Title: Carbon stocks in southern England's intertidal seagrass meadows

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Abstract

This study analyses total carbon stock (C_{stocks}) from the Isle of Wight, Solent, and adjacent harbours in southern England, including organic carbon (C_{org}) stored in the sediment and plant. Results from this study contribute to global blue carbon research by reporting the first direct assessment of sediment C_{stocks} in the top metre of intertidal seagrass meadows from the Solent region, with significant C_{stocks}, on average 103.12 ± 71.45 MgC ha^{-1}, comparable to other global regions. This study also compared sediment %C_{org} and percentage of organic matter (%OM) within seagrass meadows and adjacent, un-vegetated, sampling points, showing that un-vegetated mudflats had higher %C_{org} and %OM than seagrass for most sites, apart from Hayling Island. This study shows that %OM can be confidently used as a proxy to determine sediment %C_{org} values in intertidal seagrass meadows. These results support the inclusion of the region's seagrass meadows in conservation and restoration projects, aiming not only to conserve the C stored in their soils, but also increase their future C uptake potential.

Introduction

Many studies have identified seagrass meadows as highly productive ecosystems that act as effective carbon sinks by trapping large amounts of organic carbon (C_{org}) in their sediments, with a recently estimated average of 3.76-21 PgC, adding to the total global blue carbon stocks (C_{stocks}) of > 30 PgC across ~185 million ha (Fourqurean *et al*., 2012a; Lavery *et al*., 2013; Macreadie *et al*., 2021). This is due to their ability to retain allochthonous and autochthonous particles by reducing water flow, and sediment resuspension, coupled with slow decomposition rates from their typically oxygen poor sediments, making their plant material less labile than other marine plants (Kennedy and Björk, 2009; Pedersen *et al*., 2011; Rohr *et al*., 2018). In addition, the ability of seagrass ecosystems to capture and retain C within their sediments may be at least two times higher than terrestrial habitats per unit area, when compared to tropical (40 g C m $^{-2}$ yr $^{-1}$) and temperate (22.5 g C m $^{-2}$ yr $^{-1}$) forests (Grace *et al*., 2006;Taillardat *et al*., 2018).

In addition to their role as carbon sinks, seagrass meadows have historically provided numerous ecosystem services to humans, directly or indirectly, such as seagrass litter being used as bedding, straw substitutes for thatching stoned roofs in Scotland, and even in agriculture (Urquhart, 1824; Terrados and Bodrum, 2004; Campagne *et al*., 2015). Moreover, their high productivity and ability to trap organic matter (OM) make seagrass beds a fundamental part of marine food webs, being the primary food source of large, threatened, species such as dugongs, manatees, sea turtles, and water birds (Nordlund *et al*., 2016; Whitehead *et al*., 2018; Kurniawan *et al*., 2020).

In recent years, a number of organisations have produced guidelines to place a monetary value on ecosystem services provided by vegetated coastal environments, among them, carbon stocks to be included in carbon trading initiatives as nature-based solutions (Villa and Bernal, 2017; Kurniawan *et al*., 2020; Gregg *et al*., 2021). Fourqurean *et al*. (2012a), compared reported seagrass carbon stocks, represented by the plant biomass and sediment organic carbon, from a range of global regions. The results suggest a global mean of 7.29 ± 1.52 MgC ha^{-1} stored in plant biomass and 329.5 ± 55.9 MgC ha^{-1} in the top metre of soil, with Mediterranean meadows (dominated by *Posidonia oceanica*) containing the highest average sediment carbon stock (372.4 ± 56.8 MgC ha^{-1}) (Fourqurean *et al*. 2012a; Lavery *et al*., 2013). In comparison, North Atlantic temperate seagrass meadows showed lower carbon stock values, with 48.7 ± 14.5 MgC ha^{-1} in sediment organic carbon (Fourqurean *et al*., 2012a). There were no data for the Southeast and Western Pacific in their study, evidencing the knowledge gaps for global seagrass carbon stocks (Fourqurean *et al*., 2012a).

However, one of the main challenges in attributing a value to ecosystem services relates to the lack of sufficient data to quantify the service's scale and geographical extent (Dewsbury *et a*l., 2016; Villa and Bernal, 2017; Nordlund *et al*., 2017). The majority of seagrass blue carbon assessments in the UK have been restricted to basic estimations using data from studies in different regions (Garrard and Beaumont, 2014), estimated values based on extrapolations (Green *et al*., 2018), or outdated standing stock assessments, making them unreliable (Green *et al*., 2021; Gregg *et al.,* 2021). For example, Green *et al*, (2018) assessed the variability of subtidal *Zostera marina* seagrass sediment carbon, along the west coast of England. The study highlighted the lack of published data on seagrass meadows from the British Isles but provided a representative assessment of the UK's seagrass carbon stocks, based on extrapolated data, reporting an estimated standing stock of 66,337 MgC in the top metre of sediment (Green *et al*., 2018).

Given the diversity of biological and environmental factors that influence carbon storage potential, such as nutrient availability, species' production, sediment accretion, hydrology, and geomorphological conditions (Lima *et al*., 2020), indirect quantification can lead to inaccuracies and possible overestimations (Johannessen and Macdonald 2016; Macreadie *et al*., 2018). Therefore, this paper contributes to global seagrass blue carbon research by providing the first direct measurement of carbon storage values for temperate, intertidal, seagrass ecosystems in England. The aim is to provide the most comprehensive assessment to date of total carbon stock from seagrasses in the Isle of Wight, the Solent and adjacent harbours, hereafter referred to as the Solent Region, southern England. The objectives are to determine: 1) above-ground biomass carbon stock; 2) below-ground biomass carbon stock; 3) sediment carbon stock to a depth of 1 m; 4) total carbon pool for each studied site by combining vegetative and soil carbon stocks.

Methods

Sampling Sites

The three largest natural harbours found in the Solent Region have been included in this study, Portsmouth Harbour, Langstone Harbour, and Chichester Harbour (Williams *et al*., 2018). The Isle of Wight and the harbours of Portsmouth, Langstone and Chichester form an extensive coastal system consisting of natural and man-made environments with high habitat diversity, providing an important wildlife resource (McLeod *et al*., 2005; King, 2010).

Samples used for carbon stock analyses were collected between June and August 2017, from six fieldwork sites selected within this area, namely Creek Rythe (CRST) in Chichester Harbour, Farlington Marshes (FMST) and Hayling Island (LGST) in Langstone Harbour, Porchester (PMST) in Portsmouth Harbour, and Cowes (CWST) and Ryde (RYST) on the Isle of Wight **(Supplementary table A),** following an assessment of the most recent seagrass distribution inventory (Marsden and Chesworth, 2015). The chosen study sites encompass soft mud sediment regions, represented by sheltered, estuarine areas, such as Creek Rythe and Hayling Island, areas exposed to anthropogenic stress and nutrient runoff, Farlington Marshes and Porchester, with similar fine-grained sediments, and areas with sandy substrates, and more exposed to hydrodynamic activity from waves and tides, namely Ryde and Cowes (Marsden and Chesworth, 2015). The combined area of seagrass meadows from the six study sites investigated is 406.03 ha, accounting for nearly 10% of the reported intertidal seagrass meadows in the UK (Dickie *et al.,* 2014; Luisetti *et al.,* 2019).

Field methods

Five temporary plots were randomly selected from each sampling site, without permanent demarcations, since this project did not aim to evaluate carbon stocks changes over time or make precise comparisons, but to produce a single blue carbon measurement (Pearson et al., 2007; Howard, et al., 2014). Variation in seagrass patches within the meadows on each site was very limited, based on visual assessment, allowing a random selection of plots. Therefore, plot location was randomly determined to enhance the chances of making a true assessment of the C_{stocks} variation within meadows, while also taking into consideration the time taken for measurements during low tide, and minimising disturbance to the habitats (Howard, *et al.*, 2014). Plots were selected within a radius of at least 5m from the edge of the meadow, and each other.

At each sampling plot, above-ground biomass (AGB) was collected from within a 0.25 m^2 quadrat by cropping all of the plant biomass (leaves - to stem base) (Howard *et al.*, 2014). After AGB removal, two sediment cores were collected from within each quadrat using a Russian corer, with a 5cm diameter and 0.5 m vertical length. Cores for soil carbon stocks and sediment particle size analyses were collected by first coring the top 50cm of sediment and dividing this section into 5 cm depth subsamples (10 in total), followed by an additional 50-100cm core, collected from the same point, as a larger subsample, giving a total of 11 subsamples per 1m core (total depth). Additionally, one, 50 cm deep, core was collected for below-ground biomass (BGB) analysis from the same sampling plot. Additionally, five, 1 m deep (or to refusal), sediment cores were collected from unvegetated mudflats adjacent to the seagrass meadows from all sites, apart from Ryde and Cowes, for carbon stocks analyses (%OM and %C_{org}), using the same methods described above. Unvegetated sediment samples were not collected from Ryde and Cowes due to the gravelly, and rocky characteristics of the substrate near the seagrass beds.

Laboratory methods and calculations

In the laboratory, each AGB sample was transferred to a 1 mm sieve, and carefully washed free of soil, following Howard *et al.*, (2014). Identified seagrass species were recorded, as well as the presence of epiphytes. Filamentous macroalgae and invertebrates were separated from the seagrass biomass during the washing procedure, however, microalgae epiphytic load, when found, was not scraped from the leaves, to prevent loss of vegetative organic matter.

