

# Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows

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## Abstract

Organic carbon (OC) storage in coastal vegetated ecosystems is increasingly being considered in carbon financing and climate change mitigation strategies. However, spatial heterogeneity in these “blue carbon” stocks among and within habitats has only recently been examined, despite its considerable implications. Seagrass meadows have potential to store significant amounts of carbon in their sediments, yet studies comparing sediment OC content at regional and meadow scales remain sparse. Here, we collected sediment cores from six temperate eelgrass (*Zostera marina*) meadows on the coast of British Columbia, Canada, to quantify sediment OC stocks, accumulation rates, and sources, and to examine local and regional drivers of variability. Sediment OC content was highly variable—across all sites, stocks in the top 0–5 cm ranged from 83 to 1089 g OC m<sup>-2</sup>, while the 15–20 cm stocks exhibited a 24-fold difference, from 59 to 1407 g OC m<sup>-2</sup>. Carbon accumulation rates ranged from 4 to 33 g OC m<sup>-2</sup> yr<sup>-1</sup>. Isotopic mixing models revealed that sediment OC was primarily terrestrial carbon (41.3%) and canopy-forming kelps (33.3%), with a smaller contribution of eelgrass (25.3%). Here, we show that regional variability in OC content exceeds meadow-scale variability. This result is likely driven by landscape factors, most notably relative water motion, representing a more dominant control on seagrass OC accumulation than meadow-scale factors such as canopy complexity. These findings elicit caution when scaling up seagrass meadow OC content and demonstrate that measures of the hydrodynamic environment could improve estimates of carbon storage in temperate soft sediment habitats.

Among a suite of important ecosystem services, vegetated habitats worldwide have the capacity to store atmospheric carbon dioxide (CO<sub>2</sub>) in their tissues and in the soils beneath them, thereby acting as potential agents in climate change mitigation (Barbier et al. 2011; Pan et al. 2011; Griscom et al. 2017). Mangroves, salt marshes, and seagrass meadows—termed “blue carbon” ecosystems—have recently gained global attention, as they exhibit high rates of carbon accumulation and can store organic carbon (OC) long term in their sediments (Laffoley and Grimsditch 2009; Nellemann et al. 2009; Lovelock and Duarte 2019). These same coastal ecosystems, however, are in accelerating decline worldwide, with anthropogenic conversion rates ranging from 0.4% to 3% annually (Waycott et al. 2009; Howard et al. 2017c). The degradation and loss of blue carbon habitats not only limits capacity for ongoing carbon sequestration and storage, but can also rerelease carbon that has accumulated over decades, centuries, or millennia (Mateo et al. 1997; Pendleton et al. 2012; Lovelock et al. 2017). Thus, there is a policy push to include

mangroves, tidal marshes, and seagrass meadows in national greenhouse gas inventories and carbon financing projects (IPCC 2014; Hejnowicz et al. 2015; Sutton-Grier and Moore 2016; Needelman et al. 2018). Yet, many regions and habitats, including the Pacific coast of North America, have only recently been explored for their blue carbon potential. The scarcity of data on the spatial heterogeneity in carbon stocks and accumulation rates creates challenges for scaling up carbon estimates and incorporating blue carbon into such climate policies (Lavery et al. 2013; Oreska et al. 2017; Mazarrasa et al. 2018). Furthermore, the mechanisms that regulate spatial variability across different scales are only beginning to be understood (Samper-Villarreal et al. 2016; Kindeberg et al. 2018; Mazarrasa et al. 2018; Santos et al. 2019).

Seagrasses are widely distributed marine flowering plants that form meadows along temperate and tropical coastlines (Short et al. 2007). In addition to supporting high biodiversity, buffering wave action, and stabilizing sediments, seagrass meadows have potential for globally significant rates of carbon storage, with most recent estimates ranging from 41.4 to 82.8 Tg of carbon sequestered annually (Barbier et al. 2011; Mtwana Nordlund et al. 2016; Howard et al. 2017c). Seagrasses often exhibit high rates of primary productivity, and this biomass can become incorporated into the

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sediment carbon pool. Seagrass canopies also facilitate particle capture and settlement from the water column, which can further enhance carbon stocks and accretion rates (Hendriks et al. 2008; Duarte et al. 2013; Macreadie et al. 2014). Thus, the OC found in seagrass meadow sediments can be autochthonous—produced within a given meadow—or allochthonous—produced outside the meadow (Kennedy et al. 2010; Miyajima et al. 2015; Oreska et al. 2018). The OC buried in seagrass sediments is generally subject to low rates of remineralization, as the sediments tend to be low in oxygen below the first few millimeters, resulting in reduced microbial decomposition (Fourqurean et al. 2012; Duarte et al. 2013; Greiner et al. 2016). Although these characteristics—high primary productivity, ability to capture particles and low oxygen sediments—yield high potential for significant carbon storage, the specific biological, chemical, and physical environments are inevitably variable among seagrass meadows, regions, and species. Understanding regional and local-scale factors controlling the magnitude of blue carbon stocks and accumulation rates could improve estimates of blue carbon potential and assist with effective local management of seagrass ecosystems (Lavery et al. 2013; Mtwana Nordlund et al. 2016; Gullström et al. 2017).

Previous studies have highlighted variability in OC stocks and accumulation rates at both the local level, within meadows, and at regional scales, among meadows (Lavery et al. 2013; Ricart et al. 2015; Oreska et al. 2017; Green et al. 2018). Such heterogeneity has been attributed to a wide array of habitat characteristics, including species composition, hydrodynamic regimes, and seagrass and sediment characteristics (Rozaimi et al. 2013; Serrano et al. 2014, 2016; Samper-Villarreal et al. 2016; Kindeberg et al. 2018; Mazarrasa et al. 2018; Santos et al. 2019). At the regional or seascape scale, enhanced carbon stocks are typically associated with higher seagrass structural complexity (Jankowska et al. 2016; Samper-Villarreal et al. 2016; Mazarrasa et al. 2018), higher proportions of fine sediments (Dahl et al. 2016; Röhr et al. 2016; Gullström et al. 2017; Miyajima et al. 2017), and sheltered sites with reduced wave height and exposure (Samper-Villarreal et al. 2016; Mazarrasa et al. 2017a). However, many of these same factors, such as seagrass density and sediment grain size, also vary at the meadow scale. For example, higher OC stocks have been found in meadow interiors relative to edges, likely due to increased turbulence, and thus more resuspension and less deposition along meadow edges (Ricart et al. 2015; Oreska et al. 2017). Furthermore, relationships between environmental factors and carbon storage may not hold true in all seagrass systems, and the mechanisms that regulate spatial variability in carbon stocks and accumulation rates require continued investigation (Mazarrasa et al. 2018; Santos et al. 2019).

Here, we quantified variability in OC stocks, accumulation rates, and OC sources in temperate eelgrass (*Zostera marina*) meadows on the northwest coast of North America, a relatively unexplored area for seagrass carbon storage potential (CEC 2013). We examined these parameters at both the local level of individual meadows and across a larger regional

landscape—two spatial scales that have not received much attention to date yet are important for carbon accounting and management. Furthermore, we investigated local and regional drivers of variability in OC stocks. We hypothesized that OC stocks and accumulation rates would vary regionally among the six meadows sampled due to known gradients in biophysical characteristics. Building off of previous work, we expected that at the meadow scale, interior OC stocks would be enhanced relative to those along meadow edges and in adjacent bare sediment (Ricart et al. 2015; Oreska et al. 2017). At the regional scale, we predicted higher OC stocks would be found in areas with reduced water motion, higher proportions of fine sediments, and more complex seagrass canopies. Finally, we review our local and regional results in the context of emerging global seagrass blue carbon trends to illustrate variability across different spatial scales.

