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Geographic variation in organic carbon storage by seagrass beds

Jennifer McHenry,[1*] **Andrew Rassweiler**,[2] **Gema Hernan**,[2,3] **Alexandra K. Dubel**,[2] **Carolyn Curtin**,[1] **Jakob Barzak**,[1] **Nicholas Varias**,[1] **Sarah E. Lester**[1,2]
[1]Department of Geography, Florida State University, Tallahassee, Florida
[2]Department of Biological Science, Florida State University, Tallahassee, Florida
[3]Department of Marine Ecology, Mediterranean Institute of Advanced Studies, Esporles, Balearic Islands, Spain

Abstract

Since seagrasses are efficient sinks for marine organic carbon, there is growing interest in incorporating seagrass protection and restoration into climate mitigation schemes, that is, offering credit for accumulated carbon to offset carbon dioxide emissions. However, patterns and drivers of organic carbon storage by seagrasses are not well resolved, especially at scales relevant to management decisions. Here, we quantified geographic variation in standing stocks of sedimentary organic carbon (Mg C_{org} ha^{-1}) associated with seagrasses along the northern Florida Gulf Coast using field surveys and sediment cores. We measured plant biomass, organic carbon, and sediment composition in each core. Using a multivariate modeling approach, we evaluated the relative importance of ecological, physical, oceanographic, and seascape drivers, developing the first spatially explicit predictions of seagrass-associated carbon stocks for this region. Applying model predictions to confirmed seagrass beds and potential recovery areas, we also estimated the carbon storage value of potential seagrass conservation and restoration as the resulting stock enhancement value per hectare of seagrass (Δ Mg C_{org} ha^{-1}). We found that organic carbon stored by seagrass sediments varied considerably across this region, with stocks significantly increasing with seagrass cover, proximity to oyster reefs, and distance from river outlets, highlighting potential synergies for coordinated management. We also found that current seagrass beds could offer nearly double the carbon storage value of potential recovery areas, emphasizing the importance of conservation as well as restoration. Our results have important implications for management, restoration, and understanding biogeographic patterns of seagrass ecosystem services.

Coastal ecosystems, including seagrass beds, mangrove forests, and salt marshes, sequester and store large quantities of organic carbon in their biomass and sediments (30,000 Tg C_{org}), thereby preventing carbon dioxide from entering the atmosphere and oceans (304 Tg CO_2 yr^{-1}) and contributing economic and social benefits as measured by the avoided social cost of carbon (US$ 22.8 billion per year) (Nellemann and Corcoran 2009; Duarte et al. 2013; Bertram et al. 2021; Macreadie et al. 2021). Seagrass beds, comprised of marine flowering plants, are among the most efficient natural carbon sinks, occupying 0.2% of the ocean floor but accounting for 10–18% of annual organic carbon burial in the ocean (Mcleod et al. 2011; Fourqurean et al. 2012). The anoxic sediment conditions of seagrass beds can prevent organic carbon from decomposing over long timescales (i.e., decades to centuries or even millennia; Fourqurean et al. 2012; Howard et al. 2017). However, the carbon storage potential of these systems is rapidly eroding because of large-scale environmental degradation and disturbance (Pendleton et al. 2012; Trevathan-Tackett et al. 2018; Salinas et al. 2020).

Improved seagrass management and conservation have been promoted to prevent the release of stored carbon, and seagrass restoration is increasingly considered as a potential ocean climate solution (Nellemann and Corcoran 2009; Hejnowicz et al. 2015; Macreadie et al. 2017*a*; Cullen-Unsworth and Unsworth 2018; Macreadie et al. 2021). “Blue carbon initiatives”, focused on coastal and marine ecosystems that promote the sequestration, storage, and burial of organic carbon, are laying the groundwork for incorporating seagrass beds into climate change mitigation schemes, that is,

*Correspondence: jennmchenry1@gmail.com

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Present address: Department of Biology, University of Victoria, British Columbia, Canada

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providing financing for conservation and restoration projects that offset carbon dioxide emissions (Hejnowicz et al. 2015; Herr et al. 2017). However, these schemes are only feasible in regions where there is evidence of long-term organic carbon burial (> 100 yr) and are sufficient data to predict how management interventions would affect carbon storage (Needelman et al. 2018; Johannessen 2022; Williamson and Gattuso 2022).

A growing body of work quantifies organic carbon stocks and burial rates in nearshore marine systems, but efforts for seagrasses lag behind other systems (Macreadie et al. 2021). Global syntheses have shown considerable variability in the amount of sedimentary organic carbon stored by seagrass beds across regions and seagrass species (Fourqurean et al. 2012), but these estimates are typically based on a small number of sediment cores, offering limited scope for assessing subregional variability in stocks associated with seagrass beds or the potential storage value of seagrass restoration. There are also geographic biases in existing data for seagrasses, with substantial sampling gaps outside of a few discrete locations in Western Europe, Australia, and the United States (Fourqurean et al. 2012; Macreadie et al. 2019). To reduce this uncertainty, assessments of subregional to regional patterns and drivers of sedimentary carbon storage by seagrasses are essential.

Previous studies indicate that a range of interrelated ecological, physical, oceanographic, and seascape factors can influence sedimentary organic carbon storage by seagrasses (Mazarrasa et al. 2018). Seagrass beds accumulate carbon in their sediments through the growth and senescence of canopy and rhizome biomass, which in turn enhances the deposition and burial of detritus, particulates, and associated carbon from the water-column. Therefore, rates of local organic carbon production and deposition can vary depending on seagrass community characteristics, such as seagrass canopy cover, species composition, areal extent, and the configuration of seagrass beds (Lavery et al. 2013; Samper-Villarreal et al. 2016; Ricart et al. 2017). In addition, stocks are likely influenced by environmental conditions controlling the supply and deposition of sediments and organic material from elsewhere, such as the water depth, turbidity, and current dynamics; as well as the seascape configuration in relation to nearby allochthonous carbon sources, such as rivers and oyster reefs (Lavery et al. 2013; Ricart et al. 2020; Asplund et al. 2021; Veenstra et al. 2021). All of these factors have the potential to create considerable spatial variation in organic carbon storage by seagrasses, but the resulting patterns and relative importance of different drivers is still unknown (Lavery et al. 2013; Oreska et al. 2017).

