Blue Carbon Stocks and Exchanges Along the Pacific West 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 Pacific coast of California. 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 seagrass and salt marsh 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 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'

39   habitats for their ability to store disproportionally high levels of organic carbon (OC) in their

40   sediments relative to other habitat types (McLeod et al., 2011). This can be attributed largely to

41   the tendency for these habitats to exhibit high sediment accretion rates and low decomposition

42   rates, driven by their exposure to permanent or regular inundation (Peck et al., 2020; Serrano et

43   al., 2019). This value has led to increasing interest in blue carbon habitats, given their

44   conservation can prevent significant emissions of carbon (Lovelock et al., 2017; Pendleton et al.,

45   2012) and their restoration can lead to increased drawdown of atmospheric CO_2 (Freedman et al.,

46   2009; Greiner et al., 2013).

47

48   **1.1 Carbon stock assessments and their significance**

49   Despite global interest, many regions are still lacking basic information on carbon stocks

50   and burial rates in blue carbon habitats. This information forms the foundation for more

51   advanced scientific research and can be extremely valuable within management contexts to

52   develop informed local and regional climate assessments. Salt marshes and seagrass meadows

53   cover extensive portions of North America's west coast, yet their carbon stocks have been

54   relatively understudied compared to other habitats in North America and other blue carbon

55   habitats in different regions of the world (Ouyang and Lee, 2014; Postlethwaite et al., 2018).

56   Eelgrass (*Zostera marina*) is the dominant seagrass species in North America and

57   occupies coastal waterways from Alaska to Mexico (Green & Short, 2003). Until recently,

58   seagrass carbon stock data were almost entirely absent along the west coast of North America

59   (See Capece et al., 2019; Kauffman et al., 2020; O'Donnell et al., 2017; Poppe & Rybczyk, 2018;

60   Postlethwaite et al., 2018; Röhr et al., 2018). Of these studies, very few data came from Central

61   or Southern California seagrass meadows, despite the fact that this region represents a key

62   temperate to subtropical transition in *Z. marina*'s range (Cabello-Pasini et al., 2003). As a result

63   of the previous paucity of data from the west coast of North America, this region was not

64   represented in previous global syntheses of seagrass carbon stocks (Duarte et al., 2010;

65   Fourqurean et al., 2012; Mazarrasa et al., 2015). Existing work on global seagrass carbon storage

66   identifies that two species of seagrasses in the Mediterranean (*Posidonia oceanica)* and Australia

67   (*Posidonia australis*) store significantly more carbon than other seagrass species, including *Z.*

68   *marina* (Fourqurean et al., 2012; Lavery et al., 2013; Prentice et al., 2020). These *Posidonia*

69   species were overrepresented in some early assessments of total global seagrass carbon storage –

70   making these global estimates unreliable when applied to management decisions or climate

71   models (Johannessen & Macdonald, 2016; Kennedy et al., 2010). In reality, the geographic and

72   interspecies variability in carbon stocks is likely greater than was initially anticipated (Macreadie

73   et al., 2018; Postlethwaite et al., 2018).

74   Salt marsh carbon stocks are similarly understudied in western North America, with

75   published carbon stock data from only four estuaries in the region and very minimal spatial

76   coverage and analyses performed in three of these locations (Brevik and Homburg, 2004;

77   Callaway et al., 2012; Kauffman et al., 2020; Patrick and DeLaune, 1990). Existing analyses of

78   North American freshwater wetlands and salt marshes are typically dominated by studies along

79   the east coast (Nahlik & Fennessy, 2016; Wilkinson et al., 2018; with the exception of Holmquist

80   et al. 2018). Within west coast studies, considerable variation in carbon stocks is observed

81   (Callaway et al., 2012; Chmura et al., 2003). Similar to seagrass meadows, these regions have

82   distinctly different oceanographic and geomorphological regimes, which can drive differences in

83   sediment carbon storage. Thus, seagrass and salt marsh carbon storage data collected from

84   understudied regions and across varying environmental gradients are necessary for understanding

85   carbon stock variability and its drivers.

86

87   **1.2 Blue carbon sources and drivers**

88   Despite an increasing breadth of information on blue carbon habitats in the last decade, a

89   number of questions remain before we can fully understand their role in regional carbon cycling

90   and climate adaptation (Macreadie et al., 2019). We do not yet fully understand what drives

91   variation in carbon stocks – a key aspect of ensuring the protection and enhancement of these

92   carbon services in the future. Previous work demonstrates that numerous factors can control

93   carbon accumulation in coastal sediments including overlying biomass, topography, hydrology,

94   mineralogy, and remineralization rates (Kelleway et al., 2016; Lima et al., 2020; Mazarrasa et

95   al., 2018; Prentice et al., 2019). In particular, sediment grain size has been demonstrated as a

96   significant predictor of carbon stocks (Dahl et al., 2016; O'Donnell et al., 2017; Serrano et al.,

97   2016), as it affects decomposition rates, which is likely related to the deposition of small

98   particles and low resuspension from the attenuation of water flow by seagrasses (Bos et al.,

99   2007; Conley et al., 2017; Gambi et al., 1990; Hendriks et al., 2008). Through similar pathways,

100   fine, silty sediments trapped in tidal salt marshes can also increase carbon storage (e.g. Zhou et

101   al., 2007).

102   The relative importance of each potential driver of carbon stock variability may be highly

103   dependent on the environmental setting, species under study, and the interactive effects of these

104   drivers. For example, in Australian salt marshes, overlying vegetation was shown to only

105   significantly affect carbon stocks in sandy and mixed grain size sediments, having no effect on

106   stocks in fine sediments (Kelleway et al., 2016). However, in other cases vegetation has been the

107 primary predictor of carbon stocks in salt marshes, irrespective of grain size (Lovelock et al.,

108 2014; Saintilan et al., 2013). Similar region and species-specific complexities between carbon

109 stocks, overlying vegetation, and mineralogy have been described in seagrass meadows (e.g.

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

111 complex interactions.

112   Knowing the relative contributions of locally produced (autochthonous) and imported

113 (allochthonous) carbon also elucidates the underlying mechanisms by which blue carbon habitats

114 store and accumulate carbon. Overlying vegetation can significantly impact sediment carbon

115 stocks; however, it is rarely the dominant source of carbon buried within blue carbon habitats

116 (Kennedy et al., 2010; Lewis et al., 2020; Mazarrasa et al., 2015; Prentice et al., 2019). In many

117 cases, contributions from terrestrial habitats, macroalgae, and suspended particulate organic

118 material contribute as much or more to carbon buried in blue carbon sediments than do

119 autochthonous sources (Drexler et al. 2020; Kennedy et al., 2010; Leorri et al., 2018; Ricart et

120 al., 2020). Thus, local primary production could significantly contribute to net annual carbon

121 drawdown within a given habitat yet play a minor role in carbon burial due to lateral export or

122 remineralization of this carbon. Understanding this phenomenon elucidates the role of blue

123 carbon habitats in broader, system-wide energy flows and carbon cycling (Hyndes et al., 2014;

124 Ricart et al., 2015). For instance, much of the carbon from laterally exported biomass may be

125 remineralized in the water column or as wrack in nearby habitats (Attard et al., 2019; Liu et al.,

126 2019), serving an important ecological role and altering the production and biogeochemical

127 cycles of recipient systems (Hyndes et al., 2014; Ince et al., 2007; Valiela and Cole, 2002).

