Blue Carbon Stocks and Exchanges Along the California Coast

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Abstract. Salt marshes and seagrass meadows can sequester and store high quantities of organic carbon (OC) in their sediments relative to other marine and terrestrial habitats. Assessing carbon stocks, carbon sources, and the transfer of carbon between habitats within coastal seascapes are each integral in identifying the role of blue carbon habitats in coastal carbon cycling. Here, we quantified carbon stocks, sources, and exchanges in seagrass meadows, salt marshes, and unvegetated sediments in six bays along the California coast. The salt marshes studied here contained approximately twice as much OC as did seagrass meadows, 23.51 ± 1.77 kg OC m^{-3} compared to 11.01 ± 1.18 kg OC m^{-3}, respectively. Both salt marsh and seagrass sediment carbon stocks were higher than previous estimates from this region but lower than global and U.S.-wide averages, respectively. Seagrass-derived carbon was deposited annually into adjacent marshes during fall seagrass senescence. However, isotope mixing models estimate that negligible amounts of this seagrass material were ultimately buried in underlying sediment. Rather, the vast majority of OC in sediment across sites was likely derived from planktonic/benthic diatoms and/or C3 salt marsh plants.

Keywords: Carbon cycling, lateral fluxes, seagrass meadow, salt marsh, carbon sequestration

1 Introduction

As carbon dioxide (CO_2) concentrations in the oceans and atmosphere continue to rise, interest in measuring the relative quantities of carbon stored within natural ecosystems has increased. These assessments can help improve global and regional climate models, the prediction of future CO_2 concentrations related to sources and sinks, and our broader understanding of nature-based climate change solutions (Serrano et al., 2019). Coastal habitats including seagrasses, salt marshes, and mangroves have earned the moniker 'blue carbon' habitats for their ability to store disproportionally high levels of organic carbon (OC) in their sediments relative to other habitat types (Lovelock and Duarte, 2019; McLeod et al., 2011). This can be attributed largely to the tendency for these habitats to exhibit high sediment accretion rates and low decomposition rates (Peck et al., 2020; Serrano et al., 2019). This value has led to increasing interest in blue carbon habitats, given their conservation can prevent significant emissions of carbon (Lovelock et al., 2017; Pendleton et al., 2012) and their restoration can lead to increased drawdown of atmospheric CO_2 (Freedman et al., 2009; Greiner et al., 2013).

1.1 Carbon stock assessments and their significance

Despite global interest, many regions are still lacking basic information on carbon stocks and burial rates in blue carbon habitats. This information forms the foundation for more advanced scientific research and can be extremely valuable within management contexts to develop informed local and regional climate assessments. Salt marshes and seagrass meadows cover extensive portions of North America's west coast, yet their carbon stocks have been relatively understudied compared to other habitats in North America and other blue carbon habitats in different regions of the world (Ouyang and Lee, 2014; Postlethwaite et al., 2018).

Eelgrass (*Zostera marina*) is the dominant seagrass species in North America and occupies coastal waterways from Alaska to Mexico (Green & Short, 2003). Until recently, seagrass carbon stock data were almost entirely absent along the west coast of North America (see Capece et al., 2019; Kauffman et al., 2020; O'Donnell, 2017; Poppe & Rybczyk, 2018; Postlethwaite et al., 2018; Röhr et al., 2018). Of these studies, very few data came from Central or Southern California seagrass meadows, despite the fact that this region represents a key temperate to subtropical transition in *Z. marina*'s range (Cabello-Pasini et al., 2003). As a result of the previous paucity of data from the west coast of North America, this region was not represented in previous global syntheses of seagrass carbon stocks (Duarte et al., 2010; Fourqurean et al., 2012; Mazarrasa et al., 2015). Existing work on global seagrass carbon storage identifies that two species of seagrasses in the Mediterranean (*Posidonia oceanica)* and Australia (*Posidonia australis*) store significantly more carbon than other seagrass species, including *Z. marina* (Fourqurean et al., 2012; Lavery et al., 2013; Prentice et al., 2020). These *Posidonia* species were overrepresented in some early assessments of total global seagrass carbon storage – making these global estimates unreliable when applied to management decisions or climate models (Johannessen & Macdonald, 2016; Kennedy et al., 2010). In reality, the geographic and interspecies variability in carbon stocks is likely greater than was initially anticipated (Macreadie et al., 2018; Postlethwaite et al., 2018).

Salt marsh carbon stocks are similarly understudied in western North America, with published carbon stock data from only four estuaries in the region and very minimal spatial coverage and analyses performed in three of these locations (Brevik and Homburg, 2004; Callaway et al., 2012; Kauffman et al., 2020; Patrick and DeLaune, 1990). Existing analyses of North American freshwater wetlands and salt marshes are typically dominated by studies along the east coast (Nahlik & Fennessy, 2016; Wilkinson et al., 2018; with the exception of Holmquist et al. 2018). Within west coast studies, considerable variation in carbon stocks is observed (Callaway et al., 2012; Chmura et al., 2003). Similar to seagrass meadows, these regions have distinctly different oceanographic and geomorphological regimes, which can drive differences in sediment carbon storage. Thus, seagrass and salt marsh carbon storage data collected from understudied regions and across varying environmental gradients are necessary for understanding carbon stock variability and its drivers.

1.2 Blue carbon sources and drivers

Despite an increasing breadth of information on blue carbon habitats in the last decade, a number of questions remain before we can fully understand their role in regional carbon cycling and climate adaptation (Macreadie et al., 2019). We do not yet fully understand what drives variation in carbon stocks – a key aspect of ensuring the protection and enhancement of these carbon services in the future. Previous work demonstrates that numerous factors can control carbon accumulation in coastal sediments including overlying biomass, topography, hydrology, mineralogy, and remineralization rates (Kelleway et al., 2016; Lima et al., 2020; Mazarrasa et al., 2018; Prentice et al., 2019). In particular, sediment grain size has been demonstrated as a significant predictor of carbon stocks (Dahl et al., 2016; O'Donnell, 2017; Serrano et al., 2016), as it affects decomposition rates, which is likely related to the deposition of small particles and low resuspension from the attenuation of water flow by seagrasses (Bos et al., 2007; Conley et al., 2017; Gambi et al., 1990; Hendriks et al., 2008). Through similar pathways, fine, silty sediments trapped in tidal salt marshes can also increase carbon storage (e.g. Zhou et al., 2007).

The relative importance of each potential driver of carbon stock variability may be highly dependent on the environmental setting, species under study, and the interactive effects of these drivers. For example, in Australian salt marshes, overlying vegetation was shown to only significantly affect carbon stocks in sandy and mixed grain size sediments, having no effect on stocks in fine sediments (Kelleway et al., 2016). However, in other cases vegetation has been the primary predictor of carbon stocks in salt marshes, irrespective of grain size (Lovelock et al., 2014; Saintilan et al., 2013). Similar region and species-specific complexities between carbon stocks, overlying vegetation, and mineralogy have been described in seagrass meadows (e.g.

Lima et al., 2020; Serrano et al., 2016), meriting further investigation to understand these complex interactions.

Knowing the relative contributions of locally produced (autochthonous) and imported (allochthonous) carbon also elucidates the underlying mechanisms by which blue carbon habitats store and accumulate carbon. Overlying vegetation can significantly impact sediment carbon stocks; however, it is rarely the dominant source of carbon buried within blue carbon habitats (Kennedy et al., 2010; Lewis et al., 2020; Mazarrasa et al., 2015; Prentice et al., 2019). In many cases, contributions from terrestrial habitats, macroalgae, and suspended particulate organic material contribute as much or more to carbon buried in blue carbon sediments than do autochthonous sources (Drexler et al. 2020; Kennedy et al., 2010; Leorri et al., 2018; Ricart et al., 2020). Thus, local primary production could significantly contribute to net annual carbon drawdown within a given habitat yet play a minor role in carbon burial due to lateral export or remineralization of this carbon. Understanding this phenomenon elucidates the role of blue carbon habitats in broader, system-wide energy flows and carbon cycling (Hyndes et al., 2014; Ricart et al., 2015). For instance, much of the carbon from laterally exported biomass may be remineralized in the water column or as wrack in nearby habitats (Attard et al., 2019; Liu et al., 2019), serving an important ecological role and altering the production and biogeochemical cycles of recipient systems (Hyndes et al., 2014; Ince et al., 2007; Valiela and Cole, 2002). Given that blue carbon habitats are highly productive (Duarte & Cebrián, 1996), support high carbon burial (e.g. McLeod et al., 2011), and can co-occur within small geographic ranges (Alongi, 2018; Bouillon & Connolly, 2009), laterally exported carbon from one blue carbon habitat may be entrapped and buried in a neighboring habitat. From this landscape-scale perspective, exchanges between blue carbon habitats could increase their capacity for carbon burial or alter the sources of buried carbon. While some coastal studies have estimated lateral carbon fluxes (Jiménez et al., 2017; Liu et al., 2019), very few studies place these lateral fluxes into landscape-scale contexts that also address carbon burial in recipient habitats (Bouillon & Connolly, 2009; Duarte & Krause-Jensen, 2017; Ricart et al., 2017).

