Blue Carbon Stocks and Exchanges Along the California Coast

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

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

1   Introduction

As carbon dioxide (CO_2) concentrations in the oceans and atmosphere continue to rise,

interest in measuring the relative quantities of carbon stored within natural ecosystems has

increased. These assessments can help improve global and regional climate models, the

prediction of future CO_2 concentrations related to sources and sinks, and our broader

understanding of nature-based climate change solutions (Serrano et al., 2019). Coastal habitats

including seagrasses, salt marshes, and mangroves have earned the moniker 'blue carbon'

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

39 sediments relative to other habitat types (Lovelock and Duarte, 2019; McLeod et al., 2011). This

40 can be attributed largely to the tendency for these habitats to exhibit high sediment accretion

41 rates and low decomposition rates (Peck et al., 2020; Serrano et al., 2019). This value has led to

42 increasing interest in blue carbon habitats, given their conservation can prevent significant

43 emissions of carbon (Lovelock et al., 2017; Pendleton et al., 2012) and their restoration can lead

44 to increased drawdown of atmospheric CO_2 (Freedman et al., 2009; Greiner et al., 2013).

45

46 **1.1 Carbon stock assessments and their significance**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

83   carbon stock variability and its drivers.

84

1.2 Blue carbon sources and drivers

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

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

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

108   complex interactions.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

123   2019), serving an important ecological role and altering the production and biogeochemical

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

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

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

127   (Alongi, 2018; Bouillon & Connolly, 2009), laterally exported carbon from one blue carbon

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

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

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

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

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

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

134

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

136   understudied region by answering the following questions:

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

138   California latitudinal gradient?

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

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

141

142   **2   Methods**

143   **2.1 Study Sites**

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

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

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

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

148   2017) and are included here for comparison. The number of cores collected in each site and

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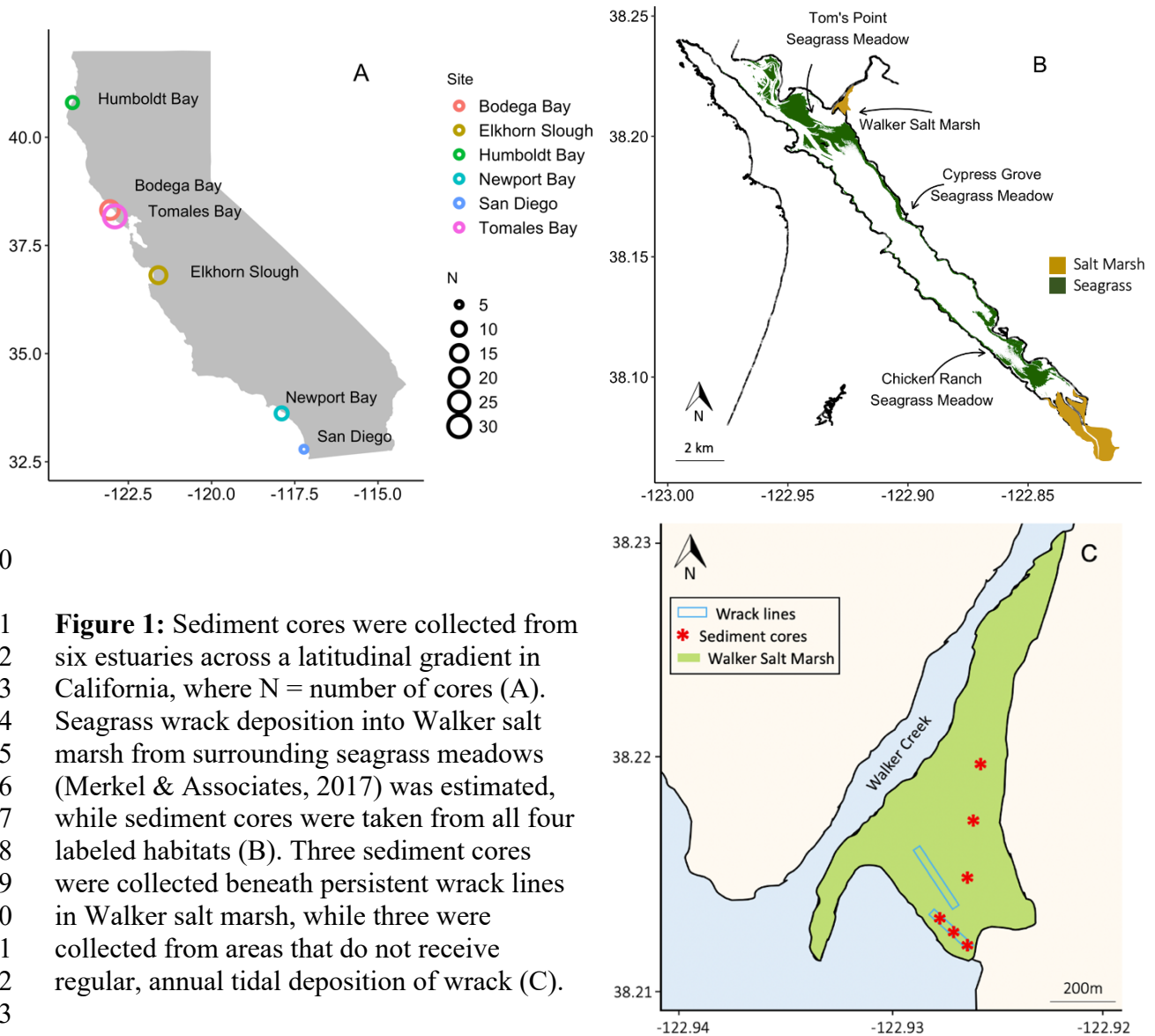
Figure 1: Sediment cores were collected from six estuaries across a latitudinal gradient in California, where N = number of cores (A). Seagrass wrack deposition into Walker salt marsh from surrounding seagrass meadows (Merkel & Associates, 2017) was estimated, while sediment cores were taken from all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

