Title: Environmental drivers of sediment carbon storage in temperate seagrass meadows

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Abstract

Seagrass meadows are productive ecosystems that contribute to climate change mitigation by accumulating 'Blue Carbon' in their plant biomass and sediments. However, there is wide variation in reported sediment carbon stocks (C_{stocks}) across different global regions and between meadows composed by different seagrass species. Therefore, understanding the drivers for sediment carbon stocks (C_{stocks}) variation is crucial to developing effective conservation and restoration projects for seagrass ecosystems. This study compares and analyses the influence of a range of environmental variables on the variation in sediment C_{stocks} for six intertidal seagrass meadows within the Solent, in southern England. There were significant differences between sites for all variables except leaf density, and concentrations of the sediment pore water nutrients, nitrites and sulphates. Sediment dry bulk density, mean grain size, sorting coefficient, % mud, elevation above sea level, and pore water salinity showed the highest levels of association with C_{stocks} when assessed individually. Multivariate analyses showed that sediment dry bulk density, sorting coefficient, % mud, and pore water pH and concentration of nutrients showed the greatest influence on C_{stocks}. Moreover, sediment characteristics such as dry bulk density, sorting coefficient and % mud, acted in

conjunction to explain the bulk of the variation in C_{stocks} among sites. Therefore, sediment characteristics should be considered as important indicators for carbon storage potential in intertidal temperate seagrass meadows used for climate change mitigation.

Keywords: Blue carbon, temperate, intertidal, sediment carbon stocks, Seagrass.

Introduction

"Blue Carbon" is a concept that represents carbon stored in coastal ecosystems, including salt marshes, mangroves and seagrass meadows (Pendleton *et al*., 2012). These ecosystems store carbon within their sediments, living aboveground biomass (leaves, branches, and stems), living belowground biomass (roots), and non-living biomass (e.g., sedimentary organic matter, litter and dead wood) (McLeod *et al*., 2011). The majority of the blue carbon stored within coastal ecosystems, can be found in their sediments (Murray *et al*., 2011). These systems are able to sequester and store large amounts of carbon, not only through photosynthesis, but also by trapping sediments and allochthonous organic debris derived from proximate ecosystems and transported by rivers or tides (McLeod *et al.*, 2011; Howard *et al.*, 2017). Whilst mangroves are limited to tropical and sub-tropical zones, salt marshes and seagrass meadows have a pan-global distribution, therefore providing significant carbon storage and sequestration potential (Garrard & Beaumont, 2014). It has been suggested that seagrasses provide a higher contribution to carbon accumulation per unit area than terrestrial soils, mainly due to their ability to trap suspended particles by reducing water flow and wave energy (Fonseca & Cahalan, 1992; Gacia & Duarte, 2001; Agawin & Duarte,

2002; Gacia *et al*., 2002; Koch *et al*., 2006; Bos *et al*., 2007; Hendriks *et al*., 2008; Kennedy & Björk, 2009; Rohr *et al*., 2018).

Seagrasses are found in widely varied environments, from sheltered estuaries to highly exposed shores, and from intertidal zones to a depth of 90m in the ocean (Duarte, 1991; Hemminga & Duarte, 2000, Chmura & Hung, 2003; Carruthers *et al*., 2007; Mazarrasa *et al*., 2018). This variation in distribution and setting, is one of the factors responsible for the highly variable estimates of sediment organic carbon (C_{org}) and sequestration rates among seagrass communities and species (Lavery *et al*., 2013; Miyajima *et al*., 2015; Mazarrasa *et al*., 2017a). Global estimations report that seagrass sediment carbon storage is believed to average 830 Mg ha^{-1}, resulting in a total estimated global carbon storage of 19.9×10^9 Mg (Fourqurean *et al*., 2012; Macreadie *et al*., 2013). However, recent studies have described the influence of habitat characteristics on sequestration and storage of C_{org} in seagrass sediments, which highlights the risks of extrapolating to regional and global estimates from limited data sets represented by only a few species and sites (Nelleman *et al*., 2009; Fourqurean *et al*., 2012; Lavery *et al*., 2013; Garrard & Beaumont, 2014; Serrano *et al*., 2014; Samper-Villarreal *et al*., 2016; Serrano *et al*., 2016; Maxwell *et al*., 2017; Mazarrasa *et al*., 2018).

The deposition of organic carbon in seagrass meadow sediments (C_{stock}) is regulated by three main mechanisms: meadow productivity and biomass build-up (particularly below-ground); the retention of allochthonous carbon in the sediment; and carbon burial efficiency in seagrass sediments (Mazarrasa *et al*., 2018). These mechanisms have been reported to be positively related to the anoxic conditions of the sediments, the proportion of clay particles, and of refractory, molecularly complex carbon being stored (Mateo *et al*., 2006; Serrano *et al*., 2016; Mazarrasa *et al*., 2018). However, seagrass meadows are experiencing a global area decline estimated at 7% per

year, potentially resulting in CO_2 emissions as sediments are increasingly being eroded and C_{stocks} exposed to aerobic conditions (Waycott et al., 2009; Marbà *et al*.,2014; Serrano *et al.*, 2016; Lovelock *et al*., 2017; Mazarrasa *et al*., 2018). Santos *et al*., (2019) highlighted similar trends in seagrass decline in Europe, despite efforts to include these ecosystems as sensitive quality elements to provide diagnostic of ecosystem health under the European Union (EU) Water Framework Directive (WFD). The decline in seagrass C_{stocks} is due to a range of anthropogenic impacts related to eutrophication, shading, shoreline erosion, sea warming, and physical removal of shoots by trawling and anchoring (Duarte, 2002; Orth *et al*., 2006; Ralph *et al*., 2006; Macreadie *et al*., 2012; Marbà *et al*., 2013; Duarte, 2014; Santos *et al*., 2019). Conversely, studies have shown that eutrophication and nutrient loading might favor the accumulation of allochthonous carbon (e.g. microalgae and epiphyte blooms) in sediment deposits, leading to an increase in the total carbon sequestered in seagrass meadows (Macreadie *et al*., 2012; Serrano *et al*., 2016; Mazarrasa *et al*.,2017b; Samper-Villarreal *et al*., 2018).

