Carbon Sequestration in a Pacific Northwest Eelgrass (Zostera marina) Meadow

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Abstract

Coastal wetlands are known to be efficient carbon sinks due to high rates of primary productivity, carbon burial by mineral sediments, and low rates of sediment organic matter decomposition. Of the three coastal wetland types: tidal marshes, tidal forests, and seagrass meadows, carbon burial by seagrasses is relatively under-studied, and reported rates range widely from 45 to 190 g C m^{-2} yr^{-1}. Additionally, most of these seagrass rates are biased toward tropical and subtropical species, particularly *Posidonia oceanica*, with few focused on *Zostera marina*, the most widespread species in the northern hemisphere. We measured sediment organic content, carbon content, and long-term accretion rates to estimate organic carbon stocks and sequestration rates for a *Z. marina* meadow in Padilla Bay, a National Estuarine Research Reserve in Washington. We found rates of carbon sequestration to be quite low relative to commonly reported values, averaging 9 to 11 g C m^{-2} yr^{-1}. We attribute this to both low sediment organic content and low rates of accretion. We postulate here that Padilla Bay's low carbon sequestration capacity may be representative of healthy *Z. marina* meadows rather than an anomaly, and that *Z. marina* meadows have an inherently low carbon sequestration capacity because of the species' low tolerance for suspended sediment (which limits light availability) and sediment organic content (which leads to toxic sulfide levels). Further research should focus on measuring carbon sequestration rates from other *Z. marina* meadows, particularly from sites that exhibit, *a priori*, the potential for higher rates of carbon sequestration.

Keywords: blue carbon, seagrass, *Zostera marina,* carbon sequestration

Introduction

Coastal wetland ecosystems, including seagrass meadows, salt marshes, and mangrove forests, are known to be efficient and long-term (century-scale) carbon sinks because of their potential for high rates of productivity, low rates of organic matter decomposition in hydric sediments, and carbon burial by mineral sediments (Mcleod et al. 2011). Additionally, coastal waters, high in sulfate compared to freshwater wetlands, inhibit the generation of methane, a potent greenhouse gas (Reddy and DeLaune 2008). The resulting stored sediment carbon, particular to coastal ecosystems, is referred to as "blue carbon" (Nelleman et al. 2009). This carbon sequestration capacity is a newly recognized ecosystem service, giving coastal wetlands the potential to mitigate climate change and allowing them to be entered into the voluntary carbon market (Emmer et al. 2015), once estimates of the actual carbon stocks and sequestration rates are determined.

Of all coastal wetland habitats, carbon sequestration by seagrasses is the least studied or published (Grimsditch et al. 2013). Based on a review of seven available studies summarizing a total of 123 sites, Mcleod et al. (2011) reported carbon accumulation rates in seagrass meadows ranging from 45 to 190 g C m^{-2} yr^{-1}, with a mean rate of 138 ± 38 g C m^{-2} yr^{-1}. The relatively high variability in seagrass carbon sequestration rates can be attributed to variability among species and habitats (Duarte et al. 2010, Kennedy et al. 2010, Grimsditch et al. 2013, Lavery et al. 2013, Rozaimi et al. 2013), or possibly to the relative

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difficulty in obtaining reliable long-term accretion rates in these environments. In any event, existing reviews of carbon sequestration rates are disproportionately dominated by tropical and subtropical species, particularly *Posidonia oceanica*, despite *Zostera marina* being the most widespread seagrass species in the northern hemisphere (Green and Short 2003), including the Pacific Northwest. *Posidonia oceanica* has an exceptional capacity for carbon storage and sequestration because of its thick, dense mat of roots and rhizomes, not necessarily representative of all seagrass species (Gacia et al. 2002, Mateo et al. 1997, Serrano et al. 2012). The few existing studies of *Z. marina* carbon sequestration have reported relatively low rates, ranging from 0 to 37 g C m^{-2} yr^{-1} (Greiner et al. 2013, Miyajima et al. 2015, Spooner 2015).

