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The sediment carbon stocks of intertidal seagrass meadows in Scotland

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Abstract

Seagrasses are highly productive ecosystems and hotspots for biodiversity, providing a plethora of benefits to the environment and to people. Their value in sequestering and storing carbon is increasingly being recognised, as the world searches for ways to mitigate the effects and slow the pace of climate change. However, many uncertainties remain, with basic information such as average carbon stocks, variability and species-specific differences missing for many regions. This study evaluates, for the first time, the carbon storage capacity of *Zostera noltii* and *Zostera marina* from intertidal seagrass meadows in Scotland. Sediment carbon stocks in the top 50cm from vegetated and reference unvegetated plots were quantified at 10 estuaries distributed along the Scottish east and west coasts. The organic carbon stocks in the top 50 cm of the seagrass sediment ranged from a minimum of 14.94 Mg C ha^{-1} at the Moray Firth to a maximum of 105.72 Mg C ha^{-1} at the Firth of Forth, with a mean (±SD) of 54.79 ± 35.02 Mg C ha^{-1} across the 10 estuaries sampled. Moreover, seagrass areas showed enhanced carbon storage compared to reference unvegetated ones, however this was highly variable across depth, and among sites and estuaries. This paper addresses key gaps in knowledge concerning the role of intertidal Scottish seagrass meadows as carbon sinks and discusses the implication of this emerging information for their effective management and conservation.

Keywords: blue carbon; *Zostera marina*; *Zostera noltii;* eelgrass; sediment

1. Introduction

Seagrass meadows, along with mangrove forests and tidal marshes - collectively termed coastal blue carbon habitats - are considered to be among the most productive and valuable ecosystems on the planet (Barbier et al., 2011). These habitats provide a wide range of ecosystem services. For example, they act as nursery sites, foraging grounds and predator refuges; they filter the water by recycling nutrients and removing pathogens; and they improve coastal safety by stabilising the sediment bed level (Costanza et al., 1997; Green and Short, 2003; Nordlund et al., 2016; Potouroglou et al., 2017).

Despite their importance, these vegetated coastal habitats have suffered rapid and extensive loss and degradation worldwide, with 29% of seagrass meadows, 50% of tidal marshes and >35% of mangrove forests being lost over the last 20-50 years (Barbier et al., 2011; Mcleod et al., 2011; Waycott et al., 2009). Of the known distribution of seagrasses, only one quarter (26 %) occurs within Marine Protected Areas (MPAs). In contrast, 40 % of warm-water coral reefs, 43 % of mangroves, 42 % of saltmarshes and 32 % of cold-water corals are found in MPAs, making seagrasses the least protected major marine ecosystem (United Nations Environment Programme, 2020). Most seagrass losses have been driven by poor coastal zone management creating increases in nutrient concentrations and decreases in water clarity (Short and Wyllie-Echeverria, 1996). In the British Isles, there is strong evidence that most seagrass meadows have been detrimentally affected as a result of excess nutrients and turbid conditions, along with other anthropogenic impacts, such as moorings and anchoring (Green et al., 2021; Jones and Unsworth, 2016).

International climate and conservation discussions have recently focused on blue carbon habitats due to the growing recognition of their role as sites of significant carbon sequestration and storage (Himes-Cornell et al., 2018). Despite early evidence indicating that marine macrophytes can act as global carbon sinks (Smith, 1981), little policy attention was paid to carbon storage in these environments before Nellemann et al. (2009) defined ‘blue carbon’ as ‘the carbon stored and sequestered in coastal and marine ecosystems, including tidal and estuarine salt marshes, seagrass meadows, and mangrove forests’. Although estimates of the organic carbon stocks of tidal salt marshes and mangroves have been readily available, there are still large uncertainties in the figures for seagrass meadows. The large variation among datasets demonstrated by a range of studies reveals the challenge of using global estimates, or those derived from other areas, as proxies for assessing local carbon budgets (Dahl et al., 2016; Fourqurean et al., 2012; Lavery et al., 2013; Miyajima et al., 2017; Röhr et al., 2018). In addition, unvegetated areas adjacent to seagrass meadows are usually not included in such analyses. Including unvegetated areas in sampling design is important, since large stocks of sedimentary organic carbon may occur in coastal sediments free of vegetation. In assessing the current and potential contribution of seagrass to carbon storage, their 'net impact' - the difference in storage between vegetated and unvegetated sediments - is of most relevance.

The World Atlas of Seagrasses indicates that Scotland has more records of seagrass meadows than much of the Western European coastline (Green and Short, 2003). These records typically include only 'presence' data although two noteworthy exceptions provide additional information on coverage (Davison and Hughes, 1998): firstly, the 1200 ha of intertidal meadows of *Zostera marina* and *Zostera noltii* in the Moray Firth Special Area of Conservation (SAC) (east coast) (RSPB, 1995), within which Cromarty Firth is considered to have the largest seagrass meadow in the UK; secondly, the Solway Firth SAC (west coast) with a coverage of 200 ha (Hawker, 1993). To date there are no complete estimates of the total areal extent in Scotland, with the most conservative figure being 1600 ha (Burrows et al., 2014). In addition, a recent study reported a seagrass area of 1316 ha (with moderate to high confidence) for the whole of the UK; however, the authors acknowledge that inconsistences and inaccuracies occur within the datasets, with as much as a 30000-fold difference between documented and actual (ground-truthed) areas (e.g. in Hawaii, USA) (McKenzie et al., 2020). The growing interest in developing a blue carbon strategy in Scotland has led to an audit of the potential blue carbon resources in the coastal waters around Orkney (Porter et al., 2020), which includes subtidal seagrass meadows, whereas other published reports include seagrass values derived from the literature (e.g. average global sequestration rates or standing stocks) (Burrows et al., 2014, 2017). The carbon stocks of intertidal Zostera meadows for the whole of Scotland have yet to be quantified, and published carbon stocks estimates for *Zostera noltii* globally are very limited. To fill a major gap in available knowledge, the carbon storage capacity of the intertidal seagrasses *Zostera noltii* and *Zostera marina* was evaluated in Scotland, to the best of our knowledge for the first time. Our study aimed a) to quantify the sedimentary carbon stocks of intertidal seagrass meadows and of appropriate reference unvegetated areas, in order to infer the impact of seagrass on sediment carbon storage in Scotland, and b) to describe the variability between a range of different estuaries.

2. Materials and Methods

2.1 Study sites and samples collection

The study was conducted at 22 sites in 10 estuaries, distributed along the east - from the Firth of Forth in the south to Dornoch Firth in the north - and the west - from Solway Firth in the south to Clyde Firth in the north - coastlines of Scotland (Fig.1; Table 1). The sites were chosen to be representative of intertidal seagrass meadows around Scotland that are normally located in protected, muddy to sandy bed types. Out of the 22 sites, 11 contained only *Zostera noltii* or *Zostera marina* (monospecific meadows) and 11 contained both species (dispecific meadows) (Table 1). At each site, 1-5 sediment cores were taken from vegetated and unvegetated areas (in the interior of the meadow) from June to September (peak seagrass growing season) at low tide, sampling all the seagrass species present to capture all potential variability. A total of 92 cores were collected, 51 from vegetated plots and 41 from adjacent unvegetated areas within the seagrass meadow (Table 1). Unvegetated areas were identified as reference sites for vegetated areas on the basis of proximity; in some cases, a single unvegetated area was used as a reference for more than one vegetated area where it was equidistant. All east coast sediment cores and those at Rockcliffe (west coast) were collected by driving a Russian peat corer into the sediment to a depth of 50cm or until refusal was reached. The sites along the west coast, except Rockcliffe, were sampled using 0.5 m and 1m PVC pipes (internal diameter 53 mm). The pipes were pushed down gradually until refusal. If the pipe was not submerged to 40 cm, it was hammered to 50cm, where possible. The cores were then removed using suction created by rubber stoppers. Due to the potential disturbance of the PVC method, the samples were continually measured to provide accurate depth values before and after extraction from the study sites, and then before being removed from the pipes at the laboratory to produce an accurate compaction factor (ranging from 0.78 to 0.94) (Howard et al., 2014). After collection, each sediment core was carefully packed by opening the corer chamber and moving the sediment onto a longitudinally sliced piece of plastic tubing of suitable internal diameter. The sediment was covered with cling film and stored at ambient temperature to protect it from compaction and desiccation during transport to the laboratory. The cores sampled with PVC pipes were transported to the lab upright to reduce potential mixing and disturbance. GPS coordinates and a 50 × 50 cm photo quadrat were taken at each core location. Seagrass cover (%) and species composition in each quadrat were obtained through visual estimates (Table 1).

