

Global Biogeochemical Cycles

RESEARCH ARTICLE

10.1029/2019GB006345

Special Section:

Carbon cycling in tidal wetlands and estuaries of the contiguous United States

Key Points:

- Sediment carbon content varied both within and among Northeast Pacific eelgrass meadows, yet there was no clear latitudinal trend
- Carbon in eelgrass meadow sediments appears to be derived largely from noneelgrass sources
- Northeast Pacific carbon stocks and accumulation rates are comparable to other *Z. marina* meadows but lower than global seagrass values

Supporting Information:

- Supporting Information S1

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Citation:

Prentice, C., Poppe, K. L., Lutz, M., Murray, E., Stephens, T. A., Spooner, A., et al. (2020). A synthesis of blue carbon stocks, sources, and accumulation rates in eelgrass (*Zostera marina*) meadows in the Northeast Pacific. *Global Biogeochemical Cycles*, 34, e2019GB006345. <https://doi.org/10.1029/2019GB006345>

Received 2 JUL 2019

Accepted 2 JAN 2020

Accepted article online 5 JAN 2020

A Synthesis of Blue Carbon Stocks, Sources, and Accumulation Rates in Eelgrass (*Zostera marina*) Meadows in the Northeast Pacific

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Abstract There is increasing urgency to implement climate change mitigation strategies that enhance greenhouse gas removal from the atmosphere and reduce carbon dioxide (CO₂) emissions. Recently, coastal “blue carbon” habitats—mangroves, salt marshes, and seagrass meadows—have received attention for their ability to capture CO₂ and store organic carbon (OC), primarily in their sediments. Across habitat types and regions, however, information about the sequestration rates and sources of carbon to local sediments remains sparse. Here we compiled recently obtained estimates of sediment OC stocks and sequestration rates from 139 cores collected from temperate seagrass (*Zostera marina*) meadows in Alaska, British Columbia, Washington, and Oregon. Across all cores sediment OC content averaged 0.75%. Organic carbon stocks in the top 25 cm and 1 m of the sediment averaged 1,846 and 7,168 g OC m⁻², respectively. Carbon sequestration rates ranged from 4.6 to 93.0 g OC m⁻² yr⁻¹ and averaged 24.8 g OC m⁻² yr⁻¹. Isotopic data from this region suggest that OC in the sediments is largely from noneelgrass sources. In general, these values are comparable to those from other temperate *Z. marina* meadows, but significantly lower than previously reported values for seagrasses globally. These results further highlight the need for local and species-level quantification of blue carbon parameters. While temperate eelgrass meadows may not sequester and store as much carbon as seagrass meadows elsewhere, climate policy incentives should still be implemented to protect existing sediment carbon stocks and the other critical ecosystem services associated with eelgrass habitats.

Plain Language Summary As we search for innovative solutions to capture and store atmospheric carbon, coastal wetlands are doing so for free and at rates greater than mature forests. The carbon market, by brokering carbon offset monies, can fund coastal wetland restoration projects where a net greenhouse gas reduction can be shown. Yet seagrass carbon sequestration capacity varies among species and even within meadows of the same species. Thus, obtaining site-specific carbon storage values is essential for restoration planning. Here we report carbon stocks and sequestration rates compiled from 30 eelgrass meadows (*Zostera marina*) in Oregon, Washington, British Columbia, and Alaska, areas underrepresented in current literature. We then compare these findings to previously reported values for *Z. marina* and for seagrasses globally. While carbon stocks and sequestration rates varied at small spatial scales, we observed no latitudinal patterns. Our values were similar to those found in other *Z. marina* meadows, but significantly lower than global seagrass averages. Through isotopic analysis we found that the majority of the carbon originated from noneelgrass sources and very little from eelgrass itself. These results, the first to reveal eelgrass carbon sequestration capacities in the Northeastern Pacific, expose the importance of obtaining local values for carbon sequestration.

1. Introduction

In the context of global climate change, it is critical to understand and quantify sinks and sources of atmospheric carbon dioxide (CO₂). Vegetated ecosystems often act as important carbon sinks, by uptaking CO₂ through photosynthesis and storing organic carbon (OC) in the form of above- or below-ground living biomass, and by capturing particulate and detrital forms of carbon via burial in soils or sediments. In addition to the carbon found in terrestrial ecosystems (e.g., forests, grasslands), significant quantities of carbon can be sequestered by, stored in, and released from coastal vegetated habitats such as mangroves, salt marshes, and seagrass meadows. This coastal carbon is now widely referred to as “blue carbon” (Duarte et al., 2013; Lovelock & Duarte, 2019; Nellemann et al., 2009). In contrast to terrestrial systems, where most carbon is stored in plant biomass or litter, between 50 and 90% of the organic carbon in coastal systems is found below ground in sediments (Duarte et al., 2005; Mcleod et al., 2011; Pendleton et al., 2012).

While the global extent of coastal blue carbon habitats is small relative to terrestrial ecosystems, blue carbon ecosystems have been shown to be more efficient at sequestering carbon, relative to their terrestrial counterparts (Donato et al., 2011; Fourqurean et al., 2012; Ouyang & Lee, 2014). Yet coastal wetlands are declining worldwide at rates of 0.4 to 3.0% annually, and their degradation and destruction can release carbon that has accumulated over centennial or millennial time scales, as well as reduce future capacity for carbon capture and storage (Irving et al., 2011; Pendleton et al., 2012; Waycott et al., 2009). In particular, there is increasing concern about declines of seagrass populations globally; not only do these declines have implications for carbon storage capacity but also for the other critical seagrass-associated ecosystem services (Orth et al., 2006; Short et al., 2011; Waycott et al., 2009). High carbon storage potential, alongside emissions associated with habitat loss, has created interest in incorporating blue carbon habitats into coastal ecosystem management and natural climate solutions through mechanisms such as carbon markets, restoration projects, marine protected area design, and ecosystem valuation (Hejnowicz et al., 2015; Howard, Mcleod, et al., 2017; Needelman et al., 2018; Fargione et al., 2018). While there is increasing interest in capitalizing on the greenhouse gas benefits of blue carbon ecosystems, limited regional and local data create challenges for accurately implementing such policies (Needelman et al., 2018; Sutton-Grier & Moore, 2016). To date, most studies have looked at carbon stocks, yet carbon finance guidelines (e.g., the Verified Carbon Standard) also require OC sequestration rates and sediment carbon sources (allochthonous versus autochthonous) to create carbon budgets (Emmer et al., 2015).

Seagrasses are globally distributed marine angiosperms that form underwater meadows along boreal, temperate, and tropical shorelines, providing some of the most biodiverse and productive habitats in coastal regions (Cullen-Unsworth & Unsworth, 2018; Green & Short, 2003; Mtwana Nordlund et al., 2016; Orth et al., 2006). Seagrass meadows can exhibit high rates of primary productivity and the tissues of many seagrass species are recalcitrant and subject to low rates of herbivory, creating excess biomass available for long-term storage (Duarte et al., 2010; Duarte & Cebrián, 1996). Furthermore, seagrass canopies can slow water movement, thereby enhancing particle deposition, trapping allochthonous carbon, and reducing resuspension and erosion of existing sediments (Gacia & Duarte, 2001; Kennedy et al., 2010; Lacy & Wyllie-Echeverria, 2011). Because seagrasses typically grow in low-energy, submerged, coastal regions, surface sediments tend to be suboxic or anoxic, which can slow the remineralization of organic matter (Borum et al., 2005; Trevathan-Tackett, Seymour, et al., 2017). The combination of these three characteristics—high primary production, particle capturing capacity, and low decomposition rates—yields high potential for seagrass meadows to act as significant carbon sinks (Duarte et al., 2013; Fourqurean et al., 2012).

Relative to other coastal blue carbon habitats (mangroves and salt marshes), species specific and local-level seagrass data remain deficient. For example, the Verified Carbon Standard includes default carbon sequestration values for marsh and mangrove ecosystems, whereas default values for seagrass systems were identified as a “key science and policy research need” (Needelman et al., 2018). This is not surprising considering that there are 72 species of seagrasses worldwide (Short et al., 2011), the carbon dynamics of which are modulated by a wide range of biological and physical factors such as plant size, seagrass characteristics (e.g., density, canopy height, root-rhizome structure), hydrodynamic conditions (e.g., exposure, depth, wave height), and sediment characteristics (e.g., sediment grain size, bulk density, porosity; Dahl et al., 2016; Mazarrasa et al., 2018; Rozaimi et al., 2013; Samper-Villarreal et al., 2016; Serrano et al., 2014, 2016). In addition to global and regional variation in seagrass blue carbon storage, large variability has been observed at

the local scale—within meadows—further emphasizing the need for local-level data on species specific carbon stocks and sequestration rates (Oreska et al., 2017; Prentice et al., 2019; Ricart et al., 2015).

Until recently, global estimates for seagrass-associated carbon stocks and accumulation rates were primarily derived from tropical and subtropical regions and species (e.g., Fourqurean et al., 2012). Although values are quickly emerging from a broader suite of regions and species (Dahl et al., 2016; Gullström et al., 2017; Jankowska et al., 2016; Kindeberg et al., 2018; Postlethwaite et al., 2018; Röhr et al., 2018), many studies focus on carbon stocks and do not include estimates of carbon sequestration rates or contributions of OC sources to the sediments. Furthermore, many of these studies sample across a broad geographic area but may overlook local or regional trends in blue carbon parameters. Thus, there remains a need to refine global estimates and expand our understanding of seagrass carbon storage and sequestration rates, particularly for eelgrass (*Zostera marina* L.), an extensively distributed temperate seagrass along the coasts of Europe, Northern Asia, and North America (CEC, 2013). The coastline of the northeast Pacific Ocean, including Southeast Alaska, British Columbia, Washington, and Oregon (a region herein referred to as the Pacific Northwest), has received little attention, and therefore, the viability of blue carbon finance in this region remains uncertain. Obtaining data from this region will not only help improve global seagrass blue carbon estimates but can also provide regional-level assessments of eelgrass carbon stocks, sequestration rates, and sources of sediment carbon.

Here we begin to fill the data gap for eelgrass blue carbon parameters in the Pacific Northwest (PNW) by compiling and comparing recently acquired estimates for sediment carbon stocks, carbon sequestration rates, and sources of carbon to the sediments. Specifically, we collected and synthesized data from temperate seagrass meadows (predominantly *Z. marina*) and adjacent unvegetated sediments across a temperate latitudinal gradient spanning roughly 1,700 km from Southeast Alaska to Southern Oregon. We then review eelgrass-associated blue carbon parameters from the Pacific Northwest in the context of data from other published *Z. marina* studies and global estimates for all seagrass species.