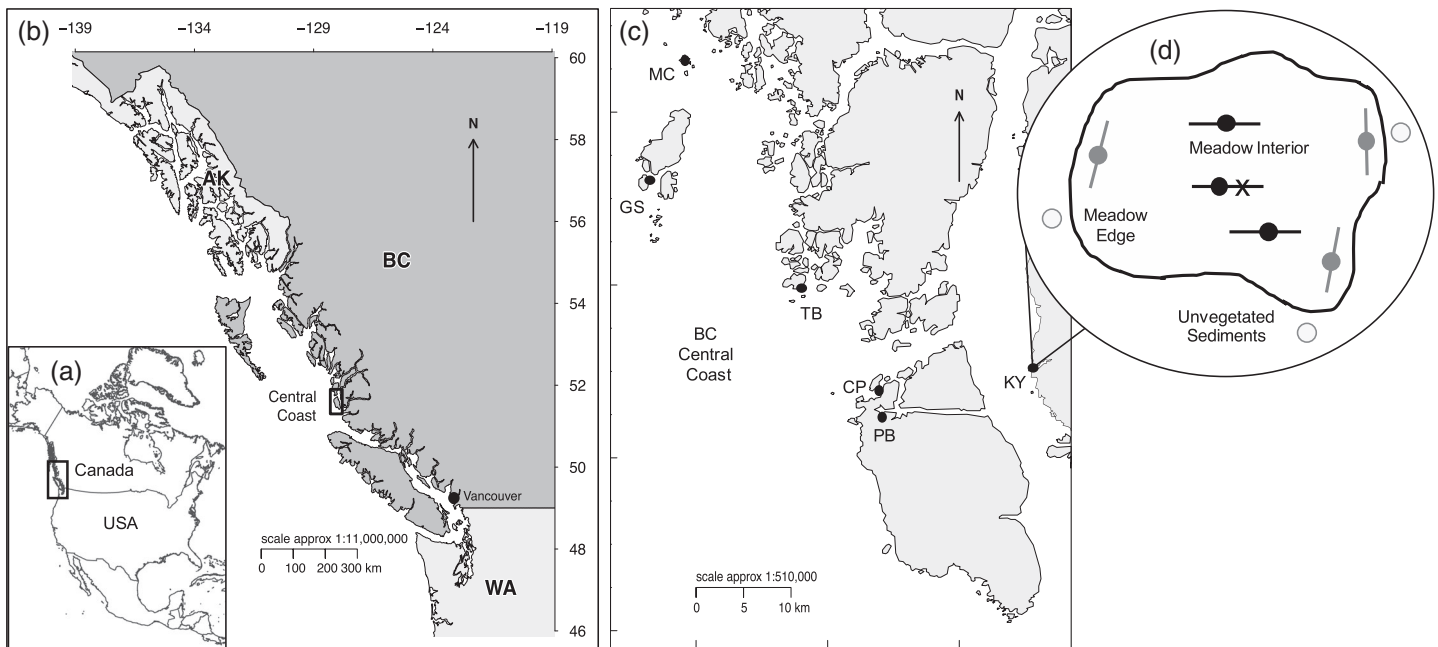
## Methods

### Study area

Sediment cores were collected from six eelgrass (*Z. marina*) meadows on the Central Coast of British Columbia (BC), Canada (Fig. 1). BC's Central Coast is a geographically complex coastline, with a suite of nearshore habitats, including eelgrass meadows of varying sizes and attributes (Table 1) (Hessing-Lewis et al. 2017). With low human population density and sparse land-based development, this area provides an opportune setting for obtaining regional estimates of eelgrass carbon storage with a focus on ecological and biophysical drivers rather than human disturbance. The six meadows sampled—Pruth Bay (PB), Choked Pass (CP), Triquet Bay (TB), McMullins North (MC), Goose Southwest (GS), and Koeys Estuary (KY)—represent the wide spectrum of environments within which *Z. marina* can grow, from sheltered, intertidal (−0.03 m deep), soft sediment estuarine systems such as Pruth Bay, to exposed, subtidal (3.34 m deep) outer coast meadows with sand or shell-hash dominated sediments such as Choked Pass (Table 1).

### Sample collection

To examine among and within-meadow variability in sediment OC content, we collected nine sediment cores (~30 cm depth, 7 cm diameter) from each meadow. Three cores were taken from three different “positions” within each meadow: (1) in the meadow interior, (2) along the vegetated meadow edge, and (3) in adjacent bare (currently unvegetated) sediments (Fig. 1). Adjacent unvegetated cores were taken approximately 5 m beyond the current edge of the meadow; this distance was standardized across meadows, as generally beyond 5 m the benthic habitat transitioned into bedrock or kelp habitat (dominant canopy species included *Macrocystis pyrifera* or *Nereocystis luetkeana*). The interior and edge cores were associated with pre-established transects for seagrass research and monitoring conducted by the Hakai Institute and



**Fig. 1.** Map showing the study area, along the northwest coast of North America (a), in British Columbia (BC), Canada (b). The sediment core sampling scheme within each of six eelgrass meadows on BC's Central Coast (c) is shown in panel (d). The circles represent short (~30 cm) cores obtained from the meadow interior (dark gray,  $n = 3$ ), meadow edge (medium gray,  $n = 3$ ), and adjacent unvegetated sediments (light gray,  $n = 3$ ). The 'X' represents the one long core (~60–80 cm), taken from the middle interior transect in each meadow. Interior and edge cores (not unvegetated) were associated with seagrass research transects (lines). Site names in panel (c) are as follows: MC, McMullins North; GS, Goose Southwest; TB, Triquet Bay; CP, Choked Pass; PB, Pruth Bay; and KY, Koeye Estuary.

contributing to the MarineGEO network. We also obtained one long core (60–80 cm in length, 10.2 cm diameter) from each meadow at one interior transect for geochronological analyses (Fig. 1).

All cores were collected manually by SCUBA divers during high tides by pounding PVC (long cores) or polycarbonate tubing (short cores) into the sediments using a sledgehammer. This method can cause compaction as sediments shift during the coring process, thus divers measured compaction once the core was fully inserted, or in some cases up to five times

during core insertion. Compaction was calculated as the distance (in centimeters) from the top of the core to the sediment surface outside of the core, minus the distance (cm) from top of core to the sediment surface inside the core, divided by the sample depth (cm of compaction/cm core depth). Average compaction values were  $17.5\% \pm 1.8\%$  (standard error [SE]). Due to time constraints associated with remote sites and SCUBA diving, we could not measure compaction at every centimeter within each core and thus could not apply a linear length correction (e.g., Morton and White

**Table 1.** Meadow area, average ( $\pm$  SE) depth relative to chart datum, seagrass shoot density, canopy height, and a qualitative description of relative exposure and freshwater for each of the six *Z. marina* meadows sampled.

Meadow	Meadow area (m <sup>2</sup> )	Chart datum depth (m)	Seagrass density (shoots m <sup>-2</sup> )	Canopy height (cm)	Relative exposure	Relative freshwater input
McMullins North	22,778	0.6 $\pm$ 0.4	102 $\pm$ 9	83 $\pm$ 4	Protected embayment	Low
Triquet Bay	31,074	0.8 $\pm$ 0.4	124 $\pm$ 13	98 $\pm$ 5	Protected embayment	Medium
Pruth Bay	34,982	-0.03 $\pm$ 0.4	216 $\pm$ 27	81 $\pm$ 28	Protected embayment	Medium
Choked Pass	354,580	3.3 $\pm$ 0.6	80 $\pm$ 7	111 $\pm$ 3	Exposed channel	Low
Koeye Estuary	26,238	0.2 $\pm$ 0.1	126 $\pm$ 16	164 $\pm$ 7	Protected narrow channel	High
Goose Southwest	215,570	2.5 $\pm$ 0.5	108 $\pm$ 9	84 $\pm$ 4	Semi-protected embayment	Low

Meadow areas were obtained by analysis of remotely piloted aerial system imagery, while depth, shoot densities, and canopy heights were measured by SCUBA divers as part of routine meadow monitoring.

1997), though we acknowledge compaction as a potential source of error in our measurements. The mass accumulation rates we employed minimize the error associated with depth compaction.

Within 24 h of collection, cores were subsectioned using an extruding device, which consisted of a 1.5 m long metal pole with a custom-sized Teflon piston attached. Each core was pressed gently downward on the piston such that the sediments were pushed out the top of the core and could be sliced with a thin piece of plastic. For the short cores, we sampled in 5 cm increments down the length of the cores (sometimes the bottom section was < 5 cm). Sampling intervals for the long cores varied with depth: we took a 6 cm section from the top surface layer, 2 cm sections from 6 to 20 cm deep, and 5 cm from 20 cm down to the bottom of the core. These sampling intervals were selected to discern variability in carbon content at a regional scale, as opposed to variation within a given core. Furthermore, the long core sampling increments were kept consistent with previous sediment cores taken from Pruth Bay in May 2016 (Short et al. 2017). Once extruded, each subsection was homogenized before taking a 30 cm<sup>3</sup> subsample for measurements of dry bulk density, carbon content, stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), and geochronological analyses. All samples were stored at  $-20^\circ\text{C}$ .