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

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

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

173 knowledge, respective vegetation has persisted through time.

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

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

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

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

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

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

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

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

182 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)

183

184 **Table 1:** Location and brief description of each bay sampled in this study, along with the total
185 number of cores collected from each habitat type in each of these bays.
186

187 **2.2 Carbon stocks**

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

189 (20 cm length, 5.08 cm diameter). Compaction occurred in 19% of cores, and a compaction

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

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

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

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

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

195   of sampling interval.

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

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

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

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

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

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

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

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

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

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

206    $^{13}C/^{12}C$). Organic carbon in each core section was then estimated using a power model developed

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

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

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

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

211   OC.

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

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

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

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

216   weighed.

217   To allow for carbon stock comparisons to previous work, a depth of 20 cm was selected

218   (Fourqurean et al. 2012; Prentice et al., 2020; Röhr et al., 2018). Previous research also suggests

219   that OC content remains relatively constant below 10 cm to depths up to 1 m (Callaway et al.,

220   2012; Prentice et al., 2020; Fig. S3), providing further justification for a 20 cm core depth

221   selection. Nonetheless, when comparing carbon stocks estimated here to those in previous

222   studies, we include these studies' sampled core depths for clarity.

223

224   **2.3 Carbon sources and exchange**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

246 (10 cm and deeper), to facilitate interpretation of changes with depth.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

273 signatures of C3 plants and diatoms, these two sources were pooled in mixing models, allowing

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

275 contributions from seagrass and C4 plants.

276

277 **2.4 Statistical Analyses**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

292 0.05). Differences in $\delta^{13}C$ (‰) or C:N ratios between sediment depth ('surface' versus 'deep'),