The Florida Gulf Coast supports some of the most extensive and biologically rich seagrass beds in North America, covering upwards of 700,000 ha (McHenry et al. 2021). Following decades of degradation and decline, significant resources have been dedicated to the restoration of seagrass beds in this region (Rezek et al. 2019). The region is characterized by heterogeneous sedimentation patterns, large-scale oceanographic gradients created by the Gulf Loop current, numerous river outlets, and a patchwork of allochthonous carbon sources (e.g., oyster reefs, salt marshes), and thus is an ideal study location for assessing patterns and drivers of organic carbon storage by seagrasses. Initial assessments for the nearby Texas Gulf Coast and southeast Florida indicate that seagrass habitats store roughly 25.7 ± 6.7 Mg C_{org} ha^{-1} and that the potential gains from seagrass restoration could reach up to 20.9 ± 8.6 Mg C_{org} ha^{-1} (Thorhaug et al. 2017). However, it is unclear how representative these assessments are for the northern Florida Gulf Coast—a region with little information on sedimentary organic carbon (outside of Florida Bay, which is located at the southern edge of the region) (Armitage and Fourqurean 2016; Howard et al. 2016). These assessments also fail to account for background levels of organic carbon that would be present in marine sediments in the absence of seagrass vegetation.

Here, we assess the geographic distribution and variability of sedimentary organic carbon stocks associated with seagrass beds along a 1500 km section of the northern Florida Gulf Coast, combining intensive field sampling with a multivariate modeling approach. We provide a novel evaluation of the importance of multiple drivers of sedimentary carbon stocks, specifically testing the effects of different seagrass bed characteristics (e.g., seagrass cover and species composition), environmental conditions (e.g., depth and sea surface temperature), and seascape drivers (e.g., proximity of river inputs and nearby oyster reefs). Furthermore, we present the first spatially explicit predictions of sedimentary carbon stocks, enabling identification of the most valuable locations for conservation and restoration and also providing estimates of total carbon storage by seagrasses in this region. By isolating the net effect of seagrasses on sedimentary organic carbon from other key drivers, we explore how the potential organic carbon storage benefits of seagrass conservation and restoration vary across the region.

Materials and methods

Study area

Our study area spans 1500 km of the Florida Gulf Coast from Mexico Beach to Spring Hill, FL, including water depths between 0 and 4 m, an area that contains over 350,000 ha of seagrass beds based on aerial surveys conducted by the Florida Fish and Wildlife Conservation Commission (FWCC 2022). According to seagrass distribution model predictions, this region also contains nearly 100,000 additional hectares of potential recovery areas possibly suitable for restoration (McHenry et al. 2021). The Florida Gulf Coast is spatially heterogenous in terms of cover of seagrasses, the freshwater, nutrient, and sediment inputs from river outlets, and the distribution of oyster reefs (Supporting Information Fig. S1). We concentrated our sampling efforts on four focal bays (Fig. 1)—St. Joseph's Bay (SJB), Apalachee Bay (AB), Deadman's Bay (DB), and Crystal Bay (CB)—which capture a representative range of mixed and monospecific seagrass beds, environmental conditions, and seascape configurations.