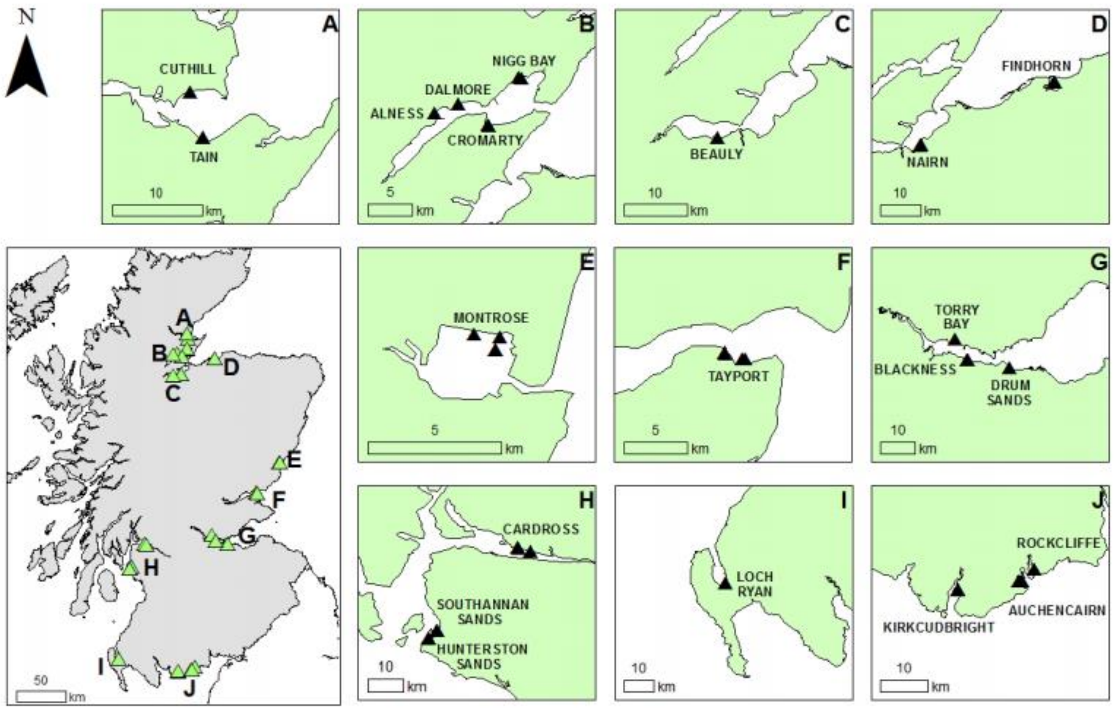


Figure 1. Location of seagrass meadow sampling sites along the East and West coasts of Scotland (A: Dornoch Firth, B: Cromarty Firth, C: Beauly Firth, D: Moray Firth, E: Montrose Basin, F: Tay Estuary, G: Firth of Forth, H: Clyde Firth, I: Loch Ryan, J: Solway Firth).

Table 1. Summary of the cores collected from both vegetated and unvegetated sediments across Scotland. (Zn: *Zostera noltii*; Zm: *Zostera marina*; Seagrass cover is presented as a range of minimum and maximum values*)*

Coast	Estuary	Sites	Type of seagrass meadow/species	Number of cores		Seagrass cover %
				Vegetated	Unvegetated	
East Coast	**Forth**	Blackness	Dispecific	3	2	50-98
		Drum Sands	Monospecific- Zn	2	2	3-25
		Torry Bay	Monospecific- Zn	2	1	50-55
	Tay	Tayport (1)	Monospecific- Zn	2	2	45-60
		Tayport (2)	Monospecific- Zm	3	3	15-70
	Montrose	Montrose	Dispecific	5	5	30-100
	Beauly	Beauly	Dispecific	4	2	30-60
	Moray	Findhorn	Monospecific- Zn	2	2	60-70
		Nairn	Dispecific	3	2	25-65
	Cromarty	Nigg Bay	Dispecific	2	2	15-45
		Dalmore	Dispecific	2	1	30-70
		Alness	Monospecific- Zn	1	1	25
		Cromarty	Dispecific	2	2	30-55
	Dornoch	Tain	Dispecific	3	1	15-65
		Cuthill	Dispecific	3	1	5-10
West Coast	**Solway**	Auchencairn	Dispecific	3	3	-
		Rockcliffe	Dispecific	2	2	-
		Kirkcudbright	Monospecific- Zn	1	1	-
	Loch Ryan	Loch Ryan	Monospecific- Zn	1	1	-
	Clyde	Southannan Sands	Monospecific- Zn	1	1	-
		Hunterston Sands	Monospecific- Zn	1	1	-
		Cardross	Monospecific- Zn	3	3	-
Total	**10**	**22**	**Dispecific (11); Monospecific-Zn (10); Monospecific-Zm (1)**	**51**	**41**	

2.2. Sediment processing and analysis

On arrival at the laboratory, the samples were sliced into 1 cm sections for the first 6cm, 2 cm sections down to 30 cm and then into 5cm sections down to 50 cm. Subsamples of 5 cm^3 of each slice, taken with a volumetric spoon, were used for the determination of dry bulk density (DBD), organic matter (OM) and organic carbon content (OC). Each sediment subsample was dried at 60 °C until constant weight was reached. DBD was calculated as follows and expressed in g cm^{-3}.

$$\text{DBD}=\frac{\text{Dry weight}}{\text{Volume of sample}}$$

Organic matter was measured by Loss on Ignition (LOI). Aliquots (ca. 1 g) of each dried sediment sample were transferred to pre-weighed porcelain crucibles which were put in a muffle furnace and subjected to a temperature of 500°C for 6 hours (Howard et al., 2014; Oreska et al., 2017). The crucibles were transferred to a desiccator to prevent moisture re-uptake. When the samples had cooled down to room temperature, their weight was recorded. LOI was used to calculate the % OM as follows.

$$\%\ \text{OM}=\frac{\text{Initial Dry Weight-Weight remaining after furnacing}}{\text{Initial Dry Weight}}\times 100$$

The most accurate method to calculate OC is by using an elemental analyser for each sample. Based on a seagrass global dataset, two equations that strongly correlate organic matter (% OM) to organic carbon content (% OC) have been suggested (Fourqurean et al., 2012; Howard et al., 2014). As there is a large range of values reported in the scientific literature, the standard ratios deriving from these equations could still introduce errors to the calculations. To improve the accuracy for our dataset, a subset of samples (26 in total) was used to measure total organic carbon content, using an automated elemental analyser (Fisons NA1500). An aliquot (ca. 60mg) of the dried sediment was first acidified with weak HCl (1-2M) to remove carbonates (Carabel et al., 2006). % OC values were plotted against % OM of the same subset of samples. The resulting linear regression equation

$$\% \, OC = (0.41 \times \% \, \mathrm{OM}) - 0.13$$

($r^2=0.59$, $p<0.001$, $SE_{intercept} = 0.07$, $SE_{slope} = 0.18$) was applied to all % OM values to convert them to % OC. Although we recognise that converting % OM to % OC does not overcome uncertainty introduced by the variation in OM composition, using LOI followed by conversion to % OC allowed for much higher replication (because of low cost) in our study and thus may give a better integrated estimate of notoriously spatially variable data.