With over 3800 ha of eelgrass (seagrasses in the genus *Zostera*), Padilla Bay is the largest eelgrass meadow in the greater Puget Sound (Berry et al. 2003) and one of the largest contiguous eelgrass stands along the North American Pacific coast (Bulthuis and Shull 2006) thus indicating a potential for significant blue carbon sequestration. However, to use blue carbon finance mechanisms, eelgrass restoration projects must use published, regionally-specific carbon stock and sequestration rate data, and the Pacific Northwest has a paucity of published eelgrass blue carbon studies available to confirm or disagree with global average values. The objective of this study was to address this data gap by measuring and documenting sediment carbon stocks and sequestration rates from this extensive temperate eelgrass meadow, and comparing those rates to other published rates for *Zostera marina*.

Methods

Study Area

Padilla Bay is a National Estuarine Research Reserve (PBNERR) in Washington State, recognized as an estuary of significant ecological value in the Puget Sound with extensive tidal mudflats and eelgrass meadows (Figure 1). The bay is largely intertidal with a maximum tidal range of 4 m (Bulthuis 1995). Freshwater inputs to Padilla Bay include several sloughs draining surrounding agricultural lands, and Skagit River discharge from the south via the Swinomish Channel. The contribution from the latter is limited, however, as the predominant currents from the channel flow northwest toward Guemes Channel, generally bypassing Padilla Bay (Bulthuis and Conrad 1995).

Two species of eelgrass (*Zostera* spp.) occur in Padilla Bay: the native *Z. marina* and the non-native *Z. japonica*. *Zostera marina* covers a much larger area (approximately 3131 ha or 82% of total eelgrass coverage) than *Z. japonica* (approximately 669 ha or 18% of total coverage) as of 2004 (Bulthuis and Shull 2006). In Padilla Bay, *Z. marina* occurs in the upper subtidal to lower intertidal zone (approximately −3.0 to +0.3 m mean lower low water height, MLLW), whereas *Z. japonica* occurs in the mid intertidal zone (approximately +0.3 to +0.8 m MLLW); (Bulthuis 1995, Thom 1990). However, *Z. japonica* appears to be expanding at both its upper and lower elevation limits in recent years, increasing the area of overlap (Bohlmann et al. 2016).

Sediment Core Collection

In 2011, PBNERR established permanent eelgrass biomonitoring plots along three 4-km transects in northern Padilla Bay. We collected one sediment core from each of six sites along the northernmost PBNERR transect in December 2013 (Figure 1) from which we measured sediment bulk density, organic content, carbon content, and long-term accretion rates to estimate sediment carbon stocks and accumulation rates. Coring site elevation ranged from +0.49 m to −0.66 m MLLW. Although the meadow overall is dominated by *Z. marina*, all sites also contained some amount of *Z. japonica*. PVC corers with an internal diameter of 10.0 cm were driven into the sediment to a depth of at least 30 cm. Sediment cores were frozen, sliced into 2-cm sections, dried for 72 hours to obtain dry bulk density, then ground through a 0.425-mm mesh screen. The organic content of each section was determined through loss on ignition by burning ground subsamples at 500 °C for 24 hours and weighing before and after burning (Craft et al. 1991). We evaluated the variation

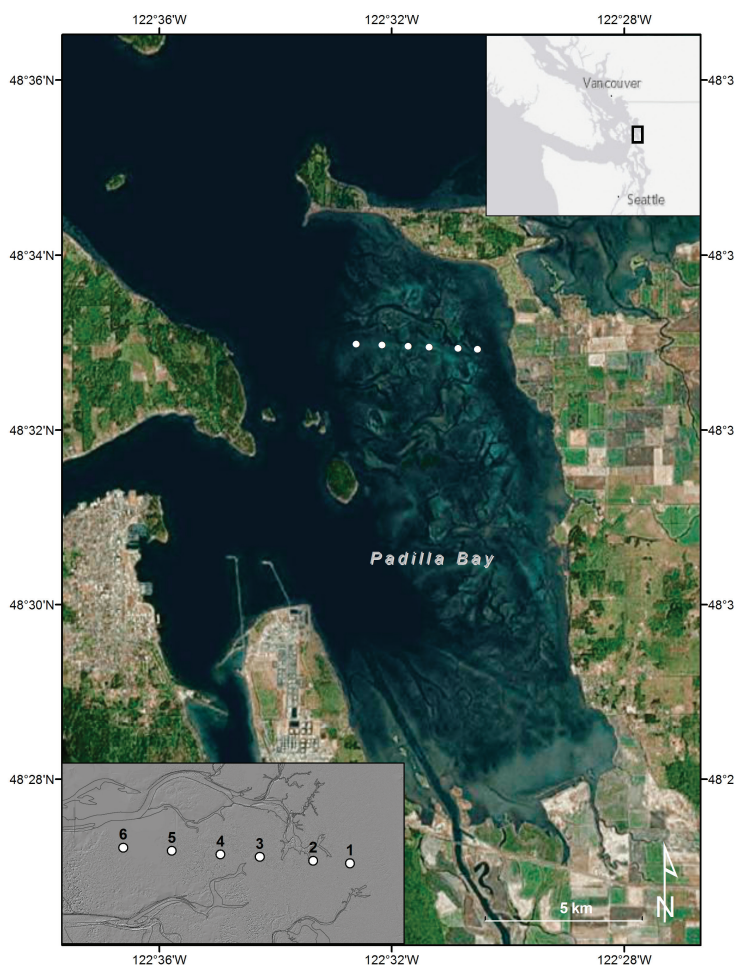Carbon Sequestration In Eelgrass Meadows   81