Whole leaves (stem to tip) were counted from each sample to determine leaf density. AGB was determined by oven-drying the vegetative biomass for 72 h at 60 ºC (Howard *et al.*, 2014). The above-ground vegetative biomass was determined by multiplying the dry weight (kg) of a sample of plant material for a given area (m^2) by a carbon conversion factor (0.34), derived from literature for seagrass AGB calculations (Duarte, 1990; Howard *et al.*, 2014).

BGB samples were transferred to 1 mm sieves and washed free of sediment under running water before careful separation of below-ground material (roots and rhizomes). The material was oven dried to a constant weight before calculations (72 h at 60 ºC) (Howard *et al.*, 2014).

Carbon in the above and below-ground biomass was calculated by the following equations:

Equation 1: Carbon in the biomass component (kg C m^{-2}) = (Estimated biomass of the plant * carbon conversion factor) / area of the plot (m^2).

Equation 2: Carbon pool (MgC ha^{-1}) = Carbon content (kgC m^{-2}) *(1 Mg/1,000 kg) * (10,000 m^2 ha^{-1}).

Sediment subsamples were stored in the freezer until analysis. Thawed sediment subsamples were weighed prior to oven drying at 60 ºC for 72 hours, and then cooled at room temperature in a desiccator for at least one hour before weighing again to determine soil moisture content (Howard *et al.*, 2014). Oven dried samples were carefully disaggregated with a pestle and mortar and 2-4 g subsamples weighed in separate beakers, before being placed in the muffle furnace for loss on ignition (LOI) at 450 ºC for 24h (Lima *et al*., 2020). Samples were cooled at room temperature in a desiccator for at least one hour before weighing to determine %OM following the equation below (Heiri *et al.,* 2001):

Equation 3: %OM = [(dry mass before combustion (mg) – dry mass after combustion (mg)) / dry mass before combustion (mg)] * 100.

To determine sediment C_{stocks}, sediment carbon density, sediment dry bulk density (DBD) and $\%C_{org}$ were calculated. DBD (g cm^{-3}) for individual depth samples were estimated using the following equation (Dadey *et al*., 1992):

Equation 4: $DBD = (1 - \varphi) * Ps$

Where φ = porosity, and Ps = grain specific gravity (see Dadey *et al*., 1992).

Additionally, to directly measure $\%C_{org}$, a total of 45 sediment subsamples (approximately 9 per site) from plots within seagrass meadows, were randomly selected from the six sampling sites to be analysed on a VarioMax CNS elemental analyser (ELEMENTAR, Germany) using the DUMAS combustion method (Dumas, 1831). The presence of carbonates was tested by three drops of 1M HCl solution to oven dried samples and observed for release of CO_2 in the form of gas bubbles (Soil Survey Staff, 1993). Out of the six sampling sites, CO_2 was only observed in samples from Ryde and Cowes. For these sites where carbonates were detected, corrected $\%C_{org}$ was calculated by removing inorganic carbon (IC) excess, using the equation below, adapted from Howard *et al*. (2014):

Equation 5: $\%C_{org\ (corrected)} = \%C_{org} - \%IC$,

Where $\%IC = (\%LOI\ 850^oC - \%LOI\ 450^oC) * 0.12$

0.12 is derived from the contribution of carbon to carbonate's total molecular weight (12%)

Values of $\%C_{org}$ from Creek Rythe, Hayling Island, Farlington Marshes and Porchester as well as corrected $\%C_{org}$ values for Ryde and Cowes were used in a regression analysis to determine the relationship between %OM and $\%C_{org}$ and formulate a regression equation to determine $\%C_{org}$ from %OM for all samples (**Equation 9** – results).

Values of %OM and $\%C_{org}$ from within the seagrass sampling plots were then compared with those calculated for the unvegetated adjacent plots for each sampling site.

Following $\%C_{org}$ calculations, sediment C density and sediment C content were calculated as the following equations for each subsample:

Equation 6: Sediment Carbon Density (g dm^{-3}) = DBD (g/cm^3) * ($\%C_{org}$) /100) (Howard *et al*., 2014).

Equation 7: Sediment C content (g cm^{-2}) = Soil Carbon Density (g cm^{-3}) * Sample thickness (cm).

Sediment C content results from each subsample were then summed to determine total carbon to 1 m depth cores, and converted to MgC ha^{-1}, using the same conversion equation described for plant biomass (**Equation 2**).
Following LOI, particle size analysis was carried out on all non-ground samples using a Malvern Mastersizer 2000 laser particle size analyser, with particle size grading undertaken in accordance with the Wentworth (1922) size classification scheme. The mean (central value) particle size for each sample was calculated following the arithmetic approach below, assuming particle sizes in phi units (Folk and Ward, 1957):

Equation 8: Mean = $\frac{D16+D50+D84}{3}$

Statistical analyses

Statistical analyses comprised Anderson-Darling tests for normality, ANOVA, Tukey's post hoc tests, two sample t-tests, paired t-tests, Pearson's correlations, and linear regression model tests. Variables analysed for homogeneity of variance (ANOVA) between sites were above-ground biomass (AGB), leaf density, below-ground biomass (BGB), dry bulk density (DBD), organic matter content (%OM), organic carbon content (%C_{org}), and sediment carbon stocks (C_{stock}). Two-sample t-tests were used to analyse differences between mean organic matter content (%OM) and organic carbon content (%C_{org}) respectively, between seagrass cores and cores from unvegetated sampling points for all sites, apart from Ryde and Cowes. Pearson's Correlation tests were used to assess the relationship between all parameters analysed and a regression model was developed to establish linear regression equations to predict values for %C_{org} from %OM. Of all variables tested, only values for BGB failed the Anderson Darling test for normality of residuals, so a Log 10(X) transformation was applied on the data prior to ANOVA analysis, to meet the assumptions of the test.

Results – Seagrass meadows

Table 1: Summary of main results for sediment carbon stocks (C_{stock}), seagrass meadows areal extent, leaf density, above and below-ground biomass (ABG and BGB, respectively), percentage of below-ground biomass per C_{stock}, sediment organic carbon content (%C_{org}), sediment organic matter content (%OM), sediment dry bulk density (DBD), mean and median (D50) grain size, for all sampling sites. Values are presented as mean (±) standard deviation for all variables, with n = 5 for each site, same letters in each the column correspond to statistically similar means for each variable where ANOVA was performed, followed by Tukey's post hoc test.

SITES	Estimated C_{stock} 1m (MgC ha^{-1})	Area (ha) *	Leaf density (m^{-2})	AGB (MgC ha^{-1})	BGB (MgC ha^{-1})	%BGB/ C_{stock}	Estimated %C_{org}	%OM	DBD (g dm^{-3})	Mean grain size (µm)	D50 (µm)
Creek Rythe (CRST)	**119.92 ± 10.00 (A)**	100.24	367.0 ± 115.1 (A)	0.50 ± 0.25 (A)	0.009 ± 0.005 (AB)	0.005 ± 0.0028 (B)	1.79 ± 0.19 (A)	6.81 ± 1.07 (A)	0.59 ± 0.02 (F)	22.00 ± 6.22 (A)	16.80 ± 1.21 (A)
Hayling Island (LGST)	**112.35 ± 6.39 (A)**	70.1	336.7 ± 95.0 (A)	0.38 ± 0.13 (AB)	0.037 ± 0.04 (A)	0.025 ± 0.026 (B)	1.57 ± 0.07 (AB)	5.87 ± 0.17 (AB)	0.74 ± 0.03 (E)	20.8 ± 4.0 (A)	15.82 ± 2.93 (A)
Porchester (PMST)	**109.49 ± 12.79 (A)**	94.92	302.0 ± 76.1 (A)	0.32 ± 0.07 (ABC)	0.013 ± 0.012 (AB)	0.011 ± 0.0085 (B)	1.28 ± 0.33 (BC)	4.73 ± 1.58 (BC)	0.86 ± 0.07 (D)	46.07 ± 21.85 (AB)	25.61 ± 10.84 (AB)
Farlington Marshes (FMST)	**117.47 ± 6.76 (A)**	31.2	584 ± 427 (A)	0.25 ± 0.14 (ABC)	0.004 ± 0.003 (B)	0.003 ± 0.0025 (B)	1.08 ± 0.10 (CD)	3.64 ± 0.51 (CD)	1.11 ± 0.09 (C)	46.79 ± 15.94 (B)	31.53 ± 5.88 (B)
Cowes (CWST)	**20.76 ± ** 2.72 (B)**	27.1	346 ± 247 (A)	0.18 ± 0.07 (BC)	0.003 ± 0.0007 (B)	0.014± 0.006 (B)	0.82 ± 0.15 (D)	2.53 ± 0.55 (DE)	1.27 ± 0.25 (B)	72.40 ± 36.91 (B)	64.82 ± 36.68 (B)
Ryde (RYST)	**30.52 ± 1.68 (B)**	82.47	427 ± 430 (A)	0.08 ± 0.03 (C)	0.008 ± 0.005 (AB)	0.084 ± 0.062 (B)	0.47 ± 0.01 (E)	0.84 ± 0.08 (E)	1.46 ± 0.01 (A)	227.99 ± 6.97 (C)	224.78 ± 4.68 (C)

*Area derived from Marsden and Chesworth, 2015

** Sediment cores for Cowes (CWST) were only 20 cm deep

Above-ground biomass (AGB)

Four seagrass species were identified in the study sites, with *Zostera angustifolia* representing the dominant species, found in all sampling sites apart from Cowes. Z. *angustifolia* formed mixed beds with *Zostera noltii* in Creek Rythe, Hayling Island and Porchester, and mainly monospecific meadows in Farlington Marshes and Ryde. *Zostera marina* was found predominantly in Cowes, while *Ruppia maritima* was only found in Creek Rythe and Hayling Island, in small mixed patches.