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

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

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

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

297

298 **3 Results**

299 **3.1 Carbon Stock Assessments**
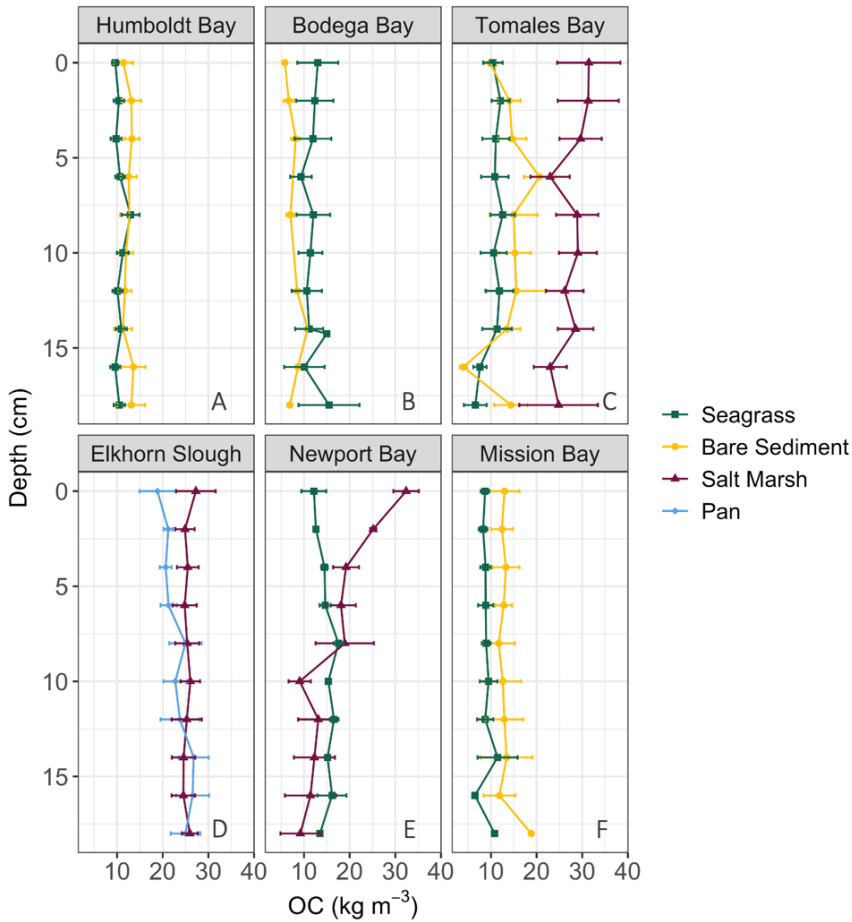
Figure 2 (left)**:** Down core trends (surface = 0 cm) in average (± SE) OC (kg m^{-3}) for each habitat type and site. Data show an insignificant decline in OC through time (downcore) in all sites except Newport Bay salt marshes.

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

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

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

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

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

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

326   = 13.3, DF =3). Specifically, salt marsh sediments contained 23.51 ± 1.77 kg OC m^{-3}, while