The study presented here addresses this globally relevant topic of research in a relatively understudied region by answering the following questions:

1) How much organic carbon is stored in seagrass and salt marsh sediments across a California latitudinal gradient?
2) What are the sources of carbon buried within these sediments?
3) Is carbon exchanged between blue carbon habitats within the coastal landscape?

2 Methods

2.1 Study Sites

Sediment cores from salt marshes and seagrass meadows, along with neighboring unvegetated sediments (hereafter 'bare sediment' near seagrass meadows, and 'pan' near salt marshes) were collected from six bays across a latitudinal gradient in California (Fig. 1a). A total of 82 sediment cores were collected, 30 of which have been discussed previously (O'Donnell, 2017) and are included here for comparison. The number of cores collected in each site and general site characteristics are described in Table 1. While all sampled seagrass meadows were

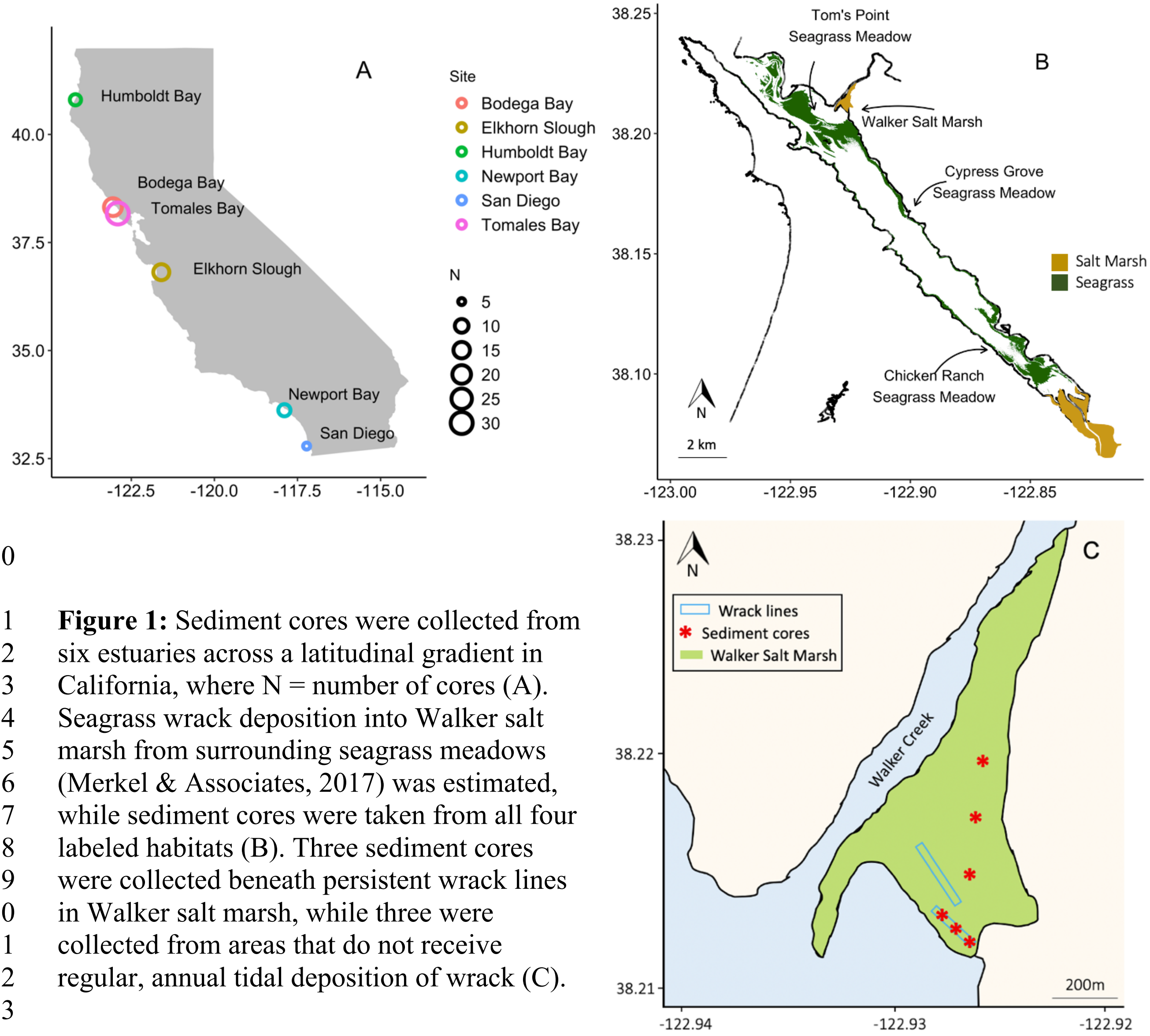


Figure 1: Sediment cores were collected from six estuaries across a latitudinal gradient in California, where N = number of cores (A). Seagrass wrack deposition into Walker salt marsh from surrounding seagrass meadows (Merkel & Associates, 2017) was estimated, while sediment cores were taken from all four labeled habitats (B). Three sediment cores were collected beneath persistent wrack lines in Walker salt marsh, while three were collected from areas that do not receive regular, annual tidal deposition of wrack (C).

dominated by a single seagrass species (*Zostera marina)*, salt marshes contained a mixed community of halophytes, predominantly composed of pickleweed (*Sarcocornia pacifica*), and to a lesser extent salt grass (*Distichlis spicata*) and marsh jaumea (*Jaumea carnosa)*. Bare sediment cores were collected in unvegetated areas nearby each seagrass meadow at a minimum of 20 meters away from the meadows and at similar depths. Pan cores were collected from patches of unvegetated sediment (2-4m diameter) found within the salt marsh interior, a natural and semi-permanent feature of salt marsh habitats formed by elevational depressions (Escapa et al., 2015). None of our sampling sites were actively restored and, to our knowledge, respective vegetation has persisted through time.

We estimated OC stocks in seagrass, salt marsh, pan, and bare sediments (see details below). In addition, we analyzed sediment OC sources for two individual salt marshes in Elkhorn Slough ('Elkhorn salt marsh') and Tomales Bay ('Walker salt marsh'), and we examined carbon exchange between a single seagrass meadow and the neighboring Walker salt marsh. Walker salt marsh is located approximately 5.5 km from the mouth of Tomales Bay and is in close proximity to extensive meadows of *Z. marina* – the dominant seagrass in each of the meadows sampled (Fig. 1b). This marsh lies where the mouth of Walker Creek meets bay waters, and thus can receive terrestrial and riverine inputs, while simultaneously receiving marine inputs from tidal exchange.

