Assessing the carbon sink potential and impacts of global change on intertidal seagrass meadows in central southern England

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Abstract

Seagrass meadows provide a multitude of ecosystem services, including the capacity to sequester carbon within their sediments and biomass. However, seagrass research in the UK is still in its infancy, with very few published data on sediment carbon stocks, and no reports of sediment accretion and carbon sequestration rates within intertidal seagrass meadows. In addition to their carbon sink potential, seagrass meadows are also important habitats for commercially important and endangered fish species in the UK. However, frequent reports on the decline of their health and extent, have raised concerns on the efficiency of current protection and management projects, especially in the face of global climatic change. Therefore, this research provides evidence of the importance of intertidal seagrass meadows in England for climate change mitigation and the need for more robust conservation strategies for UK seagrass meadows, through these objectives:

(i) to establish a regional carbon storage profile by determining aboveground and belowground biomass and carbon content of the sediments. Results showed that seagrass meadows from central southern England form significant carbon stocks, comparable to other global regions. In addition, this study also demonstrates the variability in sediment carbon stocks, sediment characteristics, above-ground biomass, shoot density, and below-ground biomass, in the form of roots and rhizomes, between the studied sites, and between seagrass meadows and neighbouring, un-vegetated, sampling points, highlighting the need for site specific assessment.

(ii) to establish relationships between carbon storage and environmental factors to promote the understanding of the features that influence seagrass carbon sink potential. Results showed that the main factors significantly related to seagrass sediment carbon stocks were: elevation in relation to mean sea-level, pore water sulphates, pH and salinity; and sorting coefficient, grain size, proportion of mud and dry bulk density. Moreover, sediment characteristics such as dry bulk density, sorting coefficient and proportion of mud, can be grouped as the factors that act in conjunction to explain the bulk of the variation in sediment carbon stocks.

(iii) to establish a geochronology to identify how organic carbon sequestration has fluctuated over time in relation to reported precipitation, storminess, and sea level. Results showed that there was significantly higher sediment accretion and carbon sequestration rates during periods with extreme weather events, suggesting that future climate change is likely to impact intertidal seagrass meadows and their role as blue carbon sinks.

This study has shown that intertidal seagrass meadows in central southern England are essential providers of carbon storage benefits, comparable to estimated global sediment carbon stocks, while also providing robust evidence on the influence of environmental factors and direct or indirect human activities, such as climate change events, on their carbon storage and sequestration potential, essential for the development of effective governance and management of these ecosystems.

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Author's Declaration

I declare that the research contained in this thesis, unless otherwise formally indicated within the text, is the original work of the author. The thesis has not been previously submitted to this or any other university for a degree and does not incorporate any material already submitted for a degree.

Signed:

Dated:

1 General Introduction

1.1 Research Context

” Blue carbon” is a modern term used to describe the carbon stored in the biomass and sediments of vegetated coastal environments, including salt marshes, mangroves and seagrass meadows (Nellemann *et al*., 2009; McLeod *et al*., 2011; Pendleton, *et al*., 2012). The biophysical process in which plants capture and securely store atmospheric carbon dioxide (CO_2) as organic carbon (C_{org}) in their biomass and sediments is known as carbon sequestration, while the amount of C_{org} is described as storage potential (Jain *et al*., 2012; Bouwer *et al*., 2018). Contrary to terrestrial forests, where much of the carbon is stored in the above-ground biomass, C_{org} reservoirs of coastal vegetated environments are mainly found in their organic rich sediments (figure 1.1) (Chmura *et al*., 2003; McLeod *et al*., 2011; Fourqurean *et al*., 2012a). This ability of enhancing and stabilising the accumulation of deposited litter and detritus in their C_{org} rich sediments give coastal wetland ecosystems an important role as natural carbon sinks (Duarte *et al*., 2005; Gallagher *et al*., 2019).

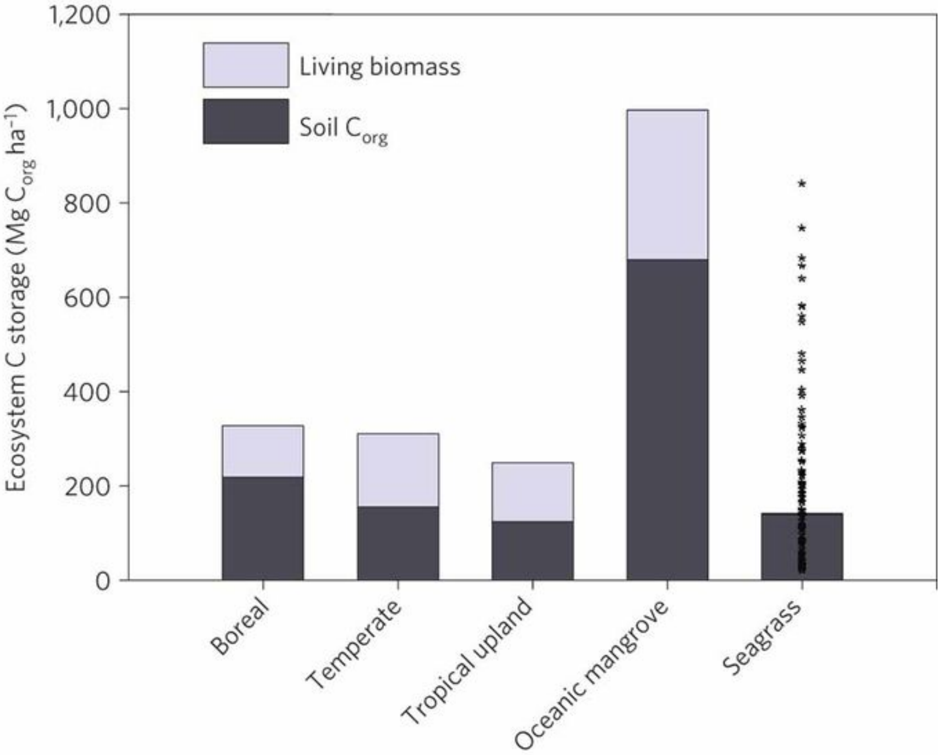


Figure 1-1: A comparison of Soil C_{org} storage in the top metre of the sediment with total ecosystem organic carbon storage, including living biomass, between major forest types: Boreal, Temperate and Tropical Upland; mangroves, and seagrass ecosystems. Based on Fourqurean *et al*., (2012a).

Furthermore, coastal vegetated environments store half the ocean's total organic carbon, despite occupying less than 2% of global area (Duarte *et al*., 2005). This disproportionate contribution results from their high rates of primary production and reduced rates of microbial activity in their permanently inundated and predominantly anaerobic sediments (Fourqurean, *et al*., 2012a; Christiansen *et al*., 2013). More specifically, seagrass ecosystems are estimated to bury 27±4 Tg C year^{-1}, roughly 10% of the yearly estimated C_{org} burial in the oceans (Duarte *et al*., 2005; Fourqurean *et al*., 2012a). This is because seagrass canopies trap allochthonous sediment particles, from adjacent habitats, which can account for as much as 50% of their total sedimentary C_{org} (Kennedy *et al*., 2010; Cathalot *et al*., 2013; Gallagher *et al*., 2019).

However, most of these figures are based on extrapolations of published values, with little attempt to directly assess the rate at which blue carbon is captured in seagrass meadows sediments, as well as regional carbon storage capacities (Duarte *et al*., 2010; Duarte *et al*., 2011; Fourqurean *et al*., 2012a; Garrard and Beaumont, 2014; Jones and Unsworth, 2016; Duarte, 2017). Therefore, reported carbon stocks and sequestration rates from seagrass meadows have been causing controversies, due to the use of estimated values based on published global literature, or extrapolations from carbon content in the top layer of sediment, using short sediment cores, to report blue carbon within entire seagrass meadows (Johannessen and Macdonald, 2016; Gallagher *et al*., 2019).

Despite these controversies, recent studies agree that further research, including biological and environmental factors from different global regions, is needed to understand the dynamics of carbon burial among seagrass ecosystems (Johannessen and Macdonald, 2016; Macreadie *et al*., 2018). Thus, directly quantifying blue carbon stored in seagrass meadows, as well as promoting conservation and restoration of meadows is of high importance (Howard *et al*., 2017; Macreadie *et al*., 2018). This includes not only preserving seagrass's potential to absorb and capture CO_2 via photosynthesis, but also maintaining the large amount of C_{org} buried in their sediments, to avoid remineralisation and re-emission to the atmosphere (Fourqurean *et al*., 2012a; Macreadie *et al*., 2018; Unsworth *et al*., 2019). Macreadie *et al*. (2018) state that the high uncertainty around global seagrass distribution might be one of the main factors contributing to the large variance in existing seagrass carbon sequestration estimates, reinforcing the need for further mapping and research aimed at determining regional contribution of seagrass meadows to climate change mitigation.

It has been reported that remineralisation of C_{org} stored in terrestrial ecosystems, as a consequence of a climate change induced carbon feedback cycle, accounts for 8-20% of anthropogenic greenhouse gases (GHG) emissions (IPCC, 2007). Chmura *et al*., (2003) suggest that climate change is also likely to influence the ability of wetlands to sequester carbon particularly in coastal and estuarine wetlands due to changes in precipitation, sea level rise and increases in storminess. Seagrasses are at great risk of being affected by global environmental change, especially those near urban areas as in this study, where plant communities are already under stress linked to human activities (Short *et al*., 2016). Global environmental change refers to planetary-scale changes in the Earth system, encompassing : planetary scale changes to atmospheric circulation, ocean circulation, climate, the carbon and nitrogen cycles, the water cycle, sea-ice changes, sea-level changes, food webs, biological diversity, pollution, health, land use, urbanisation and more (Stern *et al*., 1992).

Furthermore, the impacts of climate change on the carbon sequestration potential of blue carbon ecosystems has been highlighted as one of the most important questions to be addressed to improve and understand blue carbon science (Macreadie *et al*., 2019).

The Intergovernmental Panel on Climate Change (IPCC) predicts a rise in global sea levels during the 21st century associated with climate change models, projecting mean increases between 44 and 74cm by 2100, with a rate during 2081–2100 of 8 to 16 mm yr^{-1} (IPCC, 2013). Relative sea level (RSL) projections for the UK follow these global trends, including a worst-case scenario of 1.9m of RSL rise by 2100 published by the Met Office UK Climate Projections (UKCP) in 2009 (POST, 2017). Climate change predictions for the UK also include high impact changes in precipitation patterns, especially within estuarine ecosystems with potential habitat loss and deterioration in water quality caused by storm clusters (Robins *et al.,* 2016).

Thus, the potential impact of loss of seagrass ecosystems to global CO_2 budgets is highly relevant, enforcing the importance of establishing the magnitude of their C_{org} pools, including biomass and sediment storage. Therefore, the purpose of this research is to increase the understanding of climate change impacts on seagrass carbon sink potential in temperate, intertidal, seagrass meadows from southern

England, facilitating the inclusion of these ecosystems in future conservation and protection policies. This study provides original data on the importance of Southern England's seagrass meadows as carbon sinks, an area not yet researched, contributing to global blue carbon mapping and databases. Moreover, this project is the first to demonstrate the geochronological correlation between impacts of historical weather events, including the occurrence of storms and flooding, and seagrasses carbon sequestration and storage potential, none of which have been previously assessed for these ecosystems.

1.2 Research Aim and Objectives

This project aim is to assess how carbon sequestration and storage in central southern England's seagrass ecosystems have been influenced by recent (up to 150 years) weather events, in order to contribute towards global knowledge on the role of seagrasses as carbon sinks, and a better understanding of blue carbon regulating processes under a changing climate.

The objectives are to:

1. Establish a regional carbon storage profile by determining aboveground and belowground biomass, and carbon content of the sediment, to determine total carbon stocks.
2. Establish relationships between carbon storage and environmental factors to promote the understanding of features that influence seagrass carbon sink potential.
3. Establish a geochronology to identify how organic carbon sequestration has fluctuated in relation to reported precipitation, storminess, and sea level - as reflected in determined changes in sedimentation rate.

1.3 Research Approach

Following an assessment of the most recent seagrass inventory to determine relevant sampling locations, six fieldwork sites were selected within Southern England (Marsden and Chesworth, 2015). The region of interest, including the Isle of Wight and the harbours of Portsmouth, Langstone and Chichester, is a unique oceanographic area with unusual tidal cycles, representing a complex interconnected system of rivers, estuaries and natural harbours formed by the flooding of the river valley and coastal plains at the end of the melts the last ice age (figure 1.2) (Marsden and Chesworth, 2015).

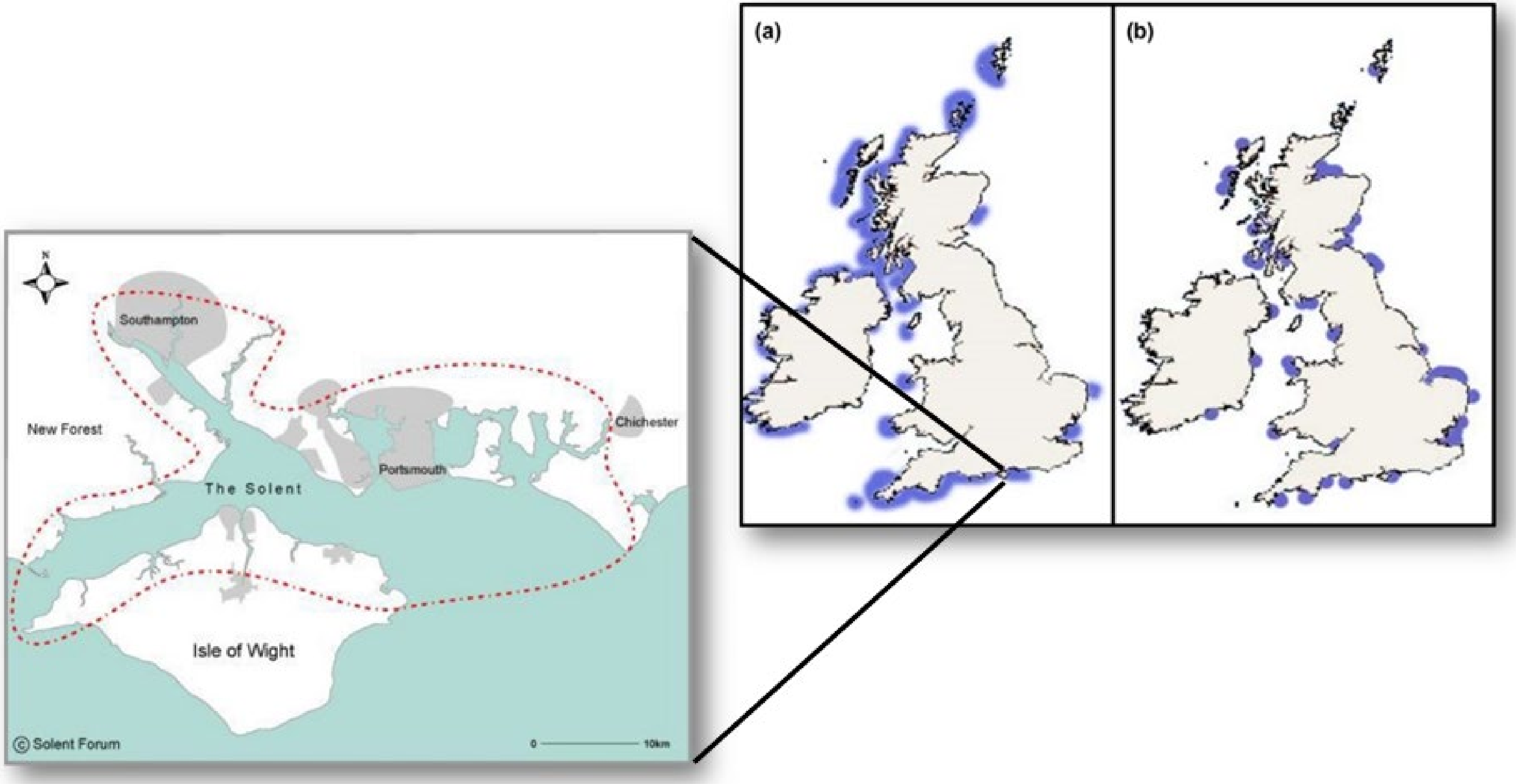


Figure 1.2: Recorded distribution of the seagrass species (a) *Zostera marina*, and (b) *Zostera noltii* around the coast of the UK and Ireland (from www.marlin.ac.uk, cited in Garrard and Beaumont, 2014). Zoom of the Solent region and adjacent harbours (Marsden and Chesworth, 2015).

This region in central southern England was chosen due to the historical distribution of seagrass on different types of sediments, from clay rich mud to sand, as well as providing a comparison between sheltered undisturbed estuaries, and ones exposed to intense anthropogenic activities, such as Portsmouth Harbour and the Isle of Wight. These factors, combined with historical flooding and high sea level rise predictions for the area, make it ideal to study recent climate change influence on seagrass carbon potential.

The sampling of intertidal seagrass, to assess below and above-ground biomass, sediment carbon storage and carbon sequestration was undertaken in the summer months, June-August, of 2017 and 2018. The geochronology and total organic carbon data were used with historical meteorological data to identify how precipitation, sea level, and occurrence of storms influenced carbon storage and sequestration at discrete time periods.

1.4 Thesis structure

Chapter 1: This chapter provides the research context, explains the aims and thesis structure.

Chapter 2: This chapter provides a review of the current and past research regarding the impacts of global environmental change on coastal vegetated ecosystems. In particular focus is placed upon literature regarding blue carbon and seagrass meadows, illustrating the importance of these ecosystems as carbon sinks globally and in the UK.

Chapter 3: This chapter introduces the characteristics of the study sites. It also provides details of general methodological techniques that are used in the analysis chapters 4, 5, and 6.

Chapter 4: This chapter contains details of total carbon stock analyses from sediment samples from seagrass meadows within the Solent region in the UK, including sediment organic carbon and living biomass carbon storage, providing a new assessment for intertidal seagrass meadows in England. These results support the inclusion of the Solent's seagrass meadows in conservation and restoration projects, aiming not only to conserve the carbon stored in their soils, but also increase their future carbon uptake potential.

Chapter 5: This chapter uses results from chapter 4 to analyse the influence of environmental factors on the variation in sediment carbon stocks for the studied seagrass meadows within the Solent region, using multivariate analyses. Results showed that sediment dry bulk density, sorting coefficient, % mud, and pore water pH and concentration of nutrients greatly influenced carbon stocks. Moreover, sediment characteristics acted in conjunction to explain most of the variation in carbon stocks among sites. Therefore, this chapter highlights the importance of considering sediment characteristics important indicators for carbon storage potential in intertidal temperate seagrass meadows.

Chapter 6: This chapter analyses past sediment accretion rates and explains variation in sediment accretion over time, and its relationship to past weather events. The sediment accretion rates were derived from an assessment of natural (^{210}Pb) radionuclides in discrete sections of sediment cores. These data were essential for any model predicting the impacts of future sea level rise scenarios on seagrass carbon sequestration potential. Moreover, there are no sediment accretion rate data available for intertidal seagrass meadows in the UK.

Chapter 7: This chapter discusses considerations regarding the results presented in the study, including comparisons to global literature. The chapter also discusses further applications of the results presented in future conservation and management environmental programs that include seagrass meadows.

Chapter 8: This chapter presents the key findings of the research project and provides recommendations for further study.

1.5 Nomenclature

Geology: Geology of the Solent region follow Dyer (1980) and Tubbs (1980)

Plants: Scientific names follow Green and Short (2003)

Units: SI units are used but salinity units are in Practical Salinity Units (PSU), elevation in relation to mean sea level is in metres, and sediment accretion is in millimetres.

2 Literature Review

2.1 Global Climate Change

Climate change has become a critical environmental challenge for modern society, representing a vital global concern (IPCC, 2018). Global concentrations of atmospheric GHG, mainly derived from anthropogenic sources, such as burning fossil fuels, land use change, industrialisation, agricultural practices and waste generation have increased significantly in comparison to pre-industrial values (IPCC, 2014). As a direct consequence, current atmospheric concentrations CO_2, methane (CH_4) and nitrous oxide (N_2O) are unprecedented in at least 800,000 years (IPCC, 2014). Analysis from ice cores and sea-floor sediments show that the current, near 410 parts per million (ppm), concentration of atmospheric CO_2 has not been experienced for at least three million years (Royal Society, 2017).

The effects of increased GHG emissions have been detected throughout the climate system, and identified as the dominant cause of observed warming since the mid-20th century, with current global atmospheric average temperature about 1°C higher (IPCC, 2014; Royal Society, 2017). Moreover, IPCC's (2018) most recent assessment reports with high confidence that global warming is likely to reach 1.5°C above pre-industrial levels between 2030 and 2052 if it continues to increase at the current rate.

The Earth's climate system has a natural seasonal variability across a range of temporal scales, including inter annual patterns such as the El Niño-Southern Oscillation (ENSO), inter decadal cycles such as the North Atlantic and Pacific oscillations and even multimillennial scale changes like glacial and interglacial transitions (Harley *et al.*, 2006). However, even considering natural and internal variability within the climate system such as the effects of a stronger El Niño between 2015 and 2016, and interactions within and between the ocean and the atmosphere, mean global surface temperatures during those years were still the highest they have ever been (Royal Society, 2017).

The urgency in addressing climate change issues comes from the many risks and impacts of global warming on natural and human systems, such as sea level rise, ocean warming and acidification, changes in precipitation, loss of ice sheets and polar ice extent, and their direct impacts on natural ecosystems and species survival (IPCC, 2014; IPCC, 2018). Walsh *et al.* (2014) analysed some of the most recent trajectories proposed by climate change models, designed to limit the global temperature increase to 2°C above pre-industrial levels. In order to achieve the limit described, not only are rapid emissions reductions by 2050 required (more than 70% decrease in human-related emissions), but also net negative emissions by 2100 (Walsh *et al*., 2014).

Hence, unless a large net removal of CO_2 from the atmosphere over a sustained period can occur, simply reducing or avoiding future GHG emissions would not be a sufficient method to mitigate climate change (IPCC, 2014). Achieving emission targets involves an extensive strategy that covers not only reducing fossil fuel based GHG emissions but also avoiding future emissions due to conversion by protecting and managing ecosystems that sequester carbon, including vegetated coastal environments (Howard *et al.,* 2017). Consequently, in December 2015, 196 nations worldwide joined forces in a legally binding agreement in order to determine individual and global efforts and actions towards a more resilient, low carbon society and an environmentally sustainable future (UNCC, 2015). Parties involved in the agreement were requested to outline clear information regarding the scope and extension of their mitigation and adaptation efforts, including detailed methodological approaches to estimate and account for anthropogenic GHG emissions and opportunities for removals (Herr and Landis, 2016).The Paris agreement (COP 21) unprecedentedly combined nations with a common cause based on their historic, current and future responsibilities, with the purpose of keeping this century's global temperature rise below 2°C, relative to pre-industrial levels, and to improve efforts to limit that increase even further, to 1.5°C (UNCC, 2015).

Moreover, COP 21 aimed to strengthen global mitigation against the impacts of climate change, by developing each country's National Climate Action Plans, or Intended Nationally Determined Contributions (INDCs), as well as promoting sustainable climate actions to rapidly reduce emissions and the present levels of atmospheric CO_2 (UNCC, 2015). Under the agreement countries have the freedom to independently develop their INDCs, reflecting their economy and environmental status (Herr and Landis, 2016).