2. Materials and Methods

2.1. Compilation of Eelgrass Sediment Carbon Data From the Pacific Northwest

We analyzed all available sediment carbon data from eelgrass meadows in the Pacific Northwest, spanning from Southeast Alaska to Southern Oregon. Collections were made independently by a number of research groups and included published manuscripts, theses, and unpublished values (Lutz, 2018; Murray, 2018; Poppe & Rybczyk, 2018; Prentice et al., 2019; Short et al., 2017; Spooner, 2015; Stephens & Eckert, 2018). While the studies varied slightly in their objectives and scope, all studies had a common goal of quantifying carbon stocks, sequestration rates, and sources of stored carbon in *Z. marina* meadows of the Pacific Northwest, to continue to fill the data gap for this region and species.

2.2. Sediment Core Collection and Subsampling

Sediments were sampled from 16 meadows on Prince of Wales Island, Southeast Alaska (Figure 1a); six meadows on the Central Coast of British Columbia, Canada (Figure 1b); one meadow in K'omoks Estuary, Vancouver Island, British Columbia, Canada (Figure 1c); three meadows in the Central Salish Sea, Washington (Figure 1d); two meadows in the Southern Salish Sea, Washington (Figure 1e); and two meadows in South Slough, Oregon (Figure 1f). The number of cores from vegetated and unvegetated sediments, tidal height, average core depth, and the sampling period for the different regions are shown in Table 1.

In general, cores were collected manually by inserting PVC tubes into the sediment using a sledgehammer. In some cases (Southern Salish Sea, Washington and South Slough, Oregon) a vibrating motor was employed to help insert the core into the sediments while minimizing compaction (Short et al., 2017). Cores were either taken at a predetermined depth (e.g., 30 cm) or inserted to the point of refusal. Intertidal cores were collected during low tides, while subtidal cores were collected by SCUBA divers. Core locations were determined either haphazardly or were associated with existing eelgrass monitoring sites (e.g., SeagrassNet long-term monitoring transects). Unvegetated cores were taken between 5 and 15 m beyond the meadow perimeter and were collected only in British Columbia (Central Coast and Vancouver Island) and the Central Salish Sea.

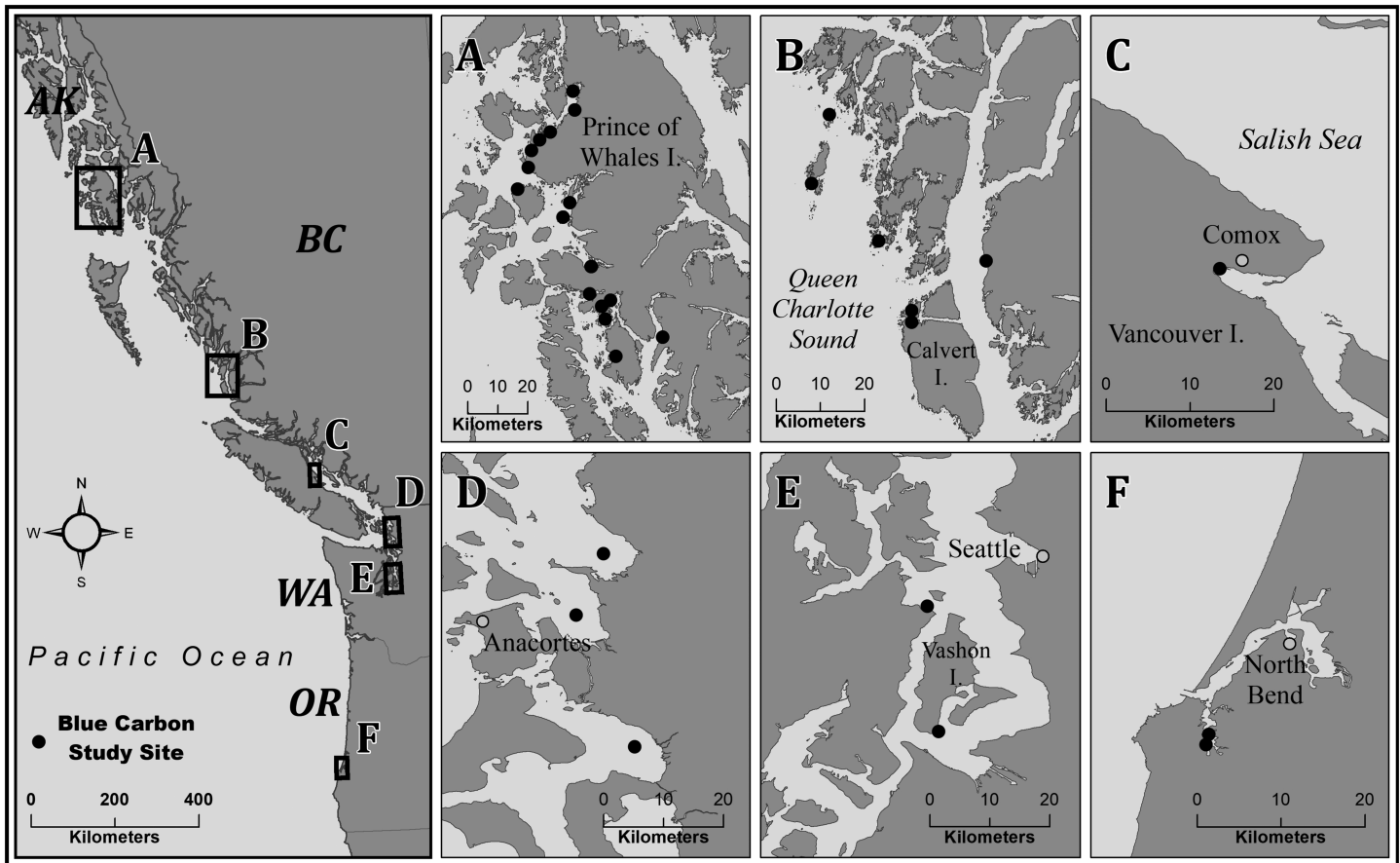


Figure 1. (left panel) locations of sediment cores collected from eelgrass (*Z. marina*) meadows and adjacent bare sediments across the Pacific northwest in (a) Southeast Alaska, USA; (b) the central coast of British Columbia, Canada; (c) K'omoks estuary on Vancouver Island, British Columbia, Canada; (d) the central Salish Sea, WA, USA; (e) the southern Salish Sea, WA, USA; and (f) South Slough National Estuarine Research Reserve, OR, USA. Meadows sampled within each region are denoted with dark circles, and nearby population centers are noted in light grey circles for reference.

When possible, sediment compaction was calculated for each core by measuring the distance from the top of the core to the sediment surface outside of the core, minus the distance from top of core to the sediment surface inside the core (Howard et al., 2014). Cores were extruded and subsectioned either immediately following collection or after being frozen. Subsection depth intervals varied by site and region ranging from 2- to 10-cm subsections. Depth intervals were adjusted based on compaction only for the Southeast Alaska cores. In all cases, sediment from each depth interval was homogenized and a subsample of known volume was taken for chemical analyses and calculation of dry bulk density. All visible plant biomass and fauna were

Table 1

Summary of the Cores Collected From Both Vegetated and Unvegetated Sediments in Six Locations Within Four Regions Across the Pacific Northwest

Region	Location (inset map)	No. of sites	Number of cores		Tidal height	Average core depth (cm) \pm SE	Sampling period
			Vegetated	Unvegetated			
AK	Southeast Alaska (A)	16	16	0	Intertidal	30 ± 0	April–August 2017
BC	BC Central Coast (B)	6	45	18	Intertidal subtidal	32.8 ± 3.4	May–August 2016
	Vancouver Island (C)	1	7	2	Intertidal subtidal	51.1 ± 1.5	May–Sept 2014
WA	Central Salish Sea (D)	3	27	12	Intertidal subtidal	62.9 ± 6.8	2014–2016
	Southern Salish Sea (E)	2	6	0	Intertidal	33.9 ± 15.9	May 2016
OR	South Slough (F)	2	6	0	Intertidal	91.1 ± 3.1	May 2016
Total	-	30	107	32	-	40.4 ± 2.9	-

removed from the sediments before chemical analyses; however, nonseagrass organic material (e.g., woody debris) was left in the samples.

2.3. Quantification of Sediment Carbon Content

Sediment OC content was determined by two methods. For British Columbia (Central Coast and Vancouver Island), Southern Salish Sea and South Slough, Oregon, total percent carbon (%TC) was determined using an Elemental Analyzer, and percent inorganic carbon (%IC) was measured using a UIC Carbon Dioxide Coulometer. Percent organic carbon (%OC) was calculated by subtracting %IC from %TC for each sample (Hodgson & Spooner, 2016; Howard et al., 2014). For the Central Salish Sea sites, %OC was estimated by creating a regression equation to relate %OM (obtained from Loss on Ignition) to %OC (obtained from Elemental Analysis using a Thermo Electron Corp. FlashEA 1112 nitrogen and carbon analyzer; equation (1) and Figure S1). Equation (1) was also used to convert %OM to %OC for the Southeast Alaska sites, since only %OM data were available from these cores.

$$\%OC = \%OM \times 0.3134 - 0.1149 \quad (1)$$

Organic carbon stocks were calculated by summing the carbon mass from each subsection up to 25-cm depth, as described by Howard et al. (2014). A depth of 25 cm was selected for carbon stock comparisons to allow inclusion of the greatest number of our cores, and to allow comparisons to carbon stocks from previous studies (e.g., Dahl et al., 2016; Lavery et al., 2013; Röhr et al., 2018). It should be noted that OC values were relatively constant below 10 cm to depths up to 100 cm, which supported both retaining the Sediment Mixed Layer and extrapolating stocks to 1-m depth for comparison across studies.

2.4. Carbon and Nitrogen Isotope Analyses

In some locations (the BC Central Coast, Southern Salish Sea, and South Slough, Oregon), an Isotope Ratio Mass Spectrometer was used to measure $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the sediments to determine whether organic matter was autochthonous (originating within the meadow) versus allochthonous (originating outside the meadow). All isotopic ratios are expressed relative to Vienna Pee Dee Belemnite for carbon, and atmospheric air for nitrogen, in per mil notation (‰). Carbon and nitrogen isotope signatures for potential sources of carbon to the sediments were compiled from existing available data from the Pacific Northwest (Table S1).