Furthermore, climate change may aggravate seagrass decline, as a result of multiple impacts including ocean acidification, and increases in sea surface temperature and water depths (Short & Neckles, 1999; Jordà *et al.*, 2012; Saunders *et al*., 2013; Valle *et al*., 2014; Marba *et al*., 2018).The effects of ocean acidification on the accumulation of autochthonous C_{org} in seagrass sediments and biomass still needs to be clarified, with some studies suggesting increases in sequestration rates under acidic conditions (Palacios & Zimmerman, 2007; Hall-Spencer *et al*., 2008; Fabricius *et al*., 2011; Russell *et al*., 2013; Garrard & Beaumont, 2014; Mazarrasa *et al*., 2018) and others reporting a substantial decrease (Martínez-Crego *et al*., 2014; Repolho *et al*., 2017). Thus, understanding the response of seagrass ecosystems to climate change and other anthropogenic impacts has become a priority for the development of effective conservation and management (Brierley & Kingsford, 2009; Hoegh-Guldberg & Bruno, 2010; Valle *et al*., 2014; Maxwell *et al*., 2017; Santos *et al*.,

2019). It is important to draw attention to the potential that environmental factors can act in synergy, and their effects will depend upon seagrass species' abilities to tolerate and adapt to different scenarios (Ralph, 1999; Sunda & Cai; 2012; Repolho *et al*., 2017). The high sensitivity of seagrasses to environmental change means it is vital to understand which factors may threaten their role as long term carbon sinks (Marbà *et al*., 2012; Cullen-Unsworth *et al*., 2014; Jones & Unsworth, 2016; Mazarrasa *et al*., 2018). Therefore, monitoring programs based either directly or indirectly on seagrass responses to environmental disturbance have increasingly been incorporated into ecosystem management (Martínez-Crego *et al*., 2008; Montefalcone, 2009; Roca *et al*., 2016). For example, the European Union's Water Framework Directive includes the monitoring of seagrass ecosystems as a reference for the ecological status of coastal areas, using characteristics such as leaf density, cover, and depth limits (Longstaff *et al*., 1999; D'Souza *et al*., 2015; Roca *et al*., 2016).

A large number of biotic and abiotic factors can potentially influence carbon stocks and accumulation rates in seagrass meadows (Maxwell *et al*., 2017). Mazarrasa *et al.*'s (2018) review found that species composition, high canopy complexity, a continuous meadow landscape, biotic interactions made of complex and stable trophic interactions, low exposure to wave energy, low levels of turbidity, and shallow water depth, were key factors contributing favourably to carbon storage. Conversely, factors that negatively impact carbon storage were, low nutrient availability, over grazing, bioturbation, eutrophication and climate change, while elevation, climatic region and acidification were amongst the unresolved components (Maxwell *et al*., 2017; Mazarrasa *et al*., 2018). However, most studies investigating relationships between environmental factors and seagrass carbon storage capacity have focussed on specific factors individually, rather than their associations (Lavery *et al*., 2013; Rozaimi *et al*., 2013; Duarte *et al*., 2013; Martínez-Crego *et al*., 2014; Armitage and Fourqurean 2016; Howard *et al*., 2016; Ricart *et al*., 2017; Oreska *et al*., 2017;

Mazarrasa *et al*., 2017; Mazarrasa *et al*., 2018). Few studies have analysed the influence of multiple environmental factors as drivers of variability in carbon storage in seagrass sediment, with some evaluating relationships at small (within meadow) scales (Samper-Villarreal *et al* 2016; Mazarrasa *et al*., 2017), and others comparing between meadows from different geographical regions (Lavery *et al*., 2013; Miyajima *et al*., 2015; Dahl *et al*., 2016; Gullstro¨m *et al* 2017; Rohr *et al*., 2018), which could make a reliable assessment of variability harder.

In addition, intertidal seagrass meadows may be particularly vulnerable to multiple stressors, such as air exposure, temperature, light intensity and salinity, which could impact photosynthetic rates and consequent carbon uptake and storage (Bjork *et al*., 1999). Intertidal populations are also prone to runoff from catchment areas, being susceptible to elevated levels of nutrients from industrial and agricultural waste, which not only affect meadow health, but increase epiphyte productivity (Short and Willie-Echeverria, 1996; Ye *et al*., 2003). Variability among seagrass species can also affect their carbon storage potential, with species-environment interactions likely to strongly impact the storage of sedimentary carbon (Lavery *et al*., 2013). To this date, no study has evaluated the interaction between environmental factors and variation in seagrass sediment carbon storage at the intermediate (regional) scale, incorporating different habitat characteristics, and mixed species meadows. Further understanding of these interactions would benefit global seagrass research, promoting conservation and protection programs with the aim of climate change mitigation, and seagrass status as a biological indicator of ecosystem status. Therefore, this study aims to identify the key environmental factors driving carbon storage in intertidal seagrass sediments from different sites within the same temperate region. In this study, i) variation in environmental factors between seagrass sites is assessed, and ii) relationships between factors that influence carbon stocks were identified, to answer the following research hypothesis: within temperate intertidal seagrass meadows, sediment characteristics most strongly influence carbon storage.

Methods

Study Sites

The Solent is considered one of the most important coastal areas in the UK composed of natural and man-made environments with high habitat diversity, providing an important wildlife resource internationally (King, 2010). The distinctive hydrographic regime of an extended or double high tide and the intricacy of different habitats are reasons why the Solent region has been selected as a Special Area of Conservation (SAC) (McLeod *et al*., 2005). Tidal amplitudes are not uniform along the Solent, with the eastern end having almost double the tidal range of the western end, providing longer inundation periods (Dyer & King, 1975). The region is defined by the body of water that encompasses the central south coast of England and the Isle of Wight, thought to have been formed during the last Ice Age, when ice melting flooded the paleo-channel Solent River system (Fletcher *et al.*, 2007).

Studies have been reporting water quality issues along the Solent (Harding *et al*., 2016; Environment Agency 2016a; 2016b). For example, the harbours and estuaries at Langstone, Chichester, Portsmouth, and Eastern Yar, on the Isle Wight, have been classified as eutrophic or at risk of eutrophication by the Environment Agency (Harding *et al.*, 2016; Environment Agency 2016a; 2016b). This increase in nutrient levels can cause algal blooms, promoting the growth of benthic algae which can potentially smother seabed habitats, like seagrass meadows (Harding *et al*., 2016). Therefore, these estuaries in the Solent have been designated as sensitive areas, or polluted waters, under the Urban Waste Water Treatment Directive and/or Nitrates Directive (Harding *et al*., 2016; SeaView, 2017). Sources of pollution include treated effluent discharges from waste water treatment works, and runoff from the surrounding catchment including waste and

industrial activities (SeaView, 2017). Combined with riverine sources, it is evident that offshore coastal background sources have been responsible for the nutrient loading input within the Solent's estuaries (Environment Agency 2016a; 2016b).

