Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows

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Abstract

Organic carbon (OC) storage in coastal vegetated habitats (blue carbon) is increasingly being considered in carbon financing and ecosystem-based management. Seagrass meadows have potential to sequester and store significant amounts of carbon, primarily belowground in the sediments beneath them. However, existing estimates are primarily from tropical and sub-tropical regions. On the northwest coast of North America, the magnitude and variability of seagrass carbon stocks, as well as local drivers of variability remain rare. We collected sediment cores from six eelgrass (*Zostera marina*) meadows on the coast of British Columbia, Canada, to quantify sedimentary OC stocks and accumulation rates. The top 20cm of sediments exhibited a 30-fold difference in OC stocks across meadows (185 – 5545 g OC m^{-2}). Stocks in meadow interiors (1392 ± 928 SD g OC m^{-2}) were 1.23 times greater than those along meadow edges (1130 ± 698 SD g OC m^{-2}) and 1.42 times greater than adjacent unvegetated sediments (977.10 ± 516 SD g OC m^{-2}). The top 20cm of sediment represented 21 to 74 years of accumulation, and OC accumulation rates ranged from 13 to 50 g OC m^{-2} $year^{-1}$. Isotopic analysis of sediments ($\delta^{13}C$ = 19.43‰ ± 3.25 SD) revealed that OC is largely derived from non-seagrass sources (terrestrial, benthic microalgae and/or macroalgae). OC stocks in the top 5 cm were most strongly influenced by water motion (Relative Variable Importance RVI = 0.81), relative to seagrass structural complexity (RVI = 0.21), and sediment size (RVI= 0.22). Specifically, higher OC stocks were associated with lower water motion, which may facilitate greater deposition of organic carbon particles and reduce rates of erosion and resuspension. This study highlights variability in carbon stocks at local scales with profound implications for estimating variability in carbon stocks at regional and global scales, typically unaccounted for in seagrass blue carbon estimates. To help account for this variability, we demonstrate that reduced water motion can indicate high potential for blue carbon storage in temperate soft sediment habitats.

Keywords: *Zostera marina*; blue carbon; carbon storage; climate change; seagrass hydrodynamics; variability

I would like to dedicate this thesis to my parents, Alison and Andrew Prentice, who instilled a love of nature and sense of curiosity in me at a young age and are still actively involved in citizen science and ecological restoration (including eelgrass planting!) to this day.

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Introduction

Blue Carbon Ecosystems

Conserving and restoring vegetated ecosystems that efficiently sequester and store carbon (C) is a climate strategy that can remove atmospheric carbon dioxide (CO_2)(Pan et al., 2011; Duarte et al., 2013). In addition to ‘green carbon’ sequestered by terrestrial ecosystems, coastal vegetated ecosystems - mangroves, salt marshes and seagrass meadows - can sequester and store significant amounts of ‘blue carbon’ (Nellemann et al., 2009; Laffoley and Grimsditch, 2009; McLeod et al., 2011). Blue carbon habitats play a disproportionally large role in carbon sequestration relative to their global extent, making them ‘hot spots’ for carbon storage (Duarte et al., 2005; McLeod et al., 2011; Fourqurean et al., 2012). Further, degradation and destruction of coastal ecosystems can release carbon that has accumulated over decadal, centennial or millennial time scales, as well as limit capacity for future sequestration and storage (Mateo et al., 1997; Pendleton et al., 2012). Thus, there is increasing interest to include mangroves, tidal marshes and seagrass meadows in national greenhouse gas inventories as well as carbon financing and offset schemes (Hejnowicz et al., 2015; Sutton-Grier and Moore, 2016; Nellemann et al., 2009; Johannessen and Macdonald, 2016). However, scarcity of data and high within and among habitat variability in carbon storage capacity create challenges for scaling-up carbon estimates and incorporating blue carbon into climate policies (Lavery et al., 2013; Oreska et al., 2017a). Here, we quantified variation in *Zostera marina* sedimentary organic carbon (OC) stocks and identified local drivers of variability on the northwest coast of North America, a relatively data deficient region for seagrass blue carbon estimates. Further, we review these results in the context of emerging global trends to illustrate variability across different spatial scales.

Carbon Sequestration and Storage in Seagrass Meadows

Seagrass meadows have potential for globally significant, yet variable, rates of carbon sequestration and storage (Mcleod et al., 2011; Fourqurean et al., 2012; Macreadie et al., 2014). Seagrasses represent some of the most productive vegetated communities on the planet, with above and belowground biomass production averaging

3.8 and 1.21 g dry weight m^{-2} day^{-1} (Duarte and Chiscano, 1999). Approximately 15.9% of this production is buried in seagrass sediments, while the remainder is decomposed (50.3%), exported (24.3%) or consumed by herbivores (18.6%) (Duarte and Cebrian, 1996; Duarte and Krause-Jensen, 2017). Seagrass canopies also facilitate particle capture and settlement from the water column, which can further enhance sedimentary OC stocks (Duarte et al., 2013; Macreadie et al., 2014). The carbon in seagrass meadow sediments can therefore be autochthonous - produced within a given meadow - or allochthonous - produced outside the meadow (Kennedy et al., 2010; Miyajima et al., 2015; Oreska et al., 2017b). The origin of OC has implications for remineralization rates, as terrestrial material and seagrass tissues are more refractory, while macroalgae and seston are more labile and vulnerable to microbial breakdown (Mazarrasa et al., 2017a; Trevathan-Tackett et al., 2017a). Seagrass meadow sediments are generally anoxic below the first few millimeters, resulting in low microbial activity and limited breakdown of organic matter. However, disturbances such as bioturbation by infaunal organisms can increase the depth of the oxic zone and subsequently enhance remineralization rates (Martinetto et al., 2016; Trevathan-Tackett et al., 2017b). The combination of high primary productivity, the ability to capture and bury allochthonous OC, and generally anoxic sediments yields high potential for seagrass meadows to act as significant blue carbon sinks. While most seagrass systems share the aforementioned characteristics to a certain extent, their specific biological, chemical and physical environments can vary substantially, thereby creating variability in blue carbon storage potential.

Factors Influencing Seagrass Blue Carbon Potential

To improve assessments of the OC storage potential of seagrass meadows, a thorough understanding of the factors influencing the magnitude and variability of carbon stocks and accumulation rates is required (Dahl et al., 2016a; Gullström et al., 2017; Lavery et al., 2013). Large differences in OC stocks and accumulation rates among seagrass habitats have been identified (Lavery et al. 2013; Serrano et al. 2014). Biological factors influencing seagrass blue carbon potential include plant size and species composition (Rozaimi et al., 2013; Gillis et al., 2017), seagrass structural complexity (Jankowska et al., 2016) and carbon origin (Mazarrasa et al., 2017a). Elevated OC in seagrass sediments is often associated with higher proportions of fine sediments, higher porosity, lower bulk density and higher specific surface area (Rohr et al., 2016; Dahl et al., 2016a; Gullström et al., 2017; Miyajima et al., 2017). At the landscape level, OC stocks are often greater in the meadow interior relative to edges (Oreska et al. 2017a; Ricart et al. 2015), and greater in large continuous meadows, relative to smaller, patchy ones (Gullström et al., 2017; Ricart et al., 2017). Physical factors such as water depth, turbidity levels, wave height and wave exposure have been shown to influence OC stocks, with higher OC content at lower wave heights and exposures, higher turbidities, and shallower depths (Serrano et al., 2014; Samper-Villarreal et al., 2016; Mazarrasa et al., 2017b). While small scale or low intensity disturbances may not influence OC stocks (Macreadie et al., 2014; Dahl et al., 2016b), clam harvesting (Barañano et al., 2017) and shading (Trevathan-Tackett et al., 2018) can result in at least a 50% reduction in sedimentary carbon content. Furthermore, the relationships between environmental factors and OC stocks may not hold true in all seagrass systems (e.g. Serrano et al., 2016), and the relative influence of factors can vary regionally (Lavery et al., 2013; Samper-Villarreal et al., 2016). Determining which physical, chemical and biological factors are most important at different scales is challenging, but crucial to fully understanding seagrass blue carbon budgets.

Objectives and Hypotheses

The objectives of this study were to: (1) quantify within and among meadow variability in OC stocks in OC accumulation rates in temperate *Zostera marina* meadows, (2) explore local drivers of variability in OC stocks, (3) examine the sources of OC in *Z. marina* associated sediments and (4) place our values in the context of seagrass meadows globally to examine regional and global variability. We hypothesized that OC stocks and accumulation rates would vary among meadows, given known differences in characteristics. Further, we expected interior OC stocks to be enhanced relative to meadow edges and adjacent bare sediment (Oreska et al., 2017a; Ricart et al., 2015). Among meadows, we predicted higher OC stocks would be associated with reduced water motion, greater proportions of fine sediments, and higher seagrass structural complexity. Fine sediments allow for more adsorption of organic particles and limit oxygen exchange, while a more complex seagrass canopy should result in more efficient particle capture and erosion reduction. Similarly, reduced water motion would allow more time for particle deposition and result in less resuspension and erosion.