2.2 Climate Change and Marine Environments

The ocean plays a key role in climate regulation, absorbing additional heat and CO_2 emissions (Royal Society, 2017). However, marine ecosystems and their related economic and social services have been suffering profound impacts due to human induced climate change (IPCC, 2018). For example, anthropogenic climate warming has been identified as the main cause of recent sea level rise, associated with oceanic thermal expansion and contraction of glaciers (Rahmstorf, 2007; Rahmstorf and Vermeer, 2011; IPCC 2013; Zickfeld *et al*., 2017; Royal Society, 2017; Nerem *et al*., 2018; IPCC; 2018). The average rate of Global Mean Sea Level (GMSL) rise has doubled, from 1.5mm to over 3 ± 0.4 mm per year, if compared between the periods of 1901-1990 and 1993-2014, representing the highest rate for over 3,000 years (Ablain *et al*., 2017; POST, 2017; Nerem *et al*., 2018). Although thermal expansion of the oceans has been the main contributor to the increase in GMSL rise during the 21st century, the uncertainty around the addition of water due to loss of ice from glaciers, which could become significantly greater after 2100, is alarming under high emission scenarios (IPCC 2013; Royal Society, 2017; IPCC 2018).

Nerem *et al*. (2018) used satellite altimetry, paired with seasonal variability and potential instrumental errors, to show that the rate of sea level rise is accelerating at 0.084 ± 0.025 mm y^{-2}, which would more than double global sea level rise predictions of approximately 65 cm for 2100. However, the predicted rate of sea-level rise is not uniformly distributed and some coastal regions might experience uplift or subsidence, due to processes unrelated to climate change, including groundwater abstraction, tectonic movement, oil and gas exploitation, and post-glacial isostasy (IPCC, 2011). Along with differences in coastal elevation, inland factors, such as variations in water or ice storage, modifications of lakes and streams, building of dams, mining of ground water and drainage into aquifers, can also influence the net effect of sea level rise on coastal ecosystems through gravimetric differences (UNEP, 2007).

Around the UK, tide gauge observations show that sea level has risen on average 1.4 ± 0.2 mm per year since 1900, with patterns of north-south spatial variability and local differences in relative sea level due to vertical land movement (Woodworth *et al*., 2009; POST, 2017). Recent studies estimate an average land uplift in western Scotland between 0.2- and 0.5-mm $year^{-1}$, lower than the 2 mm $year^{-1}$ previously suggested, which, paired with studies on marsh sedimentation rates, demonstrate that sea level rise has been outpacing coastal uplift in the country (Teasdale *et al*., 2011; Smith *et al*., 2017). Shennan and Horton (2002) reported a maximum relative land uplift of 1.6 mm year^{-1} in Scotland and a maximum subsidence in southwest England of 1.2 mm year^{-1}, with areas in the southeast of England exposed to an extra 0.5-1.1 mm year^{-1} increase in subsidence as a consequence of sediment auto compaction and land drainage.

It has been established that the observed and predicted rise in GMSL poses significant threats to coastal communities (Haigh *et al*., 2014; Poloczanska *et al*., 2014). In addition, changes in the atmospheric pressure gradient and circulation, due to continental land warming at a faster rate than oceans, and its consequences on wind fields along ocean margins, are among the main physical changes caused by climate change on coastal environments (Harley *et al*., 2006). Moreover, changes in atmospheric and ocean circulation can influence factors such as storm frequency, and precipitation patterns that could affect salinity, turbidity and runoff of terrestrial nutrients and pollutants (Harley *et al*., 2006).

The combination of waves, tides and storm surges associated with the occurrence of extreme sea level rise events, will become more frequent with the increase in GMSL (Wong *et al*., 2014; Wadey *et al*., 2015). Additionally, eroded beaches, coupled with increased sea level, will increase the occurrence of coastal flooding driven by extreme events (Wong *et al*., 2014; POST, 2017). Although stronger wind fields could increase upwelling of nutrient rich waters to the surface, increasing nutrient availability, the long-term interference and consequences of thermal stratification promoted by climate change is still a research priority (Harley *et al.*, 2006).

Another important, but often overlooked, impact of increasing atmospheric GHG concentrations is the changes in ocean biogeochemistry (Howes *et al*., 2015). For example, expected changes in ocean pH are higher than those inferred from fossil records over the past 300 million years, with uncertainties regarding adaptation by marine organisms (Poloczanska *et al*., 2014). This is because the ocean's concentration of carbon and oxygen, as well as pH and temperature levels, will continue to change even if CO_2 emissions ceased (Howes *et al*., 2015).

Furthermore, the increase in atmospheric CO_2 levels, and consequent depletion of the ozone layer by cooling the stratosphere and reducing temperature-related ozone loss processes, can potentially lead to enhanced ultraviolet radiation levels on the

Earth's surface (Stolarski *et al.*, 2015). Ecological implications of biogeochemical feedback cycles, such as cloud cover, ultraviolet radiation, planktonic productivity and the release of dimethyl sulphide (DMS) by marine algae, are complex and hard to predict under future temperatures and GHG concentrations (Harley *et al.*, 2006). Impacts on biogeochemical feedback cycles are also related to increased warming, acidification and deoxygenation of the ocean, with changes spreading into deep waters and directly impacting vulnerable ecosystems, such as coral reefs and their linked food webs, even under low emission scenarios (Heinze *et al.*, 2015; Hoegh-Guldberg and Poloczanska 2017).

Changes in sea temperature, combined with alterations in ocean chemistry and circulation can strongly impact the performance and survival of many marine species, like seagrasses and corals (Harley *et al.*, 2006; Howes *et al.*, 2015; Hoegh-Guldberg and Poloczanska 2017). Additionally, anthropogenic climatic forcing and its cascade of physical and chemical changes in marine systems can affect evolutionary adaptations, and large-scale biogeographical patterns of species and population distribution (Poloczanska *et al.*, 2014). Climate change will also impact population dynamics and ecological community structure, where responses depend on relationships between the abiotic environment and organism level processes, influencing transport, dispersal and recruitment (Harley *et al.*, 2006).

A major climate change related impact on societies and economies will be the availability and reliability of water supplies, being placed under stress not only in dry subtropical regions but also where demands are high (Flörke *et al.*, 2018; IPCC, 2018). Problems such as overfishing, chemical runoff from urbanized areas, and freshwater diversion can promote the introduction of invasive species and estuarine habitat loss (Robins *et al.*, 2016). Changes in freshwater runoff rates have been identified as one of the greatest potential impacts of climate change on estuaries, resulting in variations in physical mixing characteristics (Scavia *et al.*, 2002).

2.3 Carbon Cycling and Coastal Vegetated Environments

Research on natural carbon sinks has primarily focused on oceans (Sabine *et al.*, 2004) and terrestrial forests (Houghton *et al.*, 1999), and only more recently, on coastal systems (McLeod *et al.*, 2011). This is because the ocean represents the largest active carbon sink on Earth, absorbing 20–35% of anthropogenic CO_2 emissions (Khatiwala *et al.*, 2009; Gattuso *et al.*, 2018). Powlson *et al.* (2011)

describe five major pools of global carbon: oceanic, geologic, pedologic, atmospheric and biotic. Each of these carbon pools is interconnected through the carbon cycle, with the oceanic, pedologic, and biotic pools being recognised as important buffers to climate change, the oceanic pool is the largest and one of the most stable (figure 2.1) (Lal, 2004).

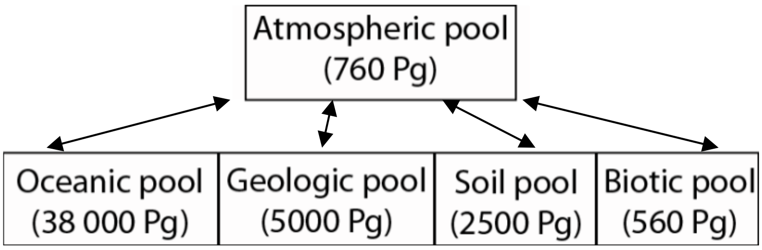


Figure 2-1: Estimated global carbon pools in petagrams (Pg), adapted from (Lal, 2004).

Carbon cycling is the main process used by most natural ecosystems to transfer energy at baseline levels, including carbon uptakes (fluxes into) and carbon release (fluxes out of) the system (Howard *et al.,* 2017). However, the climate-carbon feedback cycle still represents a point of instability in global climate change models (Huntzinger *et al*., 2017). The climate-carbon positive feedback loop can be explained by the effect of elevated CO_2 concentrations in the atmosphere increasing global temperatures, which further promotes the acceleration of sediment decomposition rates consequently releasing more CO_2 and other GHG into the atmosphere (Lal, 2004; Fung *et al*., 2005; IPCC, 2007; Huntzinger *et al.,* 2017). However, management strategies to enhance oceanic carbon sequestration and storage, like ocean iron fertilization, are currently impractical, and with potentially high ecological impacts (Russell *et al.,* 2013).

Both scientists and decision makers have recently been focusing on terrestrial and coastal vegetated ecosystems, which show high potential for climate mitigation at local and national scales (Howard *et al*., 2017). More specifically, wetland ecosystems are increasingly acknowledged as important carbon sinks, based on their ability to sequester large amounts of carbon in their biomass and, more importantly, in their sediments (Hiraishi *et al*., 2014). Wetlands are characterised by regular, seasonal or occasional inundation highly influenced by changes on adjacent land as well as surrounding waters (Burton and Tiner, 2009; Short *et al*., 2016). They encompass a range of inland and coastal ecosystems, including rivers and lakes, floodplains, swamps, marshes, peatlands, mangroves, rice fields and seagrass meadows (Burton and Tiner, 2009). Wetlands are considered important because they support vital services and provide benefits to society, including nutrient cycling, carbon storage, water purification, flood attenuation, recreation and conservation of biodiversity (Kirwan and Megonigal, 2013; Russi *et al*., 2013).

Vegetated coastal environments are twice as effective at storing carbon in their sediments and biomass as terrestrial habitats (Lovelock *et al*., 2017). Mangrove forests, seagrass meadows, and salt marshes, have carbon sequestration rates per hectare estimated at an order of magnitude greater than terrestrial forests (Chmura *et al*., 2003; McLeod *et al*., 2011; Duarte *et al*., 2013; Herr and Landis, 2016; Lovelock *et al*., 2017). In addition, losses of C_{org} through chemical conversion to CO_2 are comparatively low in vegetated coastal environments as a result of their frequent inundation by saline water, which increases the storage of organic matter by keeping sediment oxygen concentration low, decreasing microbial activity (IPCC, 2013). Another added advantage of inundation by saline water is the limitation in CH_4 production (Herr and Landis, 2016; Lovelock *et al*., 2017).

Vegetated coastal environments may accrete sediments vertically in response to rising sea level when healthy, increasing the size of their sediment carbon sink over time (Herr and Landis, 2016). Studies show that vegetated coastal environments develop feedbacks as a result of changes in sea level and flooding, including faster rates of above ground plant growth promoting greater standing biomass to reduce water velocity and erosion, consequently increasing mineral sediment deposition (Kirwan and Megonigal, 2013). These feedbacks suggest that tidal marshes, for example, might survive accelerating rates of sea-level rise by creating eco-geomorphic interactions between rates of vertical accretion and sea level (Kirwan and Megonigal, 2013).

However, land use change such as, deforestation, erosion and agricultural activities can result in CO_2 emissions from ecosystems that serve as natural carbon sinks (Solomon *et al*., 2007). This would cause the release of much of the carbon stored in their sediments back into the atmosphere and ocean, shifting these ecosystems from net sinks to sources of carbon (Pendleton *et al.* 2012; Kauffman *et al.* 2014; Howard *et al*., 2017). Therefore, many nations have been including protection, conservation and restoration of their natural coastal wetlands in their INDCs, given their significant mitigation and adaptation value as carbon sinks, for coastal protection and for food security (Mitsch *et al*., 2012; Herr and Landis, 2016; Melts *et al*., 2019).

In order to be relevant for climate change mitigation policies, including GHG inventories, carbon pools and cycling processes within a system need to be able to promote changes in atmospheric GHG above baseline levels (Howard *et al.,* 2017). For example, ecosystems included in climate mitigation policies, like vegetated coastal environments, must have responsive GHG emissions from their carbon cycling, either significantly increasing or decreasing, following habitat degradation or restoration and conservation, respectively (Howard *et al.,* 2017). For instance, carbon cycling processes in mangroves, saltmarshes and seagrass meadows would be disturbed under scenarios of anthropogenic pressure, promoting emission of previously stored C_{org} back into the atmosphere as CO_2 (figure 2.2) (McLeod *et al*., 2011; Fourqurean *et al*., 2012a; Howard *et al*., 2017).

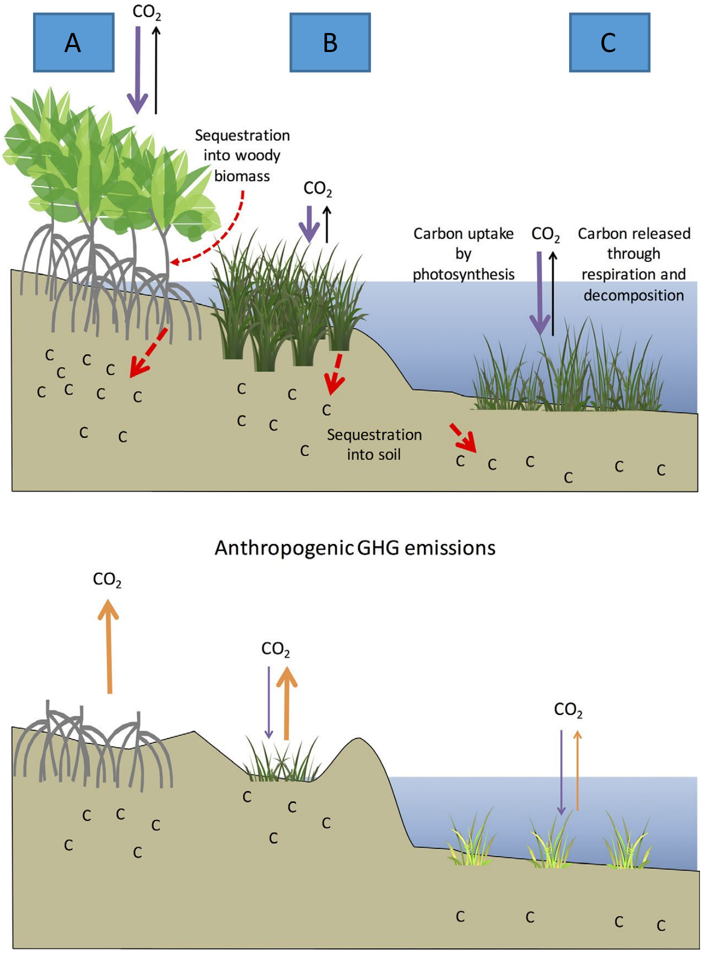


Figure 2.2: Carbon uptakes and emissions from preserved (top) and degraded (bottom) states. Purple arrows - CO_2 uptake via photosynthesis, narrow black arrows - carbon released through respiration and decomposition (top), red dotted arrows - carbon sequestration into biomass and sediments (top), upward orange arrows - CO_2 emissions due to degradation (bottom). A- Mangroves, B- Saltmarsh and C- Seagrass (Adapted from Howard *et al*., 2017)

Herr and Landis, (2016) suggested that implementing vegetated coastal environments conservation and protection programs to completely halt human related losses could prevent the release of over 450 Mt CO_2 per year, or even 230 Mt CO_2 annually if losses were reduced by half, enough to offset the reported CO_2 emission of Spain in 2013, for example. Furthermore, Mitsch *et al*. (2013) and Mitsch (2016) illustrated that the world's wetlands may currently be net carbon sinks of about 0.83 Pg year^{-1} of carbon with an average of 118 gC m^{-2} yr^{-1} of net carbon sequestration rate. Therefore, it has been proposed that restoring vegetated coastal environments would potentially increase annual carbon sequestration by 160 Mt CO_2 per year, offsetting emissions equivalent to burning 77.4 million tonnes of coal (Herr and Landis, 2016).

However, robust information needs to be accounted for in order to determine if an ecosystem should potentially be included in national GHG inventories and endorse actions to enhance or conserve their carbon uptake potential (Howard *et al*., 2017; Villa and Bernal, 2017; Mitsch and Mander, 2018; Gattuso *et al*., 2018). These would include assessing the system's carbon sequestration rate, current carbon stocks including future predictions, geographic coverage, and exposure to anthropogenic impacts, that could drive system loss leading to carbon emissions and emission rates from both degraded and intact states (Mitsch *et al*., 2012; Howard *et al.,* 2017; Mitsch and Mander, 2018; Gattuso *et al*., 2018).

2.3.1 Blue Carbon

"Blue carbon" is a modern term, introduced in 2009, designed to represent the carbon stored in vegetated coastal environments, including salt marshes, mangroves and seagrass meadows (Pendleton, *et al*., 2012; Lovelock and Duarte, 2019). UNEP's (2009) report suggests that 55% of all the atmospheric carbon captured by living organisms is stored in the oceans, with between 50% and 71% of this being captured by the ocean's vegetated blue carbon environments (Nellemann *et al*., 2009). These ecosystems store carbon within their sediment, 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). Thus, although the combined area of salt marshes, mangroves and seagrasses only covers a narrow coastal fringe, covering less than

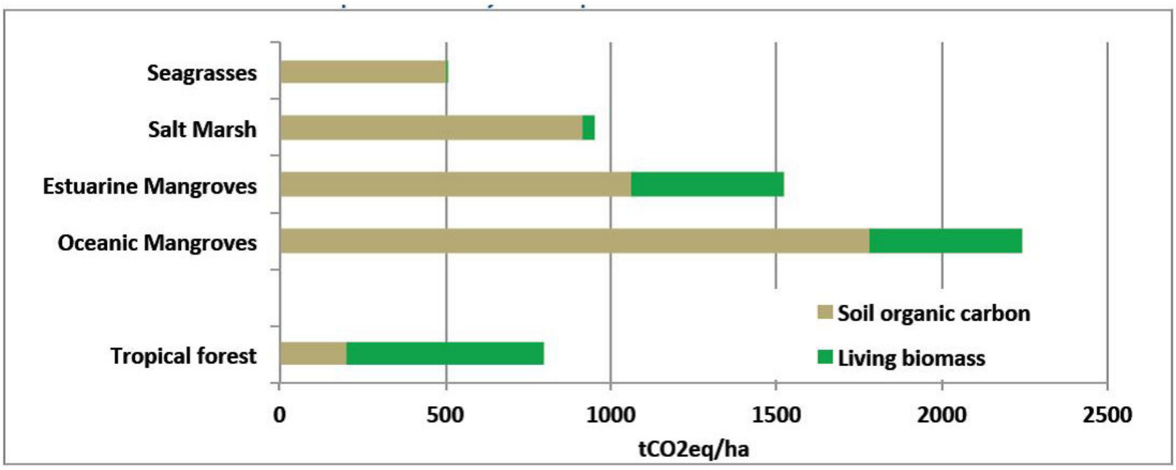
0.5% of the seabed, their potential role as GHG emissions sources is disproportionally large (Pendleton *et al*., 2012; Himes-Cornell *et al*., 2018).

Blue carbon environments also provide several other important direct and indirect ecosystem services, including the provision of nursery habitats, raw materials, coastal protection, and enhancing water quality, to name a few (Lau, 2013). Studies have indicated that large areas of these ecosystems have been, and are currently being, lost or degraded worldwide (Himes-Cornell *et al*., 2018). For instance, over the last 20–50 years, 50% of salt marshes, 35% of mangroves, and 29% of seagrasses have been lost (Waycott *et al*., 2009; Mcleod *et al*., 2011). The development of blue carbon projects in these ecosystems remains a challenge, due to the high spatial variation in GHG emissions, uncertainty around land tenure, tidal boundaries and legislative responsibilities for which research and development are still required (Herr *et al*., 2017; Lovelock and Duarte, 2019).

Even though projects focused on the protection and sustainable management of vegetated coastal environments are not a novelty, such efforts are mainly aimed at generating benefits and services to local communities and biodiversity, as well as the fisheries, forestry and tourism sectors (Herr *et al*., 2014; Mitsch and Mander, 2018). Unlike terrestrial ecosystems, few programs have been established with the goal of conserving and restoring ecosystems as potential mechanisms for climate mitigation (carbon capture/ avoided emissions) (Herr *et al*., 2011; Gattuso *et al*., 2018). Herr and Landis (2016) pointed out that even though 151 countries contain at least one blue carbon ecosystem (seagrass, saltmarsh or mangrove), with 71 containing all three, only 28 countries include references to coastal wetlands in terms of mitigation in their INDCs.

Chmura *et al*. (2003) suggested that vegetated coastal environments could contain the largest stores of pedologic and biotic carbon pools and thus provide an important ecosystem service by removing carbon from the atmosphere. Even though most of the atmospheric CO_2 captured by photosynthesis is almost immediately returned via plant and microbial respiration, or temporarily stored in living plant biomass, part of it is sequestered for significant periods of time in woody biomass and sediment (Howard *et al*., 2017).

The majority of the blue carbon stored within coastal ecosystems, can be found in their sediments (figure 2.3) (Murray *et al*., 2011; Lovelock and Duarte, 2019). These systems are able to sequester and store large amounts of carbon, not only through their natural photosynthetic processes, but also by trapping sediments and organic debris within their complex root systems (Howard *et al.,* 2017). Allochthonous organic debris can be derived from proximate ecosystem vegetation and sediment transported by river systems, tides, or wave activity (McLeod *et al.,* 2011; Howard *et al.,* 2017). These rich sediment carbon stores can be as deep as six meters below surface, remaining stored for millennia (Blue Carbon Initiative, 2012).



*Data is per unit area, where tCO2eq/ha is tons of carbon dioxide equivalents per hectare

Source: Murray, Brian, Linwood Pendleton, W. Aaron Jenkins, and Samantha Sifleet. 2011. Green Payments for Blue Carbon: Economic Incentives for Protecting Threatened Coastal Habitats. Nicholas Institute Report. NI R 11-04

Figure 2.3: Living biomass and sediment organic carbon content in vegetated ecosystems (Murray et al., 2011).

However, there might be significant differences in the amount of carbon stored in vegetated coastal ecosystems from different global regions (Fourqurean *et al*., 2012a; Villa and Bernal, 2017). For example, compared to temperate regions, seagrass meadows located in the Mediterranean have the highest average sediment carbon, of 372.4 Mg C ha^{-1}, as well as high levels of carbon storage in their plant biomass (Fourqurean *et al*., 2012a). Furthermore, global carbon stock estimations for coastal and marine systems usually only take into account the carbon stored within the top meter of their organic sediments, leading to possible underestimations (Howard *et al.,* 2017).

Moreover, healthy coastal ecosystems might have the ability to maintain rates of sediment accretion that keeps pace with sea level rise (Howard *et al.,* 2017). Chmura *et al*. (2003), suggested that climate change is likely to influence the ability of vegetated coastal environments to sequester carbon particularly in coastal and estuarine environments due to changes in precipitation, sea level rise and increases in storminess. On average, 0.23-2.25 x 10^9 Mg of CO_2 are released annually by drainage and loss of coastal ecosystems, representing 0.7-3% of total area lost (varying geographically and with vegetation type) (Howard *et al.,* 2017; Hiraishi *et al.,* 2014).

Vegetated coastal environments degradation and loss varies globally and may include conversion to aquaculture, agriculture, forest over-exploitation, industrial use, upstream damming of rivers, dredging, eutrophication of overlying waters, urban development, and conversion to open water due to accelerated sea-level rise and land subsidence (Pendleton *et al*., 2012). At current rates, 30–40% of salt marshes and seagrasses and nearly 100% of mangroves could be lost in the next 100 years (Pendleton *et al*., 2012; Wylie *et al*., 2016; Villa and Bernal, 2017; Himes-Cornell *et al*., 2018). Climate change related threats to seagrass ecosystems include rising sea levels, changing tidal regimes, UV radiation damage, sediment hypoxia or anoxia, increases in sea temperatures and increased storms and flooding events (Bjork *et al*., 2008; Herr *et al*., 2017; Macreadie *et al*., 2019).