The organic carbon density (g C cm^{-3}) was calculated by multiplying the dry bulk density by organic carbon content at a specific depth. A series of linear regression analyses of the change in organic carbon density as a function of sediment depth were run for both vegetated and unvegetated cores. The depth profiles were categorised as 'decreasing' when the slope was negative and significant (at a = 0.05), 'increasing' when the slope was positive and significant, or 'mixed' for non-significant profiles, following the methods described in Kindeberg et al.(2019).

2.3. Organic carbon stocks calculations and downcore difference in organic carbon density between vegetated and unvegetated cores

The sediment organic carbon stock (g C cm^{-2}) per sampled depth interval was calculated as follows:

$$Organic\ carbon\ stock = \text{sediment thickness or depth interval} \times Organic\ carbon\ density$$

The total sediment organic carbon stock from one core was determined by summing up the values of organic carbon stock at all depth intervals from the obtained samples (Howard et al., 2014). To allow comparison with other seagrass studies that have reported stocks to 100 cm depth, the CC100 stock was calculated by multiplying the CC50 stock by two, clearly indicated as projected organic carbon stock (Mg C ha^{-1}).

While the difference in stocks between vegetated and unvegetated cores can be achieved through simple subtraction, this does not provide any indication about the depth distribution of any OC enhancement in the vegetated sediments. To estimate the downcore distribution of any enhancement of organic carbon density in the vegetated cores, we subtracted the average 'background' organic carbon density from the organic carbon density profile measured in each depth interval of vegetated cores. The background density has been referred to as the 'reference plane', and its use is recommended by the Verified Carbon Standard methodology for determining the greenhouse gas offset potential of seagrass restoration projects (Emmer et al., 2015), and applied as a method for determining the organic carbon enhancement of sediment that can be attributed to seagrasses in a restored meadow (Oreska et al., 2020). While none of the sites in this study were restored sites, we have used the same methodology to assess any enhancement of carbon storage downcore in the vegetated sediments. The 'background' organic carbon density was calculated as the average of organic carbon density of all unvegetated cores within a site (Table S1). Deducting a single average 'background' density value from the entire seagrass organic carbon downcore profile allowed us to estimate any enhancement in the organic carbon that could be attributed to the presence of seagrass.

2.4. Data analysis

Statistical analyses were performed using Minitab 18. All data were checked for normality and homogeneity of variances. When assumptions were not met the data were log10 or log10(x+1) transformed. General Linear Models were used to test differences in sedimentary DBD and % OC between vegetated and unvegetated areas and estuaries. General Linear Models were used to test differences in sedimentary organic carbon stocks between vegetated and unvegetated areas, sites, estuaries, and types of meadow. Tukey HSD post hoc tests were used to determine significant differences and grouping. Regression analysis was performed to assess the relationship between the dry bulk density of the surface sediment (5cm and 10cm) and the average organic carbon stock of each vegetated core.

3. Results

3.1. Dry bulk density, organic carbon content and organic carbon density variation

The average (±SD) dry bulk density of the seagrass sediment across all sites was 1.31±0.25 g cm^{-3}, and ranged from 1.00±0.10 (Alness) to 1.55±0.09 g cm^{-3} (Loch Ryan) (Table 2). DBD of adjacent unvegetated areas ranged from 0.88±0.15 (Alness) to 1.63±0.10 g cm^{-3} (Southannan Sands), with an average of 1.29±0.24 g cm^{-3}, and was not significantly different than that of seagrass areas ($F_{1,1964}$=2.46; p=0.117).

The average organic carbon content (OC) % of dry weight (DW) of seagrass sediment across all sites was 0.88±0.90, and ranged from 0.26±0.26 (Nairn) to 2.52±2.69 (Tayport 1) (Table 2). The OC of adjacent unvegetated areas ranged from 0.16±0.12 (Cuthill) to 1.87±0.57 % of DW (Drum Sands), with an average of 0.71±0.55 % of DW (Table 2). Overall, the OC was significantly higher in seagrass sediments than adjacent unvegetated areas ($F_{1,1964}$= 24.38; p<0.001). OC of seagrass sediments varied significantly among sites ($F_{21,1065}$=27.34; p<0.001) and estuaries ($F_{9,1077}$= 30.62; p<0.001). The highest OC was found in the Firth of Forth, with an average (±SD) of 1.61±0.55 % DW and the lowest in Moray Firth with 0.27±0.24 % DW (Table 2).

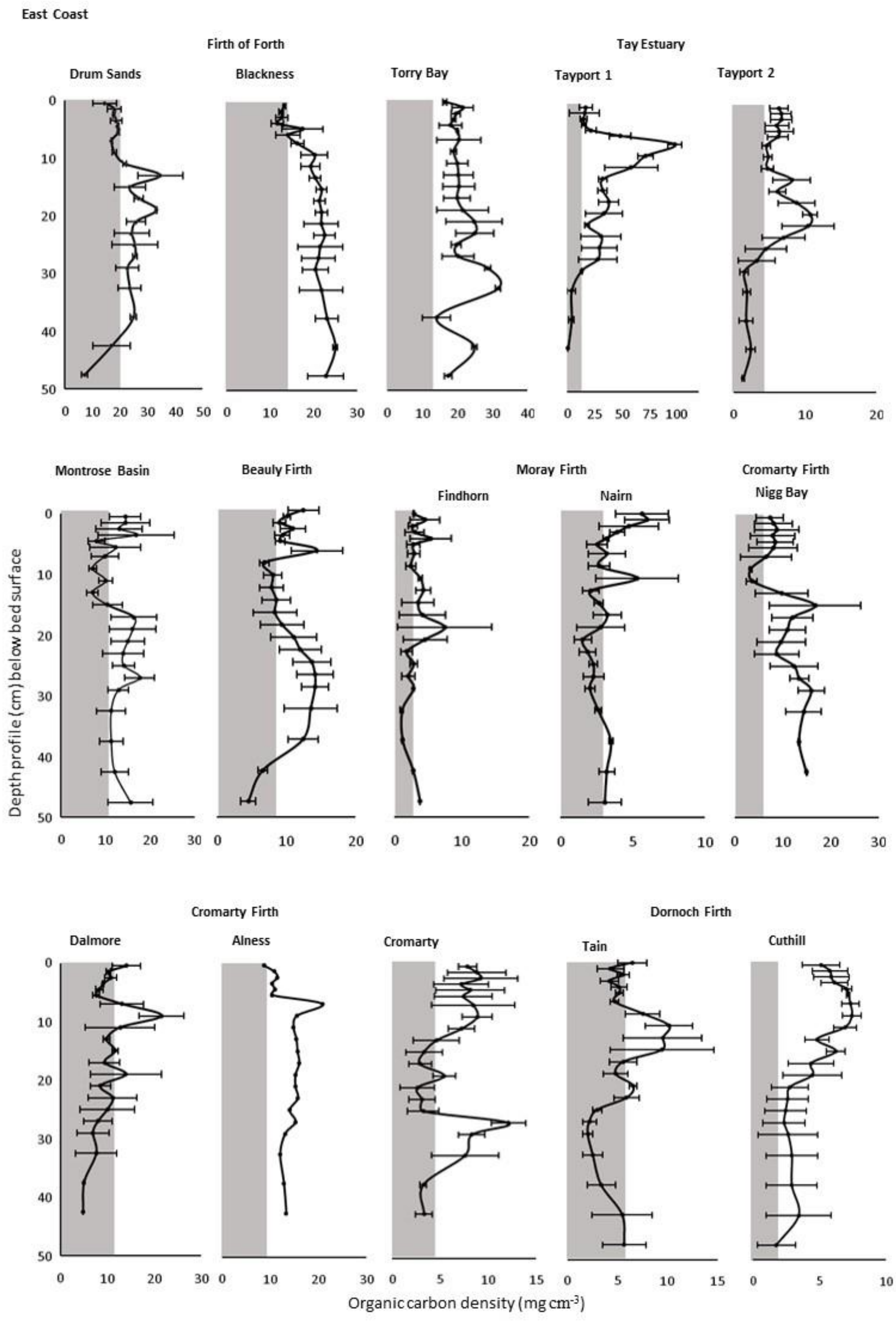
Out of the 51 seagrass cores, 9 displayed a 'decreasing', 8 an 'increasing' and 34 a 'mixed' depth profile of organic carbon density (Table S2; see also Fig. 2 for the depth profiles on a per site basis). The cores with a decreasing depth profile had the lowest mean (±SE) organic carbon density (6.04±1.24 mg C cm^{-3}) followed by the cores with mixed depth profile (11.71±1.24 mg C cm^{-3}), whereas the cores with an 'increasing' profile had the highest organic carbon density (13.28±1.99 mg C cm^{-3}). Out of the 41 unvegetated cores, 8 displayed a 'decreasing', 12 an 'increasing' and 21 a 'mixed' depth profile (Table S3; see also Fig. S1 for the depth profiles on a per site basis). The average organic carbon density of the cores displaying 'decreasing' and 'mixed' depth profiles were almost equal (8.07±1.83 and 8.00±1.04 mg C cm^{-3}, respectively), whereas the cores with an 'increasing' profile had the highest organic carbon density (10.5±1.50 mg C cm^{-3}).