Methods

Study Area

Sediment cores were collected from eelgrass (*Zostera marina*) meadows on the Central Coast of British Columbia, Canada, a relatively data deficient region for seagrass blue carbon estimates (CEC, 2013). The Central Coast is a geographically complex coastline, with a variety of nearshore habitats including expansive eelgrass meadows of varying size and attributes (Hessing-Lewis et al. 2017; Table A.1; Table A.2). The relatively undisturbed nature of this region and the variability in meadow characteristics provides an opportune setting for quantifying baselines in eelgrass carbon storage and examining within and among meadow variability. The six meadows sampled - Pruth Bay (PB), Choked Pass (CP), Triquet Bay (TB), McMullins North (MC), Goose Southwest (GO) and Koeye Estuary (KY) - represent the wide spectrum of environments within which *Z. marina* can grow, from sheltered, soft sediment estuarine systems such as Pruth Bay, to exposed, outer coasts with sand or shell-hash dominated sediments such as Choked Pass (Figure 1; Figure A.1). The meadows sampled also range widely in size and shape, from 22,778 m^2 (McMullins North) to 354,580 m^2 (Choked Pass) (Figure A.1).

Experimental Design and Sample Collection

To examine among and within-meadow variability in sediment carbon content, we collected nine cores (7 cm diameter, ~30cm depth) from six *Z. marina* sites (Figure 1). Three cores were taken from three different 'positions' within each site – along the meadow edge (Edge 1-3), in the meadow interior (Interior 4-6) and in adjacent bare sediment (Reference 7-9) (Figure A.1). Reference cores were taken approximately five meters beyond the current edge of the meadow. This distance was selected across sites as the habitat often changed quickly at this distance beyond the edge of the seagrass meadow, e.g. turned to bedrock, or transitioned into a kelp forest (dominant canopy species including *Macrocystis pyrifera* or *Nereocystis leutkeana*). The interior and edge cores were associated with pre-established sampling transects as part of a long-term seagrass monitoring program conducted by the Hakai Institute. We also obtained one long core (10.2 cm diameter, ~1m in length) from each meadow at one interior transect (Interior 5) for geochronological analyses (^{210}Pb dating).

SCUBA divers collected cores manually at high tides, using a small sledgehammer to pound PVC (long cores) or polycarbonate (short cores) tubing into the sediments. 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 5 times during core insertion to calculate changes with depth. Compaction was calculated as the distance (cm) 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 sample depth). Compaction values were on average 17.46 ± 13.32 SD %. 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 (Morton & White, 1997), though we do acknowledge compaction as a source of error in our measurements.

Within 24 hours of collection, cores were sliced into subsections using a custom-fabricated extruding device and pistons. Short cores were sampled in 5cm increments, though the deepest subsection was often shorter than 5cm. Sampling intervals for the long cores varied with depth: 6cm section for the top section (we considered the top 6cm the ‘mixed layer’), 2cm sections from 6 to 20cm deep, and 5cm sections >20cm deep). Once extruded, each subsection was thoroughly homogenized and a 30cc subsample was taken for measurements of dry bulk density, carbon content, stable isotopes and ^{210}Pb. The remainder of the subsection was used for grain size analysis or saved.

Sediment Characterization

Chemical Analyses. The 30cc subsamples were freeze dried for approximately one week, or until fully dry. A dry weight was obtained before each sample was ground into a fine powder using a grinding mill. Any non-living material (e.g. shell pieces, wood, rocks) was left in the sample, as these materials are part of the sedimentary carbon pool. However, all visible living biomass (e.g. shoots, roots or rhizomes, macroalgae) was removed, as it represents the biomass carbon pool. Total percent carbon (%TC) and nitrogen (%TN) were determined using an Elemental Analyzer. 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.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values were determined using an Isoprime Isotope Ratio Mass Spectrometer at the Stable Isotope Facility in the Department of Forest and Conservation Sciences (for $\delta^{13}C$) and the Department of Earth, Ocean and Atmospheric Sciences (for $\delta^{15}N$) at the University of British Columbia in Vancouver, BC, Canada. All isotopic ratios are expressed relative to Vienna Pee Dee Belemnite (VPBD) for carbon and atmospheric air for nitrogen in per mil notation (‰). Samples were acidified using sulfurous acid (H_2SO_3) to remove inorganic carbon prior to mass spectrometry. While acidification has the potential to cause analytical errors in samples with low organic matter, we found high inorganic carbon content within our samples (an average of 1.86 ± 2.37 SD % and maximum value of 7.95% of samples analyzed for isotopes), and mechanical removal of calcified structures was unfeasible (Schlacher & Connolly, 2014).

Geochronological analyses (^{210}Pb) were conducted by MyCore Scientific Inc. in Dunrobin, Ontario, Canada. An alpha spectrometer was used to measure ^{210}Po, the granddaughter radionuclide of ^{210}Pb, assuming radioactive equilibrium between the two radionuclides. The activity of ^{210}Po was determined from the ratio of counts of ^{209}Po to ^{210}Po and the known amounts of ^{209}Po in each sample. Excess ^{210}Pb was determined by subtracting background, or supported, ^{210}Pb from total ^{210}Pb activity at each depth interval.

Carbon Parameter Calculations. For each depth subsection and core, we calculated various carbon parameters. Dry bulk density (g cm^{-3}) was determined by dividing dry weights of sediment subsamples by the known sample volume (30 cm^3). OC density (g OC cm^{-3}) for each subsection was calculated by multiplying the OC fraction (%OC/100) by the dry bulk density (g cm^{-3}). OC mass (g OC m^{-2}) was calculated by multiplying the OC density (g OC cm^{-3}) by the depth of the subsection (cm). OC stocks were calculated by summing the carbon mass (g OC m^{-2}) in each subsection to a particular depth as outlined by Howard et al. (2014). From the ^{210}Pb data, excess ^{210}Pb profiles were created for the depth of each long core, and the age of each sediment layer was estimated using the Constant Rate of Supply (CRS) model, which allows sedimentation rates to vary with depth (Appleby & Oldfield, 1978; Carey et al. 2017).

Sediment accumulation rates (g cm^{-2} $year^{-1}$) were estimated at each depth interval, based on the sediment dry bulk densities. OC accumulation rates (g OC m^{-2} $year^{-1}$) were calculated by multiplying the OC fractions for each subsection by the corresponding sediment accumulation rates. For comparison, carbon accumulation rates were also calculated using the Constant Initial Concentration (CIC) model, which assumes a constant rate of sedimentation over time, as outlined in Carey et al. (2017). The known decay coefficient for ^{210}Pb (-0.03114) was divided by the slope of the regression of ln(^{210}Pb) versus depth, excluding the surface mixed layer, to obtain an accretion rate (cm $year^{-1}$). The accretion rate was multiplied by the average carbon density (g OC cm^{-3}) over the corresponding depth and converted to the appropriate units (cm^2 scaled to to m^2), to estimate OC accumulation rates for each core (g OC m^{-2} $year^{-1}$).

Grain Size Analyses. Sediment grain size analyses were conducted using an electronic sieve shaker. For all short cores, the 0-5 and 15-20 cm sections were analyzed, as well as the 0-5, 15-20, 35-40 and one deeper subsection, if applicable, from the six long cores. Samples were dried at 60°C for 24-48 hours and each sample was allowed to shake for 10 minutes. Dry weights were obtained both before and after shaking. Sieve sizes of 4mm, 2mm, 1mm, 500μm, 250μm, 125μm and 63μm were used, and the amount of sediment remaining in each category was weighed to the nearest 0.01g. Any particles that passed through the 63μm sieve were included in a <63μm category (the 'mud' or fine sediments fraction). Based on the weight of each size fraction and the total sample weight, the percentage of particles in each size class was calculated. We did not perform a hydrogen peroxide digestion prior to grain size analyses, however, the % organic matter was very low in our sediments and would influence the mass of the % fines fraction for all samples equally, if at all.

Seagrass Meadow Characterization

We characterized environmental attributes (water depth, water motion) and seagrass parameters (shoot density, canopy height, above and below-ground biomass) associated with each meadow. Water depth relative to chart datum was calculated by subtracting the tidal height (m) from the recorded water depth (m) at the time the survey was conducted. Relative water motion was characterized at the edge and interior of each meadow using the relative dissolution rate of Plaster of Paris chalk blocks; this metric integrates the effects of both tidal currents and waves (Potouroglou et al., 2017).

Similar to Potouroglou et al. (2017), we used zip ties to attach plaster blocks (~130g) 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°C, and the weight loss was standardized to time left in the field (mass before (g) – mass after (g))/time in field (hours). Canopy height (m) was obtained by averaging measurements taken from six quadrats along each of six transects within each meadow. Seagrass density (scaled up to shoots m^{-2}) was also obtained from averaging values from the six quadrats along each transect; density measurements of 0 were included in averages, as they are an indication of patchiness of the area. Aboveground biomass for each transect was the average dry weight (g) per shoot from four shoots collected along each transect. Belowground biomass was the average dry weight (g) of root and rhizome biomass per cm^3 of sediment. The canopy height, density and above and belowground measurements were obtained in August 2016 in conjunction with sediment core collection.