To represent the characteristic variation in the region, six study sites with known seagrass meadow extents, were selected within the Solent region, Southeast of England, following an assessment of the most recent seagrass distribution inventory (Marsden and Chesworth, 2015) (**Table 2**). Selected sites were Creek Rythe in Chichester Harbour, Hayling Island and Farlington Marshes in Langstone Harbour, Porchester in Portsmouth Harbour, Cowes and Ryde (**Figure 1**). Seagrass meadows from all sites are characterised as intertidal, located in both sheltered inland bays (Chichester Harbour, Langstone Harbour, and Portsmouth Harbour sites), and more exposed shorelines (Isle of Wight sites), encompassing seagrass habitats from both muddy and sandy substrates, incorporating *Zostera marina* (Eelgrass), *Zostera noltei*, *Zostera angustifolia*, and *Ruppia spp.* meadows (Marsden & Chesworth, 2015). The most recent seagrass surveys conducted at Creek Rythe, in Chichester Harbour, reported patchiness with varied meadow density, and no clear dominance between *Z. noltei* and *Z. angustifolia* species, while *Ruppia* spp. were only found within inlet channels (Marsden & Chesworth, 2015). The site has a tidal range of 0.9-4.9m, represented by mean low water springs (MLWS) and mean high water springs (MHWS) values, respectively. Surveys in Langstone Harbour and Porchester reported mainly the presence of *Z. angustifolia* and *Z. noltei*, but also *Ruppia* spp. in intertidal areas (Marsden & Chesworth, 2015), with a MLWS and MHWS tidal range of 0.8-4.8m, respectively. Here, there are reports of significant declines in seagrass due to extensive trampling and dredging, and some evidence of anoxic conditions and smothering from dense green algae mats (Marsden & Chesworth, 2015). At the Isle of Wight sites, Cowes is characterised by gravel and soft to firm sandy sediments, with

intertidal-subtidal seagrass coverage to 2m below Chart Datum and MLWS and MHWS tidal range between 0.8-4.2m, while Ryde is characterised by soft to firm sandy sediments (Marsden & Chesworth, 2015), with a MLWS and MHWS tidal range of 0.2-3.1m, respectively. Surveys at both sites reported the presence of *Zostera* spp., including *Z. marina* and *Z. noltei*, with possible *Z. angustifolia* at Ryde (Marsden & Chesworth, 2015).

Field Methods

A range of environmental variables were measured at each study site to determine factors influencing C_{stocks} (**Table 2**). Sediment variables included grain size, dry bulk density, degree of sorting and % mud. Pore water parameters were salinity, pH, and nutrients (nitrites [NO_2^-] and sulphates [SO_4^{-2}]). Elevation above sea level and the biological parameters leaft density and above-ground biomass were also recorded.

Degree of sorting, calculated as the sorting coefficient from the different sediment grain size

Fig. 1 Location of the six seagrass sampling sites in the Solent, southern England (red square). Zoomed image shows seagrass sampling sites and their respective seagrass meadows areal extent in red, collated by Marsden and Chesworth (2015): Hayling Island (100.24 ha), Creek Rythe (70.1 ha), Porchester (94.92 ha), Farlington Marshes (31.2 ha), Cowes (27.1 ha) and Ryde (82.47). Maps are adapted from Esri ArcGIS online basemaps

fractions, was used along elevation above mean sea-level as a proxy for degree of exposure of the site (see Folk & Ward, 1957). Mud content (% mud), including clay and silt particles (< 63 µm), has been suggested as a better representative fraction of seagrass bulk sediment and their C_{stocks}, than solely using clay particles (< 4 µm) (De Falco *et al*., 2004; Burdige, 2007; Pedrosa-Pamies *et al*., 2013; Serrano *et al*., 2016). Therefore, %mud (- 63 µm) was selected for analysis, including both silt and clay fractions.

Field sampling was conducted during low tide, when seagrass meadows were exposed. Five sampling points were selected within each of the six study sites, thirty sampling points in total (Howard *et al*., 2014). Sampling points were randomly selected by walking towards the middle of

the meadow, at least 3m from the edge, and randomly throwing 0.25m^2 quadrats in a clockwise orientation. From each of the thirty randomly selected sampling points, the following samples were collected during the summer (June-August) of 2017: above-ground biomass and leaf density in the form of cropped leaves within a 0.25m^2 quadrat; one, 30cm deep, sediment core for mean pooled carbon stocks and particle size analyses; one, 30cm deep, sediment core for pore water analyses. A dGPS (Leica GPS1200 Surveying System) was used to record latitude, longitude, and elevation above mean sea level (vertical accuracy, 0.02 m) from ten points within each sample quadrat (50 points per site; 300 points in total)(Ward *et al.*, 2016). Data were post processed using the Leica Geo Office software version 8.4, correction data available from the RINEX (Receiver Independent Exchange Format), downloaded from Leica Geosystems using the British National Grid coordinate system. This was plotted using the OSGB36 datum, and the reference station used was Sandown, Isle of Wight (50°39'5.69" N -1°09'39.71" W).

Seagrass species were identified, and a visual assessment of meadow landscape, very patchy (< 20% cover), patchy (20 ≤70% cover) or dense (> 70% cover), was conducted with a walkover of the sites. Above-ground biomass and leaf density was recorded from each sample plot by cropping the plant biomass (leaves to stem base) within each 0.25 m^2 quadrat, before being stored at -20 ºC prior to analysis (Howard *et al*., 2014). Cores were collected using a Russian corer, with a 5cm diameter, to avoid core compaction. Each core was divided into 5cm depth subsamples, with 6 subsamples per core (Howard, *et al*., 2014). Because the oxygenate rhizosphere layer is more likely to be affected by changes in environmental conditions, due to microbial activity and sediment deposition processes (Enriquez *et al*., 2001; Gray and Elliot, 2009), cores were taken in the top 30cm layer of sediment, or until refusal (20cm at Cowes). Post collection, the 30 sediment cores collected for carbon stocks analysis were kept in a freezer at -20ºC, and the remaining 30

sediment cores, used for pore water extraction, were kept in a cold storage room at 4ºC at the University of Brighton's sediment analysis lab, for < 48 hours.

Laboratory methods

In the laboratory, above-ground biomass was transferred to 1mm sieves, and washed free of sediment under running water to separate living above-ground components (Howard, *et al.*, 2014). The identified seagrass species were recorded and whole leaves (stem to tip) were counted from each sample to determine leaf density. Filamentous macroalgae and invertebrates were separated from seagrass biomass during the washing procedure, however, for the sake of this study, microalgae epiphytic load, when found, was not scraped from the leaves, to prevent loss of vegetative organic matter. Above-ground plant biomass was determined by oven-drying the vegetative biomass to a constant weight (72 h at 60 ºC) (Howard, *et al.*, 2014). The above-ground living vegetative component 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 above-ground biomass calculations (Duarte, 1990; Howard *et al.*, 2014).