3.2. Sediment organic carbon stocks

The organic carbon stocks over the 50cm (CC50) for each site, estuary and coast for seagrass and respective unvegetated sediments are shown on Table 2. The average organic carbon stock CC50 (± SD) for the seagrass sediments across the 10 estuaries sampled was 54.79 (± 35.02) Mg C ha^{-1}, with 55.23 (± 37.96) Mg C ha^{-1} and 53.38 (± 24.42) Mg C ha^{-1} for the East and West coast, respectively. The CC50 of seagrass sediments varied significantly among estuaries ($F_{9,41}$= 6.18; $p<0.001$) (Fig. 3; Table 2). The Firth of Forth had twofold to sevenfold higher CC50 (105.72 ± 13.13 Mg C ha^{-1}) than the rest of the studied estuaries across both coasts, whereas CC50 was the lowest in Moray Firth (14.94±3.83 Mg C ha^{-1}). The range of variation in seagrass carbon stocks between sites, from 14.55±6.25 (Findhorn) to 134.73±23.12 Mg C ha^{-1} (Tayport 1), was also substantial (Table 2) ($F_{21,29}$=10.07; $p<0.001$). The CC50 of monospecific *Z. noltii* meadows (68.90±42.10 Mg C ha^{-1}) was higher than monospecific *Z. marina* meadows (23.11±8.17 Mg C ha^{-1}) and dispecific meadows (50.69±26.69 Mg C ha^{-1}) (Fig. 4), although not significantly different ($F_{2,48}$=2.97; p=0.061). The CC50 of the seagrass cores was neither related to the sediment dry bulk density of the top 5 cm (R^2=0.03, $F_{1,49}$=1.7, p=0.198), nor the top 10cm (R^2=0.01, $F_{1,49}$=0.56, p=0.460), indicating that the grain size distribution of the surface sediment might not play an important role in the magnitude of organic carbon. The average CC50 of unvegetated sediments across all estuaries (44.58±26.32 Mg C ha^{-1}) was lower but not significantly different than that of seagrass sediments ($F_{1,90}$=2.40; p=0.125). On the estuaries level, vegetated areas had overall higher CC50 than unvegetated areas, except in Loch Ryan (Table 2; Fig. 4). Tay estuary exhibited the highest difference in CC50 between vegetated and unvegetated areas, of 36.81 Mg C ha^{-1}, while Moray Firth the lowest difference of 0.89 Mg C ha^{-1}. On a per site basis, in 5 out of 22 sites, the unvegetated areas had higher CC50 than vegetated ones (Table 2; Drum Sands, Dalmore, Tain, Rockcliffe and Loch Ryan). Of the remaining 17 sites, 8 exhibited differences in CC50 of less than 10 Mg C ha^{-1}, while there were only 4 sites with differences in CC50 of more than 30 Mg C ha^{-1} (Table 2).

3.3. Organic carbon density enhancement over depth

The depth profile of the seagrass-enhanced sediment organic carbon density varied considerably among sites (Fig. 2). There were meadows where the presence of seagrass consistently enhanced the sediment organic carbon density over the 50cm depth profile (e.g. Torry Bay in the Firth of Forth); enhanced the surface sediment (0-10cm) (e.g. Cuthhill in Dornoch Firth); enhanced the mid-layer (10-30cm) (e.g. Tayport 1&2 in Tay Estuary, Nigg Bay in Cromarty Firth, Southannan Sands in Clyde Firth); or enhanced the deeper layer (>30cm) (e.g. Auchencairn in Solway Firth, Hunterston Sands and Cardross in Clyde Firth).


East Coast
Firth of Forth
Tay Estuary
Drum Sands
Blackness
Torry Bay
Tayport 1
Tayport 2
Montrose Basin
Beauly Firth
Moray Firth
Findhorn
Nairn
Cromarty Firth
Nigg Bay
Cromarty Firth
Dalmore
Alness
Cromarty
Dornoch Firth
Tain
Cuthill
Depth profile (cm) below bed surface
Organic carbon density (mg cm-3)