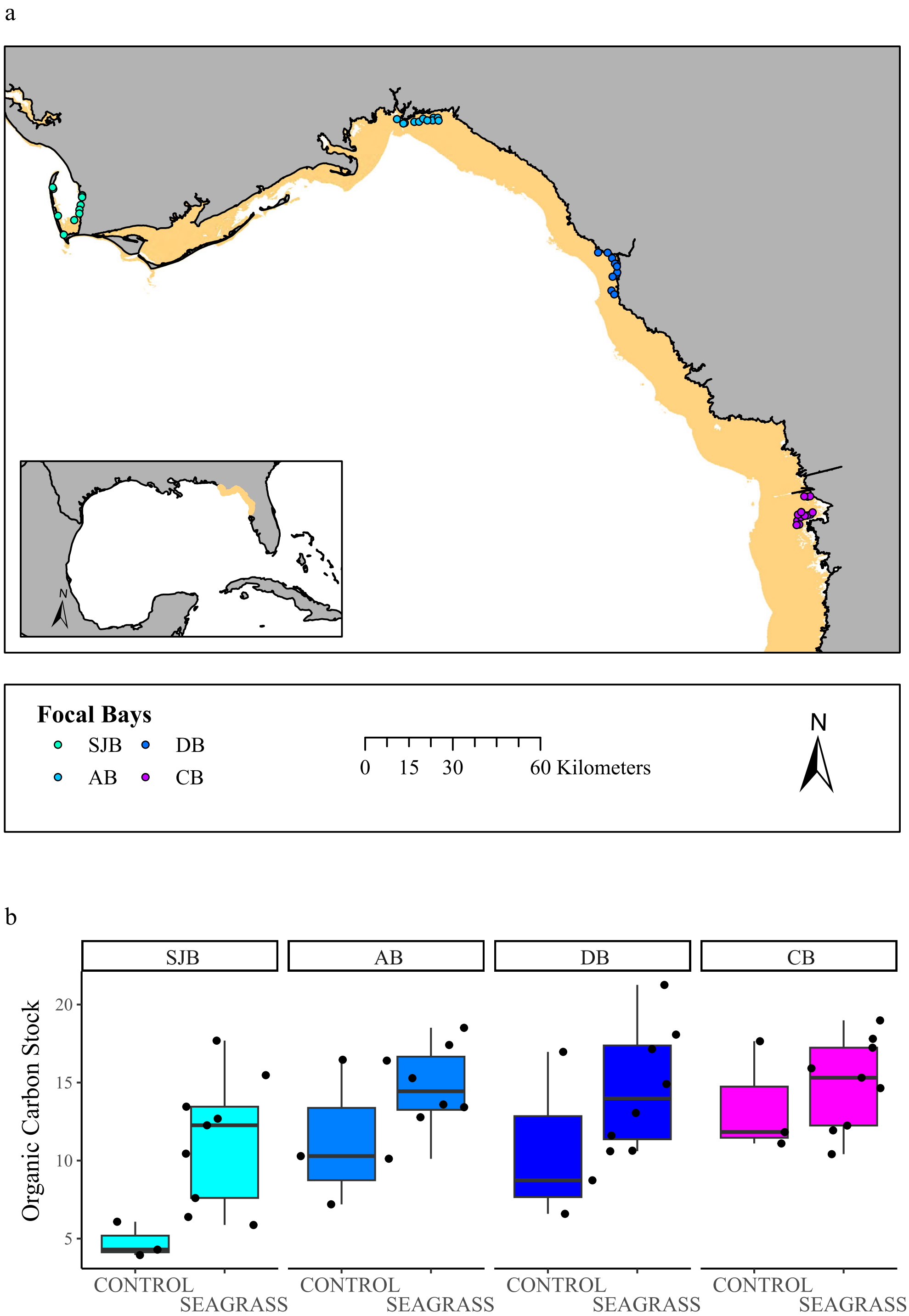

Fig. 1. (**a**) Study sites in four focal bays of the Florida Gulf Coast, with (**b**) boxplots depicting regional variation in the standing stocks of organic carbon (Mg C_{org} ha^{-1}) in the surficial sediments (i.e., 0–20 cm) of seagrass beds and unvegetated control sites. From west to east, focal bays include St. Joseph's Bay (SJB), Apalachee Bay (AB), Deadman's Bay (DB), and Crystal Bay (CB). Yellow polygon indicates the study area spanning the 4 m depth contour.

Study design

Surveys of seagrass communities and sampling for seagrass biomass and sediment cores occurred during two sampling periods (May–September of 2019 and 2021) and was permitted via the Florida Department of Environmental Protection, the U.S. Army Corps of Engineers, and the Florida FWCC. Using the "random point" function in ArcGIS, we selected potential field sites a priori, spaced at least 1 km apart, including those within seagrass beds and outside in adjacent marine sediments as control sites. We sampled up to 12 sites per focal bay (48 total), where a site represents the 1-ha area surrounding the selected coordinates. We stratified our sampling effort by seagrass canopy cover, that is, high (≥ 50%), medium (50–25%), low (25–5%), and none (≤ 5%), such that we visited roughly an equal number of sites per cover class.

Field sampling

At each site, we recorded geographic coordinates, seabed depth (m), and water clarity (measured as secchi depth). We conducted random quadrat surveys of the seagrass community ($n = 10$ per site), visually assessing the total percent cover, species composition, canopy height (cm), and epiphyte load on all seagrass and macroalgal species inside a 25 cm × 25 cm PVC quadrat. From the first three quadrats per site, we also collected all the above-ground biomass for seagrasses and macroalgae species, resulting in a total of 108 biomass samples across the four focal bays. From each cleared quadrat, we then collected a sediment core (using a 50.8 cm long × 5.08 cm diameter Wildco hand corer) to measure below-ground biomass of seagrasses (i.e., rhizomes), grain-size characteristics, and the accumulation of organic carbon in marine sediments, resulting in a total of 144 sediment cores. To ensure we were explicitly testing the influence of seagrass variables on organic carbon storage, we focused our analysis on the top 20 cm of sediment accumulation (representing approximately 100 yr of accretion; Kennedy et al. 2022), with the idea that this section of the core would be most directly impacted by observed seagrass characteristics. We determined the total sampling depth of each core using the difference between the total length of the hand corer and the height of the corer protruding above the sediment surface. We also measured the degree of compaction as the ratio between the sampling depth and the total length of the extracted core. In the field, each sediment core was subsampled into 2 cm slices (hereafter called sediment slices), which we measured and then individually bagged and stored in a −20°C freezer for laboratory analysis.

Laboratory analysis

We rinsed, sorted, and identified all seagrass and macroalgal species contained in the above-ground biomass samples, drying each species to a constant weight, and standardizing it to the area sampled (i.e., mg DW m^{-2}), and calculated the average above-ground biomass of seagrass and microalgal species at each site. In addition, we dried and weighed the sediment slices to calculate the sediment bulk density (i.e., mg DW cm^{-3}), standardizing the dry weight of each slices to its original volume. To account for sediment compaction due to sampling (~ 22%), the slice volumes were first corrected using the slice heights (h_{slice}) and the compaction ratios (CR) measured in situ (Eq. 1; Howard et al. 2014). We also determined the actual sediment depth of each sediment slice by dividing the compacted slice depth by the compaction ratio.

$$\mathrm{mg\,DW\,cm^{-3}} = \mathrm{mg\,DW}/\left(\pi \times (2.54\,\mathrm{cm})^2 \times (h_{\mathrm{slice}}/\mathrm{CR})\right) \tag{1}$$

Specific sediment slices were reserved for further analysis (Supporting Information Fig. S2). We quantified the seagrass rhizome density of each core as the total dry weight of all identifiable pieces of roots and rhizome found across the top 14 cm (i.e., the depth exceeding the typical rhizome depth of seagrasses in this region; Supporting Information Fig. S2), standardized to the slice volume (i.e., mg DW cm^{-3}) and averaged within a core. We also determined the sediment composition of each core as the fractional weight of grain sizes, averaged across the top 20 cm of sediment, by manually passing two sediment samples per core (Supporting Information Fig. S2) through a set of sieves for pebble (> 4 mm), gravel (2–4 mm), coarse sand (0.5–2 mm), medium sand (0.25–0.5 mm), fine sand (0.06–0.25 mm), and silt (≥ 0.06 mm). From this, we determined the average sediment bulk density, rhizome density, and grain-size composition per site.

Finally, we determined the average organic carbon density of each sediment core by measuring the organic content of a subset of sediment slices (Supporting Information Fig. S2) via loss-on-ignition analysis (Howard et al. 2014). Prior to analysis, we removed all shells and then homogenized each sediment sample. We heated approximately 15 g of dried sediment to 450°C for 4.5 h and used the change in weight to determine the fractional dry weight of organic content per sample (OC% of mg DW). We then determined the fraction of organic carbon content (C_{org}% of mg DW) in a smaller subset of sediment slices (i.e., one core per site for Saint Joseph's Bay, Apalachee Bay, and Deadman's Bay) via elemental analysis using a low temperature combustion approach (Chichester and Chaison 1992; Howard et al. 2014; Kim et al. 2020). For this, an aluminum capsule containing ~ 60 mg of homogenized dried sample was heated to 500°C (i.e., the temperature where organic material, but not inorganic material is fully combusted) using a CE Flash 1112 Elemental Analyzer. Since the ratio of organic content to organic carbon content was similar across our samples ($R^2 = 0.77$; $C_{org}\% = 0.31 \times OC\% - 0.03$; Supporting Information Fig. S3), we applied this ratio to our entire organic content dataset. From this, we calculated the organic carbon density (mg C_{org} cm^{-3}) of the entire dataset, using the sample bulk density and organic carbon content measurements. We found no statistically significant relationship between organic carbon density and the sampling depth (Supporting Information Fig. S4). Thus we determined the standing stock of organic carbon (Mg C_{org} ha^{-1}) in surficial sediments (i.e., the top 20 cm) at each site using Eq. 2 (Howard et al. 2014), averaging across cores within a site.