### Chemical analyses

The 30 cm<sup>3</sup> subsamples for each core interval were freeze-dried and sediment dry bulk densities were estimated by dividing sediment dry weight (g) by wet sediment volume (30 cm<sup>3</sup>) (Howard et al. 2014). Each sample was then ground into a fine powder using a Herzog HSM 100 grinding mill. Any nonliving material (e.g., shell pieces, wood, rocks) was left in the sample, while all visible living biomass (e.g., shoots, roots or rhizomes, macroalgae) was removed. Total percent carbon (%TC) and nitrogen (%TN) were determined using an Elementar Vario Micro Cube elemental analyzer (Froelich 1980; Verardo et al. 1990). A UIC Carbon Dioxide Coulometer was used to determine the percent inorganic carbon (%IC). Both elemental and coulometric analyses were conducted in the Department of Earth, Ocean and Atmospheric Sciences at the University of British Columbia, Vancouver, BC, Canada. Percent organic carbon (%OC) was calculated by subtracting %IC from %TC for each sample (Howard et al. 2014; Hodgson and Spooner 2016). OC density (g OC cm<sup>-3</sup>) for each subsection was calculated by multiplying the OC fraction (%OC/100) by the dry bulk density (g cm<sup>-3</sup>). OC mass (g OC m<sup>-2</sup>) was calculated by multiplying the OC density (g OC cm<sup>-3</sup>) by the depth of the subsection (cm). OC stocks were calculated by summing the carbon mass (g OC m<sup>-2</sup>) in each subsection to a particular depth as outlined by Howard et al. (2014). While some cores were as deep as 30 cm, OC stock depth intervals were standardized, and calculated for the top 0–5 cm as well as the bottom 15–20 cm—this allowed all cores except for one (from

Goose SW unvegetated) to be included in our comparative analyses.

### Stable isotope analyses

From the 30 cm<sup>3</sup> sediment subsamples, we also analyzed carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope values using an isoprime isotope ratio mass spectrometer at the Stable Isotope Facility in the Department of Forest and Conservation Sciences (for  $\delta^{13}\text{C}$ ) and the Department of Earth, Ocean and Atmospheric Sciences (for  $\delta^{15}\text{N}$ ) at the University of British Columbia. Isotopic ratios are expressed relative to Vienna Pee Dee Belemnite for carbon, and atmospheric air for nitrogen in per mil notation (‰). Samples were acidified using sulfurous acid (H<sub>2</sub>SO<sub>3</sub>) to remove inorganic carbon (IC) prior to mass spectrometry. We found high IC content within our samples (an average of  $1.6\% \pm 0.1\%$  [SE] and maximum value of 7.9% for isotope samples), and mechanical removal of calcified structures was unfeasible due to their small size (Schlacher and Connolly 2014). However, chemical manipulation of sediments via acidification, has the potential to cause analytical errors in samples with low organic matter. Therefore, we conducted  $\delta^{15}\text{N}$  analyses on nonacidified samples to avoid potential alteration of nitrogen signatures from the acidification step (Schlacher and Connolly 2014).

Carbon isotope ( $\delta^{13}\text{C}$ ) signatures of potential OC sources were compiled from previous studies conducted on the BC Central Coast (Supporting Information Table S1). To determine the relative percent contributions of these sources to eelgrass meadow and adjacent unvegetated sediments, we ran a one-isotope ( $\delta^{13}\text{C}$ ), three-source Bayesian mixing model using the MixSIAR package in R (Stock and Semmens 2016; R Core Team 2017). The three OC sources used in the mixing model—*Z. marina*, terrestrial vegetation, and canopy forming kelps (*Nereocystis luetkeana* and *M. pyrifera*) had distinct, non-overlapping  $\delta^{13}\text{C}$  isotope signatures. We included “site” (i.e., meadow) and “cover” (vegetated or unvegetated) as random effects in the mixing model. We used an uninformative prior and a discrimination factor of 0, as the  $\delta^{13}\text{C}$  signature of organic matter has been shown to change very little during decomposition, relative to the variability of  $\delta^{13}\text{C}$  among sources (Macko et al. 1994; Greiner et al. 2016; Miyajima et al. 2017). We chose to exclude our  $\delta^{15}\text{N}$  data, as we had a limited number of sediment samples with both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $n = 11$ ) and  $\delta^{15}\text{N}$  values have been shown to decrease once in the sediments due to bacterial reworking and thus may be less suited to tracing sources of organic matter into the sediments (Miyajima et al. 2017).

### Geochronological analyses

The <sup>210</sup>Pb dating method is commonly used to measure the rate of OC accumulation in vegetated coastal ecosystems (Arias-Ortiz et al. 2018). For our samples, <sup>210</sup>Pb analysis of sediment samples was conducted by MyCore Scientific in Dunrobin, Ontario, Canada. An alpha spectrometer measured

$^{210}\text{Po}$ , the granddaughter radionuclide of  $^{210}\text{Pb}$ , assuming radioactive equilibrium between the two. The activity of  $^{210}\text{Po}$  was determined from the count ratio of  $^{209}\text{Po}$  to  $^{210}\text{Po}$  and the known amounts of  $^{209}\text{Po}$  in each sample. Excess  $^{210}\text{Pb}$  was determined by subtracting background  $^{210}\text{Pb}$  from total  $^{210}\text{Pb}$  activity at each depth interval. Profiles of excess  $^{210}\text{Pb}$  were created for the depth of each long core, and ages and sedimentation rates were estimated using the constant rate of supply (CRS) model, which allows variable sedimentation rates with depth, but assumes a constant flux of atmospheric  $^{210}\text{Pb}$  to the sediments (Appleby and Oldfield 1978; Drevnick et al. 2016; Carey et al. 2017). Sediment mass accumulation rates ( $\text{g cm}^{-2} \text{yr}^{-1}$ ) were estimated at various depth intervals (as deep as 35 cm), based on the sediment dry bulk densities. OC accumulation rates ( $\text{g OC m}^{-2} \text{yr}^{-1}$ ) were calculated by multiplying the OC fractions for each subsection by the corresponding sediment mass accumulation rates. The OC mass accumulation rates from different depths were then averaged to determine an overall rate ( $\pm \text{SE}$ ) for each core. If the CRS model was not an optimal linear regression fit, we additionally estimated ages and sediment accumulation rates using the constant flux:constant sedimentation (CF:CS) model, which assumes a constant sediment accumulation rate and a constant flux of atmospheric  $^{210}\text{Pb}$  to the sediments and is often a better option for sediments with high rates of bioturbation and resuspension (Bonotto and García-Tenorio 2014).

### Characterization of the biophysical environment

We characterized biophysical attributes in each meadow along pre-established, permanent subtidal transects (30 m long), the same interior and edge transects from which sediment cores were collected (Fig. 1). Relative water motion was characterized using the dissolution rates of Plaster of Paris chalk blocks, which integrates the effects of both tidal currents and waves (Potouroglou et al. 2017). We attached preweighed ( $\sim 130 \text{ g}$ ) plaster blocks to PVC stakes, which were inserted into the sediments such that the blocks were approximately mid-canopy. Blocks were weighed before and after deployment after drying at  $60^\circ\text{C}$ , and the weight loss was standardized to time left in the field (mass before [g] – mass after [g]/time in field [hours]). Blocks were left in the field for an average of 2.7 d (ranging from 1 to 9 d) and thus blocks at all sites experienced several tidal cycles. Canopy height (m) was obtained on a transect-level by averaging measurements taken from seven quadrats ( $0.25 \text{ m}^2$ ) located every 5 m along the 30 m long transects. Similarly, shoot density (scaled up to shoots  $\text{m}^2$ ) was obtained by averaging densities from the seven quadrats along each transect. We calculated a metric of “seagrass complexity,” by multiplying seagrass canopy height by shoot density, to give a measure of the vertical meters of seagrass per unit area ( $\text{m seagrass m}^{-2} \text{ sediment}$ ).

Sediment grain size analyses were conducted on the 0–5 cm and 15–20 cm depth sections of all cores, and two additional deeper sections from long cores, when applicable,

using an electronic sieve shaker and a 10-min shaking interval. The amount of sediment remaining in 4 mm, 2 mm, 1 mm, 500  $\mu\text{m}$ , 250  $\mu\text{m}$ , 125  $\mu\text{m}$  and 63  $\mu\text{m}$  and < 63  $\mu\text{m}$  size classes were determined to the nearest 0.01 g. Based on the weight of each size fraction and the total sample weight, the percentage of particles in each size class was calculated. The < 63  $\mu\text{m}$  category is herein referred to as the fine sediment content (%fine sediments).

### Statistical analyses

We used an information theoretic approach to examine the strength of evidence for the effects of core position (interior, edge, or unvegetated) and meadow (site) on surface (0–5 cm) and deeper (15–20 cm) OC stocks (Burnham and Anderson 2002). Due to the crossed nature of the data (three cores for every combination of meadow and position) and a non-normal error distribution, we fit generalized linear models of OC content with a Gamma distribution and log link function using the `glm` function in the `lme4` package in R (Bates et al. 2015; R Core Team 2017). To test for an effect of core position and meadow location, we compared the relative strength of evidence for (1) position alone, (2) meadow alone, and (3) an interaction between meadow and position, in explaining the variation in OC stocks from 0–5 cm and 15–20 cm. We treated both position and meadow as fixed effects and allowed both slopes and intercepts to vary in all models.