261

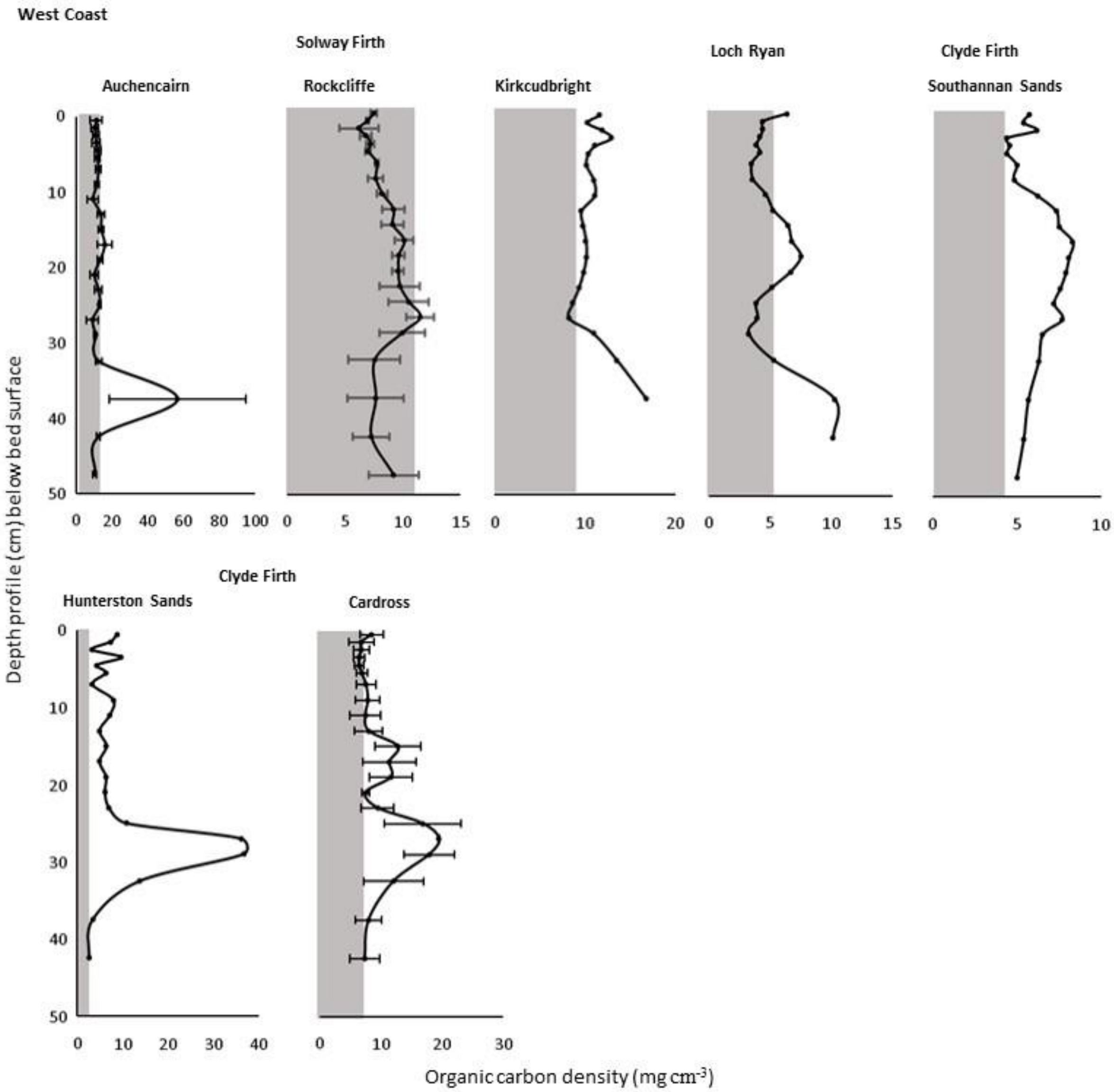


Figure 2. The seagrass-enhanced sediment organic carbon density at all sampled sites along the east and west coasts of Scotland. The black line is the seagrass organic carbon density integrated across depth intervals of the sampled vegetated cores per site. The grey area is the 'background' organic carbon density at a given site (Table S1). Error bars represent standard error. Note the variations in x axis among the sites.

Table 2. Average sediment characteristics for vegetated and unvegetated areas across all sampled sites, estuaries and coasts. [DBD = dry bulk density, g cm^{-3}; %OC = organic carbon content, % of dry weight; CC50 = organic carbon stock in the top 50cm, Mg C ha^{-1}; Difference in CC50 between vegetated and unvegetated areas, Mg C ha^{-1}].

	Vegetated						Unvegetated						Difference in CC50
Sites	DBD	SD	% OC	SD	CC50	SD	DBD	SD	% OC	SD	CC50	SD	
East Coast	1.26	0.26	0.93	0.94	55.23	37.96	1.21	0.23	0.75	0.60	44.11	28.99	11.12
Firth of Forth	1.30	0.24	1.61	0.55	105.72	13.13	1.19	0.18	1.41	0.60	85.86	26.34	19.86
Blackness	1.33	0.27	1.51	0.56	104.26	17.88	1.18	0.23	1.15	0.46	72.93	6.80	31.33
Drum Sands	1.16	0.12	1.89	0.63	106.41	10.53	1.13	0.09	1.87	0.57	109.68	27.97	-3.28
Torry Bay	1.41	0.24	1.49	0.32	107.22	16.48	1.33	0.14	1.02	0.25	64.04	-	43.18
Tay Estuary	1.31	0.25	1.26	1.96	67.76	62.49	1.38	0.19	0.51	0.46	30.95	19.15	36.81
Tayport (1)	1.43	0.33	2.52	2.69	134.73	23.12	1.54	0.13	0.78	0.62	49.80	14.09	84.93
Tayport (2)	1.23	0.14	0.46	0.35	23.11	8.17	1.28	0.14	0.34	0.18	18.38	6.44	4.73
Montrose Basin	1.21	0.27	1.05	0.65	62.21	21.97	1.12	0.19	0.97	0.53	55.37	19.55	6.84
Montrose	1.21	0.27	1.05	0.65	62.21	21.97	1.12	0.19	0.97	0.53	55.37	19.55	6.84
Beauly Firth	1.37	0.32	0.81	0.38	51.62	13.25	1.19	0.32	0.76	0.27	41.76	2.86	9.86
Beauly	1.37	0.32	0.81	0.38	51.62	13.25	1.19	0.32	0.76	0.27	41.76	2.86	9.86
Moray Firth	1.31	0.30	0.27	0.24	14.94	3.83	1.25	0.21	0.24	0.11	14.05	3.80	0.89
Findhorn	1.14	0.17	0.28	0.20	14.55	6.25	1.21	0.13	0.25	0.11	13.56	0.66	0.99
Nairn	1.43	0.31	0.26	0.26	15.20	3.08	1.30	0.27	0.22	0.11	14.54	6.47	0.66
Cromarty Firth	1.19	0.25	0.88	0.55	49.27	17.15	1.13	0.24	0.67	0.49	39.85	21.55	9.42
Nigg Bay	1.12	0.20	1.00	0.65	58.01	3.97	1.21	0.16	0.56	0.57	40.13	26.25	17.88
Dalmore	1.23	0.32	0.88	0.42	50.89	17.74	1.30	0.16	0.89	0.27	65.88	-	-14.98
Alness	1.00	0.10	1.39	0.32	69.50	-	0.88	0.15	1.10	0.46	52.68	-	16.82
Cromarty	1.32	0.17	0.51	0.33	28.78	5.16	1.09	0.26	0.45	0.27	20.14	3.68	8.64
Dornoch Firth	1.20	0.11	0.43	0.28	23.00	7.61	1.16	0.09	0.35	0.32	19.76	16.08	3.25
Tain	1.17	0.10	0.47	0.33	25.90	5.04	1.12	0.08	0.54	0.35	31.13	-	-5.23
Cuthill	1.23	0.11	0.38	0.22	20.11	9.70	1.20	0.08	0.16	0.12	8.38	-	11.72
West Coast	1.45	0.14	0.72	0.76	53.38	24.42	1.49	0.13	0.62	0.39	45.70	19.43	7.67
Solway Estuary	1.41	0.10	0.83	0.80	64.98	28.81	1.44	0.11	0.84	0.37	60.52	11.62	4.46
Auchencairn	1.41	0.10	0.99	1.09	82.55	32.70	1.38	0.10	1.00	0.45	68.53	7.92	14.02
Rockcliffe	1.45	0.10	0.58	0.12	42.56	4.22	1.54	0.06	0.71	0.17	56.87	7.15	-14.31
Kirkcudbright	1.35	0.06	0.81	0.16	57.11	-	1.43	0.04	0.64	0.11	43.80	-	13.31
Loch Ryan	1.55	0.09	0.35	0.15	30.75	-	1.58	0.11	0.36	0.19	32.58	-	-1.84
Loch Ryan	1.55	0.09	0.35	0.15	30.75	-	1.58	0.11	0.36	0.19	32.58	-	-1.84
Clyde Firth	1.47	0.18	0.66	0.75	43.98	12.72	1.52	0.13	0.40	0.26	30.55	14.50	13.43
Southannan Sands	1.54	0.09	0.41	0.09	31.10	-	1.63	0.10	0.27	0.13	22.61	-	8.50
Hunterston Sands	1.52	0.32	0.88	1.50	45.77	-	1.55	0.09	0.19	0.07	13.11	-	32.65
Cardross	1.42	0.12	0.67	0.37	47.67	14.79	1.47	0.12	0.51	0.27	39.00	11.39	8.67
Scotland	1.31	0.25	0.88	0.90	54.79	35.02	1.29	0.24	0.71	0.55	44.58	26.32	10.22