Bay	**Coordinates**	**Number of cores**	**Site description**
Humboldt Bay	40°48'12 N, 124°10'52 W	Seagrass: 4 Bare sediment: 3	A large semi-enclosed bay with a narrow mouth, stabilized by jetties. Primary freshwater sources come from the Elk River and its tributaries, with Freshwater Creek inputs entering the bay near the sampling site. Freshwater input is small relative to tidal flushing but can locally effect sedimentation rates within the bay (Schlosser and Eicher, 2012)
Bodega Harbor	38°19'60 N, 123°02'53 W	Seagrass: 15 Bare sediment: 3	There are no significant rivers or creeks that provide freshwater or sediment inputs. Sediment input in Bodega Bay is largely controlled by jetties at the mouth of the harbor and is influenced by its history of routine dredging to maintain shipping channels and control wind-blown sand entering from nearby dunes

Tomales Bay	38°10’17 N, 122°54’46 W	Seagrass: 15 Bare sediment: 9 Salt Marsh: 6	A long, narrow bay that receives periodic freshwater inputs from two primary tributaries, Walker Creek and Lagunitas Creek, which peaks seasonally during winter storms.
Elkhorn Slough	36°49'15 N, 121°45'06 W	Salt Marsh: 11 Pan: 3	Receives periodic freshwater inputs from the Old Salinas River and Bennett and Moro Coho Sloughs. After a long history of increasing sediment deposition and slowing tidal flow to the bay, levee breaches and removals in 1953 rapidly converted it to a higher tidal energy, erosional system, as it remains today (Van Dyke and Wasson, 2005). As a result, the extent of ‘high-quality’ salt marsh in 2000 was 23% of what it had been a century earlier (Van Dyke and Wasson, 2005)
Newport Bay	33°38'07 N, 117°53'17 W	Seagrass: 4 Bare sediment: 4	An urban bay, that receives terrestrial and urban inputs from the San Diego Creek Watershed. After a long history of high sedimentation and water quality nutrient impairments from urban and agricultural sources, a program was implemented in 1998 to meet water quality targets. Since its commencement, both sedimentation and nutrients in the bay have significantly decreased (Trimble, 2003).
Mission Bay	32°47'24 N, 117°13'40 W	Seagrass: 3 Bare sediment: 2	An urban, enclosed bay, that receives terrestrial and urban input from the San Diego River watershed and the Rose Creek tributary. Experiences long residence times and is primarily controlled by tidal flushing processes rather than the minimal freshwater inputs (Cyronak et al., 2018; Largier et al., 1997)

Table 1: Location and brief description of each bay sampled in this study, along with the total number of cores collected from each habitat type in each of these bays.

2.2 Carbon stocks

All sediment cores were sampled by manually inserting transparent, open-barrel PVC pipes (20 cm length, 5.08 cm diameter). Compaction occurred in 19% of cores, and a compaction factor was applied when calculating carbon stocks according to Howard et al. (2014). Once extracted, cores were capped and transported to the laboratory upright to prevent mixing of sediment layers. Cores were then immediately extruded into sections at 2 cm intervals. Coarse living plant material (> 1cm) was manually removed. Each section was dried at 60°C and weighed, and dry bulk density (DBD) was determined by dividing dry bulk mass by the volume of sampling interval.

Each section was then homogenized and divided into three subsamples of 10 g each, and the remaining sample was archived. One of the three subsamples was acidified using 1.12 M HCl to remove and measure total inorganic carbon (Milliman, 1974). The second subsample was analyzed for total organic material (TOM) by loss-on-ignition method for 4 hours at 550° C (Dean, 1974). Total C content (%) and $\delta^{13}C$ were additionally determined on a set of 44 of the acidified subsamples randomly selected across each habitat type using an elemental analyzer (PDZ Europa ANCA-GSL, SD ± 0.25 %) integrated with a continuous flow isotope ratio mass spectrometer (PDZ Europa 20-20, SD ± 0.2 ‰) at the UC Davis Stable Isotope Facility. $\delta^{13}C$ ratios are expressed in parts per thousand (‰) relative to VPDB (Vienna Pee Dee Belemnite) according to standard notation ($\delta^{13}C = [(R_{sample} / R_{standard}) - 1] \times 1000$, where R is the ratio $^{13}C/^{12}C$). Organic carbon in each core section was then estimated using a power model developed between measured TOM and measured OC in this set of subsamples (as in Craft et al., 1991). Specifically, the equation $y = 0.22x^{1.1}$ was applied ($r^2 = 0.84$; Fig. S1). A power model was selected over a linear model for these data to avoid negative estimates of carbon stocks at low levels of TOM (Fig. S1). Carbon stocks were determined by multiplying DBD (g cm^{-3}) by % OC.

In each core section, the proportion of fine sediments – the silt and clay fraction (<63 µm), hereafter "mud" – was quantified. The grain size analysis was conducted by mass loss in the third subsample from each section in 70 of the 82 total cores. The subsample was rinsed through a 63 µm sieve with deionized water, and the remaining sediments were dried at 60°C and re-weighed.

To allow for carbon stock comparisons to previous work, a depth of 20 cm was selected (Fourqurean et al. 2012; Prentice et al., 2020; Röhr et al., 2018). Previous research also suggests that OC content remains relatively constant below 10 cm to depths up to 1 m (Callaway et al., 2012; Prentice et al., 2020; Fig. S3), providing further justification for a 20 cm core depth selection. Nonetheless, when comparing carbon stocks estimated here to those in previous studies, we include these studies' sampled core depths for clarity.

2.3 Carbon sources and exchange

We applied mixing models to assess salt marsh sediment carbon sources to understand within-estuary exchange of carbon among the sampled habitats. Two separate mixing models were produced for 1) Elkhorn salt marsh in Elkhorn Slough and Walker salt marsh in Tomales Bay, and 2) salt marsh sediments under seagrass wrack, versus not under wrack in Walker salt marsh. At Walker salt marsh, a total of six sediment cores were collected. Three of these sediment cores were collected from the interior marsh, while three were collected from underneath a seagrass wrack line along the tidal edge of the marsh (Fig. 1c). *Z. marina* in this region is known to undergo a period of senescence as photoperiod shortens in the fall, as is common in all temperate seagrasses (Fourqurean et al., 1997). Historical imagery of the site shows persistent seagrass wrack concentrated along these tide lines that consistently appears in early fall as seagrass senesces (Fig. S2; Google Earth, 2020). The biomass of seagrass wrack along this tide line at the time of core collection was quantified along an 80 m transect within the marsh by collecting all seagrass present in a 1 m^2 quadrat every 10 meters. This material was taken back to the lab, sorted into above ground biomass (AGB) and below ground biomass (BGB), rinsed, dried (60°C), and weighed. Biomass data from seagrass in nearby meadows was previously published (see O'Donnell, 2017) and is used here for reference. Sediment cores collected from beneath wrack lines were sectioned at 2 cm intervals, analyzed for total OC and δ^{13}C content according to the methods described above. Total nitrogen content was also determined on an unacidified portion of the same 44 sediment subsamples used in carbon analyses (ThermoFinnigan Flash 1112 Series elemental analyzer, SD ± 0.02%). Data from Walker salt marsh are also displayed as 'shallow' (surface sediment to 10 cm deep) and 'deep' (10 cm and deeper), to facilitate interpretation of changes with depth.

The contributions of carbon sources to each core section were then estimated with a mixing model using δ^{13}C and N:C ratios as tracers. Given δ^{15}N can be altered during early diagenesis (e.g. Benner et al., 1991), we selected δ^{13}C and C:N ratios as the primary geochemical tracers, and therefore did not include fractionation factors into the model (Craven et al., 2017). N:C ratios are utilized rather than C:N ratios because mixed fractions returned by the model are based on the denominator, and thus ^{13}C /^{12}C and N:C both estimate the fractional contribution of ^{12}C (Craven et al., 2017; Perdue and Koprivnjak, 2007). However, C:N ratios are used in text and figures given this format is more typically presented in the literature. We used a Bayesian mixing model SIAR 4.2 (Parnell and Jackson, 2013) to estimate the contributions of several source groups selected according to the dominant plant and algal species observed within the selected salt marshes. The sources included C3 salt marsh plants, C4 salt marsh plants (*Distichlis* *spicata)*, seagrass *(Z. marina)*, and plankton/benthic diatoms. Seagrass geochemistry was estimated from seagrass leaves collected from meadows near the selected salt marshes in Newport Bay, Tomales Bay, and Bodega Bay (Fig. 1a; Capece et al., 2019). Representative geochemistry for all other sources has been published previously and was used here, from samples collected in San Francisco Bay, approximately 60 km south of Walker salt marsh (see Cloern et al., 2002 for full methods). All salt marsh sediment cores were collected from areas of the marsh that were dominated by the aforementioned species, and as such, other marsh species were not considered (e.g., *Spartina sp.).* While lower densities of other C3 marsh plants may have been present in some cored sites, the variability demonstrated by the selected source samples likely encompasses much of this variability given the utilization of the same photosynthetic pathway (Cloern et al., 2002). Plankton samples were collected from estuarine water samples while benthic diatom samples were collected from both salt marsh surface sediments and neighboring mudflats (Cloern et al., 2002). These sources have similar signatures and are pooled here and referred to as “diatoms” for simplicity, acknowledging that this encompasses contributions from multiple planktonic and benthic sources. Given the overlapping signatures of C3 plants and diatoms, these two sources were pooled in mixing models, allowing an estimate of diatoms and/or C3 plants contributions to marsh sediments, in addition to contributions from seagrass and C4 plants.