2.5. Sediment and Carbon Accumulation Rates

Sediment accumulation rates were determined using an alpha spectrometer for samples from the BC Central Coast, Southern Salish Sea and South Slough, Oregon and a gamma spectrometer for sites in the Central Salish Sea. Gamma spectrometry was performed at Western Washington University, Bellingham, USA, with a Canberra Germanium Detector (model GL2820R), with gamma emissions at 46 and 351 keV recorded by Genie 2000 software (Canberra 2002). Alpha spectrometry was performed by MyCore Scientific in Dunrobin, Ontario, Canada. Both alpha and gamma spectrometry are used to measure excess ^{210}Pb concentrations at various sediment depths, by subtracting supported, or background, ^{210}Pb from total ^{210}Pb concentrations. The rate of decline of this excess ^{210}Pb can be used to estimate the sediment age at various depths and thereby sediment accumulation rates. There are three models that can be used to interpret the excess ^{210}Pb profiles, outlined in Arias-Ortiz et al. (2018). Here we calculated sediment accumulation rates using the Constant Rate of Supply for the BC Central Coast, Southern Salish Sea, and South Slough sites, and we calculated accretion rates using the Constant Initial Concentration model for the Central Salish Sea sites. Carbon accumulation rates were calculated in one of two ways: as the product of sediment accumulation rates and %OC or as the product of sediment accretion rates and carbon density.

3. Results

3.1. Overview of Cores Collected

Sediment carbon data were amalgamated from 30 intertidal and subtidal eelgrass meadows within six geographic regions, spanning from the northernmost site in Southeast Alaska (Prince of Wales Island) to the southernmost site in the South Slough National Estuarine Research Reserve, Oregon (Figures 1a–1f). In

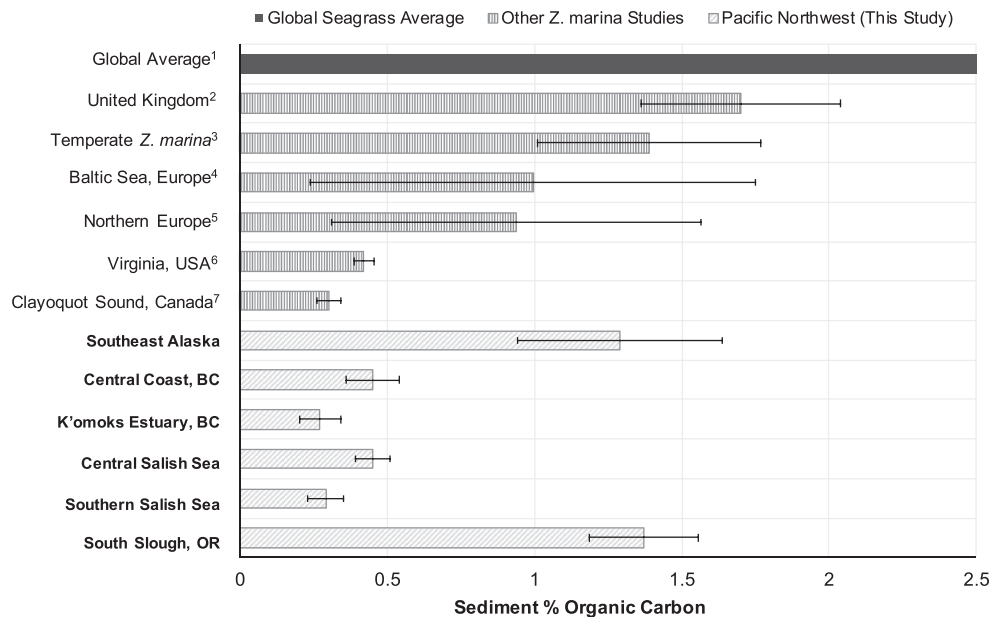


Figure 2. The percent organic carbon (%OC) in the sediments of *Z. marina* meadows in the six Pacific northwest regions (light grey, diagonal hatched bars), compared with the average %OC from other published studies in *Z. marina* meadows (medium grey, vertical hatched bars) and the global average for all seagrass species (dark grey bars). Error bars represent standard error. Sources for %OC values are as follows: 1 = Fourqurean et al. (2012), 2 = Green et al. (2018), 3 = Röhr et al. (2018), 4 = Röhr et al. (2016), 5 = Dahl et al. (2016), 6 = Greiner et al. (2013), 7 = Postlethwaite et al. (2018).

total, 139 cores were collected, with 107 from vegetated sediments (*Z. marina*) and 32 from unvegetated sediments. The cores ranged from 10 to 105 cm in length (Table 1).

3.2. Sediment Carbon Content and Dry Bulk Density

The average (\pm SE) dry bulk density across all sites was 1.4 ± 0.04 g cm⁻³ and ranged from 1.1 to 1.7 g cm⁻³. Total carbon (TC) content in the sediments across all regions sampled averaged 1.2% and ranged from 0.4 to 2.5%. Inorganic carbon (IC) content averaged 3.1% and ranged from 0 to 9.7% (Table S2). The inorganic carbon in the sediments was primarily due to bivalve shells or shell hash incorporated into the sediments. Average % OC in *Z. marina* sediments was 0.7% and ranged from 0.1 to 2.3% (Figure 2). The overall %OC, with both vegetated and unvegetated cores combined, was $0.8\% \pm 0.09$ (SE). Dry bulk density and sediment carbon content values on a per site basis are shown in Table S3.

Unvegetated cores were only collected in the central Salish Sea and British Columbia (Central Coast and Vancouver Island), and thus, we opted to compare vegetated and unvegetated sediment parameters only within sites where both core types were collected, as opposed to across the entire study region. In general, sediment %OC in vegetated areas was higher than that in unvegetated sediments except in the central Salish Sea (Figure 3).

3.3. Sediment Organic Carbon Stocks

The overall average OC stock in the top 25 cm of sediment was $1,811 \pm 154$ g OC m⁻², including both vegetated and unvegetated cores. The 25-cm OC stocks ranged from 600 to 5,125 g OC m⁻². Stocks in the top 25 cm were highest at the Oregon South Slough sites, and lowest in the Southern Salish Sea (Figure 4). When extrapolated to 1-m depth, OC stocks ranged from 752 to 20,501 g OC m⁻² and averaged 6,512 g OC m⁻². There were four cores (all from South Slough, Oregon) that were at least 1 m in length, from which OC stocks averaged 14,837 g OC m⁻² and ranged from 11,052 to 17,304 g OC m⁻². Organic carbon stocks over the top 25 cm and the extrapolated values to 1 m at each specific site are shown in Table S3.

3.4. Carbon Accumulation Rates Obtained From ²¹⁰Pb Dating

For five cores (two from British Columbia and three from the central Salish Sea) where ²¹⁰Pb data were obtained, the sediments were too mixed to determine accumulation rates with confidence; potential

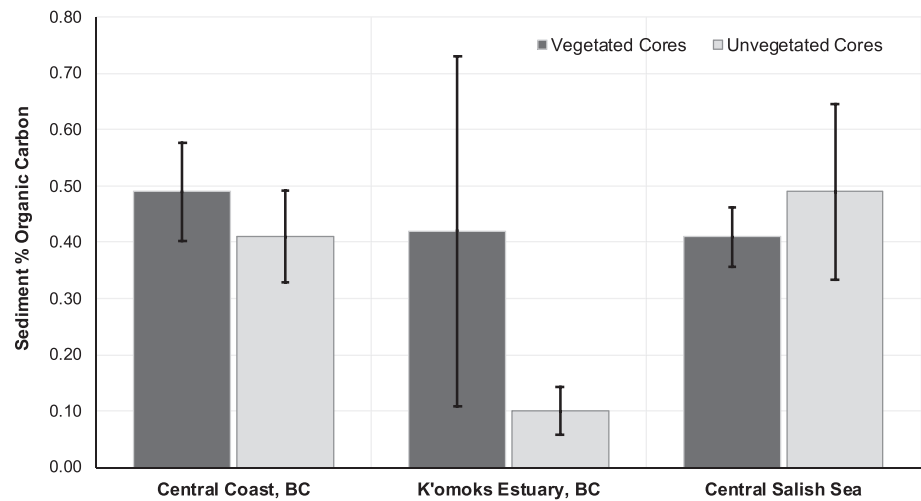


Figure 3. The mean percent organic carbon (%OC) in vegetated (dark grey) and adjacent unvegetated cores (light grey) in three PNW regions: The BC central coast, Vancouver Island, BC, and the central Salish Sea. Note that unvegetated cores were not collected from other regions. Error bars are standard errors.

mechanisms of mixing include hydrodynamic driven resuspension of sediments and bioturbation by infaunal organisms. Presence of ^{210}Pb at background levels also prevented accurate dating in four cores from Washington and one core from British Columbia. Obvious mixing was minimal in 23 cores from vegetated sediments and 2 cores from adjacent unvegetated sediments, allowing these to be used for ^{210}Pb dating. Across these 25 cores, sediment accretion rates ranged from 0.08 to 0.95 cm/year and averaged 0.39 ± 0.05 cm/year (Table 2 and Figure 5). Carbon sequestration rates ranged from 4.6 to 93.0 g OC $\text{m}^{-2} \text{yr}^{-1}$ and

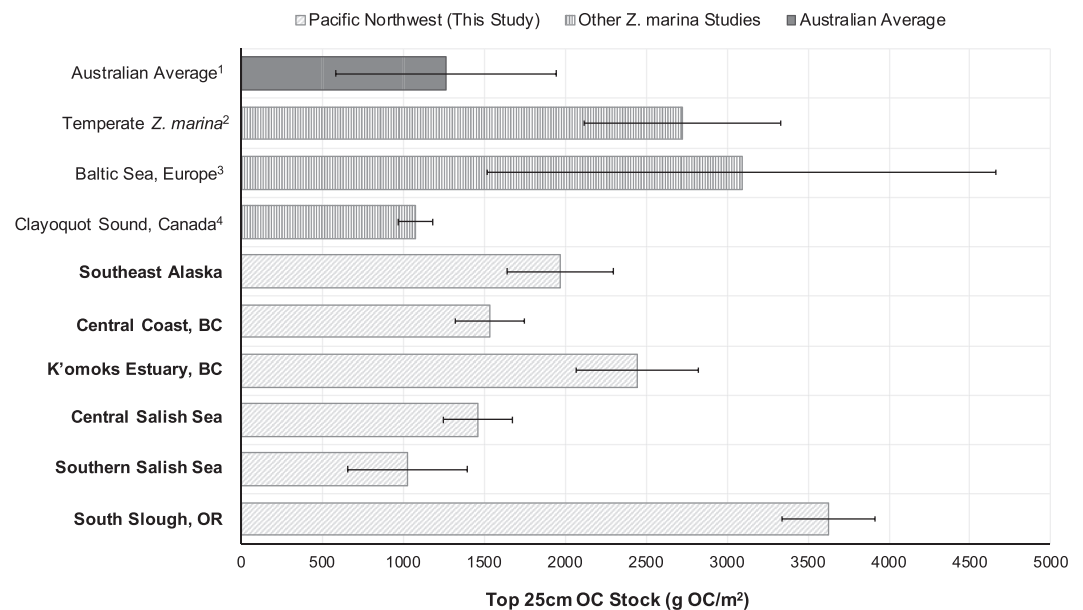


Figure 4. Organic carbon stocks integrated over the top 25 cm of sediment from *Z. marina* meadows in the six Pacific northwest regions from this study (light grey, diagonal hatched bars), compared with 25-cm OC stocks from other published studies in *Z. marina* meadows (medium grey, vertical hatched bars) and a published average for Australian seagrass species (dark grey bar). Error bars denote standard errors. Sources for OC stock values are as follows: 1 = Lavery et al. (2013), 2 = Röhr et al. (2018), 3 = Röhr et al. (2016), 4 = Postlethwaite et al. (2018). Note that these were the only studies found that calculated OC stocks to 25 cm.

