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Key Points:

- Seagrass sediment organic carbon storage varies as much within a meadow as across regions
- Grain size predicts seagrass sediment organic carbon storage regionally, but not consistently at the local-meadow scale
- Seagrass-derived organic matter makes up approximately one fourth of sedimentary organic carbon in vegetated sediments

Supporting Information:

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

Correspondence to:

L. R. Capece,
lcapece@ucsb.edu

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Author Contributions:

Conceptualization: Lena R. Capece
Data curation: Lena R. Capece
Formal analysis: Lena R. Capece
Funding acquisition: Tessa M. Hill
Investigation: Lena R. Capece, Jolie Lobrutto
Methodology: Lena R. Capece
Project administration: Tessa M. Hill
Resources: Tessa M. Hill
Supervision: Alyssa J. Griffin, Tessa M. Hill
Validation: Lena R. Capece, Alyssa J. Griffin, Tessa M. Hill
Visualization: Lena R. Capece
Writing – original draft: Lena R. Capece

Multi-Scale Variability of Blue Carbon in Seagrass Sediments From Three California Estuaries

Lena R. Capece[1,2], Alyssa J. Griffin[2,3], Melissa A. Ward[3,4], Aurora M. Ricart[3,5], Priya Shukla[3], Jolie Lobrutto[3], and Tessa M. Hill[2,3]

[1]Department of Earth Science, University of California, Santa Barbara, CA, USA, [2]Department of Earth and Planetary Sciences, University of California, Davis, CA, USA, [3]Bodega Marine Laboratory, University of California, Davis, CA, USA, [4]San Diego State University, San Diego, CA, USA, [5]Institut de Ciències del Mar—Consejo Superior de Investigaciones Científicas, Barcelona, Spain

Abstract Seagrass meadows are a significant global carbon sink. Most of the carbon sequestered in these ecosystems is found as sedimentary organic carbon, which can vary spatially across seagrass meadows and can be derived from a variety of sources. Here, we investigate intra- and inter-meadow spatial variability in sediment organic carbon storage and quantify potential organic matter sources in three *Zostera marina* seagrass meadows spanning three estuaries across California (USA). Seagrass sediment organic carbon storage varies as much intra-meadow as it varies across regions. At the intra-meadow scale we find significant correlations between organic carbon content and mud content (fraction of sediment grains <63 μm, %), C/N ratios and $\delta^{13}C$ values in surface sediments across two meadows. At the regional scale greater organic carbon storage in the presence of seagrass compared to adjacent unvegetated sediments. Additionally, we find that mud content is the best predictor of sediment organic carbon content at the regional scale, indicating an enhanced role for mineral interaction in organic carbon preservation, but not consistently at the localized meadow scale. Approximately one fourth of organic carbon preserved in seagrass sediments is derived from seagrass. This research provides insights into the variability of organic carbon storage in seagrass meadows in California at multiple spatial scales. We demonstrate the need to account for small-scale variation of organic carbon storage in seagrass meadows to better estimate the capacity for these ecosystems to serve as effective long-term carbon sinks.

Plain Language Summary Blue carbon ecosystems, including mangrove forests, tidal marshes, kelp forests, and seagrass meadows are natural carbon sinks, and their conservation and restoration are considered a climate change mitigation strategy. While there is abundant data on seagrass meadow carbon stocks and carbon burial rates globally, it is critical to evaluate carbon storage on more localized scales to improve estimates of specific seagrass meadows as carbon sinks. Here, we investigate the capacity of seagrass meadows in three California estuaries to act as carbon sinks by evaluating the spatial variability of carbon storage within individual meadows and between them.

1. Introduction

In recent decades, seagrass meadows have become recognized as globally significant carbon sinks with the ability to store carbon on the timescale of decades to millennia (Duarte et al., 2005, 2013; Mcleod et al., 2011). Despite covering less than 0.2% of the world's oceans, seagrasses may be responsible for about 10% of organic carbon burial in marine sediments and their restoration and management is a potential nature-based solution with multiple co-benefits including climate change mitigation (e.g., Fourqurean et al., 2012; Mcleod et al., 2011). While there is a wealth of available data on global seagrass organic carbon stocks and burial rates (Cebrián et al., 1997; Duarte et al., 2005, 2013; Fourqurean et al., 2012; Gagnon et al., 2024; Röhr et al., 2018), it is becoming increasingly important to assess organic carbon storage at the local or site-specific scale to (a) adequately compare storage in seagrass (vegetated) sediments relative to baseline (unvegetated) sediments, (b) provide accurate estimates of carbon stocks for potential use in carbon crediting, and (c) understand the underlying drivers of organic carbon storage (Macreadie et al., 2019).

Global studies have demonstrated that the factors driving organic carbon storage at larger, regional scales, such as geomorphology, hydrodynamics, canopy structure and biomass coverage, sediment mud content (grain size), and carbon source, can also drive organic carbon storage in seagrass meadows on smaller, localized intra-meadow scales (Hyndes et al., 2014; Janousek et al., 2025; Oreska, Wilkinson, et al., 2017; Prentice et al., 2019; Ricart

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et al., 2015, 2017). In particular, there has been a focus on sediment grain size and carbon source as drivers of enhanced organic carbon preservation in seagrass and other blue carbon ecosystems.

Small sized grains in sediment, such as high mud or clay content, are thought to aid organic carbon storage by potentially slowing decomposition and remineralization via enhanced mineral-organic matter interactions (Hemingway et al., 2019). Sediment grain size also provides clues into the depositional environment of seagrass meadows where hydrographic data are not available, as higher mud content is typically correlated to reduced hydrodynamic energy where sediment can more easily settle and accumulate than in higher energy environments (Burdige, 2007; Hedges & Keil, 1995).

The reactivity of organic matter sources within seagrass meadow sediments also has an impact on organic carbon storage (Blair & Aller, 2012; Burdige, 2007). There are multiple potential sources of organic matter to seagrass meadows including seagrass, epiphytic algae, macroalgae, phytoplankton, and terrestrially derived organic matter such as marsh plants—which are thought to have distinct reactivities toward degradation remineralization based on their chemical or structural composition (Kristensen, 1990, 1994; Trevathan-Tackett et al., 2015). These sources can be produced within the meadow (autochthonous) or be imported into the ecosystem (allochthonous). Seagrass and terrestrial derived organic matter is generally considered less reactive than marine-derived organic matter such as algae or phytoplankton (Enríquez et al., 1993; Kristensen, 1990, 1994; Trevathan-Tackett et al., 2015; Twilley et al., 1986; Wada et al., 2008); and therefore, might contribute more to sediment organic carbon storage than other more reactive organic matter types. However, previous work has shown that approximately half of organic carbon deposited in seagrass sediments is non-seagrass derived and likely sourced from algae (phytoplankton and macroalgae) and marsh plant-derived organic matter (Kennedy et al., 2010; Oreska, McGlathery, & Porter, 2017, Oreska, McGlathery, & Porter, 2017; Prentice et al., 2019; Ricart et al., 2017; Röhr et al., 2018, 2018, 2018).

Similar to global studies, foundational work on *Zostera marina* along the Pacific Coast of North America emphasizes the spatial heterogeneity of organic carbon storage and attributes observed variation in organic carbon storage between regional study sites to differences in mud content, presence or absence of seagrass, local hydrodynamic conditions, and differences in the dominant sources of organic matter (Poppe & Rybczyk, 2018; Prentice et al., 2019; Röhr et al., 2018; Ward et al., 2021). However, comprehensive assessments of how organic carbon storage and potential drivers such as mud content and organic matter source vary across the intra- and inter-meadow spatial scale within California seagrass meadows are lacking.

Here, we assess organic carbon storage across three seagrass meadows in three distinct California estuaries (Figure 1). We ask (a) How does organic carbon storage vary across local (within-meadow, across vegetation status) and regional (between meadows) scales? And (b) Are patterns in organic carbon storage associated with mud content or with differences in organic matter sources? Taken together, we fill important gaps in our understanding of the spatial heterogeneity of organic carbon storage in seagrass meadows at several spatial scales in California and provide insights for restoration and management strategies aimed at carbon preservation with implications for crediting.

2. Methods

2.1. Study Sites

We sampled seagrass meadows in three estuaries within California: two in Northern California, Cypress Grove in Tomales Bay (38.16607°N, 122.90131°W) and Bodega Harbor (38.31859°N, 123.05284°W), and one in Southern California, Newport Back Bay (33.61936°N, 117.90300°W) (Figures 1a and 1b).