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

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

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

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

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

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

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

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

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

336

337
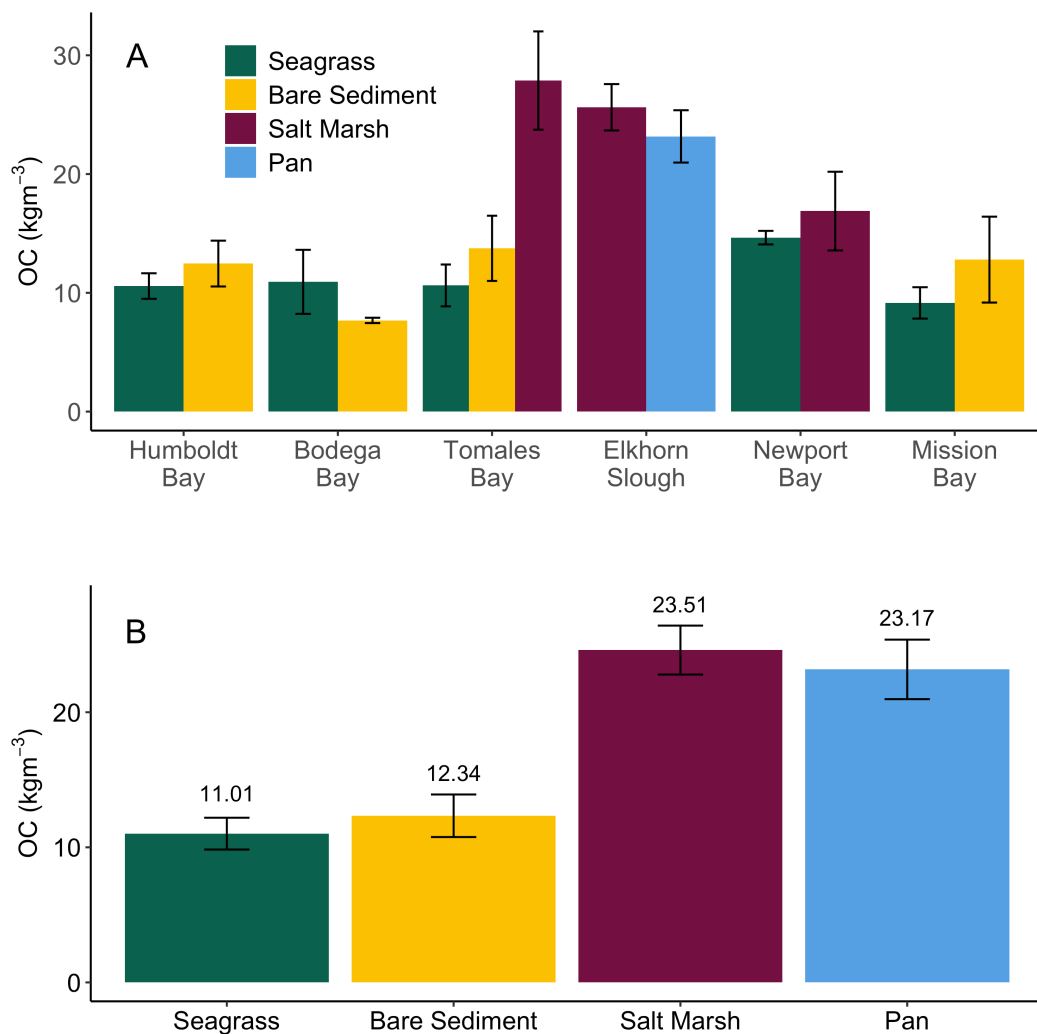
Figure 3: Average ($\pm$ SE) total organic carbon (OC) stocks (kg m^{-3}) across all cores collected
from each habitat type within each site in this study (A). Average ($\pm$ SE) total organic carbon
stocks (kg m^{-3}) across all cores collected within each habitat type in this study (B).

341

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

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

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

345 0.95, p <0.05, F-statistic = 4957, DF = 269). However, as the proportion of fine sediments in

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

347 0.73 to 0.53) after sediments consisting of more than 82% mud are included (linear model, p

348 <0.05, $r^2 = 0.53$, F-statistic = 233.1, DF = 201). Our results indicate that grain size was similar

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

350 5a; SLM, p < 0.05, F-statistic = 5.7, DF = 3), with salt marsh sediments demonstrating

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

352 < 0.05). Recognizing that the sample size of pan cores was low, pan sediments displayed

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

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

355 Tukey's post-hoc analyses did not indicate any significant differences in grain size between

356 habitat types within each site (Fig. 5a; p > 0.05).