$$\mathrm{Mg\,C_{org}\,ha^{-1}} = \mathrm{mg\,C_{org}\,cm^{-3}} \times 20\,\mathrm{cm} \times \left(1.0 \times 10^{-9}\,\mathrm{Mg\,mg^{-1}}\right) \times \left(1.0 \times 10^{8}\,\mathrm{cm^2\,ha^{-1}}\right). \tag{2}$$

Spatial datasets

We described geographic variation in potential predictors across the study area and extrapolated model predictions to unsampled locations using existing spatial data layers (Supporting Information Table S1). We used global remote sensing and data-assimilating model products assembled by BioOracle to characterize the long-term annual sea surface temperature, salinity, nitrates, current velocity, and chlorophyll concentration of coastal waters (Tyberghein et al. 2012). We used sediment property layers describing the percent composition of three grain sizes (i.e., silt, sand, and gravel) from U.S. Geological Survey's usSEABED products and a depth layer from the National Oceanic and Atmospheric Administration's Coastal Relief Modeler. We calculated the distances to the nearest shoreline and river outlet as proxies for the influence of land-based sources of organic material, nutrients, and sediments using ArcGIS Version 10.7. We also calculated the distances to the nearest oyster reef and salt marsh, using aerial survey maps from Florida FWCC's Geodata Library. These habitats may represent allochthonous organic carbon sources or may otherwise modify carbon cycling (Fodrie et al. 2017). In addition, we used aerial maps of confirmed seagrass beds from FWCC to calculate the extent of spatially contiguous seagrass vegetation at our study sites based on the area of the seagrass polygon overlapping each study site (FWCC 2022). Finally, we used models and mapped predictions from McHenry et al. (2021) to describe the expected total seagrass cover of seagrass beds under current environmental conditions (*see* Supporting Information Text S1 for model description). All spatial layers were resampled to a 93-m resolution using the nearest neighbor method ("raster" R library) (Hijmans et al. 2015). All further analyses were conducted using R version 4.0.4 (R Core Team 2021) and RStudio version 1.2.1335 (RStudio Core Team 2020).

Spatial models

We used a generalized additive model (GAM; "mgcv" R package) with a Gaussian error structure to quantify geographic patterns and drivers of sedimentary organic carbon storage in seagrass beds on the Florida Gulf Coast (Wood 2012). GAMs are increasingly used to explore spatial variability in marine ecosystems because they provide a highly flexible modeling framework and allow for both linear and nonlinear relationships between responses and predictors (Zuur et al. 2009). We modeled the standing stock of organic carbon (Mg C_{org} ha^{-1}) in surficial sediments as the response variable, relating site-level estimates to potential predictors that have been found to influence organic carbon storage in seagrasses and other habitats. Specifically, we tested the effects of different seagrass bed characteristics (e.g., seagrass presence, canopy cover, and species composition), environmental conditions (e.g., depth and sea surface temperature), seascape drivers (e.g., the distance to river inputs and nearby oyster reefs), and geographic position on sedimentary organic carbon (Table S1).

Prior to model development, we examined Pearson's correlation coefficients between the standing stocks and potential predictor variables to rule out uncorrelated variables ($r \leq |0.25|$; Supporting Information Table S2), leaving 14 variables for further analysis. We performed stepwise model selection to identify the most important predictors using Akaike's information criterion (AIC). We allowed for possible nonlinear relationships by applying a thin plate spline parameter to significant model predictors and noting the change in AIC. We also allowed for interactions between seagrass, environmental, seascape, and geographic variables. We selected the final model configuration based on the greatest reduction in AIC. We verified the absence of multicollinearity using the variance inflation factor (i.e., VIF < 3). Finally, because sampling was clustered within four focal regions, we evaluated and ruled out spatial autocorrelation of the residuals using variograms and a Mantel test ($r_M = -0.04$; $p = 0.17$).

The predictive capability of the final model was evaluated using a Monte Carlo cross-validation procedure that randomly splits the full dataset 50 times into 75% training and 25% testing data, and then refits each model to quantify the relationship between observed and predicted values in the testing datasets. From the cross-validation procedures, we calculated the average performance and predictive skill of each model in terms of the adjusted R-squared (adj-R^2), explained deviance (%), delta AIC (ΔAIC), and root mean squared error.

Mapped predictions of sedimentary organic carbon stocks

We mapped standing stocks of organic carbon in the surficial sediments of seagrass beds, i.e., megagrams of organic carbon per hectare of seagrass (Mg C_{org} ha^{-1}) for the top 20 cm of sediment, using the final model and spatial layers of the retained predictors (Fig. S1). To quantify standing stocks associated with contemporary seagrass beds, we constrained the model predictions to the extent of confirmed seagrass beds, that is, areas that have been previously surveyed and found to have seagrass beds by Florida FWCC aerial surveys between 1985 and 2019 (Supporting Information Fig. S5) (FWCC 2022). We also estimated potential standing stocks resulting from successful seagrass restoration in all suitable areas of potential recovery, that is, areas where seagrasses are currently absent according to FWCC datasets but could survive if restored according to seagrass distribution models (Fig. S5) (McHenry et al. 2021). Each 1-ha map pixel represents the expected standing stock of organic carbon in seagrass beds and with successful restoration (Mg C_{org} ha^{-1}), given current environmental conditions and the seagrass cover level predicted by McHenry et al. (2021). Areas with no potential to support seagrasses according to model predictions were not mapped.