After thawing, each sediment subsample was weighed prior to oven drying at 60 ºC for at least 72 hours, and then cooled at room temperature in a desiccator for at least one hour before weighing again to determine moisture content (Howard*et al.*, 2014). Oven dried sediment samples were disaggregated with a pestle and mortar and weighed in individual beakers, 2-4g for each sample, prior to analysis of organic matter. To estimate sediment organic carbon, sequential Loss on Ignition (% LOI) at 450 °C for 24h was selected as this method has been found to correlate well with estimation of C_{org} in seagrass meadows (Fourqurean *et al*., 2012b; Macreadie *et al*., 2014).

Samples were cooled at room temperature in a desiccator for at least one hour before weighing to determine percentage of organic matter (% OM) (Heiri *et al.*, 2001). To determine sediment C_{stocks}, dry bulk density, organic carbon content (C_{org}), and carbon density were calculated for each subsample. Dry bulk density (g/cm^3) for each subsample was estimated using the equation by Dadey *et al*., 1992:

*Equation 1: Pd = (1 – φ) * Ps*

Where Pd = bulk density, φ = porosity, and Ps = grain specific gravity**.**

%C_{org} was determined using regression equations derived from the literature for seagrass (Fourqurean *et al*., 2012a/b):

$$\%\,Corg = 0.43 * \%\,OM - 0.33, presuming\ \%\,OM > 0.2$$

$$\%\,Corg = 0.40 * \%\,OM - 0.21, presuming\ \%\,OM < 0.2$$

Following %C_{org} calculations, carbon density and carbon content were determined using the equations described by Howard *et al*. (2014). C_{stock} results from each subsample were summed to determine total carbon in each core and converted to Mg C/ha.

Following LOI, particle size analysis was carried out on all non-ground sediment samples using a Malvern Mastersizer 2000 laser analyser, with particle size grading undertaken in accordance with the Wentworth (1922) size classification scheme. Samples were washed with 10 ml of sodium hexametaphosphate prior to analysis and then stirred for 5 minutes in order to deflocculate clay particles (Ward *et al*., 2014). A small sub-sample ~1 – 1.5 g, dependent on laser obscuration related to particle size, was analysed using a basic ultrasonic setting, which improves dispersion of particles during analysis by breaking up aggregates using vibrating sound waves (Malvern Instruments, 1980). The final data for each size classification (clay, silt, and sand), represented an average of three separate analytical runs (standard error < 1 %) (Ward *et al*., 2014).

The mean (central value), and sorting coefficient (standard deviation) were calculated for each sample following Folk & Ward's method (1957).

Each 5cm increment from the 30 remaining sediment cores kept in cold storage were divided into two subsamples, one for analysis of the concentration of nitrites and sulphates, and one for pH and salinity. Sediment pore water has been described as the main provider of nutrients for seagrass growth, being several orders of magnitude higher in concentration than nutrients in the water column (Fourqurean *et al*., 1992; McGlathery *et al*., 2001). Thus, pore water was extracted from each sediment subsample within 48h of collection, to prevent organic decomposition (Michalski and Kurzyca, 2005; EPA, 2007). For pore-water extraction, each sediment subsample was centrifuged using an Eppendorf™ 5702 Series Centrifuge for 15 min at 4,400 rpm. Supernatant was collected to perform dilution trials and determine the most suitable dilution factor

to better identify relevant peaks. Dilution ratios of 1:100; 1:10; 1:5 and 1:2 were tested, between the extracted pore water and deionised water, adding up to a total volume of 5ml (Jackson, 2000). Due to the instability of the nitrogen oxide ions, and problems related to pairing separations of Cl^- /NO_2^- in saline samples (Michalski and Kurzyca, 2005), only nitrites and sulphates peaks were clearly detected (using a dilution factor of 2), and the concentration of both anions was converted from mg/L into μM prior to analysis.

Salinity and pH of each pore water subsample was measured, following the 2:5 ratio proposed by Head (2006). Approximately 3g of dry sediment sample was mixed with 7.5ml of distilled water in a temperature controlled orbital shaker for 10 min to dissolve particles for analysis (Head, 2006). Samples were allowed to stand overnight and stirred again immediately before testing (Head, 2006). pH analysis was conducted using a Mettler Toledo™ FE20 FiveEasy™ Benchtop pH Meter. Tests were conducted with three replicates, stirring briefly between readings to ensure accuracy, and an average was calculated. Probes were washed with distilled water between tests and dried before use (Head, 2006; Burnside *et al*., 2008). Equipment was calibrated using buffer solutions of pH 4.0 and 7.0. Supernatants from the same (previously stirred) samples used for pH analysis were used to determine salinity. Small droplets were applied to a Bellingham + Stanley™ Eclipse Hand Held Refractometer 45-63, to measure salinity ($^0/_{00}$). Three replicates of each reading were measured and an average was calculated. The refractometer was calibrated between cores, by taking a reading using distilled water.

Statistical Analysis

All statistical analysis was performed on Minitab 2017. Normality probability plots and histogram frequency of residuals were tested using the theory-driven Anderson-Darling method for each of the 12 variables (Anderson and Darling, 1954): pooled sediment C_{stock} (30cm), dry bulk density [DBD], mean grain size, sorting coefficient, %mud, pH, salinity, nitrite (NO_2^-), sulphate (SO_4^{-2}), elevation,leaf density and above-ground biomass. When assumptions of normality were not met, variables were transformed using Log_{10} (X) and retested for normality (**Supplementary Table A**). Site differences between each variable were tested using ANOVA Post-hoc Tukey's test was used to identify significantly different means for each variable, when present. Means are expressed as mean values for each variable from the sampled quadrats, 30 (5 per site) samples in total, to assess for the relationships between each variable and pooled carbon stocks (30cm deep). Individual relationships between variables and sediment C_{stocks} were examined using the following tests. A linear regression was used to derive an equation to determine sediment C_{stocks} based on DBD values as predictors, since DBD is commonly used in standard calculations of sediment carbon density (Howard *et al*., 2014). A Pearson's correlation test, or where data were not normally distributed a Spearman's Rho correlation, was used to assess the relationship between variables and C_{stocks}. A Partial least squares (PLS) regression multivariate analysis was used to assess the influence of different types of factors on sediment C_{stocks} (Dahl *et al*., 2016; Gullström *et al*., 2018; Rohr *et al*., 2018). The advantage of using PLS as a model for multivariate regression is that it can tolerate collinear explanatory factors, with a large number of predictors that might not be fixed, or that might contain measurement errors (Carrascal *et al*., 2009; Dahl *et al*., 2016). Results from the PLS analysis were used to identify variables with higher correlation coefficients, showing stronger relationships with sediment C_{stocks} These variables were analysed by principal component analysis (PCA) to better visualise and understand their level of association, by aggregating and summarising

groups of highly inter-correlated variables and explaining the variation in C_{stocks} among sites (ter Braak, 1995; Marin-Guirao *et al*., 2005). All results assume a significance of $p < 0.05$.