The relative support for four candidate models (position only, meadow only, meadow\*position, and a null model) was evaluated using Akaike’s information criterion corrected for small sample size ( $\text{AIC}_c$ ; Burnham and Anderson 2002) in the `MuMIN` package in R (Bartoń 2018).  $\text{AIC}_c$  values were calculated based on the number of parameters ( $K$ ) and Log Likelihoods ( $\text{Log } L$ ) of each model. The most parsimonious models were determined based on  $\Delta\text{AIC}_c$ , or the difference between the  $\text{AIC}$  score of the top model and each subsequent model. Akaike weights ( $W_i$ ) were calculated as the relative likelihood of each model ( $e^{-0.5 \times \Delta\text{AIC}_c}$ ) divided by the sum of the relative likelihoods across all models. Adjusted  $R$ -squared values ( $\text{adj}R^2$ ) were calculated based on the sample size ( $n$ ) and the number of model parameters ( $K$ ).

We further examined the strength of evidence for the relative effects of biophysical characteristics on both 0–5 cm and 15–20 cm OC stocks. We narrowed down our suite of explanatory biophysical factors to three, based on previous literature and our a priori ecological understanding of the system (Burnham and Anderson 2002). The three factors selected were water motion, seagrass complexity, and %fine sediments; these factors represent major physical, seagrass and sediment characteristics at each meadow and have been shown to be important in other seagrass systems (Dahl et al. 2016; Samper-Villarreal et al. 2016; Mazarrasa et al. 2018). Due to the hierarchical nature of the data (cores nested within meadows) and a non-normal error distribution, we fit generalized linear mixed-effects models with a Gamma distribution and log link

function using the glmer function in the lme4 package in R (Bates et al. 2015). Water motion, seagrass complexity, and % fine sediments were included as continuous fixed effects, while meadow and position were included as random effects in all models.

We checked for collinearity among model factors using Pearson correlation coefficients and variance inflation factors (VIF). Correlation coefficients  $> 0.6$  and VIF scores  $> 3.5$  indicate variables with a high degree of collinearity that may be problematic if included in the same model (Zuur et al. 2009). Correlation coefficients in this analysis ranged from 0.2 to 0.5 (Supporting Information Fig. S1), and all VIF scores ranged from 1.1 to 1.3, thus variables were not collinear. To facilitate direct comparison of parameter coefficients among continuous variables on different scales, we standardized all continuous variables by subtracting their mean and dividing by two times the standard deviation (Gelman 2008).

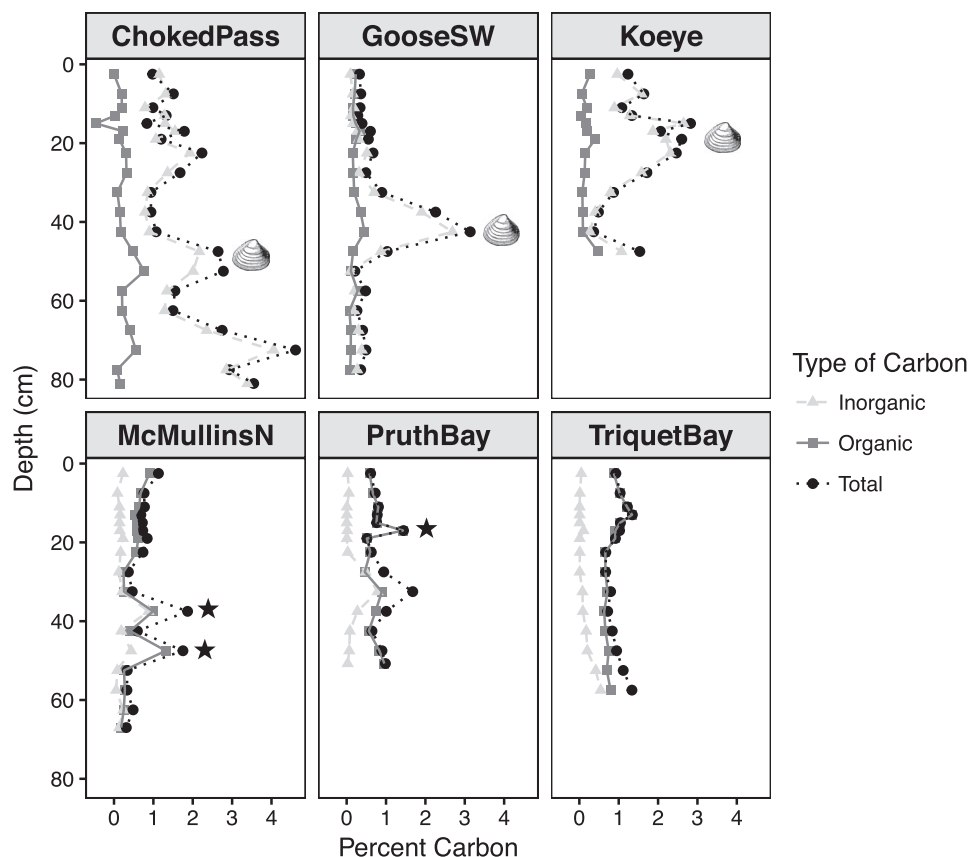
We evaluated relative support for models with all possible combinations of fixed factors using  $AIC_c$ . All combinations of factors in the model were biologically realistic, and thus we included all subsets of the global model, for a total of eight candidate models. As with our first model set, the most parsimonious model or models explaining variation in 0–5 cm and

15–20 cm OC stocks were determined based on  $\Delta AIC_c$ . Where  $\Delta AIC_c$  values between the top two candidate models were  $< 2$ , we used model averaging of these top candidate models to calculate the relative variable importance (RVI) for each variable. We also calculated RVI values, or the sum of Akaike weights across all models in which a specific variable appears, to estimate the relative importance of each individual variable.

## Results

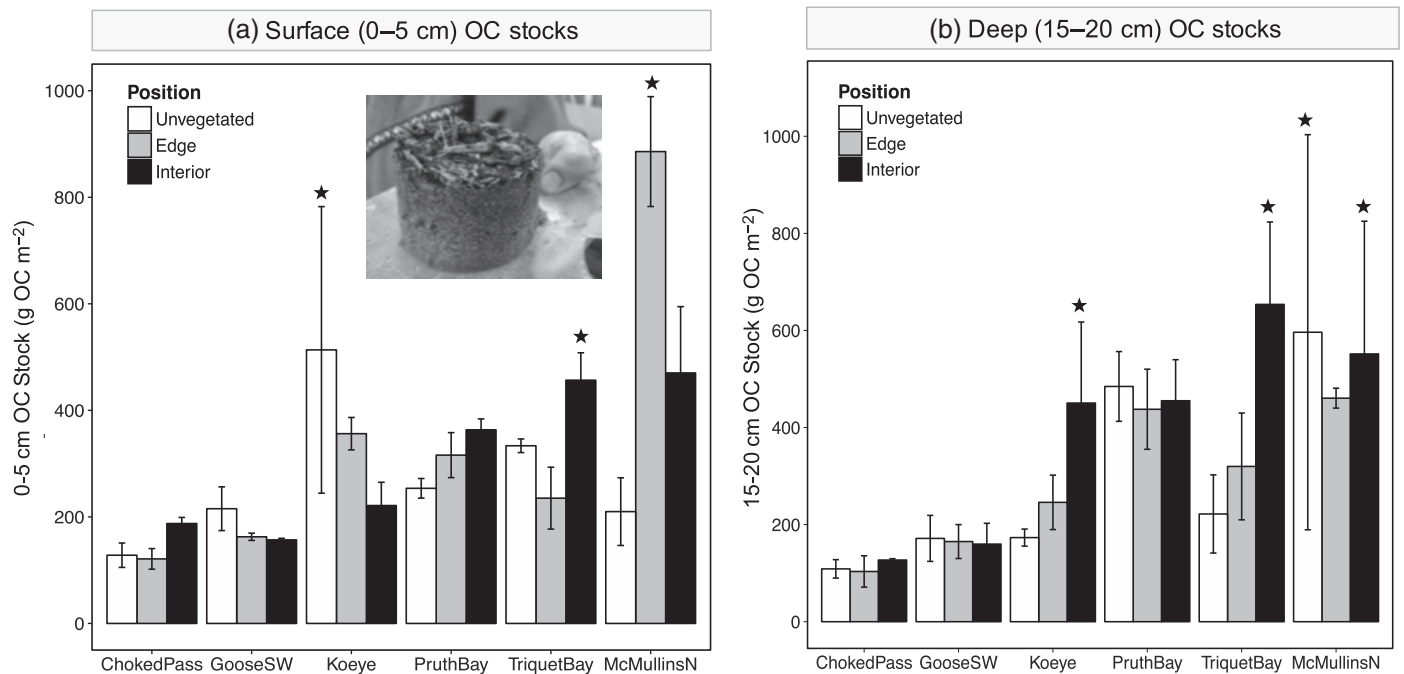
### Sediment carbon content

Combining all subsections from both long and short cores across the six meadows sampled ( $n = 399$  sections), the average percentage organic carbon (%OC) was  $0.45\% \pm 0.02\%$  (SE) and ranged from 0% to 2.98%. Relatively high OC content ( $> 2\%$ ) was associated with deposits of woody debris, accounted for qualitatively during laboratory processing and indicated with stars in Figs. 2–3. The average %inorganic carbon (%IC) was  $1.6\% \pm 0.1\%$  (SE) and ranged from 0% to 7.95%. High carbonate values were associated with bivalve shells within the sediments, also documented qualitatively and indicated with shell icons in Fig. 2. In some meadows, most of the total carbon was organic (e.g., Pruth Bay, Triquet