Figure 1. Location of study sites within Padilla Bay, a National Estuarine Research Reserve in northern Puget Sound, Washington. Bottom inset shows LiDAR imagery with study sites relative to tidal channels.

remaining inorganic portions of the samples were analyzed again with the CN analyzer for inorganic carbon content. Organic carbon content was calculated by subtraction. The LOI−C_{org} conversion was then applied to all samples to produce the reported organic carbon contents ($C_{org} = 0.3134*OM$ content − 0.1149; $R^2 = 0.97$, $P < 0.001$).

Radioisotope Dating

Long-term sediment accretion rates were determined for each core using the downcore distribution of ^{210}Pb with both the constant initial concentration (CIC) model (Robbins et al. 1978) and the constant rate of supply (CRS) model (Appleby and Oldfield 1978). The CIC model produces a single accretion rate for each core, assuming that ^{210}Pb activity at the surface is constant over time, and that migration within the soil column is negligible. The CRS model produces a separate accretion rate for each sample from various core depths and assumes a constant rate of supply of ^{210}Pb to the sediment. Excess ^{210}Pb activity was determined using a Canberra Germanium Detector (model GL2820R, Mirion Technologies (Canberra) Inc., Meriden, CT), with gamma emissions at 46 keV and 351 keV recorded by Genie 2000 software (Canberra 2002). Excess (unsupported) ^{210}Pb was calculated as the difference between total ^{210}Pb (at 46 keV) and supported ^{210}Pb (at 351 keV) to distinguish between excess ^{210}Pb deposited at the sediment surface and supported ^{210}Pb that has decayed from radium in the sediment. Cores were analyzed in 2-cm sections from the surface to the depth at which the excess ^{210}Pb concentration declined to zero. A linear regression of the natural log of excess ^{210}Pb activity versus depth was used to determine the

in organic content across depths with a one-way ANOVA comparing 2-cm depth sections, followed by Tukey HSD *post hoc* pairwise comparisons.

Carbon Analysis

We directly measured carbon content (% by weight) for a subset of samples ($n = 46$) using a FlashEA 1112 CN analyzer (Thermo Fisher Scientific, Waltham, MA). to establish a conversion from organic content to organic carbon content. These samples were first analyzed for total (organic and inorganic) carbon content. Organic matter was then removed by loss on ignition (LOI), and the

CIC-based accretion rate, which is equal to $-\lambda/s$, where λ is the half-life of ^{210}Pb (22.2 yr^{-1}) and s is the slope of the regression. The CRS-based accretion rate was calculated using the equation:

$$Q_x = Q_0 e^{-\lambda t}$$

Where Q_x is the inventory of excess ^{210}Pb below depth x, Q_0 is the total inventory, and t is the age of depth x. After the model was used to solve for the age (t) of each depth, the accretion rate for each depth was then calculated as its depth divided by its age. The range of rates within each core were averaged to produce one accretion rate per core, to compare with the CIC-based rates.