128 Given that blue carbon habitats are highly productive (Duarte & Cebrián, 1996), support high

129 carbon burial (e.g. McLeod et al., 2011), and can co-occur within small geographic ranges

130 (Alongi et al., 2018; Bouillon & Connolly, 2009), laterally exported carbon from one blue carbon

131 habitat may be entrapped and buried in a neighboring habitat. From this landscape-scale

132 perspective, exchanges between blue carbon habitats could increase their capacity for carbon

133 burial or alter the sources of buried carbon. While some coastal studies have estimated lateral

134 carbon fluxes (Jiménez et al., 2017; Liu et al., 2019), very few studies place these lateral fluxes

135 into landscape-scale contexts that also address carbon burial in recipient habitats (Bouillon &

136 Connolly, 2009; Duarte & Krause-Jensen, 2017; Ricart et al., 2017).

137

138 The study presented here addresses this globally relevant topic of research in a relatively

139 understudied region by answering the following questions:

140 1) How much organic carbon is stored in seagrass meadow and salt marsh sediments across

141   a California latitudinal gradient?

142 2) What are the sources of carbon buried within these sediments?

143 3) Is carbon exchanged between blue carbon habitats within the coastal landscape?

144

145 **2 Methods**

146 **2.1 Study Sites**

147 Sediment cores from salt marshes and seagrass meadows, along with neighboring

148 unvegetated sediments (hereafter 'bare sediment' near seagrass meadows, and 'pan' near salt

149 marshes) were collected from six bays across a latitudinal gradient in California (Fig. 1a). A total

150 of 82 sediment cores were collected, 30 of which have been discussed previously (O'Donnell et

151 al., 2017) and are included here for comparison. The number of cores collected in each site and

152 general site characteristics are described in Table 1. While all sampled seagrass meadows were

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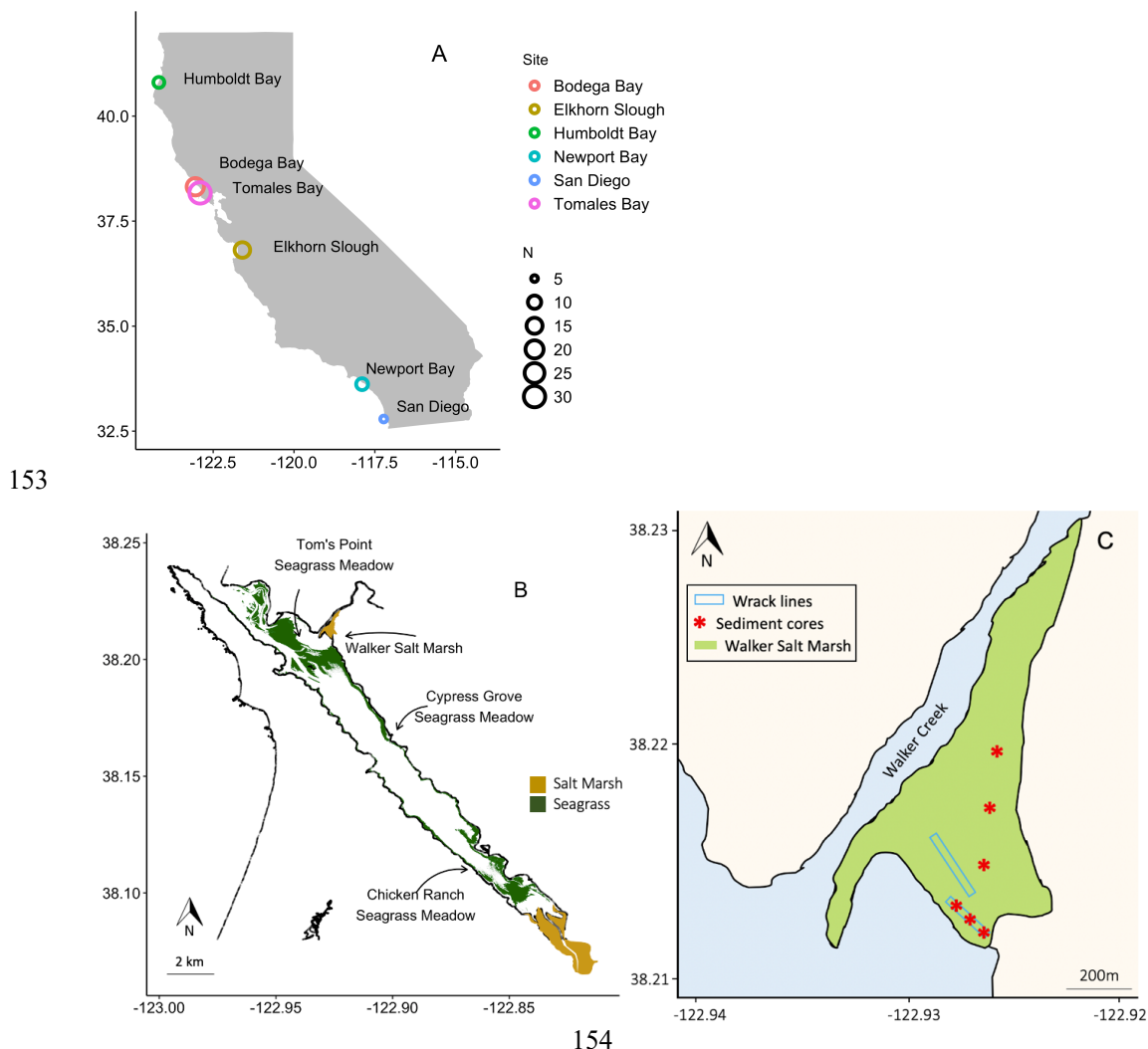
Figure 1: Sediment cores were collected from six estuaries across a latitudinal gradient in California, where N = number of cores (A). Seagrass wrack deposition into Walker salt marsh from surrounding seagrass meadows (Merkel & Associates, 2017) was estimated, while sediment cores were taken from all 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 (*Sarcornia pacifica*), and

164   to a lesser extent salt grass (*Distichlis spicata*) and marsh jaumea (*Jaumea carnosa)*. Bare

165   sediment cores were collected in unvegetated sediment nearby each seagrass meadow at a

166   minimum of 20 meters away from the meadows and from similar depths. Pan cores

167   were collected from patches of unvegetated sediment (2-4m diameter) found within the salt

168   marsh interior, a natural and semi-permanent feature of salt marsh habitats formed by elevational

169   depressions (Escapa et al., 2015). None of our sampling sites were actively restored and, to our

170   knowledge, have persisted through time.