**Fig. 2.** Profiles for the six long sediment cores ( $n = 1$  per site, **a–f**), showing changes in percent total carbon (black circles, dotted lines), inorganic carbon (light gray triangles, dashed lines), and organic carbon (medium gray squares, solid lines) with depth. Stars indicate trends associated with OC (woody debris), while shells indicate those associated with IC.





**Fig. 3.** Sediment OC stocks ( $\text{g OC m}^{-2}$ ) in (a) the surface (0–5 cm) sediments and (b) deeper (15–20 cm) sediments. Trends are shown for each meadow (along the x-axis) and for the three positions within each meadow indicated with shading. Interior cores are indicated with dark gray, edge cores with light gray, and adjacent unvegetated cores with white. Bars represent average OC stocks ( $\pm$  SEs) for each site and position. Stars indicate areas where high woody debris content was observed in the sediments. The photo in panel (a) shows an example of a deposit of woody debris found within the sediments.

Bay); while in others, it was mostly inorganic (e.g., Choked Pass, Goose SW) (Fig. 2). Further, carbon content exhibited some variability with depth, though trends did not exhibit patterns, but rather irregularities that were largely driven by spikes in either woody debris or carbonate material (Fig. 2). The sediment OC:IC ratios were also highly variable among meadows, with averages ranging from  $0.14 \pm 0.05$  (SE) in Triquet Bay unvegetated cores to  $51.17 \pm 13.24$  (SE) in Pruth Bay vegetated cores. Furthermore, in five of the six meadows, vegetated OC:IC ratios were higher than those in adjacent unvegetated sediments (Supporting Information Table S2).

### OC stocks

OC stocks exhibited substantial variability among meadows on the Central Coast of British Columbia. Among all 54 short cores, surface (0–5 cm) sediment OC stocks varied 13-fold, ranging from  $83 \text{ g OC m}^{-2}$  in Choked Pass to  $1089 \text{ g OC m}^{-2}$  at McMullins North (Fig. 3). There was the greatest support for an interaction between meadow and core position explaining patterns in 0–5 cm OC stocks (section [a] of Table 2). In other words, the effect of core location—whether a core was taken from the meadow interior, edge, or adjacent unvegetated sediments—differed depending on the meadow sampled. Three

**Table 2.** Strength of evidence for alternative candidate models of OC stocks including meadow and sediment core position (interior, edge, or unvegetated) explaining variation in (a) the top 0–5 cm and (b) bottom 15–20 cm of the sediment cores.

Model	K	Log L	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	df	$W_i$	adjR <sup>2</sup>
(a) Response ( $n = 54$ ): 0–5 cm OC stock ( $\text{g OC m}^{-2}$ )							
Meadow*Position	2	−307.08	674.5	0	19	0.795	0.798
Meadow	1	−330.39	677.2	2.71	7	0.205	0.522
Null	1	−350.31	704.9	30.34	2	0	0
Position	1	−349.60	708.0	33.50	4	0	0.026
(b) Response ( $n = 53$ ): 15–20 cm OC stock ( $\text{g OC m}^{-2}$ )							
Meadow	1	−334.55	685.6	0	7	1	0.528
Null	0	−354.44	713.1	27.52	19	0	0
Meadow*Position	2	−326.86	714.7	29.15	2	0	0.647
Position	1	−353.25	715.3	29.75	4	0	0.044

**Table 3.** Organic carbon accumulation rates and sediment ages estimated from  $^{210}\text{Pb}$  geochronological analyses using the constant rate of supply (CRS) and constant flux:constant sedimentation (CF:CS) models.

Meadow	Top 50 cm OC stocks ( $\text{g OC m}^{-2}$ )	CRS OC accumulation rate ( $\text{g OC m}^{-2} \text{yr}^{-1}$ )	CRS age of top 20 cm (yr)	CF:CS OC accumulation rate ( $\text{g OC m}^{-2} \text{yr}^{-1}$ )	CF:CS age of top 20 cm (yr)
Triquet Bay	5073	33.05	71	33.98	68
Pruth Bay	5066	29.42	73	36.74	60
McMullins North	4488	22.28	88	NA	NA
Choked Pass	1207	4.63	75	3.47	102
Koeye Estuary	1220	*Profile indicated high rate of mixing and erosion			
Goose Southwest	1673	*Not enough excess $^{210}\text{Pb}$ in core to be dated			

\* indicates cores from which  $^{210}\text{Pb}$  dating information was available, but accumulation rates were not estimated due to the reasons indicated.

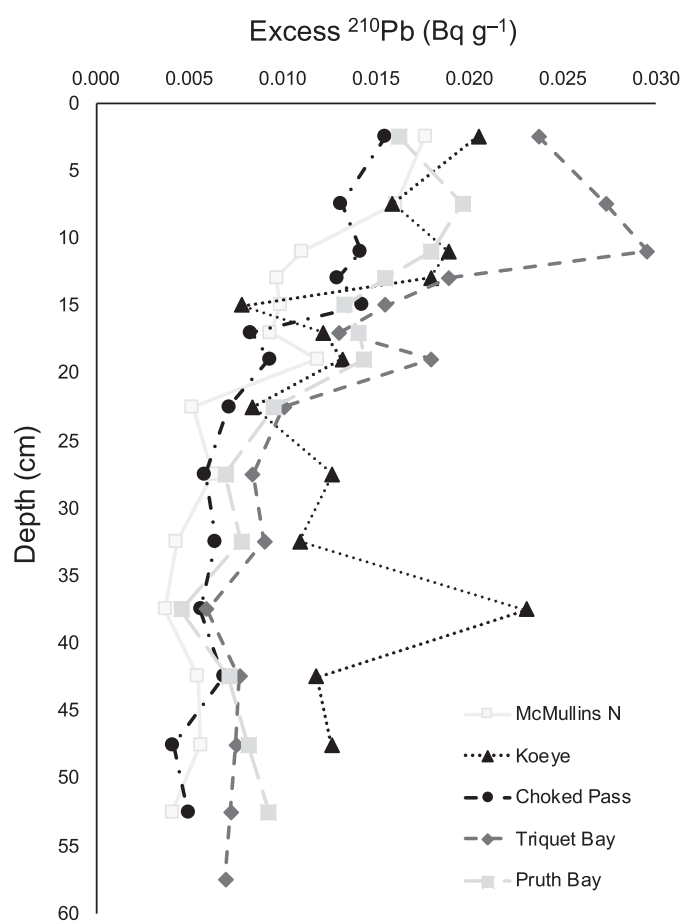
of the six meadows sampled followed hypothesized trends of higher OC stocks in the interior followed by edge and unvegetated cores, while the location patterns from the other three meadows were not consistent (Fig. 3). Similar to surface OC stocks, deeper (15–20 cm) OC stocks varied widely (24-fold) among meadows, ranging from  $59 \text{ g OC m}^{-2}$  in Choked Pass to  $1407 \text{ g OC m}^{-2}$  at McMullins North (Fig. 3). However, for the deeper sediments, meadow alone explained the most variation in 15–20 cm OC stocks, meaning there was greater variation among meadows than among locations within meadows.