Statistical Analyses

We used an information theoretic approach to examine the strength of evidence for the effects of position (interior, edge or unvegetated) and site on surface (5cm) and deeper (20cm) OC stocks (Burnham and Anderson 2002). Due to the crossed nature of the data (n=3 cores for every combination of site and position) and a non-normal error distribution, we fit generalized linear models (GLMs) 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). We compared the strength of evidence for (1) position alone, (2) site alone, (3) an interaction between site and position explaining the most variation in OC stocks in (a) the top 5cm and (b) the top 20cm. We allowed both slopes and intercepts to vary in all models.

The relative support for four candidate models (position only, site only, site*position and a null model) was evaluated using Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002) and the MuMIN package in R (Bartoń 2016). AIC_c values were calculated based the number of parameters (K) and Log Likelihoods (Log L) of each model. The most parsimonious model (or models) was determined based on ΔAIC_c, or the difference between the AIC score of the top model and each subsequent model. Akaike weights (W_i) were calculated as the relative likelihood of each model (exp ($-0.5 \times \Delta AIC_c$)) divided by the sum of the relative likelihoods across all models. Adjusted R-squared values ($adjR^2$) were calculated based on the sample size (n) and the number of parameters in the model (K).

We also examined the strength of evidence for the relative effects of environmental factors on surface (5cm) OC stocks. Since we had a sample size of 36 cores (n=6 from each of the 6 meadows, interior and edge cores only), we narrowed down our suite of potential factors to three, based on previous literature and our understanding of the system. The three factors selected were % fine sediments (particles < 63μm), water motion and seagrass complexity. These factors represent major sediment, physical and eelgrass characteristics at each site and have been shown to be important in other seagrass systems (e.g. Dahl et al. 2016a; Samper-Villarreal et al. 2016).

Due to the hierarchical nature of the data (cores nested within sites) and a non-normal error distribution, we fit generalized linear mixed-effects models (GLMMs) with a Gamma distribution and log link function using the glmer function in the lme4 package in R (Bates et al. 2015; R Core Team 2017). Water motion, seagrass complexity and % fine sediments were included as continuous fixed effects, and site was included as a random effect in all models. We tested the explanatory power of these factors on OC stocks in the top 5cm of sediment (g OC/m^2). Surface OC stocks were selected as the response because grain size data was available for all top 5cm sections (but not all deeper sections), and additionally, 20cm represents a much longer time period (as much as 74 years), over which current-day seagrass characteristics and water motion are unlikely to be good predictors.

We checked for collinearity among model factors using Pearson correlation coefficients and Variance Inflation Factors (VIF; Zuur et al. 2010, 2013). VIFs account for linear dependence among three or more variables. 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 (Zurr et al. 2009). Correlation coefficients in this analysis ranged from 0.20 to 0.40, and all VIF scores ranged from 1.09 to 1.25, 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 Akaike's Information Criterion corrected for small sample size (AIC_c; Burnham and Anderson 2004) and the MuMIN package in R (Bartoń 2016). We had no reason to think that any combination of factors in the model was not biologically realistic and thus included all subsets of the global model, for a total of 8 candidate models (Table 3). As with our first model set, the most parsimonious model (or models) explaining variation in surface carbon stocks was determined based on ΔAIC_c.

Results

Carbon Content, Stocks and Accumulation Rates

Carbon Content. Combining all sections from all cores at all sites (n=399), the average %OC was 0.45 (± 0.38 SD) and ranged from 0 - 2.98%. High OC values can be attributed to deposits of woody debris (Table A.2). The average %IC (carbonate) was 1.58 ± 2.10 SD % and ranged from 0 to 7.95%. High carbonate values can be attributed to bivalve shells within the sediments (Table A.2). Site averages (± standard deviations) ranged from 0.15 ± 0.02 % OC in Choked Pass to 0.71 ± 0.37 % in McMullins North. For inorganic carbon, site averages (± standard deviations) ranged from 0.18 (± 0.24 SD) in Pruth Bay to 4.54 (± 2.68 SD) in Triquet Bay (Table A.2). In some sites (e.g. Pruth Bay, Triquet Bay), most of the total carbon was comprised of organic carbon, while in other most of the carbon was inorganic (e.g. Choked Pass, Goose SW). Carbon content varied with depth down the core, but irregularities in depth trends were largely driven by spikes in either woody debris or carbonate material (Figure A.3).

Carbon Stocks. Organic carbon stocks exhibited substantial variability among sites on the Central Coast of British Columbia. Amongst all cores (n=60), surface (5cm) sediment OC stocks ranged from a minimum value of 0 g OC m^{-2} in Choked Pass to a maximum of 1089 g OC m^{-2} at McMullins North. Within meadows, there was the greatest strength of evidence that an interaction between site and position best explained these patterns in 5cm OC stocks (Table 1). That is, the effect of position (interior, edge or unvegetated) varied among sites (Figure A.2.) OC stocks were highest in the meadow interior, followed by the meadow edge and unvegetated bare sediments at four of six sites (Figure A.2). Similarly, 20cm OC stocks varied widely among sites, ranging from 185 g OC m^{-2} in Choked Pass to 5147 g OC m^{-2} at McMullins North (Figure 2). There was the greatest strength of evidence for site alone explaining the most variation in 20cm OC stocks, with a ΔAIC_c of 25.11 relative to the next best model (site*position) and a W_i of 1 (Table 1). In other words, there was greater variation among sites than among positions within sites.

Carbon Accumulation Rates. There was sufficient excess ^{210}Pb in the sediments to obtain estimates of sediment ages and accumulation rates at all sites except Goose SW (Table 2). However, due to low levels of organic matter in the sediments, there were large margins of error around the estimates. OC accumulation rates (± SD) ranged from 12.6 (± 12.5) g OC m^{-2} $year^{-1}$ in Choked Pass to 50.5 (± 29.1) g OC m^{-2} $year^{-1}$ in McMullins North using the Constant Rate of Supply (CRS) Model and 9.0 g OC m^{-2} $year^{-1}$ in Choked Pass to 39.8 g OC m^{-2} $year^{-1}$ in Koeye using the Constant Initial Concentration (CIC) Model. The age of the top 20cm of sediment ranged from 21 years of accumulation in the Koeye Estuary to 74 years at McMullins North, with an average of 54.2 ± 20.1 SD years of accumulation (Table 2).

Local Drivers of Variability in Surface Carbon Stocks

Seagrass and physical characteristics were variable both within and among sites (Table A.1; A.2). There was the greatest strength of evidence for a negative effect of water motion on surface (top 5cm) OC stocks (Figure 3; Table 3). Compared to other models that included % fine sediments and seagrass complexity, water motion alone had the highest relative weight (0.512) and a ΔAIC_c 2.64 units higher than the next best candidate model. The Relative Variable Importance (RVI) for water motion (0.814), was 3.9 times higher than seagrass complexity (0.205) and 3.7 times higher then % fine sediments (0.218) (Figure 3). The adjusted R^2 value for the top model was 0.60 and R^2 values for all candidate models ranged from 0.53 to 0.60. Model validation indicated homoscedasticity.

Sedimentary Carbon Sources

The mean isotopic carbon values ($\delta^{13}C$) in the surface (top 5cm) of seagrass sediments on the Central Coast of BC were 18.82 ± 3.23 SD ‰. The average values for the top 5cm varied among sites, ranging from -17.28‰ in Pruth Bay to -21.48‰ at Koeye (Figure 4). Mean $\delta^{13}C$ values in deeper sediments (15-20cm) were slightly more depleted, with an average of -19.79 ± 3.84 SD ‰, ranging from -16.71 to –23.22 ‰. Due to very low % nitrogen values in our sediments, we had limited replicates (n=12) for δ15N values. With all sites combined, the average δ15N value was 6.83 ± 0.62 SD ‰.

Discussion

High Spatial Variability in OC Stocks

Sedimentary OC stocks in eelgrass meadows and adjacent bare sediments on the Central Coast of British Columbia exhibited substantial local variability along a small stretch of coastline spanning approximately 5° of latitude. Our results suggest that for surface OC stocks, the influence of position within a meadow varies among sites. That is, in three of six meadows, we observed the expected trend of highest OC stocks in the meadow interior, followed by the edge and adjacent bare sediments (Ricart et al., 2015; Oreska et al., 2017a). However, in the other three meadows, either the unvegetated or edge OC stocks were greatest. The latter case suggests that factors influencing OC stocks (e.g. seagrass density, water motion, grain size) do not always differ between the interior and edge of a given meadow, and thus OC stocks can be relatively homogenous. Along these lines, the effect of site was much greater than position within the meadow for 20cm OC stocks (Table 1), suggesting that over longer time periods, larger-scale landscape factors are more important than smaller-scale, meadow-level factors, namely position within the meadow.

Water Motion Best Explains Surface OC Stock Variation

Variation in surface OC stocks was best explained by a negative relationship with water motion, relative to other key biological and sedimentary factors (% fine sediments and seagrass complexity). Specifically, meadows with lower water motion exhibited higher sedimentary OC stocks. These results agree with previous work examining the role of hydrodynamics on seagrass carbon storage potential, where greater sedimentary carbon content was associated with lower wave heights (Samper-Villarreal et al., 2016) and lower wave exposure (Mazarrasa et al., 2017b). Aside from these studies, few others have examined the role of hydrodynamic factors within the context of blue carbon; however, the role of seagrasses in influencing fluid dynamics and particle deposition has been well studied (Koch et al., 2006). Eelgrass canopies can reduce near-bottom mean velocities by 70 to 90% and wave heights by 45 to 70% compared to an adjacent unvegetated habitats (Hansen and Reidenbach, 2012). This reduction in water velocity allows more time for deposition of fine sediments with high organic content. In addition to increasing deposition, seagrasses may also significantly buffer against sediment resuspension, as much as three-fold compared to unvegetated bottoms (Gacia & Duarte, 2001). This combination of enhanced deposition and reduced resuspension increases potential for OC sequestration and storage.