Bioturbation can inflate the apparent accretion rate with the transport of surface sediment downward in the ^{210}Pb profile. Since the influence of bioturbation cannot necessarily be identified based on the shape of the profile, the only way to assess the relative effect of bioturbation is by analyzing the ^{210}Pb inventory and flux. We calculated the excess ^{210}Pb inventory for each core to obtain the ^{210}Pb flux to the sediment, to compare our calculated flux to the expected flux for the region (Nevissi 1985). The inventory calculation included all core sections with positive excess ^{210}Pb values. An observed flux lower than expected implies that the site sees little to no sediment deposition, and the apparent long-term accretion rate could be attributed to bioturbation instead of sediment deposition. Conversely, an observed flux higher than expected implies that the site is depositional, and the apparent long-term accretion rate is a reflection of both accretion and bioturbation. This comparison can be done with either the ^{210}Pb inventory or the flux (e.g., Baskaran and Santschi 2002, Bentley and Kahlmeyer 2012, Muhammad et al. 2008), depending on the available reference for the region of interest.

Carbon Stock and Sequestration Rate Calculations

We calculated carbon stocks by summing the carbon mass across the top 30 cm of the sediment profile, similar to Callaway et al. (2012) and Crooks et al. (2014), using carbon density and sediment volume. The top 30 cm was considered a sufficient depth to capture the decline of sediment carbon to a stable value and the decline of excess ^{210}Pb to zero, based on previous studies in Padilla Bay (Kairis 2008, Kuhlmann 2011). Carbon density was based on bulk density and carbon content of each 2-cm core section. We obtained a representative carbon density for each core by averaging carbon density from the surface to the depth at which excess ^{210}Pb declined to zero, which ranged from 8 to 20 cm. We calculated carbon accumulation rates for each core as the product of carbon density and the long-term accretion rate. The resulting carbon accumulation rates thus represent average rates over the past 100 years. We evaluated the effect of *Zostera japonica* presence on sediment characteristics using regression analyses on both *Z. japonica* biomass versus sediment organic content, and *Z. japonica* biomass versus sediment carbon stock. Since *Z. japonica* biomass did not explain variability in sediment organic content (R^2 = 0.40, P = 0.18) or carbon stock (R^2 = 0.48, P = 0.12), all cores were considered representative of an eelgrass meadow dominated by *Z. marina*.

Results

Mean organic matter content of each of the six cores ranged from 1.33% to 2.27% by weight, with an overall mean ($\pm$ SE) of 1.68 $\pm$ 0.09% (Table 1). Organic matter content was fairly consistent across the entire sediment profile. Only the top 2 cm was significantly higher than lower core sections (P < 0.05 for Tukey *post hoc* pairwise comparisons between top 2 cm and all other sections from 4 to 36 cm depth) (Figure 2). Carbon content across all cores ranged from 0.30% to 0.60% with a mean of 0.41 $\pm$ 0.03% (Table 1). Carbon stocks in the top 30 cm of sediment cores ranged from 1.18 to 1.90 kg C m^{-2}, with a mean of 1.42 $\pm$ 0.11 kg C m^{-2} (Table 1).

Accretion rates determined with the CIC model ranged from 0.08 to 0.49 cm yr^{-1}, with a mean of 0.23 $\pm$ 0.04 cm yr^{-1} (Table 2). Rates determined with the CRS model ranged from 0.08 to 0.31 cm yr^{-1}, with a mean of 0.19 $\pm$ 0.01 cm yr^{-1} (Table 2). The CIC and CRS accretion rates were significantly correlated (r = 0.89, P < 0.01), similar to comparisons by Carey et al. (2017) and Bricker-Urso et al. (1989).

TABLE 1. Sediment characteristics and organic carbon stocks for each core. Sediment characteristics are reported as the average value from the surface to the depth at which excess ^{210}Pb declined to zero, representing an approximately 100-year timeframe. Means and standard errors are shown for each core, as well as the means and standard errors across cores.