The Tomales Bay site was located in the outer bay region (outermost 8 km), which is highly influenced by tidal exchange with the coastal ocean (Hearn & Largier, 1997). The bay is formed from a drowned rift-valley and receives freshwater input from Walker Creek and Lagunitas Creek which bring in sediments, nutrients, and terrestrial sources of organic matter to the bay (Chambers et al., 2000). Ocean-derived phytoplankton are another important source of organic matter to the bay, particularly during periods of upwelling when cold, nutrient-rich waters support phytoplankton production in shelf waters (Smith & Hollibaugh, 1997). Seagrass *Z. marina* covers at most 13% of the estuary and is primarily found along tidal flats adjacent to the shoreline (Basta & Bamford, 2013). Although these meadows are perennial, meadows experience annual variations in biomass extent or coverage, senescing in fall and winter months. At the time of sampling, the meadow sampled at Cypress Grove

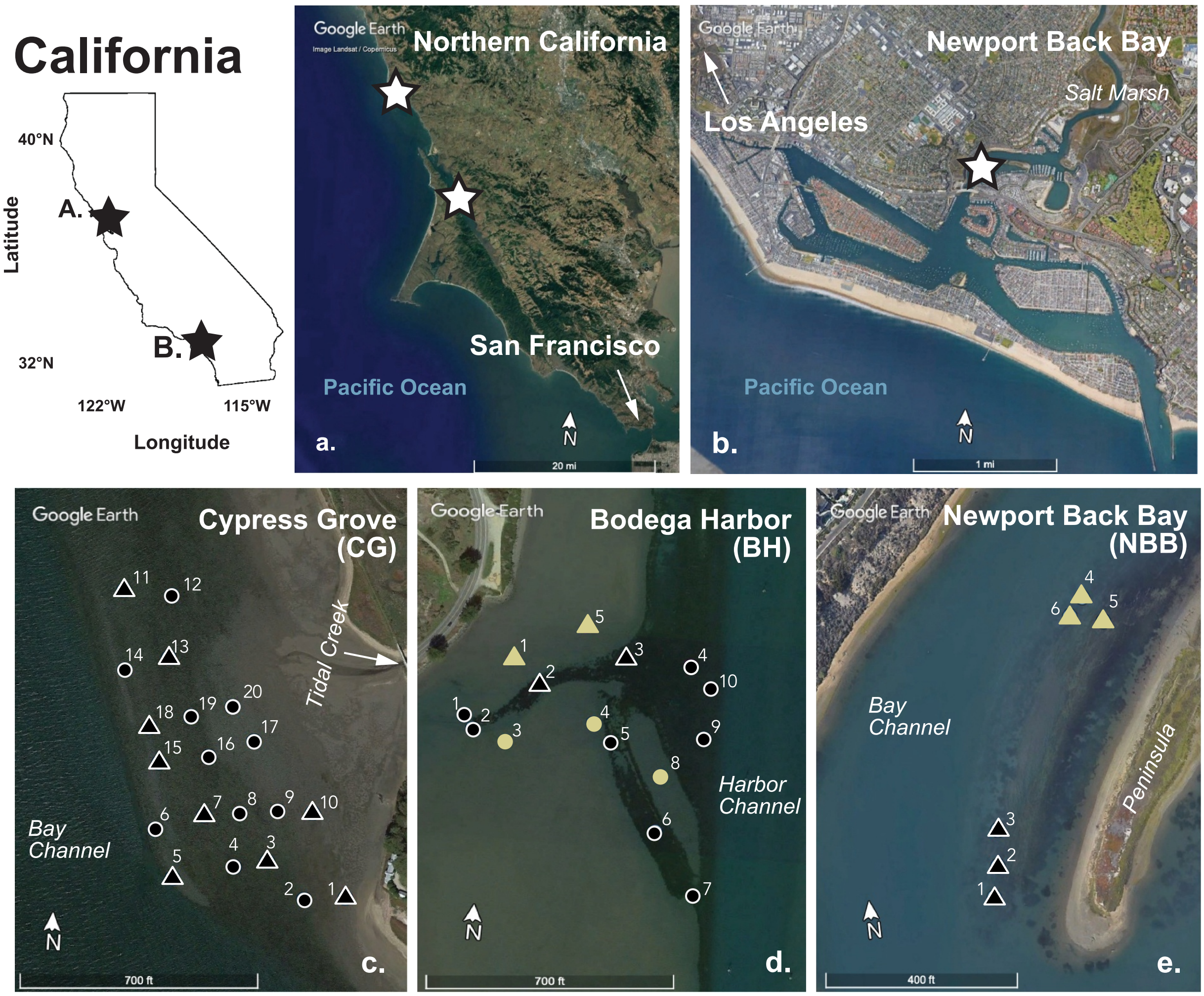

Figure 1. Map of California. (a) From north to south, the location of Bodega Harbor (BH) and Cypress Grove (CG) at Tomales Bay (shown as white stars). (b) Study site at Newport Back Bay (white star). (c) Cypress Grove vegetated core sampling locations. Black circles denote locations where surface samples were collected and black triangles denote locations where surface, intermediate, and deep samples were collected. (d) Bodega Harbor vegetated core sampling locations. Black and tan circles denote locations where surface vegetated and unvegetated samples were collected; black and tan triangles denote locations where surface, intermediate, and deep vegetated and unvegetated samples were collected. (e) Newport Back Bay vegetated and unvegetated core sampling locations shown as black triangles and tan triangles, respectively. See Table S1 in Supporting Information S1 for GPS coordinates.

(CG) in Tomales Bay occupied approximately 1 km^2 (Figure 1c). The meadow itself is adjacent to a tidal creek inhabited by marsh and land plants (Figure 1c). Previous work using ^{210}Pb chronologies on 20 cm sediment cores suggest that sedimentation rates at Tomales Bay and specifically at CG range from 0.1 to 1.0 cm/yr in reflecting approximately 100 years/20 cm (L. Capece, 2019).

Bodega Harbor (BH) is an actively dredged ~2.9 km^2 shallow embayment located approximately 11 km north of the mouth of Tomales Bay and dominated by mud flats and *Z. marina* meadows (Ronan et al., 1981). There are no significant creeks or rivers contributing to freshwater inputs to BH although there are natural springs and groundwater flow into the bay. Sediment supply to the harbor is controlled by jetties, wind-driven transport from adjacent dunes, and dredging (Ward et al., 2021). At the time of sampling the seagrass meadow at BH was approximately 1 km^2 and was situated next to the main dredged channel as well as a neighboring tidal flat creek (Figure 1d).

Newport Bay receives sediment and nutrients from the San Diego Creek watershed, surrounding urban environment and coastal ocean. Newport Back Bay (NBB) is an ecological marsh preserve that along with the rest of the bay, has been negatively impacted by eutrophication and high sedimentation rates (Ward et al., 2021).

Table 1

The Average and Range for Mud Content (%), TOM (%), Organic Carbon Content (mg C/cm³), C/N Ratios, and δ¹³C Signatures (‰) for Vegetated and Unvegetated Sediments at All Sites

Site	Interval	Mud (%)	Range	TOM (%)	Range	C (mg/cm³)	Range	C/N (molar)	Range	δ¹³C (‰)	Range	n =
Depth Averaged Sediment Characteristics Measured in Seagrass Meadows												
Cypress Grove Vegetated	Surface	16.0	4.8–39.1	3.8	1.9–11.9	4.7	0.9–11.4	9	6–12	−19.8	−21.5–−18.4	19*, 20
	Intermediate	18.1	8.0–39.2	2.1	1.3–4.8	3.4	0.9–8.9	8	6–11	−20.2	−21.8–−19.6	10*, 13
	Deep	13.9	5.3–43.1	1.8	1.1–3.6	3.2	1.1–7.9	8	6–12	−20.3	−22.7–−16.1	10*, 13
	Top 18 cm	**16.0**		**2.6**		**3.8**		**9**		**−20.1**		
Bodega Harbor Vegetated	Surface	27.1	18.5–37.6	3.2	2.0–3.9	8.7	2.7–12.4	9	8–11	−18.1	−20.7–−18.0	10*, 15
	Intermediate	24.6	13.5–35.7	3.0	1.9–3.7	8.4	0.8–14.7	10	9–13	−18.8	−20.6–−17.0	10*, 12
	Deep	21.3	–	3.6	3.2–4.0	8.1	7.3–8.9	10	9–10	−18.1	−18.4–−17.8	2
	Top 18 cm	**24.3**		**3.2**		**8.4**		**10**		**−18.3**		
Bodega Harbor Unvegetated	Surface	15.6	8.7–22.1	2.3	1.7–2.9	5.4	3.3–8.6	8	8–9	−17.7	−18.7–−16.9	5*, 8
	Intermediate	10.8	4.8–15.4	1.8	1.3–2.4	3.3	2.2–5.9	8	8–9	−18.8	−19.6–−18.0	5*, 6
	Deep	13.2	3.7–8.6	1.4	1.3–1.5	4.3	0.8–14.7	8	8–9	−18.3	−19.5–−18.6	2
	Top 18 cm	**13.2**		**1.8**		**4.3**		**8**		**−18.3**		
Newport Back Bay Vegetated	Surface	32.4	26.4–36.9	3.4	2.9–3.8	5.7	4.4–6.5	10	1–8	−22.6	−23.0–−22.1	3*, 4
	Intermediate	38.0	33.6–42.3	2.6	1.6–3.2	6.4	5.0–7.5	12	10–12	−23.5	−24.2–−23.0	3*, 4
	Deep	36.3	30.7–40.5	3.8	2.9–4.8	4.8	3.6–6.7	14	11–18	−22.6	−24.3–−19.0	3*, 4
	Top 18 cm	**35.6**		**3.3**		**5.6**		**12**		**−22.9**		
Newport Back Bay Unvegetated	Surface	8.0	6.0–10.5	1.2	0.8–1.7	1.3	0.2–3.1	4	6–12	−24.5	−25.0–−23.8	3*, 4
	Intermediate	26.4	24.2–28.5	2.3	1.9–2.5	4.7	3.3–5.5	11	6–11	−23.8	−25.3–−22.7	3*, 4
	Deep	26.1	22.6–28.0	2.3	2.3–2.4	4.2	3.6–5.1	13	6–12	−23.3	−25.7–−18.8	3*, 4
	Top 18 cm	**20.2**		**2.0**		**3.4**		**12**		**−23.9**		

Note. The * denotes the sample size (n) for measurements of the parameter mud content whereas the number without the * is the sample size for all other parameters.

Seagrass *Z. marina* is actively being restored and occupies approximately 1 km² of the bay as of 2015 (Orange County Coastkeeper, 2015). The seagrass meadow at NBB that we sampled is located on the western side of a tidally connected marsh peninsula where at the time of sampling a meadow occupied an area of approximately 0.03 km² (Figure 1e).

