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. In the top 20 cm of sediment, the salt marshes contained approximately twice as much OC as did seagrass meadows, 4.92 ± 0.36 kg OC m^{-2} compared to 2.20 ± 0.24 kg OC m^{-2}, 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 and sequester disproportionally high levels of organic carbon

39 (OC) in their sediments relative to other habitat types, thereby potentially serving in a

40 management context to provide carbon mitigation (Lovelock and Duarte, 2019; McLeod et al.,

41 2011). This can be largely attributed to the tendency for these habitats to exhibit high sediment

42 accretion rates and low decomposition rates (Peck et al., 2020; Serrano et al., 2019). This ability

43 has led to increasing interest in blue carbon habitats, given their conservation can prevent

44 significant emission of stored carbon (Lovelock et al., 2017; Pendleton et al., 2012) and their

45 restoration can lead to increased drawdown of atmospheric CO_2 (Freedman et al., 2009; Greiner

46 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, 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 paucity of data from the west coast of North America, this region was not represented in

64   previous global syntheses of seagrass carbon stocks (Duarte et al., 2010; Fourqurean et al., 2012;

65   Mazarrasa et al., 2015). Existing work on global seagrass carbon storage identifies that two

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

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

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

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

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

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

72   variability in carbon stocks is likely greater than was initially anticipated (Macreadie et al., 2018;

73   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 increasing information on blue carbon habitats in the last decade, a number of

89 questions remain before we can fully understand their role in regional carbon cycling and climate

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

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

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

93 in coastal sediments including overlying biomass, topography, hydrology, mineralogy, and

94 remineralization rates (Kelleway et al., 2016; Lima et al., 2020; Mazarrasa et al., 2018; Prentice

95 et al., 2019). In particular, sediment grain size has been demonstrated to be a significant

96 predictor of carbon stocks (Dahl et al., 2016; O'Donnell, 2017; Serrano et al., 2016), as it affects

97 decomposition rates, likely related to the deposition of small particles and low resuspension from

98 the attenuation of water flow by seagrasses (Bos et al., 2007; Conley et al., 2017; Gambi et al.,

99 1990; Hendriks et al., 2008). Through similar pathways, fine, silty sediments trapped in tidal salt

100 marshes can also increase carbon storage (e.g. Zhou et al., 2007).

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

102 dependent on the environmental setting, species composition, and the interactive effects of these

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

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

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

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

4

107   2014; Saintilan et al., 2013). Similar region and species-specific complexities between carbon

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

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

110   complex interactions.

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

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

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

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

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

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

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

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

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

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

121   remineralization of particulate organic carbon. Understanding lateral carbon transport elucidates

122   the role of blue carbon habitats in broader, system-wide energy flows and carbon cycling

123   (Hyndes et al., 2014; Ricart et al., 2015). For instance, much of the carbon from laterally

124   exported biomass may be remineralized in the water column or as wrack in nearby habitats

125   (Attard et al., 2019; Liu et al., 2019), serving an important ecological role and altering the

126   production and biogeochemical cycles of recipient systems (Hyndes et al., 2014; Ince et al.,

127   2007; Valiela and Cole, 2002). Given that blue carbon habitats are highly productive (Duarte &

128   Cebrián, 1996), support high carbon burial (e.g. McLeod et al., 2011), and can co-occur within

129   small geographic ranges (Alongi, 2018; Bouillon & Connolly, 2009), laterally exported carbon

130   from one blue carbon habitat may be entrapped and buried in a neighboring habitat. From this

131   landscape-scale perspective, exchanges between blue carbon habitats could increase their

132   capacity for carbon burial or alter the sources of buried carbon. While some coastal studies have

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

134   these lateral fluxes into landscape-scale contexts that also address carbon burial in recipient

135   habitats (Bouillon & Connolly, 2009; Duarte & Krause-Jensen, 2017; Ricart et al., 2017).

136

137   This study addresses these globally relevant topics of research in a relatively understudied region

138   by answering the following questions:

139   1) How much organic carbon is stored in seagrass and salt marsh sediments across a

140   latitudinal gradient?

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

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

143

144   **2   Methods**

145   **2.1 Study Sites**

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

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

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

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

150   2017) and are included here for comparison. The number of cores collected in each site and