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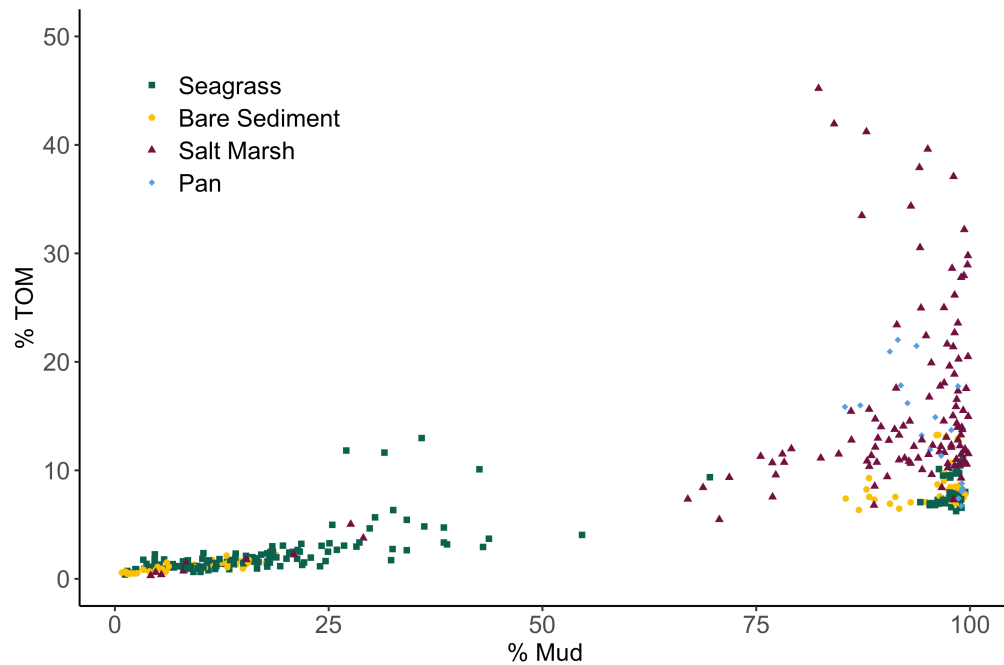
358
359 **Figure 4:** Biplot showing the relationship among total organic material (TOM) (%) of each 2-cm
360 core section from each habitat type plotted against sediment grain size (% Mud).
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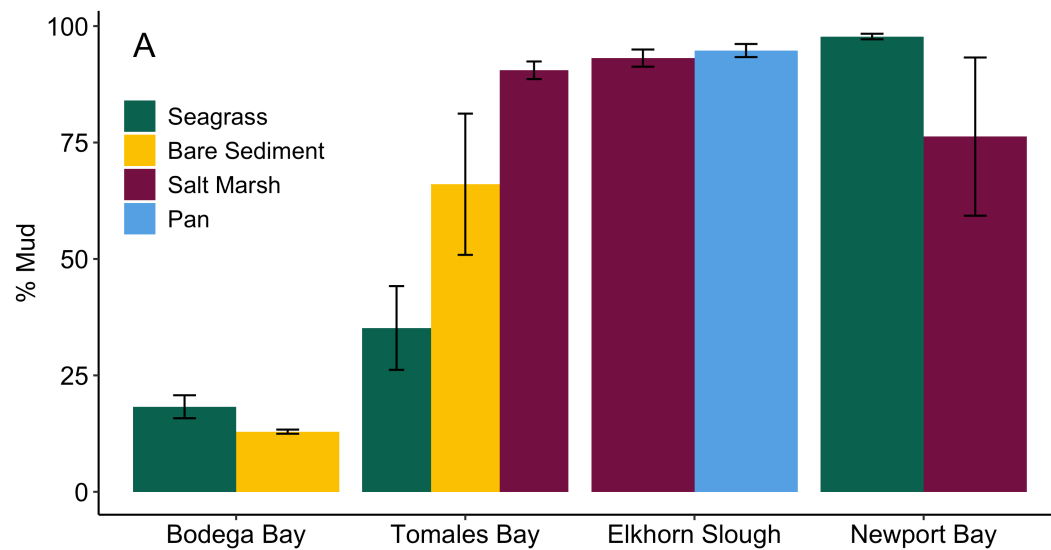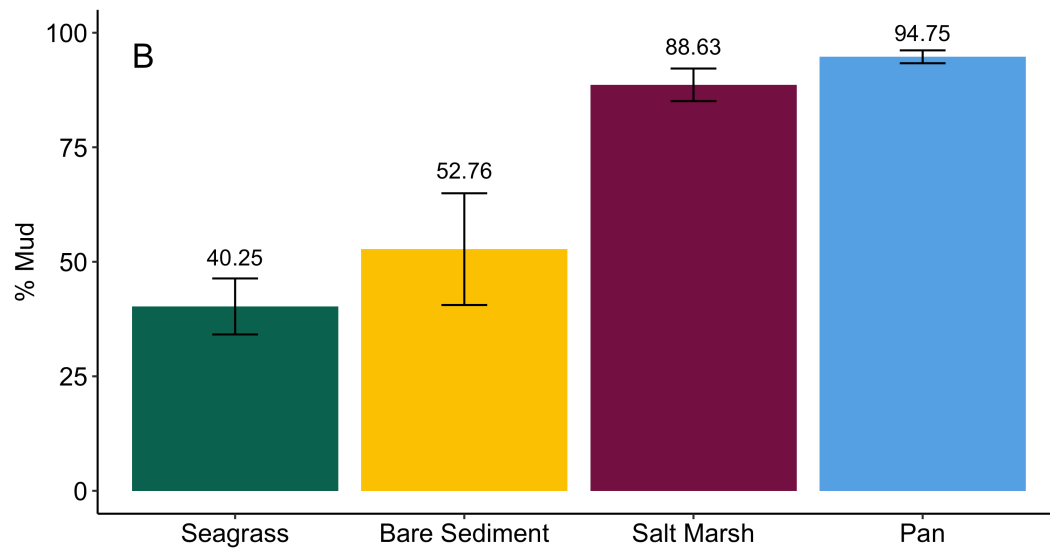
Figure 5: Average (± SE) % mud of all sediments quantified in each site within each habitat type (A), average (± SE) % mud in each habitat type across all sites measured (B).