The inclusion of blue carbon ecosystems into GHG inventories and climate change mitigation programs has been recommended by the IPCC (Howard *et al.,* 2017; Hiraishi *et al.,* 2014; Lovelock and Duarte, 2019; Macreadie *et al*., 2019). In order to develop or revise national strategies to manage vegetated coastal environments carbon sinks and sources, following the IPCC's guidance, countries should provide a background carbon assessment of their coastal systems, covering existing carbon stocks and estimates of emissions from conversion (Howard *et al.,* 2017). To date, blue carbon ecosystems represent important climate change mitigation opportunities, being included in United Nations Frameworks Convention on Climate Change (UNFCCC), such as Nationally Appropriate Mitigation Actions (NAMAs); Reducing Emissions from Deforestation and Forest Degradation (REDD+); Land use, Land Use Change and Forestry (LULUCF), and relevant climate change funding schemes (Howard *et al.,* 2017; Mitsch and Mander, 2018; Lovelock and Duarte, 2019; Macreadie *et al*., 2019).

2.4 Seagrass

Seagrasses are a group of marine angiosperm flowering plants that have adapted to exist fully submersed in saline water (Orth *et al*., 2006). They are a unique taxon, believed to have evolved from terrestrial plants who were able to acclimatise to marine life, becoming the only flowering plants able to function and reproduce under permanent submersion in saline water (Björk *et al.,* 2008; Marsden and Chesworth, 2015). Seagrasses can act as ecological engineers, by profoundly influencing physical, chemical, and biological environments in coastal waters (Wright and Jones 2006). Moreover, seagrasses provide numerous important ecological services to the marine environment, such as nutrient cycling, and food web structure (Costanza *et al*., 1997; Hemminga and Duarte 2000; Björk *et al.,* 2008). They are an important food source for mega-herbivores such as green sea turtles, dugongs, and manatees, and provide critical habitat for many animals, including commercially and recreationally important fishery species (Orth *et al*., 2006; Björk *et al.,* 2008).

Seagrasses are currently classified into 5 families: Hydrocharitaceae, Cymodoceaceae, Posidoniaceae, Zosteraceae and Ruppiaceae, which are subdivided into 14 genera and approximately 60 species, although these classifications are currently in flux due to taxonomic controversies brought about by new developments in genetic analysis (table 2.1) (Björk *et al.,* 2008; Papenbrock, 2012; Kilminster *et al*., 2015).

Table 2-1: Seagrass families and respective genus, including number of species in brackets, and global distribution. Sensu stricto according to the definitions by Larkum *et al*. (2006). Adapted from Papenbrock, (2012).

Family	Genus	Distribution*
Hydrocharitaceae	*Enhalus* (1)	5
	Thalassia (2)	2, 5
	Halophila (14)	2, 3, 4, 5, 6
Cymodoceaceae	*Amphibolis* (2)	6
	Cymodocea (4)	1, 3, 5
	Halodule (8)	1, 2, 5
	Syringodium (4)	2, 5
	Thalassodendron (2)	5, 6
Posidoniaceae	*Posidonia* (1)	3, 6
Zosteraceae	*Heterozostera* (1)	6
	Phyllospadix (5)	4
	Nanozostera (8)	1, 3, 4, 5, 6
	Zostera (4)	1, 3, 4, 5, 6
Ruppiaceae	*Ruppia* (11)	1, 3, 4, 5, 6

*1 Temperate North Atlantic, 2 Tropical Atlantic, 3 Mediterranean, 4 Temperate North Pacific, 5 Tropical Indo-Pacific, 6 Temperate Southern Oceans.

The distribution of seagrass has been broken down into six global bioregions, encompassing three distinct temperate areas which are: The Temperate North Atlantic, the Temperate North Pacific, and the Temperate Southern Oceans (table 2.1), with the Mediterranean bioregion containing both tropical and temperate species (Short *et al.* 2007). Out of the regions described, the Temperate North Atlantic is considered to have the lowest seagrass biodiversity, with eelgrass, *Zostera spp.,* as predominant species (Björk *et al.,* 2008).

Seagrass meadows are formed by one or more plant species and can be classified as enduring or transitory (Kilminster *et al*., 2015). Enduring meadows are persistent over time and dominated by persistent species such as *Posidonia spp.* or colonising species, like *Zostera spp.* and *Halophila spp.* (Guidetti *et al*., 2002; Papenbrock, 2012). Persistent species show smaller seasonal variation in abundance than opportunistic ones, but in both cases the structure and size of the meadows in the seascape can be followed over periods of decades (Hillman *et al*., 1995; Kendrick *et al*., 2000; Campbell and Miller, 2002; Kendrick *et al*., 2008).

In contrast, transitory meadows are not persistent over time; presenting periods of diebacks, with complete absence of seagrass (Papenbrock, 2012). These can only be formed by colonising and opportunistic species but can also show variation in species composition and abundance over time (Papenbrock, 2012). Examples include deep water meadows of *Halophila decipiens O.* in the Caribbean (Kenworthy, 2000), *Zostera spp.* meadows in the Gulf of California (van Lent and Verschuure, 1994; Meling-López and Ibarra-Obando, 1999; Santamaría-Gallegos *et al*., 2000), and estuarine *Ruppia spp.* meadows (Kantrud, 1991).

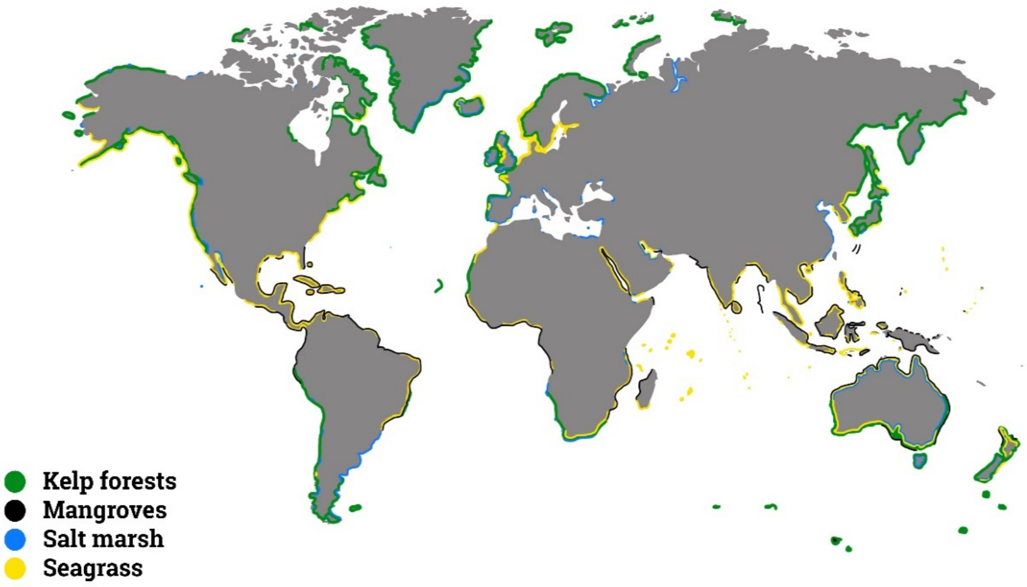


Figure 2.4: The Global distribution of marine blue carbon ecosystems, including Kelp forests (green), Mangroves (black), Salt marshes (blue) and Seagrasses (yellow). (Map: Lærke Rosenberg/ ScienceNordic. Kelp distribution from Filbee-Dexter and Wernberg, (2018). Mangroves, salt marsh, and seagrass distributions from The Blue Carbon Initiative, (2009)). Source: Krause-Jensen *et al*., (2018).

There is high variance in seagrass meadows estimated global areal coverage, ranging from 17 x 10^6 to 60 x 10^6 ha worldwide (Hemminga & Duarte, 2000). This uncertainty highlights the need for more research, to better map and understand seagrass global distribution, including seasonal and temporal variations (Macreadie *et al*., 2018). Seagrass meadows, like salt marshes, have a pan-global distribution, being found in shallow coastal areas of all continents, with the exception of Antarctica (figure 2.4) (Garrard and Beaumont, 2014). However, Garrard and Beaumont (2014) also notethat even though seagrasses have the widest global distribution of all vegetated coastal environments, they remain comparatively unstudied.

Dispersal capacity is one of the factors that influences seagrass distribution, with the greatest species richness found in South East Asia (Hogarth, 2015). Species number declines with distance from this region, both with latitude and longitude, following the main ocean currents (Hogarth, 2015). In terms of distribution *Ruppia maritima* L. has been described as the most widely dispersed seagrass species being found in both tropical and temperate bioregions, successfully adapted to a broad salinity range (Björk *et al.,* 2008). Tidal height is one of the main factors that regulates the upper limit of species occurring up to the low intertidal zone, whereas the lower limit is generally set by light penetration, determining the ultimate depth at which seagrass can live (Hogarth, 2015).

All seagrass plants, regardless of species, have similar morphology, consisting of ramets (units) formed by leaf bundles connected to a root-rhizome matrix (figure 2.5) (Marsden and Chesworth, 2015). The root-rhizome system may represent 50-60% of seagrass biomass, being more extensive in nutrient poor sediments, or in plants exposed to increased water turbulence, acting as an anchoring system (Hogarth, 2015). The below ground mat of horizontal rhizomes branches during clonal growth, resulting in a lateral expansion of patches, with high demand of resources and energy from species such as *Zostera* spp. (Marsden and Chesworth, 2015). The root and rhizome system oxygenate the sediment and can spread vertically and horizontally, altering the topography of the sea floor, even after plant death (Hogarth, 2015).

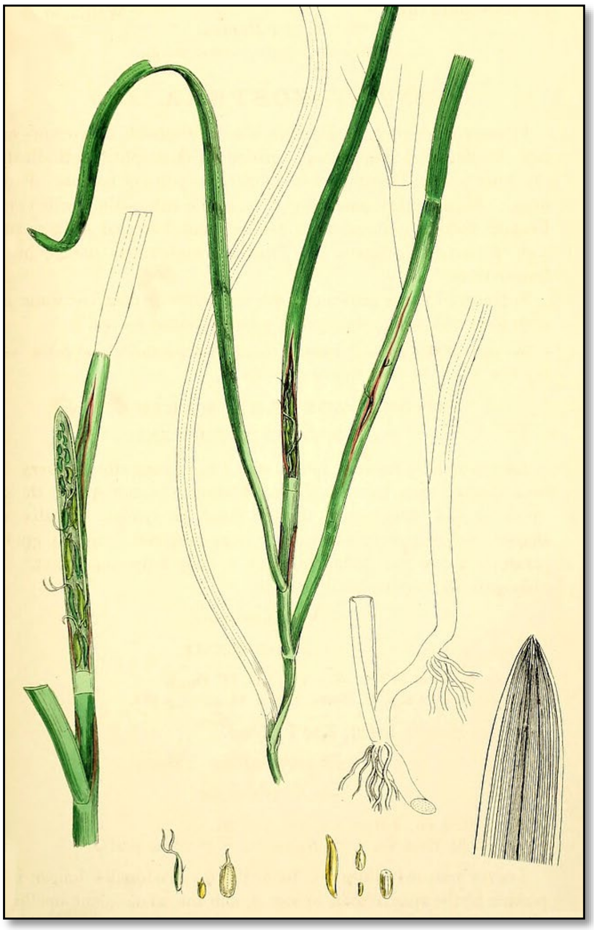


Figure 2.5: Anatomical scientific drawing of the seagrass Zostera marina (eelgrass), showing living above-ground (shoots and blades), below-ground (roots and rhizomes) components and seeds. (From: Watson, and Dallwitz, 1992).

Under favourable conditions, seagrass plants can form extensive and dense stands, also known as meadows or beds, for example, *Zostera marina* L. can form dense beds with leaves that trail up to 1m long (Marsden and Chesworth, 2015). Biomass and production in seagrass meadows can be related to species richness, and the size variability between species (Hogarth, 2015). Species differ in size and growth strategies, with pioneering species such as *Halodule spp*. and *Halophila spp.* focusing on rapid vegetation expansion and new shoot generation, with low carbon storage, whereas slower spreading, persistent, species like *Thalassia* spp. and *Posidonia oceanica* L. accumulate larger carbon reserves (Björk *et al.,* 2008).

The high primary productivity of seagrasses allows the development of a rich associated fauna as it provides a vital food source for fauna that feeds directly on the plant or on its associated epiphytic colonies (Cook *et al*., 2011; Ebrahim *et al*., 2014; Marsden and Chesworth, 2015). A diverse epiphytic community grows on seagrass leaves, including bacteria, fungi, and algae, as well as sessile animals, sometimes accumulating a biomass accountable for 60% of the plant's aboveground productivity (Hogarth, 2015). However, excessive epiphytic cover, often related to eutrophic conditions, can restrict the plant's CO_2 and mineral nutrients uptake, as well as light availability, reducing productivity and even causing mortality (Brodersen *et al*., 2015; Mabrouk *et al*., 2017).

The structure of seagrass canopies can form a barrier that reduces wave and current velocity, helping stabilise sediment and prevent erosion (Potouroglou *et al*., 2017). Depending on species, and canopy height and density, seagrasses may reduce current velocity by up to 90%, facilitating high rates of sedimentation, with net accretion rates of up to 2mm year^{-1} (Hogarth, 2015). The below-ground network of roots and rhizomes further prevent re-suspension of sediment particles by binding them together, which combined with the removal of fine particles from the water column decreases turbidity and increases light penetration, benefiting submerged photosynthetic organisms (Gacia and Duarte, 2001; Paquier *et al*., 2014; Serrano *et al*., 2016; Potouroglou *et al*., 2017).

Björk *et al.* (2008) describe light, temperature, salinity and nutrient availability to be some of the main regulating abiotic factors for seagrass growth. Seagrasses generally require irradiance greater than about 11% at the sea surface, although *Halophila spp*. can thrive at light intensities as low as 5% (Hogarth, 2015). Levels of low light tolerance vary between species and can be related to their ability to store carbohydrates in their rhizomes, suggesting that species with smaller rhizomes, such as *Zostera noltii,* have limited capacity to tolerate low light levels (Marsden and Chesworth, 2015). The average maximum depth at which seagrasses occur is around 90m, although some *Halophila spp.* has been found around 145 m deep (Hogarth, 2015).

Coastal development and industry can alter abiotic factors, and negatively impact seagrass ecosystems (Marsden and Chesworth, 2015). Impacts can be physical, resulting in direct removal of plants by dredging, or fishing practices such as bait digging, mooring or anchoring boats, or chemical interference with the sediment and water (Mazarrasa *et al*., 2017b). Moreover, storms and severe weather events, associated with climate change, can also affect seagrass populations by uprooting plants and mobilizing sediments, increasing turbidity and reducing water quality and light penetration (Cardoso *et al*., 2008).

Fluctuations in sea temperature, are considered the primary climate change related threat to seagrass ecosystems, and therefore the most studied (Garthwin *et al*., 2014; Collier and Waycott *et al*., 2014; Potouroglou *et al*., 2014; Short *et al*., 2016; Egea *et al*., 2018; George *et al*., 2018). More specifically, warming of temperate regions could lead to a reduction of seagrass biomass and productivity and an increase in leaf turnover rates, i.e. the rate in that they are produced, senesce and fall (Duarte, 1989; Duarte and Chiscano, 1999; Clausen *et al*., 2014; Olesen *et al*., 2015; Mazarrasa *et al*., 2018). This alteration in seagrass distribution and metabolism, driven by increasing sea temperatures, could subsequently reduce net autochthonous C_{org} sequestration potential (Clausen *et al*., 2014; Hyndes *et al*., 2016; Mazarrasa *et al*., 2018).

Sea level rise may also alter habitat availability for intertidal species, along with coastal squeeze as light penetration decreases with depth (Kirwan and Megonigal, 2013; Marsden and Chesworth, 2015). Human activity could also remove natural predators from the ecosystem, inducing seagrass loss by overgrazing from sea urchins and molluscs (Ibarra-Obando *et al*., 2004; Hogarth, 2015). Another anthropogenic factor that would promote loss of seagrass ecosystems is reduced water quality, caused by sediment and nutrient runoff (Lee *et al*., 2007; Howard *et al.,* 2017; Mazarrasa *et al*., 2018). In addition, seagrass is also exposed to natural disturbances, such as the occurrence of a wasting disease that almost exterminated eelgrass (*Z. marina*) communities on both sides of the Atlantic in the 1930s (Björk *et al.,* 2008).

Wasting disease is caused by a marine slime mould *Labyrinthula zosterae,* occurring widely on seagrasses throughout the world and normally causing no harm (Muehlstein *et al*., 1988; Ralph and Short, 2002; Hogarth, 2015). However, studies suggest that the fungus may have become a serious pathogen because plants were vulnerable as a result of environmental stressors, possibly human-induced, including pollution and abnormal temperature and salinity fluctuations (Hughes *et al*., 2018). A decline in fish and wildfowl biodiversity has also been observed following wasting disease events, highlighting the ecological importance of seagrass meadows (Waycott *et al*., 2009; Sullivan *et al*., 2013; Marsden and Chesworth, 2015). Anthropogenic, climate change related, or natural, impacts on seagrass meadows, are also likely to directly affect their productivity and ability to capture and store atmospheric CO_2 by photosynthesis, and therefore their capacity to act as global carbon sinks (Duarte *et al*., 2005; Kennedy *et al*., 2009; Nellemann *et al*., 2009).

Seagrass species can be found in terrigenous and carbonate organic rich sediments and have the ability to incorporate and cycle nutrients from both sediment and the water column (Björk *et al.,* 2008). Seagrass detritus can be bound to the sediment within the seagrass habitat or transported to deeper ocean habitats, thus providing a major carbon sink and long-term carbon burial (Suchanek *et al*., 1985; Kennedy and Björk, 2009; Tanaya *et al*., 2018). The turnover time, which is the rate at which the biomass is decomposed and replaced within an ecosystem, of seagrass leaf and root biomass is between two weeks and five years, with rhizomes sometimes persisting for millennia before being broken down (Mateo and Romero, 1996; Kennedy and Björk, 2009; Liu *et al*., 2017).

In addition to their environmental contribution as potential carbon sinks, seagrasses have had many traditional social and economic uses over time, ranging from filling mattresses and house insulation to providing shelter and attracting numerous species of animals, thus acting as rich fishing grounds (Björk *et al.,* 2008). Seagrasses can rival coral reefs in terms of supporting biodiversity, and when associated with barrier reef profiles they can supply more protection services than live corals themselves, compensating for long-term degradation of the reef (Guannel *et al*., 2016). Therefore, the indirect value of seagrass meadows as shelter and nutrition providers for many commercially important species, adds to their ecological importance (Hogarth, 2015; Nordlund *et al*., 2016; Nordlund *et al*., 2018).

Due to their many ecological roles, including their sensitivity to disturbances and wide geographical range, seagrass ecosystems are considered excellent biological indicators (Pergent *et al*., 2015). Jones and Unsworth (2016), further indicate the potential risks of poor environmental management of seagrass meadows for food security, given their relevant fisheries nursery value, supporting the need to preserve these habitats. However, unlike coral reefs and other ecosystems which also benefit society, seagrasses often receive little attention and are often not considered in coastal management decisions (Duarte *et al*., 2008; Grech *et al*., 2012; Nordlund *et al*., 2014; Nordlund *et al*., 2018).

2.4.1 Seagrasses in the UK

Seagrasses can be found throughout the UK coast, but mainly in the south and west of England, eastern England and Scotland (figure 2.6) (Marsden and Chesworth, 2015). Five species of seagrass have been reported in the UK: *Zostera marina*, *Zostera angustifolia*, *Zostera noltii*, *Ruppia maritima* and *Ruppia cirrhosa* (Garrard and Beaumont, 2014). *Z. marina*, a temperate seagrass found throughout Europe, the USA and the northwest Pacific, is the UK's dominant seagrass species (figure 2.6) (Green *et al*., 2018).

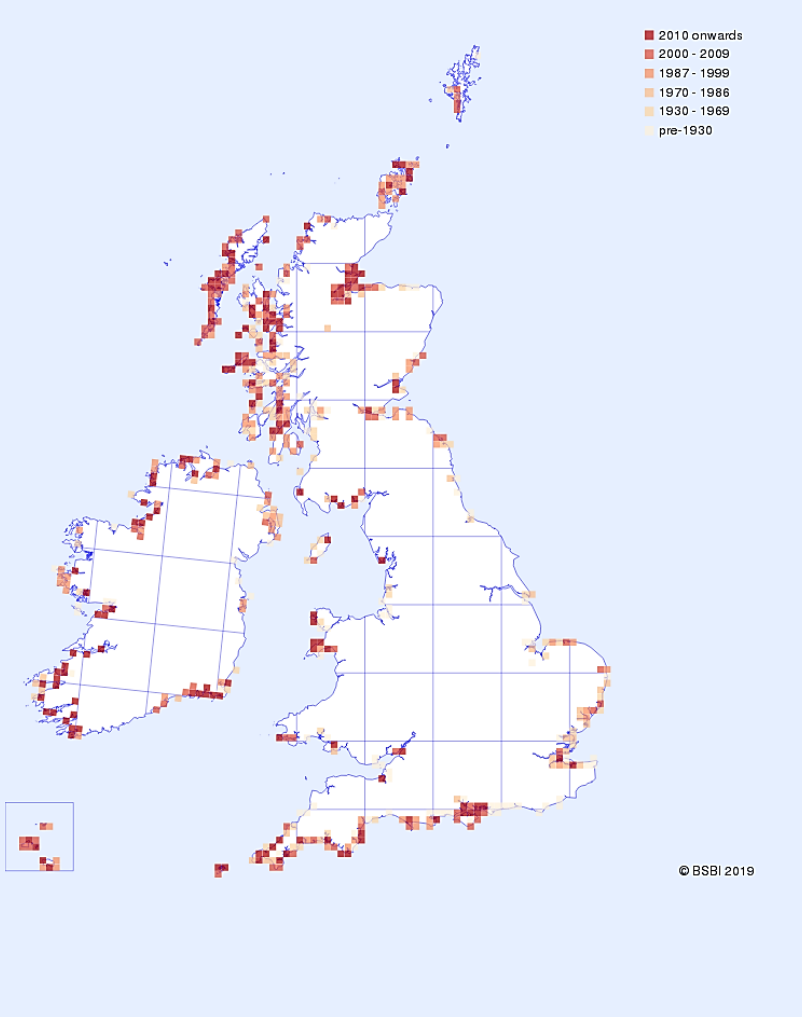


Figure 2-6: Distribution of *Zostera marina* meadows in the UK, based on recorded meadows dating from pre-1930's until present day. Source BSBI (2019), online.

Seagrass meadows were abundant around the UK, but their extent has been drastically reduced by 'wasting disease', which destroyed over 90% of *Z. marina* populations on the Atlantic coasts of Europe and the USA during the 1930's

(Muehlstein *et al*., 1988; Davison and Hughes, 1998). Following the outbreak of wasting disease, *Z. marina* was restricted to only the most sheltered sites, such as lagoons, and is now considered nationally scarce (Davison and Hughes, 1998; Jones and Unsworth, 2016). Since then, *L. zosterae* continues to affect seagrass meadows in the UK, possibly due to ongoing impacts and the poor dispersal capabilities of most species, but with no outbreaks as dramatic as the epidemic of the 1930s (Short *et al*., 1988). Unfortunately, seagrasses in the U.K. are in decline with estimates that at least 49% of UK seagrass coverage has been lost in the last 35 years (Hiscock *et al*., 2005).