Table 2

Organic Carbon Accumulation Rates and Accretion Rates Estimated From 25 Cores Obtained From British Columbia, Washington and Oregon, From Both Vegetated and Unvegetated Sediments

Region	Site	Cover	OC accumulation rate (g OC m ⁻² yr ⁻¹)	Accretion rate (cm/year)	Source
BC	Choked Passage	Vegetated	4.6	0.28	1
	McMullins N	Vegetated	22.3	0.26	1
	Pruth Bay	Vegetated	29.4	0.29	1
	Pruth Bay	Vegetated	6.5	0.13	5
	Triquet Bay	Vegetated	33.1	0.30	1
	K'omoks Estuary	Vegetated	28.0	0.35	2
	K'omoks Estuary	Vegetated	24.0	0.20	2
	K'omoks Estuary	Unvegetated	17.0	0.19	2
	K'omoks Estuary	Unvegetated	4.3	0.46	2
WA	Padilla Bay	Vegetated	7.5	0.18	3
	Padilla Bay	Vegetated	13.4	0.20	3
	Padilla Bay	Vegetated	5.0	0.08	3
	Padilla Bay	Vegetated	11.9	0.24	3
	Padilla Bay	Vegetated	8.5	0.21	3
	Padilla Bay	Vegetated	21.7	0.49	3
	Padilla Bay	Unvegetated	13.6	0.18	3
	Padilla Bay	Vegetated	29.5	0.57	4
	Padilla Bay	Vegetated	40.1	0.84	4
	Padilla Bay	Vegetated	41.0	0.70	4
	Skagit Bay	Vegetated	44.4	0.64	4
	Skagit Bay	Vegetated	93.0	0.95	4
	Samish Bay	Vegetated	13.9	0.26	4
	Skagit Bay	Unvegetated	45.3	0.93	4
OR	Valino Island	Vegetated	16.5	0.14	5
	Hidden Creek	Vegetated	29.6	0.20	5

Note. Sources are as follows: 1 = Prentice et al. (2019), (2) Spooner (2015), (3) Poppe and Rybczyk (2018), (4) Lutz (2018), and (5) Short et al. (2017).

the overall average \pm SE, based again on all cores, was 24.8 ± 4.5 g OC m⁻² yr⁻¹. Accretion rates and carbon accumulation rates for each core individually are shown in Table 2.

3.5. Carbon and Nitrogen Stable Isotopes

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic signatures of the sediments were obtained from six sites in British Columbia, three sites in Washington, and two sites in Oregon. Across these 11 sites, the average $\delta^{13}\text{C}$ signature of the sediments was $-20.3 \pm 0.5\text{‰}$ (SE) and the average $\delta^{15}\text{N}$ signature was $6.3 \pm 0.3\text{‰}$ (SE). The carbon signatures were most depleted in Oregon (-23.2‰), followed by Washington (-20.7‰) and British Columbia (-19.8‰). Carbon and nitrogen isotope signatures of common macrophytes available from the Pacific Northwest include *Z. marina* from various locations, phytoplankton, benthic diatoms, and riverine and marine particulate organic matter (Table S1).

4. Discussion

4.1. Summary of Findings

Here we provide estimates of sediment organic carbon content (%OC), OC stocks over the top 25 cm and projected to 1-m depth, OC accumulation rates, and sediment carbon sources from eelgrass meadows in the Pacific Northwest. These data add to the growing body of knowledge on carbon sequestration and storage in temperate *Z. marina* meadows and provide values for a relatively data-deficient region, where there is interest in harnessing the climate benefits of coastal wetlands. In general, these OC stocks and sequestration rates align with those from other *Z. marina* meadows but are lower than values reported for seagrasses globally. Furthermore, the OC in Pacific Northwest eelgrass sediments appears to be largely derived from noneelgrass (allochthonous) sources.

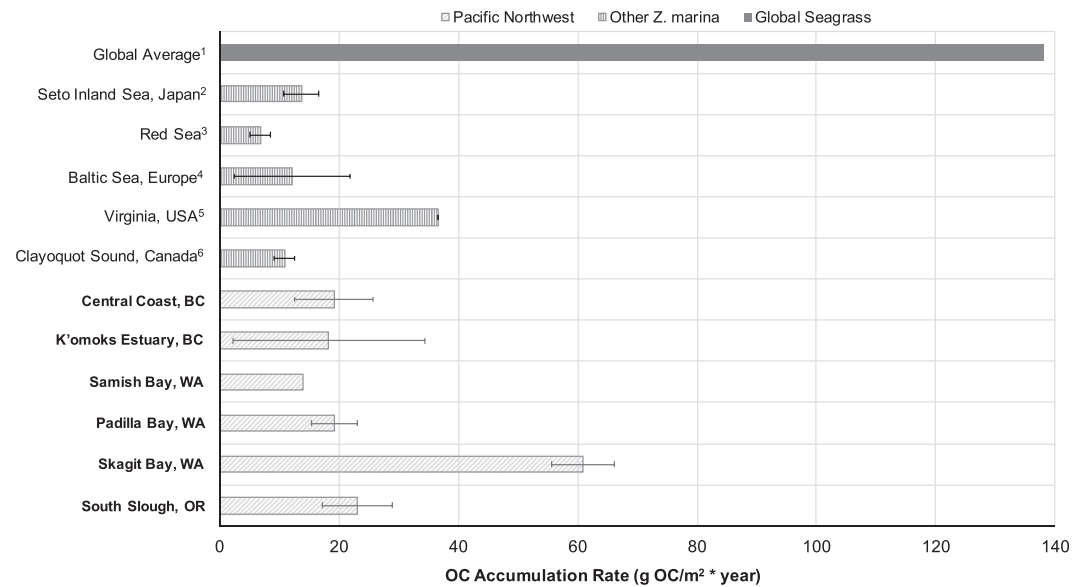


Figure 5. Organic carbon accumulation rates from *Z. marina* meadows in some of the Pacific northwest regions from this study (light grey, diagonal hatched bars), compared with accumulation rates from other published studies in *Z. marina* meadows (medium grey, vertical hatched bars) and a published average for seagrasses globally (dark grey bar). Error bars denote standard error. Sources for OC accumulation rate values are as follows: 1 = McLeod et al. (2011), 2 = Miyajima et al. (2015), 3 = Serrano et al. (2018), 4 = Jankowska et al. (2016), 5 = Greiner et al. (2013), 6 = Postlethwaite et al. (2018).

4.2. Sediment Carbon Content Trends and Comparisons

Across all samples from the six Pacific Northwest regions sampled here, OC content in the sediments of *Z. marina* meadows ranged from 0.1 to 2.3%. The highest sediment OC content was found in Southeast Alaska and South Slough, Oregon, while the lowest values were found in the Southern Salish Sea (Figure 2). As such, we did not identify a latitudinal trend in the data, consistent with Röhr et al. (2018), who found that latitude explained relatively little variation in OC stocks in *Z. marina* meadows across the Northern Hemisphere. For example, although the highest %OC values were measured in Alaska (2.32%), some sites in Alaska also had very low values (0.09%).

The sediment carbon content values reported here fall within the range of those reported from other temperate *Z. marina* meadows globally. The mean OC content for the entire Pacific Northwest region (0.7%) is within the range of values reported from eelgrass meadows in the Black Sea (0.2%), Portugal (0.6%), and the Baltic Coast of Sweden (0.2%; Dahl et al., 2016), albeit slightly lower than the average value of 1.4% reported from *Z. marina* across the globe (Röhr et al., 2018) and the Gullmarn Fjord in Sweden (2.8%; Dahl et al., 2016). Our PNW values also align with those reported from meadows on the Atlantic coast of North America of 0.4% (Greiner et al., 2013) as well as from Denmark (1.7%) and Finland (0.2%; Röhr et al., 2016). However, it is noteworthy that most of the values from temperate eelgrass meadows, including those from the Pacific Northwest, are lower than the global average OC content for all seagrass species combined (2.5%), reported by Fourqurean et al. (2012).

Similar to sediment OC content, the OC stocks in the top 25 cm of sediment exhibited high variability throughout the Pacific Northwest, ranging from 600 to 5,125 g OC m⁻². Reflecting trends in %OC values, OC stock values align with those from other temperate *Z. marina* meadows but are lower than global seagrass averages. For example, Dahl et al. (2016) reported stocks in the upper 35 cm ranging from 500 to 3,500 g OC m⁻², while Röhr et al. (2016, 2018) reported stocks in the upper 25 cm ranging from 627 to 6,005 g OC m⁻² and 318 to 26,523 g OC m⁻², respectively. Furthermore, the average OC stock from eelgrass meadows across all temperate latitudes, reported by Röhr et al. (2018), is 2,721 g OC m⁻², is somewhat similar to our Pacific Northwest average of 1,752 g OC m⁻². Additionally, our values align with stocks in the upper 25 cm from Australia, which range from 262 to 4,833 g OC m⁻² and average 1,262 g OC m⁻² (Lavery et al., 2013). While there were no 25-cm OC stocks for seagrass species globally to which we could

compare our values, we could compare our results to those reported for the upper 1 m by extrapolating our 25-cm stocks to 1-m depth. Once we extrapolated to 1 m and included four cores for which 1-m stocks had been directly measured, Pacific Northwest values averaged $6,526 \text{ OC m}^{-2}$. These OC stocks are significantly lower than the 1-m OC stock of $13,970 \text{ g OC m}^{-2}$ reported for all seagrass species globally (Fourqurean et al., 2012).