2.4 Statistical Analyses

To evaluate decay of carbon through time, we tested for significant changes in OC in each habitat type with core section depth (a proxy for time) by fitting data to a generalized linear mixed model (GLMM) using maximum likelihood with ‘depth’ and ‘site’ as fixed effects and ‘core’ as a random effect, using a gamma distribution and log link function to account for non-normality. In sites and habitats that demonstrated significant OC changes with depth, the rate of decay was estimated from the slope of its associated model. In all analyses to follow, OC across all sections in each core were averaged, and statistics were performed on these core averages. After inspecting data for normality and homogeneity of variance, differences in OC and grain size between habitat types and between sites were analyzed using simple linear models (SLM; significance defined by $\alpha = 0.05$). Specifically, these data were fit to a linear model using ordinary least squares with ‘site’ and ‘habitat’ (i.e., seagrass, salt marsh, bare sediment, pan) as fixed effects, including their interaction. The relationships between TOM (%) and grain size were analyzed using simple linear regressions, whereby a grain size filter was selectively applied to determine the point at which the relationship between the two was no longer significant ($p < 0.05$). Differences in $\delta^{13}C$ (‰) or C:N ratios between sediment depth (‘surface’ versus ‘deep’), and between sediments collected under wrack versus not under wrack, were also tested with SLMs using ordinary least squares with ‘depth’ or ‘under wrack’ as fixed effects. When necessary, data were log transformed. Tukey’s post-hoc analyses were conducted for multiple comparisons. All statistical analyses were performed in R software (R Core Team, 2018).

3 Results

3.1 Carbon Stock Assessments

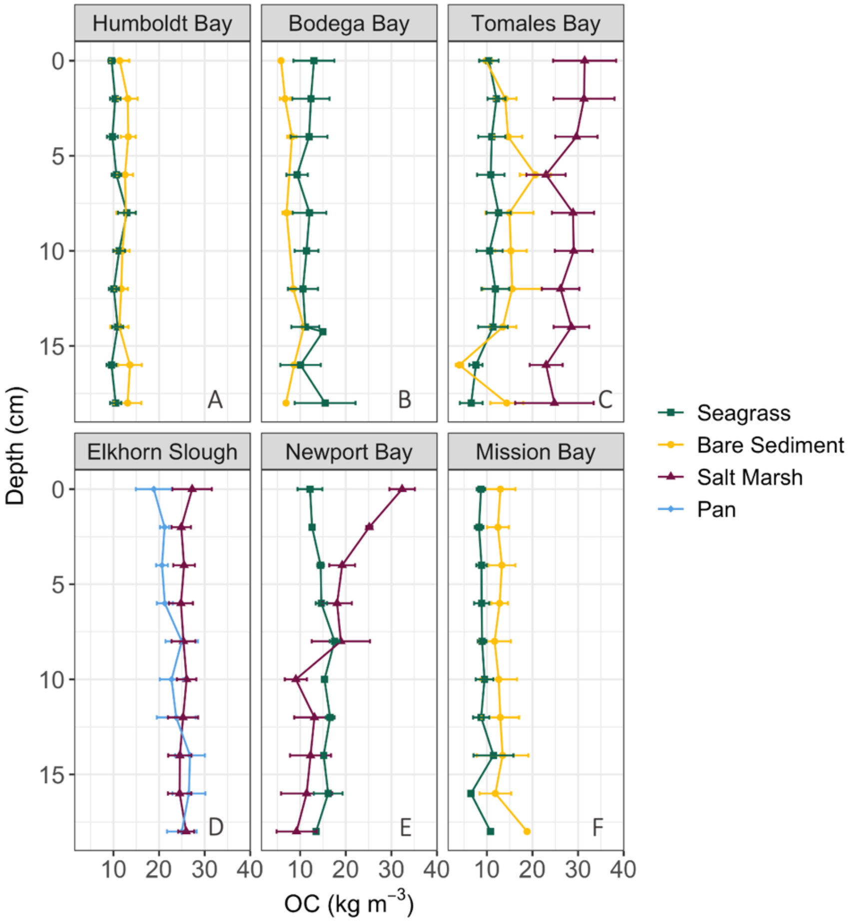


Figure 2 (left)**:** Down core trends (surface = 0 cm) in average (± SE) OC (kg m^{-3}) for each habitat type and site. Data show an insignificant decline in OC through time (downcore) in all sites except Newport Bay salt marshes.

Down core OC demonstrates high variability, resulting in few significant differences in OC with depth (Fig. 2). Specifically, only Newport Bay salt marsh sediments exhibited significant loss of OC down core, which declined at a rate of 0.95 kg C m^{-3} per cm (Fig 2e; GLMM, T-value = -4.7, SE = 0.01, $p < 0.05$). Significant differences between OC stocks emerged when cores were compared between habitats, with salt marshes containing significantly more carbon than both bare sediment and seagrass meadows (Fig. 3b; SLM, $p < 0.01$, F-statistic = 13.3, DF =3). Specifically, salt marsh sediments contained 23.51 ± 1.77 kg OC m^{-3}, while seagrass meadows contained 11.01 ± 1.18 kg OC m^{-3} (Fig. 3b; mean ± SE). Seagrass meadow carbon stocks were not significantly different than those of nearby bare sediments (Tukey's post-hoc analysis, $p > 0.05$), which contained an average of 12.34 ± 1.57 kg OC m^{-3}. Pan sediments also contained higher carbon than did seagrass meadows (Tukey's post-hoc analysis, $p > 0.05$). A full list of carbon stocks is displayed in Table S1. Tukey's post-hoc analysis indicates that in Tomales Bay, salt marshes contained significantly more carbon than seagrass meadows (Fig. 3a; $p < 0.05$) while bare sediment and seagrass carbon stocks did not significantly differ from one another ($p > 0.05$). We did not detect any other significant differences when comparing carbon stocks across habitat types within each individual site (Tukey's post-hoc analysis, $p > 0.05$).