151   general site characteristics are described in Table 1. While all sampled seagrass meadows were
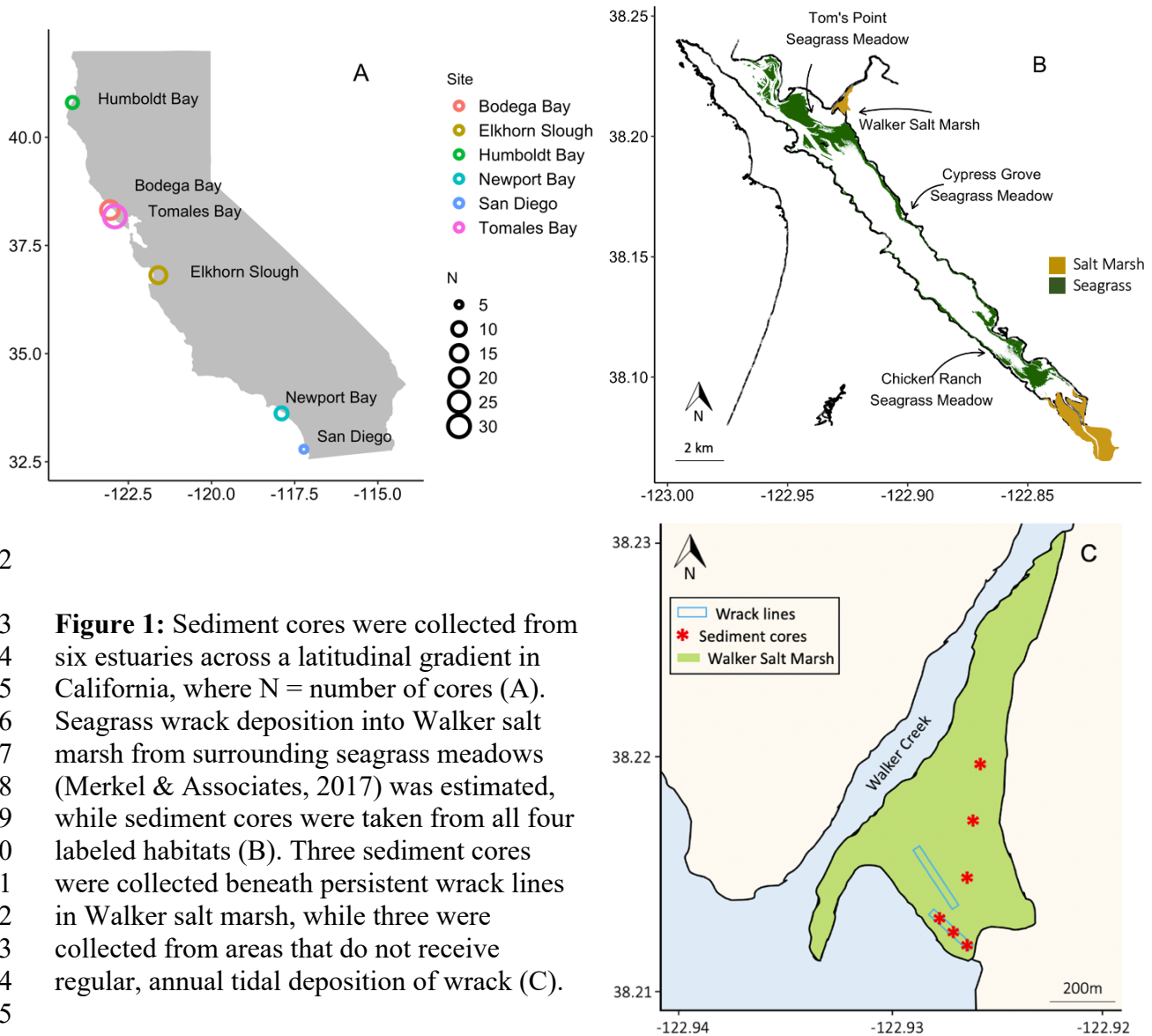
Figure 1: Sediment cores were collected from six estuaries across a latitudinal gradient in California, where N = number of cores (A). Seagrass wrack deposition into Walker salt marsh from surrounding seagrass meadows (Merkel & Associates, 2017) was estimated, while sediment cores were taken from all 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

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

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

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

175   knowledge, respective vegetation has persisted through time.

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

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

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

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

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

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

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

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

184   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

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

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

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

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

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

197   of sampling interval.

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

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

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

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

202   (Dean, 1974). Total C content (%) and $\delta^{13}C$ were additionally determined on a set of 44 of the

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

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

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

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

207   according to standard notation ($\delta^{13}C = [(R_{sample} / R_{standard}) - 1] \times 1000$, where R is the ratio

208    $^{13}C/^{12}C$). Organic carbon in each core section was then estimated using a power model developed

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

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

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

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

213   OC.

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

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

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

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

218   weighed.

219   Comparable to previous studies, a core depth of 20 cm was selected (Fourqurean et al. 2012;

220   Prentice et al., 2020; Röhr et al., 2018). As such, stock estimates are presented in kg OC m^{-2} in

221   the top 20 cm of sediment. However, given the selected depths for stock estimates vary

222   throughout the literature, we extrapolate all data to 1 m when comparing across studies. Some

223   research suggests that OC content remains relatively constant below 10 cm to depths up to 1 m,

224   making this extrapolation appropriate (Callaway et al., 2012; Prentice et al., 2020; Fig. S3),

225   while evidence of downcore variability in other studies makes extrapolation less appropriate

226   (e.g., St. Laurent et al., 2020; Serrano et al., 2012). When comparing the carbon stocks estimated

227   here to those in previous studies, we include each studies' sampled core depths for clarity.