2.2. Sample Collection

Cypress Grove (CG) in Tomales Bay was sampled in July 2018. Bodega Harbor (BH) was sampled in October 2018 and then again in January 2019. Newport Back Bay (NBB) was sampled in May 2018 (Figures 1a–1e). Short sediment cores (20 cm deep, 5 cm in diameter) were manually taken from all sites during low tide (Table 1). Cores from CG and BH were taken across the surface area of each meadow every 30–50 m in order to assess variability of intra-meadow OC storage. CG sediment cores ($n = 20$) were primarily taken from centrally located fully vegetated sediments and edge regions of the meadow that had more patchy seagrass coverage but are still considered part of the meadow (CG Vegetated) (Figure 1c). At BH, sediment cores were taken within the meadow (BH Vegetated, $n = 10$) and in adjacent unvegetated sediments no more than 30–50 m away (BH Unvegetated, $n = 5$) (Figure 1d). At the time of sampling adjacent unvegetated sampling locations had been absent of dense seagrass since at least 2005 (Google Earth). A total of six cores were collected from NBB, three from within the meadow (NBB Vegetated, $n = 3$) and three in adjacent unvegetated sediment (NBB Unvegetated, $n = 3$; Figure 1e). At NBB all cores were roughly 20 m apart from each other, and vegetated and unvegetated sampling

Table 2
Average and 1σ Standard Deviation of C/N Ratios and Carbon Isotope Compositions of Biomass Used to Establish Endmembers in Figure 5

Sample type	C/N (molar)	1σ SD	δ13C (‰)	1σ SD	n =
Average Isotope and Elemental Composition of Potential Organic Matter Sources.					
Phytoplankton (Cloern et al., 2002)	8	3	−22.6	1.7	91
SPOM (this study)	8	3	−21.5	2.2	8
C3 Plants (Cloern et al., 2002)	29	18	−27.2	3.6	118
C4 Plants (Cloern et al., 2002)	27	10	−14.9	2.1	104
Seagrass (this study)	22	9	−9.3	0.9	14

Note. Data are from this study and Cloern et al., 2002.

locations were within 200 m of each other. At the time of sampling these adjacent bare sediment sampling locations at NBB had been unvegetated since at least 2012 (Orange County Coastkeeper, 2015). Samples from adjacent bare or unvegetated sediments to seagrass meadows were collected to represent potential control sites to vegetated seagrass sediments. All cores were transported upright to the University of California, Davis Bodega Marine Laboratory (BML) using ice packs and kept refrigerated until they could be extruded 1–2 days after retrieval. Cores taken at NBB were frozen and then transported on ice to BML and extruded 1–2 days after retrieval.

2.3. Sediment Geochemistry

All cores were extruded at 2 cm intervals and evaluated at surface (2–4 cm), intermediate (8–10 cm) and deep (16–18 cm) sediment sections. After removal of seagrass below ground biomass components (rhizomes) sediment samples were dried for 72 hr at 60°C. Homogenized subsamples from all sections were taken for analysis of dry bulk density (DBD = g sediment/cm^3), total organic matter (TOM), mud content was quantified as the proportion of sediment grains smaller than 63 μm and is expressed as a percent (%), the carbon to nitrogen ratio (C/N), and organic carbon content (mg C/cm^3 = DBD *percent organic carbon) and isotopic composition ($\delta^{13}C$ values) of organic carbon following the methods outlined below.

Mud content was measured as percent mass loss after wet sieving sediment with a 63 μm sieve. TOM was determined as percent mass loss following loss on ignition for 4 hr at 550°C for all sediment samples (Heiri et al., 2001). A subset of extruded sediment samples from each site were sampled for decarbonation via rinsing with 1.12 M HCl following methods used in (Ward et al., 2021) and were then used to determine the $\delta^{13}C$ values and organic carbon content of organic matter for all samples from. Element and isotopic composition analyses were carried out at the UC Davis Stable Isotope Facility on an Elementar vario MICRO cube elemental analyzer interfaced to an Elementar VisION isotope ratio mass spectrometer (Elementar Analysensysteme GmbH, Langenselbold, Germany). Results are expressed relative to Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$ values and precision for analyses is within 0.2‰. See Supporting Information S1 (Tables 1 and 2, Figures 1a–1e and 2) for a more detailed description of the methods used to determine the carbon isotope composition and organic carbon in organic matter.

2.4. Modeling Organic Matter Sources Using $\delta^{13}C$ Values and C/N Ratios

We used the Bayesian simmr model (Govan et al., 2023) to determine the sources of OC to seagrass meadows using the $\delta^{13}C$ values and C/N ratios of potential sources including seagrass, phytoplankton/SPOM, C3 and C4 plants as tracers to unmix sediment $\delta^{13}C$ values and C/N ratios (Meyers, 1994; Meyers & Ishiwatari, 1993; Thornton & McManus, 1994). Seagrass leaf and rhizome samples were collected in the field at CG, BH, and NBB and transported back to BML where they were subsequently cleaned of epiphytic and epifaunal growth and dried. Water samples for suspended particulate organic matter (SPOM, inclusive of plankton) were collected in July 2018 at CG and used to determine the $\delta^{13}C$ values and C/N ratios of the suspended particulate organic matter (SPOM) endmember. Water samples were filtered through pre-weighed and combusted 0.45 μm GF/F Whatman filters which were subsequently acid fumigated with 12M HCl for 6 hr (Ricart et al., 2015). The remaining solid material on the filters (SPOM) as well as the dried and homogenized bulk. The SPOM and combined seagrass leaf

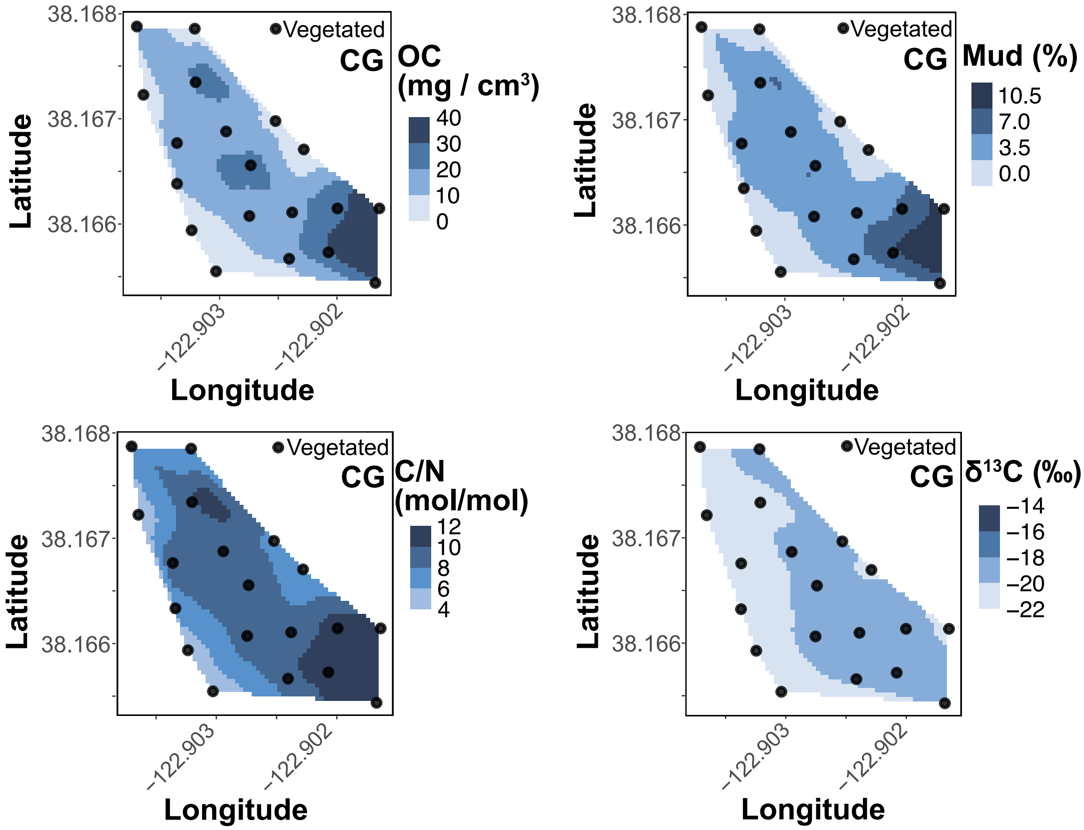

Figure 2. Cubic interpolated mud content (%), organic carbon content (mg C/cm^3), C/N ratios and δ^{13}C values (‰) of surface sediments at CG.

and rhizome biomass were then measured for their δ^{13}C values and C/N ratios. Carbon and nitrogen elemental and isotopic analyses were carried out at the UC Davis Stable Isotope Facility on an Elementar vario MICRO cube elemental analyzer interfaced to an Elementar VisION isotope ratio mass spectrometer (Elementar Analysensysteme GmbH, Langenselbold, Germany). Results are expressed relative to VPDB (Vienna Pee Dee Belemnite) for δ^{13}C and precision for analyses is within 0.2‰. The δ^{13}C values and C/N ratios of other potential endmembers including phytoplankton, C3 marsh plants, and C4 marsh plants which are found locally at CG, BH, and NBB (Ward et al., 2021) were evaluated as potential source material for the organic matter buried in seagrass sediments using endmember data from Cloern et al. (2002) (see Table 2).