4.3. Comparing Carbon Content in Vegetated and Unvegetated Sediments

When comparing vegetated areas with adjacent unvegetated areas, we found that carbon content in vegetated sediments was only marginally higher than in unvegetated sediments (Figure 3). Based on previous work (Dahl et al., 2016; Oreska et al., 2017; Ricart et al., 2015), we expected to find higher carbon content in vegetated sediments relative to unvegetated sediments because seagrass is thought to enhance carbon accumulation in these areas. While we did observe slightly higher carbon content in vegetated sediments on the BC Central Coast and Vancouver Island, in the Central Salish Sea, unvegetated sediments had marginally higher carbon content than nearby vegetated sediments (Figure 3). Moreover, it is worth noting that in all three locations, the variance in vegetated and unvegetated sediment carbon content was sufficiently large that the observed trends were not definitive (Figure 3). The vegetated and unvegetated values observed here are similar to those observed by Postlethwaite et al. (2018) and Prentice et al. (2019) in Clayoquot Sound, Vancouver Island, and the BC Central Coast, respectively. The observed similarity between vegetated and unvegetated OC content in the PNW may be due to the characteristically shallow root systems of *Z. marina*, its patchy and sparse nature, and/or its tendency to occupy coarse sandy sediments that are relatively ineffective at retaining carbon (Howard, 2018), resulting in limited enhancement of OC accumulation relative to bare sediments. Further, the lack of difference could be attributed to those unvegetated areas having been potentially previously vegetated. Due to the lack of monitoring and mapping data in these regions, it is difficult to discern where the meadows were previously, and thus, current conditions may not be reflective of historical eelgrass meadow distributions. Furthermore, if we did not sample far enough away from the meadow, the adjacent unvegetated areas may have still been subject to the carbon capturing effect of the nearby seagrass canopy.

4.4. PNW Carbon Sequestration Rates

The OC accumulation rates from eelgrass meadows in the Pacific Northwest ($n = 21$ vegetated cores, $n = 4$ unvegetated cores) ranged from 4.3 to $93.0 \text{ g OC m}^{-2} \text{ yr}^{-1}$ and averaged 24.1 g OC m^{-2} . Again, these values align with rates from other *Z. marina* meadows, such as those from Clayoquot Sound, British Columbia (3.9 – $22.3 \text{ g OC m}^{-2} \text{ yr}^{-1}$; Postlethwaite et al., 2018), Poland (0.84 – $41 \text{ g OC m}^{-2} \text{ yr}^{-1}$; Jankowska et al., 2016), Japan (3 – $10 \text{ g OC m}^{-2} \text{ yr}^{-1}$; Miyajima et al., 2015), and the Atlantic coast of North America ($36.7 \text{ g OC m}^{-2} \text{ yr}^{-1}$; Greiner et al., 2013; Figure 5). Again, our PNW rates are lower than those reported for global seagrasses, which average $138 \text{ g OC m}^{-2} \text{ yr}^{-1}$ and range from 45 to $190 \text{ g OC m}^{-2} \text{ yr}^{-1}$ (McLeod et al., 2011).

It is important to note that bioturbation can inflate the apparent accretion rates by transporting sediment from the surface downward in the sediment column, mixing the ^{210}Pb profile. Although we eliminated any obvious mixed layers (or entirely mixed cores) from our analysis, effects of bioturbation, erosion, and resuspension are not necessarily apparent in the ^{210}Pb profile and therefore may have unknowingly affected some cores. This mixing reduces the downcore rate of ^{210}Pb decline and thereby artificially inflates the accretion rate. The reported accretion and carbon sequestration rates should thus be considered maximum possible rates and may be overestimates. Although this uncertainty presents a challenge for carbon valuation efforts, our methods are comparable to other blue carbon studies, which allows for comparison of carbon sequestration rates across studies. For future studies, we highlight the importance of greater depth subsampling resolution toward the top of the core to accurately measure where the mixed layer terminates. The thickness of this bioturbation depth is another variable that may control carbon storage.

Z. marina has some habitat requirements that may partially explain its low carbon sequestration potential relative to some other seagrass species. The species appears to be limited to sediments with low carbon content to avoid damage from toxic sulfides, and areas with low suspended sediment concentrations to receive enough light for photosynthesis. Yet both these factors, while limiting to eelgrass growth, are necessary for carbon sequestration (Poppe & Rybczyk, 2018). *Z. marina* also has physical characteristics that may limit its ability to trap and retain sediments. For example, although the canopy can exceed 3 m in our study areas

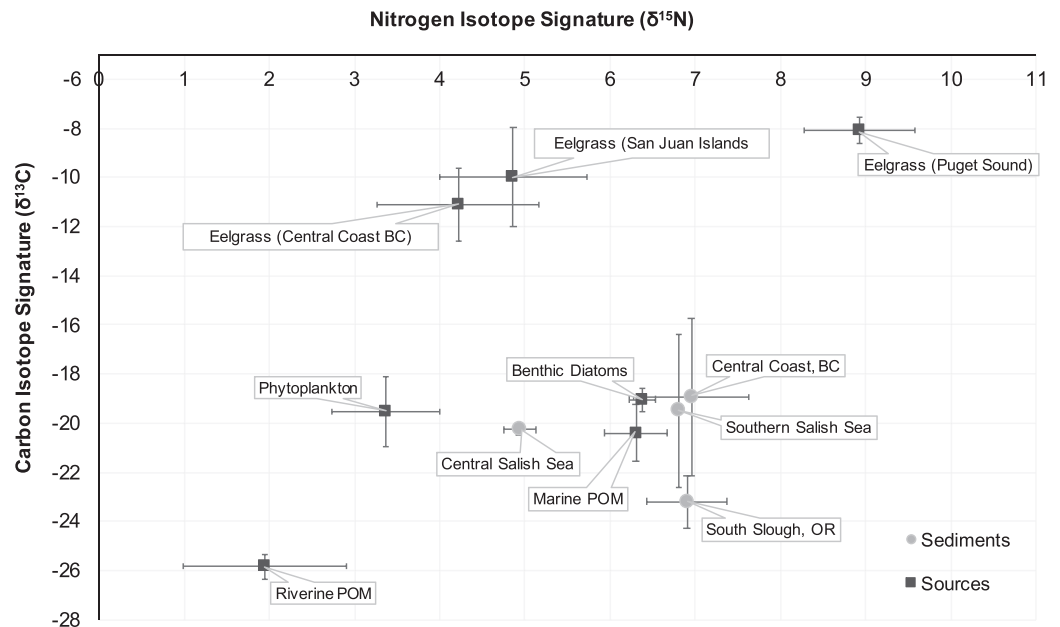


Figure 6. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope signatures of the sediments from various regions across the Pacific northwest (dark grey squares) compared with signatures of potential sources of organic carbon (light grey circles).

(Bulthuis, 2013), the leaves are thin and supple, and high currents can lay them quite flat near the sediment surface, nearly eliminating their particle-trapping ability (Prentice et al., 2019). In addition, *Z. marina* rhizomes spread just under the sediment surface, primarily within the top 4 cm (Phillips 1984), which may enhance sediment stability relative to unvegetated areas, but provide much less stability than other seagrass species with thick root mats such as *Posidonia oceanica*. Although their rhizomes do provide some sediment stabilization (Cheap et al., 1985), their shallow hold enables uprooting by brant geese grazing (Pacific Flyway Council, 2002; Rivers & Short, 2007), bioturbation (Bulthuis, 2013), and orbital wave motion, which has been found to penetrate the canopy and induce wave-enhanced bottom shear stress (Hansen & Reidenbach, 2013).

4.5. Sources of Carbon Contributing to PNW Eelgrass Sediments

Our isotopic data suggest that the organic carbon that ends up in eelgrass meadow sediments is largely derived from noneelgrass sources, which aligns with previous findings that upward of 50% of carbon in seagrass sediments may be allochthonous in origin (Kennedy et al., 2010; Miyajima et al., 2017; Oreska et al., 2018; Prentice et al., 2019). While we did not have enough replicates of sediment isotope values or enough localized signatures of potential carbon sources to determine the relative proportion of carbon sources using an isotope mixing model, the biplot shows a clear separation of signatures in the sediments from those of *Z. marina* across various regions (Figure 6). However, beyond this observation, it becomes difficult to distinguish among the other noneelgrass sources to the sediments (e.g., relative contributions of marine and river particulate organic matter, phytoplankton, and other macroalgae). Future work should continue to obtain finer resolution data on the sources of carbon to coastal sediments. For example, using environmental DNA has recently been suggested as having promising potential to precisely identify the sources and contributions of different primary producers to sediment carbon in coastal ecosystems (Gerald et al., 2019; Reef et al., 2017).

Understanding the relative contributions of allochthonous versus autochthonous carbon stored in eelgrass meadow sediments is important from multiple perspectives. First, it is important to understand how carbon flows among coastal ecosystems to gain perspective on seascape connectivity and to better inform conservation of nearshore habitats (Hyndes et al., 2012, 2014). Second, different sources of carbon may vary in their persistence in the sediments, as some sources (e.g., seston, macroalgae) are more labile and can be remineralized at a faster rate than recalcitrant sources such as terrestrial carbon or seagrass tissues (Holmer et al.,

2004; Mazarrasa et al., 2017b; Trevathan-Tackett, Macreadie, et al., 2017). Finally, the relative contribution of allochthonous versus autochthonous carbon is an important component of carbon accounting, as projects may not receive credit for allochthonous carbon unless it would have been returned to the atmosphere in the baseline scenario (Emmer et al., 2015; Needelman et al., 2018).

4.6. Drivers of Variability in Blue Carbon Parameters

Many habitat characteristics have been shown to influence the carbon content of seagrass meadow sediments, including seagrass species composition, canopy complexity, hydrodynamic regime, water depth, nutrient availability, and biotic interactions (Mazarrasa et al., 2018). Here we observed notable variability in sediment carbon content (percentage and stocks) as well as carbon sequestration rates both among and within regions. This variability is likely driven by a multitude of interacting abiotic and biotic factors, and without finer resolution data on such variables, it is difficult to discern the specific drivers of variability in carbon parameters. Moreover, the hydrodynamic environment (e.g., exposure, depth, wave height) has been shown to play a key role in the magnitude of carbon storage in seagrass meadows in various regions around the globe (Dahl et al., 2018; Mazarrasa et al., 2017a; Prentice et al., 2019; Samper-Villarreal et al., 2016), and likely plays an important role across the meadows sampled herein. While we do not have explicit measures of the hydrodynamic environment associated with these cores, we anecdotally observed higher carbon stocks in some of the more sheltered sites (e.g., South Slough in Oregon, Dundar Inlet, Salt Lake Bay, and Soda Bay in Southeast Alaska, Pruth Bay on the BC Central Coast).