AGB values ranged from a minimum of 0.08 MgC ha^{-1} in Ryde and a maximum of 0.497 Mg C ha^{-1} in Creek Rythe, with an average of 0.28 ± 0.08 MgC ha^{-1} (n = 30) across all sites (table 1). Creek Rythe and Hayling Island, the sites with denser meadows, showed significantly higher (F = 5.97, p = 0.001) AGB values than Ryde (table 1). Sites with monospecific *Z. angustifolia* beds, Farlington Marshes and Ryde, presented the highest mean leaf densities, of 584 ± 427 leaves/m^2 and 427 ± 430 leaves/m^2, respectively (table 1).

Below-ground biomass (BGB)

Mean BGB for all sites was 0.0122 ± 0.013 Mg C ha^{-1} (n = 30). Cowes had the lowest BGB amongst all sites, with 0.003 Mg C ha^{-1}, significantly lower (F = 2.89; p = 0.035) than the highest BGB value found in Hayling Island, 0.0373± 0.04 Mg C ha^{-1} (table 1). There was no statistically significant relationship between AGB and BGB (r = 0.122, p = 0.519).

Dry Bulk Density

Dry bulk density (DBD) in the studied sites ranged from 0.59 ± 0.02 gcm^{-3} in Creek Rythe to 1.46 ± 0.01 g cm^{-3} in Ryde (table 1). The mean DBD for all sites was 1.01 ± 0.32 g cm^{-3} (n = 30). Ryde had significantly higher DBD than all other sites, whilst Creek Rythe presented the lowest values. No significant relationship was found between dry bulk density and BGB for seagrass sediments (r = -0.333, p = 0.072) however, there was a negative, statistically significant, strong correlation between DBD and AGB (r = -0.750, $p < 0.001$). This association shows that sites with lower sediment DBD, like Creek Rythe and Hayling Island, had higher AGB, than Ryde and Cowes on the Isle of Wight, with higher sediment DBD.

Particle Size Analysis

Ryde had 99% of the sediment within the fine sand class (125 - 205 µm). Conversely, silt (3.9 - 63µm) particles represented the majority (>50%) of total sediment volume at Creek Rythe, Hayling Island, Farlington Marshes, Porchester and Cowes. Particles from these five silt rich sites, ranged between medium and coarse silt (15.6 - 63µm), with the highest percentage of silt found in Hayling Island, representing 76.6 ± 1.28% of total volume. All cores, apart from those collected at Ryde (0.01± 0.03%), contained clay (0.06 - 3.9 µm) in similar proportions with an average of 14.31 ± 2.41%. Mean grain size (µm), and median particle size D50 (µm) were also analysed for the sediment cores. Hayling Island presented the lowest mean grain size (µm) (20.81 ± 4.0), and lowest median particles size D50 (µm) (15.82 ± 5.02), both representing particles within the medium to fine silt classification (table 1). Conversely, the highest mean grain size (µm) (227.99 ± 6.97) and highest median particles size D50 (µm) (224.05 ± 5.68), were found in Ryde, being classified as fine sand.

There was a strong and statistically significant positive relationship between D50 and DBD ($r = 0.767$, $p < 0.001$), a moderately significant relationship between D50 and AGB ($r = -0.564$, $p = 0.001$), but no statistically significant association between D50 and BGB ($r = -0.176$, $p = 0.353$).

Organic Matter Content (%OM)

Creek Rythe had the highest %OM with 6.82 ±1.01 %, and Ryde the lowest, representing 0.84 ± 0.07 % of dry weight (table 1). Creek Rythe showed significantly higher %OM values than all other sites, apart from Hayling Island. Additionally, the %OM values for Ryde were significantly lower than all other sites, apart from Cowes (table 1).

Organic Carbon Content (%C_{org})

Mean estimated %C_{org} values were significantly different ($F = 71.13$; $p = 0.000$) between sites, ranging from 0.46 ± 0.01% of dry weight in Ryde to 1.79 ± 0.19% of dry weight in Creek Rythe (table 1). Most sites showed declines in %C_{org} with depth, however, Cowes, with only 20 cm deep cores, and Creek Rythe, displayed an overall increase in %C_{org} with depth from 1.36% at the surface layer, up to 2.11% between 50-100 cm deep (figure 1). For all sites, apart from Cowes, down-core distribution in %C_{org} was not monotonic, showing alternative increase and decrease with depth.

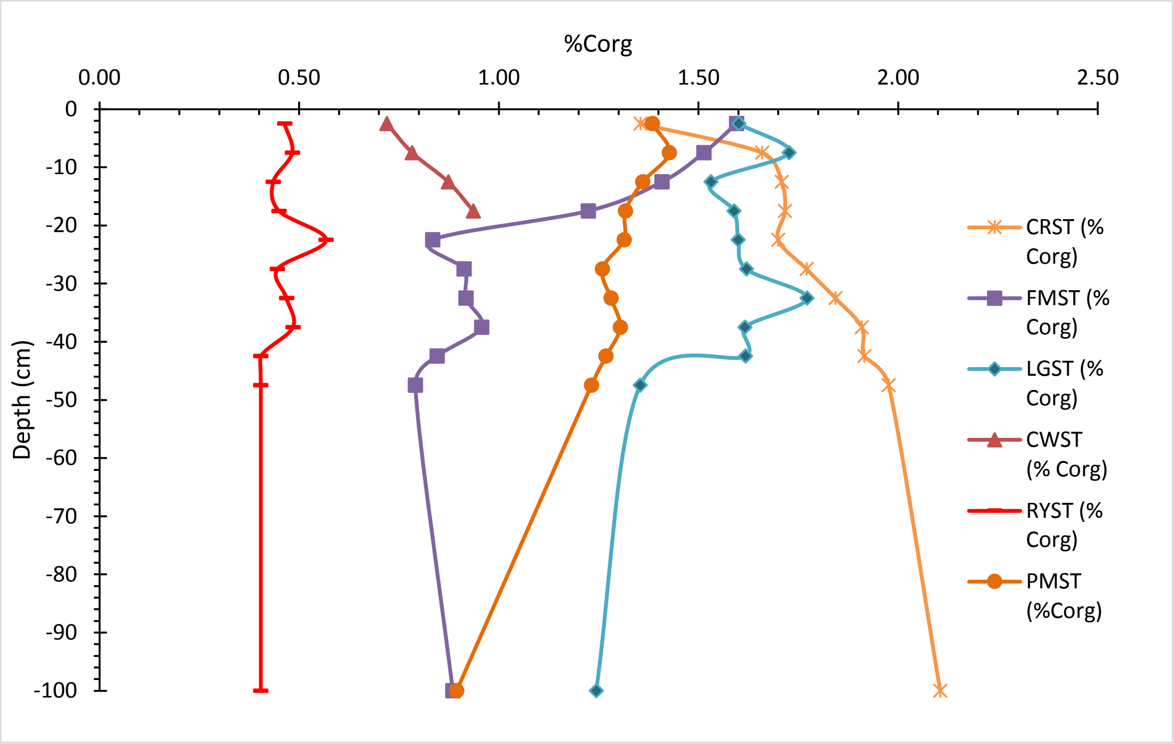

Figure 1: Down-core profile of the mean estimated organic carbon content (%C_{org}) from the cores for all sampling sites, Creek Rythe (CRST), Hayling Island (LGST), Farlington Marshes (FMST), Porchester (PMST), Ryde (RYST) and Cowes (CWST). All sites had five 1m deep cores, apart from Cowes with 20cm deep cores. Each core was divided into 5 cm subsamples, down to 50cm deep, and one larger 50cm subsample between 50 and 100cm deep.

The relationship between %OM, derived by LOI, and directly measured %C_{org} was strong (R^2=81.2%) and statistically significant ($p < 0.001$) resulting in regression equation 12 (figure 2), after removing outliers (n=.39).