Z. marina is declining globally, by approximately 1.4% per year, with large scale losses in some locations, particularly Europe and the east coast of the USA (Short *et al*., 2011). In the UK, only 20 among the 155 estuaries containing seagrass have *Z. marina* meadows larger than 1 hectare in extent (Hiscock *et al*., 2005; Marsden and Chesworth, 2015). This loss not only leads to a reduction of nursery and feeding habitat for commercially important and endangered species, such as plaice and Atlantic cod, but can also remineralise sedimentary C_{org} that has accumulated over long periods of time (Jackson *et al*., 2001; Peters *et al*., 2015). However, despite recognition by the European Union Water Framework Directive (EU-WFD) of seagrass as bio indicators for ecosystem health, research related to UK's seagrass habitats is lacking relative to other regions (e.g., Mediterranean and Australia) (Fourqurean *et al*., 2012a; Marba *et al*., 2013; Green *et al*., 2018).

North Atlantic seagrass meadows have recently been recognised for their biodiversity value by their inclusion in Marine Habitat Action Plans, and as a focal part of the UK Biodiversity Action Plan (Jackson *et al*., 2006; Marsden and Chesworth, 2015). Although intertidal seagrasses in the UK have recently been included in government programmes, these EU-WFD focused assessments do not assess environmental condition, and therefore provide very little information pertinent to the development of long-term management programs (Jones and Unsworth, 2016). To date, only results from the Isles of Scilly monitoring programme, a long-term study that provides detailed data of shoot morphology, density, disease and epiphytic content, present information pertinent to understanding the status of their seagrass meadows (Potouroglou *et al*., 2014; Jones and Unsworth, 2016). More specifically, there are few published estimates for the C_{org} stored in UK's seagrass ecosystems, apart from a recent study published by Green *et al*. (2018), investigating sub-tidal *Z. marina* meadows in England.

2.5 Summary

This review emphasises the role of seagrass meadows as important blue carbon ecosystems, with the potential to be included in climate change mitigation projects. The chapter critically identifies the need for further research on the potential of seagrass ecosystems as carbon sinks, highlighting the lack of studies in the UK, and the infancy of global research using direct estimations of sediment carbon stocks and sequestration rates. An analysis of future climate change impacts, not only globally but also specifically for the UK, is presented. These outline the impacts of climate change on coastal ecosystems, providing a source of information to establish a relationship between those events and seagrass carbon sequestration and storage potential. No assessment of the impact of historical weather events, like frequency of storm surges and flooding, as well as sea level rise, on seagrass carbon storage and sequestration rates has yet been conducted.

3 Study Area and General Methods

3.1 Study Area

The Isle of Wight and the harbours of Portsmouth, Langstone and Chichester are located on the south coast of England, and form an extensive coastal system containing two physiographic sub-types, coastal plain and bar-built estuaries (McLeod *et al*., 2005). The area is considered one of the most important coastal zones in the UK and consists of natural and man-made environments with high habitat diversity, providing an important wildlife resource internationally (King, 2010). Six fieldwork sites were selected within this area, one in Chichester Harbour, two in Langstone Harbour, one in Portsmouth Harbour, and two sites at the Isle of Wight (figure 3.1). Sites were selected following an assessment of the Hampshire and Isle of Wight Wildlife Trust's most recent seagrass distribution inventory (Marsden and Chesworth, 2015). The Wildlife Trust's inventory forms part of a greater enterprise, The Solent Seagrass Project, started in 2006, focusing on surveying and reporting the region's seagrass meadows, to promote public awareness and inform conservation (Marsden and Chesworth, 2015).

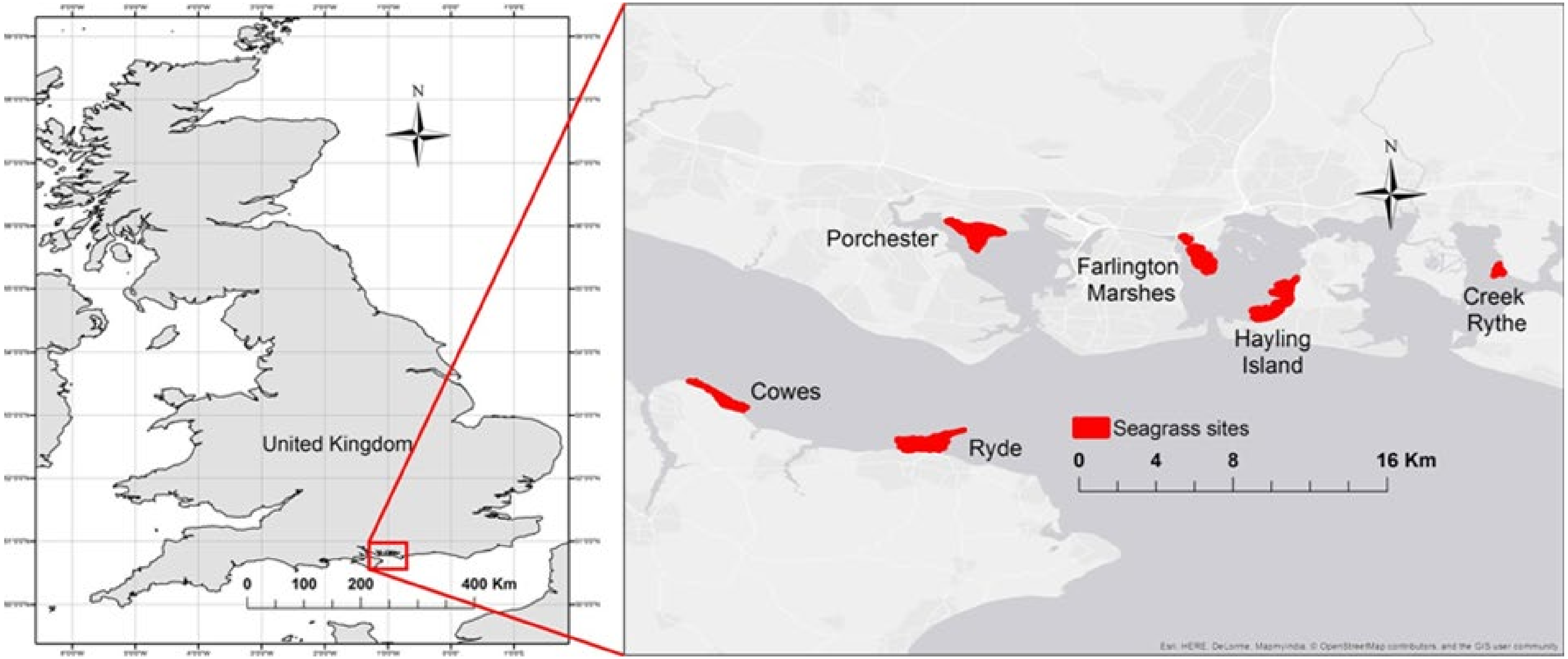


Figure 3-1: Location of the six seagrass sampling sites in the Solent, southern England (red square). Zoomed image shows seagrass sampling sites and their respective seagrass meadows areal extent in red, collated by Marsden & Chesworth (2015) Maps are adapted from Esri ArcGIS online basemaps, white lines represent roads

3.1.1 Site Characterisation

As a tidally dominated coastal complex, the harbours of Portsmouth, Langstone, Chichester and the Isle of Wight, comprise a series of coastal environments including intertidal mud and sand flats, extensive and scattered salt-marshes, and ecologically valuable coastal grazing marshes, supporting a range of species of national and international importance (Fletcher *et al*., 2007). Conservation projects like The Solent Waders, Brent Goose Strategy and the Solent Oyster conservation project, promote the implementation of site protection policies, including conservation of seagrass meadows (King, 2010; Harding *et al*., 2016). Moreover, the distinctive hydrographic regime and the intricacy of different habitats within the area, are some of the reasons why the region has been selected as a Marine Protected Areas (MPA) in the UK, including Special Protection Areas (SPA) and Special Areas of Conservation (SAC) (figure 3.2) (McLeod *et al*., 2005; MCS, 2019).

Figure 3.2: Top- Designated Special Areas of Conservation (SACs) highlighted in blue. Bottom – (a) Designated Special Protection Area (SPA) along the coast of the Isle of Wight. b) Special Area of Conservation (SAC), including Chichester and Langstone Harbours. Source: Marine Conservation Society (MCS, 2019).

The two Special Areas of Conservation (SACs) in the region are: the Solent and Isle of Wight Lagoons and The Solent Maritime (Harding *et al*., 2016). There are also three Special Protection Areas (SPAs) in the region, the Solent and Southampton Water SPA, Portsmouth Harbour SPA and Chichester and Langstone Harbours SPA, which form, together with the Solent Maritime SAC, the Solent European Marine Sites (EMS) (Harding *et al*., 2016).

The area has good transport links to the rest of the UK and Europe, which has resulted in the development of ports and industries, leading to an increase in population density in addition to the seasonal flow of tourists attracted to recreational resources along the coastline (King, 2010). This historical increase in anthropogenic activity, paired with land subsidence and resultant exacerbated rates of sea level rise in the region, make it ideal for the assessment of the impacts of global environmental change on seagrass meadows. The area also provides a range of different substrates, including sand flats and mudflats that provide a good range of comparable data across different seagrass ecosystems.

The Solent – a mesotidal estuarine strait situated in the central English Channel - has been categorised as one of the major sheltered channel systems in Europe, with unique oceanographic conditions (Marsden and Chesworth, 2015; Ozsoy *et al*., 2016). 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 paleochannel Solent River system (Fletcher *et al*., 2007). The low lying, low energy characteristics of the Solent's estuarine complex results in a shallow area of sea about 40km long, with a western width of 4km and 10km on the eastern end (Marsden and Chesworth, 2015).

The post-glacial flooding of the river valley and adjacent coastal plain formed 12 separately defined estuaries and natural harbours, the largest of which are Portsmouth, Langstone and Chichester (Marsden and Chesworth, 2015; Fletcher *et al*., 2007). A complex, interconnected, network of channels and creeks in the harbours drain a catchment of approximately 3000 km^2 through their linked intertidal basins, making the whole system function as a uniform body (Marsden and Chesworth, 2015; Fletcher *et al*., 2007). Spits and bars have been formed at the entrance of the harbours by the predominant eastward drift, leading to accumulation of sediment in these sheltered areas in the form of extensive mud and sand flats (Allen, 2009).

The land area surrounding the Solent and adjacent harbours is highly urbanised, with economic activities such as shipping, sailing, petrochemical refinery, fisheries, and marine aggregate extraction contrasting with the predominant agricultural aspects of the river basins (Marsden and Chesworth, 2015). Fletcher *et al.* (2007) estimated that over a million people live in the region, being attracted by its natural physical conditions and shelter provided by the Isle of Wight. More recent studies, however, report that one and a half million inhabitants live along the north coast of the Solent and adjacent harbours, predominantly in the cities of Portsmouth and Southampton, growing together with Gosport and Fareham to form the third largest metropolitan coastal area in the UK (Ozsoy *et al*., 2016). These two major cities, Southampton and Portsmouth, are major ports of national importance, with Southampton being a major commercial port offering services for bulk and fresh cargo, while Portsmouth has been a centre for Royal Navy shipbuilding since medieval times (Fletcher *et al.*, 2007).

A variety of anthropogenic radionuclides can be found in coastal sediments in the Solent region, derived from the global fallout from nuclear testing and accidental discharge with peaks in 1963, and 1986 for the Chernobyl accident, including Cesium (^{137}Cs), Plutonium (^{238}Pu) and Americium (^{241}Am), which can be used as markers of recent sediment accumulation rates in the region (Cundy and Croudace, 1996). Signs of eutrophication are also present in the adjacent harbours, Portsmouth, Langstone and Chichester, in the form of excessive macroalgal growth on mudflats, high levels of tri-butyl tin, other metals, and polycyclic aromatic hydrocarbons are also found (Cundy and Croudace, 1996; Marsden and Chesworth, 2015). Agricultural run-off is mainly responsible for the increased nutrient loading in the region, which has been consequently classified as a Sensitive Area under the Urban Waste Water Treatment Directive (Marsden and Chesworth, 2015).

As an area shaped by the sea, both from its physical environments and predominant economic and social conditions, the Solent and adjacent harbours is highly liable to be influenced by coastal flooding events (Fletcher *et al*., 2007). Percival and Teeuw (2012) indicated through predictive analysis that the city of Portsmouth and Havant Borough (Langstone) had the greatest risk of future high intensity coastal flooding in the region, which could directly impact coastal ecosystems in the region, like seagrass. The city of Portsmouth has 45km of open coastal frontage, making 47% of the city's area vulnerable to rising sea levels according to the Environment

Agency (Percival and Teeuw, 2012; Ozsoy *et al*., 2016). Conversely, 22% of the Borough of Havant's 48km coastline, mostly around Hayling Island and its southern half, have been reported as being the most sensitive area to sea level rise (Percival and Teeuw, 2012). Both sites have been included in this study given their economic and environmental importance, sensitivity to sea level rise, and coastal flooding.

3.1.1 Geology and Sedimentation

The estuaries of the Solent lie in the centre of the Hampshire Basin, being the latest of a series of shallow water bodies that have existed in the UK since the deep chalk sea-floor was uplifted, about 65 million years ago (Tubbs, 1999; LIFE, 2003). Solent estuaries were created during the Flandrian Transgression, which flooded the valleys of local rivers that had been previously excavated below present sea level during glacial phases of the Pleistocene (1.8 million years ago to 11,000 years ago) (West, 1980). Organic rich sedimentary deposits, that now exist beneath and around the modern estuaries and adjacent harbours, accumulated from a variety of plant and animal remains in shallow seas, lakes, and lagoons, during the Paleogene Period (Eocene and Oligocene, 65 to 24 million years ago) (West, 1980).

Historic sea level rise promoted erosion, caused by flooding events combined with wave activity, on shores facing open water like Portsmouth (Allen, 2009). More sheltered areas, particularly ones with predominant southwesterly winds, formed tidal mud-flats and saltmarshes from organic rich silty clay sediments deposited following sea level stabilization (Allen, 2009). The proportion of shallow areas gradually increased as the estuary has extended, showing that sedimentation has kept pace with rising sea level, however an equilibrium might not have been achieved yet from indications from continuous erosion (West, 1980; Dyer, 1980; Arch-Manche, 2014).

Holocene (Flandrian) deposits in the region range from marine shingle and sand to fine-grained, organic-rich sediments along more sheltered areas (West, 1980). Historic weathering and periglacial conditions in Southern England left thick deposits formed by solifluction, extending southwards (LIFE, 2003). An almost continuous belt of shingle and sand mixed with marine molluscs runs across the east Solent, being particularly thick on spits outside Porstmouth Harbour, reaching 21m depth (West, 1980). The offshore, exposed, area of the English Channel was the site of major fluvial, including river terrace, deposits (LIFE, 2003). Some organic rich sediments developed in river valleys prior to inundation by rising sea-level, including fluvial silty clays, peat, and calcareous tufa, while the uppermost deposits originated along or within estuarine waters (West, 1980).

Seismic profiling of the area has shown that most of the sediment is less than 2m thick, with longshore drift ruled by changes in the tidal cycle, establishing different sedimentation patterns (Dyer, 1980). Thicker sediments are found where the old river valleys have been filled, where a depth of 25m can be found (e.g. Calshot Spit) (Dyer, 1980).

Dyer (1980), reported four dominant sediment particle sizes after an extensive sampling of sea bed sediments including: gravel, coarse sand, medium sand, and clay. Recent studies found a clear relationship between the mean grain size and the stress from tidal flow velocity, with smaller grains being found under lower ambient current conditions (Arch-Manche, 2014). In general, rivers along the south coast of England have relatively small discharges and do not contribute much to deposition of fine-grained sediment (Velegrakis, 2000; LIFE, 2003).

Within the Solent and as far east as Chichester Harbour there seems to be a general influx of material into the deeper water areas, with sand and mud predominantly entering from the eastern end (Dyer, 1980; Allen, 2009). In sheltered estuaries and harbours of the region, considerable areas of intertidal mudflats can be found, some of which have been colonised by saltmarsh vegetation at higher elevations (Arch-manche, 2014). Coastal erosion is reported to be a significant source of mud sediment deposition, especially from the unlithified mud-rich Tertiary formations in the region (LIFE, 2003). Exposure to waves in littoral areas and beaches promote the predominance of gravel and bedrock, whereas on sheltered areas, the mouths of inlets have adjusted such that coarse sediment is swept outwards along the entrance channel or recirculated onto the beach (Dyer, 1980; Collins *et al*., 2000).

3.1.2 Hydrology

On average, maximum water depths along the western Solent are 10-15m and 10-20m at the eastern end, however, at a number of deeper bathymetric depressions, most commonly in the western Solent, water depths can reach 60m below Chart Datum (LIFE, 2003). Anthropogenic influences, like the construction of ports and Harbour developments, have led to historical dredging in the vicinities of the estuary to provide berthing, with the first reported commercial dredging dating from 1889, deepening the channel from Fawley to the Docks to 7.5m below present-day chart datum (Webber, 1980; Haigh *et al*., 2009; Wadey *et al*., 2012).

Other than anthropogenic influences, the overall bed configuration of the Solent has changed very little during the Holocene (Arch-Manche, 2014). Webber (1980) lists some of the local changes worth noting, including the recession of the low water mark on the mainland side of the west Solent and a landward swing of East Head spit in Chichester Harbour. The marked upward trend in relative sea level in the Solent region, although still not completely explained, suggests that crustal subsidence might have been occurring in this area for the past 4000 years, with varying types of land movement (Cundy and Croudace, 1996; Wadey *et al*., 2012).

The total catchment area draining freshwater into the Solent and adjacent harbours is approximately 3000km^2, with the Isle of Wight contributing to about 200km^2 of that total (Webber, 1980). The annual inflow of freshwater into the Solent, computed by statistical models of rainfall and evaporation, was of the order of 10^9m^3, equivalent to 1.4 x 10^6m^3 per tidal cycle, 10% of which is probably in the form of untreated sewage effluent discharge (Webber, 1980; Wadey *et al*., 2012).

Distinctive water temperature contributions in the Solent are provided by river and outfall discharges, with patterns of variation controlled by processes such as solar heating, evaporative cooling of the sea water influx, mixing of saline and freshwater and the thermal effect of the regular contact of sea water with intertidal mud flats, combined with warming derived from industrial outfalls (Carr *et al*., 1980). Changes in sea level largely controlled the form and extent of the region until progressive development and land reclamation began in the 18th century, especially in large urban centres like Portsmouth (Wadey *et al*., 2013). To date, meteorological induced sea level effects on the UK's South coast are generally less severe than on the East and West coasts; although surge events and Atlantic swells have been associated with coastal flooding (Haigh *et al*., 2011).

Coastal flooding in central southern England during the 20th and early 21st centuries has been frequent but usually involving low water depths (Ruocco, 2011). However, a national assessment of flood risk identified that the south coast of England would experience some of the largest increases in flood events during the 21st century, with Portsmouth presenting the greatest coastal flood risk for any city in the UK, after London and Hull (Evans, 2004; RIBA, 2009; Wadey *et al*., 2013). The risk of flood events in the region may become greater due to the marked upward trend in relative sea level reported for the region, matched with changes in the tidal regime, and a possible acceleration in crustal subsidence (Shennan, 1983; Emery & Aubrey, 1985; Woodworth, 1987; Shennan, 1989; Cundy and Croudace, 1996; Wadey *et al*., 2012). This subsidence trend has been confirmed by Cundy and Croudace's (1996) reported rate of sea level rise for the Solent of 4–5 mm year^{-1} since the early 1900's, indicating a substantial increase from previous estimations of 1–2 mm year^{-1}. However, the region is mostly sheltered from south-westerly Atlantic waves by the Isle of Wight, and a managed shingle barrier at the western end, known as Hurst Spit (Bradbury and Kidd, 1998; Wadey *et al*., 2012). Storm surges in the region mainly occur as a result of low-pressure systems that move from the Atlantic eastward over Southern England, or as a result of North Sea storm surge events transmitted into the English Channel through the Dover Strait (Haigh *et al*., 2014).

Tidl residuals in the region rarely exceed 1m, with only a 0.33 m difference between a 1 in 10 and 1 in 1000-year water-level (Haigh *et al*., 2009; Wadey *et al*., 2012). Tidal regimes in basin inlet systems can be represented by their main tidal constituents, where M_2 represents the amplitude of the principal lunar constituent, M_4 the lunar quarter-diurnal tide, and M_6 can be represented by cubing the semi diurnal tide (Aubrey and Weishar, 1988). Double high waters occur and are particularly pronounced during large spring tides, and at mid-flood tide the tide is constant for about an hour (Wadey *et al*., 2012). Tidal features of the Solent are considered one of the most complex in the world, being mainly controlled by tidal characteristics of the English Channel (Webber, 1980; Ozsoy *et al.,* 2016). The M_2 tide acts as the dominant tidal component along the English Channel, with tidal ranges between 6-10m, also acting as the main tidal forcing within the Solent (Quinn *et al*., 2012). What happens within the Solent depends on external tidal conditions as well as the hydraulic characteristics of the system, including physical configuration of the various estuarine alignments and the resistance flow that they might offer (Webber, 1980). The particular influences of the physical configuration of the region, including its irregular shape, narrow channel and average shallow depth, act to enhance the shallow water constituents of the M_4 and M_6 tides (Quinn *et al*., 2012).

Moreover, tidal streams of the West Solent are much faster (~4 knots) than in the East Solent (~2.5 knots), due to the closer proximity to a tidal node and smaller sectional area of the channel (Webber, 1980). Following an inverse pattern, mean spring tidal range increases from 2m in the west to 4m in east, while storm surges rarely exceed 1m, usually being related to low pressure systems from the North Atlantic spreading eastward through southern England (Ozsoy *et al*., 2016). Quinn *et al.,* (2012) state that at the Southampton tide gauge, for example, the M_2, M_4 and M_6 tidal constituent amplitudes are approximately 1.34, 0.24 and 0.17m respectively.

The unique tidal cycle in Southampton water shows a flow phase divided into two sub-phases, separated by a period of flood stand when the sea-level rise pauses, creating salck conditions throughout the water column (Ribeiro *et al*., 2004; Levasseur, 2008). These high water slacks remain for about two hours, due to the double high water before the ebb phase, creating the ebb dominance aspect of the tide, with tidal mixing more intense during the ebb tide, due to its higher velocities (Ribeiro *et al*., 2004; Levasseur, 2008).

The Solent has a well-known history of coastal flooding, such as when the extreme sea level events of 14th-18th December 1989 were responsible for the most extensive flooding in the area over the last half-century, generating a storm surge of between 0.5 m and 1.25m (Wadey *et al*., 2012; Ozsoy *et al*., 2016). In 1953, a notable storm surge impacted the area, resulting in significant loss of life (Quinn *et al*., 2012). Even though these extreme sea levels have frequently been exceeded since, advances in coastal defences across the area have prevented further flooding events or controlled the expected damage (Ozsoy *et al*., 2016).

Storm surges in this area are most frequently related to eastward propagation of low-pressure systems from the Atlantic, or as a consequence of storm surges propagating southwards from the North Sea (Quinn *et al*., 2012). Even though coastal flooding within the Solent is considered a frequent event, it usually involves small water depths and no loss of life (Quinn *et al*., 2012). However, under climate change predictions, the mean tidal range to the east of the Isle of Wight would increase, while decreasing to the west, with changes less than 5cm (LIFE, 2013). Accretion rates from saltmarsh cores from the area indicate that the rate of sea level rise over the last century for the Solent region ranges between 4-5 mm year^{-1}, showing a good relationship with short-term tide gauge data (Cundy and Croudace, 1996). These data suggest that an increase in the Solent's rate of sea level rise occurred prior to this century, increasing from 1.2mm year^{-1} to 4-5.5mm year^{-1} (Cundy and Croudace, 1996).

3.1.3 Sampling Sites

The six sampling sites selected for this study were: Creek Rythe (CRST) in Chichester Harbour; Hayling Island (LGST) and Farlington Marshes (FMST) in Langstone Harbour; Porchester (PMST) in Portsmouth Harbour, and the two sites at the Isle of Wight, Cowes (CWST) and Ryde (RYST) (figure 3.1 and Table 3). Permission to access the sites was obtained from the Hampshire and Isle of Wight wildlife trust before sampling collection. The selected sites, described in the sections below, encompass seagrass habitats from both muddy and sandy substrates, incorporating *Zostera marina* (Eelgrass), *Zostera noltii*, *Zostera angustifolia*, *Ruppia cirrosa* and *Ruppia maritima* (common Wigeonweed) meadows, thus providing comparable data between these habitats (Marsden and Chesworth, 2015).