171   We estimated OC stocks in seagrass, salt marsh, pan, and bare sediments (see details below).

172   In addition, we analyzed sediment OC sources for two individual salt marshes in Elkhorn Slough

173   ('Elkhorn salt marsh') and Tomales Bay ('Walker salt marsh'), and we examined carbon

174   exchange between a single seagrass meadow and the neighboring Walker salt marsh. Walker salt

175   marsh is located approximately 5.5 km from the mouth of Tomales Bay and is in close proximity

176   to extensive meadows of *Z. marina* – the dominant seagrass in each of the meadows sampled

177   (Fig. 1b). This marsh lies where the mouth of Walker Creek meets bay waters, and thus can

178   receive terrestrial and riverine inputs, while simultaneously receiving marine inputs from tidal

179   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 (County of Orange, 2019).
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)

180
181 **Table 1:** The location and a brief description of each bay sampled is included here, along with
182 the total number of cores collected from each habitat type in each of these bays.
183

184 **2.2 Carbon stocks**

185   All sediment cores were sampled by manually inserting transparent, open-barrel PVC pipes

186 (20 cm length, 5.08 cm diameter). Compaction occurred in 19% of cores, and a compaction

187 factor was applied when calculating carbon stocks according to Howard et al. (2014). Once

188   extracted, cores were capped and transported to the laboratory upright to prevent mixing of

189   sediment layers. Cores were then immediately extruded into sections at 2 cm intervals. Coarse

190   living plant material (> 1cm) was manually removed. Each section was dried at 60°C and

191   weighed, and dry bulk density (DBD) was determined by dividing dry bulk mass by the volume

192   of sampling interval.

193   Each section was then homogenized and divided into three subsamples of 10 g each, and the

194   remaining sample was archived. One of the three subsamples was acidified using 1.12 M HCl to

195   remove and measure total inorganic carbon (Milliman 1974). The second subsample was

196   analyzed for total organic material (TOM) by loss-on-ignition method for 4 hours at 550° C

197   (Dean 1974). Total C content (%) and δ^{13}C were additionally determined on a set of 44 of the

198   acidified subsamples randomly selected across each habitat type using an elemental analyzer

199   (PDZ Europa ANCA-GSL, SD ± 0.25 %) integrated with a continuous flow isotope ratio mass

200   spectrometer (PDZ Europa 20-20, SD ± 0.2 ‰) at the UC Davis Stable Isotope Facility. δ^{13}C

201   ratios are expressed in parts per thousand (‰) relative to VPDV (Vienna Pee Dee Belemnite)

202   according to standard notation (δ^{13}C = [(R_{sample} / $R_{standard}$) − 1] × 1000, where R is the ratio

203   ^{13}C/^{12}C). Organic carbon in each core section was then estimated using a power model developed

204   between measured TOM and measured OC in this set of subsamples (as in Craft et al., 1991).

205   Specifically, the equation y = 0.22x$^{1.1}$ was applied (r^2 = 0.84; Fig. S1). A power model was

206   selected over a linear model for these data to avoid negative estimates of carbon stocks at low

207   levels of TOM (Fig. S1). Carbon stocks were determined by multiplying DBD (g cm^{-3}) by %

208   OC.

209   In each core section, the proportion of fine sediments – the silt and clay fraction (<63 μm),

210   hereafter "mud" – was quantified. The grain size analysis was conducted by mass loss in the

211   third subsample from each section in 70 of the 82 total cores. The subsample was rinsed through

212   a 63 μm sieve with deionized water, and the remaining sediments were dried at 60°C and re-

213   weighed.

214

215   2.2 Carbon sources and exchange

216   We applied mixing models to assess salt marsh sediment carbon sources to understand

217   within-estuary exchange of carbon in the sampled habitats. Two separate mixing models were

218   produced in 1) Elkhorn salt marsh in Elkhorn Slough and Walker salt marsh in Tomales Bay, and

219   2) salt marsh sediments under seagrass wrack, versus not under wrack in Walker salt marsh. At

220   Walker salt marsh, a total of six sediment cores were collected. Three of these sediment cores

221   were collected from the interior marsh, while three were collected from underneath a seagrass

222   wrack line along the tidal edge of the marsh (Fig. 1c). *Z. marina* in this region is known to

223   undergo a period of senescence as photoperiod shortens in the fall, as is common in all temperate

224   seagrasses (Fourqurean et al., 1997). Historical imagery of the site shows persistent seagrass

225   wrack concentrated along these tide lines that consistently appears in early fall as seagrass

226   senesces (Fig. S2; Google Earth, 2020). The biomass of seagrass wrack along this tide line at the

227   time of core collection was quantified along an 80 m transect within the marsh by collecting all

228   seagrass present in a 1 m^2 quadrat every 10 meters. This material was taken back to the lab,

229   sorted into above ground biomass (AGB) and below ground biomass (BGB), rinsed, dried

230   (60°C), and weighed. Biomass data from seagrass in nearby meadows was previously published

231   (see O'Donnell et al., 2017) and is used here for reference. Sediment cores collected from

232   beneath wrack lines were sectioned at 2 cm intervals, analyzed for total OC and δ^{13}C content

233   according to the methods described above. Total nitrogen content was also determined on an

234   unacidified portion of the same 44 sediment subsamples used in carbon analyses

235   (ThermoFinnigan Flash 1112 Series elemental analyzer, SD ± 0.02%). Data from Walker salt

236   marsh are also displayed as 'shallow' (surface sediment to 10 cm deep) and 'deep' (10 cm and

237   deeper), to facilitate interpretation of changes with depth.

238   The contributions of carbon sources to each core section were then estimated with a mixing

239   model using $\delta^{13}C$ and N:C ratios as tracers. Given $\delta^{15}N$ can be altered during early diagenesis

240   (e.g. Benner et al., 1991), we selected $\delta^{13}C$ and C:N ratios as the primary geochemical tracers,

241   and therefore did not include fractionation factors into the model (Craven et al., 2017). N:C

242   ratios are utilized rather than C:N ratios because mixed fractions returned by the model are based

243   on the denominator, and thus $^{13}C/^{12}C$ and N:C both estimate the fractional contribution of ^{12}C

244   (Craven et al., 2017; Perdue and Koprivnjak, 2007). However, C:N ratios are used in text and

245   figures given this format is more typically presented in the literature. We used a Bayesian mixing

246   model SIAR 4.2 (Parnell and Jackson, 2013) to estimate the contributions of four source groups

247   selected according to the dominant plant and algal species observed within the selected salt

248   marshes. The four sources included C3 salt marsh plants (*Sarcocornia sp., Grindelia stricta)*, C4

249   salt marsh plants (*Distichlis spicata)*, seagrass *(Z. marina)*, and plankton/benthic diatoms.