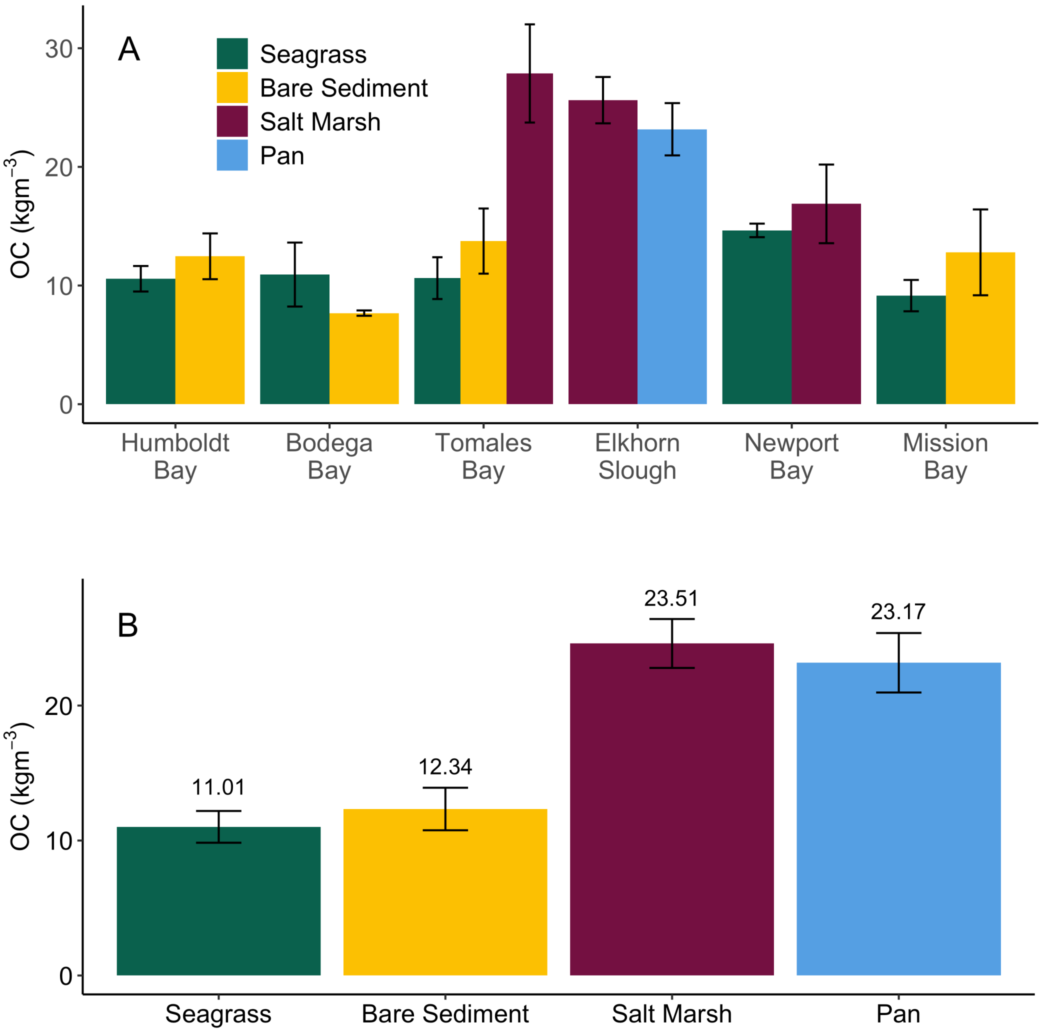


Figure 3: Average (± SE) total organic carbon (OC) stocks (kg m^{-3}) across all cores collected from each habitat type within each site in this study (A). Average (± SE) total organic carbon stocks (kg m^{-3}) across all cores collected within each habitat type in this study (B).

We observed a very strong relationship between grain size and storage of organic material, especially at lower TOM (%) values (Fig. 4). Specifically, the observed linear relationship between grain size and TOM is strongest when sediment is 8.5% TOM or less (linear model, $r^2 = 0.95$, $p < 0.05$, F-statistic = 4957, DF = 269). However, as the proportion of fine sediments in each sample increases, the relationship between grain size and TOM weakens rapidly (from $r^2 = 0.73$ to 0.53) after sediments consisting of more than 82% mud are included (linear model, $p < 0.05$, $r^2 = 0.53$, F-statistic = 233.1, DF = 201). Our results indicate that grain size was similar between sites (SLM, $p > 0.05$, F-statistic = 2.7, DF = 3) but differed between habitat types (Fig. 5a; SLM, $p < 0.05$, F-statistic = 5.7, DF = 3), with salt marsh sediments demonstrating significantly greater % mud than both seagrass and bare sediment (Tukey's post-hoc analysis, $p < 0.05$). Recognizing that the sample size of pan cores was low, pan sediments displayed comparable % mud to salt marsh sediments but there were no significant differences between pan grain size and the other habitat types' grain sizes (Tukey's post-hoc analysis, $p > 0.05$). Tukey's post-hoc analyses did not indicate any significant differences in grain size between habitat types within each site (Fig. 5a; $p > 0.05$).

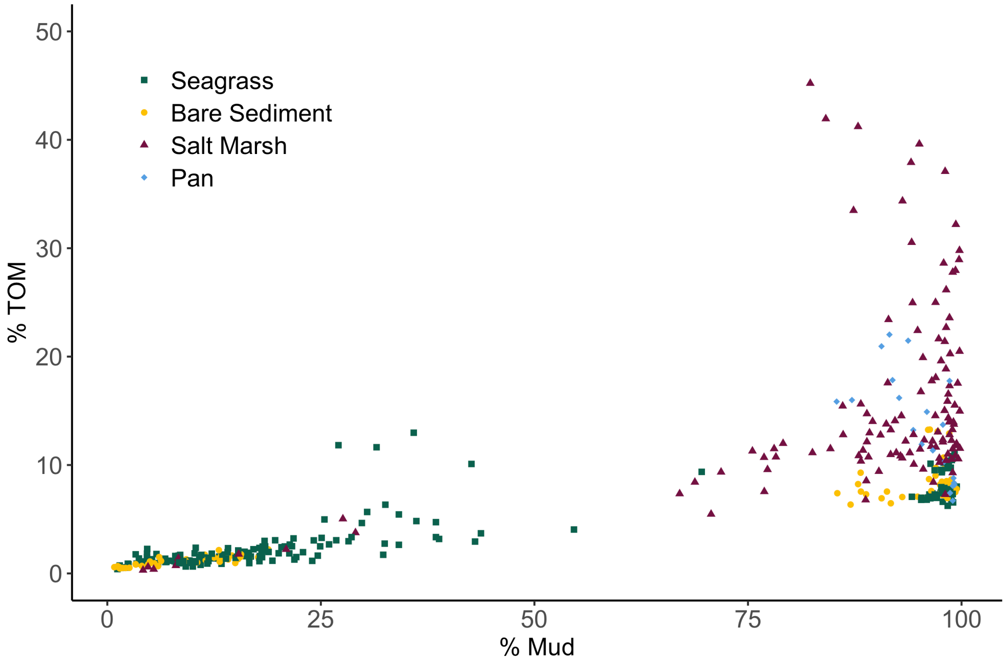
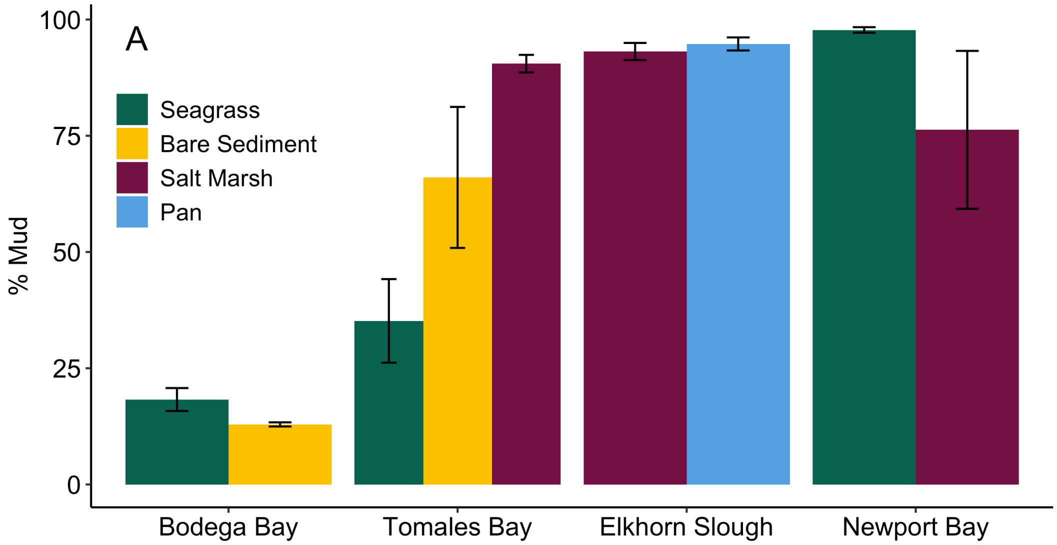


Figure 4: Biplot showing the relationship among total organic material (TOM) (%) of each 2-cm core section from each habitat type plotted against sediment grain size (% Mud).