Table 3-1:Sites Characteristics, including areal extension, as reported by Marsden and Chesworth, 2015, GPS coordinates, predominant vegetation, and main threats to 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

3.1.3.1 Chichester Harbour – Creek Rythe

The first record of seagrass beds in Chichester Harbour dates from 1915, with latest data recorded in June 2013 (Tubbs, 1999; Collins 2008; Marsden and Chesworth, 2015). Substrates are characterised by muddy sand and soft mud sediments, with patchy to dense seagrass coverage (Velegrakis, 2000; Marsden and Chesworth, 2015). The most recent seagrass survey in Chichester Harbour estimated coverage of approximately 100.24ha (2006-2013), with reports of significant decline due to past episodes of wasting disease and seasonal variation of leaf cover, increased during summer months (figures 3.1 and 3.3) (Marsden and Chesworth, 2015; MMO, 2019). This survey reported mainly the presence of *Z. marina* (including *Z. angustifolia)* and *Z. noltii*, but also mentions the presence of *Ruppia* spp. stands in intertidal beds. The inventory conducted at Creek Rythe, also reported patchiness with varied density, ranging from 10-80%, with no clear dominant species between *Z. noltii* and *Z. angustifolia*, while *Ruppia* spp. were found within the channels, sometimes extending into the saltmarsh (Marsden and Chesworth, 2015). Large amounts of *Ulva intestinalis* (gut weed or grass kelp) were also recorded in the area, mixed with seagrass beds (Collins, 2008; Marsden and Chesworth, 2015).

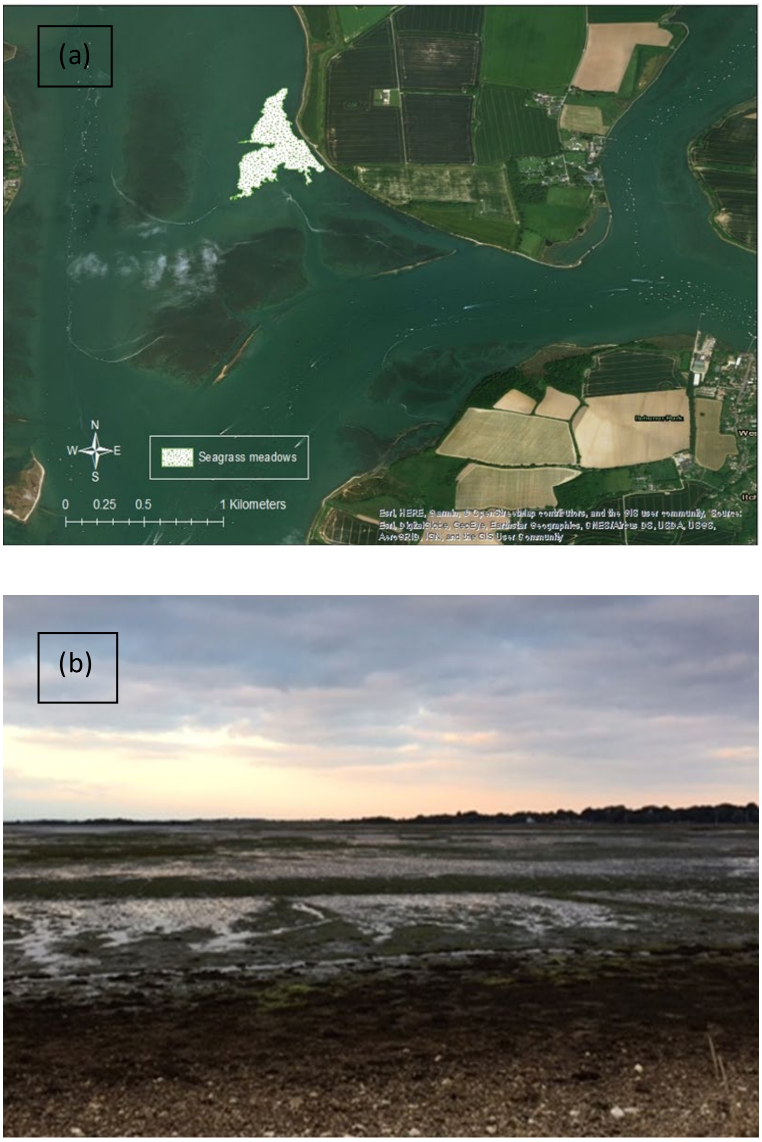


Figure 3.3: (a) - Distribution of seagrass meadows along Creek Rythe, in Chichester Harbour (Figure 3.1), as reported by Marsden and Scott (2015). (b) – Picture of Creek Rythe sampling site showing seagrass meadows at low tide (2017).

3.1.3.2 Langstone Harbour – Hayling Island and Farlington Marshes

Two sampling sites were selected in Langstone Harbour, one along the western shore of Hayling Island (figures 3.1 and 3.4) and the second by Farlington Marshes (figures 3.1 and 3.5).

Figure 3.4: (a) - Distribution of seagrass meadows along Hayling Island, in Langstone Harbour (Figure 3.1), as reported by Marsden and Scott (2015). (b) – Picture of Hayling Island sampling site showing seagrass meadows at low tide (2017).

Figure 3.5: (a) - Distribution of seagrass meadows along Farlington Marshes, in Langstone Harbour (Figure 3.1), as reported by Marsden and Scott (2015). (b) – Picture of Farlington Marshes sampling site showing seagrass meadows at low tide (2017).

The first record of seagrass beds in Langstone Harbour dates from 1956, with the most recent survey data recorded in September 2014 (Tubbs, 1999; Ralphs, 2004; Collins, 2008; Marsden & Chesworth, 2015). The substrate in the area is characterised by muddy sand and mud sediments, with dense seagrass coverage, estimated as 350 plants per m^2 (Velegrakis, 2000; Marsden & Chesworth, 2015). The most recent seagrass survey in the area estimated a coverage of approximately 117.48ha (2010-2014), with reports of significant decline due to past episodes of wasting disease and extensive trampling and dredging (Ralphs, 2004; Marsden and

Chesworth, 2015). Surveys in 2014 found that the largest seagrass bed previously recorded on Farlington Marshes in 2010 was no longer present, although a smaller bed to the north was still present, but had relocated. The survey also reported dense grass kelp, *Ulva intestinalis,* spread through the area, often with anoxic conditions below (Marsden and Chesworth, 2015).

Intertidal seagrass surveys along Langstone Harbour have been carried out on foot yearly since 2010, reporting mainly the presence of *Z. angustifolia* and *Z. noltii* beds, but also the presence of *Ruppia* spp. stands, all in intertidal areas (Ralphs, 2004; Marsden & Chesworth, 2015). Foot surveying around Hayling Island recorded *Z. noltii* dominating mid-tide levels and above, while *Z. angustifolia* dominated mid-tide levels and below (Collins 2008; Marsden and Chesworth, 2015). There is informal evidence that *Zostera* spp. used to be widespread in the area in the 1920's prior to the offset of wasting disease, however information regarding location is lacking (Butcher 1941; Tubbs, 1983; Ralphs, 2004; Marsden and Chesworth, 2015).

3.1.3.3 Portsmouth Harbour – Porchester

The first record of seagrass beds in Portsmouth Harbour dates from 1886, with the most recent survey data recorded in June 2014 (Marsden & Chesworth, 2015). The substrate is characterised by mud sediments, with patchy to dense seagrass coverage intertidal to shallow subtidal areas (Velegrakis, 2000; Marsden and Chesworth, 2015). The latest seagrass survey in the area estimated a coverage of approximately 94.92ha (2009-2014), with reports of significant decline due to extensive trampling and dredging and some evidence of anoxic conditions and smothering from dense filamentous green algal mats (figures 3.1 and 3.6) (Wicks, 2001; King, 2010; Marsden and Chesworth, 2015).

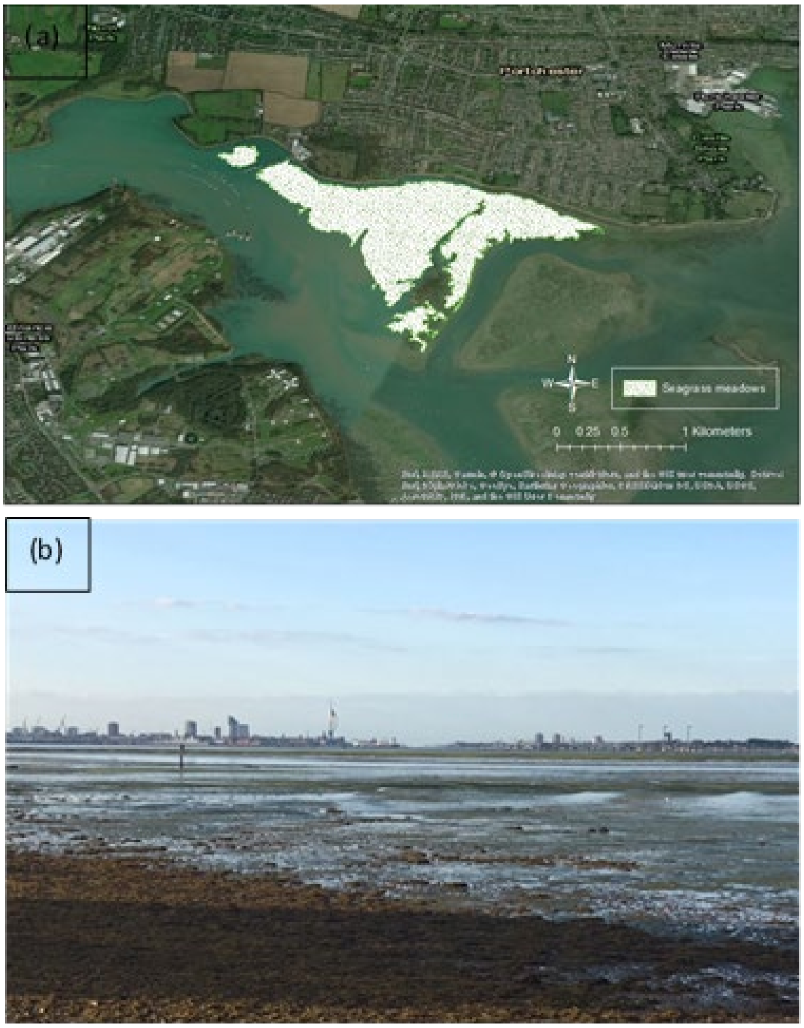


Figure 3.6: (a) - Distribution of seagrass meadows along Porchester, in Portsmouth Harbour (Figure 3.1), as reported by Marsden and Scott (2015). (b) – Picture of Porchester sampling site showing seagrass meadows at low tide (2017).

Intertidal seagrass surveys conducted in 2008 reported the presence of *Z. angustifolia* and *Z. noltii*, but also mention the presence of *Ruppia* spp. stands, all in intertidal beds (Marsden and Chesworth, 2015). Surveys in 2014 along the north of Bedenham pier reported predominance of *Z. noltii* patches on gravel along with clumps of *Z. angustifolia* (Marsden and Chesworth, 2015).

3.1.3.4 *Isle of Wight – Cowes and Ryde*

Two sampling sites were selected at the Isle of Wight, one in Cowes and another in Ryde (figures 3.1 and 3.7). The first record of seagrass beds in Cowes dates from 1979, with latest data recorded in 2008 (Cox, 2004; Marsden and Chesworth, 2015). The substrate along the Isle of Wight is characterised by gravel and soft to firm sandy mud sediments, with dense seagrass coverage mainly intertidal to shallow subtidal (2m below Chart Datum) (Velegrakis, 2000; Marsden and Chesworth, 2015). The most recent seagrass survey in the area estimated coverage of approximately 27.1ha (2008) (Collins 2008; Marsden and Chesworth, 2015).

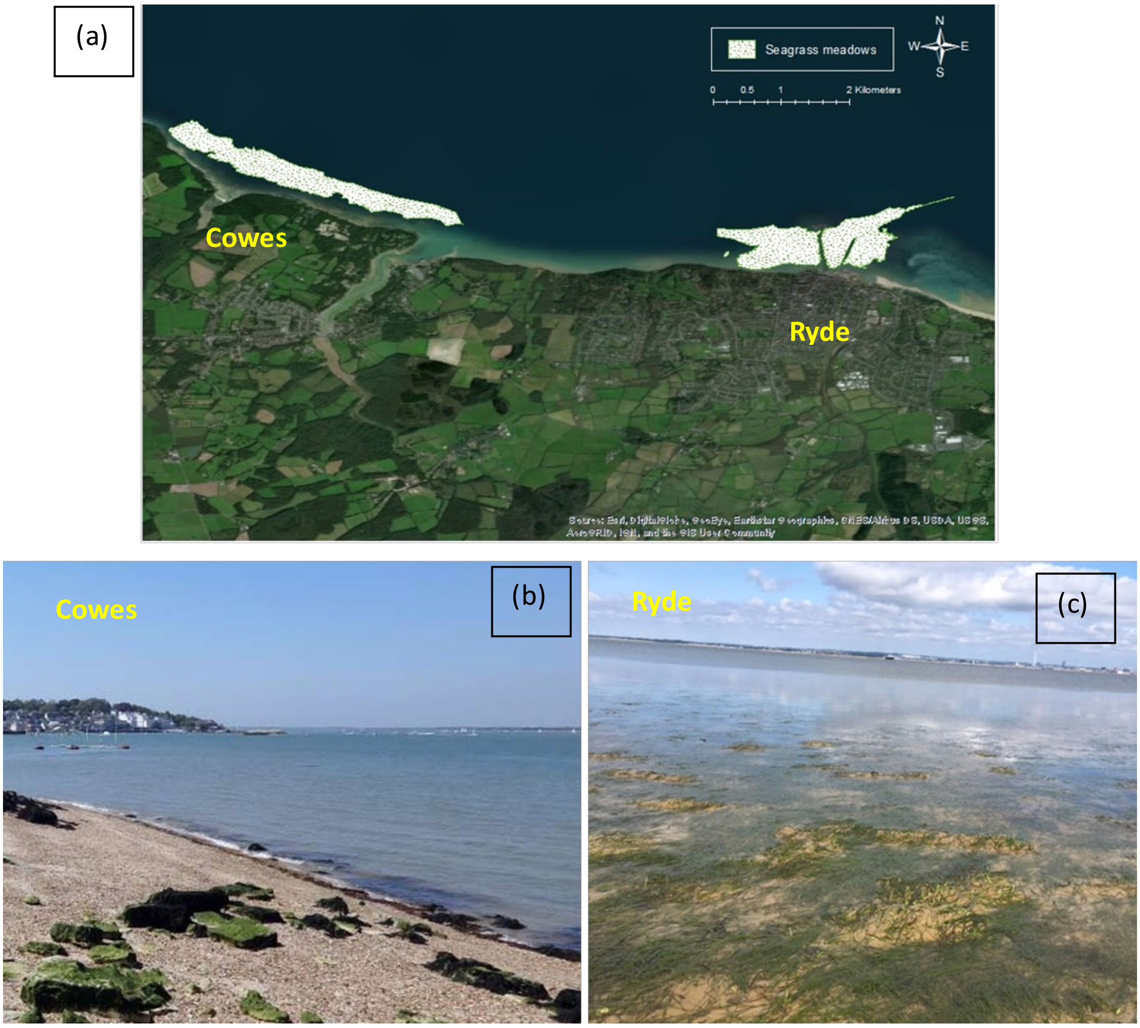


Figure 3.7: (a) - Distribution of seagrass meadows along Cowes and Ryde, at the Isle of Wight (Figure 3.1), as reported by Marsden and Scott (2015). (b) – Picture of Cowes sampling site, and (c) - Picture of Ryde sampling site showing seagrass meadows at low tide (2017).

The first record of seagrass beds in Ryde dates from 1977, and the most recent survey data was recorded in September 2014 (Tubbs, 1999; Marsden and Chesworth, 2015). The substrate in the area is characterised by soft to firm sandy mud sediments, with seagrass coverage ranging between 40-100%, estimated as up to 975 plants per m^2 (Velegrakis, 2000; Marsden and Chesworth, 2015). The most recent seagrass survey in the area estimated a coverage of approximately 82.47ha (2012-2014) (Marsden and Chesworth, 2015).

Surveys at both Isle of Wight sites reported the presence of *Zostera* spp. beds including *Z. marina* and *Z. noltii*, with possible indication of *Z. angustifolia* in Ryde (Cox, 2004; Collins 2008; Marsden and Chesworth, 2015). The 2010 Environment Agency survey in Ryde described shoot coverage of 20-100% in the 72 quadrats sampled, with no epiphytic growth observed on seagrass blades (Marsden and Chesworth, 2015).

3.2 General Methods

This section provides an overview of the general methodology applied to reach each objective. Detailed methods for each section are provided in their specific individual chapters. At all sites, the sampling of intertidal seagrasses was undertaken at low tide, during summer (June- August) in 2017 and 2018. The number of samples for total carbon stock (C_{stock}), at each site, was determined after a preliminary sampling effort, described below, resulting in a minimum optimum number of five sampling point per site, 30 (5x6) in total. A preliminary study was also conducted to determine the optimal temperature and exposure time for the loss in ignition (LOI) method applied to measure organic carbon content in sediment samples, further described below.

From each of the thirty randomly selected sampling points, the following samples were collected during the summer of 2017: Above-ground biomass in the form of cropped leaves within a $0.25m^2$ quadrat; one, 1m deep, sediment core for carbon stocks and particle size analyses; one, 50 cm deep, sediment core for below-ground biomass analyses (figure 3.8). In addition, two, 50cm deep, PVC sediment cores were also collected from two of the five seagrass sampling points, for carbon sequestration analyses using radionuclide dating, for all six sampling sites. The same sampling points were revisited the following year, 2018, to collect one, 30cm deep, sediment core for pore water analyses (figure 3.8). Furthermore, five, 1m deep sediment cores were collected from random points on adjacent un-vegetated mudflats from all sampling sites, apart from Cowes, where they did not occur, for carbon stocks analysis (figure 3.8).

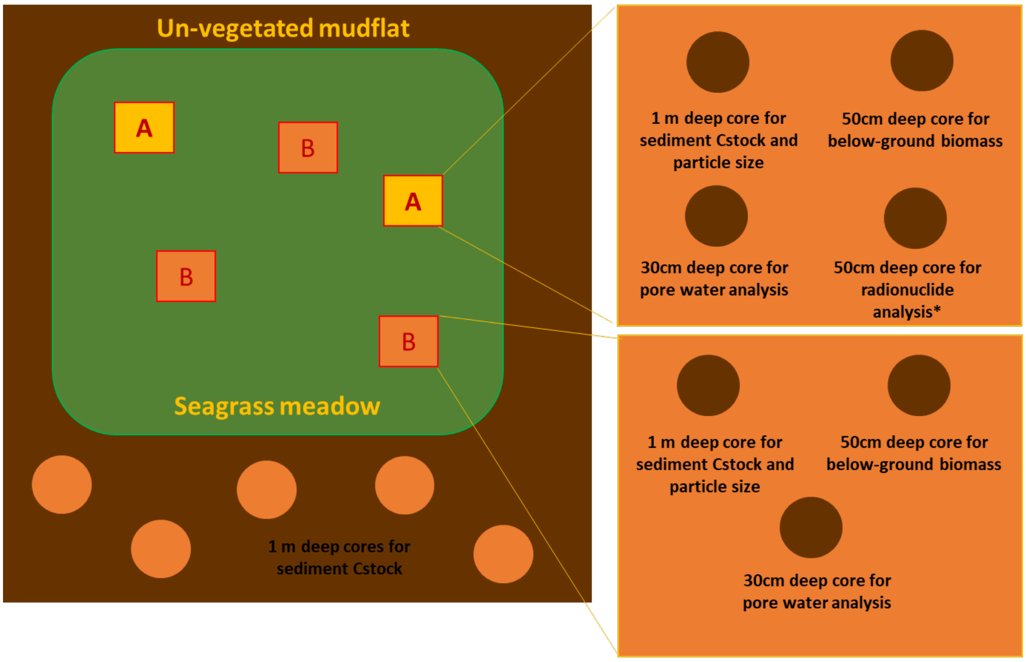


Figure 3.8: Diagram representing five sampling points within selected seagrass meadow sites and five points within neighbouring un-vegetated mudflats. A and B, represent 0.25m^2 quadrats used for above-ground biomass sampling, including: one, 1 m deep sediment core for Cstock analysis, one 50cm deep sediment cores for below-ground biomass analysis, and one 30cm deep sediment core for pore water analysis. Quadrats A, specifically, also included an additional 50cm deep core for radionuclide analyses.

A dGPS (Leica GPS1200 Surveying System) was used to record latitude, longitude, and elevation in relation to mean sea level data values within all sampling points, with ten recordings within each quadrat (25 cm^2) (vertical accuracy, 0.02 m) (Ward *et al.*, 2016). Elevation data were recorded to take into account inundation frequency and duration. 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). GPS points obtained in 2017 were used to revisit the same sampling points in 2018.

3.2.1 Statistical analyses

All statistical analyses were performed with Minitab 17 and all results assume a 95% confidence interval (α = 0.05). Statistical tests applied thought this study are listed below and will be individually described in specific chapters.

3.2.1.1 Normality test

Normality probability plots and histogram frequency of residuals were tested using the theory-driven Anderson-Darling (AD) method for each variable (Anderson and Darling, 1954). The AD test compares the empirical distribution function of the data giving more weight to the distribution tails (Farrel and Stewart, 2006; Razali and Wah, 2011). AD has been classified as one of the most powerful normality tests, comparable with Shapiro-Wilk, which is less robust for small sample sizes (<30) (Razali and Wah, 2011).

3.2.1.2 Analyses of Variance

ANOVA (one or two-way), was used as a parametric test, to identify significant differences between sampling sites (Conover and Iman, 1981). If the assumption of normality of residuals tested by AD, required to perform ANOVA, was not met, mean values were previously transformed using Log_{10} (X). As explained by Kozak and Piepho (2018), the assumption of normality for ANOVA should be checked with residuals, since raw data might display heterogeneous variance between means even when variance of errors are constant. Thus, residual diagnostic plots from the fitted model are the most suitable way of checking ANOVA assumptions (Kozak and Piepho, 2018). A post-hoc Tukey's HSD test was used to identify significant differences between groups (Tukey, 1973).

3.2.1.3 Difference between means

Two-sample and paired T-tests, in the case of paired observations, were used as parametric tests on normal, or previously transformed, data to analyse difference between two groups of means.

3.2.1.4 Correlation tests

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. Additionally, a regression model was developed to establish linear regression equations to determine outcome dependent, variables, using predictor variables.

3.2.1.5 Multivariate tests

A Partial least squares (PLS) multivariate regression 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 then 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} between sites (ter Braak, 1986; Marin-Guirao *et al*., 2005). This technique explains the maximum amount of variance with the fewest number of components, reducing data dimensions to identify a smaller number of uncorrelated variables (principal components) which are linear combinations of the observed factors (Jenerette, *et al*., 2002; Marin-Guirao *et al*., 2005).

3.2.2 Carbon stocks Analyses

To analyse C_{stocks} in seagrass meadows, studies should measure the C_{org} stored in the: (i) above ground (plant tissue, a minor component) and below ground (roots and rhizomes) biomass; and, (ii) sediment, including organic (bacteria, microalgae, macroalgae and detritus) and when relevant, inorganic (carbonates) components (Macreadie *et al*., 2014). Living biomass C_{stock}, although minor in comparison to sediment C_{stocks}, can be a good parameter to determine changes in biomass and abundance, representing periodic changes in C_{stock} over time (Macreadie *et al*., 2014).