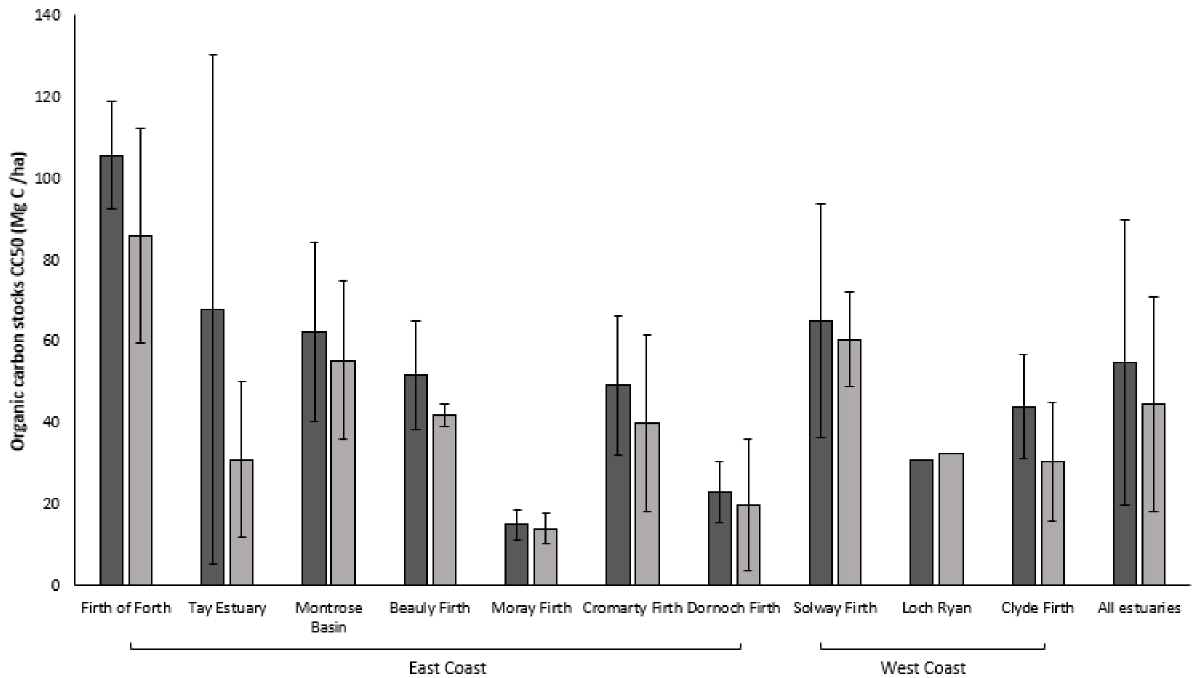


Figure 3. Organic carbon stocks in the top 50cm CC50 (Mg C ha^{-1}) in vegetated (dark grey) and unvegetated (light grey) areas from all sampled estuaries. Error bars represent SD.

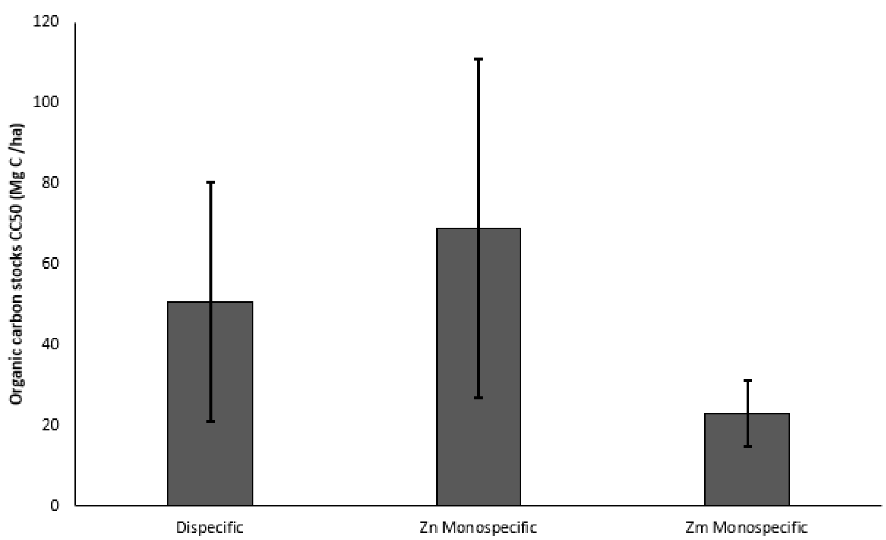


Figure 4. Organic carbon stocks in the top 50cm CC50 (Mg C ha^{-1}) in monospecific (Zn: *Zostera noltii* or Zm: *Zostera marina*) and dispecific meadows across all sampled estuaries. Error bars represent SD.

4. Discussion

The current study quantified the sedimentary organic carbon stocks for intertidal seagrass meadows on the Scottish coast. To compare to the global and regional seagrass carbon stocks, when extrapolated to 100 cm depth, the projected organic carbon stocks CC100 of the seagrass sediments averaged 109.59±70.05 (SD) Mg C ha^{-1} and 89.15±52.64 Mg C ha^{-1} in unvegetated 'bare' sediments. Whilst this is low compared to the global seagrass average of 194.2±20.2 (CI) Mg C ha^{-1}, it is well above the average for the seagrass meadows occurring in the temperate North Atlantic bioregion, at 48.7 ± 14.5 (CI) Mg C ha^{-1} (Fourqurean et al., 2012). The average sediment organic carbon stocks reported here are similar to worldwide estimates for *Z. marina*, at 108.9 Mg C ha^{-1} (Röhr et al., 2018), and twice as high as the projected carbon stocks for eelgrass meadows previously reported for the Western and Eastern Atlantic, at 54.0 and 55.4 Mg C ha^{-1} respectively, although the values for the Eastern Atlantic derive from only three short cores (25 cm) (2 from Porth Dinllaen, Wales, UK and 1 from Culatra, Portugal) (Röhr et al., 2018).

Across the UK, seagrass sediment carbon stocks have been published for subtidal *Z. marina* meadows along the southwest coast of England (Green et al., 2018), intertidal multispecific meadows (Lima et al., 2020) in South England, and subtidal *Z. marina* meadows in Northeast Scotland (Porter et al., 2020) (Fig. 5). The projected organic carbon stocks CC100 reported here are lower than those of subtidal *Z. marina* meadows in South England (140.98±73.32 Mg C ha^{-1}) (mean±SD) (Green et al., 2018), but higher than those documented for subtidal *Z. marina* meadows for Orkney in Scotland (77.94 Mg C ha^{-1}) (Porter et al., 2020). The mean organic carbon stocks in multispecific intertidal seagrass meadows (*Z. marina* / *Z. angustifolia* / *Z. noltii* / *Ruppia spp*) in Solent, Southwest England, reported for the top 30cm, are 33.80±18.40 (SD) Mg C ha^{-1}, similar to those reported here 32.87±22.81 Mg C ha^{-1} (direct conversion to 30cm stocks for this comparison).

Z. noltii carbon stocks in the top 100 cm reported in the global dataset from an unpublished source, ranged from 46 to 152 Mg C ha^{-1} (Fourqurean et al., 2012), representing a lower variability than those presented in this study for monospecific *Z. noltii* meadows, ranging from 20 to 302 Mg C ha^{-1}. The sediment organic carbon stocks for monospecific *Z. noltii* meadows here were over 8 times higher (1.38±0.8 kg C m^{-2}; direct conversion to 10cm stocks) than those obtained for *Z. noltii* in Ria de Aveiro, Portugal (0.1628±0.0109 kg m^{-2} for the top 10cm) (Sousa et al., 2019).