| Site	Elevation (m above MLLW)	Depth of excess ^{210}Pb (cm)	Bulk density (g cm^{-3})	Organic content (% by weight)	Carbon content (% by weight)	Carbon density (g C cm^{-3})	Carbon stock in top 30 cm (kg C m^{-2})
1	0.49	14	1.35 (0.05)	1.35 (0.09)	0.31 (0.03)	0.0041 (0.0002)	1.24
2	0.30	10	1.18 (0.06)	2.27 (0.29)	0.60 (0.09)	0.0068 (0.0006)	1.90
3	0.09	8	1.17 (0.12)	2.24 (0.45)	0.59 (0.14)	0.0064 (0.0008)	1.59
4	−0.01	10	1.32 (0.05)	1.57 (0.11)	0.38 (0.03)	0.0049 (0.0003)	1.33
5	−0.23	16	1.37 (0.03)	1.33 (0.08)	0.30 (0.03)	0.0041 (0.0002)	1.18
6	−0.67	20	1.49 (0.02)	1.33 (0.06)	0.30 (0.02)	0.0045 (0.0002)	1.30
Mean (SE)			1.31 (0.03)	1.68 (0.09)	0.41 (0.03)	0.0051 (0.0002)	1.42 (0.11)
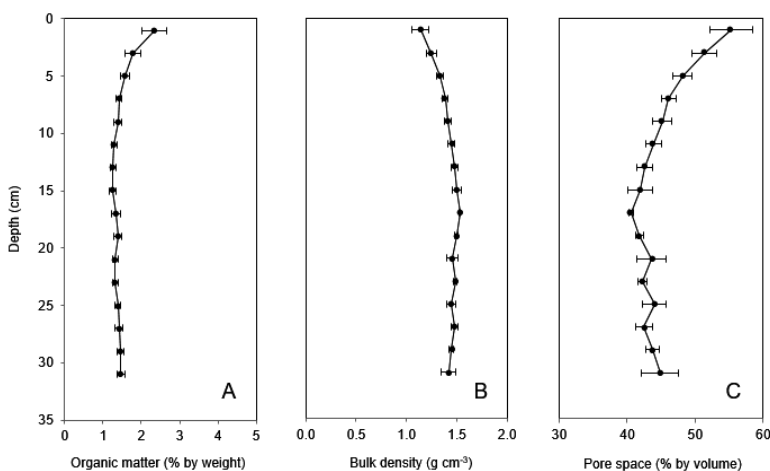
Figure 2. Sediment core profiles of A) organic matter, B) bulk density, and C) pore space. Profiles show the mean (± SE) of each 2-cm core section across six sites from within Padilla Bay's eelgrass meadow.

Carbon accumulation rates calculated with the CIC-based accretion rates ranged from 5.03 to 21.72 g C m^{-2} yr^{-1}, with a mean rate of 11.34 ± 1.74 g C m^{-2} yr^{-1} (Table 2). Carbon accumulation rates using the CRS-based accretion rates ranged from 5.40 to 13.82 g C m^{-2} yr^{-1}, with a mean rate of 9.14 ± 0.59 g C m^{-2} yr^{-1} (Table 2).

No obvious mixed layers were observed in the downcore ^{210}Pb profiles (Figure 3). The ^{210}Pb flux analysis revealed that all sites had a lower ^{210}Pb flux to the sediment than expected based on the reference atmospheric flux of 0.44 disintegrations per minute (dpm) cm^{-2} yr^{-1} for the region (Nevissi 1985). This suggests that the sites experience little sediment deposition, and that the reported accretion rates should be considered maximum possible rates and possibly overestimated.

Discussion

Carbon Stocks

Padilla Bay's sediment carbon stocks of 1.42 kg C m^{-2} are low compared to other coastal wetland habitat types such as tidal marshes and mangroves (Fourqurean et al. 2012). For example, a natural (unimpacted) Pacific Northwest tidal marsh had a reported stock of 7.17 kg C m^{-2}, and nearby tidal swamp sites had up to 9.85 kg C m^{-2} (Crooks et al. 2014). However, Padilla Bay's eelgrass meadow stocks are similar to stocks reported for most other seagrass sites globally, with the exception of mat-forming species such as *P. oceanica* (Campbell et al. 2015, Fourqurean et al. 2012, Rohr et al. 2016, Schile et al. 2016).