Results

Table 2: Environmental data for each seagrass study site in the Solent region, UK. Sites are presented in decreasing order of mean sediment C_{stock}. Values are presented as mean (± SD), n=30 for all variables, with Tukey's grouping results following ANOVA where the same letters correspond to means that are not statistically different, for each variable.

Variation among sites

The mean C_{stock} within the seagrass sediment across all six sites was 33.80 ± 18.40 $MgCha^{-1}$ (n=30). However, there was a significant variance in mean sediment carbon storage (30cm) between sampling sites, with those on the Isle of Wight, Cowes and Ryde, having significantly lower sediment C_{stock} values than all other sites, but not significantly different between themselves **(Table 2).** The mean DBD values for all sites was 0.99 ± 0.03 g/cm^3 (n=30). The mean sediment DBD values at Ryde and Cowes were significantly higher than all other sites **(Table 2).** All sites were classified as muddy, silt rich, sediments according to the Wentworth scale, apart from Cowes and Ryde, which contained average grain size (µm) within the class of very fine and fine sand respectively. The sorting coefficient at Ryde was significantly higher than all other sites **(Table2).** Porchester and Creek Rythe presented the lowest sorting coefficients respectively, both significantly different than Cowes. However, all sites were classified as very well sorted. Ryde had by far the lowest mean %mud compared to all other sites (1.14%). Hayling Island had the highest mean %mud (93.85%), followed by Creek Rythe (87.50%), both significantly higher than Cowes and Ryde (**Table 2**).

The average pore water pH across all sites was 7.28 ± 0.28 (n=30) with relatively little, but significant, variation across all sites (**Table 2**). Mean salinity showed significantly lower levels in the Isle of Wight's sites when compared against all others. Ryde had the lowest sediment pore water salinity (1.4 ± 0.55 ‰), followed by Cowes (2.0 ± 0.0 ‰), whilst the highest values were found in Hayling Island (15.6 ± 0.89 ‰) **(Table 2)**. Mean pore-water concentrations of nitrites and sulphates showed no significant differences between sampling sites **(Table 2)**. However, there was large variation in concentration of both nutrients with depth within cores, with both sites in the Isle of Wight only presenting detectable levels of pore water nutrients in the upper layers, Cowes to 10cm and Ryde to 15cm depth (**Figure 2).** Cowes showed the largest decrease in concentration of both pore water nutrients, however, Ryde presented an increase in nitrite concentration and a decrease in sulphate levels with depth (**Figure 2**). Down core variation in the concentration of both nutrients was the same in Farlington Marshes and Porchester, but did not follow the same pattern in Creek Rythe and Hayling Island (**Figure 2**).

Fig. 2 Concentrations of (a) nitrites NO_2^- ($\mu mol/L$) and (b) sulphates SO_4^{-2} ($\mu mol/L$) down-core for all study sites: Cowes, Ryde, Creek Rythe, Hayling Island, Porchester and Farlington Marshes

Seagrass meadows at Cowes were located at a significantly lower elevation above mean sea level than all other sites, at -1.82 ± 0.05m. **(Table 2)**. Out of all sites, only Farlington Marshes and Creek Rythe presented positive values of elevation above mean sea level, significantly different than all other sites, of 0.06 ± 0.07m and 0.0008 ± 0.06m, respectively. The elevation of the three remaining study sites (Hayling Island, Porchester and Ryde) were all significantly different to each other **(Table 2).**

Average leaf density across all sites was 394 ± 268 leaves/m^2 (n=30). There was no significant difference in leaf density between sampling sites, but large standard deviations were recorded **(Table 2)**. *Z. angustifolia* was the dominant species in Farlington Marshes and Ryde, and

was present at all sites apart from Cowes. At Farlington Marshes and Cowes, seagrass meadows presented very patchy landscape patterns, with un-vegetated patches within the seagrass beds. At Ryde and Porchester, the landscape was characterised as patchy, with less un-vegetated space between seagrass beds, while Hayling Island and Creek Rythe supported dense beds with continuous seagrass meadows **(Table 2)**. There were significant differences in mean above-ground biomass between sampling sites, with Creek Rythe presenting significantly higher above-ground biomass values, of 0.497 $\pm$ 0.25 $MgCha^{-1}$ (n=5), than both sites on the Isle of Wight **(Table 2).** Ryde had the lowest above-ground biomass values amongst all sites, of 0.07 $\pm$ 0.03 $MgCha^{-1}$ (n=5), significantly lower than Creek Rythe and Hayling Island **(Table 2)**.

Relationships between environmental variables and sediment C_{stock}

A regression analysis demonstrated a significant negative relationship between C_{stock} and DBD (R^2 = 87.7%, p = 0.000) (**Figure 3a**). There was a significant negative relationship between mean grain size and sediment C_{stock} (r = -0.712 and p = 0.000) **(Figure 3b),** and between sorting coefficient and sediment C_{stocks}, (r = -0.761, p = 0.000) **(Figure 3c)**. There was a significant positive correlation between %mud and sediment C_{stocks} (r = 0.761, p = 0.004) (**Figure 3d**). The association between pore water pH levels and sediment C_{stock} represented a significant negative relationship, (r = -0.545, p = 0.003) (**Figure 3e**). There was a significant positive relationship between salinity and sediment C_{stocks} (r = 0.876, p = 0.000) (**Figure 3f**) and between elevation and sediment C_{stock} (r = 0.719, p = 0.000) **(Figure 3g).** The concentration of sulphates was significantly

Fig. 3 Relationships between sediment C_{stocks} and (a) dry bulk density (DBD) including linear regression line and equation, R^2 and n values. Spearman's rho relationships between sediment C_{stocks} and (b) mean grain size, (d) %mud and g) sulphate levels represented by $Log_{10}(X)$ values, including r, p and n values. Pearson's relationship between sediment C_{stocks} and (c) degree of sorting, (e) pH, (f) salinity, and (h) elevation, (i) above-ground biomass, including r, p and n values, for all sites: Creek Rythe, Cowes , Farlington Marshes, Hayling Island, Porchester and Ryde

negatively correlated with sediment C_{stock} (r = -0.522, p = 0.004) **(Figure 3h)**, but concentration of nitrites was only moderately significantly correlated to sediment C_{stock} (r = -0.423, p = 0.031). There was no significant relationship between sediment C_{stock} and leaf density (r = -0.095, p = 0.616), but above-ground biomass was significantly related to sediment C_{stocks} (r = 0.595, p = 0.001) (**Figure 3i**).