Equation 9: %C_{org} = -0.091 + 0.2881 %OM

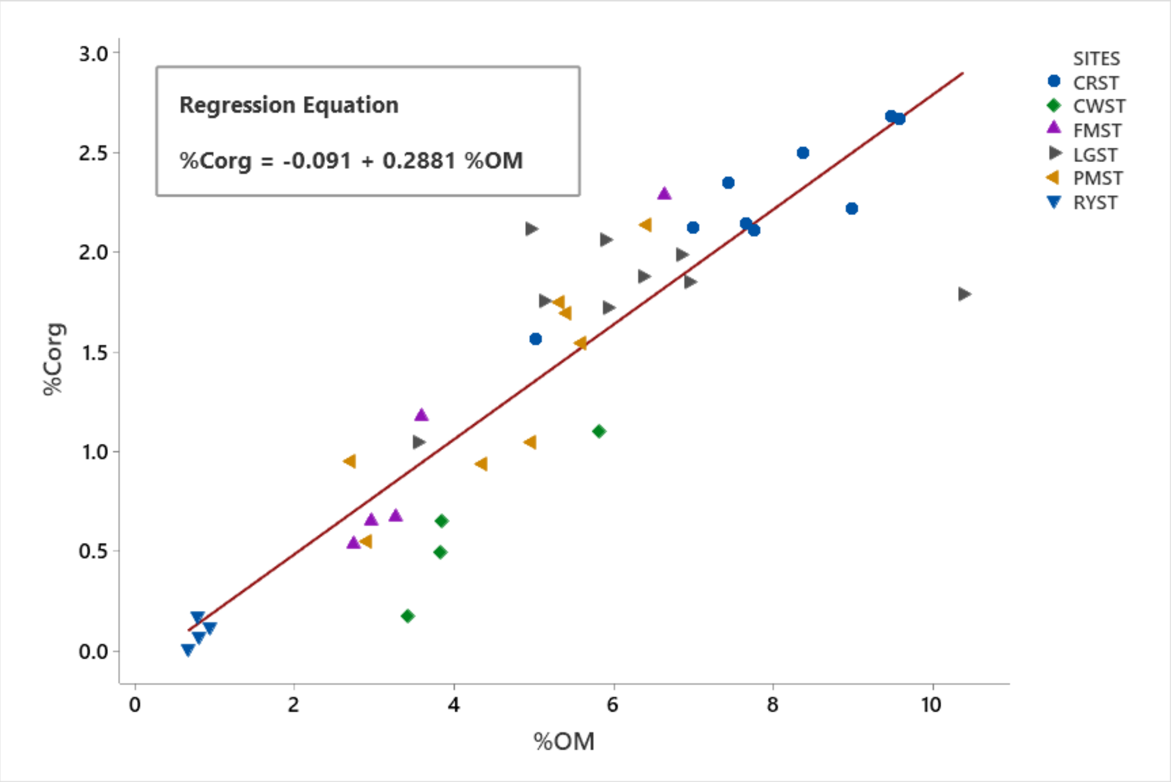

Figure 2: Relationship between directly measured sediment organic carbon content (%C_{org}) derived from elemental analysis and organic matter content (%OM) calculated via loss on Ignition (LOI), for all sites, Creek Rythe (CRST), Hayling Island (LGST), Farlington Marshes (FMST), Porchester (PMST), Ryde (RYST) and Cowes (CWST). Model equation and R-sq value included.

Sediment Carbon Stock (C_{stock})

Mean soil C_{stock}, including BGB, for the top metre of soil (or until refusal at Cowes) varied significantly (F = 176.99; p <0.001) between sampling sites, ranging from 20.76 ± 2.72 MgC ha^{-1} to 117.48 ± 6.77 MgC ha^{-1}(table 1). Mean sediment C_{stock} between all mainland sites, including Creek Rythe, Hayling Island, Porchester and Farlington Marshes was 115.34 ± 9.12 MgC ha^{-1} (n=20), significantly higher than the sites on the Isle of Wight, with 25.64 ± 5.57 MgC ha^{-1} (n=10) in Cowes and Ryde, respectively (p<0.001) (table 1). Creek Rythe had the highest mean values for sediment C_{stock} (117.47 ± 6.76 MgC ha^{-1}), AGB (0.50 ± 0.25 MgC ha^{-1}) and %OM (6.81 ± 1.07%) (table 1). This site also had the greatest seagrass meadow extent (100.24 ha), in the most recent seagrass assessment conducted in the region (Marsden and Chesworth, 2015) (table 1).

Results - Comparison between seagrass and unvegetated sediment organic matter and carbon content

Mean %OM was significantly higher in sediment cores from unvegetated sampling points than those within seagrass beds for all sampled sites, apart from Hayling Island and Porchester (supplementary table B). Unvegetated sediment cores from Creek Rythe had the highest %OM of 9.97 ± 0.98%, followed by Ryde 7.14 ±1.96%, which had the highest difference in %OM between seagrass and unvegetated sediments (**supplementary table B**).

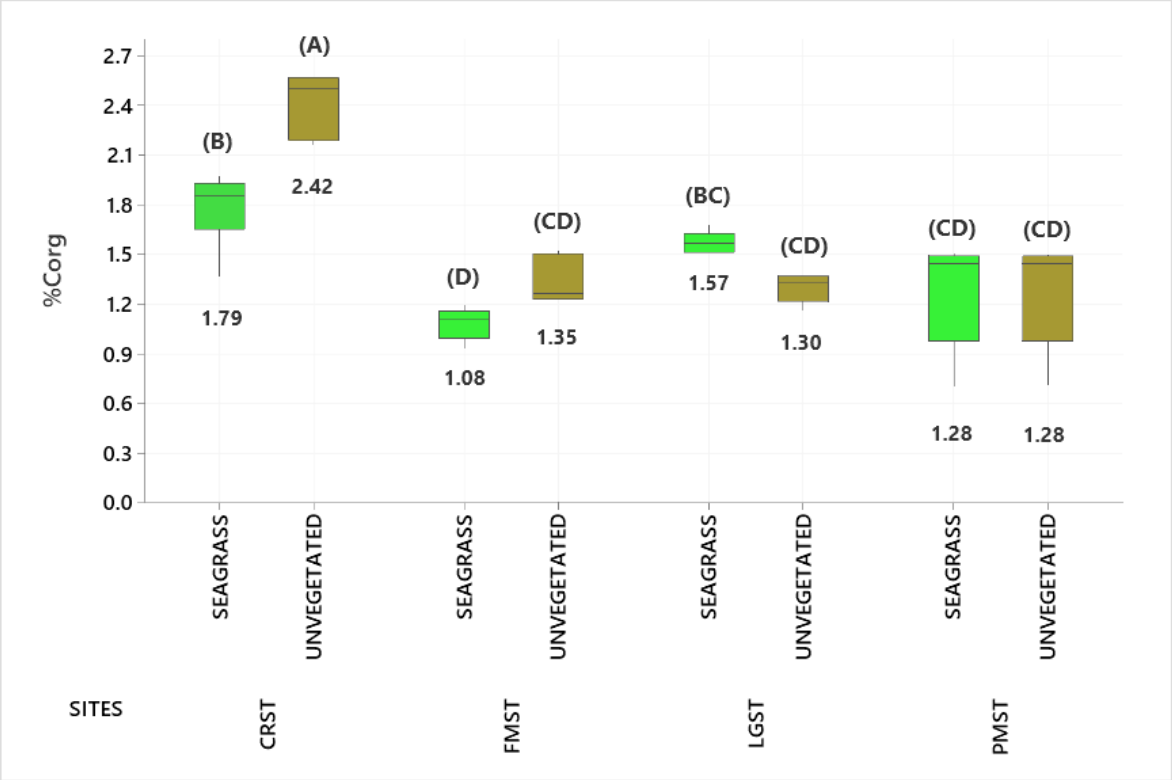

Figure 3: Mean estimated organic carbon content (%C_{org}) from seagrass and adjacent mudflat sediment cores for the sampling sites, Creek Rythe (CRST), Hayling Island (LGST), Farlington Marshes (FMST) and Porchester (PMST). Tukey's grouping results show the same letters for means that are not significantly different. Mean values in bold, n=5. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

Mean estimated %C_{org} was significantly higher in unvegetated sediment cores at Creek Rythe ($p < 0.001$), and Farlington Marshes ($p=0.015$), but significantly lower at Hayling Island ($p=0.001$) (figure 3 and **supplementary table C**). Unvegetated sediment cores from Creek Rythe also had the highest %C_{org} out of all sites, at 2.42 ± 0.19% (figure 3).

Discussion

Plant Biomass

The older seagrass meadows at Chichester Harbour, Hayling Island and Portsmouth Harbour, presented higher AGB than the younger sites from the Isle of Wight. The first records for seagrasses in the study region were: Portsmouth Harbour in 1886; Chichester Harbour in 1915; Langstone Harbour in 1956; Ryde in 1977; and Cowes in 1979 (Marsden and Chesworth 2015). This conforms with results obtained by Serrano *et al*. (2016), showing a tendency for high-biomass, persistent, older meadows to accumulate greater amounts of carbon in their sediments than ephemeral and low-biomass meadows (Lavery *et al*., 2013; Serrano *et al*., 2014).

Average AGB from the studied seagrass meadows was 0.28 ± 0.008 MgC ha^{-1}, which is below the global estimated average of 0.76 ± 0.13 MgC ha^{-1}, but within the reported global range of 0.001–5.54 MgC ha^{-1} (Fourqurean *et al*., 2012a). Settling speed, directly related to seagrass canopy, can increase sedimentation rates by altering flow and trapping particulates, which influences the deposition of suspended organic particles, which could explain why denser meadows, such as Farlington Marshes, presented higher C_{stock} values than patchier meadows, like Ryde and Cowes (Kennedy *et al*., 2010; Fourqurean *et al*., 2012b). Furthermore, the age and maturity of the seagrass meadow, combined with anthropogenic influences, can impact long term changes in nutrient supply in the ecosystem, controlling productivity related to both biomass and sediment C_{stocks} (Armitage and Fourqurean, 2016).