Z. marina meadows in the temperate Northern Hemisphere exhibit substantial regional and local variation in carbon storage (over eightfold differences between the organic carbon stocks in the Mediterranean Sea and Kattegat-Skagerrak compared to the Baltic Sea) (Röhr et al., 2018). Three sedimentary variables (mud content, sediment density, and degree of sediment sorting), and two environmental variables (water depth and salinity) explained over 62% of this variation in the study by Röhr et al. (2018). Earlier studies in other regions with *Z. marina* meadows (Dahl et al., 2016; Dahl et al., 2020; Miyajima et al., 2015; Röhr et al., 2016) or other species of seagrass (Macreadie et al., 2013 Serrano et al., 2016) have also indicated that sediment characteristics, specifically the sediment grain size distribution and sediment density, appear to be the most important predictors for seagrass carbon stocks. However, the seagrass organic carbon stocks here were not related to the sediment dry bulk density (top 5cm or 10cm). While we did not obtain explicit measures of sediment grain size, we overlayed our sampling locations with previously published contour maps showing the distribution of median grain size along the whole UK coastline (Bricheno et al., 2015). On the east coast, the sampled estuaries appearing to have larger sediment grain size are related to lower carbon stocks (e.g. Dornoch Firth: grain size 0.3<0.5 mm), and vice versa. However, on the west coast, this pattern was not observed, with the Firth of Clyde having only the seventh highest carbon stocks across all sampled estuaries (Table 2), despite having the smallest grain size (0.0<0.1 mm; (Bricheno et al., 2015)).

Variability in organic carbon stocks among and within estuaries could additionally be attributed to differences in hydrodynamics (e.g. turbidity and water flow), which also influence sedimentary characteristics (Dahl et al., 2020). Local hydrodynamics and turbulence can also affect export rates of the organic matter produced in the meadows to further adjacent locations. ~25% of the net primary production in seagrass meadows can be exported to some distance beyond the meadow (Duarte and Cebrián, 1996), even into shelf and deep-sea sediments (Duarte and Krause-Jensen, 2017). A recent study conducted in Port Curtis, a macrotidal estuary in Australia, demonstrated that seagrass organic carbon stocks were five times higher in the upper regions than in the lower regions of the estuary (Ricart et al., 2020). *Z. marina,* a generally subtidal species, can also occur in the eulittoral zone of an estuary, growing in the lower and middle part, and co-existing with *Z. noltii,* which grows in the middle and upper zones (Green and Short, 2003). Although there were no significant differences in the organic carbon stocks between monospecific (*Z. noltti* or *Z. marina* alone) and dispecific meadows (core sampling in different zones of the estuary) in the present study, the variability within some estuaries was large (e.g. average CC50 was 67.8 ± 62.5 Mg C ha^{-1} in the Tay estuary, where the only monospecific *Z. marina* meadow of our study exists), suggesting that environmental settings can influence carbon deposition. Larger seagrass species have taller canopies making them more effective at trapping and facilitating the settling of suspended matter and burial of allochthonous carbon (Mazarrasa et al., 2018). Despite having thinner and shorter leaves, *Z. noltii* meadows have been shown to have similar influences on near-bed flow dynamics and energy reduction with those of *Z. marina* (Wilkie et al., 2012). Previous studies in the Firth of Forth and Tay estuary have shown that *Z. noltii* meadows enhance the retention of underlying sediments and decrease the resuspension of large particles compared to bare sediments (Potouroglou et al., 2017; Wilkie et al., 2012). However, it seems more probable that the higher organic carbon stocks observed in *Z. noltii* meadows can be attributed to the fact that this species is adapted to living in naturally depositional environments subject to low wave energy, compared to *Z. marina* that generally occurs further offshore and thus is exposed to additional hydrodynamic forces (e.g. tidal flow and riverine currents).In addition to these drivers of variability causing differences between geomorphological settings, other sources of variability may operate at smaller scales. For example, the composition (plot/patch size and type of vegetation), the configuration (spatial arrangement) and the immediate surrounding environmental conditions may influence the functioning of mosaically structured habitats such as seagrasses (Gullström et al., 2018; Ricart et al., 2017). There is evidence that such smaller scale variability may be particularly pertinent in coastal or aquatic systems in comparison with terrestrial carbon storage. For example, terrestrial soil carbon showed no difference along a gradient of landscape heterogeneity (Williams and Hedlund, 2013). In terrestrial forests, fragmentation and edge effects had no influence on carbon sequestration in temperate regions (Ziter et al., 2014) (although tropical areas did show effects; de Paula et al., (2011)). In contrast, carbon stocks in coastal and marine ecosystems are routinely shown to exhibit spatial variability, with this non-uniform distribution being attributed to several seascape-scale factors. As seagrasses can occur either as continuous meadows or in the form of patches of various compositions, shapes and sizes, variables such as structural complexity (Gullström et al., 2018; Samper-Villarreal et al., 2016; Trevathan-Tackett et al., 2015), small-scale patch heterogeneity (Ricart et al., 2015), size of the meadow (Gullström et al., 2018; Ricart et al., 2017) and edge proximity (Oreska et al., 2017) may all significantly affect their carbon storage capacity and the rates of fluxes and transfers of material between habitat patches (Hyndes et al., 2014). Carbon stocks have been shown to be significantly higher in innermost seagrass patches compared with seagrass-edge patches (Ricart et al., 2015) and continuous meadows store more carbon than patchy ones (Gullström et al., 2018; Ricart et al., 2017). Hence, the structure of seagrass meadows can also be a potentially important predictor for the magnitude and source of seagrass carbon stocks. All these factors might contribute to the high variability that we found among the sites within an estuary, as well as among different estuaries (Table 2), and we highlight the importance for obtaining them in future studies.

Differences were observed in the OC content between vegetated and unvegetated sediments, with higher OC content on average in vegetated (0.88 % DW) than unvegetated (0.71 % DW). Although the difference here is similar to that reported globally (0.17 % DW), the absolute OC content in Scottish sediments was much lower than that globally (1.8 % DW) (Kennedy et al., 2010). The majority of the cores, whether vegetated or not, displayed no particular trend with depth ('mixed pattern'), indicating that the environmental settings did not provide locations with temporally constant fluxes of organic and mineralogical matter, and/or little post depositional disturbance. Small changes in the delivery of allochthonous material derived either from the catchment or other parts of the coast, will alter the downcore distribution of dry bulk density and carbon density, as they would by erosion and reworking of the sediments (Kindeberg et al., 2019; Röhr et al., 2016). The depths at which changes in organic carbon density occur, were generally different for vegetated and unvegetated cores at the same location (Fig.2 and Fig. S1), indicating that the processes leading to carbon sediment delivery, supply and storage differed between the two 'settings', even though they were located adjacent to each other. This emphasises the significant role of sediment mixing and remineralisation, which can result in spatio-temporal heterogeneity between and within sites, settings and species (Johannessen and Macdonald, 2016). It further emphasises the need for regular mapping and monitoring, as these patterns would have been better explained if such information existed, e.g. unvegetated areas having been previously vegetated, or disturbances leading to seagrass declines. Better understanding would be obtained through intense downcore sampling of physical parameters such as grain size, measurement of tracers that differentiate between allochthonous and autochthonous OC, and measurement of sediment carbon sequestration rates.