228

229   **2.3 Carbon sources and exchange**

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

231   within-estuary exchange of carbon among the sampled habitats. Two separate mixing models

232   were produced for 1) Elkhorn salt marsh in Elkhorn Slough and Walker salt marsh in Tomales

233   Bay, and 2) salt marsh sediments under seagrass wrack, versus not under wrack in Walker salt

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

235   sediment cores were collected from the interior marsh, while three were collected from

236   underneath a seagrass wrack line along the tidal edge of the marsh (Fig. 1c). *Z. marina* in this

237 region is known to undergo a period of senescence as photoperiod shortens in the fall, as is

238 common in all temperate seagrasses (Fourqurean et al., 1997). Historical imagery of the site

239 shows persistent seagrass wrack concentrated along these tide lines that consistently appears in

240 early fall as seagrass senesces (Fig. S2; Google Earth, 2020). The biomass of seagrass wrack

241 along this tide line at the time of core collection was quantified along an 80 m transect within the

242 marsh by collecting all seagrass present in a 1 m^2 quadrat every 10 meters. This material was

243 taken back to the lab, sorted into above ground biomass (AGB) and below ground biomass

244 (BGB), rinsed, dried (60°C), and weighed. Biomass data from seagrass in nearby meadows was

245 previously published (see O'Donnell, 2017) and is used here for reference. Sediment cores

246 collected from beneath wrack lines were sectioned at 2 cm intervals, analyzed for total OC and

247 δ^{13}C content according to the methods described above. Total nitrogen content was also

248 determined on an unacidified portion of the same 44 sediment subsamples used in carbon

249 analyses (ThermoFinnigan Flash 1112 Series elemental analyzer, SD ± 0.02%). Data from

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

251 (10 cm and deeper), to facilitate interpretation of changes with depth.

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

253 model using δ^{13}C and N:C ratios as tracers. Given δ^{15}N can be altered during early diagenesis

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

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

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

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

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

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

260   model SIAR 4.2 (Parnell and Jackson, 2013) to estimate the contributions of several source

261   groups selected according to the dominant plant and algal species observed within the selected

262   salt marshes. The sources included C3 salt marsh plants, C4 salt marsh plants (*Distichlis*

263   *spicata)*, seagrass *(Z. marina)*, and plankton/benthic diatoms. Seagrass geochemistry was

264   estimated from seagrass leaves collected from meadows near the selected salt marshes in

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

266   geochemistry for all other sources has been published previously and was used here, from

267   samples collected in San Francisco Bay, approximately 60 km south of Walker salt marsh (see

268   Cloern et al., 2002 for full methods). All salt marsh sediment cores were collected from areas of

269   the marsh that were dominated by the aforementioned species, and as such, other marsh species

270   were not considered (e.g., *Spartina sp.)*. While lower densities of other C3 marsh plants may

271   have been present in some cored sites, the variability demonstrated by the selected source

272   samples likely encompasses much of this variability given the utilization of the same

273   photosynthetic pathway (Cloern et al., 2002). Plankton samples were collected from estuarine

274   water samples while benthic diatom samples were collected from both salt marsh surface

275   sediments and neighboring mudflats (Cloern et al., 2002). These sources have similar isotopic

276   values and are pooled here and referred to as "diatoms" for simplicity, acknowledging that this

277   encompasses contributions from multiple planktonic and benthic sources. Given the overlapping

278   isotopic values of C3 plants and diatoms, these two sources were pooled in mixing models,

279   allowing an estimate of diatoms and/or C3 plants contributions to marsh sediments, in addition to

280   contributions from seagrass and C4 plants.

281

282   **2.4 Statistical Analyses**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

297   0.05). Differences in $\delta^{13}C$ (‰) or C:N ratios between sediment depth ('surface' versus 'deep'),

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

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

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

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

302

303   **3   Results**
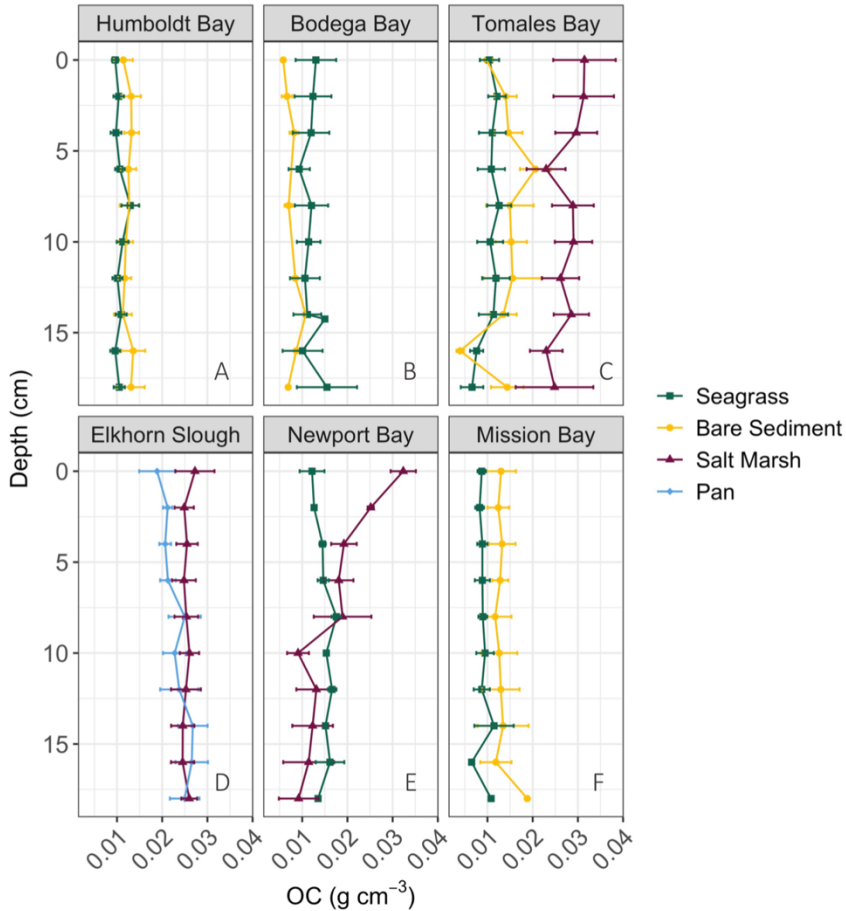
304   **3.1 Carbon Stock Assessments**

14

Figure 2 (left)**:** Down core trends (surface = 0 cm) in average (± SE) OC (g cm^{-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.