Macreadie *et al*. (2014) evaluated different methods to assess seagrass carbon stocks, listing core sampling as the best to determine above and below ground, as well as sediment C_{stocks}, since it captures all components. However, most coring work included in seagrass C_{stocks} research have used short cores, since long (≥1m) cores can be hard to obtain, especially for subtidal species (Macreadie *et al*., 2014). Using short cores, although simpler and inexpensive, only provides shallow C_{stock}

observations, whereas deeper cores can give better results regarding site history and stocks, including long-term, millennial scales (Macreadie *et al*., 2014). Therefore, for the purpose of this study, 1 m deep (or to refusal) cores have been collected for C_{stock} analysis.

The minimum number of sampling points required to provide sufficient accuracy can vary depending on the project's goals. For example, assessments to determine national or regional seagrass carbon stocks require relatively lower sampling density, covering extensive areas, than carbon market projects, which need a higher degree of precision and increased sampling effort (Howard, *et al*., 2014). Due to the lack of previous carbon stocks data from the study area, it was difficult to estimate sediment carbon and biomass variability, and consequent uncertainty, therefore, this pioneer assessment can be used as a proxy to determine variance associated with each sampling site.

Therefore, temporary plots were randomly selected, 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). However, the D-GPS location of each plot was determined, not only to evaluate elevation data, but also to allow a revisit of the same sampling location during the summer period of 2017. Variation in seagrass patches within the meadows on each site was very limited, based on naked eye 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 and minimising disturbance to the habitats (Howard, *et al*., 2014).

A preliminary sampling effort field study was conducted in Creek Rythe – Chichester Harbour, the most diverse of the sites, to determine the optimum sampling number to representatively assess C_{stock} in seagrass meadows from the studied sites. Ten, 1m deep (or to refusal), cores were collected in December 2016, from randomly selected sampling points, following Howard *et al*.'s (2014) methods. Mean sediment C_{stock} (MgC ha^{-1}) for each core was estimated, using the loss on ignition (LOI) methods, described below, and compared between 2, 3, 4, 5, 8 and 10 cores, using ANOVA, since AD results showed that samples were normally distributed (AD= 0.788; p= 0.037). There was no significant difference between the grouped means when compared by ANOVA (p = 0.909, n= 6), against the groups of cores analysed: N2, N3, N4, N5, N8 and N10 (figure 3.9). However, groups with smaller number of cores, such as N2, N3 and N4, showed skewed distribution of mean C_{stock} values, therefore, based on this result, it was established that the optimum number of sediment cores that would effectively and significantly represent the mean organic carbon content of the study sites would be 5, to perform robust statistical tests (figure 3.9).

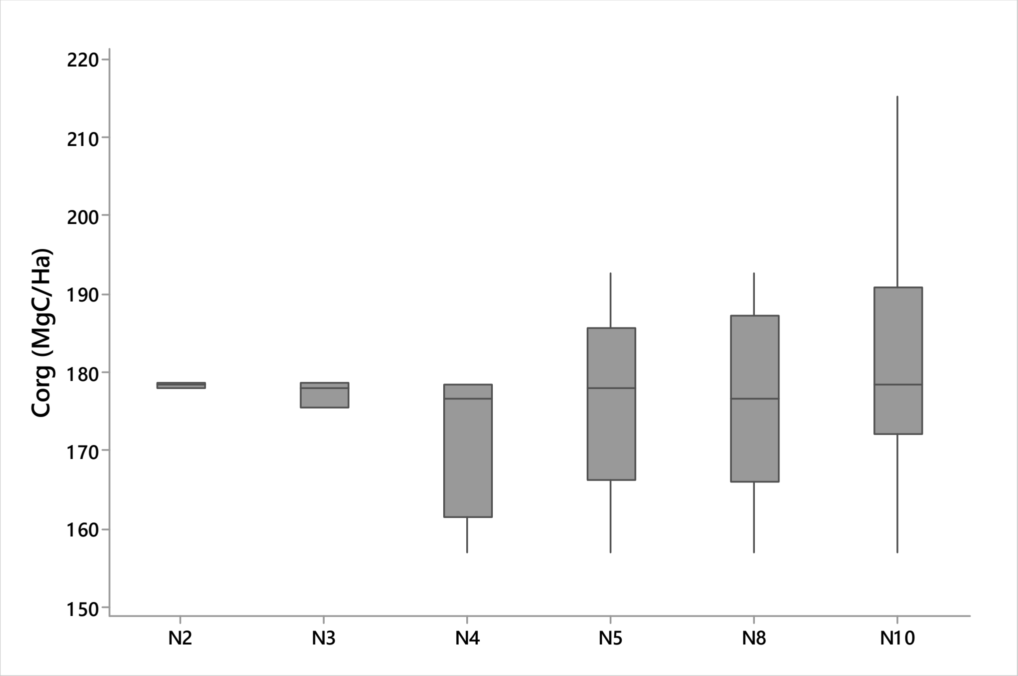


Figure 3.9: Cumulative means for sediment C_{stocks} (MgC ha^{-1}) cores collected from Creek Rythe, in December 2016. Progressively increasing number of cores (N) per sample, where N2 = average C_{stocks} between two cores, N3 = average C_{stocks} between three cores, N4 = average C_{stocks} between four cores, N5 = average C_{stocks} between five cores, N8 = average C_{stocks} between eight cores, N10 = average C_{stocks} between ten cores. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

3.2.2.1 Living above-ground and below-ground C_{stock}

According to Howard *et al.* (2014), seagrass plot size should be directly proportional to species size, with larger species like *Posidonia* spp requiring bigger (~ 1 m^2) plots than *Halophila* spp or *Zostera* spp (~0.25m^2). Living above-ground biomass samples were collected when the standing stocks are greatest, during summer months, by cropping the living biomass (leaves to stem base) from five marked quadrats (0.25 m^2) (Howard *et al.*, 2014). Belowground living biomass has been suggested as representing only 0.3% of the total carbon pool found below the surface in seagrass beds (Fourqurean *et al.*, 2012a). Litter components in seagrass meadows typically consists of dead leaves, rhizomes, fruits, and algae. In most seagrass meadows the contribution of litter to carbon stock is minimal, due to the high remineralization efficiency of leaves as well as export through hydrodynamic energy (Howard *et al.*, 2014). Therefore, litter carbon content was not measured in this study.

3.2.2.2 Sediment C_{stock}

The largest carbon pool in seagrass ecosystems is the sediment carbon stock, with variation of carbon content described as most significant in the upper 20 to 50cm of sediment (Fourqurean *et al.*, 2012b). Therefore, sediment samples were collected using a Russian gouge corer, with a 0.5m section length. Coring was done in two stages; first, the surface to 50 cm sample, followed by a deeper, 50-100cm (or to refusal) sample on the same spot. For a more detailed depth profile, subsamples were taken every 5 cm to a depth of 50 cm, followed by one larger 50 cm subsequent subsample, between a depth of 50-100 cm (Howard *et al.*, 2014).

To accurately determine the sediment carbon density, sediment dry bulk density and organic carbon content (C_{org}) were identified, using the methods further described in chapter 4.

To calculate sediment organic carbon, sequential Loss on Ignition (% LOI) was chosen as the most suitable method, given the equipment availability and budget constraints. Using other methods reported in the literature, like automated elemental analysis or wet chemistry (Walkley-Black method – H_2O_2 and Potassium Dichromate Digestion) could have some advantages, like allowing a more accurate quantitative measurement of carbon content for the first method and the low cost and absence of equipment requirements for the second (Howard *et al.*, 2014). However, studies report LOI as a reliable and inexpensive method to access C_{org} in sediments, showing strong relationships with quantitative values found via elemental analysis (Fourqurean *et al.*, 2012b).

LOI can be broken down into stages, namely when organic matter is oxidized to carbon dioxide and ash up to 500-550 ºC, and when carbon dioxide is evolved to carbonate at 900-1000 ºC, leaving oxides as a product (Henri *et al.*, 2001; Wood, 2015). Consequently, overestimated loss of mass during LOI can be problematic in samples with high concentrations of calcium carbonate, or from dehydration of clay minerals or metal oxides (Henri *et al*., 2001; Fourqurean *et al*., 2012b). It has been reported in the literature that loss of structural water from clay minerals (dewatering) happens at temperatures > 450 ºC (De Vos *et al*., 2005; Salehi *et al*., 2011; Wood, 2015). Conversely, loss of volatile salts, metal oxides and loss of CO_2 from carbonates have been reported at temperatures ≥ 500 ºC (Henri *et al*., 2001; Wood 2015).

Therefore, even though organic matter can still be decomposed up to 550 ºC, such high temperatures can cause overestimation of total organic carbon TOC, and are mostly suitable for predominantly organic samples, with small clay mineral fractions (Wood, 2015). Adopting LOI procedures with lower ignition temperatures can provide a solution to avoid TOC overestimation, as demonstrated by Davies (1974), who tested the use of LOI for 24h at 430 ºC and found good results compared to the Walkley-Black chemical digestion method (Wood, 2015). Carbonates purposely added to the samples on the aforementioned study were also intact after ignition, showing that at low temperatures (< 500 ºC), no previous treatment for carbonate removal is required (Davies, 1974; Schulte and Hopkins, 1996; Wood, 2015). Thus, it is important to check and determine ignition temperature carefully for organic matter determination, making it suitable for the type of sediment analysed (Henri *et al*., 2001). Studies suggest that heating seagrass sediment at 450 °C for LOI has been found to correlate well with estimation of C_{org} in seagrass meadows, therefore being adopted as an alternative, and inexpensive method (Fourqurean *et al*., 2012b; Macreadie *et al*., 2014). Therefore, for the purpose of this study, and to provide the most reliable results, a range of ignition temperatures and exposure times were preliminarily tested using the sediment cores collected from Creek Rythe in December 2016, to identify which LOI method would be most suitable and cost effective (table 3.1).

Table 3-2: Temperature and Exposure times for Preliminary LOI tests performed on sediment core samples from Creek Rythe, collected in December 2016.

Temperature ºC		Exposure Times (h)	
360	6	8	24
400	6	8	24
450	6	8	24

LOI temperatures and exposure times were tested using two-way ANOVA, results from this test showed that the organic matter content (%OM), calculated using the methods described in chapter 4, using 450 °C temperature was significantly higher than 360 °C and 400 °C, for all exposure times (6h; 8h and 24h), when compared with Tukey's pairwise grouping analysis (table 3.2).

Table 3-3: Summary of statistical results for two-way ANOVAS, with temperature (°C) and Exposure time (h). Where Df represents the degree of freedom, p significance value for two-way ANOVA $p<0.05$, AD (p) Anderson-Darling test for normality result ($p<0.05$).

Parameter	Df	F	p	R-sq	AD (p)
Temperature (°C)	2	89.76	0.000	91.97	0.546 (0.145)
Exposure time (hours)	2	0.35	0.712		
Interaction (Temp*Hours)	4	6.48	0.002		

Moreover, there was no significant difference between %OM at 450 °C, for all burning times tested. However, as the mean %OM values using 450 °C were slightly higher than the other two temperatures (figure 3.10), it was decided that the time and temperature combination of 450 °C for 24h would be most representative for %OM on all samples and therefore used in this study.

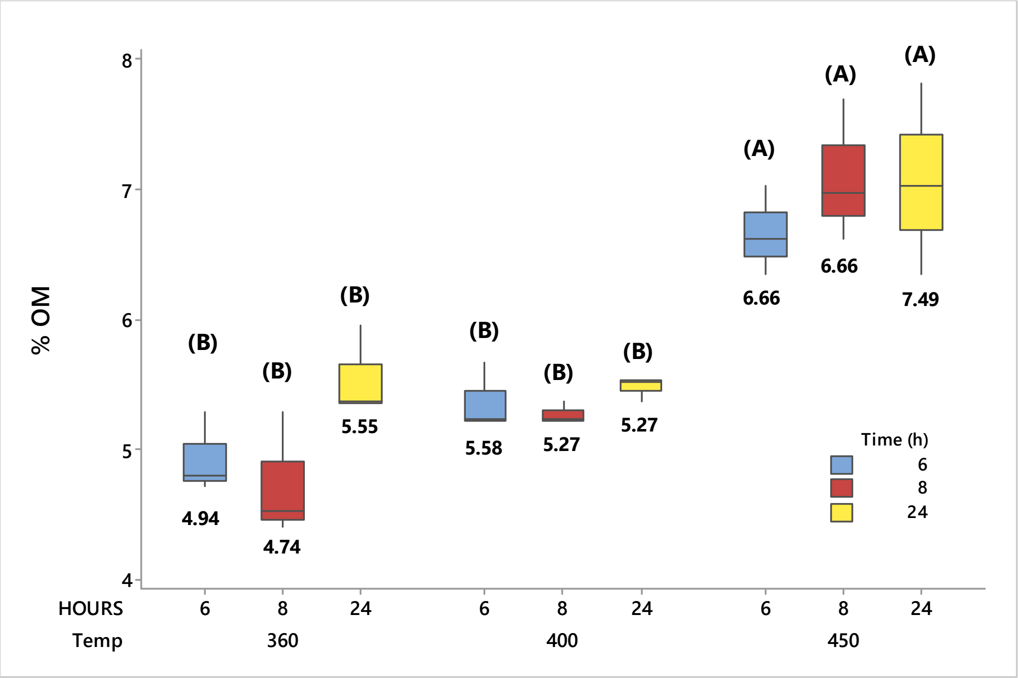


Figure 3.10: Average %OM tested under different LOI temperatures (°C) and exposure times (h), including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold. Median line represented in the 50% interquartile boxes, and whisker lines representing minimum and maximum 25% values range.

Standardising samples should be a practice, even though sample volume and mass are not essentially described in LOI methods, as it has been shown that an increase in sample size could lead to a reduction in TOC estimation by LOI (Henri *et al*., 2001; Wood, 2015). Therefore, oven dried samples used for LOI were disaggregated carefully with a pestle and mortar and weighed into individual beakers, 2-4g for each sample, before being placed in the muffle furnace.

Macreadie *et al*. (2014), also listed complementary laboratory analysis available as methods for C_{stocks} estimations, including radio-isotope dating; sediment particle size and elemental analysis to determine C:N:P ratio. Alternatively, stable isotope ^{13}Carbon can also be used as a method to identify C_{org} sources in seagrass sediment, when access to an isotope-ratio mass spectrometer is available (Kennedy *et al*., 2010; Macreadie *et al*., 2012; Macreadie *et al*., 2014). Furthermore, seismo-acoustic sounding can be a useful, albeit expensive, method to provide an accurate and high-resolution estimation of the depth and extension of the seagrass meadow, reducing the number of core samples needed for C_{stocks} quantification (Lo Iacono *et al*., 2008; Macreadie *et al*., 2014).

Due to the wide range of reported ratios of carbon content (% C_{org}) to % OM for seagrasses in the literature, it was best to determine the ratio for the particular sediment samples from this study, to obtain a more suitable conversion factor, rather than standard literature values. In order to obtain this ratio, a total of 45 sediment subsamples, were selected to be sent for C:N elemental analyses, providing data to develop a C_{org} conversion factor for seagrass sediments in the Solent region. Further detailed in chapter 4.

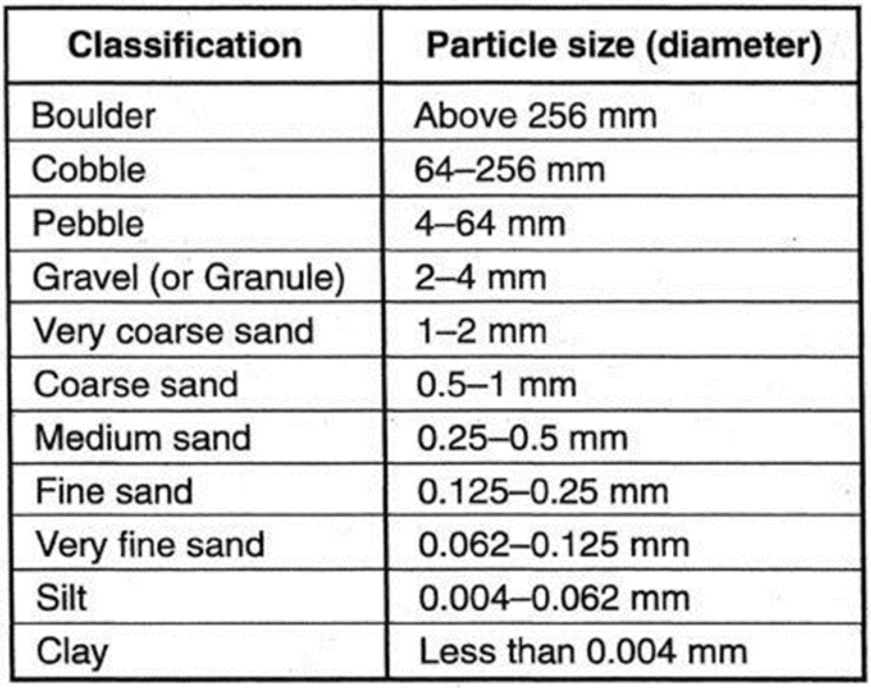
Furthermore, for cores deeper than 50cm, but that did not reach 1m depth, values for sediment C_{org} were assumed as constant and equal to the bottommost sample values up to 1m (Fourqurean *et al*., 2012b). Average sediment C_{stock} were assessed for each sampling site, and scaled up derived from the sampling area, based on seagrass area data from Marsden and Chesworth, (2015).

3.2.3 Particle Size Analyses

Seagrass meadow canopies are known to reduce water velocity and facilitate sedimentation processes, consequently promoting an increase in the number of fine particles in their sediments, enhancing carbon storage (Dahl *et al*., 2016; Potouroglou *et al*., 2017). It has been reported that sediment grain size can influence the aggregation of organic particles in coastal environments, with a positive relationship between finer grain size and sediment organic matter content (Mayer, 1994; Dahl *et al*., 2016; Mazarrasa *et al*., 2018). Grain size and degree of sorting also correlates with sediment density and porosity, influencing redox conditions in the sediment and consequent organic matter decomposition rates (Dahl *et al*., 2016).

Grain size is determined by measuring three particle axes that compose the three-dimensional shape of a particle (Bunte and Abt, 2001). Sediment size gradation can be classified into six major categories, following the Wentworth (1922) scale: boulders (256 – 4096 mm); cobbles (64 – 256 mm); gravel (2 – 64 mm); sand (0.063 – 2 mm); silt (0.0039 – 0.063 mm) and clay (0.00024 – 0.0039 mm) (table 3.3) (Wentworth, 1922). Seagrass species, like *Z. marina* for example, have been found in a wide range of substrates, from coarser gravel-sand to finer silt and clay sediments (Dahl *et al*., 2016).

Table 3-4: Scale of sediment particle sizes classification according to Wentworth, (1922).



Classification	Particle size (diameter)
Boulder	Above 256 mm
Cobble	64–256 mm
Pebble	4–64 mm
Gravel (or Granule)	2–4 mm
Very coarse sand	1–2 mm
Coarse sand	0.5–1 mm
Medium sand	0.25–0.5 mm
Fine sand	0.125–0.25 mm
Very fine sand	0.062–0.125 mm
Silt	0.004–0.062 mm
Clay	Less than 0.004 mm

To measure and classify a sediment a few descriptive analyses must be made, including mean particle diameter (MPD), particle size frequency and cumulative distribution, as well as standard deviation and sorting coefficient (Bunte and Abt, 2001; Gray and Elliot 2009). The cumulative distribution curve for a sediment is given by percentile values, where the percentile represents the “percentage finer than” a particular grain size (i.e., D_{25} is the particle size for which 25% of the distribution is finer) (Bunte and Abt, 2001). The most commonly used percentiles for grain distribution analysis are D_{50} (median); D_{25} and D_{75} (quartiles); D_{16}; D_{84}; D_{5} and D_{95} (Bunte and Abt, 2001).

Additionally, the sorting coefficient represents the degree of mixing of different grain sizes, with well sorted, more homogenous, sediments occurring in low energy areas (wave and current activities) and poorly sorted, heterogeneous, sediments, found in high energy areas (Gray and Elliot 2009). The standard deviation (σ) will express the spread of the particle size data set, otherwise known as the degree of sorting (table 3.4) (Folk and Ward, 1957; Bunte and Abt, 2001). Assuming a normal distribution, one standard deviation from the median includes all data between D_{16} and D_{84}, therefore, for this study, those percentiles were used for mean particle size and degree of sorting calculations (Bunte and Abt, 2001).

Table 3-5: Degree of sorting classification (Folk and Ward, 1957)

Sorting Coefficient (φ)	Classification
> 4	extremely poor
2 - 4	very poor
1 - 2	Poor
0.71 - 1	moderate
0.50 – 0.71	moderately well
0.35 – 0.5	well
< 0.35	very well

Therefore, 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. 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 of 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 sound waves (Malvern Instruments, 2007). 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) for each sample were calculated following the arithmetic approaches further described in chapter 4, assuming particles sizes in φ units (Folk and Ward, 1957).

3.2.4 Pore Water Analyses

Pore water variables, including concentration of nitrites and sulphates, salinity (super saturated solution) and pH (super saturated solution) were analysed. Further details are described in chapter 5.

Studies investigating the effects of biotic (e.g. microbial cycling and grazing) and abiotic (e.g. redox potential, salinity and waves exposure) factors on seagrass carbon storage and sequestration potential, typically focus on the top (brown – oxygen rich) layers of sediment (Enriquez *et al*., 2001; Dahl *et al*., 2016; Macreadie *et al*., 2014; Miyajima *et al*., 2015; Röhr *et al*., 2016; Serrano *et al*., 2016; Röhr *et al*., 2018). This is 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). For this reason, this study investigates the effects of biotic and abiotic factors on seagrass carbon stocks in the top 30cm (rhizosphere) layer of sediment from the selected sampling sites, or until refusal. Therefore, five, 30cm deep, sediment cores were collected from each sampling site, to perform this analysis (figure 3.8).

Furthermore, 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, even though seagrasses, like most rooted aquatic plants, might uptake nutrients from the water column through their leaves, root uptake from sediments is considered the predominant nutrient source (Carignan & Kalff 1980; Barko & Smart 1981; Fourqurean *et al*., 1992; McGlathery *et al*., 2001).

3.2.5 Carbon sequestration rates

Sequestration rates for seagrass meadows should consider the levels of submergence of the habitats, the effects of water and sediment chemistry in carbon remineralization processes and sediment accretion rates (Villa and Bernal, 2017). Additionally, determination of mean carbon sequestration rates is partially dependent on the timescale of interest and the dating methods used (Arias-Ortiz *et al*., 2018a). Sediment radionuclide dating readings can be a useful tool to determine carbon sequestration, by assessing sediment accretion rate coupled with the amount of C_{org} per dated section, providing long term accumulation data (up to 150 years) (Duarte *et al*., 2011; Villa and Bernal, 2017). Depending on the habitat, sediment accretion rates can be measured directly, by using markers like brick dust, glitter, and sand to create visible horizons, or via radionuclide dating methods (Harter and Mitsch, 2003; Villa and Bernal, 2017).

Common dating techniques include those using radioactive isotopes of lead (^{210}Pb), carbon (^{14}C), as and for Cesium (^{137}Cs) (Duarte *et al*., 2011; Villa and Bernal, 2017). The decay rates of these radionuclides are well known, with half-lives (time for half of the original amount to be undecayed) of ^{210}Pb and ^{14}C established at 22.26 and 5730 years, respectively (Duarte *et al*., 2011). Therefore, radiocarbon dating can be useful to provide age estimations of much older coastal sediments (58,000-62,000 years), whilst ^{210}Pb dating is the most widely utilised method for more recent (~100 years) sediment profiles (Wise,1980; Thompson *et al*., 2001; Teasdale *et al*., 2011; Duarte *et al*., 2011; Ward *et al*., 2014).