### Carbon accumulation rates

There was sufficient excess  $^{210}\text{Pb}$  in the sediments to obtain estimates of sediment ages and accumulation rates at all meadows except Goose SW (Table 3). Furthermore, there were high levels of mixing and erosion in one meadow (Koeye Estuary), impeding estimates of age or sediment accumulation rates (Fig. 4). For the remaining four meadows, OC accumulation rates ranged from  $4.6 \text{ g OC m}^{-2} \text{yr}^{-1} \pm 1.5$  (SE) in Choked Pass to  $33.1 \text{ g OC m}^{-2} \text{yr}^{-1} \pm 4.5$  (SE) in Triquet Bay and averaged  $22.4 \text{ g OC m}^{-2} \text{yr}^{-1}$ . The estimated age of the top 20 cm of sediment ranged from 71 to 88 yr (average = 76.8 yr) using the CRS model (Table 3). CF:CS estimates are included in Table 3 for comparison. Meadows with higher OC accumulation rates also tended to have higher OC stocks in the top 50 cm (Table 3).

### Drivers of OC variability

Seagrass and physical characteristics were highly variable both within and among the meadows sampled (Tables 1, 4). Of the eight candidate models evaluating biophysical characteristics—water motion, seagrass complexity, and %fine sediments—as predictors of surface (0–5 cm) OC content, the top models included both water motion and %fine sediments (%fines). The  $\Delta\text{AIC}_c$  was  $< 2$  between the top two candidate models, suggesting no strong support for one particular model (section [a] of Table 5). However, model averaging across all candidate models revealed that water motion had the highest RVI (0.81) and exhibited a strong inverse relationship with surface OC stocks (Fig. 5). The %fine sediments had a positive effect on surface OC stocks, though this effect was

**Fig. 4.** Changes in excess  $^{210}\text{Pb}$  with increasing sediment depth for the long cores obtained from each of the six sites (see legend). Note the high levels of mixing observed in Koeye (triangles, dotted line), which precluded estimating an OC accumulation rate at this site.

3.3 times weaker, and 2.5 times less important ( $\text{RVI} = 0.32$ ) than water motion. The effect of seagrass complexity on surface OC stocks was the weakest and least important ( $\text{RVI} = 0.19$ ) compared to water motion and %fine sediments (Fig. 5; section [a] of Table 5).

Of the eight candidate models evaluating biophysical characteristics—water motion, seagrass complexity, and %fines—



as predictors of deeper (15–20 cm) sediment OC content, the top models again included water motion and %fines. The  $\Delta AIC_c$  was  $< 2$  between the top two candidate models, suggesting no strong support for one particular model (section [b] of Table 5). Model averaging across all candidate models revealed a strong negative effect of water motion (RVI = 0.75), but also a strong positive effect of %fines (RVI = 0.74) (Fig. 5; section [b] of Table 5). The effect of water motion was only 1.5 times stronger and equally as important as the effect of fine sediments. Again, seagrass complexity had the weakest and least important (RVI = 0.22) influence on OC stocks (Fig. 5; section [b] of Table 5).

**Table 4.** Biophysical characteristics of the six *Z. marina* meadows on the Central Coast of British Columbia, Canada, where sediment cores were collected in August 2016.

Meadow	Canopy complexity (m m <sup>-2</sup> )	Water motion (g lost h <sup>-1</sup> )	% Fine sediments (< 63 $\mu$ m)
McMullins North	99.8	0.7 $\pm$ 0.10	0.4 $\pm$ 0.07
Triquet Bay	112.5	1.5 $\pm$ 0.2	1.0 $\pm$ 0.16
Pruth Bay	141.0	0.6 $\pm$ 0.01	6.0 $\pm$ 0.62
Choked Pass	86.4	2.5 $\pm$ 0.12	0.1 $\pm$ 0.02
Koeye Estuary	186.5	1.0 $\pm$ 0.06	0.7 $\pm$ 0.19
Goose Southwest	95.3	1.0 $\pm$ 0.01	0.2 $\pm$ 0.04

Canopy complexity is a combination of seagrass density and canopy height (Table 1), water motion is the relative mass loss from chalk blocks, and %fine sediments was obtained using a sieve shaker. Values are averages  $\pm$  SEs.

**Table 5.** Strength of evidence for alternative models of OC content including combinations of three biophysical variables: water motion, %fine sediments, and seagrass complexity in explaining variation in (a) top 0–5 cm and (b) bottom 15–20 cm of sediment cores.

Model	K	Log L	AIC <sub>c</sub>	$\Delta AIC_c$	W <sub>i</sub>	adjR <sup>2</sup>
(a) Response (n = 36): 0–5 cm OC stock (g OC m <sup>-2</sup> )						
Water motion	5	–212.144	436.3	0.00	0.455	0.602
Water motion + %fines	6	–211.5	437.9	1.61	0.203	0.616
Water motion + seagrass complexity	6	–212.14	439.2	2.88	0.108	0.602
Null	4	–215.06	439.4	3.13	0.095	0.532
% Fines	5	–214.218	440.4	4.15	0.057	0.554
Water motion + seagrass complexity + %fines	7	–211.5	441.0	4.71	0.043	0.616
Seagrass complexity	5	–215.062	442.1	5.84	0.025	0.532
Seagrass complexity + %fines	6	–214.206	443.3	7.02	0.014	0.554
(b) Response (n = 36): 15–20 cm OC stock (g OC m <sup>-2</sup> )						
Water motion + %fines	6	–226.635	468.2	0.00	0.424	0.555
Water motion	5	–228.987	470	1.81	0.172	0.493
% Fines	5	–229.046	470.1	1.92	0.162	0.491
Water motion + seagrass complexity + %fines	7	–226.448	470.9	2.73	0.108	0.560
Seagrass complexity + %fines	6	–228.748	472.4	4.23	0.051	0.499
Water motion + seagrass complexity	6	–228.802	472.5	4.33	0.049	0.498
Null	4	–232.299	473.9	5.72	0.024	0.390
Seagrass complexity	5	–231.837	475.7	7.51	0.01	0.406

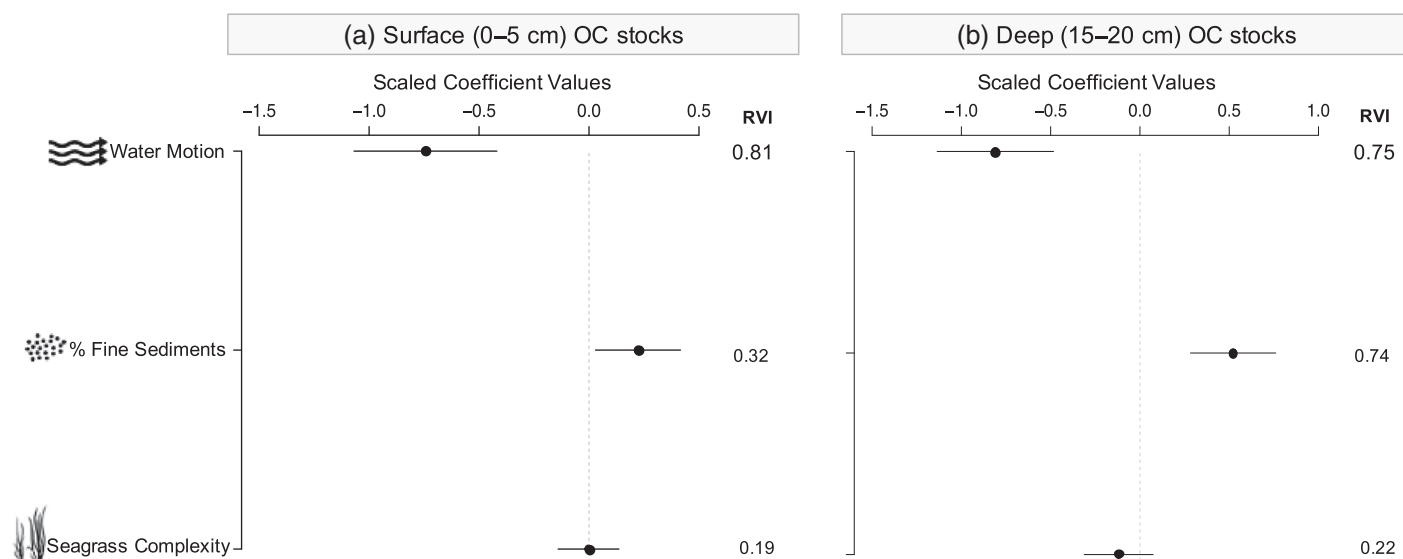
## Sources of OC to the sediments

The overall average isotopic carbon value ( $\delta^{13}C$ ) in eelgrass sediments, including all sediment depths, was  $-20.0\text{‰} \pm 0.4\text{‰}$  (SE). Signatures for the top 0–5 cm were on average of  $19.4\text{‰} \pm 0.4\text{‰}$  (SE) and ranged from  $-17.9\text{‰}$  in Pruth Bay to  $-22.0\text{‰}$  at Koeye.  $\delta^{13}C$  signatures in deeper sediments (15–20 cm) were slightly more depleted, with an average of  $-20.7\text{‰} \pm 0.6\text{‰}$  (SE) and a range from  $-18.1\text{‰}$  in Pruth Bay to  $-23.7\text{‰}$  at McMullins North. Due to very low %nitrogen values in our sediments, we had limited replicates ( $n = 12$  from all meadows,  $n = 1$ –3 per meadow) for  $\delta^{15}N$  values. For all meadows combined, the average  $\delta^{15}N$  value was  $6.8\text{‰} \pm 0.6\text{‰}$  (SE). The three-source, one-tracer ( $\delta^{13}C$ ) mixing model revealed that allochthonous OC sources contributed most to sediment OC, with terrestrial vegetation and canopy forming kelps (*Nereocystis luetkeana* and *M. pyrifera*) contributing 41.3% and 33.3%, respectively. Autochthonous carbon (*Z. marina*) contributed the remaining 25.3% (Fig. 6). All percent contributions are reported as the median values of the posterior distributions.