Estimating the carbon storage value of seagrasses

We estimated the carbon storage value of seagrasses at the hectare scale over a 1500 km stretch of the Florida Gulf Coast from water depths between 0 and 4 m. To estimate the stock enhancement value of seagrass beds, we compared model predictions of standing stocks assuming seagrass beds are present at their current levels to counterfactual predictions where all current seagrass beds are lost (i.e., seagrass predictors are set to zero prior to generating organic carbon stock predictions). To estimate the potential stock enhancement value with restoration, we compared standing stock predictions for potential recovery areas if seagrasses were successfully restored to predictions if seagrass beds remain absent. In both cases, stock enhancement values represent the net effect of seagrasses on the amount of sedimentary organic carbon stored per hectare over baseline unvegetated conditions in units of delta megagrams of organic carbon per hectare of seagrass (Eq. 3).

$$\Delta\,\mathrm{Mg\,C_{org}\,ha^{-1}} = \mathrm{Standing\ Stock_{Seagrass\ Present}} - \mathrm{Standing\ Stock_{Seagrass\ Absent}}. \quad (3)$$

We quantified the overall uncertainty of the mean estimates for organic carbon stocks, stock enhancement values of seagrass beds, and stock enhancement values with restoration (Supporting Information Text S2).

Results

Sedimentary organic carbon stocks

Seagrass beds had significantly higher standing stocks of organic carbon in surficial sediments compared to unvegetated control sites (ANOVA, df = 1, $***p \leq 0.005$). Seagrass beds on average stored 13.9 ± 0.1 SE Mg C_{org} ha^{-1} whereas unvegetated controls stored 10.1 ± 0.4 SE Mg C_{org} ha^{-1}. However, estimates varied by an order of magnitude across sites within each habitat, indicating that carbon storage by seagrasses is highly context dependent. Organic carbon content in seagrass beds ranged from 0.3% to 6.7% of mg DW and standing stock estimates ranged from 5.9 to 21.3 Mg C_{org} ha^{-1}. Meanwhile the organic carbon content and

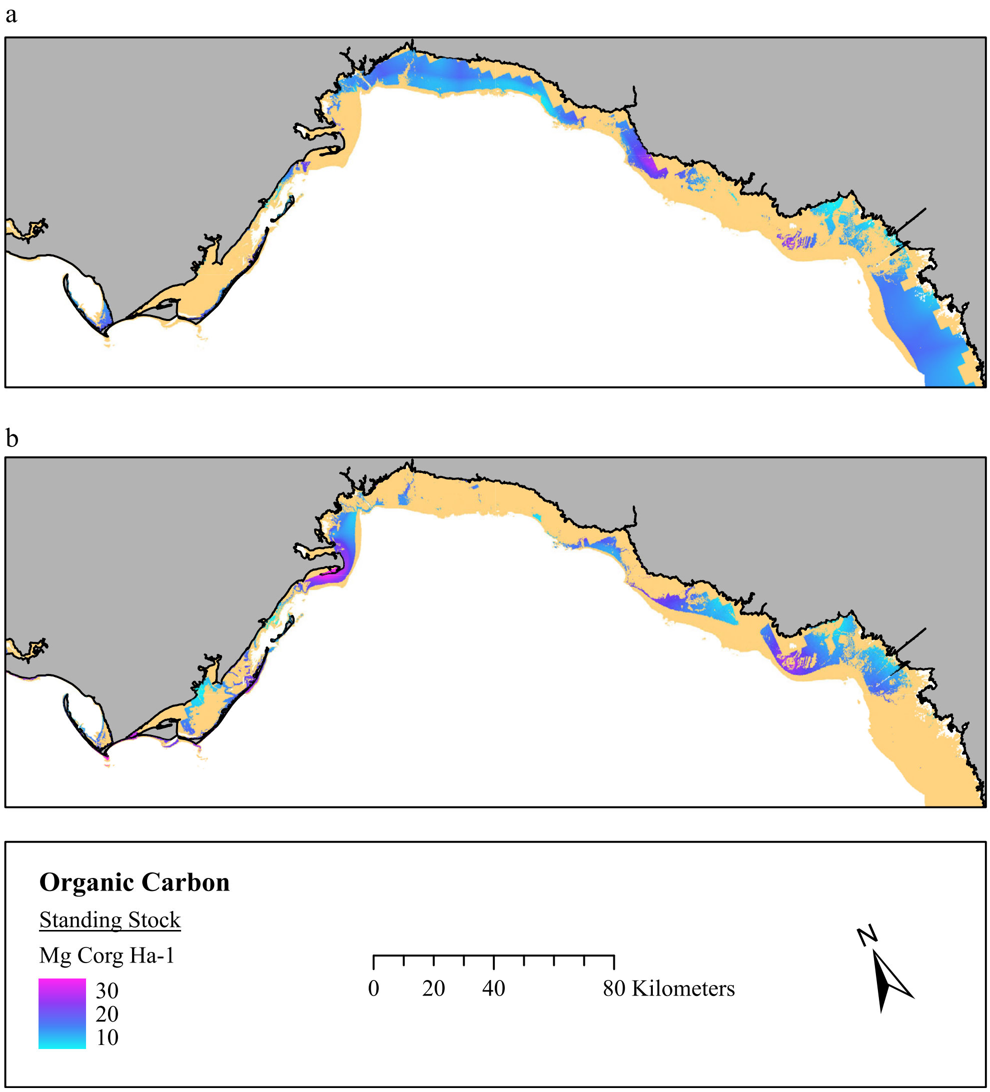

Fig. 2. Predicted standing stocks of organic carbon (Mg C_{org} ha^{-1}) associated with surficial sediments in (**a**) confirmed seagrass beds and (**b**) potential recovery areas across the northern Florida Gulf Coast. Yellow polygon indicates the study area extending to the 4 m depth contour.

Table 1. The total estimated organic carbon stock and storage value of seagrass beds and potential recovery areas with successful seagrass restoration in the northern Florida Gulf Coast. Carbon storage value is quantified in terms of the total stock enhancement (Mg C_{org}) value resulting from the persistence of seagrasses in all suitable areas. Errors represent overall uncertainty estimates on the total estimates.

	Total organic carbon stock (Mg C_{org})	Total stock enhancement (Mg C_{org})
Confirmed beds	3,251,651 (± 1766)	402,784 (± 2497)
Potential recovery areas	1,960,253 (± 1269)	147,960 (± 1795)

standing stocks of unvegetated areas ranged from 0.2 to 1.4 C_{org}% and 3.9 to 17.7 Mg C_{org} ha^{-1}, respectively. There was also considerable variation within and across focal bays (ANOVA, df = 3, $^{***}p \leq 0.001$), with the difference between standing stocks in seagrass beds and unvegetated areas generally narrowing from the northwest to southeast of the study area (Fig. 1).