Furthermore, there is undoubtedly an important interaction between the hydrodynamic environment and sediment grain size, with greater percentages of fine sediments typically found in more sheltered sites (Mazarrasa et al., 2017a). Sediment grain size likely plays a role in controlling the amount of carbon stored in eelgrass sediments, as finer sediments are found to contain higher proportions of organic carbon (Dahl et al., 2016; Mazarrasa et al., 2018; Serrano et al., 2016). In Southeast Alaska, we found a positive relationship between OC content and a qualitative measure of sediment grain size ($R^2 = 0.47$, $p = 0.004$), suggesting that sites with sediments classified as mud or sandy mud tended to have higher %OC (Figure S2a). Moreover, at sites where % fine sediments (particle size $<63 \mu\text{m}$) was measured quantitatively, we found that %OC increased with an increase in % fine sediments, although little variance in %OC was accounted for by the model ($R^2 = 0.05$, $p = 0.04$; Figure S2b). Some outliers in the regression (e.g., high %OC values associated with low % fines) may be attributed to deposits of woody debris, which are high in organic matter, causing high %OC values regardless of sediment grain size.

In meadows influenced by large river systems or any high unidirectional currents such as channels, it is important to consider areas of deposition versus erosion, as these smaller-scale processes likely create heterogeneity in sediment carbon content across the area of riverine influence. For example, the highest sediment accretion rates (0.95 cm/year) were found in the Skagit River delta, near the mouth of a new tributary that resulted from a recent avulsion. This redistributed the bank sediments over a five-year time span, elevating accretion at this site, while lower rates (0.35 cm/year) were found nearby. Furthermore, at some sites located in restricted channels with high tidal exchanges (e.g., Koeys Estuary, Choked Pass on the BC Central Coast), erosional processes likely restrict the carbon accumulation potential and result in the loss of buried carbon.

4.7. Other Factors to Consider for Eelgrass Carbon Budgets

There are a variety of other factors to consider when examining the overall carbon budget in seagrass meadows, and when determining whether a given area is a net sink or source of CO_2 . For example, anthropogenic disturbances such as coastal development, shading, clam harvesting, and dredging can expose sediments to oxygen, thereby facilitating microbial remineralization of carbon stocks and diminished carbon storage capacity (Barañano et al., 2017; Trevathan-Tackett et al., 2018; Macreadie et al., 2019). Furthermore, even natural disturbances such as wave action and bioturbation by infaunal organisms can result in favorable conditions for microbial degradation of sediment carbon by changing oxygen penetration depths (Thomson, 2017). In the Pacific Northwest, local disturbances such as active infaunal communities, dredging, diking, log boom shading, increasing sedimentation, and erosion should be further considered in the context of sediment carbon storage. Furthermore, on the Central Coast of British Columbia and in Southeast Alaska where sea otter (*Enhydra lutris*) populations are expanding, the bioturbation effects of

otters digging for prey such as clams could be further investigated to determine potential effects on carbon stocks (Eckert et al., 2018).

To date, most work on seagrass blue carbon has focused on organic carbon stocks, whereas the inorganic carbon fraction of the sediments, primarily calcium carbonate (CaCO_3), has been largely unaccounted for (Mazarrasa et al., 2015; Howard, Creed, et al., 2017; Gullstrom et al., 2017). Seagrass ecosystems can support active communities of calcifying organisms, and calcification and carbonate dissolution both cause CO_2 exchange with the atmosphere. In particular, the process of calcium carbonate production produces CO_2 , and thus, in seagrass ecosystems with high calcium carbonate production, carbon sequestration may be offset by CO_2 produced by calcifying organisms (Macreadie et al., 2017; Howard, Creed, et al., 2017). In some of the PNW meadows sampled herein, the sediment carbon was largely composed of inorganic carbon, and thus, the organic to inorganic carbon ratio (OC: IC) was less than 1 (Table S2). The inorganic carbon component was primarily made up of bivalve shell deposits (shell hash) within the sediments. Shell hash-dominated sediments were particularly prominent at some sites in Southeast Alaska and the BC Central Coast, regions which had the lowest OC: IC ratios, of 0.3 and 0.2, respectively. In meadows with such active bivalve communities and naturally low organic carbon content, it will be important to investigate the balance between CO_2 exchange during calcium carbonate shell production and carbon sequestered by means of community photosynthesis or particle capture to determine if the meadow ecosystem is acting as a net sink or source of CO_2 (Mazarrasa et al., 2015; Howard, Creed, et al., 2017; Macreadie et al., 2017).

The fate of exported eelgrass tissue is not well understood but is likely either assimilated into nearshore food webs in situ and in adjacent ecosystems, buried in nearby sediments, or exported to the deep sea. Although much of the carbon sequestered in Pacific Northwest eelgrass meadows appears to be from noneelgrass sources, the carbon contained in seagrass tissues could potentially still contribute to carbon storage elsewhere depending upon the transport and fate of the senescing seagrass leaves (Duarte & Cebrian, 1996; Mateo et al., 2006; Duarte & Krause-Jensen, 2017). This exported biomass has the potential to be sequestered elsewhere, either in sediments of surrounding ecosystems or in the deep sea (below 1,000 m), where it is unlikely to come in contact with the atmosphere for significant time scales (Duarte & Krause-Jensen, 2017). Thus, future research should expand beyond seagrass meadows themselves, to investigate the fate of exported eelgrass biomass to gain a more holistic understanding of coastal carbon budgets.

5. Conclusions

For the first time, we report latitudinal trends in seagrass-associated sediment carbon at multiple sites from Southeast Alaska to South Slough, Oregon. We present measurements of eelgrass organic carbon stocks, accumulation rates, and estimates of sediment carbon sources—essential components of project qualification under the Verified Carbon Standard (Emmer et al., 2015). We were able to amalgamate data from 139 cores across the Pacific Northwest, providing a range of empirical estimates for this region. However, broader spatial coverage and more replication is critical to refine estimates for such a long and geographically complex coastline. This is especially true considering the small-scale variability and uncontrolled factors that can cause “spikes” in both organic and inorganic carbon content (e.g., woody debris, bivalve shells). The meadows included in this study appear representative of the range of Pacific Northwest environments within which *Z. marina* grows, from sheltered sites with finer sediments, to exposed sites on the outer coast with coarser sediments. Thus, the range of parameters reported here may be considered to provide a realistic estimate of the true range of blue carbon sequestration and storage potential for Pacific Northwest eelgrass meadows.

As shown by other recent work in temperate *Z. marina* meadows (Hodgson & Spooner, 2016; Jankowska et al., 2016; Oreska et al., 2017; Poppe & Rybczyk, 2018; Postlethwaite et al., 2018; Prentice et al., 2019; Röhr et al., 2018), eelgrass carbon stocks and accumulation rates appear substantially lower than previously published global estimates for seagrass meadows (Fourqurean et al., 2012; Mcleod et al., 2011). These trends emphasize the importance of obtaining local values for carbon sequestration and storage in coastal habitats, particularly in the context of carbon credits and offset schemes. Furthermore, our results suggest the importance of characterizing habitat features (e.g., exposure, sediment grain size) across different spatial scales to help refine blue carbon estimates that can be accurately used for carbon accounting. Finally, it is important

to consider carbon storage as one of a multitude of reasons to conserve and restore eelgrass meadows in the Pacific Northwest and seagrass meadows globally.

Acknowledgments

This work was supported by a Commission for Environmental Cooperation (CEC) grant to F. Short, M. Helling-Lewis, J. Gaeckle, and A. Helms; a Tula Foundation scholarship to C. Prentice; National Science Foundation grants awarded to G. Eckert (NSF 1635716, 1600230); and a Padilla Bay Research Assistantship awarded to M. Lutz, E. Murray, and K. Poppe. We would also like to thank the many field and lab technicians who helped with the field and laboratory data collection. Specifically, we thank A. Olson, D. VanMaanen, and Z. Monteith (Hakai Institute) for their assistance collecting the BC Central Coast cores; Shauna Bjornson for her contributions to the Padilla Bay cores; and Lisa Ferrier and Dolores Sare (WA State DNR) for their assistance with the Southern Salish Sea cores. We also thank we thank K. Holmes (Hakai Institute) for the creation of the map in Figure 1. Data from this manuscript are freely accessible through the Hakai Institute Metadata Catalogue at the following link: <https://doi.org/10.21966/20SJ-J017>. Additionally, the data from Southeast Alaska are available through the Knowledge Network for Biocomplexity at the following link: <https://knbn.ecoinformatics.org/view/doi:10.5063/F1ZS2TTH>.