The sites sampled here varied widely in their physical attributes. Choked Pass is a highly marine-influenced meadow with strong current velocities channelled through rocky, exposed islets. The Koeye estuary is a narrow river system with large tidal exchanges that create high currents through the meadow. Both of these sites with high water motion had relatively low carbon stocks. In contrast, McMullins North and Pruth Bay are enclosed embayments that experience less water motion and exhibited higher surface carbon stocks (Figure 2). Thus, our results suggest that local oceanographic conditions, driven by geomorphology, currents and exposure, influence the water motion of a meadow, and play a more important role in carbon sequestration than site-level seagrass canopy attributes or sediment properties. Given that seagrass canopies are generally thought are to reduce water motion, we expected seagrass canopy complexity to potentially enhance sediment carbon stocks. Similarly, multiple studies have found sediment characteristics to be strongly correlated with seagrass sediment carbon content (Dahl et al., 2016a; Miyajima et al., 2017; Serrano et al., 2015). Instead, water motion alone dominated, overriding local variation in seagrass and sediment characteristics, perhaps due to the wide range of water motion experienced among sites, and particularly high current velocities in some meadows. Differences in water motion explain much of the variability at the regional level of this study and can inform management and policy at this scale. However, scaling up to global trends and international carbon sequestration policy requires examining our trends in light of emerging values from seagrass habitats spanning the globe.

Putting Regional Estimates in the Global Context

Overall, the sedimentary OC stocks within the Central Coast region of British Columbia agree with other temperate *Z. marina* meadows but are lower than global averages reported for other seagrass species and latitudes (Table 4). The average OC stocks in the top 25cm on the Central Coast (1482 g OC m^{-2}), assuming a relatively consistent carbon profile to 1m (~5928 g OC m^{-2}), are approximately 3 times lower than the global median for 1m OC stocks in seagrass meadows (19420 g OC m^{-2}) reported by

Fourqurean et al. (2012). Likewise, the average %OC reported here (0.45%) is much lower than the global median of 1.4% and average of 2.5% (Fourqurean et al., 2012). Thus, our findings reconfirm the emerging notion that seagrass meadow carbon stocks can be highly variable and patchy, even at the meadow and regional scale. Due to this regional variability, observed in our study and others, the global estimates for seagrass carbon stocks are likely to be overestimates of seagrass blue carbon storage potential (Johannessen and Macdonald, 2016).

Similar to OC stocks, our OC accumulation rates are within the range of those reported from other *Z. marina* meadows, but lower than reported global averages for seagrasses. OC accumulation rates in this study ranged from 12.6 to 50.5 g OC m^{-2} $year^{-1}$. These estimates are similar to those from *Z. marina* sites near Japan (3.13 – 10.14 g OC m^{-2} $year^{-1}$; Miyajima et al., 2015) and in Virginia (36.68 g OC m^{-2} $year^{-1}$; Greiner et al. 2013). Moreover, our values are slightly higher than those reported by Jankowska et al. (2016) in Baltic Sea eelgrass meadows (0.84 to 3.85 g OC m^{-2} $year^{-1}$). However, the accumulation rates found here are at least 3 times lower than the global average reported for seagrass (138 g OC m^{-2} $year^{-1}$) and at the low end of the range reported for all seagrass species (45-190 g OC m^{-2} $year^{-1}$) (McLeod et al., 2011).

Sediment OC Primarily from Non-Seagrass Sources

Sedimentary isotopic carbon signatures (19.43 ± 3.25 SD‰) are much more depleted than *Zostera marina* signatures from this region (-11.10 ± 1.52‰), suggesting that the OC in seagrass sediments is derived largely from allochthonous and/or non-seagrass sources, such as benthic microalgae, terrestrial sources and macroalgae. However, the potential non-seagrass sources of OC have similar, overlapping δ13C values, ranging from approximately -19 to -23 ‰ (Figure 4). With limited replication of sediment samples, overlapping end member signatures from the Central Coast region, and sufficient replication for only one stable isotope (δ13C), it is difficult to distinguish amongst these potential OC sources. Even so, it does appear that the OC across all meadows originates primarily from non-seagrass sources. This finding is similar to seagrass meadows elsewhere that have exhibited largely allochthonous contributions to sedimentary OC stocks, with 50% or more of the carbon originating from non-seagrass sources (Kennedy et al., 2010; Miyajima et al., 2015; Oreska et al., 2017b). Understanding the sources of OC in seagrass meadow sediments has important implications for the long-term persistence OC stocks, as sources that are more refractory (seagrass, terrestrial) are likely to be more resistant to microbial degradation and persist for longer than labile sources such as benthic microalgae and macroalgae (Trevathan-Tackett et al., 2017a; Mazarrasa et al. 2017a). Additionally, isotopic data can provide important insights into carbon flow and connectivity amongst nearshore ecosystems, adding credence to the notion of a broad, ecosystem-based approach to coastal management.

Additional Considerations for Nearshore Carbon Budgets

While water motion clearly plays an important role in determining sedimentary OC stocks in this region, an array of other factors may also affect OC stocks, as well as the persistence of carbon in the sediments. Recent literature has highlighted the importance of molecular composition and recalcitrance of OC sources (litter quality), sediment mineralogy and microbial activity and diversity in determining the quantity and quality of carbon sequestered in seagrass meadows (Belshe et al., 2017; Trevathan-Tackett et al. 2017a,b). Furthermore, it is important to consider and quantify the amount of seagrass biomass exported out of the meadow, consumed by herbivores and/or decomposed within the system (Duarte and Cebrián, 1996). The fate of exported seagrass biomass is often unknown and thus not accounted for in blue carbon studies. If biomass ends up in the deep sea, it could potentially be considered ‘sequestered’; in contrast, if seagrass biomass is washed ashore, it is more likely to be re-mineralized and returned to the atmosphere as CO_2 (Duarte and Krause-Jensen, 2017). Benthic disturbance is also an important factor that can influence OC stocks (Barañano et al., 2017; Trevathan-Tackett et al. 2018), and may vary substantially among sites. On the Central Coast of British Columbia, bioturbation by sea otters digging for prey, infaunal communities, 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.

Implications for Blue Carbon Policy

The low OC stocks and high variability found in our study are not uncommon to other *Zostera marina* seagrass meadows (e.g. Rohr et al., 2016; Jankowska et al., 2016, Spooner, 2015). These low and variable values, along with a lack of data on seagrass meadow extent, present challenges for including them in national and international blue carbon policies (Lavery et al., 2013; Hejnowicz et al., 2015). No climate change policy mechanisms are currently in place for seagrass meadows, or other blue carbon habitats, in British Columbia or Canada, though there is growing interest in markets nationally and internationally (Hejnowicz et al., 2015; Sutton-Grier and Moore, 2016). Further, there is potential to consider blue carbon benefits in existing policy frameworks, such as marine protected area creation (Howard et al., 2017). In British Columbia, this could include targeting seagrass for their blue carbon contributions within current planning processes such as the Marine Planning Partnership (MaPP) and the Northern Shelf Bioregion MPA Initiative. Our results can help contribute to incorporating blue carbon into coastal planning and management by providing blue carbon estimates for temperate eelgrass meadows where few data exist. Here, we present a range of OC stocks over various sediment depths, and OC accumulation rates for *Z. marina*, including metrics of uncertainty and variability within and among meadows. We also investigated factors that may indicate high potential for seagrass carbon sequestration and storage. Our results suggest that water motion, or other metrics of the hydrodynamic environment, 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 reduced compared to tropical 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.

Conclusions

Here, we characterized the blue carbon potential of six *Zostera marina* meadows along a relatively undisturbed stretch of coastline in British Columbia, Canada – a previously data deficient region for seagrass blue carbon estimates. Sediment OC stocks exhibited high natural variability, with stocks in the top 20cm ranging from 185 g OC m^{-2} to 5147 g OC m^{-2}. In addition to OC stocks, we quantified OC accumulation rates, which also varied (12.6 – 50.5 g OC m^{-2} $year^{-1}$) amongst meadows in relatively close proximity. Both OC stocks and accumulation rates were similar to values reported from other *Zostera marina* meadows but lower than global averages for seagrasses. Variation in surface OC stocks was best explained by differences in water motion, where meadows with lower water motion exhibited higher OC stocks. Our results suggest that larger-scale landscape factors (e.g. water motion) have a greater influence on OC stocks than finer-scale meadow characteristics (e.g. seagrass canopy complexity and % fine sediments). These findings highlight substantial variability in seagrass carbon stocks at local, regional and global scales. The data herein can help contribute to incorporating blue carbon into coastal planning and management by providing estimates for temperate eelgrass meadows where few data exist. Further, our findings suggest that water motion should be considered when determining potential 'hot spots' for OC stocks in temperate regions. While the blue carbon potential of temperate eelgrass meadows may be reduced relative to other seagrass species and regions, their capacity to sequester and store carbon at a regional scale should be considered in conjunction with other valuable ecosystem services they provide.