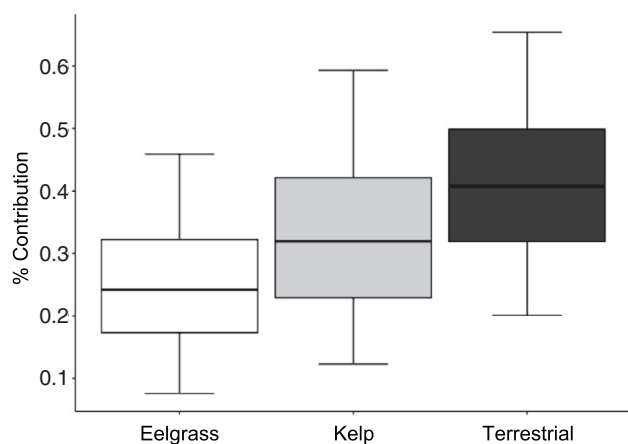
## Discussion

### OC content within and among meadows

Eelgrass sediment carbon content on the Central Coast of British Columbia, Canada, exhibited substantial variability along a stretch of coastline spanning ~ 50 km. As hypothesized, OC stocks exhibited high regional variability, with a 13-fold and a 24-fold difference between the minimum and maximum values for



**Fig. 5.** Scaled coefficient values (dots) and 95% confidence intervals (lines) for the three biophysical factors (water motion, %fine sediments, seagrass complexity) included in the generalized linear mixed effects models. The models examined the strength of evidence for the relative effects of biophysical characteristics on (a) 0–5 cm OC stocks and (b) 15–20 cm OC stocks ( $\text{g OC m}^{-2}$ ). Estimates greater than 0 (dashed line) indicate a positive effect on OC stocks and estimates less than 0 indicate a negative effect. The 95% confidence intervals indicate the precision around the estimate of the effect. The RVI values are the sums of Akaike weights across all models in which a specific variable appears and estimate the relative importance of each variable.



**Fig. 6.** Box plots of the posterior distributions of the percent contributions of each OC source (eelgrass, canopy-forming kelps, and terrestrial vegetation) to the sediments, obtained from Bayesian mixing models. The middle of the box represents the median (50<sup>th</sup> percentile), outer edges represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and whiskers represent the 5<sup>th</sup> and 95<sup>th</sup> percentiles. Carbon isotope values ( $\delta^{13}\text{C}$ ) of the sources used in the mixing model are shown in Supporting Information Table S1.

surface (0–5 cm) and deeper (15–20 cm) OC stocks, respectively. Contrary to the hypothesized decrease in OC content from the meadow interior to the edge and into unvegetated sediments, we did not observe consistently higher OC stocks in vegetated cores relative to unvegetated, but rather only observed this trend in three of six meadows (Fig. 3). This inconsistency may be partially attributed to deposits of woody debris, which caused spikes in OC content regardless of seagrass presence. The similarity of OC

content in vegetated and unvegetated sediments may also be due to the close proximity of the unvegetated cores to the current meadow edges (e.g., 5 m distance). The temporal dynamics and migration of the meadow edge are unknown at these sites due to their remote nature, and it is possible that unvegetated areas beyond the meadow were recently vegetated. Finally, the similarity of OC content in vegetated and unvegetated patches could be because a large proportion of sediment OC came from allochthonous sources, and seagrass canopies could not effectively enhance deposition of this allochthonous carbon relative to unvegetated sediments. If there were a larger contribution from autochthonous (seagrass) sources, perhaps we would have observed a greater difference between vegetated and unvegetated patches.

### Contributing sources to sediment OC stocks

Our isotopic mixing model suggested that most of the sediment OC in Central Coast eelgrass meadows is derived from allochthonous sources, specifically terrestrial organic matter and kelp-derived carbon—*M. pyrifera* and *Nereocystis luetkeana*, as opposed to autochthonous sources (Fig. 6). These findings align with other studies that have found largely allochthonous contributions to seagrass sediment OC stocks, with 50% or more of the carbon originating from non-seagrass sources such as macroalgae, salt marsh vegetation, benthic microalgae, plankton, or terrestrial sources (Kennedy et al. 2010; Miyajima et al. 2015; Greiner et al. 2016; Oreska et al. 2018). While the isotope sources used here are distinct from one another, overlapping source signatures can make it challenging to decipher relative contributions to the sediments. Furthermore, it should be noted that there are overlapping

error bars around the estimates of the percent contributions of the sources examined here (Fig. 6), likely due to limited replication of isotopic measurements (range of  $n = 10\text{--}18$   $\delta^{13}\text{C}$  values per meadow). Future work in the Pacific Northwest and in seagrass meadows more generally should continue to resolve the sources of OC in seagrass meadow sediments. Not only is knowing the relative contributions of different sources important for understanding the long-term persistence of OC stocks (Mazarrasa et al. 2017b) and discerning carbon flow and connectivity in nearshore seascapes (Hyndes et al. 2014), the allochthonous:autochthonous OC ratio is critical for undertaking greenhouse gas benefit accounting in accordance with the Verified Carbon Standard (Needelman et al. 2018). Finally, using environmental DNA has recently been highlighted as a novel method for more precisely determining OC contributions to sediments, and should be further investigated as a tool to resolve sources contributing to seagrass carbon stocks (Reef et al. 2017).

### Biophysical drivers of variation in OC stocks

Variation in surface OC stocks at our sites was best explained by a negative relationship with water motion, relative to other key biophysical factors (%fine sediments and seagrass complexity). In other words, meadows with lower water motion exhibited higher sediment OC stocks, likely due to enhanced particle deposition and reduced rates of erosion and resuspension in these calmer hydrodynamic environments. Our results agree with previous field studies examining the role of hydrodynamics on seagrass meadow carbon storage, where greater sediment carbon content was associated with lower wave heights (Samper-Villarreal et al. 2016), lower wave exposure (Mazarrasa et al. 2017a), and lower current velocities (Santos et al. 2019). Carbon stocks have also been shown to be significantly higher in inner fjords compared to outer fjords and open coasts (Kindeberg et al. 2018), which aligns with our finding that more sheltered inner-coast sites such as Pruth Bay had much higher OC stocks than exposed outer coast sites such as Choked Pass (Table 1; Fig. 3). Furthermore, our findings corroborate recent laboratory studies, which demonstrated that higher flow velocities greatly increased the loss of OC from seagrass sediments (Dahl et al. 2018).

Seagrass canopies are typically thought to be effective at reducing water motion (Lacy and Wyllie-Echeverria 2011; Hansen and Reidenbach 2012) and buffering against sediment resuspension (Gacia and Duarte 2001). Thus, we expected seagrass complexity to have a positive influence on sediment OC stocks. Instead, there was no clear relationship (positive or negative) between seagrass complexity and sediment OC content (Fig. 5), and seagrass complexity was the least important (had the lowest RVI value) for predicting OC content at both sediment depths. The finding that seagrass complexity may have relatively little influence on sediment OC content is also supported by Dahl et al. (2018), who compared vegetated and unvegetated sediments and found that shoot density had no influence on OC resuspension. They attributed this to the relatively low shoot densities used in the experiment (253 shoots  $\text{m}^{-2}$ ). However, the shoot densities reported

therein were higher than the densest meadow among our sites (Pruth Bay—216 shoot  $\text{m}^{-2}$ ; Table 1), and all other sites in our study had even lower shoot densities, which is not unusual for *Z. marina*. The lower densities, resulting in lower canopy complexity, of the meadows sampled here could help explain why seagrass canopy complexity was relatively unimportant in our models, and also why we observed little difference between carbon content of vegetated and unvegetated sediments. As highlighted by Santos et al. (2019), the trade-offs between current velocities and structural complexity of vegetation must be considered when attempting to attain blue carbon estimates for nearshore vegetated habitats.