3.2 Carbon Sources and Exchange

3.2.1 Wrack Deposition

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

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

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

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

384 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

385

386 **Table 2:** Living seagrass above ground biomass (AGB) and below ground biomass (BGB) was
387 collected in Tom's Point seagrass meadow (Fig. 1b) in both summer and winter (g m^{-2}). Total
388 seagrass wrack delivered to Walker salt marsh was quantified as AGB and BGB (g m^{-2}) and
389 converted to carbon (g C m^{-2}) using a 31.6% carbon conversion rate.
390

391 **3.2.2 Sediment Carbon Sources**

392   In Walker salt marsh, surface (< 10 cm) wrack sediments had higher δ^{13}C values than

393 sediments collected from the interior of the marsh (non-wrack sediments) and thus were more

394 similar to the δ^{13}C values of seagrass (Fig. 6; SLM, $p < 0.05$; F-statistic $=27.3$; DF $= 18$).

395 Shallow wrack sediments had an average δ^{13}C of -22.5 $\pm$ 0.38 ‰, while non-wrack sediments

396 had an average δ^{13}C of -24.9 $\pm$ 0.26 ‰ (mean $\pm$ SE). However, when both shallow and deep

397 (>10cm) sediments were included, wrack sediment δ^{13}C did not significantly differ from non-

398 wrack sediments (SLM, $p > 0.05$, F-statistic $= 0.34$, DF $= 31$). C:N sediment ratios did not

399 significantly differ from one another regardless of collection depth or location (SLMs, $p > 0.05$).

400 When data were applied to a mixing model, apparent discrepancies in seagrass-derived carbon

401 contributions between shallow and deep, and wrack and non-wrack sediments were insignificant

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

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

404   estimate that sediments were derived almost entirely from either diatoms or C3 plants – 83% in

405   Elkhorn Slough and 88% in Walker salt marsh (Fig. 7; Table S2). Thus, regardless of site, depth,

406   or the presence of wrack, model results estimate no significant storage of seagrass-derived

407   carbon in sediment (Table S2). Instead, C3 plants and/or diatoms are the primary significant

408   contributors to underlying carbon storage across salt marshes in all locations.