250   Representative geochemistry for all of these sources (aside from seagrass) have been published

251   previously and were used here, from samples collected in San Francisco Bay, approximately 60

252   km south of Walker salt marsh (see Cloern et al., 2002 for full methods). All salt marsh sediment

253   cores were collected from areas of the marsh that were dominated by these four species, and as

254   such, other marsh species were not considered (e.g. *Spartina sp.)*. While lower densities of other

255   C3 marsh plants may have been present in some cored sites, the variability demonstrated by the

256   selected source samples likely encompasses much of this variability given the utilization of the

257   same photosynthetic pathway (Cloern et al., 2002). Plankton samples were collected from

258   estuarine water samples while benthic diatom samples were collected from both salt marsh

259   surface sediments and neighboring mudflats (Cloern et al., 2002). Isotopic signatures from the

260   benthic diatoms and estuarine plankton measured here are distinct from the other selected

261   sources but overlap with one another (Cloern et al., 2002). Thus, we pooled these data and refer

262   to this source as 'diatoms' hereafter, acknowledging that this also encompasses contributions

263   from other planktonic and benthic sources. Seagrass geochemistry was estimated from seagrass

264   leaves collected from meadows near the selected salt marshes in Newport Bay, Tomales Bay,

265   and Bodega Bay (Fig. 1a; Capece et al., 2019).

266

267   **2.3 Statistical Analyses**

268   To evaluate decay of carbon through time, we tested for significant changes in OC in each

269   habitat type with core section depth (a proxy for time) by fitting data to a generalized linear

270   mixed model (GLMM) using maximum likelihood with 'depth' and 'site' as fixed effects and

271   'core' as a random effect, using a gamma distribution and log link function to account for non-

272   normality. In sites and habitats that demonstrated significant OC changes with depth, the rate of

273   decay was estimated from the slope of its associated model. In all analyses to follow, OC across

274   all sections in each core were averaged, and statistics were performed on these core averages.

275   After inspecting data for normality and homogeneity of variance, differences in OC and grain

276   size between habitat types and between sites were analyzed using simple linear models (SLM;

277   significance defined by $\alpha = 0.05$). Specifically, these data were fit to a linear model using

278   ordinary least squares with 'site' and 'habitat' (i.e. seagrass, salt marsh, bare sediment, pan) as

279   fixed effects, including their interaction. The relationships between TOM (%) and grain size

280   were analyzed using simple linear regressions, whereby a grain size filter was selectively applied

281   to determine the point at which the relationship between the two was no longer significant (p <

282   0.05). Differences in $\delta^{13}C$ (‰) or C:N ratios between sediment depth ('surface' versus 'deep'),

283   and between sediments collected under wrack versus not under wrack, were also tested with

284   SLMs using ordinary least squares with 'depth' or 'under wrack' as fixed effects. When

285   necessary, data were log transformed. Tukey's post-hoc analyses were conducted for multiple

286   comparisons. All statistical analyses were performed in R software (R Core Team, 2018).

287

288   **3   Results**

289   **3.1 Carbon Stock Assessments**
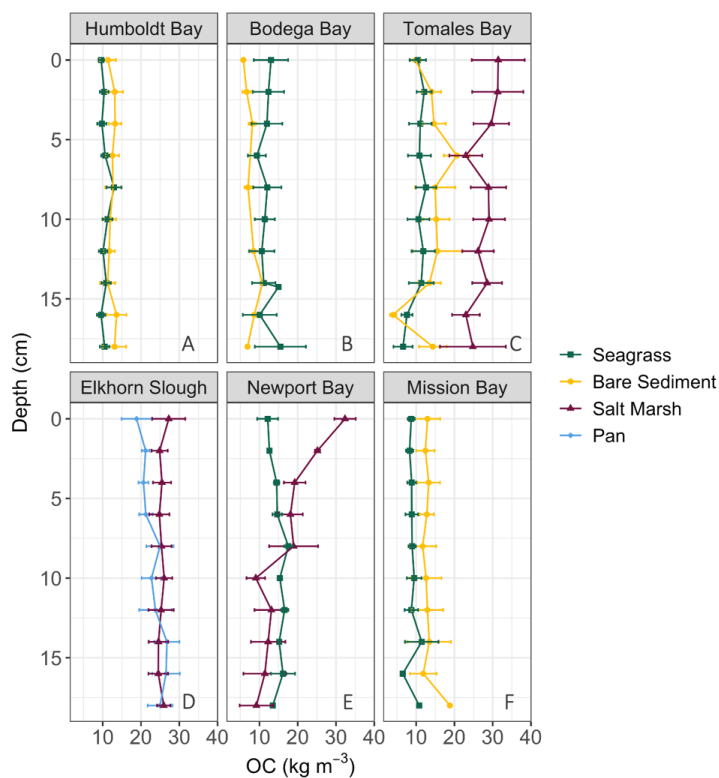
Figure 2 (left)**:** Down core trends (surface = 0 cm) in average (± SE) OC (kg m^{-3}) for each habitat type and site. Data show an insignificant decline in OC through time (downcore) in all sites except Newport Bay salt marshes.

309   Down core OC demonstrates high variability, resulting in few significant differences in

310   OC with depth (Fig. 2). Specifically, only Newport Bay salt marsh sediments exhibited

311   significant loss of OC down core, which declined at a rate of 0.95 kg C m^{-3} per cm (Fig 2e;

312   GLMM, T-value = -4.7, SE = 0.01, $p < 0.05$). Significant differences between OC stocks

313   emerged when cores were compared between habitats, with salt marshes containing significantly

314   more carbon than both bare sediment and seagrass meadows (Fig. 3b; SLM, $p < 0.01$, F-statistic

315   = 13.3, DF =3). Specifically, salt marsh sediments contained 23.51 ± 1.77 kg OC m^{-3}, while

316   seagrass meadows contained 11.01 ± 1.18 kg OC m^{-3} (Fig. 3b; mean ± SE). Seagrass meadow

317   carbon stocks were not significantly different than those of nearby bare sediments (Tukey's post-

318   hoc analysis, $p > 0.05$), which contained an average of 12.34 ± 1.57 kg OC m^{-3}. Pan sediments

319   also contained higher carbon than did seagrass meadows (Tukey's post-hoc analysis, $p > 0.05$).

320   A full list of carbon stocks is displayed in Table S1. Tukey's post-hoc analysis indicates that in

321   Tomales Bay, salt marshes contained significantly more carbon than seagrass meadows (Fig. 3a;

322    $p < 0.05$) while bare sediment and seagrass carbon stocks did not significantly differ from one

323   another ($p > 0.05$). We did not detect any other significant differences when comparing carbon

324   stocks across habitat types within each individual site (Tukey's post-hoc analysis, $p > 0.05$).