Carbon Sequestration Rates

Although the carbon sequestration rates measured here are below the range reported by Mcleod et al. (2011) in their review of all seagrass species, they are within the range of values recently reported

84   Poppe and Rybczyk

TABLE 2. Accretion rates and carbon accumulation rates calculated with both CIC and CRS dating models. Rates were determined for portion of each core with positive excess ^{210}Pb activity values, representing an approximately 100-year timeframe. Means and standard errors are shown for each core, as well as the means and standard errors across cores.

| Site	Elevation (m above MLLW)	Depth of excess ^{210}Pb (cm)	Accretion rate (CIC) (cm yr^{-1})	Accretion rate (CRS) (cm yr^{-1})	Carbon accumulation rate (CIC) (g C m^{-2} yr^{-1})	Carbon accumulation rate (CRS) (g C m^{-2} yr^{-1})
1	0.49	14	0.18 (0.07)	0.16 (0.01)	7.51 (2.82)	6.37 (0.50)
2	0.30	10	0.20 (0.07)	0.15 (0.01)	13.38 (4.70)	10.09 (1.27)
3	0.09	8	0.08 (0.00)	0.08 (0.01)	5.03 (0.72)	5.40 (0.79)
4	−0.01	10	0.24 (0.04)	0.19 (0.05)	11.88 (2.14)	9.39 (2.31)
5	−0.23	16	0.21 (0.15)	0.24 (0.03)	8.52 (6.31)	9.75 (1.53)
6	−0.67	20	0.49 (0.13)	0.31 (0.03)	21.72 (5.86)	13.82 (1.49)
Mean (SE)			0.23 (0.04)	0.19 (0.01)	11.34 (1.74)	9.14 (0.59)
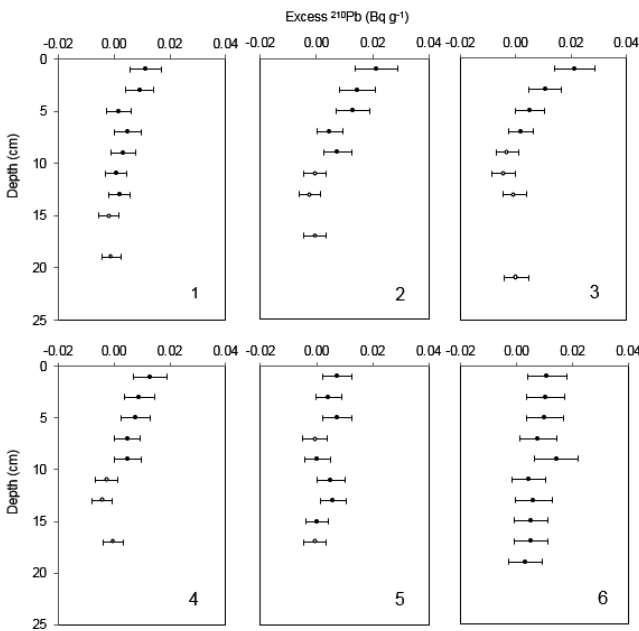
Figure 3. Excess ^{210}Pb activity versus depth in the sediment column at each site in Padilla Bay. Error bars represent ± 1 standard deviation. Hollow points represent excess ^{210}Pb values less than 0 Bg g^{-1}, which were not included in the natural log regression used to calculate the accretion rates.

for *Z. marina* specifically (Greiner et al. 2013, Miyajima et al. 2015, Spooner 2015). Spooner (2015) reported carbon accumulation rates from *Z. marina* sites in British Columbia, Canada, ranging from 0 to 13 g C m^{-2} yr^{-1}. Miyajima et al. (2015) measured carbon accumulation rates of 3.13, 7.10, and 10.14 g C m^{-2} yr^{-1} from three *Z. marina* sites near Japan. However, they used radiocarbon dating to obtain sediment accretion rates, which would result in lower rates than would be expected using the shorter-termed ^{210}Pb method. Greiner et al. (2013) measured the highest carbon accumulation rate of 36.68 g C m^{-2} yr^{-1} from a 10-year restored *Z. marina* meadow in the coastal bays of Virginia, which is over three times the average we measured in Padilla Bay. Note, however, that this accretion rate reflects only the 10 years following site restoration. It is thus expected that the 10-year accretion rate would be higher than a longer-term (100-year) rate measured by ^{210}Pb, which incorporates long-term processes of compaction and decomposition (Callaway et al. 1996, Neubauer et al. 2002).