Studies show that the current attenuation effects of *Z. marina* canopies can reduce bottom shear stress by up to 90%, promoting trapping and accumulation of allochthonous particles (Hansen and Reidenbach, 2012). Even though AGB only contributes a small proportion of total C_{stock}, leaf density might play an important role in trapping allochthonous particles from the water column, therefore increasing seagrass carbon sink potential (Mazarrasa *et al*., 2018; Githaiga *et al*., 2019).

The high standard deviation in plant density found in some of the sites, like Ryde, suggests a less uniform cover and patchiness and could be related to differences in meadow canopy, age, complexity, and landscape. The average leaf density across all sites was 394 ± 268 leaves/m^2, with no significant difference between sites. This variation in leaf numbers could also be associated with species and age of the meadows, as some species, e.g. *Z. marina* and *Z. angustifolia,* have longer and wider leaves. Green *et al*. (2018), suggested that a high standard deviation in leaf numbers per area, and related patchiness, could also be linked to poor ecosystem health or physical anthropogenic impacts (Jones and Unsworth, 2016). Additionally, a study on sub-tidal *Z. marina* meadows from Calshot spit, western Solent, reported a seagrass density of 150 leaves/m^2, lower than the mean value found in this study (Lefebvre *et al*., 2009). However, the only seagrass species recorded in Calshot was *Z. marina*, unlike the intertidal meadows analysed in this study, where *Z. angustifolia* was found in all sites apart from Cowes, forming mixed beds with *Z. noltii* in Creek Rythe, Hayling Island and Porchester, and mainly monospecific meadows in Farlington Marshes and Ryde. Moreover, *R. maritima* was found in Creek Rythe and Hayling Island, in small mixed patches. Cowes was the only sampling site with a predominance of *Z. marina*, exhibiting a mean leaf density of 346 ± 247 leaves/m^2, still higher than reported by Lefebvre *et al*. (2009). However, the average leaf density recorded in this study related well with values reported from temperate *Z. marina* meadows from the Baltic Sea, of 417 ± 75 leaves/m^2 in Finland, varying between 112–773 leaves/m^2, and 418 ± 32 leaves/m^2 in Denmark, ranging between 300–652 leaves/m^2 (Rohr *et al*., 2016).

Seagrass rhizomes and roots have important roles in binding and stabilising the sediment. Many studies focus on estimating sediment carbon stocks and AGB linked to net primary production, but there is increased attention being given to BGB and carbon stocks in seagrass roots and rhizomes (Wittman, 1984; Paling and McComb, 2000; Fourqurean *et al*., 2012a). In some seagrass communities (e.g. *Posidonia*, *Zostera* and *Thalassia*), 50 to 90% of biomass is below-ground, while in others (e.g. *Amphibolis*) only 20% of the biomass is in the sediment (Hillman *et al*., 1989; Duarte and Chiscano, 1999). Several studies suggest that the contribution of rhizomes and roots to total seagrass primary production is 20 to 60% in tropical species (Patriquin, 1973; Brouns, 1987) and 20 to 40% in temperate ones (Kenworthy and Thayer, 1984; Wittman, 1984; Dennison *et al*., 1987). These results from temperate seagrass meadows in the Solent Region, dominated by *Zostera* spp., showed that most of the biomass was found above-ground, rather than in roots and rhizomes.

Average BGB from the Solent Region's seagrass meadows was 0.012 ± 0.013 MgC ha^{-1}, below the global estimated average of 1.756 ± 0. 375 MgC ha^{-1}, but within the reported global range of 0.001–17.835 MgC ha^{-1} (Fourqurean *et al*., 2012a). This could be explained by the potential bias of global estimates, which mainly focus on the review of reported values from tropical and Mediterranean seagrass meadows dominated by larger species, like *Posidonia spp*., which can form enormous root mats several metres deep (Romero *et al.,* 1994, Lo Iacono *et al*., 2008; Johannessen and Macdonald, 2016; Serrano *et al*., 2018). Moreover, Fourqurean *et al*. (2012a), report that two-thirds of seagrass biomass is buried in their soil as rhizomes and roots, which contradicts results found for the temperate species studied in this paper. Here, the highest BGB was found in sites with carbon rich sediments, where seagrass formed denser meadows, like Hayling Island and Creek Rythe. However, sites with lower sediment carbon stocks and higher degree of wave exposure, like Ryde, presented higher BGB/ sediment carbon stocks of 0.084 ±0.062 %. Furthermore, due to the overall low contribution of root and rhizome biomass to below-ground sediment C_{stocks} (<1%), it is safe to quantify sediment carbon stocks for temperate seagrass meadows in the Solent Region without removing roots and rhizomes.

Particle size and sediment DBD

Lima *et al*., (2020), in a recent study conducted on the same sampling sites, concluded that a higher degree of exposure, wave activity and tidal flow, promotes erosion and flushing of sediments, which would explain why sites like Ryde, with lower AGB, have sediments with a larger mean grain size. Furthermore, the study also suggests that factors that influence the magnitude of sediment carbon storage in seagrass ecosystems include mineral and physical characteristics, as sediments with a higher concentration of clay particles typically contain a greater amount of carbon (Armitage and Fourqurean, 2016; Mazarrasa *et al*., 2018; Lima *et al*., 2020). This could explain why the Isle of Wight sites, Ryde and Cowes, with predominantly sand sediments, showed the lowest organic carbon storage among the studied sites.

DBD, linked to sediment porosity and organic matter content, are important predictors for erosion rates, as cohesive sediments formed mainly by clay particles, may reduce erosion (de Boer, 2007). Average DBD for all sediment cores analysed was 1.01 ± 0.32 g/cm^3, in accordance with the reported global seagrass mean DBD of 1.03 ± 0.02 g/cm^3 (Fourqurean *et al*., 2012a). Moreover, DBD in the collected top metre of sediment cores was close to the mean value reported by Green *et al*. (2018), for the top 30cm of sediment from subtidal UK seagrass meadows (0.96 ± 0.22 g/cm^3).

These results indicate that the seagrass plants themselves play a key role in determining the amount of C_{org} available for burial, due to the capacity of their canopy to trap and retain sediment particles, which tends to reduce remineralisation rates due to lower oxygen exchange and redox potentials (Middelburg *et al*., 1993; Hedges *et al*., 1995; Burdige, 2007; Serrano *et al*., 2016; Serrano *et al*., 2018). Therefore, sediments with larger, particles (e.g., sand), and larger interstitial spaces, result in higher rates of remineralisation of stored carbon, and lower sediment C_{stocks}, as seen at Ryde and Cowes (Serrano *et al*., 2016, Serrano *et al*., 2018; Gullström *et al*., 2018).

Sediment C_{stock}

The mean carbon stock value for the top metre of sediment from mainland sites of 115.34 ± 9.12 MgC ha^{-1} found in this study falls below Green *et al*.'s (2018) estimations from subtidal *Z. marina* meadows from the West coast of the UK (table 2). However, it is important to highlight that results from this present study are based on direct assessments and calculations of sediment carbon stocks, rather than estimations and/or extrapolations, which can lead to inaccuracies (Johannessen and Macdonald, 2018). Estimations of sediment C_{org} stores can vary with depth, as some deposits can be several metres thick, representing accumulation over millennia. However, the top 1m of sediment is considered the one most vulnerable to remineralization, therefore the one most conventionally studied where possible (Fourqurean *et al*., 2012b).

The total organic carbon stored in the top metre of sediment at all studied sites, including BGB, was 54.7 x 10^3 MgC ha^{-1}, based on the meadow extents reported in Marsden and Chetsworth (2015). Garrard and Beaumont (2014) estimated a mean standing stock of 1.61 MgC ha^{-1} for seagrass meadows in the UK, using data reported from previous studies conducted in different geographical areas. Based on these values, the amount of carbon stored in the Solent Region's seagrass meadows' sediments is ten times higher than the reported estimated average for sediment blue carbon in UK seagrass meadows. Therefore, these results highlight the importance of direct carbon stock measurements to corroborate estimations and extrapolations, helping in the development of a regional profile of seagrass carbon storage in the British Isles.

Table 2 shows seagrass sediment C_{stocks} reported in previous studies, from different regions of the world. The high carbon storage variability between studies can be explained by a range of factors that influence seagrass carbon sink potential, including: species, hydrodynamic regime, geographical variability, grain size and sediment depth profile (Jankowska *et al*., 2016; Mazarrasa *et al*., 2017; Ricart *et al*., 2020; Lima *et al*., 2020). The mean value of sediment organic carbon content stored in the Creek Rythe site at 119.92 ± 10.00 MgC ha^{-1}, within the same order of magnitude as the suggested global mean range of 165.6 MgC ha^{-1} (table 2).

Table 2: Comparison between sediment organic carbon stocks (C$_{stock}$ Mg ha^{-1}) reported for different seagrass species and geographic regions, including the overall mean value for mainland sites in the present study (in bold). * represents studies where C$_{stocks}$ down to 1 metre were calculated using estimations based on shorter cores.