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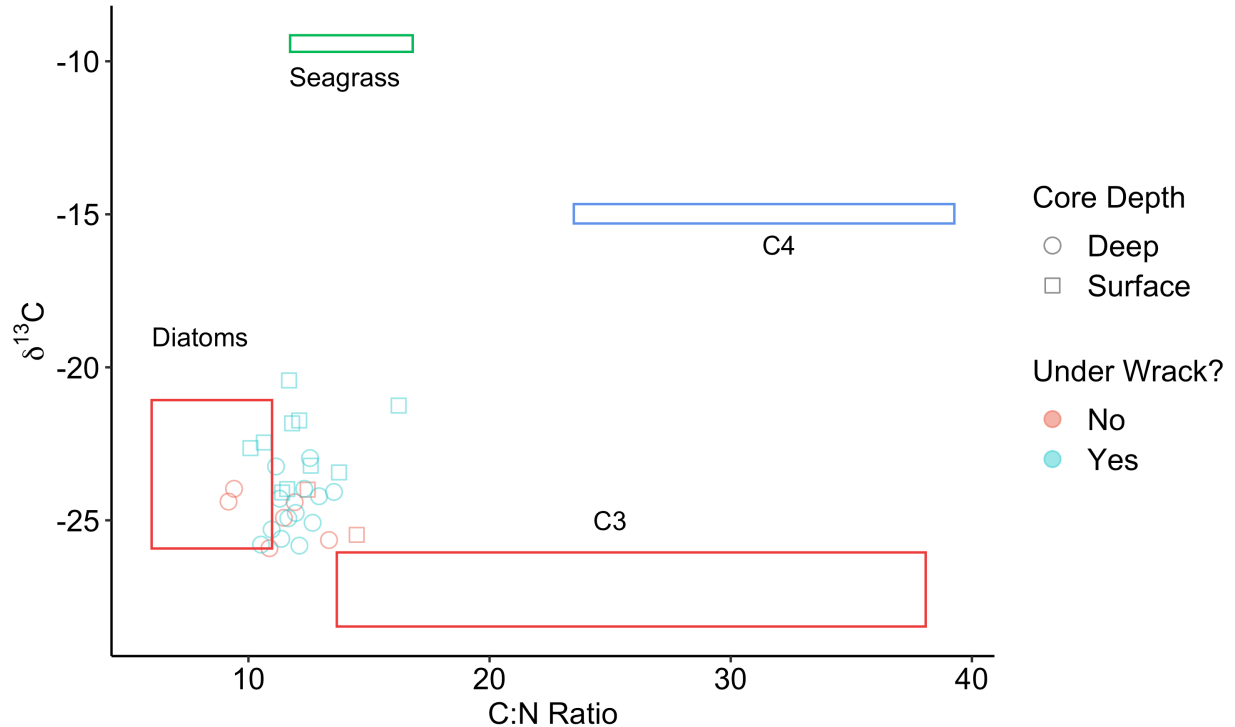
410
411
412   **Figure 6**: Points represent the $\delta^{13}C$ and C:N ratios of Walker Salt Marsh sediment data, collected
413   from underneath persistent wrack lines (blue) and from areas free of wrack (red) (see Fig. 1c).
414   Sediment subsamples collected from the surface to 10cm deep are labelled as surface samples
415   (square) and below 10cm are labelled as deep samples (circle). Colored boxes represent sources
416   (means ± SD) from diatoms (red), seagrass (green), C4 salt marsh plants (blue), and C3 salt
417   marsh plants (red).
418
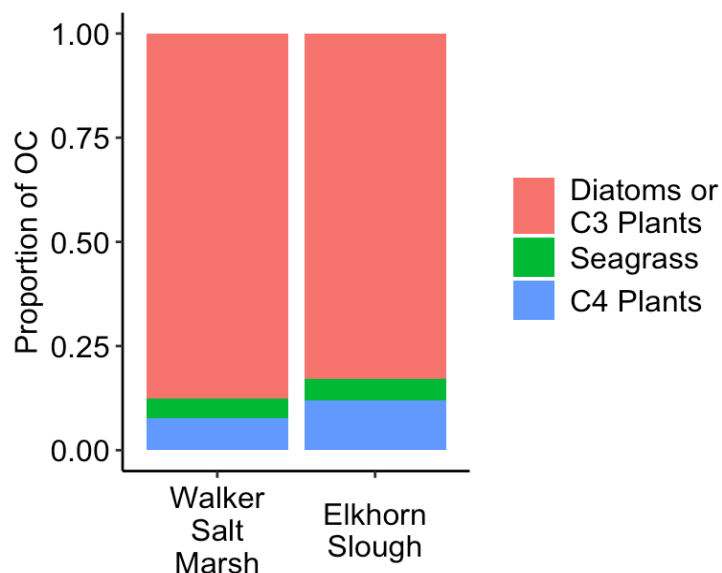
Figure 7 (left)**:** Mixing model results displaying the average source contributions to salt marsh sediment organic carbon (OC) for two salt marshes. Exact values and significance are shown in Table S2.

4 Discussion

4.1 Carbon Stocks

The lack of clear downcore trends (Fig. 2) could suggest relative OC stability with depth and

through time or that there have been minimal changes to factors such as vegetation and grain size

through time. The persistence of this pattern is supported by the longer cores sampled in seagrass

and bare sediment sites (Fig. S3). One possible explanation for significant downcore OC losses

in Newport Bay salt marsh is change in historic hydrography. Specifically, previous sediment

profiles from this region also found finer surface sediments above coarser materials – associated

with the conversion from an erosional to a depositional system in the early 20th century due to

urbanization of the surrounding area (Trimble, 2003). This change in grain size down core may

drive the associated OC loss down core, discussed further below. Although we did not quantify

sediment carbon accumulation rates here, previous work in Tomales Bay seagrass meadows

indicate rates of 11.37 - 15.16 g C m^{-2} yr^{-1} via ^{210}Pb dating (O'Donnell, 2017). By these

accumulation rate estimates, we estimate the top 20 cm of sediment sampled here accumulated

446   over approximately 100-130 years. Given the relatively slow accumulation rates and lack of

447   down core trends, we interpret that our data represent realistic stock assessments for each

448   respective habitat and location, rather than being reflective of shallow surface sediment carbon

449   stocks.