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

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

330   significant loss of OC down core, which declined at a rate of 0.001 g C cm^{-3} per cm depth (Fig

331   2e; GLMM, T-value = -4.7, SE = 0.01, p < 0.05). Significant differences between OC stocks

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

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

334   = 13.3, DF =3). Specifically, within the top 20 cm of sediment, salt marsh sediments contained

335   4.92 ± 0.36 kg OC m^{-2}, while seagrass meadows contained 2.20 ± 0.24 kg OC m^{-2} (Fig. 3b;

336   mean ± SE). Seagrass meadow carbon stocks were not significantly different than those of

337   nearby bare sediments (Tukey's post-hoc analysis, p > 0.05), which contained an average of 2.47

338   ± 0.32 kg OC m^{-2}. Pan sediments also contained higher carbon than did seagrass meadows

339   (Tukey's post-hoc analysis, $p > 0.05$). A full list of carbon stocks is displayed in Table S1.

340   Tukey's post-hoc analysis indicates that in Tomales Bay, salt marshes contained significantly

341   more carbon than seagrass meadows (Fig. 3a; $p < 0.05$) while bare sediment and seagrass carbon

342   stocks did not significantly differ from one another ($p > 0.05$). We did not detect any other

343   significant differences when comparing carbon stocks across habitat types within each individual

344   site (Tukey's post-hoc analysis, $p > 0.05$).

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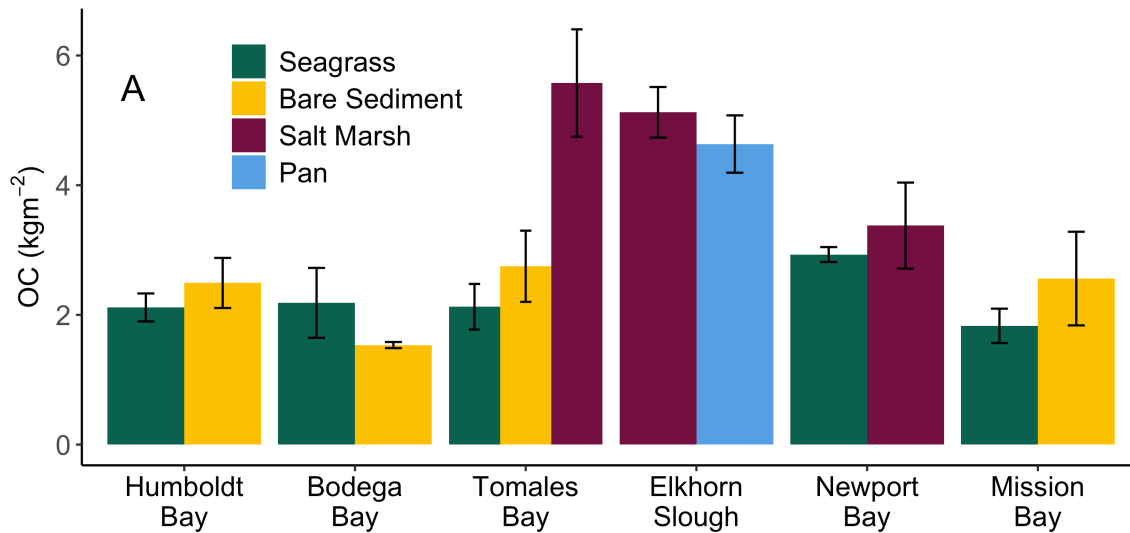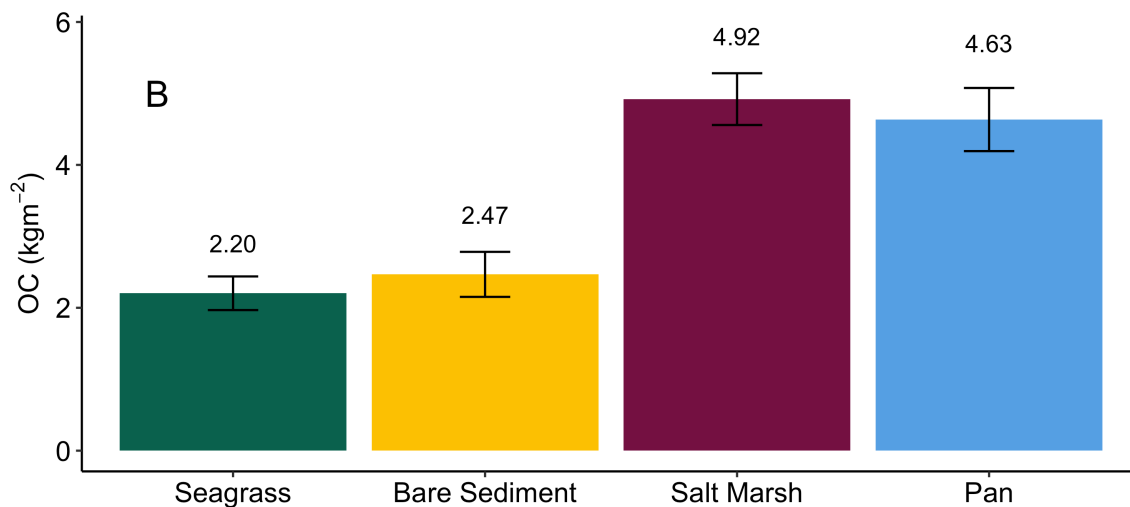
Figure 3: Average (± SE) total organic carbon (OC) stocks (kg m^{-2}) across all cores collected from each habitat type within each site in this study (A). Average (± SE) total organic carbon stocks (kg m^{-2}) across all cores collected within each habitat type in this study (B). Stocks are representative of the top 20 cm of sediment.