The multivariate relationship between sediment C_{stock} and the predictor variables was explained in a PLS regression model. The cumulative fraction (R-sq) of the first four components (DBD, Sorting, %Mud and pH) was 0.90, showing a high degree of determination, meaning they explain 90% of the variation in the model data. According to the model, the most important factors responsible for the variation in sediment C_{stocks} were DBD, followed in rank order by sorting coefficient, %mud, pH, sulphates, nitrites, elevation, salinity, above-ground biomass, mean grain size and leaf density **(Figure 4)**. DBD, sorting coefficient, %mud, sulphates, elevation, mean grain size, and leaf density showed negative relationships with sediment C_{stocks}, while pH, nitrites, above-ground biomass and salinity were positively related to sediment C_{stocks}.

Fig. 4 Partial least square regression model coefficient plot. The model assesses the relative influence of different predictors in sediment C_{stocks}. Predictors are dry bulk density (DBD), sorting coefficient, %mud, pH, nitrites (NO_2^-), sulphates (SO_4^{-2}), elevation, salinity, above-ground biomass, mean grain size, and leaf density, ranked by level of importance from left, most important, to right, least important

The six predictors indicated by PLS as main drivers for variation in sediment C_{stocks}, with a coefficient > 5, were selected for inclusion in the PCA, namely DBD, sorting coefficient, %mud, pH, sulphates and nitrites. The first two principal components cumulatively explained 78.3% of the variation in the data, with eigenvalues > 1. The first principal component (PC1) explained 62.6% of the variation, with 15.7% being explained by the second principal component (PC2). Sediment characteristics showed the largest influence on PC1, with DBD and sorting coefficient

with positive loadings on the component, closely related to sediment C_{stock} and %mud with negative loadings **(Figure 5)**. This indicates that PC1 primarily expresses sediment characteristics. PC2 was mainly negatively influenced by the concentration of nitrites (**Figure 5).** The relationship between sediment C_{stocks} and the different variables was not uniform between sampling sites, with points from Ryde, Cowes and Farlington Marshes grouped separately from other sites, while points from Creek Rythe, Hayling Island and Porchester were closer together **(Figure 5)**. Points from Creek Rythe and Hayling Island had low values for both PC1 and PC2, representing sites with highest C_{stock}, high %mud and lowest DBD. Points for Ryde had high positive values for PC1 and three points had high negative values for PC2, with the other 2 points exhibiting low values for PC2.Ryde was the site with lowest C_{stock}, lowest %mud, highest DBD, highest degree of sorting and higher concentration of both pore water nutrients (nitrites and sulphates). Cowes and Farlington Marshes had positive relationships with both principal components, representing sites with similar sorting, %mud and pH levels. However, Cowes had higher values for PC1, while points from Farlington Marshes was grouped closer to the centre of both axis. This could be explained by the higher values for C_{stock} and lower DBD in Farlington Marshes **(Figure 5).**

Fig. 5 Principal component analysis (PCA) showing the six seagrass study sites, Creek Rythe, Cowes, Farlington Marshes, Hayling Island, Porchester and Ryde, related to the five most relevant predictor variables, dry bulk density (DBD), sorting coefficient, %mud, pH, nitrites (NO_2^-) and sulphates (SO_4^{-2}) (Figure 4) in terms of sediment C_{stocks} as the response variable

Discussion

Results from this study provide valuable insights into the environmental factors influencing sediment carbon storage in temperate seagrass ecosystems, specifically within intertidal seagrass meadows in the Solent region, England. Seagrass meadows with different species composition,

showed significantly different sediment $C_{stocks,}$ dry bulk density, mean grain size, degree of sorting, proportion of mud and pore water pH and salinity. Overall, the main factors significantly related to seagrass sediment C_{stocks} were: elevation, pore water sulphates, pH and salinity; and sediment degree of sorting, grain size, proportion of mud and dry bulk density. Indeed, dry bulk density can be used as a predictor for sediment C_{stocks} as indicated by the regression equation developed by this study. However, when the combined association of factors was analysed, dry bulk density, sorting coefficient, proportion of mud, pH, nitrites and sulphates showed the greatest influence on sediment C_{stocks}. Moreover, sediment characteristics such as dry bulk density, sorting coefficient and proportion of mud, acted in conjunction to explain the bulk of the variation in sediment C_{stocks}.

There was no significant difference in leaf density between sampling sites. However,meadows with mixed species, and dense continuous beds, namely Creek Rythe, Hayling Island and Porchester, supported higher sediment C_{stocks} than sites that formed beds with single species, such as Farlington Marshes and Ryde, or were very patchy as at Cowes. Higher species diversity, can increase seagrass efficiency in reducing currents and consequent sediment resuspension, therefore contributing to organic matter deposition, especially in species such as *Zostera spp*. and *Thalassia spp*., with blade-like leaves (Verduin and Backhaus, 2000; Koch *et al*., 2006; Peralta *et al*., 2008; Hendricks *et al*., 2008, Mazarrasa *et al*., 2018). Additionally, dense and continuous meadows retain more autochthonous carbon, such as leaf detritus, which combined with their ability to accumulate finer sediment particulates, enhances their carbon storage and sequestration capacity (Miyajima *et al*., 2017; Oreska *et al*., 2017; Rocart *et al*., 2017; Mazarrasa *et al*., 2018).