Compared to the range of sequestration rates reported by Mcleod et al. (2011), the carbon sequestration rates we measured in Padilla Bay are low because both long-term accretion rates and sediment organic content are low. Based on results from this study and similar *Z. marina* studies, we postulate that Padilla Bay's low carbon sequestration capacity may be representative of healthy *Z. marina* meadows rather than an anomaly, and that *Z. marina* meadows have an inherently low carbon sequestration capacity due to multiple species-specific habitat requirements discussed below.

Sediment Organic Matter Limitation

A system that sequesters carbon must have both carbon in the sediment, and an ongoing accumulation of new material. One possible reason why eelgrass meadows have a limited carbon storage capacity is that *Z. marina* itself can tolerate relatively little sediment carbon. Multiple studies have pointed to an upper threshold of approximately 5% sediment organic content (% by weight) for submerged aquatic vegetation and *Z. marina* in particular (Barko and Smart 1983, Batiuk et al. 2000, Kemp et al. 2004, Koch 2001), above which the plants may be unable to defend against toxic sulfide concentrations (Goodman et al. 1995, Koch and Erskine 2001, Mascaro et al. 2009). Although this threshold may vary somewhat depending on other factors such as hydrological conditions (Wicks et al. 2009), sulfides may be one of the more important limiting factors as they can cause decreased growth rates, reduced aboveground biomass, and increased mortality (Burkholder et al. 2007, Pérez et al. 2007, Walser 2014).

The empirical organic content limit of 5% is consistent with the occurrence of *Z. marina* in Padilla Bay, where surface (top 2 cm) organic content ranges from 1.7% (this study) to 5.0% (Kairis 2008). Kairis (2008) and Kuhlmann (2011) reported similar surface organic content from at least 16 eelgrass sites across Padilla Bay, averaging 2.9% and 2.6%, respectively. The organic content we have observed in Padilla Bay's eelgrass meadow is similar to that seen in other Pacific Northwest eelgrass meadows. Yang et al. (2013) reported a range of 0.6 to 3.2% organic content from 17 Puget Sound eelgrass meadows (with the highest value in Padilla Bay). Thom et al. (2001) reported a range of approximately 0.25 to 2.5% carbon content from 10 eelgrass meadows across the Pacific Northwest, which points to approximately 0.5 to 5% organic content. Ruesink et al. (2010) found that both *Z. marina* and *Z. japonica* occupied sediments with 1 to 4% organic content in Willapa Bay. More recently Ruesink et al. (2015) reported *Z. marina* sediment organic contents ranging from < 1 to 9%, although these were from surface sediment scrapes which are expected to be somewhat higher than subsurface

sediments. Data compiled by Fourqurean et al. (2012) from multiple studies worldwide showed an average *Z. marina* sediment organic content of 2.5%, a median of 1.7%, and less than 5% organic content in nearly all *Z. marina* sediment samples, with the exception of one study reporting a sample with 6.98% organic content (Holmer et al. 2006), and another reporting sediment organic contents up to 16.5% (Krause-Jensen et al. 2011). Although there may be instances of *Z. marina* growing in relatively organic-rich sediment, the large majority of *Z. marina* appears to be found in organic-poor sediments.

This low observed sediment organic content may be surprising given high rates of annual net primary productivity (NPP), averaging 351 g C m^{-2} in Padilla Bay (Thom 1990). Much of the plant material produced in eelgrass beds is likely decomposed (Kairis and Rybczyk 2010) or exported, although few studies have quantified seagrass export because measurement can be difficult (Mateo et al. 2006). Duarte and Cebrian (1996) reviewed carbon budgets for a variety of coastal habitats and estimated that seagrass ecosystems on average export 24.3% of their total NPP, with 50.3% lost to decomposition, 18.6% to herbivory, and only 15.9% stored in the seagrass bed sediments. Lacking a more regionally-specific estimate of export, it may be reasonable to assume that only a small fraction of the plant material produced in Pacific Northwest eelgrass meadows is buried in situ. A portion of the exported fraction may be sequestered elsewhere, either outside the meadow or in deep sea sediments (Duarte and Krause-Jensen 2017).