Figures

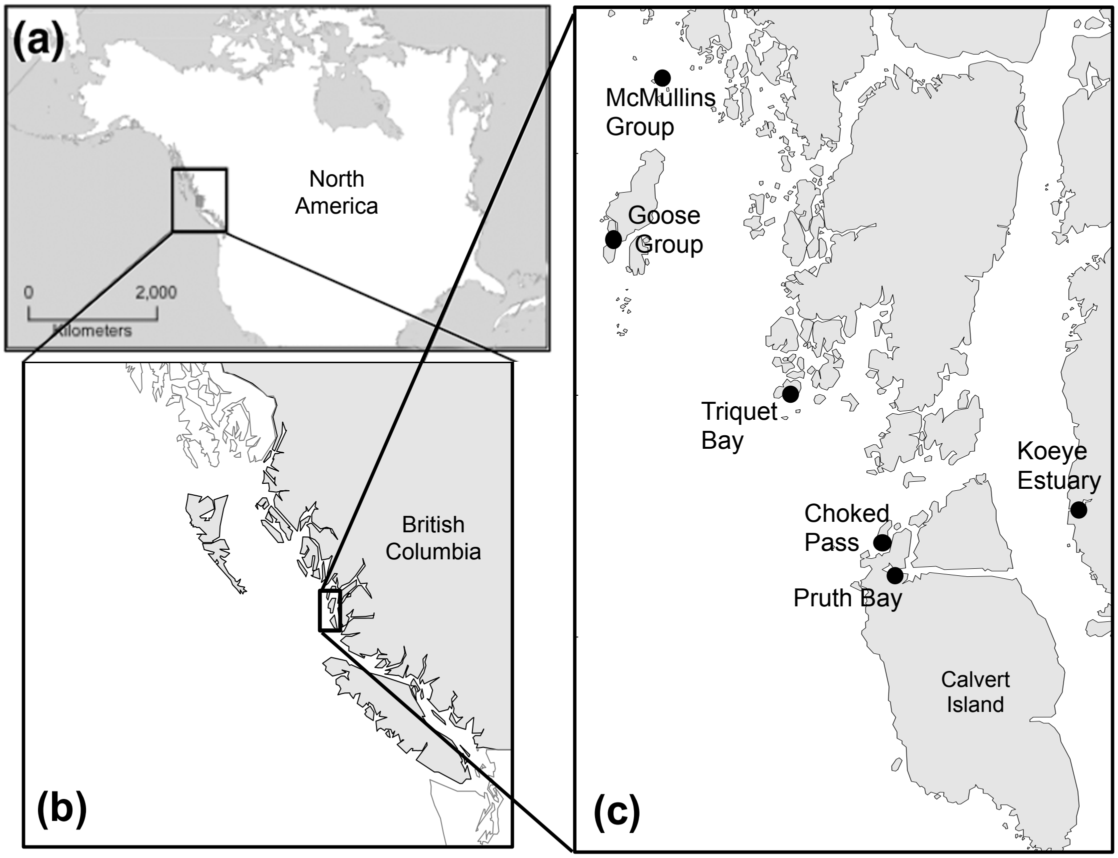

Figure 1: We sampled sediments within six eelgrass (*Zostera marina*) meadows located along the northwest coast of North America (a), on British Columbia's (b) Central Coast (c). Nine cores were obtained from three positions within each meadow (interior, edge and adjacent bare sediment). Specific sampling locations at each site are shown in Figure A.1. Figure adapted from Keeling et al. (2017).

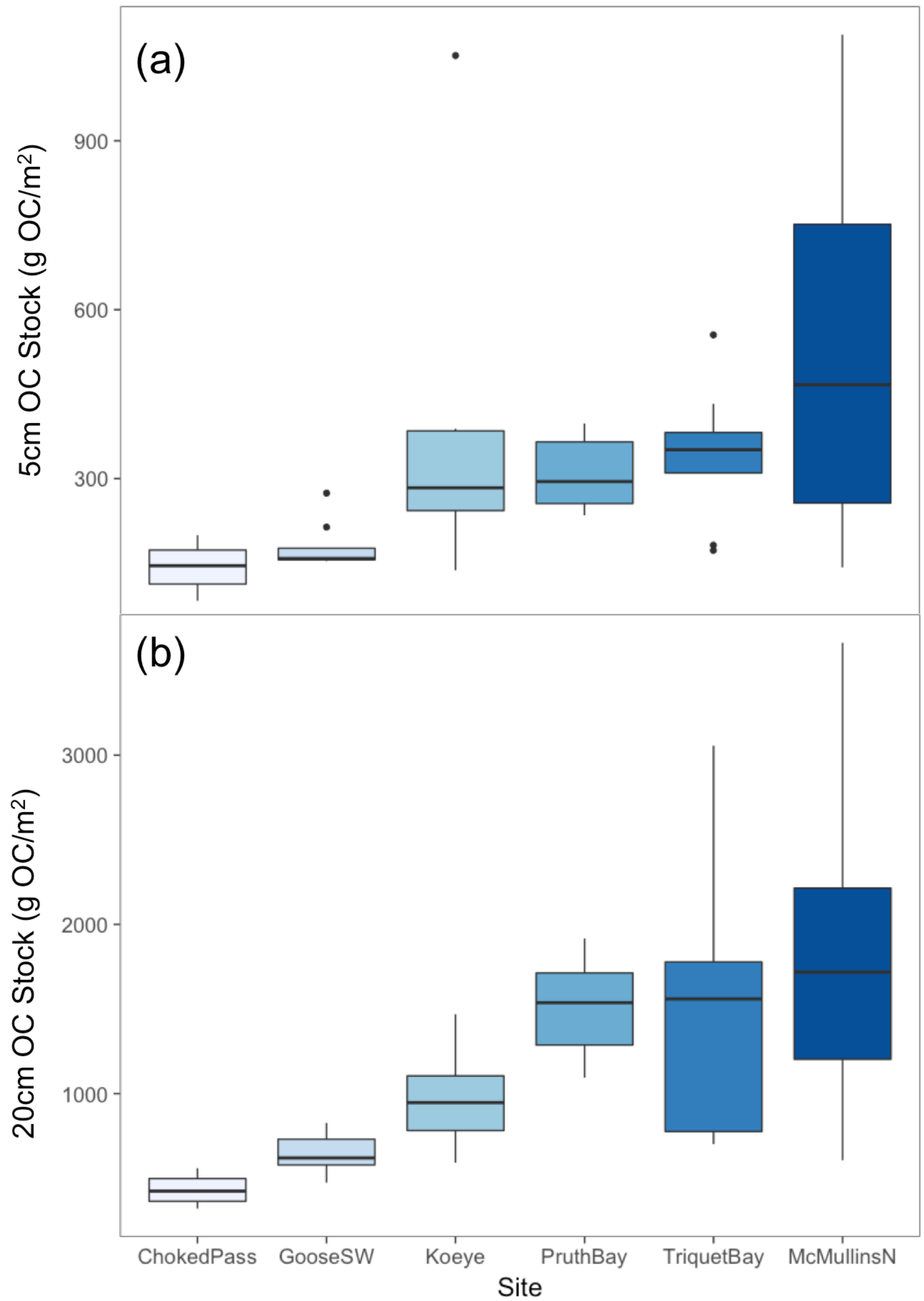

Figure 2: Surface organic carbon (OC) stocks in the top 5cm of sediment (a) and deeper OC stocks in the top 20cm (b) at each site sampled on the Central Coast of British Columbia, Canada. The middle line represents the median OC stock for each site, while the lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers extend to 1.5 times the inter-quartile range, while any points beyond the end of the whiskers are outlying points.