351

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

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

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

355   0.95, p <0.05, F-statistic = 4957, DF = 269). However, as the proportion of fine sediments in

356   each sample increases, the relationship between grain size and TOM weakens rapidly (from r^2 =

357   0.73 to 0.53) after sediments consisting of more than 82% mud are included (linear model, p

358   <0.05, r^2 = 0.53, F-statistic = 233.1, DF = 201). Our results indicate that grain size was similar

359   between sites (SLM, p > 0.05, F-statistic = 2.7, DF = 3) but differed between habitat types (Fig.

360   5a; SLM, p < 0.05, F-statistic = 5.7, DF = 3), with salt marsh sediments demonstrating

361   significantly greater % mud than both seagrass and bare sediment (Tukey's post-hoc analysis, p

362   < 0.05). Recognizing that the sample size of pan cores was low, pan sediments displayed

363   comparable % mud to salt marsh sediments but there were no significant differences between

364   pan grain size and the other habitat types' grain sizes (Tukey's post-hoc analysis, p > 0.05).

365   Tukey's post-hoc analyses did not indicate any significant differences in grain size between
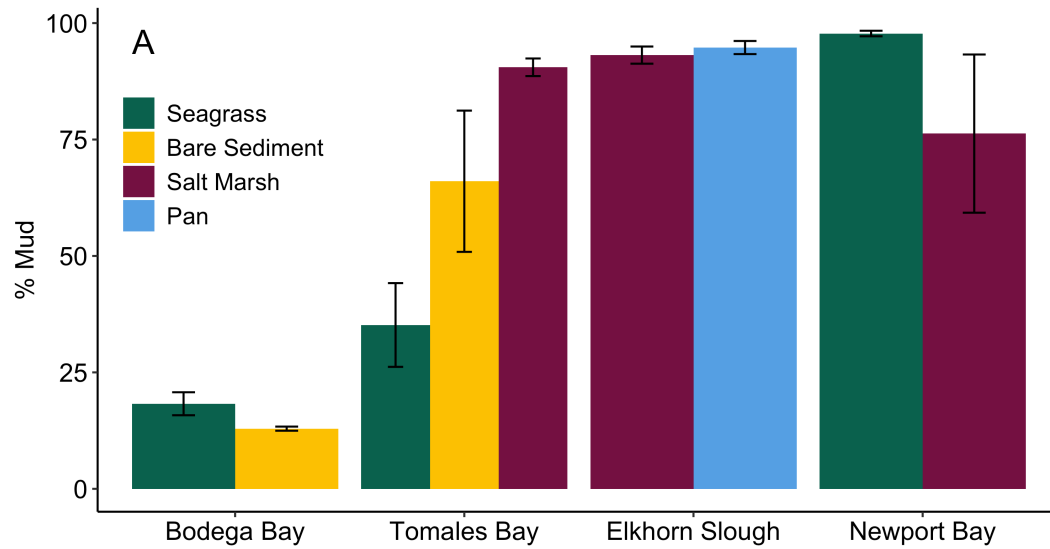
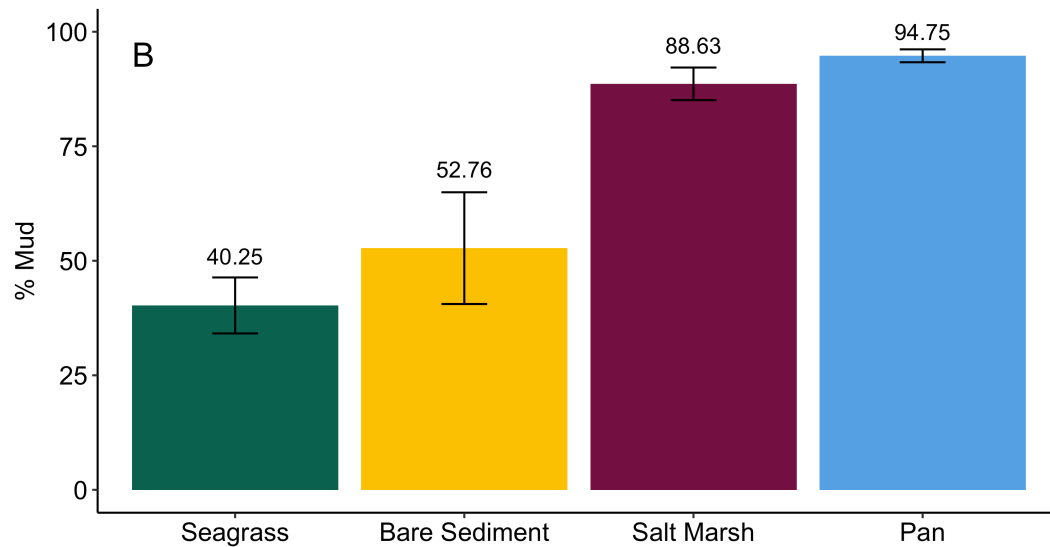366   habitat types within each site (Fig. 5a; p > 0.05).