Drivers of variation in sedimentary organic carbon stocks

Three variables—seagrass cover, distance from river outlets, and proximity to oyster reefs—collectively explained a substantial portion of the variation in the standing stocks of organic carbon (adj-$R^2 = 0.43$; deviance explained = 46.4%; Supporting Information Table S3). These were the only variables identified as statistically significant predictors and retained out of the 14 considered during model selection. Model coefficients indicated that standing stocks significantly increase with distance from river outlets by 0.47 Mg C_{org} ha^{-1} km^{-1} from river outlet and decreased with distance to oyster reefs by 0.1 Mg C_{org} ha^{-1} km^{-1} from oyster reefs (Supporting Information Fig. S6). Finally, organic carbon stocks were positively associated with the total cover of seagrasses, increasing by 0.04 Mg C_{org} ha^{-1} per percentage increase of seagrass. High model performance and predictive skill was maintained during cross-validation, indicating the final model is suitable for spatial extrapolation of predictions across our study area (Supporting Information Table S4).

Mapped predictions of organic carbon stocks

Standing stocks of organic carbon associated with seagrass beds varied considerably across the study area according to mapped predictions (CV = 13.2; Fig. 2a). On average, seagrass beds stored 15.7 ± 0.007 Mg C_{org} ha^{-1} with some locations storing up to 28 Mg C_{org} ha^{-1} where seagrasses had higher seagrass cover and occurred nearer to oyster reefs and further away from river outlets (e.g., Cedar Key and Horseshoe Beach). Potential recovery areas for seagrasses could support similar mean standing stocks compared to confirmed beds following successful seagrass restoration (Fig. 2a; mean = 15.6 ± 0.010 Mg C_{org} ha^{-1}), with the greatest stock potential (e.g., off Cedar Key and Alligator Point) reaching up to 29.6 Mg C_{org} ha^{-1} (Fig. 2b). However, the coefficient of variation was considerably higher (CV = 19.8). In total, we estimate that the surficial sediments of confirmed seagrass beds contain 3.3 million Mg C_{org} and that potential recovery areas could store up to 1.9 million Mg of C_{org} following successful restoration (Table 1).

Estimating the organic carbon storage value of seagrasses

The organic carbon storage value of seagrasses varied across the Florida Gulf Coast, with stock enhancement values ranging from 0.2 to 4.2 Δ Mg C_{org} ha^{-1} over baseline conditions, increasing with higher total cover of seagrass beds. Seagrass beds and potential recovery areas differed significantly in

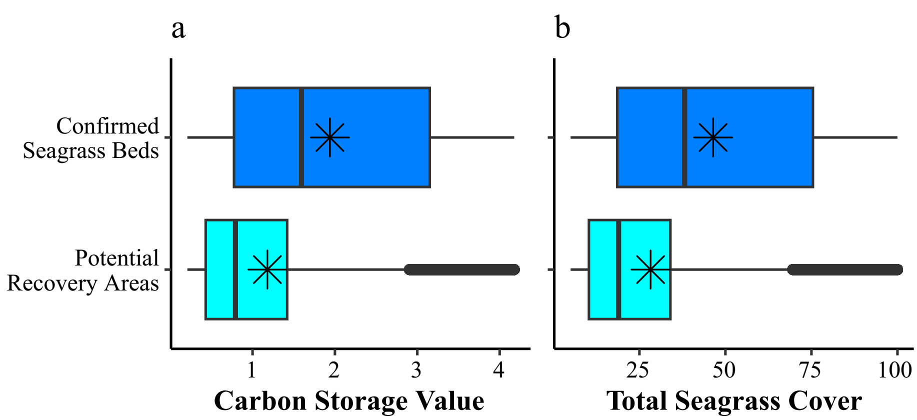

Fig. 3. The (**a**) organic carbon storage value and (**b**) predicted total seagrass cover of confirmed seagrass beds and potential recovery areas following successful restoration in the northern Florida Gulf Coast. The organic carbon storage values generated by seagrasses is calculated in terms of the stock enhancement value (Δ Mg C_{org} ha^{-1}) resulting from the persistence of seagrasses for a given 1-ha pixel. Stars indicate the mean pixel value from the spatial predictions for the study area.