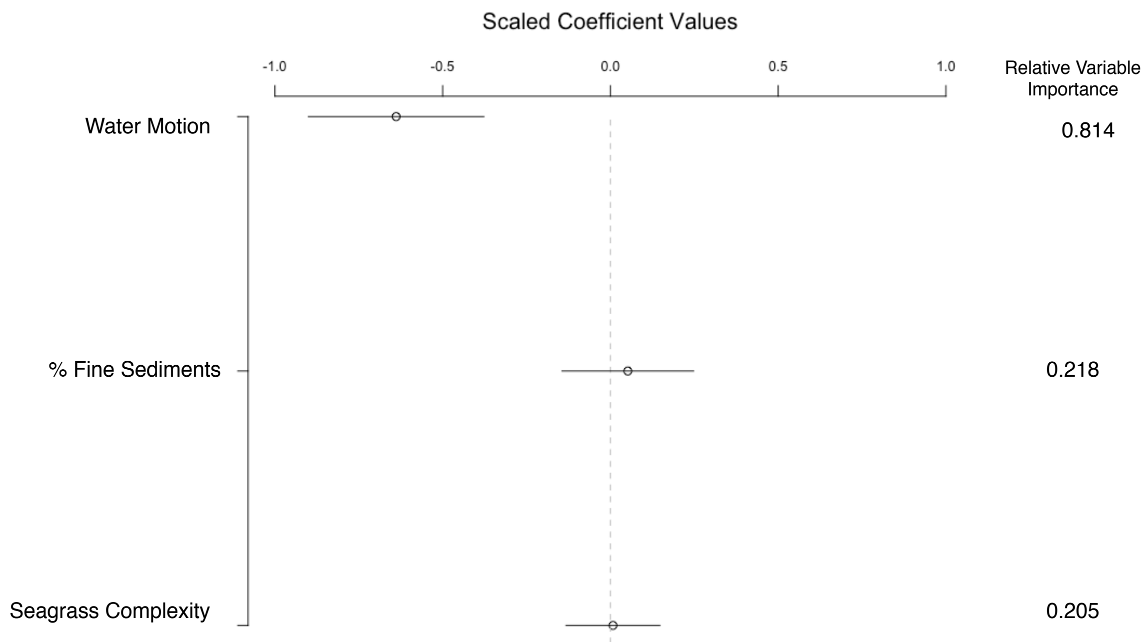

Figure 3: Scaled coefficient values (dots) and 95% confidence intervals (lines) for the three factors included in the generalized linear mixed effects model examining factors driving variation in surface organic carbon (OC) stocks (Table 3). Relative variable importance (RVI) values for each factor were calculated by summing the Akaike weights (W_i) of each model containing that factor. Estimates greater than 0 (dashed line) indicate a positive influence on OC stocks and vice versa. The 95% confidence intervals indicate the precision around the estimate of the effect; if the line crosses zero, there is little confidence in the direction and magnitude of the effect.

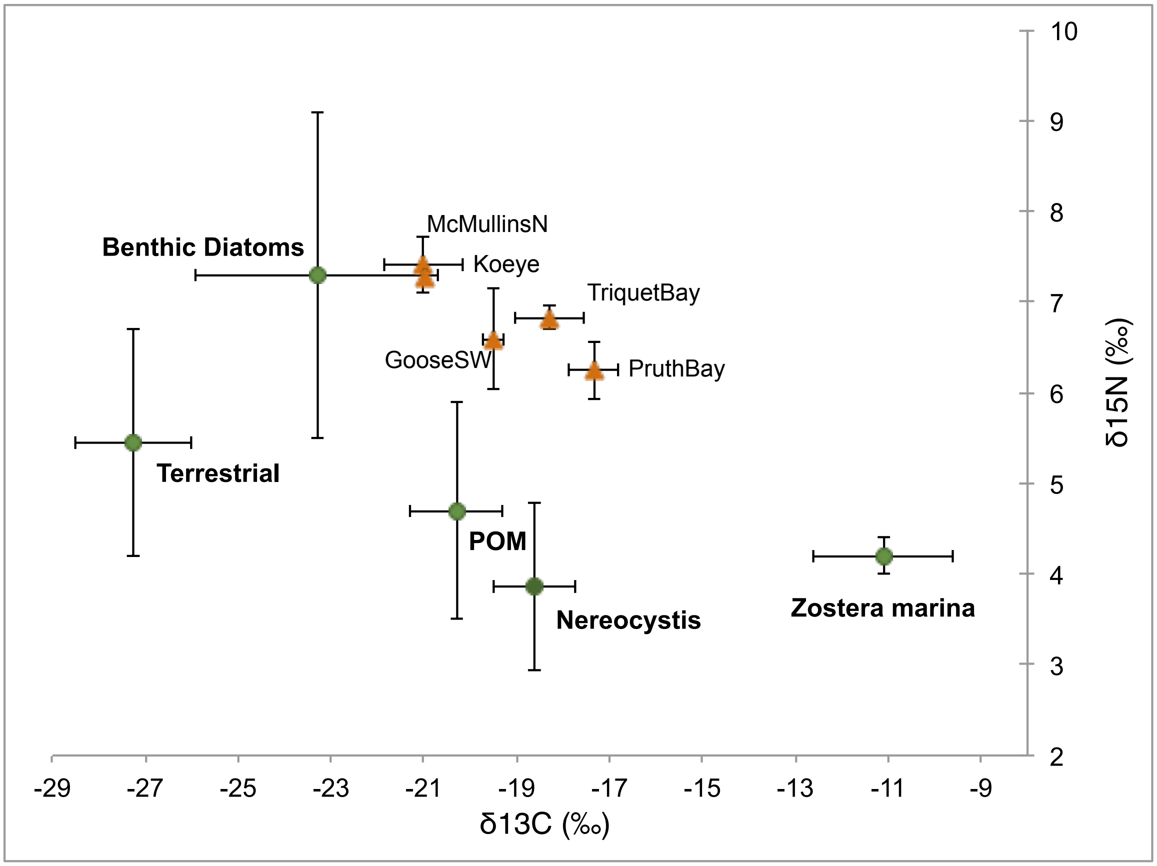

Figure 4: $\delta^{13}C$ and $\delta^{15}N$ signatures for sediment mixtures from five of the six sites sampled (orange triangles) and from potential OC sources (green circles). Choked Pass is not shown, as sediment N values were too low to conduct isotopic analyses. Error bars are standard errors for sediment mixtures and standard deviations for sources, for ease of visualization. Benthic diatom signatures are from 51 benthic diatom samples in San Francisco Bay Estuary (Cloern et al., 2002); POM data represent the mean value for the Central Coast of British Columbia, *Zostera marina* signatures are from Choked Pass, Central Coast, BC (Olson et al. 2015); terrestrial values represent the range reported in Cloern et al. (2002).

Tables

(a) Response (n=54): Top 5cm Organic Carbon Stock (g OC/m^2)							
Model	**K**	**Log L**	**AIC_c**	**ΔAIC_c**	**DF**	**W_i**	**$adjR^2$**
Site*Position	2	-307.08	674.5	0	19	0.795	0.798
Site	1	-330.393	677.2	2.71	7	0.205	0.522
Null	1	-350.31	704.9	30.34	2	0	0
Position	1	-349.601	708	33.5	4	0	0.0260
(b) Response (n=53): Top 20cm Organic Carbon Stock (g OC/m^2)							
Model	**K**	**Log L**	**AIC_c**	**ΔAIC_c**	**DF**	**W_i**	**$adjR^2$**
Site	1	-384.506	785.5	0	7	1	0.683
Site*Position	2	-374.792	810.6	25.11	19	0	0.781
Null	0	-414.981	834.2	48.7	2	0	0.061
Position	1	-413.322	835.5	49.98	4	0	0

Table 1: Strength of evidence for alternative candidate models explaining variation in (a) surface (5cm) and (b) 20cm organic carbon (OC) stocks. Models with varying numbers of parameters (K) were ranked by differences (Δ) in small sample size corrected Akaike Information Criterion (AIC_c) based on their log likelihoods (Log L) and K. Akaike weights (W_i) were calculated as the relative likelihood of each model (exp(-0.5*ΔAIC_c) divided by the sum of the relative likelihoods across all models. Adjusted R-squared values ($adjR^2$) were calculated based on the sample size (n) and the number of parameters in the model (K). All values were calculated using the MuMIN package in R.

Site	Sediment Accumulation Rate (g/m^2×yr)	OC Density (mg OC/cm^3)	CRS OC Accumulation Rate (g OC/m^2×yr)	CIC OC Accumulation Rate (g OC/m^2×yr)	Age of Top 20cm (years)	Age-based OC Stock (g OC/m^2 ×50 years)
McMullins North	7507.9 (3028.9)	7.4 (1.9)	50.45 (29.06)	25.14	74 (25)	2724.3
Triquet Bay	4056.8 (18054.0)	11.0 (2.4)	41.31 (15.39)	35.44	58 (11)	2230.7
Pruth Bay	4375.8 (2593.1)	10.7 (4.3)	32.31 (14.17)	34.37	65 (38)	1744.7
Koeye	12619.8 (4039.8)	2.0 (1.8)	25.74 (20.14)	39.79	21 (9)	1390.0
Choked Pass	10727.3 (4075.6)	1.8 (1.5)	12.57 (12.46)	9.00	53 (34)	678.8
Goose SW	*No excess ^{210}Pb					

Table 2: Geochronological analyses (^{210}Pb dating) and elemental analysis of carbon content were used to estimate mean (±SD), sediment accumulation rates, organic carbon (OC) densities, Constant Rate of Supply (CRS) OC accumulation rates, Constant Initial Concentration (CIC) OC accumulation rates, and the age of the top 20cm of sediment. Aged-based (in contrast with depth-based) OC stocks were calculated by multiplying the OC accumulation rate (g OC/m^2 × year) for each site by the average number of years that 20cm represents (54 years). Note that Goose SW did not have enough excess ^{210}Pb to obtain age or accumulation rate estimates.