Seagrass species	**Region**	**Sediment Layer (cm)**	**C stock (Mg ha^{-1})**	**References**
Multispecies	Global	0-100	165.6	Fourqurean *et al*. (2012a)
	Florida, Western Mediterranean, Western Australia	0-100*	329.5 ± 55.9	
Posidonia australis	Jervis Bay, NSW Australia	0–100	7.50 ± 2.12	Macreadie *et al*. (2014)
Multispecies	Indonesia	0-100	129.9 ± 9.6	Alongi *et al*. (2015)
Posidonia australis	Oyster Harbour, Western Australia	0–150	107.90 ± 1.2	Rozaimi *et al*. (2016)
Posidonia ocenica	Mediterranean Sea	0-100*	202 ± 79	Mazarrasa *et al*., (2017)
Zostera marina	Baltic Sea	0-100*	23.1	Rohr *et al*., (2018)
Zostera marina	Global	0-100*	108.9	Rohr *et al*., (2018)
Zostera marina	West Coast, UK	0-100*	140.0 ± 73.32	Green *et al*. (2018)
Multispecies	Zanzibar, Tanzania	0.100*	33.9 ± *7.7*	Belshe *et al*., (2018)
Multispecies	Red Sea	0-100	33.5	Serrano *et al*., (2018)
Cymodocea nodosa	Canary Islands, Spain	0-100*	86.20 ± 19.06	Banolas *et al*., 2020

Multispecies	**Central Southern England, UK Mainland Sites**	**0-100 (or to refusal)**	**115.34 ± 9.12**	**Present Study**

Villa and Bernal (2017) describe changes in hydrological regime as another factor which could disturb the equilibrium in vegetated coastal environments, affecting soil aeration and consequent decomposition of recalcitrant sediment organic matter by increased enzyme activity. This could explain the lower sediment C_{stocks} found on sites with greater history of dredging, such as Porchester and Farlington Marshes, and higher wave exposure, like Cowes and Ryde, when compared to more sheltered and undisturbed sites like Creek Rythe and Hayling Island, which had the highest C_{stocks} (Marsden and Chesworth, 2015).

Seagrasses at Farlington Marshes showed higher values of $\%C_{org}$ on the surface, decreasing down-core. This could suggest a larger input of allochthonous carbon in Farlington Marshes’ sediments, due to its reported links to anthropogenic discharge (Marsden and Chesworth, 2015). Better preserved and sheltered sites like Creek Rythe, showed an increase in $\%C_{org}$ down-core, which could also be related to age and maturity of the meadow, with older and deeper sediments representing higher stored organic matter before wasting disease episodes, while younger, closer to the surface, sediments could represent $\%C_{org}$ from restored younger meadows (Marsden and Chesworth, 2015). Moreover, Ricart *et al*. (2020) reported a decrease in $\%C_{org}$ when they compared seagrass meadows between inland, estuarine, and seaward sites.

Our study provided a comparison between $\%C_{org}$ from cores within unvegetated mudflats and adjacent seagrass meadows (table 1 and figure 3). Creek Rythe, the site with the highest reported seagrass meadow areal extent, of 100.24 ha, and highest mean seagrass sediment C_{stock} of 119.92 ± 10.00 MgC ha^{-1}, also presented the highest $\%C_{org}$ (2.42 ± 0.19 %) from neighbouring unvegetated sediment cores.

It is important to factor in the accumulation of allochthonous carbon in seagrass meadows, which could contribute up to 50% of the total C_{org} buried in their sediments (Kennedy *et al*. 2010). However, the fate of allochthonous carbon in coastal waters is still uncertain, with studies suggesting that it could be either intercepted by seagrass meadows and stored in their sediments or transported elsewhere to neighbouring ecosystems (Johannessen and Macdonald, 2016; Macreadie *et al*., 2019; Githaiga *et al*., 2019; Prentice *et al*., 2019).

It has been reported that the loading of allochthonous carbon in the water column depends on local factors and is usually higher in coastal areas influenced by river discharges, such as at Creek Rythe, and/or nearby urbanised areas, as at Farlington Marshes and Ryde (Short and Burdick, 1996; Mazarrasa *et al*., 2017). Serrano *et al*. (2016) also reported that seagrass meadows and unvegetated sediments in environments conducive for depositional processes (i.e., estuaries) accumulated up to 400% more mud compared to other coastal ecosystems. Moreover, Duarte and Krause-Jensen (2017), concluded that seagrass carbon export represents a significant contribution to carbon sequestration, both in sediments outside seagrass meadows in adjacent unvegetated areas and deeper ocean zones, based on a review of 65 published reports. However, the same pattern was not reported by Colarusso *et al*. (2016), who found that sediments within eelgrass meadows stored more carbon than sediments in adjacent, unvegetated reference sites. Even so, they also report a higher variability in sediment C_{stocks} within meadows than the ones found in this study, which could explain the differing results (Colarusso *et al*., 2016).

Results from this study showed the variability in carbon storage, and biomass, between studied sites. Such results can potentially contribute to the implementation of more relevant regional policymaking, by identifying areas with the highest potential for carbon storage and offsetting atmospheric CO_2 emissions. Even though seagrass meadows in the UK and northern Europe have been directly or indirectly included in conservation law and initiatives, including nature-based solutions (Jackson *et al*., 2016; Jones and Unsworth, 2016; Jones *et al*., 2018), studies suggest that these have not generally been effective in protecting and preserving these ecosystems, with declines being consistently reported, including in the UK (Smale *et al*., 2019; Green *et al*., 2021; Gregg *et al*., 2021). Therefore, identifying and understanding the factors that drive seagrass meadow variability, and the threats to seagrass at local scales, is a fundamental requirement for effective management and to harmonise conservation goals with sustainable economic development (Jones *et al.,* 2018; Green *et al*., 2021).

Conclusions

Results from this study address gaps in the existing global database on seagrass meadow carbon stocks, which currently lack information from seagrasses in the UK and from intertidal temperate environments. Results showed that even meadows comprised of smaller, temperate seagrass species can play an important role in global blue carbon inventories, with considerable sediment C_{stocks}. Even though there were significant differences in carbon storage between sites, seagrass meadows in southern England provide important carbon sink potential, comparable with some tropical regions. These results confirm the importance of seagrass ecosystems as carbon sinks and the need to protect them to avoid remineralisation of sediment C_{org}.

Results from this study also indicate that temperate intertidal seagrass meadows in southern England play an important role in carbon storage, as suggested by comparisons between organic matter in seagrass and unvegetated sediments. The significant difference in C_{stocks} between sites shows that there is a pressing need to better map and estimate carbon pools associated with seagrass meadows and adjacent ecosystems worldwide, in order to accurately assess and quantify their contribution as carbon sinks and understand the potential impacts of degradation and conversion of these ecosystems in a changing climate scenario. These findings can be used as a baseline to promote protection and restoration of coastal seagrass habitats, as well as incorporate seagrass conservation into climate change policies. However, more geographically wide-ranging studies should be undertaken to understand the principal factors that influence seagrass carbon storage potential, such as the sedimentary environment, and levels of disturbance.

Supplementary tables

Table A: Site characteristics, including extent, as reported by Marsden and Chesworth, 2015, GPS coordinates, predominant vegetation, and main threats to the seagrass meadows.

SITES	Areal Extension (ha)	Coordinates	Predominant Vegetation	Main Threats
Creek Rythe (CRST)	100.24	50°49'3''N, 0°53'33''W	*Z. marina/Z. angustifolia/ Z. noltii / Ruppia spp.* Dense beds	Past episodes of wasting disease, eutrophication
Hayling Island (LGST)	70.1	50°47'54''N, 0°59'48''W	*Z. marina/Z. angustifolia/ Z. noltii /Ruppia spp.* Dense beds	Past episodes of wasting disease, trampling, dredging
Farlington Marshes (FMST)	31.2	50°50'2''N, 1°2'24''W	*Z. angustifolia* Very patchy	Past episodes of wasting disease, trampling, dredging and eutrophication.
Porchester (PMST)	94.92	50°50'13''N, 1°7'51''W	*Z. angustifolia/ Z. noltii* Patchy	Extensive trampling, dredging, evidence of anoxic conditions and smothering from algal mats
Ryde (RYST)	82.47	50°44'02''N, 1°09'23''W	*Z. angustifolia* Patchy	Past episodes of wasting disease, trampling, dredging and eutrophication
Cowes (CWST)	27.1	50°45'55''N, 1°16'56''W	*Z. marina/ Z. noltii* Very patchy	Past episodes of wasting disease, trampling, dredging and eutrophication

Table B: Summary of statistical results for T-Tests examining organic matter content (%OM) (mean ± standard deviation) from sediment cores on seagrass and unvegetated sampling points, including n, df, T and p, for all study sites. Where df represents the degree of freedom, and significance value for two sample T-test, p<0.05.

Study Site	Sediment core	%OM	N	df	T	p
Creek Rythe (CRST)	Seagrass	6.82 ± 1.07	10	13	-5.53	<0.001
	Un-vegetated	9.97 ± 0.98	5			
Hayling Island (LGST)	Seagrass	5.87 ± 0.17	5	8	1.26	0.243
	Un-vegetated	5.20 ± 1.17	5			
Farlington Marshes (FMST)	Seagrass	3.64 ± 0.51	5	12	-3.74	0.003
	Un-vegetated	5.70 ± 1.15	9			
Porchester (PMST)	Seagrass	4.73 ± 1.58	5			
	Un-vegetated	5.58 ± 1.15	5	8	-0.97	0.36

Table C: Summary of statistical results for T-Tests examining organic carbon content (%C_{org}) (Mean ± standard deviation) from sediment cores on seagrass and unvegetated sampling points, including n, df, T and p, for all study sites. Where df represents the degree of freedom, and significance value for two sample T-test, p<0.05.