2.5. Statistical Approach

To determine if spatial correlation existed across environmental controls of organic carbon content in surface sediments at CG and BH we used spatial error models. Linear models (LM) were used in place of spatial error models to understand relationships between organic carbon, mud content, C/N ratios, and δ^{13}C values if the spatial error coefficient (λ) was not statistically significant. To compare differences in sediment organic carbon content across sites we calculated the depth-integrated mean of measured parameters (mud content, C/N ratios, and δ^{13}C values) for depth intervals surface (0–2 cm), intermediate (8–10 cm), and deep (16–18 cm) (hereon "depth-integrated mean"). We then used linear mixed-effects models (LMM) to evaluate differences in depth-integrated mean between vegetated and unvegetated sediments, using "vegetation status" (vegetated = V or unvegetated = UV) as a fixed effect, and "site" (CG, BH, NBB) as a random effect. We then ran a Kruskal-Wallis test to determine if significant differences between the depth-integrated mean organic carbon content, mud content, C/N ratios and δ^{13}C values also varied across study sites given their vegetation status (CGV, BHV, BHUV, NBBV, NBBUV) performing Dunn's Test to reveal drivers of significant differences among sites. To explore the relationships between organic carbon content and the potential drivers of interest (i.e., grain size and source of organic matter) we first used linear models (LM) to understand relationships between organic carbon

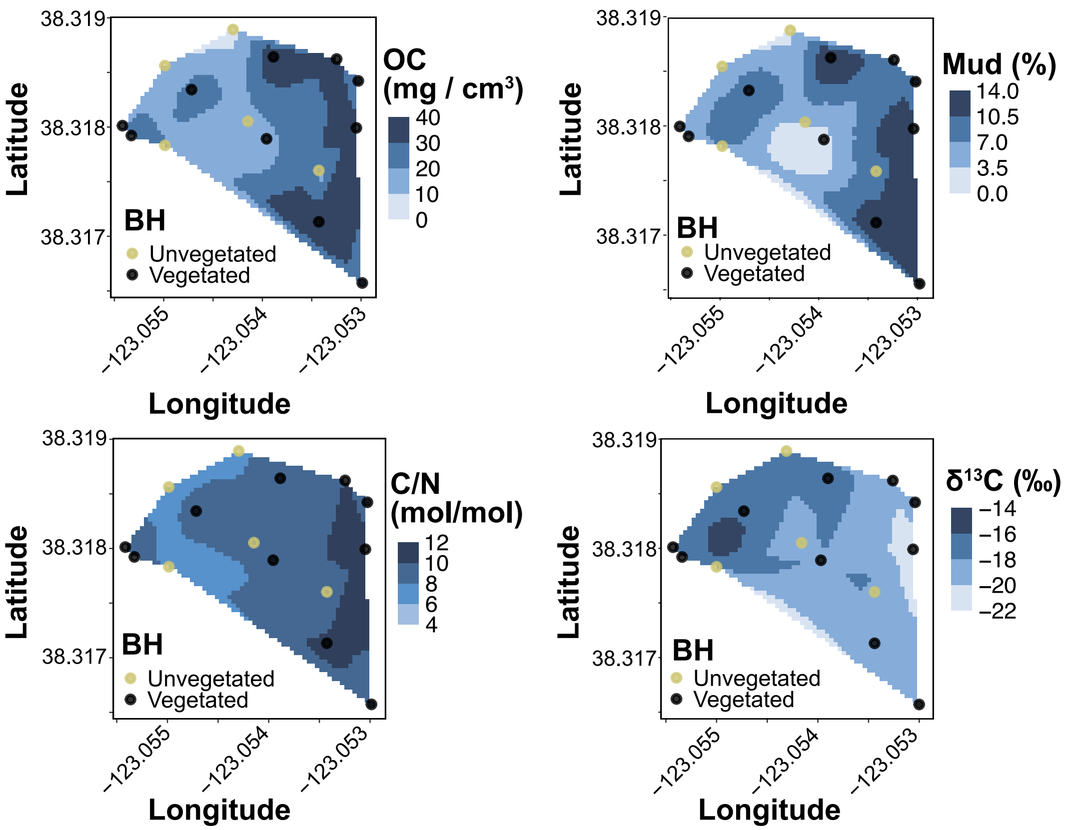

Figure 3. Cubic interpolated mud content (%), organic carbon content (mg C/cm3), C/N ratios and δ^{13}C values (‰) of surface sediments at BH. Black and tan dots represent vegetated and unvegetated sediments, respectively.

content, mud content, C/N ratios across all sample intervals. We then used LMMs to understand relationships between organic carbon content and potential drivers with depth-integrated mean mud content, C/N ratios, and δ^{13}C values as fixed effects and site vegetation status as random effects (CGV, BHV, BHUV, NBBV, and NBBUV). To predict organic carbon, we used Akaike Information Criterion (AIC) to determine the most parsimonious models relative to a null model. While p-values < 0.05 were considered statistically significant for all tests, we report the actual value in text if p > 0.01. All statistical analyses were conducted in *R* Statistical Software (R version 4.4.3, 2025) using built-in functions, akima, gstat, spdep, spatialreg, simmr, and lme4 packages.

3. Results

3.1. Intra-Meadow Spatial Patterns in Organic Carbon Storage Across Surface Sediments

CG mud content (LM: $R^2 = 0.97$, $p < 0.01$) and C/N ratios (LM: $R^2 = 0.85$, $p < 0.01$) of surface sediments (2–4 cm depth) were significantly correlated with organic carbon while δ^{13}C values were not (Figure 2). Sediments with a higher mud content, higher organic carbon content and higher C/N ratios were located in the east and southeast corner of the meadow (shallower water, closer to shore) while lower mud (%), lower organic carbon content, and lower C/N ratios sediments were located in deeper water, closer to the channel of the bay. Additionally, δ^{13}C values of organic matter are more ^{13}C-enriched in the east portion of the meadow compared to the west (Figure 2).

At BH, the mud content and organic carbon (LM: $R^2 = 0.79$, $p < 0.01$) were significantly correlated and were highest in the southeast corner of the meadow closest to the harbor channel (Figure 3). C/N ratios and δ^{13}C values were also significantly correlated with organic carbon, but spatial error models confirmed residual spatial autocorrelation such that organic carbon varies beyond what C/N ratios and δ^{13}C values explain (Figure 3). Higher C/N ratios are observed primarily in the eastern side of the meadow, whereas the lowest C/N ratios are

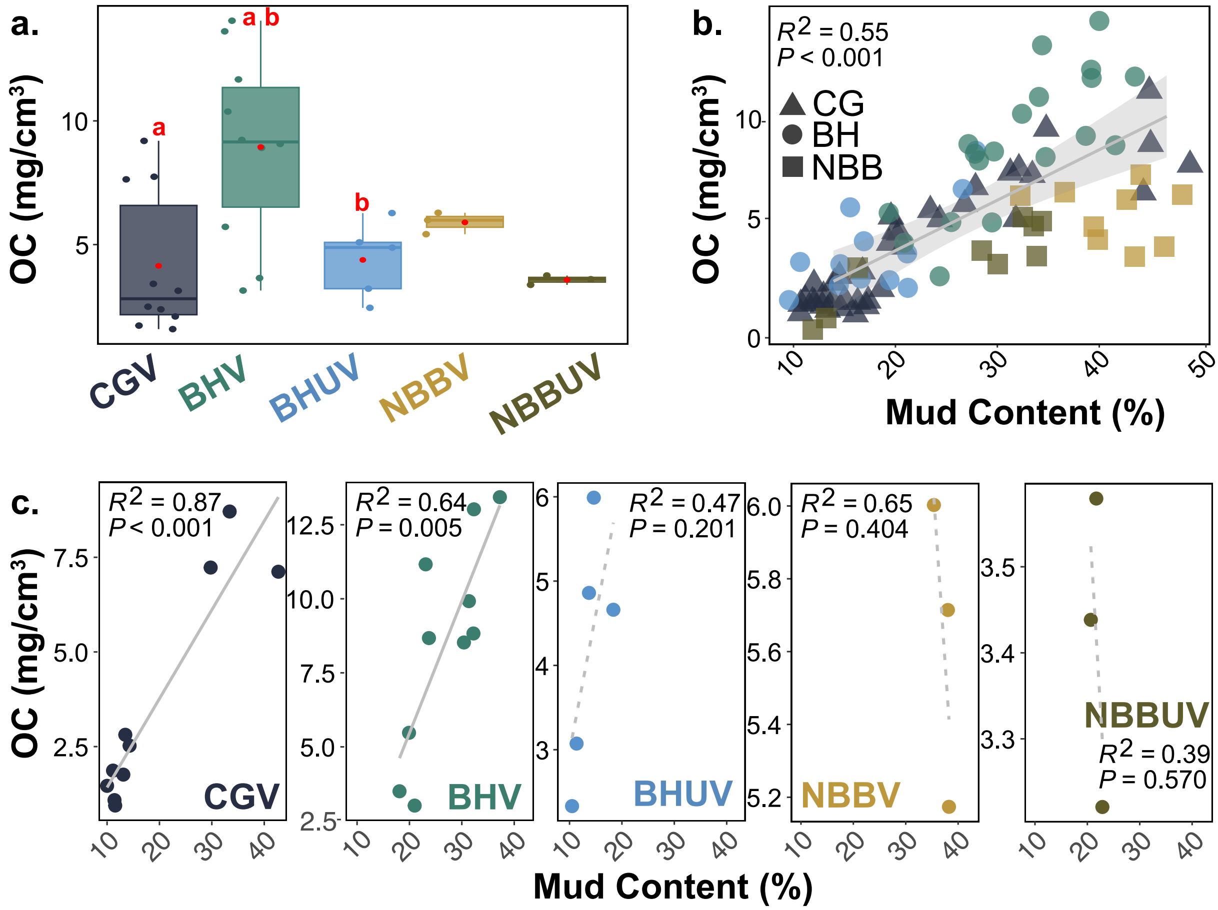

Figure 4. (a) From left to right boxplots showing the distributions of organic carbon (mg C/cm3) in depth-integrated mean vegetated and unvegetated sediment cores at CG, BH, and NBB. Red dots represent the mean sediment organic carbon for each site. Significant differences in sediment organic carbon between sites following pairwise comparisons are denoted by letter "a" with $p < 0.01$ or "b" $p = 0.04$. (b) The overall regional relationship between organic carbon and mud content. (c) Left to right, the relationship between depth-integrated mean organic carbon and mud content at CG, BH, and NBB vegetated and unvegetated sediments.

found in the western side of the meadow. ^{13}C-depleted δ^{13}C values were found in the southeast part of the meadow whereas ^{13}C-enriched δ^{13}C values were found in the northwest part of the meadow (Figure 3).