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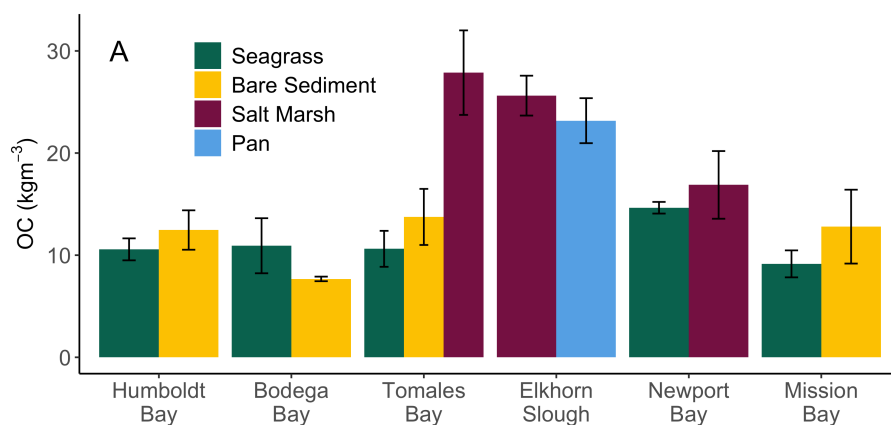
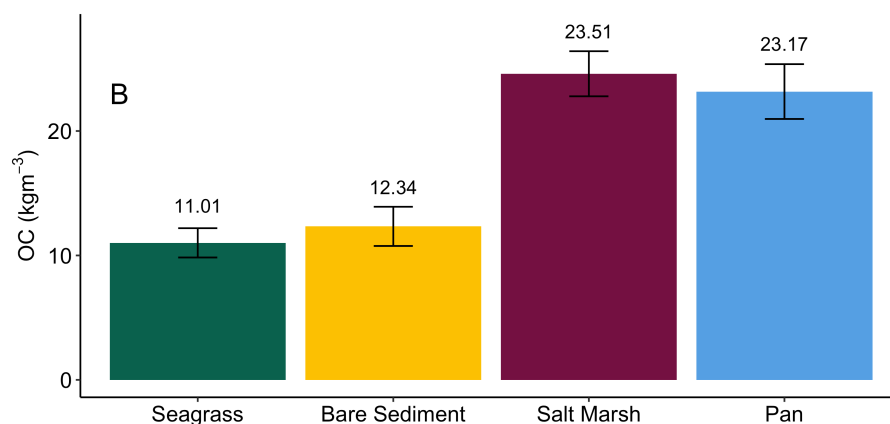


Figure 3: Average (± SE) total organic carbon (OC) stocks (kg m^{-3}) across all cores collected
from each habitat type within each site in this study (A). Average (± SE) total organic carbon
stocks (kg m^{-3}) across all cores collected within each habitat type in this study (B).

330

331   We observed a very strong relationship between grain size and storage of organic material,

332   especially at lower TOM (%) values (Fig. 4). Specifically, the observed linear relationship

333   between grain size and TOM is strongest when sediment is 8.5% TOM or less (linear model, r^2 =

334   0.95, $p < 0.05$, F-statistic = 4957, DF = 269). However, as the proportion of fine sediments in

335   each sample increases, the relationship between grain size and TOM weakens, with no

336   significant relationship between the two in sediments consisting of more than 36% mud (SLM, p

337   > 0.05, F-statistic = 3.9, DF = 232). Our results indicate that grain size was similar between sites

338   (SLM, $p > 0.05$, F-statistic = 2.7, DF = 3) but differed between habitat types (Fig. 5a; SLM, p <

339   0.05, F-statistic = 5.7, DF = 3), with salt marsh sediments demonstrating significantly greater %

340   mud than both seagrass and bare sediment (Tukey's post-hoc analysis, $p < 0.05$). Recognizing

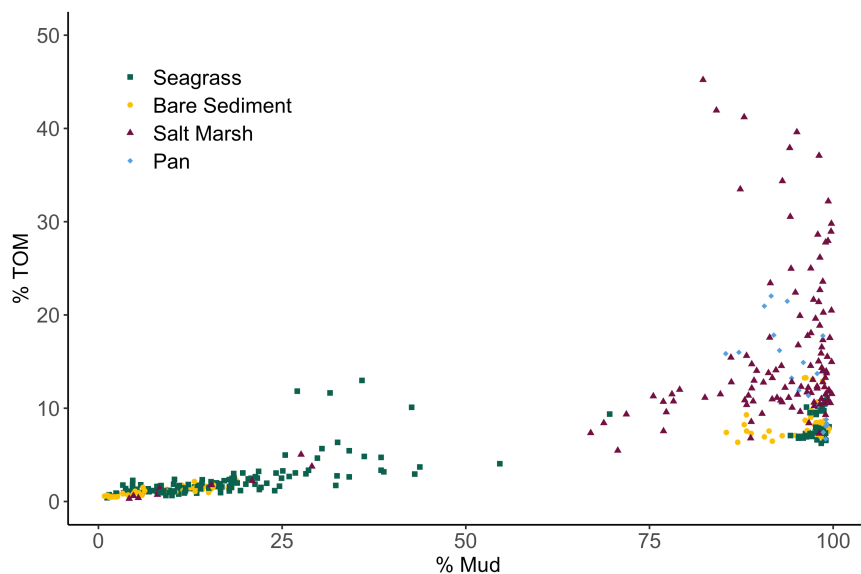
341   that the sample size of pan cores was low, pan sediments displayed comparable % mud to salt

342   marsh sediments but there were no significant differences between pan grain size and the other

343   habitat types' grain sizes (Tukey's post-hoc analysis, $p > 0.05$). Tukey's post-hoc analyses did

344   not indicate any significant differences in grain size between habitat types within each site (Fig.

345   5a; p > 0.05).