Sites	Sediment core	%C_{org}	N	df	T	p
Creek Rythe (CRST)	Seagrass	1.79 ± 0.19	10	13	-5.72	< 0.001
	Un-vegetated	3.96 ± 0.42	5			
Hayling Island (LGST)	Seagrass	1.57 ± 0.07	5	7	-5.43	0.001
	Un-vegetated	1.30 ± 0.09	5			
Farlington Marshes (FMST)	Seagrass	1.08 ± 0.10	5	12	-3.74	0.005
	Un-vegetated	2.12 ± 0.49	9			
Porchester (PMST)	Seagrass	1.28 ± 0.33	5			
	Un-vegetated	2.14 ± 0.61	5	8	-0.95	0.371

Reference List

Alongi, D., D. Murdiyarso, J. Fourqurean, J. Kauffman, A. Hutahaean, S. Crooks, C. Lovelock, J. Howard, D. Herr, and M. Fortes. (2015). Indonesia's blue carbon: a globally significant and vulnerable sink for seagrass and mangrove carbon. *Wetlands Ecology and Management* **24:**3–13.

Armitage A.R., Fourqurean J.W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences* **13:**313–321.

Bañolas, G., S. Fernández, F. Espino, R. Haroun, and F. Tuya. 2020. "Evaluation of Carbon Sinks by the Seagrass Cymodocea Nodosa at an Oceanic Island: Spatial Variation and Economic Valuation." *Ocean & Coastal Management* **187:** 105112.

Belshe, E. F., Hoeijmakers, D., Herran, N., Mtolera, M., and Teichberg, M. (2018). Seagrass community-level controls over organic carbon storage are constrained by geophysical attributes within meadows of Zanzibar, Tanzania. *Biogeosciences* **15:** 4609–4626.

Campagne, C.S., Salles, J.-M., Boissery, P., Deter, J., (2015). The seagrass *Posidonia oceanica*: ecosystem services identification and economic evaluation of goods and benefits. Mar. Pollut. Bull. **97:** 391–400.

Colarusso P, Simpson J, Novak A, Ford K, DiBona P, Vella P, Deane J, Stanley S (2016) Blue carbon, green eelgrass: estimating carbon storage in eelgrass in the Gulf of Maine. US EPA Climate Ready Estuaries Program Technical Report: 18 pp

Connell SD, Gillanders BM. (2007). *Marine ecology*. South Melbourne: Oxford University Press.

Costanza, R., d'Arge, R., de Groot, R., Farberk, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Suttonkk, P. And Marjan van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature* **387:** 253-260.

Cullen-Unsworth LC, Nordlund LM, Paddock J, Baker S, McKenzie LJ, Unsworth RKF (2014). Seagrass meadows globally as a coupled social–ecological system: Implications for human wellbeing. *Marine Pollution Bulletin*. **83:** 387–397. pmid:23800460.

Dadey, K., Janecek, T., Klaus, A. (1992). Dry bulk density: its use and determination. Proceedings of the Ocean Drilling Program. *Scientific Results,* **26**: 551-554.

Davison, D.M., Hughes, D.J., (1998). *Zostera biotopes. An Overview of Dynamics and Sensitivity Characteristics for Conservation management of SAC.* Vol. I. Scottish Association for Marine Science (UK Marine SACs Project), pp. 95.

Dewsbury B.M., M. Bhat, J.W. Fourqurean (2016). A review of seagrass economic valuations: gaps and progress in valuation approaches. *Ecosystem Services*, **18:** 68-77.

Dickie, I., Cryle, P., Maskell, L. (2014). UK National Ecosystem Assessment Follow-on. Work Package Report 1: Developing the evidence base for a Natural Capital Asset Check: What characteristics should we understand in order to improve environmental appraisal and natural income accounts?

Duarte, C.M. (1990). Seagrass nutrient content. *Marine ecology progress series. Oldendorf*, **6**: 201–207.

Duarte, C.M., Chiscano, C.I. (1999) Seagrass biomass and production: A reassessment. *Aquatic Botany.* **65:** 159-174.

Duarte CM and Krause-Jensen D (2017) Export from Seagrass Meadows Contributes to Marine Carbon Sequestration. *Front. Mar. Sci.* ***4:****13.*

Dumas, J.B.A., (1831). Procedes de l'Analyse Organique, *Ann. Chim. Phys.* ***247*****:**198–213.

Folk, R. L. and Ward, W. C. (1957). Brazos river bar: a study of significance of grain size parameters, *J. Sediment Petrol*. **27:** 3–26.

Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marba, N., Holmer, M., Mateo, M.A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J. & Serrano, O. (2012a). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience,* **5:** 505-509.

Fourqurean, J.W., Kendrick, G.A., Collins, L.S., Chambers, R.M. & Vanderklift, M.A. (2012b). Carbon, nitrogen and phosphorus storage in subtropical seagrass meadows: examples from Florida Bay and Shark Bay. *Marine and Freshwater Research*, **63:** 967–983.

Garrard, S. L. and Beaumont, N. J. (2014). The effect of ocean acidification on carbon storage and sequestration in seagrass beds; a global and UK context. *Marine Pollution Bulletin,* **86:** 138-46.

Githaiga MN, Frouws AM, Kairo JG and Huxham M (2019) Seagrass Removal Leads to Rapid Changes in Fauna and Loss of Carbon. *Front. Ecol. Evol*. **7:**62.

Grace, J., José, J.S., Meir, P., Miranda, H.S. and Montes, R.A. (2006), Productivity and carbon fluxes of tropical savannas. Journal of Biogeography, 33: 387-400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Green, E.P., Short, F.T., (2003). World Atlas of Seagrasses. University of California Press.

Green, A., M. A. Chadwick, and P. J. S. Jones. (2018). Variability of UK seagrass sediment carbon: Implications for blue carbon estimates and marine conservation management. *PLoS One*. **13:** e0204431. doi:10.1371/journal.pone.0204431.

Green AE, Unsworth RKF, Chadwick MA and Jones PJS. (2021) Historical Analysis Exposes Catastrophic Seagrass Loss for the United Kingdom. *Frontiers in Plant Science,* **12:**629962. doi: 10.3389/fpls.2021.629962

Gregg R., Elias J. L., Alonso I., Crosher I.E. and P. Muto and M.D. Morecroft (2021). Carbon storage and sequestration by habitat: a review of the evidence (second edition) Natural England Research Report NERR094. Natural England, York.

Hansen JCR, Reidenbach MA (2012). Wave and tidally driven flows in eelgrass beds and their effect on sediment suspension. *Mar Ecol Prog Ser* **448:**271-287.

Heiri, O., Lotter, A.F. & Lemcke, G. (2001). Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of paleolimnology*, **25:** 101–110.

Howard, J., Hoyt, S., Isensee, K., Pidgeon, E., Telszewski, M. (ed[s].) (2014). *Coastal Blue Carbon: Methods for assessing carbon stocks and emissions factors in mangroves, tidal salt* *marshes, and seagrass meadows*. Conservation International, Arlington, Virginia, USA: Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature.

Jackson, E. L., Cousens, S. L., Bridger, D. R., Nancollas, S. J., & Sheehan, E. V. (2016). Conservation inaction in action for Essex seagrass meadows? *Regional Studies in Marine Science*, **8:** 141–150.

Johannessen S. C. and Macdonald R. W. (2016) Geoengineering with seagrasses: is credit due where credit is given? *Environ Res,.* **Lett. 11:** 113001. Doi: doi:10.1088/1748-9326/11/11/113001.

Jones, B. L. & Unsworth, R. K. (2016). The perilous state of seagrass in the British Isles. *R Soc Open Sci,* **3:** 150596.

Jones, B. L., Unsworth, R. K. F., McKenzie, L. J., Yoshida, R. L., & Cullen-Unsworth, L. C. (2018). Crowdsourcing conservation: The role of citizen science in securing a future for seagrass. *Marine Pollution Bulletin*. **134:** 210–215. https://doi.org/10.1016/j. marpolbul.2017.11.005.

Kennedy, H., & Björk, M. (2009). Seagrasses. In D. d'A Laffoley & G. Grimsditch (Eds.), The management of natural coastal carbon sinks in coastal ecosystems: Investigating and realizing the potential (pp. 23–30). Switzerland: IUCN, Gland.

Kennedy, Hilary & Beggins, Jeff & Duarte, Carlos & Fourqurean, James & Holmer, Marianne & Marba, Nuria & Middelburg, Jack. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles - GLOBAL BIOGEOCHEM CYCLE*. **24.** GB4026. 10.1029/2010GB003848.

King, D. (2010). Solent Waders and Brent Goose Strategy 2010. Hampshire and Isle of Wight Wildlife Trust.