References

- Arias-Ortiz, A., Masqué, P., Garcia-Orellana, J., Serrano, O., Mazarrasa, I., Marbà, N., et al. (2018). Reviews and syntheses: 210Pb-derived sediment and carbon accumulation rates in vegetated coastal ecosystems—Setting the record straight. *Biogeosciences*, 15(22), 6791–6818. <https://doi.org/https://doi.org/10.5194/bg-2018-78>
- Borum, J., Pedersen, O., Greve, T. M., Frankovich, T. A., Zieman, J. C., Fourqurean, J. W., & Madden, C. J. (2005). The potential role of plant oxygen and sulphide dynamics in die-off events of the tropical seagrass, *Thalassia testudinum*. *Journal of Ecology*, 93(1), 148–158. <https://doi.org/10.1111/j.1365-2745.2004.00943.x>
- Bulthuis, D. A. (2013). The ecology of Padilla Bay, Washington: An estuarine profile of a National Estuarine Research Reserve. Padilla Bay National Estuarine Research Reserve Shorelands and Environmental Assistance Program. Mount Vernon, WA.
- CEC (2013). *North American Blue Carbon Scoping Study*, (49pp ed.). Montreal, Canada: Commission for Environmental Cooperation. Available from: <http://www3.cec.org/islandora/en/item/11368-north-american-blue-carbon-scoping-study-en.pdf>
- Cheap, K. M., Kenworthy, W. J., Heller, D. Y., Thayer, G. W., & Fonseca, M. S. (1985). *Transplanting of the Seagrasses "Zostera marina" and "Halodule wrightii" for Sediment Stabilization and Habitat Development on the East Coast of the United States*. Vicksburg, Miss.: U.S. Army Engineer Waterways Experiment Station.
- Cullen-Unsworth, L. C., & Unsworth, R. (2018). A call for seagrass protection. *Science*, 361(6401), 44–448. <https://doi.org/10.1126/science.aat7318>
- Dahl, M., Deyanova, D., Gütschow, S., Asplund, M. E., Lyimo, L. D., Karamfilov, V., et al. (2016). Sediment properties as important predictors of carbon storage in *Zostera marina* meadows: A comparison of four European areas. *PLoS ONE*, 11(12), e0167493. <https://doi.org/10.1371/journal.pone.0167493>
- Dahl, M., Infantes, E., Clevesjö, R., Linderholm, H. W., Björk, M., & Gullström, M. (2018). Increased current flow enhances the risk of organic carbon loss from *Zostera marina* sediments: Insights from a flume experiment. *Limnology and Oceanography*, 63(6), 2793–2805. <https://doi.org/10.1002/lno.11009>
- Donato, D. C., Kauffman, J. B., Murdiyarso, D., Kurnianto, S., & Stidham, M. (2011). Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, 4(5), 293–297. <https://doi.org/10.1038/ngeo1123>
- Duarte, C. M., & Cebrián, J. (1996). The fate of marine autotrophic production. *Limnology and Oceanography*, 41(8), 1758–1766. <https://doi.org/10.4319/lno.1996.41.8.1758>
- Duarte, C. M., Kennedy, H., Marbà, N., & Hendriks, I. (2013). Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies. *Ocean and Coastal Management*, 83, 32–38. <https://doi.org/10.1016/j.ocecoaman.2011.09.001>
- Duarte, C. M., & Krause-Jensen, D. (2017). Export from seagrass meadows contributes to marine carbon sequestration. *Frontiers in Marine Science*, 4(January), 1–7. <https://doi.org/10.3389/fmars.2017.00013>
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., & Apostolaki, E. T. (2010). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4). <https://doi.org/10.1029/2010GB003793>
- Duarte, C. M., Middelburg, J. J., & Caraco, N. (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences*, 2, 1–8. <https://doi.org/10.5194/bgd-1-659-2004>
- Eckert, G., Bolwek, A., LaRoche, N., Stephens, T. A., Domke, L. and W. Raymond. (2018). *Sea Otters and Seagrass in Southeast Alaska. EarthWatch Institute Field Report*. Boston, MA: Earthwatch Institute. Available from: <https://earthwatch.org/FieldReports/earthwatch-field-report-sea-otters-sea-grass-alaska-2018.pdf>
- Emmer, I., Needelman, B., Emmett-Mattox, S., Crooks, S., Megonigal, P., Myers, D., ... Shoch, D. (2015). VM0033 Methodology for Tidal Wetland and Seagrass Restoration. Available from: <https://verra.org/wp-content/uploads/2018/03/VM0033-Tidal-Wetland-and-Seagrass-Restoration-v1.0.pdf>
- Fargione, J. E., Bassett, S., Boucher, T., Bridgham, S. D., Conant, R. T., Cook-Patton, S. C., et al. (2018). Natural climate solutions for the United States. *Science Advances*, 4(11). <https://doi.org/10.1126/sciadv.aat1869>
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., et al. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7), 505–509. <https://doi.org/10.1038/ngeo1477>
- Gacia, E., & Duarte, C. M. (2001). Sediment retention by a Mediterranean *Posidonia oceanica* meadow: The balance between deposition and resuspension. *Estuarine, Coastal and Shelf Science*, 52(4), 505–514. <https://doi.org/10.1006/ecss.2000.0753>
- Geraldi, N. R., Ortega, A., Serrano, O., Macreadie, P. I., Lovelock, C. E., Krause-Jensen, D., et al. (2019). Fingerprinting blue carbon: Rationale and tools to determine the source of organic carbon in marine depositional environments. *Frontiers in Marine Science*, 6(May), 1–9. <https://doi.org/10.3389/fmars.2019.00263>
- Green, E. P., & Short, F. T. (2003). *World Atlas of Seagrasses*. Berkeley, CA: University of California Press.
- Greiner, J. T., McGlathery, K. J., Gunnell, J., & McKee, B. A. (2013). Seagrass restoration enhances “blue carbon” sequestration in coastal waters. *PLoS ONE*, 8(8), 1–8. <https://doi.org/10.1371/journal.pone.0072469>
- Gullström, M., Lyimo, L. D. L., Dahl, M., Samuelsson, G. G. S., Eggertsen, M., Anderberg, E., et al. (2017). Blue carbon storage in tropical seagrass meadows relates to carbonate stock dynamics, plant-sediment processes and landscape context: Insights from the Western Indian Ocean. *Ecosystems*, 1–16. <https://doi.org/10.1007/s10021-017-0170-8>
- Hejnowicz, A. P., Kennedy, H., Rudd, M. A., & Huxham, M. R. (2015). Harnessing the climate mitigation, conservation and poverty alleviation potential of seagrasses: Prospects for developing blue carbon initiatives and payment for ecosystem service programmes. *Frontiers in Marine Science*, 2(June), 1–22. <https://doi.org/10.3389/fmars.2015.00032>
- Hodgson, C., & Spooner, A. (2016). *The K'ómoks and Squamish Estuaries: A Blue Carbon Pilot Project, Final Report to North American Partnership for Environmental Community Action (NAPECA)*, Grant 2014-1362. Comox: Comox Valley Project Watershed Society. British Columbia.
- Holmer, M., Duarte, C. M., Boschker, H. T. S., & Barrón, C. (2004). Carbon cycling and bacterial carbon sources in pristine and impacted Mediterranean seagrass sediments. *Aquatic Microbial Ecology*, 36(3), 227–237. <https://doi.org/10.3354/ame036227>
- Howard, J., Hoyt, S., Isensee, K., Telszewski, M., & Pidgeon, E. (Eds) (2014). *In Coastal Blue Carbon: Methods for Assessing Carbon Stocks and Emissions Factors in Mangroves, Tidal Salt Marshes, and Seagrasses*. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature. Virginia, USA: Arlington.

- Howard, J., McLeod, E., Thomas, S., Eastwood, E., Fox, M., Wenzel, L., & Pidgeon, E. (2017). The potential to integrate blue carbon into MPA design and management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(February), 100–115. <https://doi.org/10.1002/aqc.2809>
- Howard, J. L. (2018). *Patterns of Carbon Metabolism, Storage, and Remineralization in Seagrass Ecosystems*. PhD Dissertation: Florida International University.
- Howard, J. L., Creed, J. C., Aguiar, M. V. P., & Fouquereau, J. W. (2017). CO₂ released by carbonate sediment production in some coastal areas may offset the benefits of seagrass “blue carbon” storage. *Limnology and Oceanography*, 63(1), 160–172. <https://doi.org/10.1002/lno.10621>
- Hyndes, G. A., Lavery, P. S., & Doropoulos, C. (2012). Dual processes for cross-boundary subsidies: Incorporation of nutrients from reef-derived kelp into a seagrass ecosystem. *Marine Ecology Progress Series*, 445, 97–107. <https://doi.org/10.3354/meps09367>
- Hyndes, G. A., Nagelkerken, I., Mcleod, R. J., Connolly, R. M., Lavery, P. S., & Vanderklift, M. a. (2014). Mechanisms and ecological role of carbon transfer within coastal seascapes. *Biological Reviews*, 89(1), 232–254. <https://doi.org/10.1111/brv.12055>
- Irving, A. D., Connell, S. D., & Russell, B. D. (2011). Restoring coastal plants to improve global carbon storage: Reaping what we sow. *PLoS ONE*, 6(3), 1–6. <https://doi.org/10.1371/journal.pone.0018311>
- Jankowska, E., Michel, L. N., Zaborska, A., & Włodarska-Kowalczyk, M. (2016). Sediment carbon sink in low density temperate eelgrass meadows (Baltic Sea). *Journal of Geophysical Research – Biogeosciences*, 121(12), 2918–2934. <https://doi.org/10.1002/2016JG003424>
- Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., & Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24(4), 1–8. <https://doi.org/10.1029/2010GB003848>
- Kindeberg, T., Ørberg, S. B., Röhr, M. E., Holmer, M., & Krause-Jensen, D. (2018). Sediment stocks of carbon, nitrogen, and phosphorus in Danish eelgrass meadows. *Frontiers in Marine Science*, 5, 1–14. <https://doi.org/10.3389/fmars.2018.00474>
- Lacy, J. R., & Wyllie-Echeverria, S. (2011). The influence of current speed and vegetation density on flow structure in two macrotidal eelgrass canopies. *Limnology and Oceanography: Fluids and Environments*, 1, 38–55. <https://doi.org/10.1215/21573698-1152489>
- Lavery, P. S., Mateo, M.-Á., Serrano, O., & Rozaimi, M. (2013). Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS ONE*, 8(9), e73748. <https://doi.org/10.1371/journal.pone.0073748>
- Lovelock, C. E., & Duarte, C. M. (2019). Dimensions of blue carbon and emerging perspectives. *Biology Letters*, 15(3), 20180781. <https://doi.org/10.1098/rsbl.2018.0781>
- Macreadie, P. I., Atwood, T. B., Seymour, J. R., Fontes, M. L. S., Sanderman, J., Nielsen, D. A., & Connolly, R. M. (2019). Vulnerability of seagrass blue carbon to microbial attack following exposure to warming and oxygen. *Science of the Total Environment*, 686, 264–275. <https://doi.org/10.1016/j.scitotenv.2019.05.462>
- Mateo, M. A., Cebrian, J., Dunton, K., & Mutchler, T. (2006). Carbon flux in seagrass ecosystems. In A. Larkum, R. Orth, & C. Duarte (Eds.), *Seagrasses: Biology*, (pp. 159–192). Netherlands: Ecology and Conservation. Springer-Verlag.
- Mazarrasa, I., Marbà, N., Garcia-Orellana, J., Masqué, P., Arias-Ortiz, A., & Duarte, C. M. (2017a). Effect of environmental factors (wave exposure and depth) and anthropogenic pressure in the C sink capacity of *Posidonia oceanica* meadows. *Limnology and Oceanography*, 62(4), 1436–1450. <https://doi.org/10.1002/lno.10510>
- Mazarrasa, I., Marbà, N., Garcia-Orellana, J., Masqué, P., Arias-Ortiz, A., & Duarte, C. M. (2017b). Dynamics of carbon sources supporting burial in seagrass sediments under increasing anthropogenic pressure. *Limnology and Oceanography*, 62(4). <https://doi.org/10.1002/lno.10509>
- Mazarrasa, I., Marbà, N., Lovelock, C. E., Serrano, O., Lavery, P. S., Fourqurean, J. W., et al. (2015). Seagrass meadows as a globally significant carbonate reservoir. *Biogeosciences*, 12(16), 4993–5003. <https://doi.org/10.5194/bg-12-4993-2015>
- Mazarrasa, I., Samper-Villarreal, J., Serrano, O., Lavery, P. S., Lovelock, C. E., Marbà, N., et al. (2018). Habitat characteristics provide insights of carbon storage in seagrass meadows. *Marine Pollution Bulletin*, 134, 106–117. <https://doi.org/10.1016/j.marpolbul.2018.01.059>
- McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., et al. (2011). A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10), 552–560. <https://doi.org/10.1890/110004>
- Miyajima, T., Hori, M., Hamaguchi, M., Shimabukuro, H., & Yoshida, G. (2017). Geophysical constraints for organic carbon sequestration capacity of *Zostera marina* seagrass meadows and surrounding habitats. *Limnology and Oceanography*, 62(3), 954–972. <https://doi.org/10.1002/lno.10478>
- Mtwana Nordlund, L., Koch, E. W., Barbier, E. B., & Creed, J. C. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS ONE*, 11(10), 1–23. <https://doi.org/10.1371/journal.pone.0163091>
- Murray, E. (2018). *Variation in Carbon Sediment Storage across Salish Sea Eelgrass Habitats Master of Marine Affairs Thesis*. Seattle, WA: University of Washington.
- Needelman, B. A., Emmer, I. M., Emmett-Mattox, S., Crooks, S., Megonigal, J. P., Myers, D., et al. (2018). The science and policy of the verified carbon standard methodology for tidal wetland and seagrass restoration. *Estuaries and Coasts*, 41(8), 2159–2171. <https://doi.org/10.1007/s12237-018-0429-0>
- Nellemann, C., Corcoran, E., Duarte, C. M., Valdés, L., De Young, C., Fonseca, L., & Grimsditch, G. (2009). Blue Carbon. A Rapid Response Assessment. United Nations Environment Programme, GRID-Arendal, www.grida.no. Available from http://www.grida.no/files/publications/blue-carbon/BlueCarbon_screen.pdf
- Oreska, M. P. J., McGlathery, K. J., & Porter, J. H. (2017). Seagrass blue carbon spatial patterns at the meadow-scale. *PLoS ONE*, 12(4), 1–18. <https://doi.org/10.1371/journal.pone.0176630>
- Oreska, M. P. J., Wilkinson, G. M., McGlathery, K. J., Bost, M., & McKee, B. A. (2018). Non-seagrass carbon contributions to seagrass sediment blue carbon. *Limnology and Oceanography*, 63(S1), S3–S18. <https://doi.org/10.1002/lno.10718>
- Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., et al. (2006). A global crisis for seagrass ecosystems. *Bioscience*, 56(12), 987–996. [https://doi.org/10.1641/0006-3568\(2006\)56\[987:AGCFSE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2)
- Ouyang, X., & Lee, S. Y. (2014). Updated estimates of carbon accumulation rates in coastal marsh sediments. *Biogeosciences*, 11(18), 5057–5071. <https://doi.org/10.5194/bg-11-5057-2014>
- Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., et al. (2012). Estimating global “blue carbon” emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS ONE*, 7(9), e43542. <https://doi.org/10.1371/journal.pone.0043542>
- Poppe, K. L., & Rybczyk, J. M. (2018). Carbon sequestration in a Pacific northwest eelgrass (*Zostera marina*) meadow. *Northwest Science*, 92(2), 80–91. <https://doi.org/10.3955/046.092.0202>