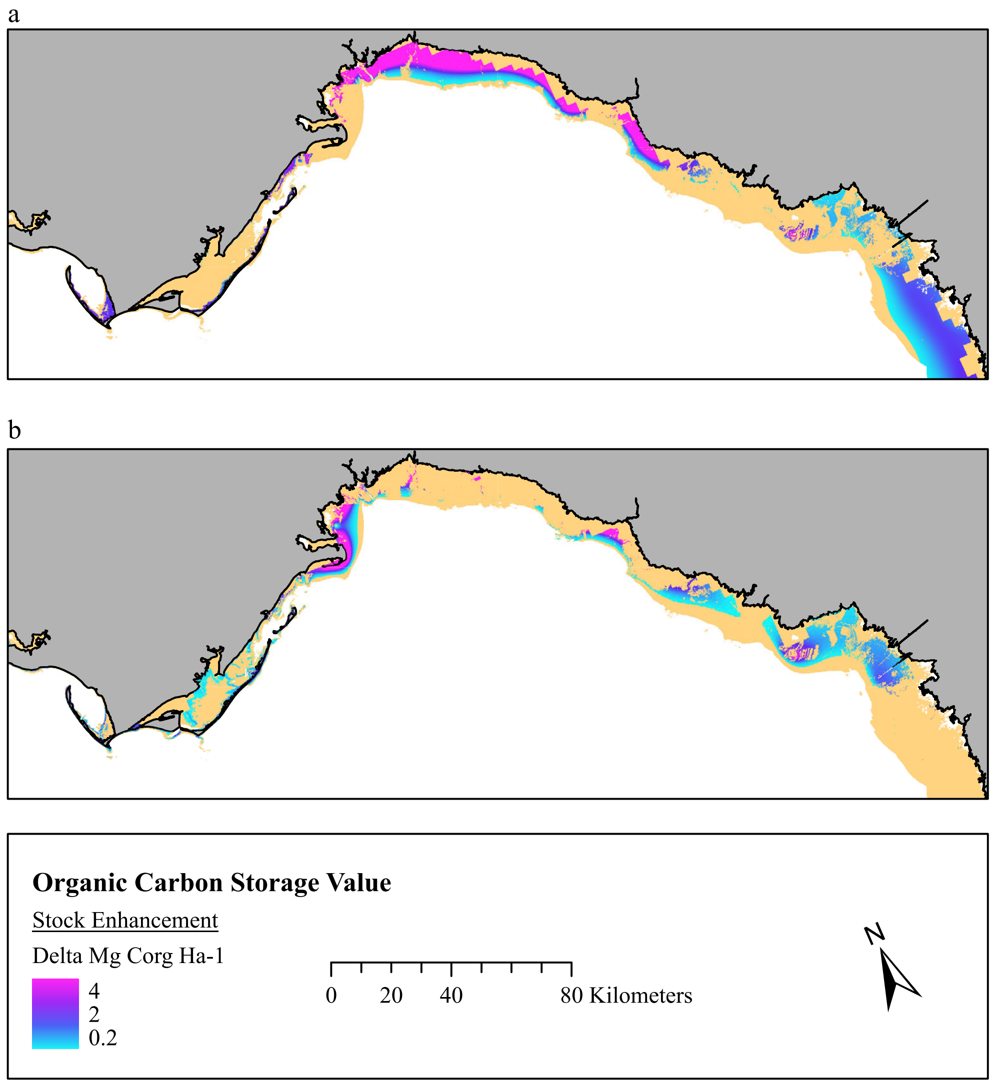

Fig. 4. Organic carbon storage value associated with surficial sediments in (**a**) confirmed seagrass beds and (**b**) potential recovery areas across the northern Florida Gulf Coast. Organic carbon storage values are shown as the stock enhancement value (Δ Mg C_{org} ha^{-1}) resulting from the persistence of seagrasses for a given map pixel. Model predictions are constrained to 4 m isobath to avoid inappropriate extrapolation. Yellow polygon indicates the study area spanning the 4 m depth contour.

terms of their mean and median carbon storage value (ANOVA and Kruskal–Wallis ****$p < 0.0001$), due to the lower seagrass cover predicted in potential recovery areas (Fig. 3). The average stock enhancement value of confirmed seagrass beds was 1.9 ± 0.010 Δ Mg C_{org} ha^{-1} (Fig. 3a). By comparison, seagrass beds had nearly double the stock enhancement value of potential recovery areas, which contributed only 1.2 ± 0.014 Δ Mg C_{org} ha^{-1} of additional carbon storage (Fig. 3a). Carbon storage values showed distinct spatial patterns from the standing stocks of blue carbon, with the highest stock enhancement occurring in Apalachee Bay and Deadman's Bay (Fig. 4). Overall, we estimate that 12.1% of standing stocks in confirmed seagrass beds and 7.7% of standing stocks in potential recovery areas are attributable to the persistence of seagrasses (Table 1).

Discussion

Seagrasses are known to be effective carbon sinks but geographic variability in their sedimentary carbon stocks and in their potential to offset emissions is still largely unknown. Here, we apply intensive field sampling and spatial modeling to document considerable variation in the standing stocks of organic carbon associated with seagrasses in the northern Florida Gulf Coast. Mapped predictions for this region show that seagrasses store up to 28.0 Mg C_{org} ha^{-1} in the top 20 cm of sediment and that potential recovery areas could reach similar stocks following successful restoration. However, our analysis shows that the carbon storage value of these areas is likely context dependent because of the positive effect of seagrass canopy cover. Importantly, we found that the stock enhancement value of seagrass beds ranged from 0.2% to 17.5% over unvegetated stock levels, representing an order of magnitude difference between low and high cover seagrass beds. We also found that most potential recovery areas had lower stock enhancement potential due to the generally lower predicted seagrass cover of these areas, emphasizing the importance of seagrass conservation and not just restoration for advancing blue carbon initiatives.

Many ecological, environmental, and seascape factors have been examined as potential predictors of sedimentary organic carbon storage by seagrasses (Mazarrasa et al. 2018). Our analysis shows that a significant portion of the variation in standing stocks in the Florida Gulf Coast can be explained by just three factors. Standing stocks significantly increased with the total cover of seagrasses, likely due to the greater local organic carbon production and deposition created by larger, more abundant seagrass canopies (Samper-Villarreal et al. 2016; Mazarrasa et al. 2018). Stocks also increased with distance from river outlets, potentially corresponding to the decreasing turbidity and hydrodynamic energy further from rivers leading to greater deposition (Ricart et al. 2020). Finally, standing stocks were positively influenced by the proximity of oyster reefs, suggesting potential synergies for coordinated management and restoration. This positive association likely relates to the allochthonous carbon subsidies and wave attenuation they produce, which has been found to enhance the rate of carbon storage and burial in nearby sediments (Sharma et al. 2016; Fodrie et al. 2017; Veenstra et al. 2021).

Surprisingly, several factors commonly proposed to influence sedimentary organic carbon stocks did not emerge as significant in our study. For one, species composition was not a significant predictor; we found no evidence of a differing effect between the three dominant species in the northern Florida Gulf Coast at this spatial scale (*Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*), despite substantial variation in species composition across our study sites and the considerable morphological differences between species (McHenry et al. 2021). However, the probability of encountering *T. testudinum* tends to increase further from river outlets, along environmental gradients in turbidity and salinity created by river outflow (McHenry et al. 2021). Thus, the effect of this larger, more persistent species on organic carbon stocks may be partly captured within the statistical effect of distance from river mouth in our model. We also found no additional explanatory power from the inclusions of either in situ or previously mapped grain sizes as indicators of the local hydrodynamics controlling deposition rates (Mazarrasa et al. 2018). Since oyster reefs and riverine outflow play a more direct role in controlling sediment deposition and sorting in this region (Davis 2017), it is likely the positive association with fine sediments size is also captured by the model.

Mapped predictions show a threefold difference between the lowest and highest standing stocks of organic carbon associated with seagrasses in the northern Florida Gulf Coast. These predictions represent the maximum potential for organic carbon stocks associated with seagrass beds, based on the expected cover of seagrasses and the current distribution of oyster reefs and rivers. The range of organic carbon stocks predicted by our model is consistent with previous field sampling from the Texas Gulf Coast (Thorhaug et al. 2017). However, stocks were generally much lower than those documented for seagrasses in southeast Florida (Thorhaug et al. 2017) and the Caribbean (Kennedy et al. 2022), likely due to the shorter growing season and greater seasonal fluctuation of seagrass biomass occurring at higher latitudes (Mazarrasa et al. 2018).