346

347
348   **Figure 4:** Biplot showing the relationship among total organic material (TOM) (%) of each 2-cm
349   core section from each habitat type plotted against sediment grain size (% Mud).
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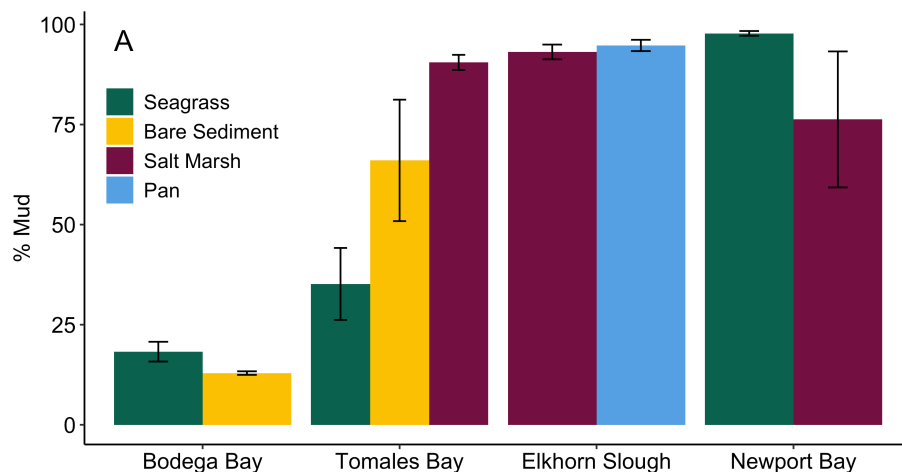
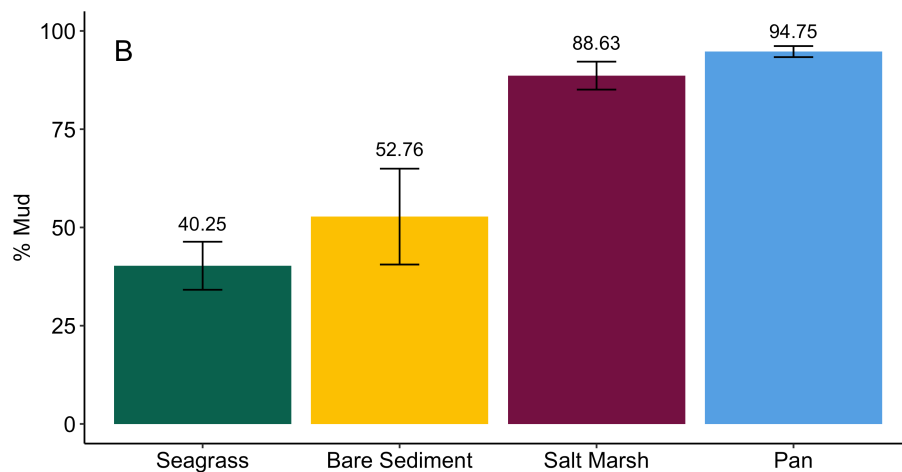


Figure 5: Average (± SE) % mud (fine grained particles) of all sediments quantified in each site within each habitat type (A), average (± SE) % mud in each habitat type across all sites measured (B).

357

358 **3.2 Carbon Sources and Exchange**

359 **3.2.1 Wrack Deposition**

360   While we conducted only one ground survey of seagrass wrack lines within Walker salt

361 marsh in October 2019, historical aerial imagery was utilized to verify that these wrack lines

362 appear reliably in this season in similar locations each year (Fig. S2). This phenomenon can be

363 viewed as far back as 2002, before which images are of low quality or unavailable (Google

364 Earth, 2020). These wrack lines typically persist throughout the winter, becoming indiscernible

365 via aerial imagery by spring. Previous data collected by the authors (O'Donnell et al., 2017)

366 demonstrated this senescence within the nearby Tom's Point seagrass meadow (Fig. 1b), where

367 average summer seagrass biomass was 440 ± 59.4 g m^{-2} and winter biomass was 115 ± 16.5 g m^{-}

368 ^{2} (AGB and BGB, mean ± SE; Table 2). Within the neighboring Walker salt marsh, fall estimates

369 of wrack demonstrated that 106 ± 24.6 g m^{-2} of seagrass (dry weight) was deposited along tide

370 lines (Table 2). While both seagrass AGB and BGB are included in this value, seagrass BGB

392   (SIAR mixing model, Table S2). Similarly, no significant quantity of seagrass-derived carbon

393   was detected in Elkhorn salt marsh sediments (SIAR mixing model, Table S2). Rather, models

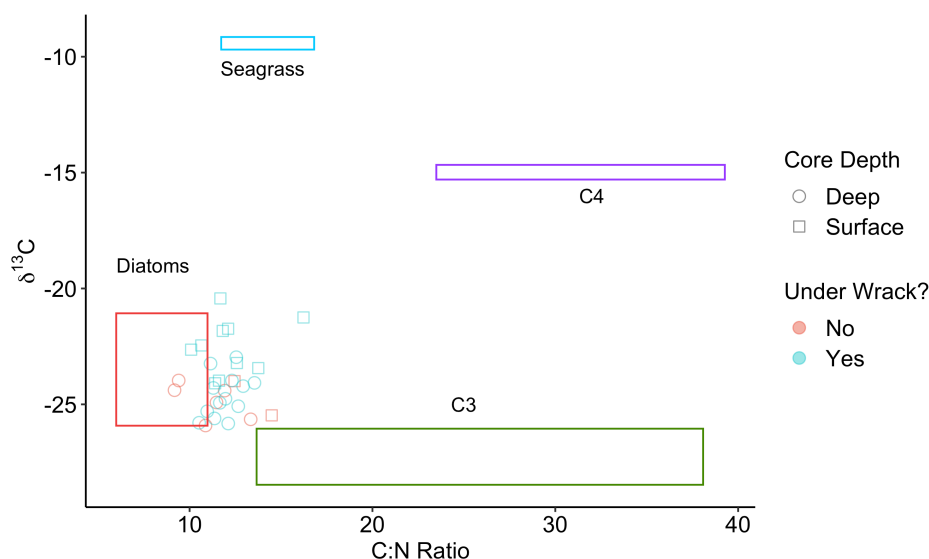
394   estimate that sediments were derived from an estimated 47% salt marsh C3 plants and 42%

395   diatoms in Elkhorn Slough, and 49% salt marsh C3 plants and 46% diatoms in Walker salt marsh

396   (Fig. 7; Table S2). Thus, regardless of site, depth, or the presence of wrack, model results

397   estimate no significant storage of seagrass-derived carbon in sediment (Table S2). Instead, C3

398   plants and diatoms are the only two significant contributors to underlying carbon storage across

399   salt marshes in all locations.

