *Global Change Biology*, *24*(6), 2498–2512. <https://doi.org/10.1111/gcb.14089>
- Watanabe, S., Kodama, M., & Fukuda, M. (2009). Nitrogen stable isotope ratio in the manila clam, *Ruditapes philippinarum*, reflects eutrophication levels in tidal flats. *Marine Pollution Bulletin*, *58*(10), 1447–1453. <https://doi.org/10.1016/j.marpolbul.2009.06.018>
- Welsh, D. T. (2003). It's a dirty job but someone has to do it: The role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. *Chemistry and Ecology*, *19*(5), 321–342. <https://doi.org/10.1080/0275754031000155474>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. Retrieved from <https://ggplot2.tidyverse.org>
- Widdows, J., Brinsley, M. D., Salkeld, P. N., & Elliott, M. (1998). Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface. *Estuaries*, *21*(4), 552. <https://doi.org/10.2307/1353294>
- Wright, R. T., Coffin, R. B., Ersing, C. P., & Pearson, D. (1982). Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. *Limnology & Oceanography*, *27*(1), 91–98. <https://doi.org/10.4319/lo.1982.27.1.0091>
- Zhou, J., Wu, Y., Zhang, J., Kang, Q., & Liu, Z. (2006). Carbon and nitrogen composition and stable isotope as potential indicators of source and fate of organic matter in the salt marsh of the Changjiang Estuary. *China*, *65*(2), 310–317. <https://doi.org/10.1016/j.chemosphere.2006.02.026>
- Zhu, J., Zarnoch, C., Gosnell, J., Alldred, M., & Hoellein, T. (2019). Ribbed mussels *Geukensia demissa* enhance nitrogen-removal services but not plant growth in restored eutrophic salt marshes. *Marine Ecology Progress Series*, *631*, 67–80. <https://doi.org/10.3354/meps13132>
- Zurburg, W., Smaal, A., Hiral, M., & Dankers, N. (1994). Seston dynamic and Bivalbe feeding in the bay of marennes-Oleron (France). *Netherlands Journal of Aquatic Ecology*, *28*(3–4), 459–466. <https://doi.org/10.1007/bf02334217>

## References From the Supporting Information

- Benner, R., Fogel, M. L., & Sprague, E. K. (1991). Diagenesis of belowground biomass of *Spartina alterniflora* in salt-marsh sediments. *Limnology & Oceanography*, *36*(7), 1358–1374. <https://doi.org/10.4319/lo.1991.36.7.1358>
- Borst, A. C. W., Verberk, W. C. E. P., Angelini, C., Schotanus, J., Wolters, J. W., Christianen, M. J. A., et al. (2018). Foundation species enhance food web complexity through non-trophic facilitation. *PLoS One*, *13*(8), 1–15. <https://doi.org/10.1371/journal.pone.0199152>
- Couch, C. A. (1989). Carbon and nitrogen stable isotopes of meiobenthos and their food resources. *Estuarine, Coastal and Shelf Science*, *28*(4), 433–441. [https://doi.org/10.1016/0272-7714\(89\)90090-5](https://doi.org/10.1016/0272-7714(89)90090-5)
- Dai, J., Sun, M., Culp, R. A., & Noakes, J. E. (2005). Changes in chemical and isotopic signatures of plant materials during degradation: Implication for assessing various organic inputs in estuarine systems. *Geophysical Research Letters*, *32*(13), L13608. <https://doi.org/10.1029/2005GL023133>
- Haines, E. B. (1976). Stable carbon isotope ratios in the biota, soils and tidal water of a Georgia salt. *Estuarine and Coastal Marine Science*, *4*(6), 609–616. [https://doi.org/10.1016/0302-3524\(76\)90069-4](https://doi.org/10.1016/0302-3524(76)90069-4)
- Haines, E. B., & Dunstan, W. M. (1975). The distribution and relation of particulate organic material and primary productivity in the Georgia Bight, 1973-1974. *Estuarine and Coastal Marine Science*, *3*(4), 431–441. [https://doi.org/10.1016/0302-3524\(75\)90043-2](https://doi.org/10.1016/0302-3524(75)90043-2)
- Morrison, E. S., Bianchi, T. S., Kenney, W. F., Brenner, M., Prince, K., Williams, S., et al. (2022). *Sediment, crab, and vegetation data from Sapelo Island, Georgia: 2017 - 2019 ver 1*. Environmental Data Initiative. <https://doi.org/10.6073/pasta/9f4f43b8bf95c28896fcb1d8ef5f020b>
- Peterson, B. J., Howarth, R. W., & Garritt, R. H. (1985). Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science*, *227*(4692), 1361–1363. <https://doi.org/10.1126/science.227.4692.1361>
- Schwinghamer, P., Tan, F. C., & Gordon, D. C., Jr. (1983). Stable carbon isotope studies on the Pecks Cove mudflat ecosystem in the Cumberland basin, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(S1), s262–s272. <https://doi.org/10.1139/f83-288>
- Windom, H. L. (2019). Elemental composition of suspended particles across the southeastern continental shelf off the coast of North Florida and South Georgia: Provenance, transport, fate and implications to mid-outer shelf water column processes. *Continental Shelf Research*, *178*, 27–40. <https://doi.org/10.1016/j.csr.2019.03.005>