Recent studies assessing the role of environmental parameters in determining seagrasses' carbon sink potential corroborate the results of this research, with sediment properties being

identified as highly influential (Lavery *et al*., 2013; Duarte *et al*., 2011; Dahl *et al.*, 2016; Mazarrasa *et al*., 2018; Rohr *et al*., 2018). Results from this study show that large sediment C_{stocks} are strongly linked to a high proportion of mud and low bulk density, suggesting that seagrass meadows with such sediment characteristics have a higher potential as natural carbon sinks (Dahl *et al*., 2016; Mazarrasa *et al*., 2018; Rohr *et al*., 2018). Grain size is strongly related to sediment porosity and density, which are important factors regulating oxygen concentrations in the sediment and consequent degradation of organic matter by microbial activity (Benner *et al*., 1984; Enriquez *et al.*, 1993; Deming and Harass, 1993; Dahl *et al*., 2016). Seagrass meadows, especially ones with a low contribution of autochthonous carbon sources to sediment pools, can increase the concentration of fine grain particles in the sediment by reducing water velocity and facilitating sedimentation, thus promoting high carbon storage (Serrano *et al*., 2016). Higher proportions of fine grains in mud substrate, with greater particle surface areas, also contribute to the preservation and accumulation of organic matter (Mayer, 1994; Dahl *et al*., 2016; Mazarrassa *et al*., 2018; Rohr *et al*., 2018). Sites with smaller grain size fractions, such as Hayling Island and Creek Rythe, are likely to have lower soil permeability and more anoxic conditions as a result of smaller interstitial spaces, which reduces organic matter degradation rates by decreasing oxygen exchange and redox potential, contributing to their higher sediment C_{stocks} (Hedges, 1995; Wilson *et al*., 2008; Dahl *et al*., 2016). The relationship between carbon storage and sediment characteristics is more evident in meadows with relatively low seagrass biomass and a high proportion of finer particle sizes, such as the temperate ones studied here, while in meadows dominated by seagrass species with a greater biomass, e.g. *Posidonia spp*., the amount of autochthonous carbon seems to be more important for carbon storage than mud and silt content (Serrano *et al*., 2016).

Dahl *et al*. (2016) demonstrated that sediment density has a negative relationship with sediment organic carbon, affirming the results for the variance in dry bulk density among sites in

this study, where sites with higher bulk density (and therefore lower porosity) had lower sediment C_{stocks}, e.g. Ryde and Cowes. In combination with particle size, the degree of exposure to hydrodynamic forces such as waves, tides and currents, is also a determinant factor for sedimentation and erosion in coastal areas (Maxwell *et al*., 2017; Mazarrasa *et al*., 2018). The level of exposure in seagrass meadows is usually reflected in the proportion of fine sediment particles (e.g. % mud), being higher in sheltered areas compared to more exposed sites (Van Keulen and Borowitzka, 2003; Mazarassa *et al*., 2018). This is likely to be the case for meadows at Ryde and Cowes on the Isle of Wight, which are more exposed to wave activity, and present lower sediment C_{stocks}, than the mainland sites. The degree of sorting can also be used as a proxy to indicate physical exposure related to movement of water masses, with better sorted particles representing slower deposition driven by stable hydrodynamic conditions (Folk and Ward, 1957; Mazarrasa *et al*., 2017; Rohr *et al*., 2018). All sites in this study had sediments classified as very well sorted, but the two on the Isle of Wight had significantly higher degrees of sorting and lower sediment C_{stock} values than the other sites. These results conform with those obtained by Rohr *et al*. (2018) for seagrasses in the Baltic, where exposure to wave activity was an important driver for sediment C_{stock} in *Z. marina* meadows, with high exposure leading to lower sediment C_{stock} due to the potential export of carbon to other adjacent ecosystems. Other factors related to sedimentation processes have previously also shown to be relevant to seagrass sediment carbon storage, such as water depth, in-situ primary productivity, sedimentation rates and the trapping of fine-grained sediment and organic matter (Serrano *et al*., 2016; Dahl *et al*., 2016; Mazarrasa *et al*., 2018).

Even though there was a limited range of pore water pH values across all six sites, they were significantly higher on sites with less sediment C_{stocks}, and showed a significant negative relationship with seagrass sediment carbon storage. This association is supported by Ivers *et al's*., (1997) findings of a decrease in photosynthetic rates when pH increased by 0.6 units for *Posidonia*

oceanica and *Cymodocea nodosa*, and 0.8 units for *Z. noltei*. Furthermore, Egea *et al*. (2018) found no effect on seagrass production with increased acidification, reporting a slight increase in carbon stocks with lower pH levels. At a broader scale, studies suggest an increase in seagrass productivity and consequent carbon storage in acidic scenarios, with Garrand and Beaumont (2014) quantifying that the reduction in pH of ocean surface waters is expected to enhance both above- and belowground biomass, leading to an 82–94% increase in seagrass carbon storage and sequestration potential, potentially increasing ocean storage of carbon by 12–14%.

It has been suggested that the amount of organic carbon in seagrass sediments can be positively linked to above and belowground plant productivity, with seagrass productivity being sensitive to nutrient input, often decreasing substantially as a result of light limitation during algal blooms when high nutrient loadings occur (Hauxwell *et al*., 2001; Schmidt *et al*., 2012; Burkholder *et al*., 2007; Kirwan and Mudd, 2012; Armitage and Fourqurean, 2016). Nutrient availability in seagrass sediments is closely related to microbial activity in their rhizosphere, associated with the release of oxygen into the sediment by seagrasses' rhizomes, enhancing bacterial activity and nitrogen fixation at depths that would otherwise be anoxic (Perry and Dennison, 2000). Thus, sediment grain size might be one of the limiting factors in nutrient cycling, with fine grain sediments having lower concentrations of oxygen with depth, decreasing microbial activity (Mazarrasa *et al*., 2018). An increase in microbial activity can potentially explain the high concentration of pore water nitrites and sulphates in the upper layer of sites in this study with lower sediment C_{stocks}, such as at Ryde and Cowes.

Elevation in relation to mean sea levelwas correlated with seagrass sediment $C_{stocks.}$ Ryde and Cowes, which were located at the lowest elevations in relation to mean sea level, had the lowest values of sediments C_{stocks}. Although all sites in this study were intertidal, differences in elevation are related to varying periods of emersion and desiccation between low and high tide, which

impacts carbon sequestration processes, since areas with higher exposed periods could have higher rates of photosynthesis, therefore sequestering and storing more carbon in their sediments (Short and Neckles, 1999; Mazarrasa *et al*., 2018). Conversely, some studies have identified increased desiccation stress as a factor that slows recovery time in intertidal seagrass beds growing at higher elevations, indicating higher vulnerability to extreme weather events linked to climatic change (de Fouw *et al*., 2016; El Hacen *et al*., 2018).