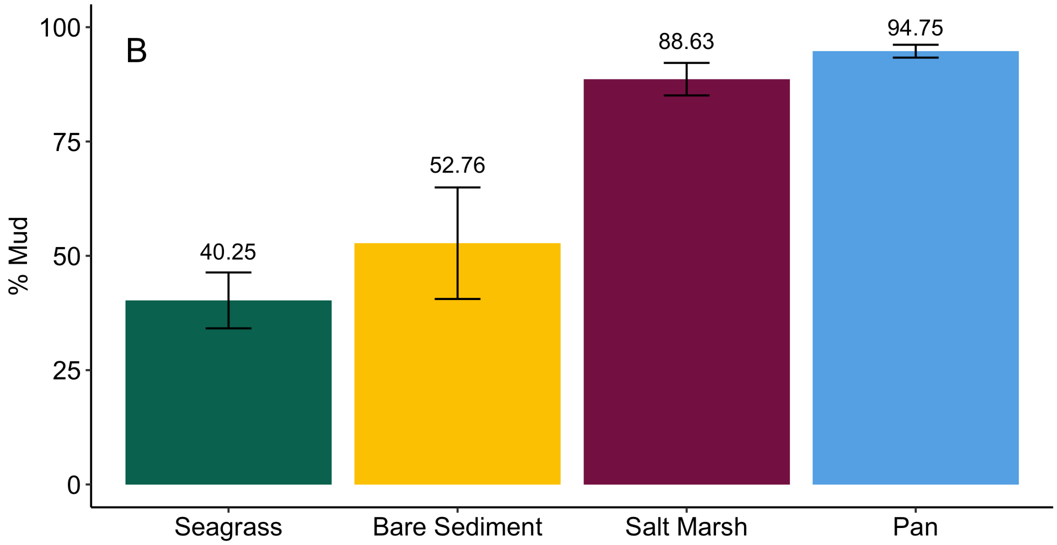


Figure 5: Average (± SE) % mud of all sediments quantified in each site within each habitat type (A), average (± SE) % mud in each habitat type across all sites measured (B).

3.2 Carbon Sources and Exchange

3.2.1 Wrack Deposition

While we conducted only one ground survey of seagrass wrack lines within Walker salt marsh in October 2019, historical aerial imagery was utilized to verify that these wrack lines appear reliably in this season in similar locations each year (Fig. S2). This phenomenon can be viewed as far back as 2002, before which images are of low quality or unavailable (Google Earth, 2020). These wrack lines typically persist throughout the winter, becoming indiscernible via aerial imagery by spring. Previous data collected by the authors (O'Donnell, 2017) quantified seagrass senescence within the nearby Tom's Point seagrass meadow (Fig. 1b), where average summer seagrass biomass was 440 ± 59.4 g m^{-2} and winter seagrass biomass was 115 ± 16.5 g m^{-2} (AGB and BGB, mean ± SE; Table 2). Within the neighboring Walker salt marsh, fall estimates of wrack demonstrated that 106 ± 24.6 g m^{-2} of seagrass (dry weight) was deposited along tide lines (Table 2). While both seagrass AGB and BGB are included in this value, seagrass BGB only accounted for 3.5% of total seagrass biomass measured (Table 2). Analysis of seagrass leaves collected from Tomales Bay demonstrated that seagrass material was composed of 31.6% of OC. Thus, we estimate Walker salt marsh receives 33.4 ± 7.6 g OC m^{-2} in the form of seagrass along wrack lines each year.

	Seagrass (winter) (g/m2)	Seagrass (summer) (g/m2)	Wrack (g/m2)	Wrack carbon (gC/m2)
AGB	58.6 ± 14	361.3 ± 47.8	102.8 ± 24	32.5 ± 7.6
BGB	57.1 ± 4.6	79 ± 15.5	3.7 ± 2.6	1.2 ± 0.8
Total	115.7 ± 16.5	440.3 ± 59.4	105.7 ± 24.6	33.4 ± 7.8

Table 2: Living seagrass above ground biomass (AGB) and below ground biomass (BGB) was collected in Tom's Point seagrass meadow (Fig. 1b) in both summer and winter (g m^{-2}). Total seagrass wrack delivered to Walker salt marsh was quantified as AGB and BGB (g m^{-2}) and converted to carbon (g C m^{-2}) using a 31.6% carbon conversion rate.

3.2.2 Sediment Carbon Sources

In Walker salt marsh, surface (< 10 cm) wrack sediments had higher δ^{13}C values than sediments collected from the interior of the marsh (non-wrack sediments) and thus were more similar to the δ^{13}C values of seagrass (Fig. 6; SLM, $p < 0.05$; F-statistic =27.3; DF = 18). Shallow wrack sediments had an average δ^{13}C of -22.5 ± 0.38 ‰, while non-wrack sediments had an average δ^{13}C of -24.9 ± 0.26 ‰ (mean ± SE). However, when both shallow and deep (>10cm) sediments were included, wrack sediment δ^{13}C did not significantly differ from non-wrack sediments (SLM, $p > 0.05$, F-statistic = 0.34, DF = 31). C:N sediment ratios did not significantly differ from one another regardless of collection depth or location (SLMs, $p > 0.05$). When data were applied to a mixing model, apparent discrepancies in seagrass-derived carbon contributions between shallow and deep, and wrack and non-wrack sediments were insignificant

(SIAR mixing model, Table S2). Similarly, no significant quantity of seagrass-derived carbon was detected in Elkhorn salt marsh sediments (SIAR mixing model, Table S2). Rather, models estimate that sediments were derived almost entirely from either diatoms or C3 plants – 83% in Elkhorn Slough and 88% in Walker salt marsh (Fig. 7; Table S2). Thus, regardless of site, depth, or the presence of wrack, model results estimate no significant storage of seagrass-derived carbon in sediment (Table S2). Instead, C3 plants and/or diatoms are the primary significant contributors to underlying carbon storage across salt marshes in all locations.

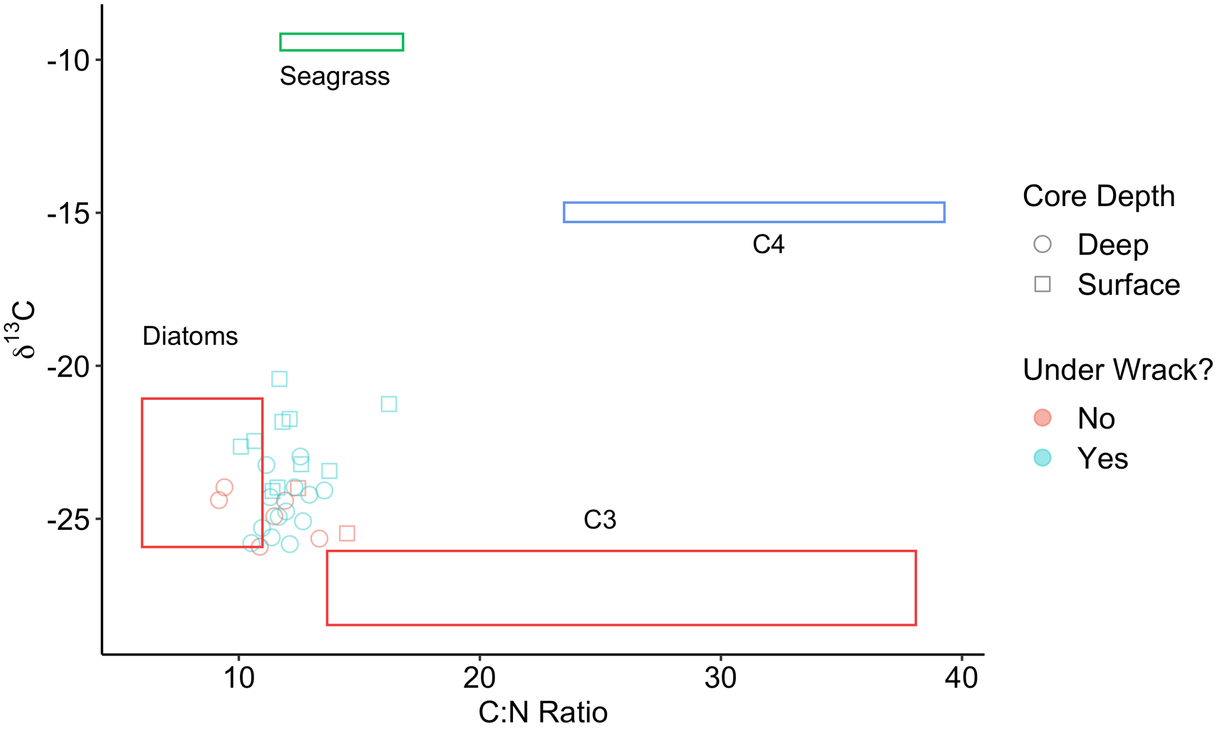


Figure 6: Points represent the δ^{13}C and C:N ratios of Walker Salt Marsh sediment data, collected from underneath persistent wrack lines (blue) and from areas free of wrack (red) (see Fig. 1c). Sediment subsamples collected from the surface to 10cm deep are labelled as surface samples (square) and below 10cm are labelled as deep samples (circle). Colored boxes represent sources (means ± SD) from diatoms (red), seagrass (green), C4 salt marsh plants (blue), and C3 salt marsh plants (red).