3.2. Regional Differences in Sediment Organic Carbon

The mean and range for measured sediment characteristics across surface, intermediate, and deep depth intervals are summarized in Table 1. No significant correlations in measured parameters were found with depth (Figure S3 in Supporting Information S1). The depth-integrated mean organic carbon content across vegetated sites was highest at BH (8.4 mg C/cm^3) and lowest at CG (3.8 mg C/cm^3) (Table 1). The variance (standard deviation) in depth-integrated mean organic carbon content in vegetated sites at the California wide scale was 3.6 mg C/cm^3 which was the same as the variance of depth-integrated mean organic carbon content at BH (3.6 mg C/cm^3), but higher than CG (2.9 mg C/cm^3) or NBB (1.4 mg C/cm^3) (Table S4 in Supporting Information S1). The depth integrated mean mud content was lowest in CG sediments (16.0%) and highest in NBB vegetated sediments (35.6%) (Table 1). The depth integrated mean C/N ratios across vegetated sediments ranged from 5.8 to 9.6 and were highest at NBB (9.6) and lowest at CG (5.8) (Table 1). The depth-integrated mean δ^{13}C values of vegetated sediments across all sites ranged from −18.3 to −22.9‰. The δ^{13}C values of vegetated sediments were the most ^{13}C-depleted at NBB and ^{13}C enriched at BH (Table 1).

The presence of vegetation had a significant influence on the depth-integrated mean organic carbon in sediments (LMM, χ^2 (1) = 8.91, $p < 0.01$), increasing it by 3.82 ± 1.22 organic carbon mg C/cm^3 (Figure 2). Across sites and vegetation status the depth-integrated mean organic carbon (Kruskal-Wallis, $\chi^2(3) = 11.56$, $p = 0.02$) (Figure 2), mud content (Kruskal-Wallis, $\chi^2(4) = 13.95$, $p < 0.01$), C/N ratios (Kruskal-Wallis, $\chi^2(4) = 16.30$, $p < 0.01$), and $\delta^{13}C$ values (Kruskal-Wallis, $\chi^2(4) = 20.94$, $p < 0.01$) varied significantly.

Across sites, vegetation status, and depth intervals higher mud content (LM, $R^2 = 0.55$, $p < 0.01$, Figure 4b), C/N ratios (LM, $R^2 = 0.27$, $p < 0.01$), and ^{13}C-enriched $\delta^{13}C$ values (LM, $R^2 = 0.32$, $p = 0.048$) were correlated with increasing organic carbon. Mud content was the best predictor of depth-integrated mean (LMM, $\chi^2(1) = 25.875$, $p < 0.01$) such that for every 1% increase in mud content, organic carbon increased by 0.26 mg C/cm^3. However, the relationship between mud content and organic carbon was not significant for sites other than CG and BH vegetated (Figure 4c) (BH Unvegetated, NBB Unvegetated, Vegetated, Figure 4c). The second-best models used mud content and C/N ratio to predict depth-integrated mean organic carbon ($p < 0.01$, ΔAIC = 1.28); however, incorporating C/N or $\delta^{13}C$ values separately or together did not improve model fit and was not significant.

3.3. Isotope and Elemental Composition of Potential Organic Matter Sources

The mean C/N ratios and $\delta^{13}C$ values of potential organic matter sources to the vegetated seagrass sediments at our sites are shown in Table 2. As anticipated, the range in $\delta^{13}C$ values and C/N ratios of the SPOM endmember is similar to those of the phytoplankton endmember and less similar to the other source endmembers. The C/N ratios and $\delta^{13}C$ values (Figure 5a) provides a qualitative assessment of potential sources of organic matter to vegetated and unvegetated seagrass sediments. The majority of sediment samples were clustered within the range for C/N ratios and $\delta^{13}C$ values of the phytoplankton and SPOM endmembers (Figure 5a). No sediment samples were close to the seagrass endmember (Figure 5a). NBB vegetated and unvegetated sediment samples were closer to the C3 plants endmember than other sediment samples (Figure 5a). These patterns in C/N ratios and $\delta^{13}C$ values are reflected in the simmr (Govan et al., 2023) output where the combined phytoplankton and SPOM inputs made up 11%–19% of organic matter across sites and C3 inputs made up 60% of organic matter at NBB (Figure 5b). Inputs of potential sources of organic matter varied across study sites (CG, BH, NBB) and were relatively evenly split between potential inputs (Figure 5b). However, seagrass and C4 inputs were highest at BH and CG, making up 17% and 26%, and 26% and 28%, of organic matter, respectively (Figure 5b).

4. Discussion

4.1. Spatial Variability in Seagrass Carbon Storage and Mud Content

Seagrass sediment organic carbon content (mg C/cm^3) varies across the intra-meadow and regional spatial gradients. Surface (2–4 cm) organic carbon at CG varies spatially between 0.9 and 11.4 mg C/cm^3, while at BH organic carbon varies spatially between 2.7 and 12.4 mg C/cm^3 (Figures 2 and 3). The highest organic carbon samples group in specific regions within each meadow suggesting that relative position within the meadow has an impact on carbon storage (Figures 2 and 3). At CG, higher organic carbon content is found in the central and southeastern areas of the meadow, farthest from the bay channel, whereas at BH organic carbon is highest in the southeastern part of meadow close to the harbor channel. In these meadows, higher organic carbon is also associated with higher mud content, suggesting that reduced hydrodynamic conditions in these regions promotes the accumulation of fine sediments and organic carbon (Figures 2 and 3). While we do not have in situ hydrographic data, previous studies have documented the correlation between higher mud content, organic carbon and lower Reynolds stress (Dahl et al., 2016; Miyajima et al., 2017; Oreska, Wilkinson, et al., 2017; Prentice et al., 2019) and suggest that the relationship is driven by the accumulation of finer size grains in lower energy environments which results in more carbon retention due to the higher surface area of smaller grains and greater availability of sediment surface interaction with organic matter and its protection (Burdige, 2007; Hedges & Keil, 1995; Hemingway et al., 2019; Mayer & Rossi, 1982). Depositional environments that enhance the settling of finer material (mud sized grains and particulate organic carbon) could be facilitated by numerous factors such as seagrass canopy structure or complexity, bathymetry, local geomorphology, and tidal current velocity and direction (Fonseca & Bell, 1998; Hansen & Reidenbach, 2012; Lei et al., 2023; Mazarrasa et al., 2021; Tecchiato et al., 2019). At CG and BH the highest organic carbon is found within seagrass vegetated sediments suggesting that seagrass canopy structure could be helping to form depositional environments that enhance settling of mud and organic matter (Figures 1c, 1d, 2a and 3a). Our sampling strategy and analysis of surface organic carbon and mud content across CG and BH, reveals significant spatial heterogeneity that could be missed if a single-point sampling strategy were used.

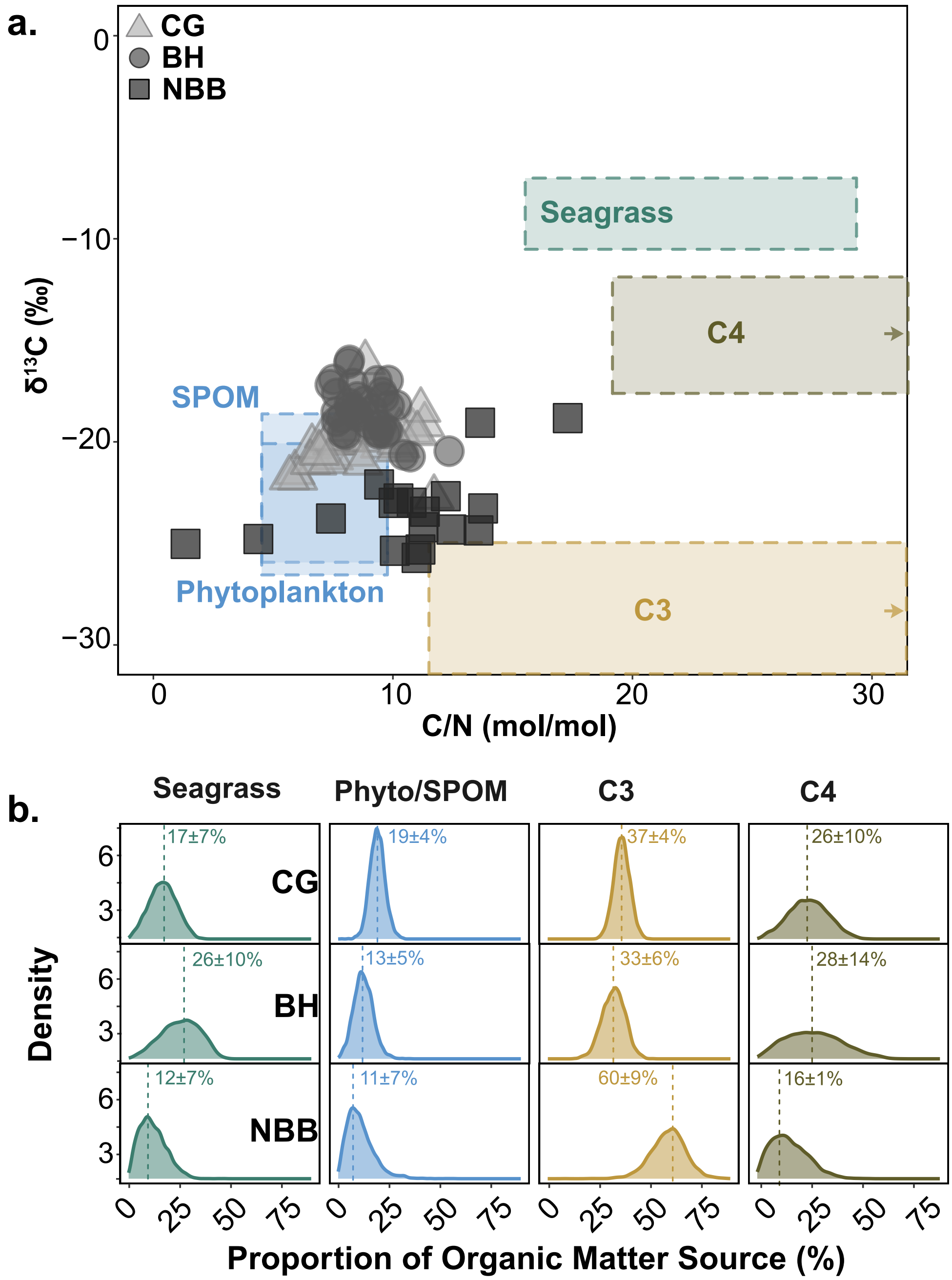

Figure 5. (a) The depth-integrated mean C/N ratios and $\delta^{13}C$ values (‰) for each sediment sample from vegetated sediment at CG, BH, and NBB. Range of C/N ratios and $\delta^{13}C$ values of endmember organic matter inputs are plotted as boxes (arrows represent range in values outside of the *x*-axis bounds of the figure). (b) Simmr model output as posterior distributions for each site and source input. The mean and standard deviation of the posterior distribution of source inputs is denoted by a dashed line.