400

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

407

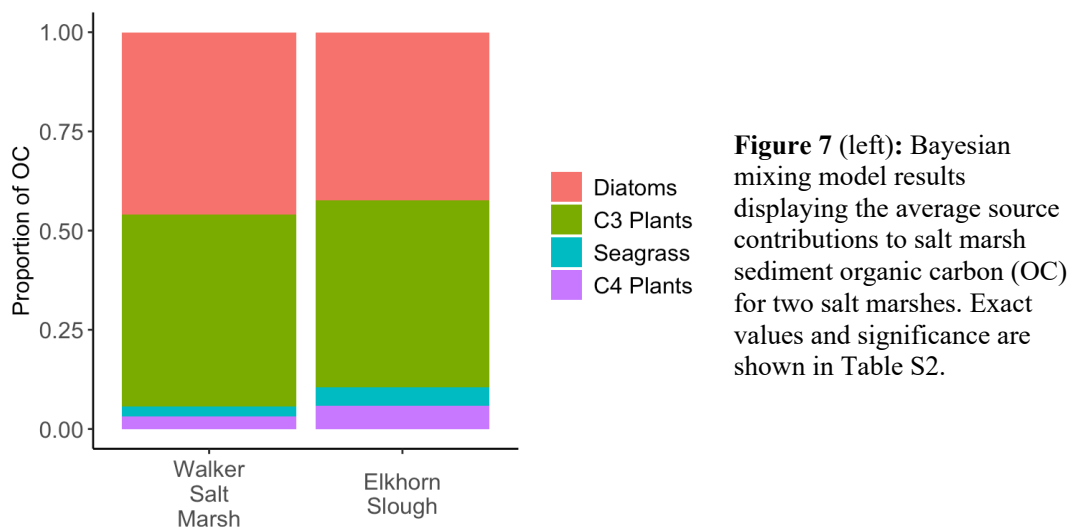



Figure 7 (left)**:** Bayesian mixing model results displaying the average source contributions to salt marsh sediment organic carbon (OC) for two salt marshes. Exact values and significance are shown in Table S2.

4   Discussion

4.1 Carbon Stocks

The lack of clear downcore trends suggests relative OC stability with depth and through time (Fig. 2). This is further supported by the persistence of this pattern in seagrass and bare sediment sites where longer cores were available (Fig. S3). In the only site with significant downcore OC losses (Newport Bay salt marsh), this pattern may be explained by historic hydrographic changes. 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 downcore 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} (O'Donnell et al., 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

435   slow accumulation rates and lack of down core trends, we interpret that our data represent

436   realistic stock assessments for each respective habitat and location, rather than being reflective of

437   shallow surface sediment carbon stocks.

438   Determining drivers of OC storage variation across habitats is notably complex, where a mix

439   of factors such as grain size, elevation, hydrodynamic energy, and vegetation type may influence

440   underlying sediment OC storage (Kelleway et al., 2016; Lima et al., 2020; Miyajima et al.,

441   2015). Here, sediment grain size and its associated drivers allow us to further examine variation

442   in sediment OC storage variation. Specifically, grain size likely contributed to the observed inter-

443   habitat differences in OC storage, given its strong correlation with TOM. Despite no significant

444   differences in grain size between habitat types within each site (likely due to high grain size

445   variability and low relative sample sizes), apparent qualitative differences elude to possible

446   explanations of stock differences. For example, seagrass sediments had lower % mud than salt

447   marsh sediments in Tomales Bay, a trend that was reversed in Newport Bay (Fig. 5a; Table S1).

448   Similarly, seagrass sediments did not always contain a higher % mud than neighboring bare

449   sediments, contrary to what is typically reported (Bos et al., 2007; Conley et al., 2017; Mazarassa

450   et al., 2015), which may explain their apparent lack of sediment OC differences. Overall, salt

451   marshes had greater OC storage and smaller average grain size than seagrass meadows. The

452   periodic, lower energy inundation of the sampled marsh and pan habitats may facilitate the

453   observed smaller grain sizes – by preventing the resuspension of small particles that might occur

454   in higher hydrodynamic energy or submerged systems (Christiansen et al., 2000; Yang et al.,

455   2008). In marsh and pan habitats, biological factors such as primary production and

456   decomposition rates may become more important drivers of carbon burial than would be true in

457   dominantly sandy sediments (Miyajima et al., 2017). Yet despite the absence of vegetation in

458   pan sites, we did not observe significant differences in carbon stocks between pan sediments and

459   surrounding salt marsh sediments. This could be attributed to 1) significant carbon contributions

460   from surrounding salt marsh biomass to pan sites overtime, 2) historical marsh recovery along

461   pan edges and subsequent burial of vegetation captured in pan cores, 3) variable decomposition

462   rates in both pan and salt marsh sediments, or 4) because the expected effect of canopy-

463   vegetation on salt marsh sediment is too small relative to other drivers, producing statistically

464   insignificant results. In sum, although seagrasses and salt marshes can facilitate carbon storage

465   by altering grain size distributions, hydrodynamics and geomorphology play a critical role in

466   grain size distributions and therefore, carbon storage. The hydrographic changes in Newport Bay

467   salt marshes associated with decreased grain sizes further emphasize this point – drawing

468   attention to the importance of watershed and sediment management to regional carbon storage.

469   Furthermore, although grain size is clearly a key driver in carbon storage, our data demonstrate

470   that it becomes of limited use as a predictor of carbon stocks after the proportion of mud exceeds

471   36% (Fig. 4). This demonstrates that using grain size as a cost-effective way to estimate carbon

472   stocks (as has been suggested, e.g. Serrano et al., 2016) only appears possible in sandy and

473   mixed grain size sediments within the sites studied here. Stocks in fine sediment sites above this

474   threshold cannot be estimated using grain size alone – a management-relevant finding for efforts

475   to incorporate habitat-specific carbon storage into regional climate plans.

476

477   **4.2 Global and Regional Comparisons**

478   With recent meta-analyses on coastal carbon stocks in salt marshes and seagrass meadows,

479   we can compare our data to global and regional averages (no sufficient syntheses of pan or bare

480 sediment carbons stocks were identified). We find that carbon storage in California seagrass

481 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})
Seagrass			
This study	Seagrass (*Z. marina*)	California	110 ± 11.8
Kauffman et al. (2020)	Seagrass (*Z. marina*)	* U.S. west coast	80 ± 12
Prentice et al. (2020)	Seagrass (*Z. marina*)	U.S. west coast	65.12
Rohr et al. (2018)	Seagrass (*Z. marina*)	* U.S. west coast	69.4 ± 8.4
		* Temperate Northern Hemisphere	108.9 ± 39.56
[1]Fourqurean et al. (2012)	Seagrass	Global	[1]139.7
Salt Marsh			
This study	Salt marsh dominated by *Sarcocornia pacifica*, *Distichlis spicata* and *Jaumea carnosa*	California	235 ± 17.7
Kauffman et al. (2020)	Salt marsh dominated by *Distichlis spicata* and *Sarcocornia perennis*	* U.S. west coast	190 ± 16
Holmquist et al. (2018)	Tidal wetlands (mixed, dominated by estuarine emergent vegetation)	* Conterminous U.S. tidal wetlands	270 ± 1.4

482
483 **Table 3:** Summary of previously reported carbon stock assessments in seagrass meadows and
484 tidal wetlands, all normalized to the top 1m of sediment. Studies that included any data from
485 California are denoted by an asterisk. Values are reported as mean ± SE, unless otherwise noted.
486 [1]Fourqurean et al. (2012) value represents median OC storage.
487

488 *marina* from the U.S. west coast (Table 3). Early estimates from the US west coast were

489 markedly low, with one study of *Z. marina* from British Columbia measuring average stocks of

490 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

491 maximum OC of 7.0 % estimated here (Postlethwaite et al., 2018). While estimates from studies

492 averaging over broader U.S. West coast regions are higher than this Canadian case study (Table

493 3), the data presented here are still higher than regional estimates, suggesting possible latitudinal

494   difference in carbon storage between the northern and southern regions of the North American

495   west coast. This is not unsurprising given the variation in environmental and geomorphic

496   conditions over this large stretch of coastline, which likely influence the carbon storage capacity

497   along with the factors discussed here such as hydrodynamics or grain size conditions.