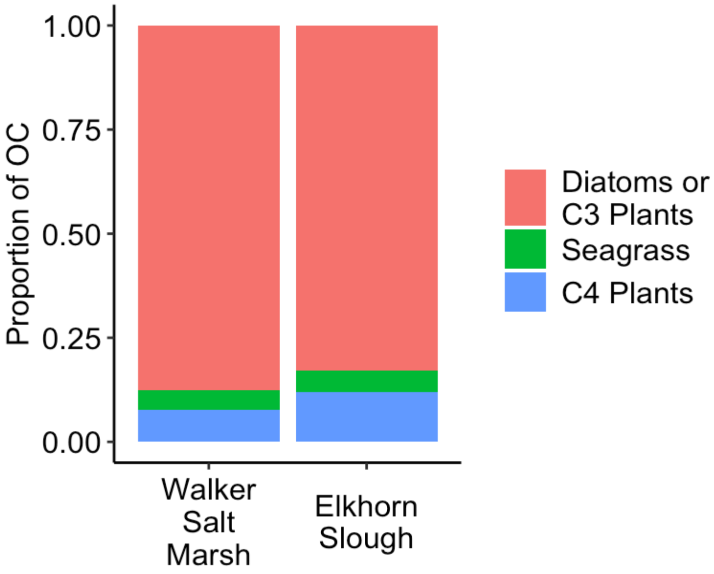


Figure 7 (left)**:** Mixing model results displaying the average source contributions to salt marsh sediment organic carbon (OC) for two salt marshes. Exact values and significance are shown in Table S2.

4 Discussion

4.1 Carbon Stocks

The lack of clear downcore trends (Fig. 2) could suggest relative OC stability with depth and through time or that there have been minimal changes to factors such as vegetation and grain size through time. The persistence of this pattern is supported by the longer cores sampled in seagrass and bare sediment sites (Fig. S3). One possible explanation for significant downcore OC losses in Newport Bay salt marsh is change in historic hydrography. Specifically, previous sediment profiles from this region also found finer surface sediments above coarser materials – associated with the conversion from an erosional to a depositional system in the early 20th century due to urbanization of the surrounding area (Trimble, 2003). This change in grain size down core may drive the associated OC loss down core, discussed further below. Although we did not quantify sediment carbon accumulation rates here, previous work in Tomales Bay seagrass meadows indicate rates of 11.37 - 15.16 g C m^{-2} yr^{-1} via ^{210}Pb dating (O'Donnell, 2017). By these accumulation rate estimates, we estimate the top 20 cm of sediment sampled here accumulated over approximately 100-130 years. Given the relatively slow accumulation rates and lack of down core trends, we interpret that our data represent realistic stock assessments for each respective habitat and location, rather than being reflective of shallow surface sediment carbon stocks.

Determining drivers of OC storage variation across habitats is notably complex, where a mix of factors such as grain size, elevation, hydrodynamic energy, and vegetation type may influence underlying sediment OC storage (Kelleway et al., 2016; Lima et al., 2020; Miyajima et al., 2015). Here, sediment grain size and its associated drivers allow us to further examine variation in sediment OC storage variation. Specifically, grain size likely contributed to the observed inter-habitat differences in OC storage, given its strong correlation with TOM. Despite no significant differences in grain size between habitat types within each site (likely due to high grain size variability and low relative sample sizes), apparent qualitative differences elude to possible explanations of stock differences. For example, seagrass sediments had lower % mud than salt marsh sediments in Tomales Bay, a trend that was reversed in Newport Bay (Fig. 5a; Table S1). Similarly, seagrass sediments did not always contain a higher % mud than neighboring bare sediments, contrary to what is typically reported (Bos et al., 2007; Conley et al., 2017; Mazarassa et al., 2015), which may explain their apparent lack of sediment OC differences. Overall, salt marshes had greater OC storage and smaller average grain size than seagrass meadows. The periodic, lower energy inundation of the sampled marsh and pan habitats may facilitate the observed smaller grain sizes – by preventing the resuspension of small particles that might occur in higher hydrodynamic energy or submerged systems (Christiansen et al., 2000; Yang et al., 2008).

In marsh and pan habitats, biological factors such as primary production and decomposition rates may become more important drivers of carbon burial than would be true in dominantly sandy sediments (Miyajima et al., 2017). It is possible that root systems of overlying vegetation add bulk organic material into available sediment space, contributing to increased carbon deposition as well as decreased space for mineral accumulation (e.g., Rogers et al., 2019). Yet despite the absence of vegetation in pan sites, we did not observe significant differences in carbon stocks between pan sediments and surrounding salt marsh sediments. This could be attributed to 1) significant carbon contributions from surrounding salt marsh biomass to pan sites overtime, 2) historical marsh recovery along pan edges and subsequent burial of vegetation captured in pan cores, 3) variable decomposition rates in both pan and salt marsh sediments, or 4) because the expected effect of canopy-vegetation on salt marsh sediment is too small relative to other drivers, producing statistically insignificant results. In sum, although seagrasses and salt marshes can facilitate carbon storage by altering grain size distributions, hydrodynamics and geomorphology play a critical role in grain size distributions and therefore, carbon storage. The hydrographic changes in Newport Bay salt marshes associated with decreased grain sizes further emphasize this point – drawing attention to the importance of watershed and sediment management to regional carbon storage. Furthermore, although grain size is clearly a key driver in carbon storage, our data demonstrate that it becomes of limited use as a predictor of carbon stocks after the proportion of mud exceeds 82% (Fig. 4). This demonstrates that using grain size as a cost-effective way to estimate carbon stocks (as has been suggested, e.g. Serrano et al., 2016) only appears possible in sandy and mixed grain size sediments within the sites studied here. Carbon stocks in fine sediment sites above this threshold cannot be estimated using grain size alone – a management-relevant finding for efforts to incorporate habitat-specific carbon storage into regional climate plans.

4.2 Global and Regional Comparisons

With recent reviews on coastal carbon stocks in salt marshes and seagrass meadows, we can compare our data to global and regional averages (no sufficient syntheses of pan or bare sediment carbons stocks were identified). We find that carbon storage in California seagrass sediments studied here is lower than global estimates yet is higher than regional estimates of *Z.*

Study	**Habitat Type/Species**	**Location(s)**	**Value (Mg C_{org} ha^{-1})**	**Methods (core length and extrapolation depth)**
Seagrass				
This study	Seagrass *(Z. marina)*	California	110 ± 11.8	20 cm cores extrapolated to 1 m
Kauffman et al. (2020)	Seagrass *(Z. marina)*	*U.S. west coast	80 ± 12	1 m cores collected (no extrapolation)
Prentice et al. (2020)	Seagrass (*Z. marina*)	U.S. west coast	65.12	25 cm cores extrapolated to 1 m
Röhr et al. (2018)	Seagrass (*Z. marina*)	*U.S. west coast *Temperate Northern Hemisphere	69.4 ± 8.4 108.9 ± 39.56	25 cm cores extrapolated to 1 m
Fourqurean et al. (2012)	Seagrass (many species)	Global	[1]139.7	A combined estimate from short cores (≥ 20cm & < 1 m) extrapolated to 1 m and full cores (1 m)
Salt Marsh				
This study	Salt marsh dominated by *Sarcocornia pacifica, Distichlis*	California	235 ± 17.7	20 cm cores extrapolated to 1m

	spicata and *Jaumea carnosa*			
Kauffman et al. (2020)	Salt marsh dominated by *Distichlis spicata* and *Sarcocornia perennis*	*U.S. west coast	190 ± 16	1 m cores collected (no extrapolation)
Holmquist et al. (2018)	Tidal wetlands (mixed, dominated by estuarine emergent wetlands)	*Conterminous U.S. tidal wetlands	270 ± 1.4	A combined estimate from short cores (≥ 10cm & < 1 m) extrapolated to 1 m and full cores (1 m)