Kurniawan F. *et al* (2020) IOP Conf. Ser.: *Earth Environ. Sci*. **414:** 01200

Lavery, Paul & Mateo, Miguel-Ángel & Serrano, Oscar & Rozaimi Jamaludin, Mohammad. (2013). Variability in the Carbon Storage of Seagrass Habitats and Its Implications for Global Estimates of Blue Carbon Ecosystem Service. *PloS one*. **8:** e73748. 10.1371/journal.pone.0073748.

Lefebvre, A., C. E. L. Thompson, K. J. Collins, and C. L. Amos. (2009). "Use of a High-Resolution Profiling Sonar and a Towed Video Camera to Map a *Zostera marina* Bed, Solent, UK." *Estuarine, Coastal and Shelf Science* **82 (2):** 323–334.

Lima, M. D. A. C., Ward, R. D., and Joyce, C. B. (2020). Environmental drivers of sediment carbon storage in temperate seagrass meadows. *Hydrobiologia* **847:** 1773–1792. doi: 10.1007/s10750-019-04153-5

Luisetti, T.; Turner, K.; Andrews, J.; Jickells, D.; Kroger, S.; Diesing, M.; Paltriguera, L.; Johnson, M.; Parker, E.; Bakker, D. (2019). Quantifying and valuing carbon flows and stores in coastal and shelf ecosystems in the UK. *Ecosystem Services.* **35:** 67–76.

Macreadie, Peter & Allen, Katie & P. Kelaher, Brendan & Ralph, Peter & G. Skilbeck. (2014). Quantifying and modelling the carbon sequestration capacity of seagrass meadows - A critical assessment. *Marine pollution bulletin*. **83:** 430-439.

Macreadie P. I., Ewers C., Whitt A., Ollivier Q., Trevathan-Tackett S., Carnell P., Thomson A. and Serrano O., (2018) Comment on Geoengineering with seagrasses: is credit due where credit is given?. *Environ. Res. Lett.*, **13:** 028002.

Macreadie, P. I, Anton, A., Raven, J. A., Beaumont, N., Connolly, R. M., Friess, D. A., *et al*. (2019). The future of Blue Carbon science. *Nature Communications* **10**: 3998.

Macreadie, P.I., Costa, M.D.P., Atwood, T.B. *et al.* (2021) Blue carbon as a natural climate solution. *Nat Rev Earth Environ* **2,** 826–839. https://doi.org/10.1038/s43017-021-00224-1

Marbà, N. *et al*. (2015) Impact of seagrass loss and subsequent revegetation on carbon sequestration and stocks. *J. Ecol.* **103**: 296–302.

Marsden, A. L. and Chesworth, J. C. (2015). *Inventory of eelgrass beds in Hampshire and the Isle of Wight 2015, Section One: Report. Version* ***7:*** *May 2015.* Hampshire, UK: Hampshire and Isle of Wight Wildlife Trust.

Mazarrasa, I., Marbà, N., Garcia-Orellana, J., Masqué, P., Arias-Ortiz, A., Duarte, C.M. (2017). Dynamics of carbon sources supporting burial in seagrass sediments under increasing anthropogenic pressure. *Limnol. Oceanogr*. **62:** 1451–1465.

Mazarrasa, I., Samper-Villarreal, J., Serrano, O., Lavery, P. S., Lovelock, C. E., Marba, N., & Duarte, C. M. (2018). Habitat characteristics provide insights of carbon storage in seagrass meadows. *Marine Pollution Bulletin.* **134:** 106–117.

Mcleod, E. Chmura, G. Bouillon, S. Salm, R. Bjork, M. Duarte, C. Lovelock, C. Schlesinger, W. Silliman, B. (2011). A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Front. Ecol. Environ,* **7:** 362_370.

Muehlstein, L.K., (1988). Perspectives on the wasting disease of eelgrass *Zostera marina*. *Dis. Aquat. Org*., **7:** 211–221.

Nordlund, L.M., Koch, E.W., Barbier, E.B., Creed, J.C., (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS One* 2016.

Nordlund, L. M., Jackson, E. L., Nakaoka, M., Samper-Villarreal, J., Beca-Carretero, P., & Creed, J. C. (2017). Seagrass ecosystem services – What's next? *Marine Pollution Bulletin.* **134:** 145-151.

Orth R. J., J. S. Lefcheck, K. S. McGlathery, L. Aoki, M. W. Luckenbach, K. A. Moore, M. P. J. Oreska, R. Snyder, D. J. Wilcox, B. Lusk, (2020). Restoration of seagrass habitat leads to rapid recovery of coastal ecosystem services. *Science Advances.* **6:** eabc6434.

Pedersen, M. Ø., Serrano O., Mateo M. A., and Holmer M. (2011) Decomposition of *Posidonia oceanica* matte in a climate change setting*, Aquat. Microb. Ecol*., **65:** 169–182.

Prentice, C., Hessing-Lewis, M., Sanders-Smith, R., & Salomon, A. K. (2019). Reduced water motion enhances organic carbon stocks in temperate eelgrass meadows. *Limnology and Oceanography*, **64**(6): 2389–2404.

Ricart, A.M., York, P.H., Bryant, C. et al. (2020). High variability of Blue Carbon storage in seagrass meadows at the estuary scale. *Scientific Reports* **10:** 5865.

Röhr, Emilia & Boström, Christoffer & Canal-Vergés, Paula & Holmer, Marianne. (2016). Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows. *Biogeosciences*. **13:** 6139-6153. 10.5194/bg-13-6139-2016.

Röhr, M. E., Holmer, M., Baum, J. K., Björk, M., Chin, D., Chalifour, L., et al. (2018). Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) meadows. *Global Biogeochemical Cycles*, **32**.

Rozaimi, M., Lavery, P. S., Serrano, O., & Kyrwood, D. (2016). Long-term carbon storage and its recent loss in an estuarine *Posidonia australis* meadow (Albany, Western Australia). *Estuarine, Coastal and Shelf Science*. ***171*:** 58–65.

Serrano, O., Lavery, P.S., Rozaimi, M., Mateo, M.A. (2014). Influence of water depth on the carbon sequestration capacity of seagrass. *Glob. Biogeochem. Cycles* **28:** 950–961. Science Society of America: Madison; 21-31.

Serrano, Oscar & Ricart, Aurora & Lavery, Paul & Angel Mateo, Miguel & Arias-Ortiz, Ariane & Masqué, Pere & Rozaimi Jamaludin, Mohammad & Steven, Andy & Duarte, Carlos. (2016). Key biogeochemical factors affecting soil carbon storage in Posidonia meadows. *Biogeosciences.* **13:** 4581-4594. 10.5194/bg-13-4581-2016.

Serrano, O., Almahasheer, H., Duarte, C. M. & Irigoien, X. (2018). Carbon stocks and accumulation rates in Red Sea seagrass meadows. *Sci. Rep.* **8**: 15037.

Short, F.T., Burdick, D.M., Kaldy, J.E., (1996). Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnol. Oceanogr*. **40:** 740–749.

Smale, DA, Epstein, G, Parry, M, Attrill, MJ. (2019) Spatiotemporal variability in the structure of seagrass meadows and associated macrofaunal assemblages in southwest England (UK): Using citizen science to benchmark ecological pattern. *Ecol Evol*. **9:** 3958– 3972.

Soil Survey Division Staff. (1993). Soil survey manual. United States Department of Agriculture Handbook 18.

Taillardat Pierre, Friess Daniel A. and Lupascu Massimo (2018) Mangrove blue carbon strategies for climate change mitigation are most effective at the national scale. *Biol. Lett.* **14** 2018025120180251 http://doi.org/10.1098/rsbl.2018.0251

Terrados, J., Bodrum, J., (2004). Why are Seagrasses Important? - Goods and Services Provided by Seagrass. pp. 8–10.

Tomasko, D., Crooks, S., Robison, D., (2017). Refining carbon sequestration estimates of seagrass meadows in Tampa Bay. Pp. 259–269. In: Burke, M. (Ed.), Proceedings, Tampa Bay Area Scientific Information Symposium, BASIS 6. 28–30 September 2015.

Unsworth, R. K. F., L. J. McKenzie, C. J. Collier, L. C. Cullen-Unsworth, C. M. Duarte, J. S. Eklöf, J. C. Jarvis, B. L. Jones, and L. M. Nordlund. (2019) Global challenges for seagrass conservation. *Ambio* **48:**801-815.

Urquhart, J.T., (1824). On the preparation of the *Zostera* or seagrass in Orkney. Prize Essays *Trans. Highl. Soc. Scotl*. 588–593.

Villa, Jorge & Bernal, Blanca. (2017). Carbon sequestration in wetlands, from science to practice: An overview of the biogeochemical process, measurement methods, and policy framework. *Ecological Engineering*. **10**.1016/j.ecoleng.2017.06.037.

Wentworth C. K. (1922), "A Scale of Grade and Class Terms for Clastic Sediments," The *Journal of Geology* **30**, no. 5 (Jul. - Aug., 1922): 377-392.

Williams C. and Davies W. (2018) A valuation of the Provisioning Ecosystem Services provided by shellfish for priority shellfish waters in the Solent. A report for Sussex IFCA and the Environment Agency. 44pp NEF Consulting Limited, London. UK.

Whitehead S, Cambridge ML, Renton M. (2018). A functional–structural model of ephemeral seagrass growth influenced by environment. *Annals of Botany*.**121:** 897–908.