### Interactions among biophysical characteristics

It is important to consider the many potential interactions among biophysical factors influencing carbon content in seagrass sediments. First, there is typically a negative relationship between hydrodynamic energy and %fine sediments, with higher fine sediment content in sheltered embayments compared to exposed outer coast regions (Samper-Villarreal et al. 2016; Santos et al. 2019). While we did observe a negative relationship between water motion and %fines, this relationship was weak ( $-0.4$  correlation coefficient; Supporting Information Fig. S1). Second, we expected a positive relationship between seagrass canopy complexity and %fines, as seagrass canopies both enhance particle deposition and reduce resuspension. Again, we observed the expected positive relationship between canopy complexity and percent fines, but it was a weak correlation ( $0.2$  correlation coefficient; Supporting Information Fig. S1). Third, we expected that greater seagrass complexity would have a dampening effect on water motion and yet again, we found a weak negative relationship between seagrass complexity and water motion ( $-0.2$  correlation coefficient; Supporting Information Fig. S1). In summary, the expected relationships among the key biophysical factors examined were confirmed in our data, but the interactions were not as strong as we hypothesized. Rather, these interactions appear to be overpowered by the dominant influence of water motion on sediment OC content. These results support our anecdotal field observations from the BC Central Coast, where the influence of high currents passing through a complex coastal landscape is visible during dive surveys. Although seagrass canopies generally have the capacity to buffer against water currents, we have observed that high-energy environments may cause the seagrass canopy to lie flat along the substrate, preventing the blades from interacting with particles passing through the water column.

### Additional factors influencing sediment OC content

While water motion appears to play a primary role in determining sedimentary OC stocks in this region, an array of other factors must be considered when examining the overall carbon budget within seagrass habitats. Carbon storage in seagrass meadows depends on species composition, canopy complexity, water depth, turbidity, and biotic interactions, among other factors (Belshe et al. 2018; Mazarrasa et al. 2018). Furthermore, the

molecular composition and recalcitrance of OC sources (litter quality), sediment mineralogy, temperature, and microbial community composition are also important in determining the quantity and quality of carbon sequestered in seagrass meadows (Belshe et al. 2017; Trevathan-Tackett et al. 2017). Benthic disturbances, such as shading, bioturbation by infauna, and wave action, can also influence OC stocks (Barañano et al. 2017; Trevathan-Tackett et al. 2018). On the Central Coast of British Columbia, bioturbation by sea otters (*Enhydra lutris*) digging for prey, the dynamics of active infaunal communities, and human activities including dredging, log boom shading, increasing sedimentation, and erosion should be investigated further to determine their impacts on the carbon sequestration and storage capacity of nearshore systems. Additionally, in some meadows sampled, sediment carbon was almost entirely inorganic (from bivalve shells), with very low fractions of OC (e.g., Choked Pass, Goose SW; Fig. 2, Supporting Information Table S2). In these meadows with active bivalve communities and low OC content, the amount of CO<sub>2</sub> produced during CaCO<sub>3</sub> shell production needs to be considered in conjunction with the OC sequestered via photosynthesis or particle capture to determine if the meadow is acting as a net sink or source for CO<sub>2</sub> (Mazarrasa et al. 2015; Howard et al. 2017a; Macreadie et al. 2017).

### Putting BC findings in context

Sediment OC values from the Central Coast region of BC align with other temperate *Z. marina* meadows (Greiner et al. 2013; Dahl et al. 2016; Jankowska et al. 2016; Kindeberg et al. 2018; Postlethwaite et al. 2018; Röhr et al. 2018), but are significantly lower than global averages reported for other seagrass species and latitudes (Mateo et al. 1997; Fourqurean et al. 2012; Serrano et al. 2016). The average OC stocks in the top 25 cm on the Central Coast (1482 g OC m<sup>-2</sup>), assuming a relatively consistent carbon profile to 1 m (~5928 g OC m<sup>-2</sup>), are approximately three times lower than the global median for 1 m OC stocks in seagrass meadows (19,420 g OC m<sup>-2</sup>) reported by Fourqurean et al. (2012). Even if the top meter stocks provided are overestimated due to not accounting for compaction, they are over three times lower, on average, than global estimates for all seagrasses. Furthermore, the median (0.34%) and average (0.45%) OC fractions reported here are much lower than the global median of 1.4% and average of 2.5% (Fourqurean et al. 2012). Our findings reconfirm the emerging notion that seagrass meadow carbon stocks can be highly variable and patchy, even at meadow and regional scales. Due to regional variability, observed in this study and others, the global estimates for seagrass carbon stocks need further empirical refinements (Johannessen and Macdonald 2016; Macreadie et al. 2018).

Similar to OC stocks, our OC sediment mass accumulation rates are within the range of those reported from other *Z. marina* meadows, but lower than reported global averages for seagrasses. OC sediment mass accumulation rates in the meadows sampled in this study ranged from 5 to 33 g OC m<sup>-2</sup> yr<sup>-1</sup>—similar to estimates from *Z. marina* meadows in Japan (3–10 g OC m<sup>-2</sup> yr<sup>-1</sup>;

Miyajima et al. 2015), Virginia (37 g OC m<sup>-2</sup> yr<sup>-1</sup>; Greiner et al. 2013), and further south on the BC coast in Clayquot Sound (10.8 ± 5.2 g OC m<sup>-2</sup> yr<sup>-1</sup>; Postlethwaite et al. 2018), though slightly higher than those reported by Jankowska et al. (2016) in Baltic Sea eelgrass meadows (1–4 g OC m<sup>-2</sup> yr<sup>-1</sup>). However, the accumulation rates reported in this study are at least three times lower than the global average reported for seagrass (138 g OC m<sup>-2</sup> yr<sup>-1</sup>) and at the low end of the range reported for all seagrass species (45–190 g OC m<sup>-2</sup> yr<sup>-1</sup>) (McLeod et al. 2011).

### Future directions

The low OC stocks and high variability found in our study are not uncommon to other *Z. marina* meadows located in temperate regions (Hodgson and Spooner 2016; Jankowska et al. 2016; Röhr et al. 2016, 2018; Kindeberg et al. 2018; Poppe and Rybczyk 2018; Postlethwaite et al. 2018). These low and variable values, along with a lack of data on meadow extent, present challenges for including seagrasses in national and international blue carbon policies (Hejnowicz et al. 2015; Green et al. 2018; Needelman et al. 2018). Building on this first regional assessment of seagrass carbon stocks in Canada, future work should continue to refine regional and local estimates for Pacific Northwest eelgrass meadows. Increased replication at the regional scale is necessary to obtain a better understanding of large-scale drivers of variability relevant to management. Additionally, finer scale within-core resolution, and the use of additional tracers, would help improve OC accumulation rate accuracy obtained through <sup>210</sup>Pb dating (Arias-Ortiz et al. 2018). Balancing sample allocations within cores, within meadows, and among meadows is an important consideration for all blue carbon studies. Finally, given the importance of the hydrodynamic environment highlighted herein, future work could begin to link laboratory hydrodynamic work (e.g., Dahl et al. 2018) with regional-scale observations.

No climate change policy mechanisms are currently in place for seagrass meadows, or other blue carbon habitats, in BC or Canada, though there is growing interest in incorporating blue carbon habitats into natural climate solutions both nationally and internationally (Hejnowicz et al. 2015; Sutton-Grier and Moore 2016; Griscom et al. 2017; Needelman et al. 2018). Furthermore, there is potential to consider blue carbon benefits in existing management frameworks, such as marine protected area creation (Howard et al. 2017b). In British Columbia, this could include targeting seagrasses for their blue carbon contributions within current planning processes such as the Marine Planning Partnership (MaPP) and the Northern Shelf Bioregion MPA Network, where eelgrass meadows have been identified as a conservation priority and an ecologically significant species (DFO 2009, 2017; MaPP 2015).

### Conclusion

For the first time, we provide meadow and regional scale blue carbon storage estimates for temperate eelgrass meadows

on the northwest coast of Canada, where few data currently exist. Our data include metrics of uncertainty and variability within and among meadows that can help inform the application of blue carbon science for coastal planning and management. This study illustrates the range of OC stocks over various sediment depths, and OC accumulation rates for *Z. marina* meadows. Our results suggest that low water motion, or other metrics of the hydrodynamic environment, and high proportions fine sediments should be considered when determining potential “hot spots” for OC stocks in temperate regions. While the blue carbon potential of temperate seagrass meadows may be low compared to larger, longer-living species such as those in the *Posidonia* genus, their capacity to sequester and store carbon at a regional scale should be considered in conjunction with other valuable ecosystem services they provide.

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## Conflict of Interest

None declared

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