Table 3: Summary of previously reported carbon stocks in seagrass meadows and tidal wetlands, all normalized to the top 1m of sediment. Studies that included any data from California are denoted by an asterisk. Values are reported as mean ± SE, unless otherwise noted. [1]Fourqurean et al. (2012) value represents median OC storage.

marina from the U.S. west coast (Table 3). Early estimates from the U.S. west coast were markedly low, with one study of *Z. marina* from British Columbia measuring average stocks of 1.34 kg C m^{-3} with a maximum OC of 1.3%, compared to the 11.01 ± 1.18 kg C m^{-3} and a maximum OC of 7.0 % estimated here (Postlethwaite et al., 2018). While estimates from studies averaging over broader U.S. west coast regions are higher than this Canadian case study (Table 3), the data presented here are still higher than regional estimates, suggesting possible latitudinal difference in carbon storage between the northern and southern regions of the North American west coast. This is not surprising given the variation in environmental and geomorphic conditions over this large stretch of coastline, which likely influence the carbon storage capacity along with the factors discussed here such as hydrodynamics or grain size conditions.

Recent studies of the U.S. west coast and of conterminous U.S. tidal wetlands allow for comparison with salt marsh data collected here. Much like with seagrass meadows, California salt marsh carbon storage was also higher than previous estimates from the U.S. west coast (Kauffman et al., 2020; Table 3). Both the data presented here as well as those from Kauffman et al. (2020) (Table 3) were collected from similar marsh elevation zones and species compositions, reducing some potential for these factors to result in the observed differences in carbon stocks. Previous work has found that high-marsh zone sediments are likely to contain greater OC than mid- and lower-marsh zones, and that less inundation can facilitate increased root productivity and increased OC (the sites presented here would be considered 'lower-marsh zones') (Blum, 1993; Connor et al., 2001; Zhou et al., 2007). Moreover, sediments beneath other common marsh species in this region (e.g. *Spartina sp.*) were not sampled, yet may have differing productivity levels, resulting in OC stock differences. This may contribute to the variation between our estimated salt marsh carbon stock and that of conterminous U.S. tidal wetlands (Holmquist et al., 2018), which includes a variety of habitat types including forested and shrub-dominated tidal wetlands.

4.3 Carbon Sources and Exchanges

Across both salt marshes assessed in this study, diatoms and/or C3 plants were the dominant carbon sources in sediment. Although the isotopic signatures resulting from C4 and seagrass sources are poorly resolved, lack of a significant signature from either source allows for interpretation. Specifically, seagrasses do not significantly contribute to any OC sources in sediment, while C4 plants may contribute minimally to OC in sediment in Elkhorn Slough (1.1-11.9%; Table S2). Thus, despite similar isotopic signatures between seagrass and C4 plants, if seagrass-derived organic matter was buried under wrack sediments, we would expect to see higher δ^{13}C values in wrack sediments with depth. The insignificant differences in δ^{13}C between wrack and non-wrack sediments suggest that seagrass is not ultimately being buried, but rather, carbon derived from C3 plants and diatoms are ultimately retained in sediment.

Several underlying causes may lead to this high proportion of diatom and/or C3-derived carbon (Fig. 7). The recalcitrance of both autochthonous and allochthonous material in sediment can vary depending on the material's composition (e.g. Burdige, 2007), and thus knowing the sources and composition of deposited material aids in understanding its chance of long-term burial. In seagrass meadows, previous work demonstrated that seagrass BGB likely contributes most to autochthonous carbon burial when compared to AGB, due to higher proportions of refractory compounds and decreased grazing pressure (Trevathan-Tackett et al., 2017). This may serve to explain our lack of seagrass signal in salt marsh sediments under wrack. Seagrass wrack material deposited on top of the salt marsh is predominantly AGB, likely breaking down or being transported elsewhere before any appreciable portion reaches long-term sediment carbon pools. Instead, the dominant C3 signal is likely driven by the presence of pickleweed species (*Sarcocornia sp.)*, which have a considerable portion of below ground biomass. Despite the presence of salt grass (*Distichilis spicata)*, the relative lack of C4-derived carbon in sediment may be due to a few potential factors: 1) salt grass is less common relative to pickleweed within our sites, 2) based on our field observations, root systems of salt grass do not seem to penetrate as deeply or contain as much BGB as do those of pickleweed, and 3) salt grass contains less woody tissue than pickleweed, making it less refractory (Jepson Flora Project, 2020). In the case of diatom and planktonic sources, their significant presence in sediment may be due to a greater abundance overall, or due to complex preservation pathways such as the facilitation of carbon burial by binding sediments through extracellular polymeric substances (Drexler et al., 2020; Macreadie et al., 2019; Oakes and Eyre, 2013).

From the seasonal senescence indicated by seagrass meadow biomass data (Table 2), we infer that a significant amount of seagrass AGB is either degraded within the meadow or exported for remineralization or deposition elsewhere. Given that strong tidal flows can occur within meadows and that high densities of seagrass wrack were observed in a neighboring salt marsh, lateral export of AGB from the meadow is likely. Nonetheless, the majority of OC deposited into the marsh in the form of seagrass wrack is likely remineralized over the course of the year – with wrack decomposition outpacing a sediment accumulation rate that might support carbon preservation. While wrack remineralization can support local estuarine food web metabolism, it can also produce emissions (Jiménez et al., 2017; Liu et al., 2019). However, these emissions are small when compared to the levels of carbon sequestration within the marsh – if all of the seagrass wrack along the wrack lines was remineralized annually, this degradation would only contribute 33 ± 7.8 g C $m^{-2}yr^{-1}$ to the atmosphere (Table 2). For comparison, dating (primarily ^{137}Cs) from salt marshes nearby estimate carbon accumulation as 174 ± 45 g C $m^{-2}yr^{-1}$ (Ouyang & Lee, 2014). Thus, even along wrack lines, carbon accumulation far outpaces carbon release from breakdown of allochthonous material. Although estimates of decomposition and accumulation rates in this site could further inform these concepts, the slow annual cycle of seagrass wrack deposition and disappearance observed in the aerial imagery (Fig. S2), and the lack of seagrass-derived carbon in underlying sediment make a compelling case that little of this material is ultimately buried.

5 Conclusions

We find that California salt marshes can store approximately twice as much carbon than do seagrass meadows within this region. Grain size – an easier metric to quantify than carbon stock – can be used to estimate regional carbon storage in sandy and mixed-grain size sediments. This information can serve to inform local and regional management plans in efforts to prioritize and quantify carbon storage across these habitat types. While seagrass meadows may act as local sinks for carbon, they also export substantial amounts of AGB annually, which can be remineralized and converted to CO_2, rather than buried in neighboring blue carbon habitats. C3 salt marsh plants and/or diatoms contributed to the OC pools in all three salt marshes under study – likely due to their prevalence within our sites and their resistance to degradation. This comprehensive study assesses several key research needs in blue carbon science informing current efforts to prioritize and quantify carbon storage across these habitat types.

6 Data Availability

All data included in this manuscript will be made publicly available on the Dryad data repository.

7 Competing Interests

All data included in this manuscript will be made publicly available on the Dryad data repository.

8 Author Contributions

Ward – conceptualization, investigation, methodology, writing (original draft preparation), formal analysis; Hill – conceptualization, funding support, writing (review & editing); Souza – investigation (field and lab support), writing (review & editing); Filipczyk – investigation (field and lab support), writing (review & editing); Ricart – methodology, investigation, writing (review & editing); Merolla – investigation (field and lab support), writing (review & editing); Capece – writing (review & editing); O'Donnell – investigation (field and lab support), methodology; writing (review & editing);); Elsmore – investigation (field and lab support), writing (review & editing); Oechel – writing (review & editing); Beheshti – investigation (field and lab support), writing (review & editing).

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