367
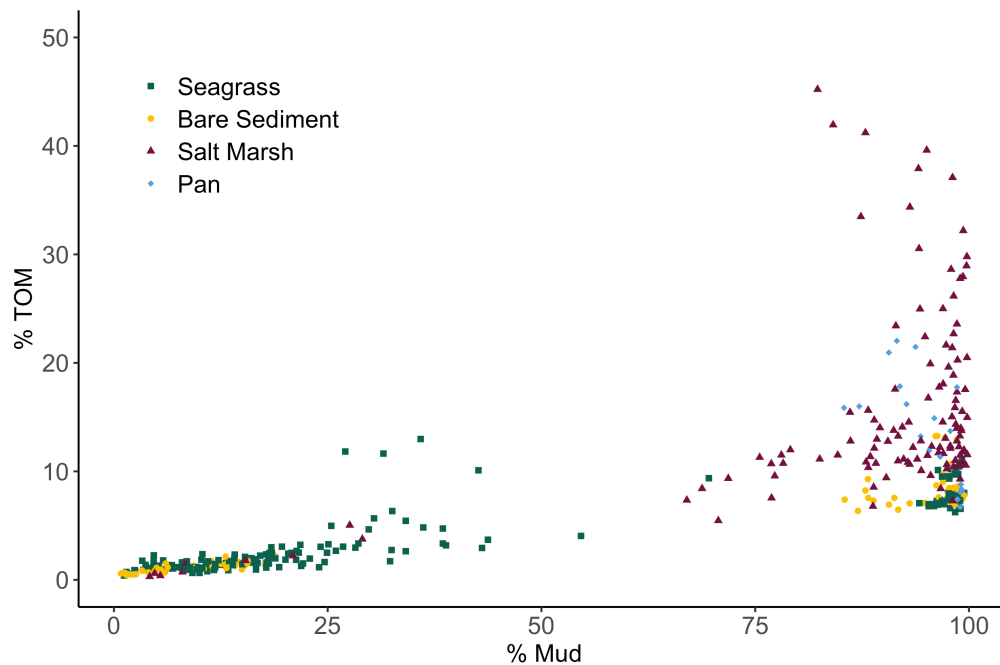
368
369   **Figure 4:** Biplot showing the relationship among total organic material (TOM) (%) of each 2-cm
370   core section from each habitat type plotted against sediment grain size (% Mud).

18

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

19

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

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

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

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

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

385 via aerial imagery by spring. Previous data collected by the authors (O'Donnell, 2017) quantified

386 seagrass senescence within the nearby Tom's Point seagrass meadow (Fig. 1b), where average

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

388 (AGB and BGB, mean $\pm$ SE; Table 2). Within the neighboring Walker salt marsh, fall estimates

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

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

391 only accounted for 3.5% of total seagrass biomass measured (Table 2). Analysis of seagrass

392 leaves collected from Tomales Bay demonstrated that seagrass material was composed of 31.6%

393 of OC. Thus, we estimate Walker salt marsh receives 33.4 ± 7.6 g OC m^{-2} in the form of seagrass

394 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

395

396 **Table 2:** Living seagrass above ground biomass (AGB) and below ground biomass (BGB) was
397 collected in Tom's Point seagrass meadow (Fig. 1b) in both summer and winter (g m^{-2}). Total
398 seagrass wrack delivered to Walker salt marsh was quantified as AGB and BGB (g m^{-2}) and
399 converted to carbon (g C m^{-2}) using a 31.6% carbon conversion rate.
400