Response (n=36): Top 5cm Organic Carbon Stock (g OC/m^2)							
Model	**K**	**Log L**	**AIC_c**	**ΔAIC_c**	**DF**	**W_i**	**$adjR^2$**
Water Motion	1	-212.22	433.7	0	4	0.512	0.601
Water Motion + % Fines	2	-212.183	436.4	2.64	5	0.137	0.601
Water Motion + Seagrass Complexity	2	-212.217	436.4	2.7	5	0.133	0.601
Null	0	-215.063	436.9	3.14	3	0.106	0.532
% Fines	1	-214.796	438.9	5.15	4	0.039	0.539
Water Motion + Seagrass Complexity + % Fines	3	-212.182	439.3	5.53	6	0.032	0.601
Seagrass Complexity	1	-215.062	439.4	5.68	4	0.03	0.532

Table 3: Strength of evidence for alternative candidate models explaining variation in surface (5 cm) organic carbon (OC) stocks. Models with varying numbers of parameters (K) were ranked by differences (Δ) in small sample size corrected Akaike Information Criterion (AIC_c) based on their log likelihoods (Log L) and K. Akaike weights (W_i) were calculated as the relative likelihood of each model ($\exp(-0.5 * \Delta AIC_c)$ divided by the sum of the relative likelihoods across all models. Adjusted R-squared values ($adjR^2$) were calculated based on the sample size (n) and the number of parameters in the model (K). All values were calculated using the MuMIN package in R.

Region	Seagrass Species	Reference	OC Stocks (g OC/m²)	
			Depth (cm)	Range
British Columbia	*Zostera marina*	This Study	5	83 - 1089
			10	123 - 2652
			20	21 - 3665
			25	185 - 5545
			50	1207 - 5073
Baltic Sea	*Zostera marina*	Jankowska et al. 2016	10	50.2 - 228
Finland & Denmark	*Zostera marina*	Rohr et al. 2016	25	627 - 4324
Northern Europe	*Zostera marina*	Dahl et al. 2016	25	500 - 3500
Australia	Multiple species	Lavery et al. 2013	25	262 - 4833
Asia	Multiple Species	Miyajima et al. 2015	100	3800 - 12000
Global	Multiple Species	Fourqurean et al. 2012	100	19420
Mediterranean Sea	*Posidonia oceanica*	Serrano et al. 2014	100	1800 - 7400

Table 4: Comparison of organic carbon (OC) stocks from this study (all sites combined) to values obtained from published literature for *Zostera marina* meadows as well as other seagrass species.

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Appendix.

Supplemental Figures and Tables

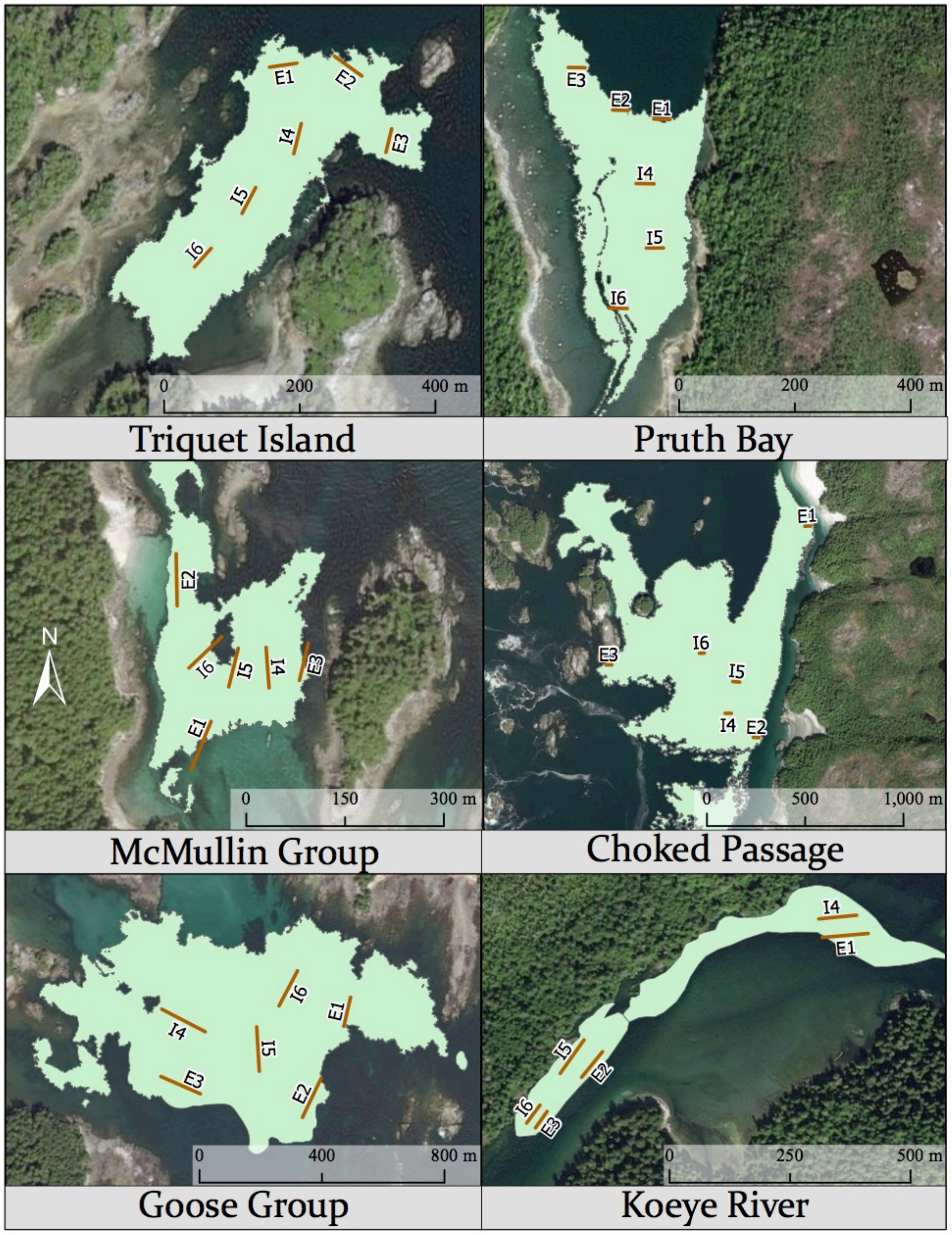

Figure A.1: The position of sampling transects (brown lines) within each of the six *Zostera marina* meadows sampled (panels) on the Central Coast of British Columbia, Canada. For unvegetated cores, divers swam approximately five meters out from the current edge of the meadow, perpendicular to edge transects 1-3. See Figure 1 for larger study area overview.

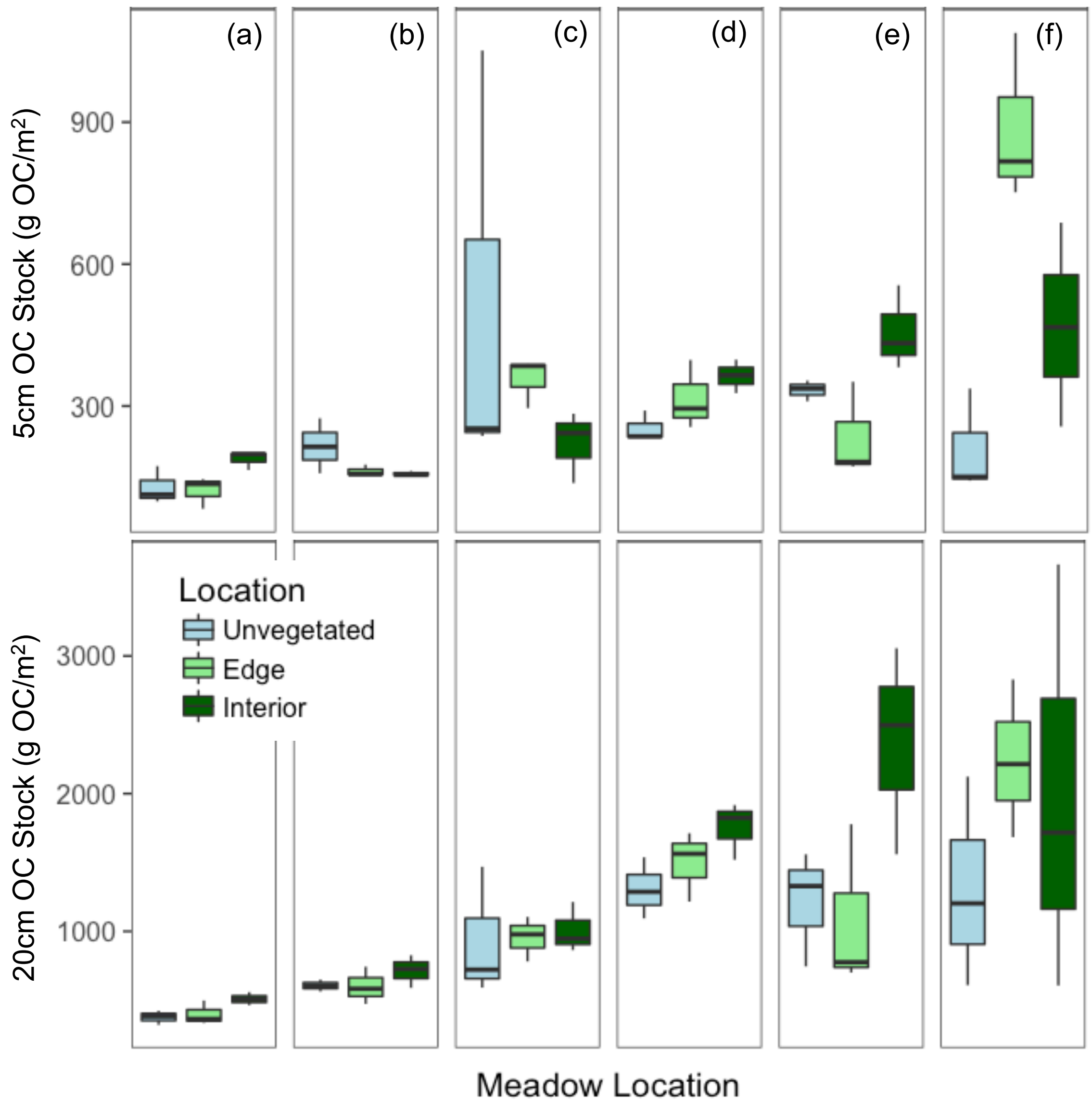

Figure A.2: Surface organic carbon (OC) stocks in the top 5cm (top row) and the top 20cm (bottom row) shown for each site (Choked Pass, Goose SW, Koeye, Pruth Bay, Triquet Bay, McMullins N; columns a-f respectively) and the three positions within each site - interior (dark green), edge (light green) and unvegetated (blue). The middle line represents the median OC stock for each site, while the lower and upper hinges correspond to the first and third quartiles. The upper and lower whiskers extend to 1.5 times the inter-quartile range, while any points beyond the end of the whiskers are outlying points.