Regionally, we find that the presence of seagrass vegetation enhances depth-integrated mean organic carbon (Figure 4a). While this finding has been reported before (Gagnon et al., 2024; Githaiga et al., 2017; Márba et al., 2015; Singh et al., 2022), previous work in seagrass meadows in California show higher average organic carbon stocks in some bare sediments compared to neighboring seagrass meadows (Ward et al., 2021). These contrasting results highlight the importance of scale and sampling resolution: our high-resolution, site-specific approach and direct measurement of organic carbon via elemental analysis likely enabled a more comprehensive assessment of localized drivers of carbon storage. Depth-integrated mean organic carbon content varies significantly across regional vegetated sites (Figure 4a); mean organic carbon in vegetated sediments at BH was highest followed by CG and NBB. Regionally, higher organic carbon is driven by higher mud content (Figure 4b), which could potentially mean that at BH, lower hydrodynamic energy enhances organic carbon storage at this site compared to others. Mean mud content in vegetated sediments at BH were highest followed by CG and NBB. Several recent studies have shown that higher organic carbon and higher mud content or smaller grain size in seagrass meadows is correlated with locations with lower wave exposure and reduced hydrodynamic conditions at the regional scale (Gagnon et al., 2024; Mazarrasa et al., 2021). As discussed above, carbon accumulation and storage at BH compared to the other sites may be aided by hydrodynamic conditions. Vegetated sediments in NBB, however, have equally high mud content as BH (>30%, Figure 4b), but organic carbon is lower than the organic carbon predicted by our regional model (Figure 4b) and no significant relationship exists between mud content and organic carbon (Figure 4c). This highlights the significance of understanding site specific drivers of carbon storage in seagrass meadows and that sediment grain size is not always the primary predictor of organic carbon content.

Taken together, our assessment of intra-meadow, vegetated and unvegetated sites, and regional organic carbon trends show that there are quantifiable differences in the spatial relationships of organic carbon at multiple spatial scales and that these differences are not quantified exclusively by mud content.

4.2. Sources of Organic Matter to Seagrass Meadows and Carbon Storage

Linear mixed models (LMMs) show that mud content and C/N ratio are significant predictors of intra-meadow and regional differences in depth-integrated mean organic carbon. Regionally higher organic carbon is associated with higher C/N ratios (depth-integrated mean > 8) and ^{13}C-enriched δ^{13}C values (depth-integrated mean, >−20‰), although the latter is not statistically significant in our LMMs. At the regional scale this could be driven by the presence of seagrass derived δ^{13}C values around −9.3 ± 0.9‰. At the regional scale, the highest modeled proportion of seagrass derived organic matter is found at BH (26%) followed by CG (17%) and NBB (12%) (Figure 5b). While the proportion of modeled allochthonous organic matter inputs (C3 and C4 plants, phytoplankton/SPOM) at all sites is larger (≥74%) than seagrass derived organic matter, at BH and CG where the proportion of seagrass derived organic matter is higher, organic carbon is also higher (Figure 5b). This further supports that the presence of seagrass biomass provides an additive benefit to carbon preservation potentially due to the input of less reactive organic compounds such as ligno-cellulose which is less easy to breakdown compared to less complexed organic matter such as algae or phytoplankton (Kristensen, 1990; Twilley et al., 1986). NBB is proximal to a large tidal marsh with abundant C3 marsh plants (*Salicornia spp*.) and is potentially influenced by terrestrial inputs from the urban watershed (Ward et al., 2021) which typically have higher C/N ratios and ^{13}C-depleted δ^{13}C values (Meyers, 1994; Meyers & Ishiwatari, 1993). This results in sediment that is ^{13}C-depleted (average = −22.9‰, range = −19.0 to −24.3‰) relative to the carbon isotope composition of seagrass inputs (δ^{13}C = −9.3 ± 0.9‰, Table 2) and is consistent with higher modeled contribution of C3 marsh plants at this site (60%) compared to the others (BH = 33%, CG = 37%) (Figure 5b). Model results also indicate that phytoplankton/SPOM (11%–20%) contribute to seagrass sediment organic matter consistent with other studies (Kennedy et al., 2010; Mazarazza et al., 2017). Typically, phytoplankton derived organic matter is considered to be more reactive and therefore less likely to be preserved (Kristensen, 1990, 1994; Trevathan-Tackett et al., 2015; Twilley et al., 1986); however, the high organic matter input to seagrass sediments create anoxic conditions favoring slow degradation and perhaps sulphurization reactions, which may be fueled by algae-like organic matter (L. R. Capece et al., 2025). Together these findings support that seagrass meadows trap and accumulate organic matter in the water column such that underlying sediments act as an additional sink for organic matter from nearby marsh habitats (C3 marsh plant/terrestrial) and marine environments (phytoplankton/SPOM) enhancing the carbon storage capacity of these ecosystems (Greiner et al., 2016; Kennedy et al., 2010; Oreska, McGlathery, & Porter, 2017; Prentice et al., 2019; Rohr et al., 2018).

The sources of organic matter as interpreted by the C/N ratios and δ^{13}C values in surface sediments at CG and BH also vary at the intra-meadows scale. At CG, higher organic carbon content in the southeastern part of the meadow is colocated with more ^{13}C-enriched δ^{13}C values and higher C/N ratios compared to the rest of the meadow suggesting that higher contributions of phytoplankton or seagrass derived organic matter occurs in this region of the meadow over the northwest region (Figure 2, Table 2). At BH the higher organic carbon content in the southeastern part of the meadow are co-located with more ^{13}C-depleted δ^{13}C values and higher C/N ratio relative indicating that higher contributions of terrestrial organic matter sources (C3 marsh plants) or another allochthonous organic matter source, potentially introduced from the harbor, occurs in this region of the meadow over the northwest region (Figure 3, Table 2). Differences in the dominant source of organic matter in surface sediments co-located with the higher organic carbon between these two sites further emphasize that organic matter source and its composition is a weaker predictor of organic carbon compared to mud content and that site specific factors govern organic carbon storage.

4.3. Impacts on Blue Carbon Accounting

Understanding the controls on the spatial variability and chemical composition of organic carbon preserved within seagrass meadows and between meadows is critical in determining the capacity of these ecosystems to serve as long-term organic carbon sinks and as potential opportunities for carbon crediting (Ward et al., 2025). Our study highlights the heterogeneity in organic carbon storage in seagrass meadows across multiple spatial scales in California. The variance in depth-integrated organic carbon at the California-wide or regional scale (3.6 mg C/cm^3) is equal to the variance at BH (3.6 mg C/cm3), and surface sediments at BH alone show nearly as much variability (3.4 mg C/cm^3) (Table S4 in Supporting Information S1, Figures 3 and 4). This highlights that local variability in organic carbon can rival regional variability, underscoring the need for adequate sampling to support accurate blue carbon stock estimates in California. This level of local meadow variability is substantial and aligns with findings from other seagrass systems in the Mediterranean and Australia where there is up to an order of magnitude difference in carbon content across regional sites (e.g., Lavery et al., 2013; Ricart et al., 2015). Such high spatial variability at our study sites highlight the challenge of scaling up carbon stock estimates from limited field samples as under-sampling could lead to overestimation or underestimation of regional carbon stocks, which directly inform statewide climate goals, greenhouse gas inventories, and carbon mitigation opportunities (Janousek et al., 2025; Lavery et al., 2013).

We also demonstrate that mud content as a predictor of organic carbon performs well at some spatial scales (e.g., regionally), but not at others (e.g., intra-meadow, site specific) and therefore should not act as a replacement for measuring carbon content in seagrass sediments in California but could serve as a preliminary assessment tool for the selection of conservation or restoration project sites. While sources of organic matter to sediment might have an impact on organic carbon storage, we find that C/N ratios and $\delta^{13}C$ values are not good predictors of organic carbon in isolation acknowledging limitations in their interpretation due to the impact of diagenetic processes such as preferential loss of nitrogen or selective preservation of more ^{13}C-depleted compounds in sediments such as lipids or lignin leading to compositions that do not match an original organic matter source (Burdige, 2007; Kennedy et al., 2010). However, by quantifying source contributions of organic matter, we assign a value of carbon storage attributed to seagrass and determine where seagrass derived—or non-point source organic matter inputs like C3 plants, C4 plants, and phytoplankton/SPOM derived—organic carbon preservation is maximized. This could aid conservation and restoration planning by informing where organic carbon storage is driven by in situ production versus ex situ production. Within the voluntary carbon market, projects seeking to restore or conserve seagrass meadows for carbon credits often deduct for allochthonous carbon (i.e., credits are discounted for carbon sourced from biomass outside the project area; Houston et al., 2024; Needleman et al., 2018). Thus, understanding the variation in allochthonous and autochthonous carbon within and across seagrass meadows can directly inform how these deductions are accurately included into carbon market projects.