In conclusion, this study showed that seagrass meadows within the same climatic region, and locality, do not share the same potential for long-term sediment carbon storage, and that environmental characteristics strongly influence this ecosystem service. Therefore, while seagrass research at global, and even continental, scales are extremely important, caution must be taken with extrapolations and generalisations across different regions. These results also show that individual seagrass meadows might not be representative of the whole ecosystem, and highlights the need for the assessment and consideration of multiple environmental features and their interactions in seagrass blue carbon research, such as dry bulk density, sorting coefficient and other sediment characteristics, above-ground biomass, nutrients, elevation in relation to mean sea level etc.. In the Solent estuary, larger stocks were associated with meadows located in sheltered bays, with high sediment mud content and well sorted particles. Conversely, exposed meadows subject to intense anthropogenic disturbance are likely to experience a decline in their capacity to sequester and store carbon in the long-term, as shown by sites with patchy seagrass landscapes, high surface nutrient levels and lower sediment $C_{stocks.}$ This indicates that the most influential factors driving temperate seagrass sediment C_{stocks}, namely dry bulk density, degree of sorting, and proportion of mud, should be monitored in conjunction with pore water sulphates, pH and salinity, elevation and mean grain size, in conservation and restoration projects that aim to promote the carbon sink potential of intertidal seagrass ecosystems. It is also evident that seagrass carbon sink potential is regulated by

a combination of multiple environmental factors, encompassing sediment and vegetation variables, highlighting the potential vulnerability of these ecosystems to climate change, such as sea level rise. Therefore, key factors should be considered, individually or ideally in combination, when developing and implementing conservation or restoration projects, and climate change mitigation strategies, using seagrass ecosystems.

Table 2

Study sites	Coordinates	Meadow extent (ha)*	C_{Stock} (30cm)** ($MgCha^{-1}$)	Vegetation	Leaf density (m^{-2})	Above-ground Biomass ($MgC\ ha^{-1}$)	Elevation (m)	Dry bulk density (gdm^{-3})	Mean grain size (µm)	Sorting coefficient (φ)	% Mud	pH	Salinity (‰)	NO_2^- ($\mu molL^-$)	SO_4^{-2} (µmolL-)
Hayling Island	50°47'54"N, 0°59'48"W	100.24	51.13 ± 7.84 (A)	*Z. marina / Z. angustifolia / Z. noltei / Ruppia spp.* Dense	336.7 ± 95.0	0.37 ± 0.13 (AB)	-0.81 ± 0.13 (C)	0.72 ± 0.04 (CD)	20.37 ± 3.28 (C)	-1.73 ± 0.07 (BC)	93.8 ± 3.2 (A)	7.07 ± 0.05 (B)	15.6 ± 0.9 (A)	18914 ± 9765	488.9 ± 199.2
Creek Rythe	50°49'3"N, 0°53'33"W	70.1	45.31 ± 3.53 (A)	*Z. marina / Z. angustifolia / Z. noltei / Ruppia spp.* Dense	367.0 ± 115.1	0.50 ± 0.25 (A)	0.0008 ± 0.06 (A)	0.68 ± 0.08 (D)	24.25 ± 10.82 (C)	-1.78 ± 0.09 (CD)	87.5 ± 3.6 (A)	7.16 ± 0.10 (B)	12.8 ± 2.8 (A)	18538 ± 15929	554 ± 254
Porchester	50°50'13"N, 1°7'51"W	94.92	45.23 ± 12.10 (A)	*Z. angustifolia / Z. noltei* Patchy	302.0 ± 76.1	0.32 ± 0.07 (ABC)	-0.55± 0.11 (B)	0.89 ± 0.20 (BC)	55.23 ± 31.09 (BC)	-1.99 ± 0.19 (D)	79.3 ± 13.0 (AB)	7.17 ± 0.08 (B)	12.6 ± 1.9 (A)	20363 ± 19780	424.8 ± 154.6
Farlington Marshes	50°50'2"N, 1°2'24"W	31.2	40.23 ± 4.16 (A)	*Z. angustifolia* Very patchy	584 ± 427	0.25 ± 0.14 (ABC)	0.059 ± 0.06 (A)	0.94 ± 0.09 (B)	48.71 ± 29.08 (BC)	-1.76 ± 0.18 (BCD)	79.7 ± 6.3 (AB)	7.59 ± 0.05 (A)	14.4 ± 3.6 (A)	10383 ± 9109	2334 ± 2317
Cowes	50°45'55"N, 1°16'56"W	27.1	14.22 ± 7.59 (B)	*Z. marina / Z. noltei* Very patchy	346 ± 247	0.18 ± 0.07 (BC)	-1.82 ± 0.05 (E)	1.27 ± 0.02 (A)	72.40 ± 36.91 (B)	-1.51 ± 0.16 (B)	66.62 ± 18.5 (B)	7.42 ± 0.34 (AB)	2.0 ± 0.0 (B)	6271 ± 5892	1011 ± 985
Ryde	50°44'02"N, 1°09'23"W	82.47	6.65 ± 1.73 (B)	*Z. angustifolia* Patchy	427 ± 430	0.07 ± 0.03 (C)	-1.48 ± 0.11 (D)	1.46 ± 0.03 (A)	225.01 ± 7.78 (A)	-0.48 ± 0.02 (A)	1.14 ± 0.03 (C)	7.66 ± 0.33 (A)	1.4 ± 0.6 (B)	69509 ± 69739	4755 ± 5628

*Area derived from Marsden and Chesworth (2015).

** Cores from Cowes (CWST) were 20cm deep.

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Supplementary Table

Table A: Summary of ANOVA results for all environmental variables between the six sampling sites. Mathematical transformation ($Log_{10}(X)$) performed when assumptions of normality of residuals were not met – AD (p) is the Anderson- Darling normality test result ($p<0.05$).

Variables	df	F	p	R-sq	Pooled StD	AD (p)	Transformation
Sediment C_{stock} (Mg C Ha^{-1})	29	34.70	0.000	0.8785	7.05	0.438 (0.277)	Normal
Dry bulk density (g dm^{-3})	29	51.08	0.000	0.9141	0.10	1.136 (<0.05)	$Log_{10}(X)$
Mean grain size (µm)	29	67.04	0.000	0.9229	21.65	1.242 (<0.05)	$Log_{10}(X)$
Sorting coefficient (φ)	29	92.62	0.000	0.9411	0.13	0.613 (0.103)	Normal
% Mud	29	17.56	0.000	0.7853	9.88	1.348 (<0.05)	$Log_{10}(X)$
pH	29	5.49	0.002	0.5664	0.28	1.090 (0.006)	Normal
Salinity (‰)	29	33.58	0.000	0.8888	2.20	0.628 (0.091)	Normal
leaf density (leaf/m^{-2})	29	0.68	0.642	0.1243	68.91	0.896 (0.019)	Normal
Above-ground Biomass (Mg C Ha^{-1})	29	5.97	0.001	0.5543	0.14	0.290 (0.587)	Normal
Nitrites NO_2^- (µmolL^-)	29	1.36	0.280	0.2542	0.57	1.757 (<0.05)	$Log_{10}(X)$
Sulphates SO_4^{-2} (µmolL^-)	29	3.29	0.026	0.4641	0.39	2.717 (<0.05)	$Log_{10}(X)$
Elevation (m)	29	332.09	0.00	0.9858	0.09	0.142 (0.968)	Normal

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