The carbon storage value maps provide new insights about the relative contributions of seagrasses to organic carbon stocks, in terms of the additional stock enhancement value resulting from seagrasses per hectare. We show that seagrass beds significantly enhance standing stocks of organic carbon, but there is a high degree of variability in their potential stock enhancement value, resulting from the heterogeneity of seagrass cover across the Florida Gulf Coast. Since we only considered the top 20 cm of sediment, it is likely that carbon storage values are even higher in areas where seagrasses promote a greater depth of sediment accretion. We also do not account for the export of seagrass plant matter and detritus to other marine foundation species, which likely further increases the carbon storage benefits of seagrass beds (Duarte and Krause-Jensen 2017). Future studies can refine our estimates as datasets for relative sediment accumulation and biomass export become available.

Several factors could also reduce the organic carbon storage value of seagrasses under certain circumstances. For example, we do not account for local stressors and disturbances, such as bioturbation, herbivory, and boating activity, which could lead to some remineralization at the sediment-surface interface (Johannessen 2022). We also do not account for the role of calcium carbonate production and dissolution in seagrass systems. Ongoing debate in the literature has yet to resolve the overall direction and magnitude of these processes (Williamson and Gattuso 2022). A growing body of work suggests that a portion of the organic carbon storage value by seagrasses could be offset by local calcification, especially in tropical settings that tend of have carbonate rich sediments due to the prevalence of calcareous epiphytes and shellfish (Macreadie et al. 2017*b*; Howard et al. 2018; Van Dam et al. 2021). As the same time, carbonate dissolution and advection from other marine habitats have the potential to significantly enhance the carbon storage role of seagrasses (Saderne et al. 2019). Ultimately, the amount of carbon dioxide that is either removed or stored by seagrass systems will depend on relative rates of calcification, primary production, carbonate dissolution, and advection of allochthonous carbonates from other habitats (Saderne et al. 2019; Williamson and Gattuso 2022). Future assessments should consider how these processes modify the spatial patterns of stock enhancement value we document here.

Counter to expectations, we found that successful restoration could offer only half of the stock enhancement value of confirmed seagrass beds, likely due to the lower limit on seagrass cover predicted for many potential recovery areas. Seagrass cover has been linked to various environmental factors controlling light availability and disturbance, including water depth, water quality, and water motion (Iverson and Bittaker 1986; Hale et al. 2004; Uhrin and Turner 2018). In the Florida Gulf Coast, seagrass cover tends to decrease with water depth and near river outlets, especially where there is higher turbidity caused by seasonal nutrient influx (McHenry et al. 2021) and watershed pollution (Greening et al. 2014). Since most potential recovery areas in the Florida Gulf Coast are expected to be in deeper waters and nearer to rivers, they may not currently be suitable for supporting dense seagrass beds (Supporting Information Fig. S7). However, there may be opportunities to increase the expected cover of these areas (and thus their stock enhancement) through local watershed management targeting improved water quality and clarity (Greening et al. 2014; Tomasko et al. 2018).

By quantifying the carbon storage value of seagrasses, our study allows for more credible estimates of the total carbon offset potential of contemporary seagrasses (Table 1). In the northern Florida Gulf Coast, we found that approximately 12% of organic carbon stocks are attributable to the presence of seagrass beds. Since carbon dioxide has the molecular weight of 3.67, this storage implies that an additional 1.5 million MT CO_2 is being stored over what would be expected in the absence of seagrass beds. Based on conservative estimates of the expected social cost resulting from CO_2 release (Ricke et al. 2018), this also suggests that maintaining seagrasses in this region may contribute up to $79.5 million USD of "blue carbon" wealth. In addition, successful restoration within all currently suitable habitats for seagrasses could lead to a further emissions reduction value on the order of 0.6 million MT CO_2 and a social cost avoidance value of $29.2 million USD. However, this additional value from restoration should be viewed as a long-term benefit, given the slow pace of seagrass recovery (Tomasko et al. 2018; Rezek et al. 2019) and the decadal to century timescales needed to reaccumulate sediments and reach predicted stock levels (Greiner et al. 2013; Kennedy et al. 2022). Furthermore, since these estimates are based on predictions for surficial sediments (i.e., the top 20 cm of sediment accumulation), future research is needed to understand how this additional carbon storage value contributes to carbon stocks persisting over decades or centuries (Johannessen 2022).

Our study has important implications for advancing blue carbon initiatives. A key barrier to incorporating seagrasses into greenhouse gas abatement schemes has been the lack of credible data about patterns of blue carbon storage (Needelman et al. 2018). Demonstrating the potential carbon offset value of proposed management and restoration sites is essential for spatial planning and site selection to maximize carbon storage benefits (Lester et al. 2020) and is often an unavoidable prerequisite to securing financing. Uncertainty about variability in the maximum potential carbon stocks associated with seagrasses can also make it difficult to develop realistic benchmarks for evaluating project success. Our study provides key datasets to advance blue carbon initiatives in the Florida Gulf Coast. For example, the carbon storage value maps we present can be used to prioritize conservation of current seagrass beds based on their predicted stock enhancement and relative risk of carbon remineralization from seagrass loss. Similarly, potential recovery areas can be prioritized based on their predicted offset benefits following seagrass restoration. However, additional research on local sediment accumulation rates is necessary to ensure proposed sites are likely to contribute to permanent carbon stocks (i.e., persisting for longer than 100 yr) (Johannessen 2022). Once projects are underway, the standing stock maps can help assess project performance through comparison of monitoring datasets to model predictions. In the long term, our models can also help managers gauge the vulnerability of organic carbon stocks to environmental changes affecting seagrasses and adjacent oyster reefs, such as sea-level rise (Macreadie et al. 2019; McHenry et al. 2021). The local to regional scale of our sampling efforts also helps to pave the way for increased accuracy in future global scale assessments for blue carbon systems. Future work could adopt our sampling and modeling framework to understand and evaluate changes in the geographic variability of the carbon storage value of these important systems.

Data availability statement

All data, R code, and model output produced by this study will be made available in a GitHub repository (https://github.com/jennmchenry1/Geographic-variation-in-organic-carbon-storage-by-seagrass-beds).

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Conflict of Interest

None declared.

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