Recognition of the role of vegetated coastal ecosystems as carbon sinks has led to the development of blue carbon strategies which aim to help mitigate and adapt to climate change through the conservation and restoration of these ecosystems (United Nations Environment Programme, 2020). One approach to increasing our understanding of the relative importance of seagrasses to blue carbon is to compare ecosystem service delivery between seagrass and other coastal and marine habitats (Huxham et al., 2018). A small but growing literature compares seagrass carbon stocks with those of other coastal habitats, at local, regional and global scales (e.g. Fourqurean et al., 2012; Hyndes et al., 2014; Luisetti et al., 2013). However, these comparisons are usually only with other vegetated coastal ecosystems such as mangrove forests and tidal marshes, whose carbon stocks have been more widely reported in the literature. Comparison with non-vegetated areas is also of interest; importantly we found that sediment organic carbon content in seagrass areas was higher than that in the reference unvegetated areas (except for Loch Ryan; Fig. 3), adding to the argument that the presence of seagrass enhances sediment carbon stocks. On average, Scottish seagrass areas retained 20% (or 1.24 times) more organic carbon (% DW) than unvegetated areas, but this 'seagrass multiplier' was as high as 2.5 times at one estuary (the Tay). Similarly, Jankowska et al. (2016) reported 1.5-4.8 times higher organic carbon densities in seagrass areas compared to unvegetated ones in the Baltic Sea. Enhancements in organic matter and organic carbon contents in seagrass compared with unvegetated plots have also been documented in other regions (e.g. Githaiga et al., 2017; Kennedy et al., 2010; Postlethwaite et al., 2018; Ricart et al., 2017). The presence of seagrasses in the Firth of Forth has been shown to result in an average difference in surface elevation rate of 9.01 mm/year, compared to adjacent unvegetated sediments (Potouroglou et al., 2017). Hence much of the enhanced carbon in Scottish seagrass is likely to come from more efficient trapping and storing of allochthonous sources. It is worth noting that although higher organic carbon content was observed in seagrass sediments in 9 out of 10 studied estuaries, in Loch Ryan, unvegetated areas had marginally higher organic carbon content than nearby seagrass areas. Due to the lack of historical information on seagrass distribution at the local scale, we recognise that current conditions can only provide a single snapshot of the seascape configuration. Thus, these unvegetated areas might have been previously vegetated, and as previously identified, future work should obtain isotopic data to determine sources and their relative contribution to sediment carbon stocks. There is a clear pattern emerging of enhanced carbon storage compared with unvegetated reference sites (e.g. Dahl et al., 2016; Githaiga et al., 2017; Novak et al., 2020; Prentice et al., 2020), although such comparisons remain surprisingly rare in the seagrass sediment carbon stocks literature.

Conserving and enhancing carbon stocks in seagrass meadows should form one part of the Scottish government's response to the climate change challenge. Our results reveal that the magnitude of sedimentary carbon stocks in intertidal seagrass meadows in Scotland is comparable not only to previously published values from the wider region, but also to other carbon rich habitats, such as saltmarshes and terrestrial peatlands within the country (see Fig. 5). Seagrass sediments from the Forth (where our highest carbon stocks of 211 Mg C ha $^{-1}$ were found) are similar in their carbon concentrations to the carbon-rich Scottish soils peaty gleys (242 Mg C ha $^{-1}$) and peaty podzols (214 Mg C ha $^{-1}$) (Rees et al., 2018). However, terrestrial peat itself, at 547 Mg C ha^{-1}, is more than 2.5 times as carbon dense as Forth sediments or 5 times as carbon dense as the average seagrass sediments found here. This comparison emphasises the exceptional carbon density of peat, and the importance of preserving this terrestrial Scottish store, rather than denigrates the possible contribution of seagrass. Also, the mean organic carbon stock of seagrasses is similar to that reported for saltmarshes in Scotland (113 Mg C ha $^{-1}$), although this value was derived from only two sites in Orkney (Porter et al., 2020). Taking the conservative estimate of 1600 ha of seagrass in Scotland (including only the known records) and using the mean value for carbon stocks found here, Scottish intertidal seagrasses store ~175,360 Mg of organic carbon in the upper 100cm of their sediments. This represents around 10 % of the total annual emissions from the Scottish residential sector (after conversion to $CO_{2\ (eq)}$; Scottish Government, 2019), and although we acknowledge the different time scales in these two processes, we argue that seagrass conservation and/or restoration could provide opportunities for enhancing carbon storage (and/or avoid CO_2 emissions) in addition to maintaining or enhancing additional ecosystem services.

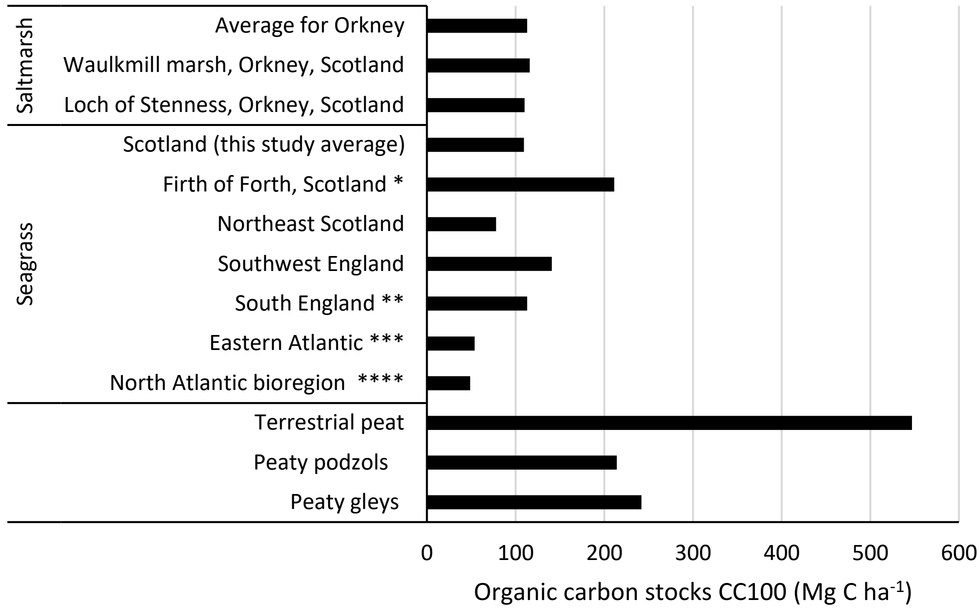


Figure 5. Organic carbon stocks in the top 100cm CC100 of soil in terrestrial and coastal and marine ecosystems in Scotland (terrestrial peat, peaty podzols, peaty gleys, saltmarshes and seagrasses), and seagrass carbon stocks from the UK and wider region (North Atlantic seagrass bioregion and Eastern Atlantic). * The highest carbon stocks reported in Scotland (from the present study). ** Direct conversion from 30 to 100cm to allow comparison with the rest of the studies. *** This includes 3 sediment cores from *Zostera marina* (n=2 from Porth Dinllaen, Wales, UK and n=1 from Culatra, Portugal) (Röhr et al., 2018). **** This includes *Ruppia maritima, Zostera marina, Zostera noltii, Cymodocea nodosa* (Fourqurean et al., 2012). Saltmarsh values from Porter et al., 2020. Peat values from Rees et al., 2018.

To ensure seagrasses can thrive in the future, it is vital to maintain high water quality with low mean turbidity and low levels of eutrophication. Seagrass meadows have been identified as Priority Marine Features in Scottish territorial waters, with 64% of the known records being in marine protected areas (Howson et al., 2012). This figure, however, is likely to overestimate the degree of protection afforded to Scottish seagrass, because of the limited number of mapping or monitoring efforts within the country. Acknowledging the possible contribution of seagrasses to maintaining and enhancing natural carbon stores in Scotland is just one more argument for the conservation of these important habitats.

Ethics Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

Conceived and designed the study: MP, MH, KD, HK. Led the study and drafted the manuscript: MP and MH. Contributed data: MP, LM (East coast of Scotland) and DW, GM (West Coast of Scotland). Analysed the data: MP, LM and DW. All co-authors commented on and provided edits to the original manuscript.

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