In marine sediments and other blue carbon habitats, organic carbon preservation is dictated by a multitude of mechanisms or drivers in addition to the ones we tested, including sedimentation rate, existence of anoxic sedimentary conditions (Burdige, 2007), bioturbation (Aller, 1994; van de Velde et al., 2020), the binding of organic components to sticky extracellular polymeric substances produced by algae or bacteria (Drexler et al., 2020; Pacton et al., 2007), chemical adsorption or physical protection by minerals like iron-oxides and clays (Hemingway et al., 2019; LaRowe et al., 2020), microbial community composition (Cavicchioli et al., 2019), and the sulphurization of organic matter (L. R. Capece et al., 2025; Raven et al., 2019). Understanding the in situ biogeochemical and ecological processes that impact the preservation of sediment organic carbon can help determine the potential of seagrass meadows to serve as long-term carbon sinks.

5. Conclusions

This study underscores the need to understand and quantify intra- and inter-meadow scale carbon storage in seagrass sediments. We find significant differences in carbon storage across study sites in California documenting spatial patterns in carbon storage within two Northern California seagrass meadows. We also find significantly higher organic carbon in vegetated seagrass sediments compared to unvegetated sediments—a finding that, while unsurprising, has been contradicted in other studies within the region. We also find mud content to be a significant predictor at the regional scale but not at the sitescales. C/N ratios and $\delta^{13}C$ values used to determine sources of organic matter do not significantly predict organic carbon and show that sediment organic carbon is primarily sourced from allochthonous sources of organic matter. However, at study sites where organic carbon is higher, contributions of seagrass derived organic matter are also highest, elucidating the potential role of preservation of less reactive organic matter, such as lignocellulose rich seagrass, in enhancing carbon storage. Overall, we emphasize the need for future research that investigates carbon storage and its underlying mechanisms at local (intra-meadow) and regional scales in order to best inform proper restoration and management of these ecosystems, and to provide accurate estimates of blue carbon storage.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data that support the findings of this study are available in the Supporting Information S1 of this article and on Dryad https://doi.org/10.5061/dryad.5hqbzkhft (L. Capece, 2025).

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References

Aller, R. C. (1994). Bioturbation and remineralization of sedimentary organic matter: Effects of redox oscillation. *Chemical Geology*, *114*(3), 331–345. https://doi.org/10.1016/0009-2541(94)90062-0

Basta, D. J., & Bamford, H. A. (2013). Tomales Bay vessel management plan.

Blair, N. E., & Aller, R. C. (2012). The fate of terrestrial organic carbon in the Marine environment. *Annual Review of Marine Science*, *4*(1), 401–423. https://doi.org/10.1146/annurev-marine-120709-142717

Burdige, D. J. (2007). Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? *Chemical Reviews*, *107*(2), 467–485. https://doi.org/10.1021/cr050347q

Capece, L. (2019). *The origin of sedimentary organic carbon in temperate seagrass meadows in California estuaries*. University of California.

Capece, L. (2025). Bulk sediment geochemistry for seagrass meadows in three California estuaries [Dataset]. *Dryad*. https://doi.org/10.5061/dryad.5hqbzkhft

Capece, L. R., Bailey, M., Morrison, M., Phillips, A. A., Sharpnack, L., Webb, S. M., et al. (2025). Evaluating sulfurization as a blue carbon sink in a southern California salt marsh. *Limnology and Oceanography, lno*, *70*(7), 70089–71991. https://doi.org/10.1002/lno.70089

Cavicchioli, R., Ripple, W. J., Timmis, K. N., Azam, F., Bakken, L. R., Baylis, M., et al. (2019). Scientists' warning to humanity: Microorganisms and climate change. *Nature Reviews Microbiology*, *17*(9), 569–586. https://doi.org/10.1038/s41579-019-0222-5

Cebrián, J., Duarte, C. M., Marbá, N., & Enríquez, S. (1997). Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species. *Marine Ecology Progress Series*, *155*, 29–44. https://doi.org/10.3354/meps155029

Chambers, R. M., Hollibaugh, J., Snively, C. S., & Plant, J. N. (2000). Iron, sulfur, and carbon diagenesis in sediments of Tomales Bay, California. *Estuaries*, *23*, 1–9. https://doi.org/10.2307/1353220

Cloern, J. E., Canuel, E. A., & Harris, D. (2002). Stable carbon and nitrogen isotope composition of aquatic and terrestrial plants of the San Francisco Bay estuarine system. *Limnology & Oceanography*, *47*(3), 713–729. https://doi.org/10.4319/lo.2002.47.3.0713

Dahl, M., Deyanova, D., Gütschow, S., Asplund, M. E., Lyimo, L. D., Karamfilov, V., et al. (2016). Sediment properties as important predictors of carbon storage in Zostera marina meadows: A comparison of four European areas. *PLoS One*, *11*(12), e0167493. https://doi.org/10.1371/journal.pone.0167493

Drexler, J. Z., Davis, M. J., Woo, I., & De La Cruz, S. (2020). Carbon sources in the sediments of a restoring vs. historically unaltered salt marsh. *Estuaries and Coasts*, *43*(6), 1345–1360. https://doi.org/10.1007/s12237-020-00748-7

Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*, *3*(11), 961–968. https://doi.org/10.1038/nclimate1970

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

Enríquez, S., Duarte, C. M., & Sand-Jensen, K. (1993). Patterns in decomposition rates among photosynthetic organisms: The importance of detritus C:N:P content. *Oecologia*, *94*(4), 457–471. https://doi.org/10.1007/BF00566960

Fonseca, M., & Bell, S. (1998). Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series*, *171*, 109–121. https://doi.org/10.3354/meps171109

Fourqurean, J. W., Duarte, C. M., Krause-Jensen, D., Apostolaki, E. T., Kendrick, G. A., Kennedy, H., et al. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, *5*(7), 505–509. https://doi.org/10.1038/ngeo1477

Gagnon, K., Thormar, J., Fredriksen, S., Potouroglou, M., Albretsen, J., Gundersen, H., et al. (2024). Carbon stocks in Norwegian eelgrass meadows across environmental gradients. *Scientific Reports*, *14*(1), 25171. https://doi.org/10.1038/s41598-024-74760-3

Githaiga, M. N., Kairo, J. G., Gilpin, L., & Huxham, M. (2017). Carbon storage in the seagrass meadows of Gazi Bay, Kenya. *PLoS One*, *12*(5), e0177001. https://doi.org/10.1371/journal.pone.0177001

Govan, E., Jackson, A. L., Inger, R., Bearhop, S., & Parnell, A. C. (2023). SIMMR: A package for fitting stable isotope mixing models in R. arXiv preprint arXiv:2306.07817. https://doi.org/10.48550/arXiv.2306.07817

Greiner, J. T., Wilkinson, G. M., McGlathery, K. J., & Emery, K. A. (2016). Sources of sediment carbon sequestered in restored seagrass meadows. *Marine Ecology Progress Series*, *551*, 95–105. https://doi.org/10.3354/meps11722

Hansen, J. C. R., & Reidenbach, M. A. (2012). Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. *Marine Ecology Progress Series*, *448*, 271–287. https://doi.org/10.3354/meps09225

Hearn, C. J., & Largier, J. L. (1997). The summer buoyancy dynamics of a shallow Mediterranean Estuary and some effects of changing bathymetry: Tomales Bay, California. *Estuarine, Coastal and Shelf Science*, *45*(4), 497–506. https://doi.org/10.1006/ecss.1996.0197

Hedges, J. I., & Keil, R. G. (1995). Sedimentary organic matter preservation: An assessment and speculative synthesis. *Marine Chemistry*, *35*. https://doi.org/10.1016/0304-4203(95)00008-F

Heiri, O., Lotter, A. F., & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. *Journal of Paleolimnology*, *25*(1), 101–110. https://doi.org/10.1023/A:1008119611481

Hemingway, J. D., Rothman, D. H., Grant, K. E., Rosengard, S. Z., Eglinton, T. I., Derry, L. A., & Galy, V. V. (2019). Mineral protection regulates long-term global preservation of natural organic carbon. *Nature*, *570*(7760), 228–231. https://doi.org/10.1038/s41586-019-1280-6

Houston, A., Kennedy, H., & Austin, W. E. N. (2024). Additionality in blue carbon ecosystems: Recommendations for a universally applicable accounting methodology. *Global Change Biology*, *30*(11), e17559. https://doi.org/10.1111/gcb.17559

Hyndes, G. A., Nagelkerken, I., McLeod, R. J., Connolly, R. M., Lavery, P. S., & Vanderklift, M. A. (2014). Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biological Reviews*, *89*(1), 232–254. https://doi.org/10.1111/brv.12055

Janousek, C. N., Krause, J. R., Drexler, J. Z., Buffington, K. J., Poppe, K. L., Peck, E., et al. (2025). Blue carbon stocks along the Pacific Coast of North America are mainly driven by local rather than regional factors. *Global Biogeochemical Cycles*, *39*(3), e2024GB008239. https://doi.org/10.1029/2024GB008239

Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., & Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, *24*(4), GB4026. https://doi.org/10.1029/2010GB003848

Kristensen, E. (1990). Characterization of biogenic organic matter by Stepwise Thermogravimetry (STG). *Biogeochemistry*, *9*(2), 135–159. https://doi.org/10.1007/BF00692169