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

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

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

453   2015). Here, sediment grain size and its associated drivers allow us to further examine variation

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

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

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

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

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

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

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

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

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

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

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

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

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

467   2008).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

488   2016) only appears possible in sandy and mixed grain size sediments within the sites studied

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

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

491   storage into regional climate plans.

492

493   **4.2 Global and Regional Comparisons**

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

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

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

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

498

Study	Habitat Type/Species	Location(s)	Value (Mg C_{org} ha^{-1})	Methods (core length and extrapolation depth)
Seagrass				
This study	Seagrass (*Z. marina*)	California	110 ± 11.8	20 cm cores extrapolated to 1 m
Kauffman et al. (2020)	Seagrass (*Z. marina*)	*U.S. west coast	80 ± 12	1 m cores collected (no extrapolation)
Prentice et al. (2020)	Seagrass (*Z. marina*)	U.S. west coast	65.12	25 cm cores extrapolated to 1 m
Röhr et al. (2018)	Seagrass (*Z. marina*)	*U.S. west coast

*Temperate Northern Hemisphere | 69.4 ± 8.4

108.9 ± 39.56 | 25 cm cores extrapolated to 1 m |
Fourqurean et al. (2012)	Seagrass (many species)	Global	[1]139.7	A combined estimate from short cores (≥ 20cm & < 1 m) extrapolated to 1 m and full cores (1 m)
Salt Marsh				
This study	Salt marsh dominated by *Sarcocornia pacifica, Distichlis*	California	235 ± 17.7	20 cm cores extrapolated to 1m

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

499
500 **Table 3:** Summary of previously reported carbon stocks in seagrass meadows and tidal wetlands,
501 all normalized to the top 1m of sediment. Studies that included any data from California are
502 denoted by an asterisk. Values are reported as mean ± SE, unless otherwise noted. [1]Fourqurean et
503 al. (2012) value represents median OC storage.
504

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

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

507 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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

524   1993; Connor et al., 2001; Zhou et al., 2007). Moreover, sediments beneath other common marsh

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

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

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

528   2018), which includes a variety of habitat types including forested and shrub-dominated tidal

529   wetlands.

530

531   **4.3 Carbon Sources and Exchanges**

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

533   dominant carbon sources in sediment. Although the isotopic signatures resulting from C4 and

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

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

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

537   11.9%; Table S2). Thus, despite similar isotopic signatures between seagrass and C4 plants, if

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

539   higher δ^{13}C values in wrack sediments with depth. The insignificant differences in δ^{13}C between

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

581   material is ultimately buried.

582

583   **5   Conclusions**

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

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

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

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

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

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

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

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

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

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

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

595

596 **6   Data Availability**

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

598 repository.

599

600 **7   Competing Interests**

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

602 repository.

603

604 **8   Author Contributions**

605 Ward – conceptualization, investigation, methodology, writing (original draft preparation),

606 formal analysis; Hill – conceptualization, funding support, writing (review & editing); Souza –

607 investigation (field and lab support), writing (review & editing); Filipczyk – investigation (field

608 and lab support), writing (review & editing); Ricart – methodology, investigation, writing

609 (review & editing); Merolla – investigation (field and lab support), writing (review & editing);

610 Capece – writing (review & editing); O'Donnell – investigation (field and lab support),

611   methodology; writing (review & editing);); Elsmore – investigation (field and lab support),

612   writing (review & editing); Oechel – writing (review & editing); Beheshti – investigation (field

613   and lab support), writing (review & editing).

614

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625   mentorship and legacy in wetland conservation has sparked lifelong collaborations and scientific

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627
628   **10 References**
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