498   Recent studies of the U.S. west coast and of conterminous U.S. tidal wetlands allow for

499   comparison with salt marsh data collected here. Much like with seagrass meadows, California

500   salt marsh carbon storage was also higher than previous estimates from the U.S. west coast

501   (Kauffman et al., 2020; Table 3). Both the data presented here as well as those from Kauffman et

502   al. (2020) (Table 3) were collected from similar marsh zones and species compositions, reducing

503   some potential for these factors to result in the observed differences in carbon stocks. Previous

504   work has found that high-marsh zone sediments are likely to contain greater OC than mid- and

505   lower-marsh zones, and that less inundation can facilitate increased root productivity and

506   increased OC (the sites presented here would be considered 'lower-marsh zones') (Blum, 1993;

507   Connor et al., 2001; Zhou et al., 2007). Moreover, sediments beneath other common marsh

508   species in this region (e.g. *Spartina sp.*) were not sampled, yet may have differing productivity

509   levels, resulting in OC stock differences. This may contribute to the variation between our

510   estimated salt marsh carbon stock and that of conterminous U.S. tidal wetlands (Holmquist et al.,

511   2018), which includes a variety of habitat types including forested and shrub-dominated tidal

512   wetlands.

513

514   **4.1 Carbon Sources and Exchanges**

515   Across both salt marshes assessed in this study, diatoms and C3 plants were the dominant

516   carbon sources in sediment. Although the isotopic signatures resulting from C4 and seagrass

517   sources are poorly resolved, lack of a significant signature from either source allows for

518   interpretation. Specifically, neither C4 plants nor seagrasses significantly contributed to the OC

519   sources in sediment. Thus, despite similar isotopic signatures, if some seagrass-derived organic

520   matter was buried under wrack sediments, we would expect to see higher $\delta^{13}C$ values in wrack

521   sediments with depth. The insignificant differences in $\delta^{13}C$ between wrack and non-wrack

522   sediments suggest that seagrass is not ultimately being buried, but rather, carbon derived from

523   C3 plants and diatoms are ultimately retained in sediment.

524   Several underlying causes may lead to this high proportion of diatom and C3-derived carbon

525   (Fig. 7). The recalcitrance of both autochthonous and allochthonous material in sediment can

526   vary depending on the material's composition (e.g. Burdige, 2007), and thus knowing the

527   sources and composition of deposited material aids in understanding its chance of long-term

528   burial. In seagrass meadows, previous work demonstrated that seagrass BGB likely contributes

529   most to autochthonous carbon burial when compared to AGB, due to higher proportions of

530   refractory compounds and decreased grazing pressure (Trevathan-Tackett et al., 2017). This may

531   serve to explain our lack of seagrass signal in salt marsh sediments under wrack. Seagrass wrack

532   material deposited on top of the salt marsh is predominantly AGB, likely breaking down or being

533   transported elsewhere before any appreciable portion reaches long-term sediment carbon pools.

534   Instead, the dominant C3 signal is likely driven by the presence of pickleweed species

535   (*Sarcocornia sp.*), which have a considerable portion of below ground biomass. Despite the

536   presence of salt grass (*Distichilis spicata*), the lack of C4-derived carbon in sediment may be due

537   to a few potential factors: 1) salt grass is less common relative to pickleweed within our sites, 2)

538   based on our field observations, root systems of salt grass do not seem to penetrate as deeply or

539   contain as much BGB as do those of pickleweed, and 3) salt grass contains less woody tissue

540 than pickleweed, making it less refractory (Jepson Flora Project, 2020). In the case of diatom and

541 planktonic sources, their significant presence in sediment may be due to a greater abundance

542 overall, or due to complex preservation pathways such as the facilitation of carbon burial by

543 binding sediments through extracellular polymeric substances (Drexler et al., 2020; Macreadie et

544 al., 2019; Oakes and Eyre, 2013).

545 From the seasonal senescence indicated by seagrass meadow biomass data (Table 2), we

546 infer that a significant amount of seagrass AGB biomass is either degraded within the meadow or

547 exported for remineralization or deposition elsewhere. Given that strong tidal flows can occur

548 within meadows and that high densities of seagrass wrack were observed in a neighboring salt

549 marsh, lateral export of AGB from the meadow is likely. Nonetheless, the majority of OC

550 deposited into the marsh in the form of seagrass wrack is likely remineralized over the course of

551 the year – with wrack decomposition outpacing a sediment accumulation rate that might support

552 carbon preservation. While wrack remineralization can support local estuarine food web

553 metabolism, it can also produce emissions (Jiménez et al., 2017; Liu et al., 2019). However,

554 these emissions are small when compared to the levels of carbon sequestration within the marsh

555 – if all of the seagrass wrack along the wrack lines was remineralized annually, this degradation

556 would only contribute 33 ± 7.8 g C m^{-2}yr^{-1} to the atmosphere (Table 2). For comparison, dating

557 (primarily ^{137}Cs) from salt marshes nearby estimate carbon accumulation as 174 ± 45 g C m^{-2}yr^{-1}

558 (Ouyang & Lee, 2014). Thus, even along wrack lines, carbon accumulation far outpaces carbon

559 release from breakdown of allochthonous material. Although estimates of decomposition and

560 accumulation rates in this site could further inform these concepts, the slow annual cycle of

561 seagrass wrack deposition and disappearance observed in the aerial imagery (Fig. S2), and the

562   lack of seagrass-derived carbon in underlying sediment make a compelling case that little of this

563   material is ultimately buried.

564

565   **5   Conclusions**

566   We find that California salt marshes can store approximately twice as much carbon than do

567   seagrass meadows within this region. Grain size – an easier metric to quantify than carbon stock

568   – can be used to estimate regional carbon storage in sandy and mixed-grain size sediments. This

569   information can serve to inform local and regional management plans in efforts to prioritize and

570   quantify carbon storage across these habitat types. While seagrass meadows may act as local

571   sinks for carbon, they also export substantial amounts of AGB annually, which can be rapidly

572   remineralized and converted to CO_2, rather than buried in neighboring blue carbon habitats. Both

573   C3 salt marsh plants and diatoms contributed to the OC pools in all three salt marshes under

574   study – likely due to their prevalence within our sites and their resistance to degradation. This

575   comprehensive study assesses several key research needs in blue carbon science informing

576   current efforts to prioritize and quantify carbon storage across these habitat types.

577
578
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