Suspended Sediment Limitation

Another potential reason why *Z. marina* meadows have a limited carbon storage capacity is that *Z. marina* tolerates relatively little suspended sediment. Carbon sequestration requires an accumulation of organic material which is often aided by mineral sediment accretion and subsequent burial, particularly in tidal wetlands (Chmura et al. 2003). *Zostera marina* tolerance for total suspended solids (TSS) is limited by the plant's light requirements. *Zostera marina* requires at least 10−20%

of surface irradiance to survive (Duarte 1991, Short and Burdick 1995), and as much as 50% of surface irradiance to thrive (Ochieng et al. 2010). Incident light is reduced by TSS, phytoplankton, and epiphytes, and these three light-attenuating factors vary from site to site. A few studies have reported the upper TSS tolerance limits for various *Z. marina* study sites, and although they differ as a result of variation in eelgrass depth and other light-attenuating factors, their limits are all low relative to typical TSS concentrations observed in other coastal wetland types. For example, tidal marshes along the East and Gulf coasts of the USA typically have TSS concentrations ranging from 10 to 100 mg L^{-1}, and many of these marshes have seen a decline relative to historical concentrations (Weston 2014). In contrast, *Z. marina* tolerates much lower TSS concentrations. Moore et al. (1996) observed eelgrass loss in Chesapeake Bay when TSS concentrations reached 15−40 mg L^{-1}. Batiuk et al. (2000) assessed water quality conditions and light requirements at several Chesapeake Bay sites and recommended a TSS target limit of 15 mg L^{-1}. A study of several Massachusetts eelgrass sites reported a lower TSS limit of 3 mg L^{-1} to 6 mg L^{-1} (Kenworthy et al. 2014). Padilla Bay has a TSS concentration of approximately 4 mg L^{-1}, with little seasonal and annual variability (Poppe 2016). This TSS concentration results in minimal long-term accretion rates.

Interactions Between Limiting Factors

An interaction between sediment organic content and eelgrass light requirements may impose an additional limit on the carbon sequestration capacity of *Z. marina* meadows. A high sediment organic content may actually increase the plant's light requirements because of the need to supply more oxygen to the rhizosphere to oxidize higher levels of sulfides (Armstrong 1978, Kenworthy et al. 2014, Krause-Jensen et al. 2011), if eelgrass is to remain healthy.

Implications for Blue Carbon Valuation

The list of ecosystem services provided by seagrass meadows is long (Batker et al. 2008, Costanza et al. 2014), and it is tempting to add carbon seques-

tration to the list, especially when this ecosystem service is an emerging tool for conservation and restoration (Crooks et al. 2010). However, the limited number of *Z. marina* blue carbon studies report carbon sequestration rates (0 to 36.68 g C m^{-2} yr^{-1}) much lower than the commonly cited rates for seagrasses (45 to 190 g C m^{-2} yr^{-1}), and results from this study (5.03 to 21.72 g C m^{-2} yr^{-1}) fall within the range of existing *Z. marina* rates. Existing global estimates of seagrass carbon sequestration rates should thus be used with caution when applied to eelgrass habitats of the Pacific Northwest, since the majority of studies to date have focused on a limited number of seagrass species, and there appears to be a great deal of variation in carbon sequestration rates among species. Applying the global average seagrass rates to eelgrass meadows of the Pacific Northwest risks overestimating their carbon sequestration potential and assigning them too many carbon offset credits for blue carbon projects, inadvertently increasing net carbon emissions to the atmosphere.

Although *Z. marina* sediment carbon sequestration rates may be minimal, some of the carbon produced within the meadow may be exported and sequestered elsewhere. In addition, *Z. marina* may still host a notable carbon stock that could potentially be lost as a result of habitat conversion. Habitat conversion in this case would most likely involve conversion to mudflat or open water with a decline in eelgrass health (Orth et al. 2006). With a sediment carbon stock of 1.42 ± 0.11 kg C m^{-2} (14.2 ± 1.1 Mg C ha^{-1}) in the top 30 cm, and a total eelgrass area of approximately 3800 ha, Padilla Bay's eelgrass meadow stores approximately 53 960 tonnes of carbon in the top 30 cm of the sediment. Extrapolating this stock to the 1-m depth recommended by Pendleton et al. (2012) results in approximately 180 000 Mg of carbon that could potentially be lost to the atmosphere, with a cost to the economy of over $27 million using the "social cost of carbon" of $41 per Mg CO$_2$ (Pendleton et al. 2012).

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