- Postlethwaite, V. R., McGowan, A. E., Kohfeld, K. E., Robinson, C. L. K., & Pellatt, M. G. (2018). Low blue carbon storage in eelgrass (*Zostera marina*) meadows on the Pacific coast of Canada. *PLoS ONE*, 13(6), 1–18. <https://doi.org/10.1371/journal.pone.0198348>
- Prentice, C., Hessing-Lewis, M., Sanders-Smith, R., & Salomon, A. K. (2019). Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows. *Limnology and Oceanography*, 64(6), 2389–2404. <https://doi.org/10.1002/lno.11191>
- Reef, R., Atwood, T. B., Samper-Villarreal, J., Adame, M. F., Sampayo, E. M., & Lovelock, C. E. (2017). Using eDNA to determine the source of organic carbon in seagrass meadows. *Limnology and Oceanography*, 62(3), 1254–1265. <https://doi.org/10.1002/lno.10499>
- Ricart, A. M., York, P. H., Rasheed, M. A., Pérez, M., Romero, J., Bryant, C. V., & Macreadie, P. I. (2015). Variability of sedimentary organic carbon in patchy seagrass landscapes. *Marine Pollution Bulletin*, 100(1), 476–482. <https://doi.org/10.1016/j.marpolbul.2015.09.032>
- Rivers, D. O., & Short, F. T. (2007). Effect of grazing by Canada geese *Branta canadensis* on an intertidal eelgrass *Zostera marina* meadow. *Marine Ecology Progress Series*, 333, 271–279. <http://doi:10.3354/meps333271>
- Röhr, M. E., Boström, C., Canal-Vergés, P., & Holmer, M. (2016). Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences*, 13, 6139–6153. <https://doi.org/10.5194/bg-13-6139-2016>
- Röhr, M. E., Holmer, M., Baum, J. K., Björk, M., Chin, D., Chalifour, L., et al. (2018). Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) meadows. *Global Biogeochemical Cycles*, 32(10), 1457–1475. <https://doi.org/10.1029/2018GB005941>
- Rozaimi, M., Serrano, O., & Lavery, P. S. (2013). Comparison of carbon stores by two morphologically different seagrasses. *Journal of the Royal Society of Western Australia*, 96, 81–83. Available from: [https://www.rswa.org.au/publications/Journal/96\(2\)/ROY%20SOC%2096.2%20ROZAIMI%20ET%20AL%2081-83.pdf](https://www.rswa.org.au/publications/Journal/96(2)/ROY%20SOC%2096.2%20ROZAIMI%20ET%20AL%2081-83.pdf)
- Samper-Villarreal, J., Lovelock, C. E., Saunders, M. I., Roelfsema, C., & Mumby, P. J. (2016). Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. *Limnology and Oceanography*, 61(3), 938–952. <https://doi.org/10.1002/lno.10262>
- Serrano, O., Lavery, P. S., Rozaimi, M., & Mateo, M. Á. (2014). Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochemical Cycles*, 28, 950–961. <https://doi.org/10.1002/2014GB004872>
- Serrano, O., Ricart, A. M., Lavery, P. S., Mateo, M. A., Arias-Ortiz, A., Masque, P., et al. (2016). Key biogeochemical factors affecting soil carbon storage in *Posidonia* meadows. *Biogeosciences*, 13(15), 4581–4594. <https://doi.org/10.5194/bg-13-4581-2016>
- Short, F. T., Hessing-Lewis, M., Prentice, C., Sanders-Smith, R., Gaeckle, J., & Helms, A. (2017). *Seagrass Sediment Sampling Protocol and Field Study: British Columbia, Washington and Oregon*. 12 Pp. Montreal, Canada: Commission for Environmental Cooperation. Available from: <http://www.cec.org/islandora/en/item/11726-seagrass-sediment-samplingprotocol-and-field-study-british-columbia-washington-en.pdf>
- Short, F. T., Polidoro, B., Livingstone, S. R., Carpenter, K. E., Bandeira, S., Bujang, J. S., et al. (2011). Extinction risk assessment of the world's seagrass species. *Biological Conservation*, 144(7), 1961–1971. <https://doi.org/10.1016/j.biocon.2011.04.010>
- Spooner, A. (2015). *Blue Carbon Sequestration Potential in Zostera marina Eelgrass Beds of the K'ómoks Estuary, British Columbia*. MSc Thesis: Royal Road University.
- Stephens, T., & Eckert, G. (2018). Sediment organic and inorganic matter within intertidal eelgrass beds in Southeast Alaska. *Knowledge Network for Biocomplexity*. <https://doi.org/10.5063/F1ZS2TTH>
- Sutton-Grier, A. E., & Moore, A. (2016). Leveraging carbon services of coastal ecosystems for habitat protection and restoration. *Coastal Management*, 44(3), 259–277. <https://doi.org/10.1080/08920753.2016.1160206>
- Thomson, A. C. G. (2017). The role of bioturbators in seagrass blue carbon dynamics. PhD Thesis, University of Technology Sydney.
- Trevathan-Tackett, S. M., Macreadie, P. I., Sanderman, J., Baldock, J., Howes, J. M., & Ralph, P. J. (2017). A global assessment of the chemical recalcitrance of seagrass tissues: Implications for long-term carbon sequestration. *Frontiers in Plant Science*, 8, 925. <https://doi.org/10.3389/fpls.2017.00925>
- Trevathan-Tackett, S. M., Seymour, J. R., Nielsen, D. A., Macreadie, P. I., Jeffries, T. C., Sanderman, J., et al. (2017). Sediment anoxia limits microbial-driven seagrass carbon remineralization under warming conditions. *FEMS Microbiology Ecology*, 93(6), 1–15. <https://doi.org/10.1093/femsec/fix033>
- Trevathan-Tackett, S. M., Thomson, A. C. G., Ralph, P. J., & Macreadie, P. I. (2018). Fresh carbon inputs to seagrass sediments induce variable microbial priming responses. *Science of the Total Environment*, 621, 663–669. <https://doi.org/10.1016/j.scitotenv.2017.11.193>
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., et al. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106(30), 12377–12381. <https://doi.org/10.1073/pnas.0905620106>

References From the Supporting Information

- Dethier, M. N., Sosik, E., Galloway, A. W. E., Duggins, D. O., & Simenstad, C. A. (2013). Addressing assumptions: Variation in stable isotopes and fatty acids of marine macrophytes can confound conclusions of food web studies. *Marine Ecology Progress Series*, 478, 1–14. <https://doi.org/10.3354/meps10310>
- Howe, E. R. (2012). *Detrital Shadows: Evaluating Landscape and Species Effects on Detritus-Based Food Web Connectivity in Pacific Northwest Estuaries*. PhD Dissertation: University of Washington.
- Olson, A. (2017). Seagrass meadows as seascape nurseries for rockfish (*Sebastes* spp.) MSc thesis. University of Victoria.