Site	Meadow Size (m^2)	Seagrass Density (shoots m^{-2})	Canopy Height (m)	Canopy Complexity (m/m^2)	BG Biomass (mg/cm^3)	AG Biomass (g/shoot)
PB	34982	215.6 (128.1)	80.8 (27.5)	140.99 (61.40)	0.66 (0.37)	0.74 (0.60)
CP	354580	79.6 (13.2)	110.2 (19.5)	86.36 (13.95)	1.25 (0.74)	1.81 (0.91)
KY	26238	125.7 (32.4)	164.1 (38.7)	186.50 (66.37)	0.94 (0.59)	1.21 (0.64)
TB	31074	124.2 (77.1)	98.2 (30.3)	112.50 (35.89)	1.65 (1.15)	1.71 (0.87)
MC	22778	102.9 (37.4)	85.1 (23.3)	99.76 (50.53)	1.17 (0.71)	1.27 (0.57)
GO	215570	107.8 (44.8)	84.9 (20.0)	95.30 (48.53)	1.30 (1.00)	1.05 (0.54)

Table A.1: Seagrass characteristics (means ± SD) in each of the six meadows sampled in August 2016. PB = Pruth Bay, CP = Choked Pass, KY = Koeye Estuary, TB = Triquet Bay, MC = McMullins N, GO = Goose SW. Meadow areas are derived from unmanned aerial vehicle (UAV) imagery. Densities and canopy heights are averages from quadrats along edge (n=3) and interior (n=3) transects (n=6 transects/meadow). Canopy complexity was calculated by multiplying density × canopy height (vertical meters (m) of seagrass/m^2). Belowground (BG) biomass is root and rhizome biomass (mg) per cubic centimeter of sediment, while aboveground (AG) biomass is the average mass of an individual shoot.

Site	Chart Datum Depth (m)	Water Motion (g lost/hr)	% Fines (<63µm)	Woody Debris Proportion	Top 5cm Sediment δ13C (‰)	% Organic Carbon	% Inorganic Carbon
PB	-0.03 (0.87)	0.59 (0.01)	6.17 (2.91)	0.4 (0.4)	-17.28 (0.54)	0.57 (0.10)	0.18 (0.24)
CP	3.34 (1.38)	2.48 (0.16)	0.12 (0.05)	0.1 (0.1)	-18.77 (2.33)	0.15 (0.02)	0.98 (0.63)
KY	0.16 (0.32)	0.97 (0.14)	0.83 (0.79)	0.3 (0.4)	-21.48 (3.39)	0.35 (0.18)	0.96 (1.06)
TB	0.77 (0.87)	1.53 (0.50)	0.98 (0.72)	0.3 (0.4)	-18.65 (3.12)	0.69 (0.29)	4.54 (2.68)
MC	0.56 (0.87)	0.70 (0.14)	0.57 (0.27)	0.8 (0.3)	-21.07 (0.93)	0.71 (0.37)	1.76 (2.39)
GO	2.45 (1.09)	1.01 (0.02)	0.20 (0.11)	0.5 (0.5)	-19.17 (0.81)	0.26 (0.07)	2.70 (2.43)

Table A.2: Physical and sediment characteristics (means ± SD) in each of the six meadows sampled in August 2016. PB = Pruth Bay, CP = Choked Pass, KY = Koeye Estuary, TB = Triquet Bay, MC = McMullins North, GO = Goose Southwest. Water depths were calculated by subtracting the tidal height (m) from the recorded water depth (m) during SCUBA surveys; negative depths indicate intertidal, positive depths indicate subtidal. Water motion is the relative dissolution rate of Plaster of Paris blocks in grams lost/hour. Percent (%) fines is the proportion of sediments passed through the 63µm sieve. Woody debris proportion is the proportion of 5cm depth intervals per core containing woody debris deposits. $\delta^{13}C$ values are from the top 5cm of sediment, while % organic and inorganic carbon values are per core averages from each site.

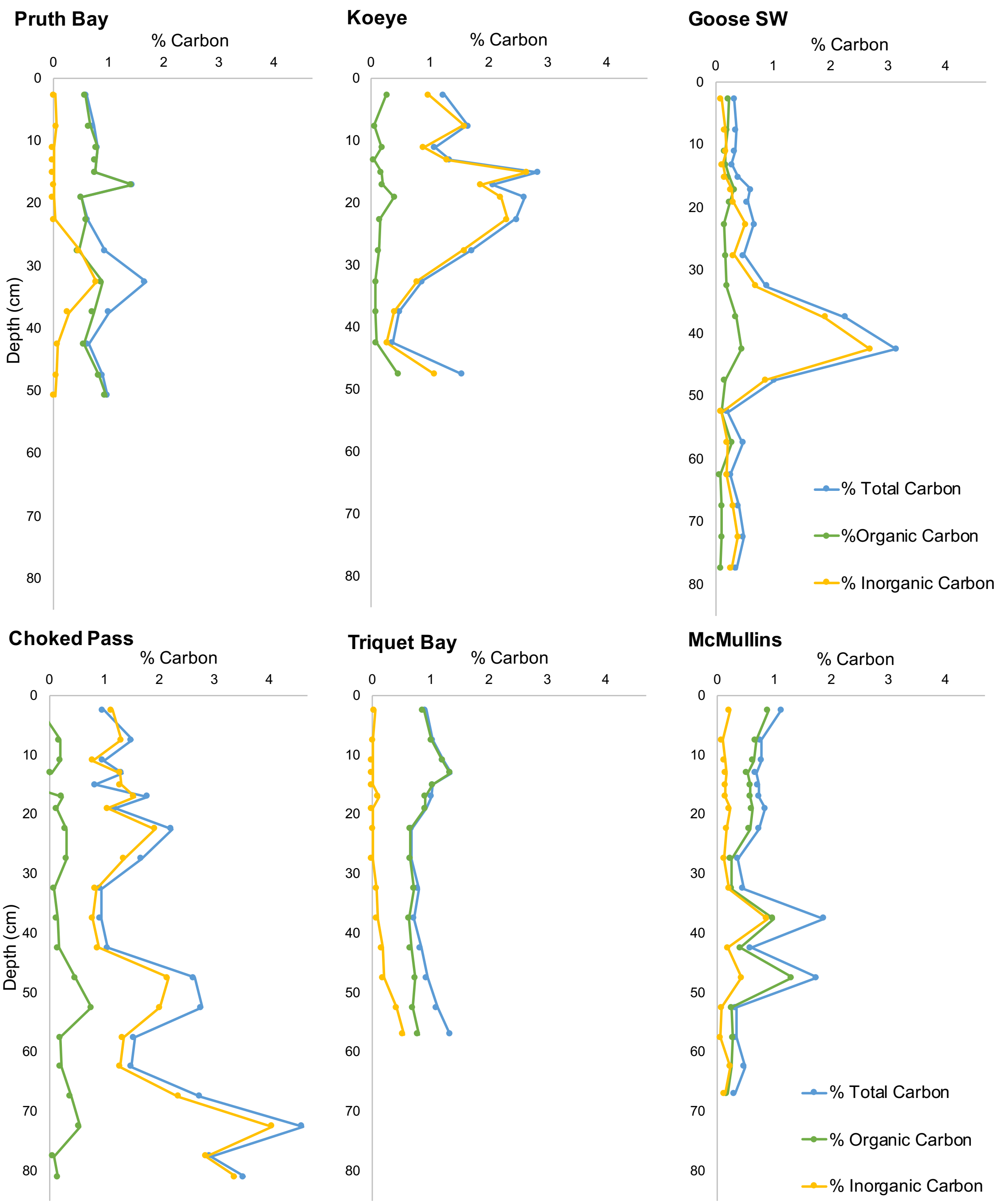

Figure A.3: Profiles for the six long sediment cores collected from each site, showing changes in % total carbon (blue), % inorganic carbon (yellow) and % organic carbon (green) with depth (cm).