3.2.2 Sediment Carbon Sources

In Walker salt marsh, surface (< 10 cm) wrack sediments had higher $\delta^{13}C$ values than sediments collected from the interior of the marsh (non-wrack sediments) and thus were more similar to the $\delta^{13}C$ values of seagrass (Fig. 6; SLM, $p < 0.05$; F-statistic =27.3; DF = 18). Shallow wrack sediments had an average $\delta^{13}C$ of -22.5 ± 0.38 ‰, while non-wrack sediments had an average $\delta^{13}C$ of -24.9 ± 0.26 ‰ (mean ± SE). However, when both shallow and deep (>10cm) sediments were included, wrack sediment $\delta^{13}C$ 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.
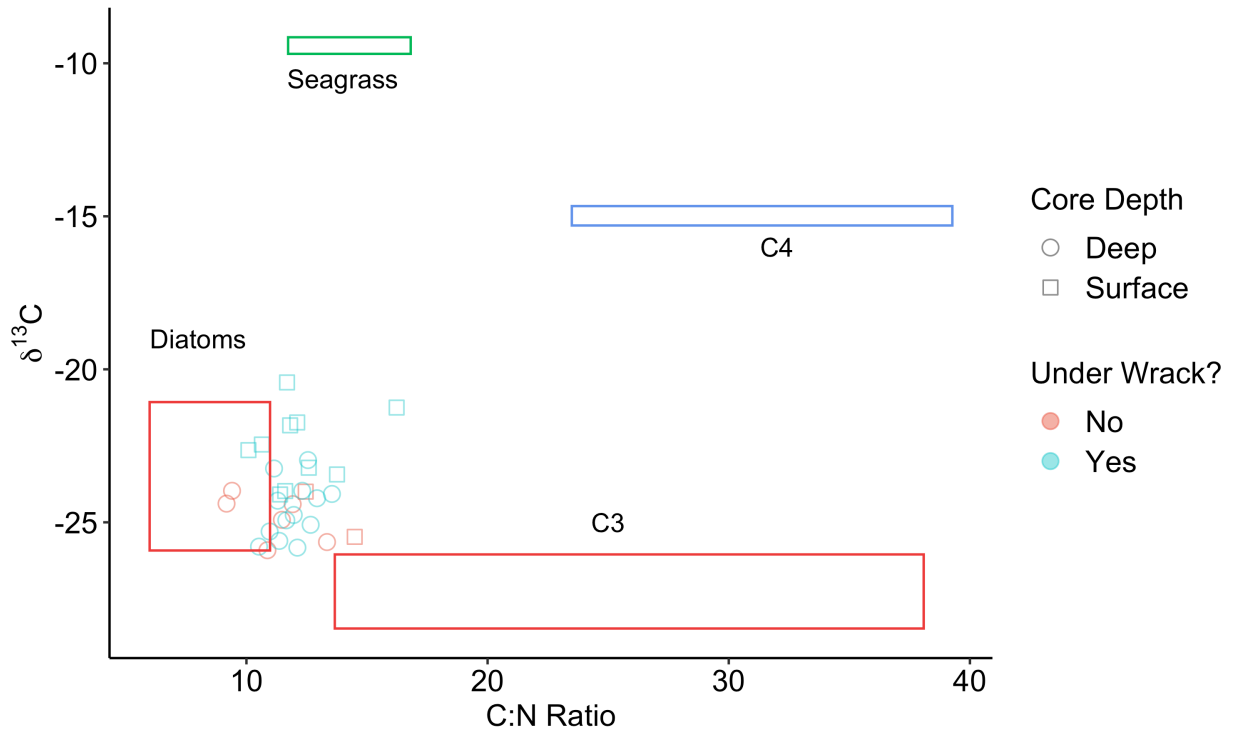
420
421
422 **Figure 6**: Points represent the $\delta^{13}C$ and C:N ratios of Walker Salt Marsh sediment data, collected
423 from underneath persistent wrack lines (blue) and from areas free of wrack (red) (see Fig. 1c).
424 Sediment subsamples collected from the surface to 10cm deep are labelled as surface samples
425 (square) and below 10cm are labelled as deep samples (circle). Colored boxes represent sources
426 (means ± SD) from diatoms (red), seagrass (green), C4 salt marsh plants (blue), and C3 salt
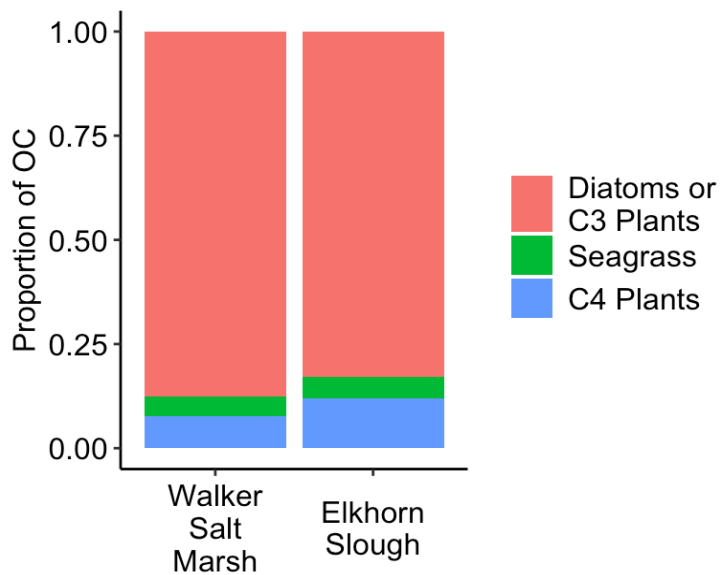427 marsh plants (red).
428

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.

22

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-

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

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

467   variability and low relative sample sizes), apparent qualitative differences allude to possible

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

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

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

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

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

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

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

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

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

477   2008).