Due to the relatively long integration period (decades to a century), mean ^{210}Pb-derived carbon sequestration rates estimates are not affected by inter annual variability, hence allowing for the assessment of shifts in carbon accumulation from the "baseline" condition (such as the C_{org} that cycles naturally through an ecosystem (Howard *et al*., 2017; Arias-Ortiz *et al*., 2018a). The ^{210}Pb technique was first applied by Koide *et al*. (1972) to date marine sediments.

3.2.5.1 210Pbtotal, 137Cs and 214Pb activities profiles

The ^{210}Pb method is based upon the assessment of $^{210}Pb_{excess}$, unsupported ^{210}Pb from the decay of atmospheric ^{222}Rn (Radon), deposition into the accumulating sediment (Ward *et al*., 2014; Villa and Bernal, 2017). Total ^{210}Pb within sediment profiles is calculated by the sum of this 'excess' activity and the 'supported', natural in-situ, radioactive ^{210}Pb decay activity (Mackenzie *et al*., 2011; Ward *et al*., 2014; Villa and Bernal, 2017). The supported ^{210}Pb component is usually measured via direct assessment of ^{226}Ra activity, and the daughter radionuclides ^{214}Bi and/or ^{214}Pb, combined with estimation of constant ^{210}Pb activity per depth (Ward *et al.,* 2014).

Such estimations can be made given the permanent radioactive (secular) equilibrium which states that in a closed, undisturbed, isotopic system the activity of parent nucleotides is similar to its intermediate or final decay product (Papadopoulos *et al*., 2013). ^{238}U, ^{230}Th, ^{226}Ra, and ^{210}Pb radioisotopes are frequently used in geochronological studies due to their chemical characteristics and half-lives, with ^{226}Ra reaching equilibrium with its parent ^{230}Th in approximately 8000 years, while ^{210}Pb reaches more than 95% of equilibrium with ^{226}Ra in hundreds of years (Papadopoulos *et al*., 2013).

Different models can be applied to calculate accumulation rates from ^{210}Pb activity, including the Constant Rate of Supply (CRS), Constant Initial Concentration (CIC) and Constant Flux: Constant Sedimentation (CF:CS or 'Simple' model) methods

(Appleby and Oldfield 1992; Appleby 2001; Ward *et al*., 2014; Sheenan *et al*., 2015; Villa and Bernal 2017). Although each ^{210}Pb model has specific assumptions, they share the following: (1) the deposition of unsupported ^{210}Pb is at steady state and (2) there is no post-depositional mobility of ^{210}Pb (Arias-Ortiz *et al*., 2018).

The CIC model assumes a constant initial ^{210}Pb activity, independent of sediment accretion rates, being ideally applied at locations where events such as erosion or hydraulic changes have occurred, causing gaps in the sediment accretion records (Appleby, 2008; Sheenan *et al*., 2015). This model permits an estimation of the age (t) at any depth at which ^{210}Pb has been measured, provided that the initial specific ^{210}Pb activity is known (Arias-Ortiz *et al*., 2018a). However, the CIC model requires a monotonic decrease, entirely non-increasing, specific activity of ^{210}Pb$_{\text{excess}}$ down-core, to avoid calculation of reversed ages (Arias- Ortiz *et al*., 2018a). Therefore, the CIC method was not used in this study, as it might be too ambitious to calculate a detailed stepwise chronology based on an often-limited number of data points decreasing monotonically.

Moreover, the CF:CS model provides an average estimation of the rate of sedimentation over the entire depth of the core sampled, determined by the slope of the least squares fit regression of the natural log of ^{210}Pb$_{\text{excess}}$ activity against sample depth (Ward *et al*., 2014; Sheenan *et al*., 2015). Moreover, the CRS model assumes a constant direct ^{210}Pb atmospheric fallout, combined with fluctuations in the sedimentation rate and variable initial specific activity, calculated in combination with mass accumulation rates (Sheenan *et al*., 2015). The model uses inventories to calculate specific ages at any depth (x) where the total inventory within the core is determined from the sum of ^{210}Pb$_{\text{excess}}$ x Dry Bulk Density x thickness of the core slice (Thompson *et al*., 2001; Ward *et al*., 2014). Implicit within this model is that the major source of ^{210}Pb is derived from direct atmospheric input with ^{210}Pb activity being inversely proportional to mass flux of sediment (Appleby and Oldfield, 1992). The CRS model has been widely applied in estuarine and vegetated coastal environments, due to its robustness against non-monotonic features in the ^{210}Pb record and is relatively insensitive to mixing (Oldfield *et al*., 1978; Appleby *et al*., 1983; Appleby and Oldfield, 1992; Breithaupt *et al*., 2014; Andersen, 2017).

Generally, ^{210}Pb dates are confirmed using artificial radionuclides ^{137}Cs profiles as date markers, when the ^{137}Cs profiles are well preserved, enabling identification of high activity peaks in the sediment profile (Ward *et al*., 2014; Villa and Bernal, 2017).

Therefore, for the purpose of this study, long-term sediment accretion rates were determined for each core using the down-core distribution of ^{210}Pb with both the Constant Flux: Constant Sedimentation (CF:CS) model and the constant rate of supply (CRS) model, as well as ^{137}Cs impulse dating method for comparison and validation, further described in chapter 6 (Krishnaswamy *et al*., 1971; Appleby and Oldfield 1978; Appleby and Oldfield, 1992; Appleby, 2001).

4 *Estimation of carbon stocks*

4.1 *Preamble*

A review of the literature established that in order to assess seagrass potential as carbon sinks and include these ecosystems in blue carbon accounting, an in depth and globally detailed estimation of seagrass's carbon stocks must be provided. This chapter directly analyses total carbon stock samples from the Solent region in the UK, including sediment organic carbon and living biomass carbon storage, a new assessment for intertidal seagrass meadows in England. The results provide a basis for analysis and comparison between seagrass ecosystems in the Solent and those in other temperate and tropical seagrass meadows worldwide, as well as comparisons between sites with different historical and environmental characteristics. These results support the inclusion of the Solent's seagrass meadows in conservation and restoration projects, aiming not only to conserve the carbon stored in their soils, but also increase their future carbon uptake potential.

4.2 *Introduction*

Several studies have identified seagrass meadows as highly productive ecosystems that act as hotspots for carbon storage by trapping high amounts of organic carbon in their sediments, with an estimated median value of 42.7 Mg ha^{-1}, adding up to a total global blue carbon storage of 19.9 × 10^{9} Mg (Duarte and Cebrián, 1996; Duarte *et al*., 2010; Hemminga and Duarte, 2000; Fourqurean *et al*., 2012a; Lavery *et al*., 2013; Macreadie *et al*., 2014; Rozaimi *et al*., 2016; Rohr *et al*., 2018). This is due to their ability to retain allochthonous particles by reducing water flow, and sediment resuspension, coupled with slow decomposition rates from their usually oxygen poor sediments, make their plant material less labile than other marine angiosperms and algae (Kennedy and Björk, 2009; Holmer *et al*., 2009; Kennedy *et al*., 2010; Pedersen *et al*., 2011; Rohr *et al*., 2018).

Studies also suggest that seagrass habitat's ability to capture and retain carbon within their sediments is thousands of times higher than terrestrial habitats, per unit area, and comparable to the total amount of organic carbon stored in the world's marine tidal salt marshes and mangrove forests combined (Chmura *et al*., 2003; Donato *et al*., 2011; Howard *et al*., 2014; Rohr *et al*., 2018). Although the importance of seagrass ecosystems for climate change research has been increasingly recognised, most studies have focused on the loss of future carbon storage potential by degradation of existing meadows, rather than the potential conversion of their previously sequestered sediment carbon pools into atmospheric CO_2 (Pendleton *et al*., 2012; Nordlund *et al*., 2017).

In addition to their role as carbon sinks, seagrass meadows have historically provided numerous ecosystem services to humans, directly or indirectly, dating back to the 16th century (Campagne *et al*., 2015; Cullen-Unsworth *et al*., 2014; Nordlund *et al*., 2016; Nordlund *et al*., 2018). A few examples of these come from centuries old records of seagrass litter being used as bedding, straw substitutes for thatching stoned roofs in Scotland, and even in agriculture (Urquhart, 1824; Willis, 1983; Terrados and Bodrum, 2004; Nurdlund *et al*; 2016). Moreover, their high productivity and ability to trap organic matter make seagrass beds a fundamental part of marine food webs, being the primary food source of large, threatened, species like dugongs, manatees, sea turtles, and water birds (Costanza *et al*., 1997; Green and Short, 2003; Connell and Gillanders, 2007; IUCN, 2010; Nordlund *et al*., 2016; Whitehead *et al*., 2018).

Another important ecosystem service of seagrass meadows relates to their provision of nursery and sheltering habitats for fish and invertebrates, estimated to support 20% of the world's fisheries productivity (Orth *et al*., 1984; Fonseca, 1989; Duarte and Cebrián, 1996; Fourqurean *et al*., 2012a; Unsworth *et al*. 2018a; Unsworth *et al*., 2018b). However, as seagrass beds become targeted fishing grounds, due to their proximity to land coupled with the provision of shelter to a diverse fauna of fish and invertebrates, they also become potentially exposed to anthropogenic disturbance that could negatively impact carbon sequestration processes (Crooks *et al*. 2011; Duarte *et al*. 2013; Cullen-Unsworth *et al*., 2014; Cullen-Unsworth and Unsworth, 2016; Grech *et al*., 2012; Nordlund *et al*., 2014).

A number of organizations have produced guidelines to place a monetary value on ecosystem services within vegetated coastal environments, listing their carbon stocks as the factor with highest potential to be included in carbon trading initiatives (Villa and Bernal, 2017). However, one of the main challenges in attributing a value to ecosystem services relates to the lack of sufficient data to quantify their scale and magnitude in each geographical location (Villa and Bernal, 2017; Nordlund *et al*., 2018). Maintenance of healthy seagrass meadows have broadly been linked with mitigation of two major human concerns, food availability and climate change mitigation, based on their high supporting biodiversity and carbon sink potential (Unsworth *et al*., 2018a).

Duarte *et al*. (2011) listed the main actions required to address uncertainties and knowledge gaps around the role of seagrasses as carbon sinks, including comprehensive carbon stock research over extensive seagrass meadows and assessments of the fate of this buried carbon upon meadows degradation. Up to date carbon storage assessments are required at an international level in order to supply information to estimate the impact of vegetated coastal environments area loss on global GHG emissions (Pendleton *et al*., 2012). Hence, estimating the magnitude of organic carbon pools in seagrasses is an important step towards a better understanding of the potential impact of conversion from their stored carbon by direct anthropogenic degradation or climate change related factors (Fourqurean *et al*., 2012a).

Pendleton *et al*. (2012) have also identified the quantification of the global extent of seagrasses and tidal marshes, with their relative carbon pools and conversion rates, as one of the most urgent requirements in order to move forwards with robust blue carbon conservation programs. It has been noted that there is limited available historical data on the health and extent of seagrass meadows throughout the British Isles, including leaf density and total area, to appropriately evaluate their overall environmental health (Jones and Unsworth, 2016). Moreover, the majority of seagrass blue carbon data in the UK have been restricted to basic estimations using data from studies in different regions, like Spanish bays, or outdated standing stock assessments, making them unreliable to accurately assess UK's seagrass carbon stock potential (Garrard and Beaumont, 2014).

A recently published paper assessed the variability of the UK's seagrass sediment carbon for the first time, covering subtidal *Zostera marina* meadows on sites along the western coast of England (Green *et al*, 2018). This study also highlighted the lack of published data from seagrass meadows from British islands, and provided a representative assessment of the UK's seagrass carbon stocks, reporting an estimated standing stock of 66,337tC in the top 100cm of sediment (Jones and Unsworth, 2016; Green *et al*., 2018). However, Green *et al.'s* (2018) carbon stock values are still based on extrapolations and estimations in subtidal meadows, evidencing the need for further research and direct assessments of seagrass carbon stocks along the British coast, including intertidal meadows, such as those in the Solent.

Fourqurean *et al*. (2012a), compared the reported seagrass carbon stocks, represented by the living biomass (MgC ha^{-1}) and sediment organic Carbon (MgC ha^{-1}), from a range of global regions. Their results suggest a global mean of 7.29 ± 1.52 MgC ha^{-1} stored in living biomass and 329.5 ± 55.9 MgC ha^{-1} in the top metre of sediment organic carbon, with Mediterranean meadows containing the highest average sediment carbon stock (372.4 ± 56.8 MgC ha^{-1}) (Fourqurean *et al*. 2012a). In comparison, North Atlantic's temperate seagrass meadows showed lower carbon stock values, with 48.7 ± 14.5 Mg C/ha in sediment organic carbon, even though both regions had the highest number of studies globally (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).

These gaps underline the existing paucity of carbon stock data, which limits the ability of current estimates to accurately evaluate regional carbon storage patterns for seagrass meadows (Howard *et al*., 2014). Even though previous global estimations have been useful to raise attention to the important role of seagrass as carbon sinks in climate change mitigation, they are regionally and species biased (Lavery *et al*., 2013; Green *et al*., 2018). Given the diversity of biological and environmental factors that could influence carbon storage potential, such as nutrient availability, species rate of production, sediment accretion, hydrology, and geomorphological conditions, indirect quantification approaches based on estimations can lead to inaccuracies and possible overestimations (Johannessen and Macdonald 2016; Macreadie *et al*., 2018). For example, most published research on seagrass carbon stocks have been conducted in carbon rich Mediterranean meadows, dominated by *Posidonia oceanica,* potentially skewing regional and global estimations (Lavery *et al*., 2013; Green *et al*., 2018).

This chapter contributes to global seagrass blue carbon research by providing the first direct measurement of carbon storage values for intertidal seagrass ecosystems in England. The aim is to provide the most comprehensive assessment to date of total carbon stock from seagrasses in the Solent Region, UK. The objectives are to determine: 1) above-ground living biomass carbon stock. 2) below-ground living biomass carbon stock. 3) sediment carbon stock. 4) total carbon pool for each studied site by adding vegetative and soil carbon stocks.

4.3 Methods

4.3.1 Sampling Sites

Samples used for carbon stock analyses were collected between June and August of 2017, from the six sampling sites, 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 (figures 3.1). The chosen study sites encompass soft mud sediment regions, represented by sheltered, estuarine areas, such as Creek Rythe (figure 3.3) and Hayling Island (figure 3.4), as well as areas exposed to anthropogenic stress and nutrients runoff, like Farlington Marshes (figure 3.5) and Porchester (figure 3.6), with similar fine-grained sediments. Two sites at the Isle of Wight were also selected, Ryde and Cowes (figure 3.7), to provide comparable data from intertidal seagrass meadows growing on sandy substrates, and more exposed to hydraulic pressure from waves and tidal activity (Marsden and Chesworth, 2015). Out of the four natural harbours found in the Solent, the three largest have been included in this study, Portsmouth Harbour, Langstone Harbour, and Chichester Harbour, the fourth being Pagham Harbour (Williams *et al*., 2018). Chichester Harbour has five main channels with three surface freshwater inputs, comprising around 44km^2 of open water, the vast majority of which is intertidal (Williams *et al*., 2018). It has a wide variety of marine habitats including extensive areas of sand and mud flats, intertidal areas supporting eelgrass (*Zostera spp.*), and saltmarshes (MMO, 2019).

Despite being under Chichester Harbour Conservancy's management since 1971, Chichester Harbour has recently been listed as in an unfavourable state, under the Habitats Regulation Monitoring process, mainly due to its littoral sediment conditions (Smale *et al*., 2019). This is because the area is exposed to pollutant inputs, which include sewage discharge and agricultural / industrial and natural runoff, even though considerable water exchange is guaranteed by frequent tidal flush (Seaview, 2017; Williams *et al*., 2018). In addition, the harbour is one of the busiest in the country for recreational activity, (estimated 12,000 regular boat users) which can also cause potential pollution and water quality impacts, as well as physical damage to existing seagrass meadows, caused by propellers, trampling and anchoring (Seaview, 2017).

Chichester and Langstone harbours are connected by a channel north of Hayling Island, both presenting mudflats and saltmarshes that protect their margins from the actions of waves generated within the harbours (figure 3.1) (Bray and Cottle, 2003). Organic sediments are generated by biological production from the intertidal mudflats and sandflats, covering around 1413ha in Langstone Harbour and 1300ha in Chichester Harbour (Barne *et al*., 1996; Bray and Cottle, 2003). The upper mudflats exhibit annual growth of algae (*Ulva* and *Enteromorpha sp.*), whereas significant areas of *Zostera spp.* (*Z. angustifolia and Z. noltii*) are present on the lower flats and towards mean low water in Chichester (220ha) and Langstone (340ha) (Raybould *et al*., 2000).

Seagrass populations in Chichester and Langstone Harbours have fluctuated with increases during the 1980's but have suffered subsequent losses due to eelgrass wasting disease (figure 3.1) (Bray and Cottle, 2003; Marsden and Chesworth, 2015). Much of the mudflat area was colonised by *Spartina anglica* from the turn of the 20th century, however the mudflats expanded in recent years, following dieback and erosion of *S. anglica* dominated lower marshes (Haynes and Coulson, 1982; Wallingford, 1994). This new mudflat area created by retreat of saltmarsh, located 1m to 2m lower than the marsh they replaced, are less accessible to bird grazing as they are covered by tides for prolonged periods, therefore providing a favourable habitat for seagrass growth (Collier and Fontana, 1996).

Portsmouth Harbour is a tidal basin, due to its narrow entrance, and although a tidal channel connects the north-eastern extremity with Langstone Harbour, the exchange of water mass between the two harbours is low (figure 3.1) (Bray and Cottle, 2003). Biological production within Portsmouth Harbour provides organic input to sedimentation, assisted by wave energy dissipation provided by existing mudflats and low-mid saltmarsh (Baily *et al*., 2000). However, the loss of *S. anglica* has increased suspended sediment concentrations due to the reduced stability of muddy substrates, and expanded intertidal mudflat areas to around 926 ha, supporting extensive growth of eelgrasses (*Zostera spp*) and high densities of green algae, mainly *Enteromorpha spp* and *Ulva spp*, in the area (Bray and Cottle, 2003; Marsden and Chesworth, 2015). Although not uniformly distributed within Porstmouth Harbour, the extent of *Zostera spp* communities is one of the largest recorded in southern England (Baily *et al*., 2000). Furthermore, as *S. anglica* declines and sea-level rises, more conversion of lower to mid-marsh to mudflat may be imminent, thus expanding the habitat available to eelgrass in the region (Wallace *et al*., 1990; Cundy and Croudace, 1996).

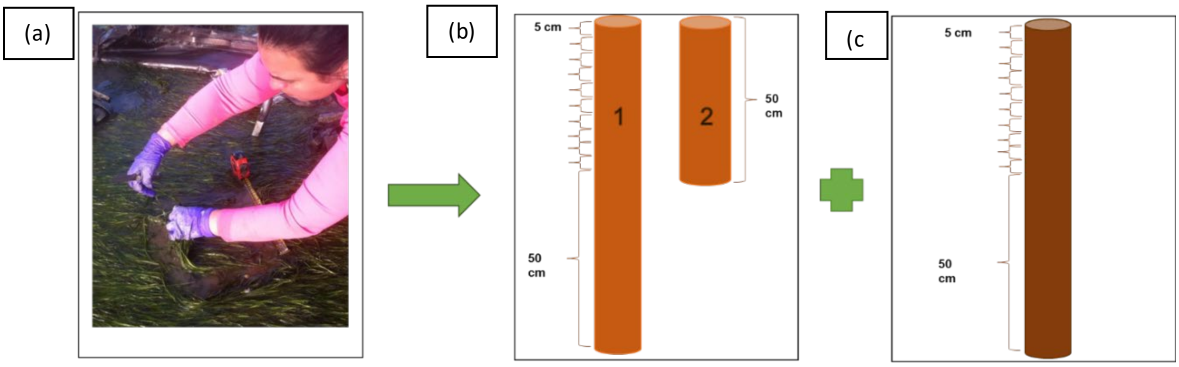
These fluctuations in areal extension of seagrass beds in the Solent are some of the best recorded historically in the UK (Tubbs, 1999; Marsden and Chesworth, 2015). Studies monitoring the distribution of seagrass beds in the region began in the 18th century (Marsden and Chesworth, 2015). Surveys conducted after wasting disease outbreaks in the 1930's, described a rapid disappearance of seagrass in most areas of the Solent and the harbours of Chichester, Langstone and Portsmouth, apart from the Isle of Wight (Butcher, 1934). However, the Isle of Wight's meadows did not appear to survive more than a decade, based on reports by Wadham in the 1940's (Tubbs, 1999).

Most eelgrass beds reported in the Isle of Wight are scattered along the north coast, where the intertidal zone consists mostly of sheltered mudflats and sandflats, being exposed to lower wave energy than the southern side of the Isle (Marsden and Chesworth, 2015). Both sampling sites in the Isle of Wight, Cowes and Ryde, are located on the central and eastern side of the north coast, mainly facing less rapid tidal currents (generally <1ms^{-1}), compared to the West Solent (>2ms^{-1}), influencing sediment transport along the shoreline, with the largest being medium sand (figures 3.1 and 3.7) (Dyer, 1980; Webber, 1980; Halcrow, 1996; SCOPAC, 2003).

4.3.2 Field methods

Five sampling points were randomly selected within each of the six study sites (30 in total) (Methods - section 3.2.2). A 0.25 m^2 quadrat was placed at each sampling point, to collect above-ground biomass by cropping the plant biomass (leaves - to stem base), and transferred into a sealed and labelled sampling bag (figures 3.8 and 4.1) (Howard *et al*., 2014). After above-ground biomass removal, two sediment cores were collected from each quadrat using a Russian corer, with a 0.5m section length. One, 1m deep (or to refusal), core was used for sediment carbon stocks and sediment particle size analyses, and one, 50cm deep (or to refusal), core was collected for below-ground biomass analysis (figures 3.8 and 4.1). Each 1m deep sediment core was divided into 5cm depth sediment subsamples from 0-50 cm, followed by one larger 50cm subsequent subsample from 50-100cm, e.g. 11 subsamples per 1m core (Howard *et al*., 2014). Additionally, five, 1 m deep (or to refusal), sediment cores were collected from un-vegetated mudflats sampling points adjacent to the seagrass meadows on all sites, apart from Cowes, for carbon stocks analysis, using the same methods described above (figures 3.8 and 4.1). Un-vegetated sediment samples were not collected from Cowes due to the gravelly and rocky characteristics of the sediment near seagrass beds.

In the field, each sediment subsample was transferred into individual bags, labelled with location, date, plot, and sample number. For the purpose of this study, sediment carbon density was calculated including below-ground carbon content from roots and rhizomes.



Above-ground biomass collected from 0.25 m^2 seagrass sampling quadrat. (5 per site – 30 in total)

Two sediment cores per seagrass quadrat (10 per site – 60 in total): Core 1 - 1m deep (or to refusal) for sediment Carbon stock analysis. Core 2 - 50cm deep (or to refusal) for below-ground biomass analysis.

Additional sediment cores from un-vegetaded mudflats, for sediment Carbon stock analysis. (5 per site – 30 in total)

Figure 4.1: Field methods showing above-ground biomass sampling within 0.25 m^2 quadrats (a), including 1 m deep sediment core for sediment C$_{\text{stocks}}$ and particle size analyses, for seagrass meadows (b) and un-vegetated mudflats (c), including subsamples division, and one 50cm deep sediment core for below-ground biomass analyses (b).

4.3.3 Laboratory methods

In the laboratory, above-ground biomass material was transferred to 1mm sieves, and washed free of soil under running water to separate living above-ground components (figure 4.2) (Howard *et al.*, 2014). Identified seagrass species were recorded, as well as observations regarding presence of epiphytes. 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.