Kristensen, E. (1994). Decomposition of macroalgae, vascular plants and sediment detritus in seawater: Use of stepwise thermogravimetry. *Biogeochemistry*, *26*(1), 1–24. https://doi.org/10.1007/BF02180401

LaRowe, D. E., Arndt, S., Bradley, J. A., Estes, E. R., Hoarfrost, A., Lang, S. Q., et al. (2020). The fate of organic carbon in marine sediments—New insights from recent data and analysis. *Earth-Science Reviews*, *204*, 103146. https://doi.org/10.1016/j.earscirev.2020.103146

Lavery, P. S., Mateo, M.-Á., Serrano, O., & Rozaimi, M. (2013). Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS One*, *8*(9), e73748. https://doi.org/10.1371/journal.pone.0073748

Lei, J., Schaefer, R., Colarusso, P., Novak, A., Simpson, J. C., Masqué, P., & Nepf, H. (2023). Spatial heterogeneity in sediment and carbon accretion rates within a seagrass meadow correlated with the hydrodynamic intensity. *Science of the Total Environment*, *854*, 158685. https://doi.org/10.1016/j.scitotenv.2022.158685

Macreadie, P. I., Anton, A., Raven, J. A., Beaumont, N., Connolly, R. M., Friess, D. A., et al. (2019). The future of blue Carbon science. *Nature Communications*, *10*(1), 1–13. https://doi.org/10.1038/s41467-019-11693-w

Marbà, N., Arias-Ortiz, A., Masqué, P., Kendrick, G. A., Mazarrasa, I., Bastyan, G. R., et al. (2015). Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. *Journal of Ecology*, *103*(2), 296–302. https://doi.org/10.1111/1365-2745.12370

Mayer, L. M., & Rossi, P. M. (1982). Specific surface areas in coastal sediments: Relationships with other textural factors. *Marine Geology*, *45*(3–4), 241–252. https://doi.org/10.1016/0025-3227(82)90112-8

Mazarrasa, I., Lavery, P., Duarte, C. M., Lafratta, A., Lovelock, C. E., Macreadie, P. I., et al. (2021). Factors determining seagrass blue carbon across bioregions and geomorphologies. *Global Biogeochemical Cycles*, *35*(6), e2021GB006935. https://doi.org/10.1029/2021GB006935

Mazarrasa, I., Marbà, N., Garcia-Orellana, J., Masqué, P., Arias-Ortiz, A., & Duarte, C. M. (2017). Effect of environmental factors (wave exposure and depth) and anthropogenic pressure in the C sink capacity of Posidonia Oceanica meadows. *Limnology & Oceanography*, *62*(4), 1436–1450. https://doi.org/10.1002/lno.10510

Mcleod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., et al. (2011). A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment*, *9*(10), 552–560. https://doi.org/10.1890/110004

Meyers, P. A. (1994). Preservation of elemental and isotopic source identification of sedimentary organic matter. *Chemical Geology*, *114*(3–4), 289–302. https://doi.org/10.1016/0009-2541(94)90059-0

Meyers, P. A., & Ishiwatari, R. (1993). Lacustrine organic geochemistry—An overview of indicators of organic matter sources and diagenesis in Lake sediments. *Organic Geochemistry*, *20*(7), 867–900. https://doi.org/10.1016/0146-6380(93)90100-P

Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., & Yoshida, G. (2017). Geophysical constraints for organic carbon sequestration capacity of Zostera marina seagrass meadows and surrounding habitats. *Limnology & Oceanography*, *62*(3), 954–972. https://doi.org/10.1002/lno.10478

Needelman, B. A., Emmer, I. M., Emmett-Mattox, S., Crooks, S., Megonigal, J. P., Myers, D., et al. (2018). The science and policy of the verified carbon standard methodology for tidal wetland and seagrass restoration. *Estuaries and Coasts*, *41*(8), 2159–2171. https://doi.org/10.1007/s12237-018-0429-0

Orange County Coastkeeper. (2015). Upper Newport Bay eelgrass restoration project.

Oreska, M. P. J., McGlathery, K. J., & Porter, J. H. (2017). Seagrass blue carbon spatial patterns at the meadow-scale. *PLoS One*, *12*(4), e0176630. https://doi.org/10.1371/journal.pone.0176630

Oreska, M. P. J., Wilkinson, G. M., McGlathery, K. J., Bost, M., & McKee, B. A. (2017). Non-seagrass carbon contributions to seagrass sediment blue carbon. *Limnology & Oceanography*, *63*(S1), S3–S18. https://doi.org/10.1002/lno.10718

Pacton, M., Fiet, N., & Gorin, G. E. (2007). Bacterial activity and preservation of sedimentary organic matter: The role of exopolymeric substances. *Geomicrobiology Journal*, *24*(7–8), 571–581. https://doi.org/10.1080/01490450701672042

Poppe, K. L., & Rybczyk, J. M. (2018). Carbon sequestration in a Pacific Northwest eelgrass (Zostera Marina) meadow. *Northwest Science*, *92*(2), 80–91. https://doi.org/10.3955/046.092.0202

Prentice, C., Hessing-Lewis, M., Sanders-Smith, R., & Salomon, A. K. (2019). Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows. *Limnology & Oceanography*, *64*(6), 2389–2404. https://doi.org/10.1002/lno.11191

Raven, M. R., Fike, D. A., Gomes, M. L., & Webb, S. M. (2019). Chemical and isotopic evidence for organic matter sulfurization in redox gradients around mangrove roots. *Frontiers in Earth Science*, *7*, 98. https://doi.org/10.3389/feart.2019.00098

Ricart, A. M., Pérez, M., & Romero, J. (2017). Landscape configuration modulates carbon storage in seagrass sediments. *Estuarine, Coastal and Shelf Science*, *185*, 69–76. https://doi.org/10.1016/j.ecss.2016.12.011

Ricart, A. M., York, P. H., Rasheed, M. A., Pérez, M., Romero, J., Bryant, C. V., & Macreadie, P. I. (2015). Variability of sedimentary organic carbon in patchy seagrass landscapes. *Marine Pollution Bulletin*, *100*(1), 476–482. https://doi.org/10.1016/j.marpolbul.2015.09.032

Röhr, M. E., Holmer, M., Baum, J. K., Björk, M., Boyer, K., Chin, D., et al. (2018). Blue carbon storage capacity of temperate eelgrass (Zostera marina) meadows. *Global Biogeochemical Cycles*, *32*(10), 1457–1475. https://doi.org/10.1029/2018GB005941

Ronan, T. E., Miller, M. F., & Farmer, J. D. (1981). Organism-sediment relationships on a modern tidal flat, bodega Harbor (Vol. *17*).

Singh, S., Lal, M. M., Southgate, P. C., Wairiu, M., & Singh, A. (2022). Blue carbon storage in Fijian seagrass meadows: First insights into carbon, nitrogen and phosphorus content from a tropical southwest Pacific Island. *Marine Pollution Bulletin*, *176*, 113432. https://doi.org/10.1016/j.marpolbul.2022.113432

Smith, S. V., & Hollibaugh, J. T. (1997). Annual cycle and interannual variability of ecosystem metabolism in a temperate climate embayment. *Ecological Monographs*, *67*(4), 509–533. https://doi.org/10.1890/0012-9615(1997)067[0509:ACAIVO]2.0.CO;2

Tecchiato, S., Buosi, C., Ibba, A., Del Deo, C., Parnum, I., O'Leary, M., & De Muro, S. (2019). Geomorphological and sedimentological surrogates for the understanding of seagrass distribution within a temperate nearshore setting (Esperance Western Australia). *Geo-Marine Letters*, *39*(3), 249–264. https://doi.org/10.1007/s00367-019-00571-5

Thornton, S. F., & McManus, J. (1994). Application of organic carbon and nitrogen stable isotope and C/N ratios as source indicators of organic matter provenance in estuarine systems: Evidence from the Tay Estuary, Scotland. Estuarine. *Coastal and Shelf Science*, *38*(3), 219–233. https://doi.org/10.1006/ecss.1994.1015

Trevathan-Tackett, S. M., Kelleway, J., Macreadie, P. I., Beardall, J., Ralph, P., & Bellgrove, A. (2015). Comparison of marine macrophytes for their contributions to blue carbon sequestration. *Ecology*, *96*(11), 3043–3057. https://doi.org/10.1890/15-0149.1

Twilley, R. R., Ejdung, G., Romare, P., & Kemp, W. M. (1986). A comparative study of decomposition, oxygen consumption and nutrient release for selected aquatic plants occurring in an estuarine environment. *Oikos*, *47*(2), 190–198. https://doi.org/10.2307/3566045

van de Velde, S. J., Hidalgo-Martinez, S., Callebaut, I., Antler, G., James, R. K., Leermakers, M., & Meysman, F. J. R. (2020). Burrowing fauna mediate alternative stable states in the redox cycling of salt marsh sediments. *Geochimica et Cosmochimica Acta*, *276*, 31–49. https://doi.org/10.1016/j.gca.2020.02.021

Wada, S., Aoki, M. N., Mikami, A., Komatsu, T., Tsuchiya, Y., Sato, T., et al. (2008). Bioavailability of macroalgal dissolved organic matter in seawater. *Marine Ecology Progress Series*, *370*, 33–44. https://doi.org/10.3354/meps07645

Ward, M., Dibble, C., Millington-Drake, M., Lynch, J., McGlathery, K., Lilley, R. J., et al. (2025). Management approach matters: Meeting seagrass recovery and carbon mitigation goals. *npj Ocean Sustain*, *4*(1), 18. https://doi.org/10.1038/s44183-025-00111-y

Ward, M. A., Hill, T. M., Souza, C., Filipczyk, T., Ricart, A. M., Merolla, S., et al. (2021). Blue carbon stocks and exchanges along the California Coast. *Biogeosciences*, *18*(16), 4717–4732. https://doi.org/10.5194/bg-18-4717-2021