478   In marsh and pan habitats, biological factors such as primary production and decomposition

479   rates may become more important drivers of carbon burial than would be true in dominantly

480   sandy sediments (Miyajima et al., 2017). It is possible that root systems of overlying vegetation

481   add bulk organic material into available sediment space, contributing to increased carbon

482   deposition as well as decreased space for mineral accumulation (e.g., Rogers et al., 2019). Yet

483   despite the absence of vegetation in pan sites, we did not observe significant differences in

484   carbon stocks between pan sediments and surrounding salt marsh sediments. This could be

485   attributed to 1) significant carbon contributions from surrounding salt marsh biomass to pan sites

486   overtime, 2) historical marsh recovery along pan edges and subsequent burial of vegetation

487   captured in pan cores, 3) variable decomposition rates in both pan and salt marsh sediments, or

488   4) because the expected effect of canopy-vegetation on salt marsh sediment is too small relative

489   to other drivers, producing statistically insignificant results. In sum, although seagrasses and salt

490   marshes can facilitate carbon storage by altering grain size distributions, hydrodynamics and

491   geomorphology play a critical role in grain size distributions and therefore, carbon storage. The

492   hydrographic changes in Newport Bay salt marshes associated with decreased grain sizes further

493   emphasize this point – drawing attention to the importance of watershed and sediment

494   management to regional carbon storage. Furthermore, although grain size is clearly a key driver

495   in carbon storage, our data demonstrate that it becomes of limited use as a predictor of carbon

496   stocks after the proportion of mud exceeds 82% (Fig. 4). This demonstrates that using grain size

497   as a cost-effective way to estimate carbon stocks (as has been suggested, e.g. Serrano et al.,

498   2016) only appears possible in sandy and mixed grain size sediments within the sites studied

499   here. Carbon stocks in fine sediment sites above this threshold cannot be estimated using grain

500   size alone – a management-relevant finding for efforts to incorporate habitat-specific carbon

501   storage into regional climate plans.

502

503   **4.2 Global and Regional Comparisons**

504   With recent reviews on coastal carbon stocks in salt marshes and seagrass meadows, we can

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

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

507   sediments studied here is lower than global estimates yet is higher than regional estimates of Z.

508

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 spicata* and *Jaumea carnosa*	California	235 ± 17.7	20 cm cores extrapolated to 1m
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)

509
510 **Table 3:** Summary of previously reported carbon stocks in seagrass meadows and tidal wetlands,
511 all normalized to the top 1m of sediment. Studies that included any data from California are
512 denoted by an asterisk. Values are reported as mean ± SE, unless otherwise noted. [1]Fourqurean et
513 al. (2012) value represents median OC storage.
514

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

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

517   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

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

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

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

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

522   west coast. This is not surprising given the variation in environmental and geomorphic

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

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

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

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

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

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

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

530   reducing some potential for these factors to result in the observed differences in carbon stocks.

531   Previous work has found that high-marsh zone sediments are likely to contain greater OC than

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

533   and increased OC (the sites presented here would be considered 'lower-marsh zones') (Blum,

534   1993; Connor et al., 2001; Zhou et al., 2007). Moreover, sediments beneath other common marsh

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

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

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

538   2018), which includes a variety of habitat types including forested and shrub-dominated tidal

539   wetlands.

540

4.3 Carbon Sources and Exchanges

542   Across both salt marshes assessed in this study, diatoms and/or C3 plants were the

543 dominant carbon sources in sediment. Although the isotopic values resulting from C4 and

544 seagrass sources are poorly resolved, lack of a significant values from either source allows for

545 interpretation. Specifically, seagrasses do not significantly contribute to any OC sources in

546 sediment, while C4 plants may contribute minimally to OC in sediment in Elkhorn Slough (1.1-

547 11.9%; Table S2). Thus, despite similar isotopic values between seagrass and C4 plants, if

548 seagrass-derived organic matter was buried under wrack sediments, we would expect to see

549 higher $\delta^{13}C$ values in wrack sediments with depth. The insignificant differences in $\delta^{13}C$ between

550 wrack and non-wrack sediments suggest that seagrass is not ultimately being buried, but rather,

551 carbon derived from C3 plants and diatoms are ultimately retained in sediment.

552   Several underlying causes may lead to this high proportion of diatom and/or C3-derived

553 carbon (Fig. 7). The recalcitrance of both autochthonous and allochthonous material in sediment

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

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

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

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

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

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

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

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

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

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

564 presence of salt grass (*Distichilis spicata)*, the relative lack of C4-derived carbon in sediment

565 may be due to a few potential factors: 1) salt grass is less common relative to pickleweed within

566 our sites, 2) based on our field observations, root systems of salt grass do not seem to penetrate

567 as deeply or contain as much BGB as do those of pickleweed, and 3) salt grass contains less

568 woody tissue than pickleweed, making it less refractory (Jepson Flora Project, 2020). In the case

569 of diatom and planktonic sources, their significant presence in sediment may be due to a greater

570 abundance overall, or due to complex preservation pathways such as the facilitation of carbon

571 burial by binding sediments through extracellular polymeric substances (Drexler et al., 2020;

572 Macreadie et al., 2019; Oakes and Eyre, 2013).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

591   material is ultimately buried.

592

593   **5   Conclusions**

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

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

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

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

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

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

600   remineralized and converted to CO_2, rather than buried in neighboring blue carbon habitats. C3

601   salt marsh plants and/or diatoms contributed to the OC pools in all three salt marshes under study

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

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

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

605

606   **6   Data Availability**

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

608   repository.

609

7   Competing Interests

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

repository.

613

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).

624

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638   10 References
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