Figure 4.2: Above-ground biomass being washed free of soil and under running water, using a 1mm sieve.

Whole leaves (stem to tip) were counted from each sample to determine leaf density. Above-ground plant biomass was determined by oven-drying the vegetative biomass (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).

Below-ground biomass samples were transferred to 1mm sieves and washed free of sediment under running water before careful separation of below-ground living 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 living above-ground and below-ground biomass was calculated by the following equations:

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

Equation 2: Carbon pool (Mg C/ha) = Carbon content (kg C/m^2) *(Mg/1,000 kg) * (10,000 m^2/ha).

Sediment subsamples were stored in the freezer until analysis. The thawed samples were then 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 moisture content (Howard *et al.*, 2014).

Oven dried samples were carefully disaggregated with a pestle and mortar and weighed into individual beakers, 2-4g for each sample, before being placed in the muffle furnace for loss in ignition (LOI) at 450 ºC (selected temperature) for 24h (selected exposure time) (Methods – Section 3.2.2 (ii)). Samples were cooled at room temperature in a desiccator for at least one hour before weighing to determine percentage of organic matter (% 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 carbon stocks (C_{stocks}), sediment carbon density, sediment dry bulk density and organic carbon content (C_{org}) were calculated. Dry bulk density (g/cm^3) for individual depth samples were estimated using the equation:

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

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

To directly determine ($\%C_{org}$), a total of 45 sediment subsamples, approximately 9 per site, were randomly selected between the six sampling sites to be analysed on a VarioMax CNS elemental analyser (ELEMENTAR) using the DUMAS combustion method (Dumas, 1831). In the DUMAS, or dry combustion, method samples are combusted at high temperature (> 950°C) for approximately 12 to 15 minutes in an oxygen atmosphere. The samples were weighed, mixed with copper (II) oxide, and heated in a tube. Any carbon present in the compound was converted into oxides, which were led over a column of hot copper to be reduced back into carbon gas molecules. The gases produced were then collected and the volume measured by a thermal conductivity detector and given as % or mg Carbon. This method measures total carbon in the samples, including carbon from carbonates, if present. The presence of carbonates ($CaCO_3$) was tested by adding a few drops of 1M HCl solution to oven dried samples and observed for the 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 Farlington Marshes, Ryde and Cowes. For these sites where carbonates were detected, $\%C_{org}$ was adjusted to remove the excess from inorganic carbon (IC), after quantification by LOI, using the equation below, adapted from Howard *et al*. (2014):

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

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

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 and Porchester as well as corrected C_{org} values for Farlington Marshes, 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.

To confirm the reliability of the equation formulated, results were compared against regression equations derived from global literature (**equations 6 and 7**) (Fourqurean *et al*., 2012a/b) and assessed for statistical differences to determine which equation should be used to determine $\%C_{org}$ from %OM values.

$$\textbf{Equation 6}: \%\ C_{org} = 0.43 * \%\ LOI - 0.33, \text{ presuming } \%\ OM > 0.2,$$

$$\textbf{Equation 7}: \%\ C_{org} = 0.40 * \%\ LOI - 0.21, \text{ presuming } \%\ OM < 0.2$$

Following C_{org} calculations, sediment carbon density and carbon content were determined as the following equations for each subsample:

Equation 8: Sediment Carbon Density (g/dm^3) = [(Dry mass (mg) * % C_{org}) / Dry mass (mg)] * 100 (Howard *et al*., 2014).

Equation 9: Sediment C content (g/cm^2) = Soil Carbon Density (g/cm^3) * Sample thickness (cm).

Sediment carbon content results from each subsample were then summed to determine total carbon to 1 m depth cores, and converted to Mg C/ha, using the same conversion equation described above for living 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 (Methods – section 3.2.3). The mean (central value) and sorting coefficient (standard deviation) for each sample were calculated following the arithmetic approaches below, assuming particles sizes in φ units (Folk and Ward, 1957):

$$\textbf{Equation 10}: \text{Mean} = \frac{D16 + D50 + D84}{3}$$

$$\textbf{Equation 11}: \text{Sorting} = \frac{\varphi 84 + \varphi 16}{4} + \frac{\varphi 95 - \varphi 5}{6.6}$$

Characterisation of the degree of sorting also followed Folk and Ward's (1957) classification.

4.3.4 Statistical analyses

Statistical analyses performed for this chapter included: Anderson-Darling test for normality, ANOVA, Tukey's post hoc test, two sample T-tests, paired T-test, Pearson's correlation and linear regression model tests (Methods – section 3.2.1). Variables analysed for homogeneity of variance between sites were: above-ground biomass (AGB), leaf density, below-ground biomass (BGB), %BGB/ C_{stock}, 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 sediment cores and cores from un-vegetated sampling points for all sites, apart from Cowes [Methods – section 3.2.1 (iii)]. A paired T-test was used to analyse the difference between %Corg calculated using an equation derived from this analysis and the one used in global literature [Methods – section 3.2.1 (iii)]. 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} and C_{stocks}, from %OM and DBD, respectively [Methods – section 3.2.1 (iv)].

For better analysis and comparability, all graphs have been standardised to show sites from left to right on an East to West geographical direction, starting with inland sites (CRST-LGST-FMST-PMST), followed by the sites on the Isle of Wight (RYST-CWST).

4.4 Results

Of all variables tested for homogeneity of variance, only values for BGB and %C_{org} 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 (table 4.1).

Table 4-1: Summary of statistical results for ANOVA tests for all variables (n=30; $p<0.05$). Where Df represents the degree of freedom, p the significance value, R-sq R-squared value and Pooled StD the pooled standard deviation for ANOVA. AD (p) is Anderson-Darling test for normality ($p<0.05$) and consequent mathematical transformation if AD (p) < 0.05. Where: Above-ground biomass (AGB), Below-ground biomass (BGB), sediment carbon stocks (C_{stock}), Dry bulk density (DBD), percentage of organic matter (% OM), percentage of organic carbon content (%C_{org}).

Variables	df	F	p	R-sq	Pooled StD	AD (p)	Transformation when AD(p) <0.05
AGB (Mg C Ha^{-1})	29	5.97	0.001	0.4615	0.14	0.290 (0.587)	No
Leaf density (m^{-2})	29	0.68	0.642	0.1243	68.91	0.896 (0.019)	No
BGB (Mg C Ha^{-1})	29	2.89	0.035	0.2461	0.017	1.938 (<0.05)	Yes -Log$_{10}$(X)
%BGB/C_{stock}	29	6.07	0.001	0.5583	0.028	1.933 (<0.005)	Yes -Log$_{10}$(X)
DBD (g/cm^3)	29	244.93	0.000	0.9816	0.048	0.592 (0.114)	No
%OM	29	39.43	0.000	0.8781	0.88	1.017 (0.010)	No
%C_{org}	29	71.13	0.000	0.9368	0.28	1.851 (<0.05)	Yes - Log$_{10}$(X)
C_{stock} (MgC ha^{-1})	29	176.99	0.000	0.9693	0.13	0.485 (0.213)	No

A summary of the mean values of all parameters analysed in this chapter is presented in table 4.2, including coordinates of all sampling sites and seagrass meadow areal extents. Creek Rythe had the highest mean values for sediment C_{stock} (181.0 ± 16.24 MgC ha^{-1}), above-ground biomass (0.50 ± 0.25 MgC ha^{-1}) and organic matter content (6.81 ± 1.07%) (table 4.2). 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 4.2).

Table 4-2: Summary of main results for sediment carbon stocks (C_{stock}), reported seagrass meadows areal extent, leaf density, above and below-ground biomass, percentage of below-ground biomass per carbon stock, sediment organic carbon content (C_{org}), sediment organic matter content (OM), sediment dry bulk density, mean and median (D50) grain size and degree of sorting, including calculated sorting coefficients (φ), for all sampling sites. Values are presented as mean (±) standard deviation for all variables, with n = 30, and the same letters correspond to statistically similar means for each variable where ANOVA was performed, followed by Tukey's post hoc test.

SITES	**C_{stock} 1m (Mg C Ha^{-1})**	**Area (ha)***	**Leaf density (m^{-2})**	**Above-Ground Biomass (Mg C Ha^{-1})**	**Below-Ground Biomass (Mg C Ha^{-1})**	**%BGB/ C_{stock}**	**%C_{org}**	**%OM**	**Dry bulk density (g dm^{-3})**	**Mean grain size (μm)**	**D50 (μm)**	**Degree of Sorting**
Creek Rythe (CRST)	**181.0 ± 16.24 (A)**	100.24	367.0 ± 115.1	0.50 ± 0.25 (A)	0.009 ± 0.005 (AB)	0.005 ± 0.0028 (B)	3.07 ± 0.15 (A)	6.81 ± 1.07 (A)	0.59 ± 0.02 (F)	22.00 ± 6.22	16.80 ± 1.21	Very poorly sorted (2.28 ± 0.06)
Hayling Island (LGST)	**154.9 ± 12.13 (B)**	70.1	336.7 ± 95.0	0.38 ± 0.13 (AB)	0.037 ± 0.04 (A)	0.025 ± 0.026 (B)	2.27 ± 0.14 (B)	5.87 ± 0.17 (AB)	0.74 ± 0.03 (E)	20.8 ± 4.0	15.82 ± 2.93	Very poorly sorted (2.48 ± 0.08)
Porchester (PMST)	**148.6 ± 21.8 (BC)**	94.92	302.0 ± 76.1	0.32 ± 0.07 (ABC)	0.013 ± 0.012 (AB)	0.011 ±0.0085 (B)	1.77 ± 0.61 (C)	4.73 ± 1.58 (BC)	0.86 ± 0.07 (D)	46.07 ± 21.85	25.61 ± 10.84	Poorly sorted (1.76 ± 0.73)
Farlington Marshes (FMST)	**124.96 ± 10.28 (C)**	31.2	584 ± 427	0.25 ± 0.14 (ABC)	0.004 ± 0.003 (B)	0.003 ±0.0025 (B)	1.34 ± 0.06 (BC)	3.64 ± 0.51 (CD)	1.11 ± 0.09 (C)	46.79 ± 15.94	31.53 ± 5.88	Poorly sorted (1.62 ± 0.02)
Cowes (CWST)	**19.3 ±** ** **5.90 (D)**	27.1	346 ± 247	0.18 ± 0.07 (BC)	0.003 ± 0.0007 (B)	0.014± 0.006 (B)	0.76 ± 0.24 (E)	2.53 ± 0.55 (DE)	1.27 ± 0.25 (B)	72.40 ± 36.91	64.82 ± 36.68	Poorly sorted (1.77 ± 0.74)
Ryde (RYST)	**10.09 ± 2.27 (D)**	82.47	427 ± 430	0.08 ± 0.03 (C)	0.008 ± 0.005 (AB)	0.084 ±0.062 (B)	0.13 ± 0.02 (D)	0.84 ± 0.08 (E)	1.46 ± 0.01 (A)	227.99 ± 6.97	224.78 ± 4.68	Moderately sorted (0.89 ± 0.02)

*Area derived from Marsden and Chesworth, 2015 ** Sediment cores for Cowes (CWST) were only 20cm deep

4.4.1 Above-ground biomass

Species found in the study sites were: *Zostera noltii, Zostera marina, Zostera angustifolia* and *Ruppia maritima*, represented in the above-ground biomass samples collected. *Z. angustifolia* was found in all sampling 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, as the dominant species. *Z. marina* was found predominantly in Cowes, while *R. maritima* was only found in Creek Rythe and Hayling Island, in small mixed patches.

Microalgae epiphyte-cover was visible to the naked eye on above-ground samples from Cowes, but not abundant, where *Zostera marina* was dominant. Associated green macro algae was found in Farlington Marshes and Hayling Island – Langstone, whilst Creek Rythe presented the most associated macro fauna, mostly small crustaceans. For the purpose of this study, above-ground biomass (AGB) was assessed without removal of epiphytic load.

Above-ground biomass 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 $\pm$ 0.08 MgC ha^{-1} (n=30) between all sites. There were significant differences on AGB between sites, with above-ground biomass in Creek Rythe being significantly higher than both sites in the Isle of Wight, Ryde and Cowes (figure 4.3). Moreover, both Creek Rythe and Hayling Island, the sites with denser meadows, showed significantly higher AGB values than Ryde (figure 4.3).

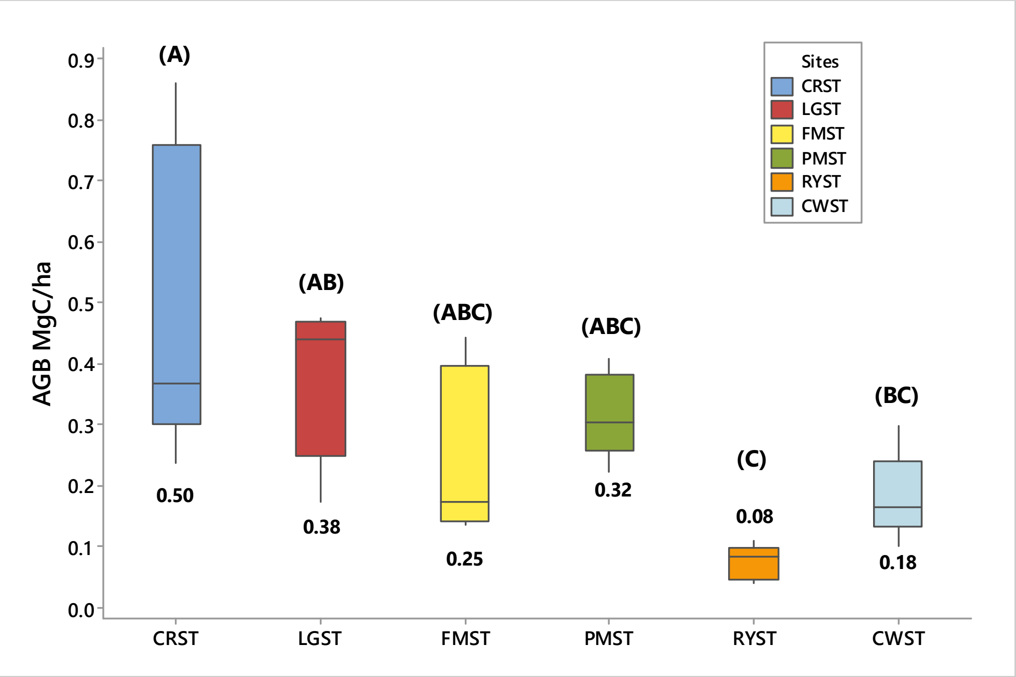


Figure 4.3: Distribution of above-ground biomass values on all sampling sites, Creek Rythe (CRST, Hayling Island (LGST), Farlington Marshes (FMST), Porchester (PMST), Ryde (RYST) and Cowes (CWST), including Tukey's grouping analysis results, where the same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

The 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 (table 4.1), but the large standard deviations around the means could be related to differences in meadow canopy, age, complexity, and landscape (table 4.2). Sites with monospecific *Z. angustifolia* beds, like Farlington Marshes and Ryde, presented the highest mean leaf densities, of 584 ± 427 leaves/m^2 and 427 ± 430 leaves/m^2, respectively (figure 4.4, table 4.2).

A Pearson's correlation test was also used to assess the relationship between the above-ground biomass (MgC ha^{-1}) and leaf density (leaves/m^2) across all six sites, respectively, but no significant relationship between the variables was found (r=0.002 and p=0.992).

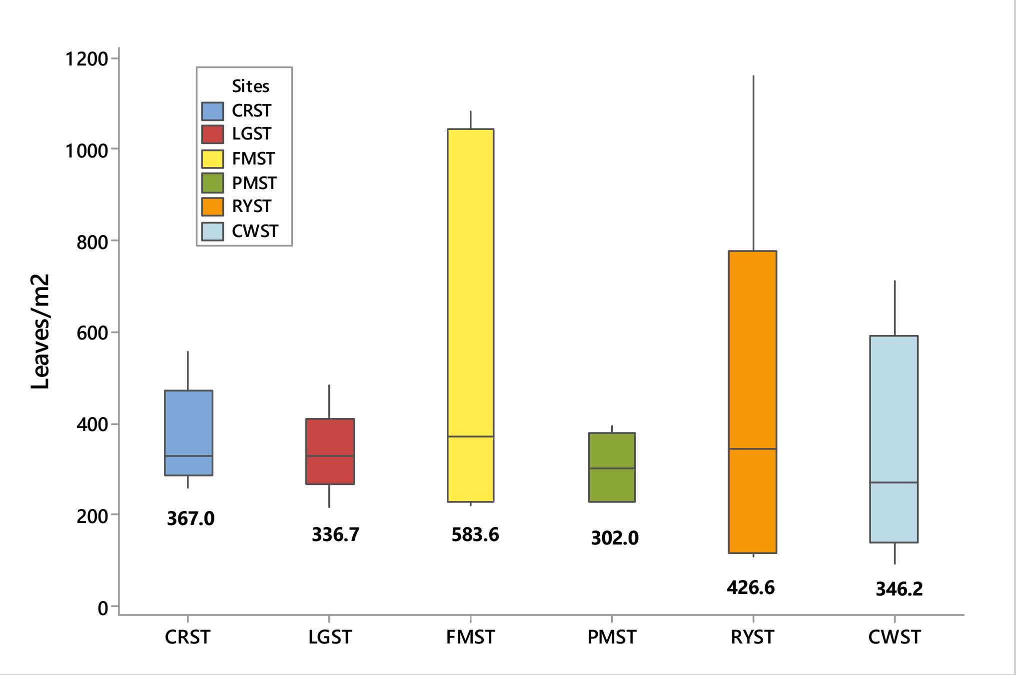


Figure 4.4: Distribution of leaf density values on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

4.4.2 Below-ground biomass

Mean below-ground biomass for all sites was 0.0122 ± 0.013 Mg C ha^{-1} (n=30). Cowes and Farlington Marshes had significantly lower below-ground carbon pools than Hayling Island (table 4.2). Cowes had the lowest below-ground biomass amongst all sites, of 0.003 Mg C/ha, whilst the highest BGB value was found in Hayling Island, 0.0373± 0.04 Mg C/ha (figure 4.5 and table 4.2). However, when comparing relative %BGB/C$_{stocks}$, Ryde's sediment cores presented a significantly higher proportion of below-ground carbon stocks composed by BGB, than all other sites (figure 4.6). Moreover, correlation analysis showed no statistically significant relationship between above and below-ground biomass (r=0.122; p = 0.519).

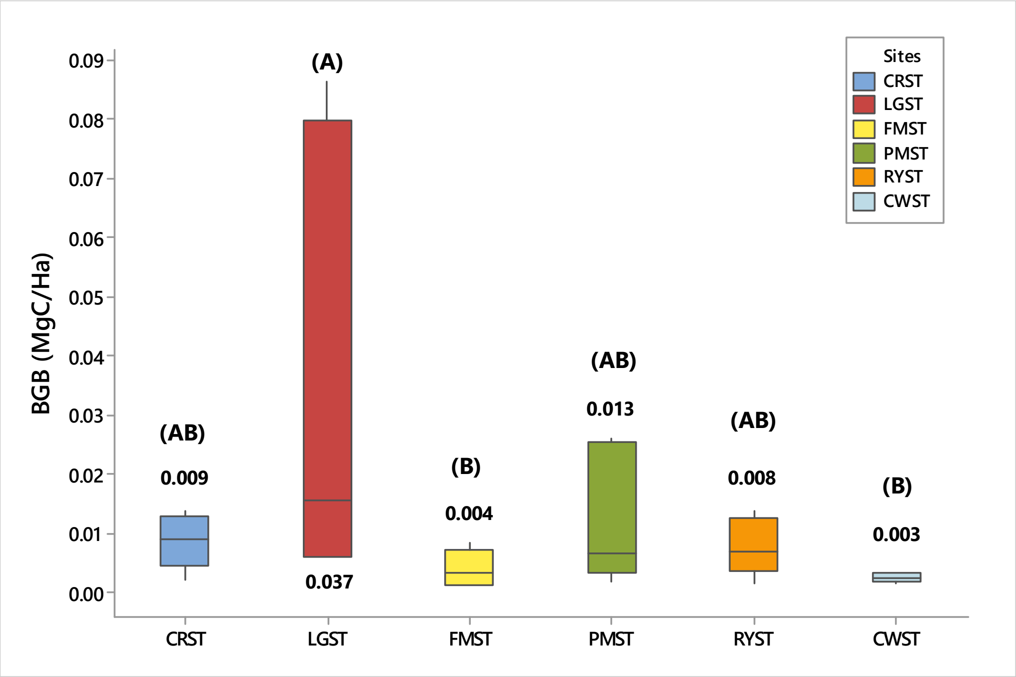


Figure 4.5: Distribution of below-ground biomass (BGB) values on all sampling sites CRST, LGST, FMST, PMST, RYST and CWST before Log$_{10}$(X) transformation, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

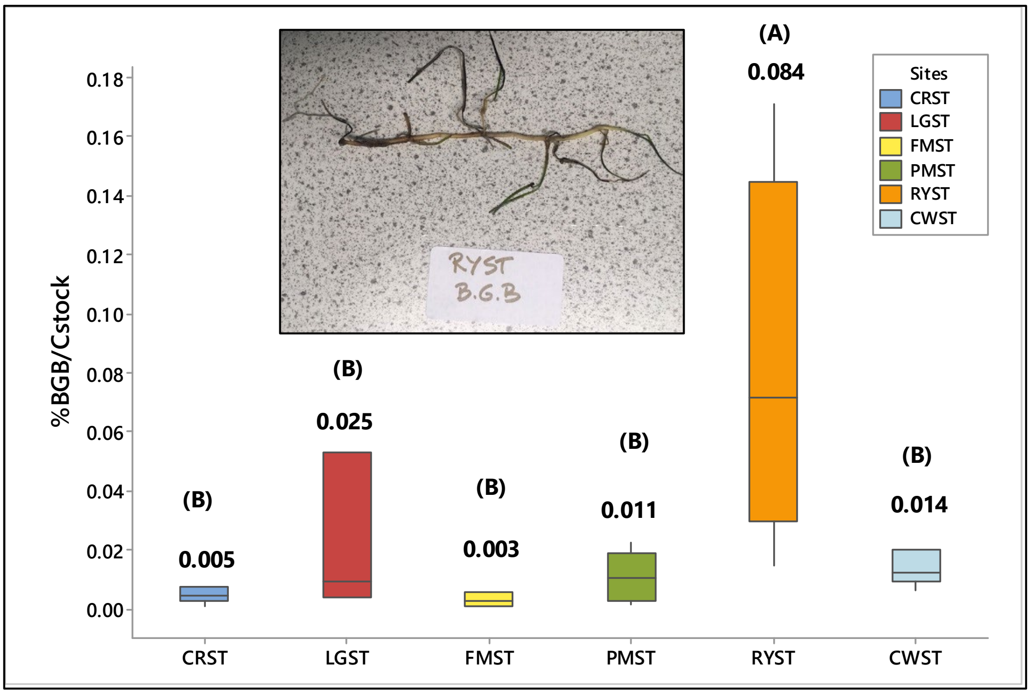


Figure 4.6: Distribution of %below-ground biomass/ C$_{stocks}$ values on all sampling sites CRST, LGST, FMST, PMST, RYST and CWST before Log$_{10}$(X) transformation, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range. Image showing rhizome and associated roots system colleted from Ryde.

4.4.3 Dry Bulk Density

Dry bulk density (DBD) in the study sites ranged from 0.59 ± 0.02 g/cm^3 in Creek Rythe to 1.46 ± 0.01 g/cm^3 in Ryde (table 4.2). The mean dry bulk density for all sites was 1.01 ± 0.32 g/cm^3 (n=30). There were significant differences in DBD between sampling sites (table 4.1), with Ryde having significantly higher DBD than all other sites, whilst Creek Rythe presented the lowest values (figure 4.7).

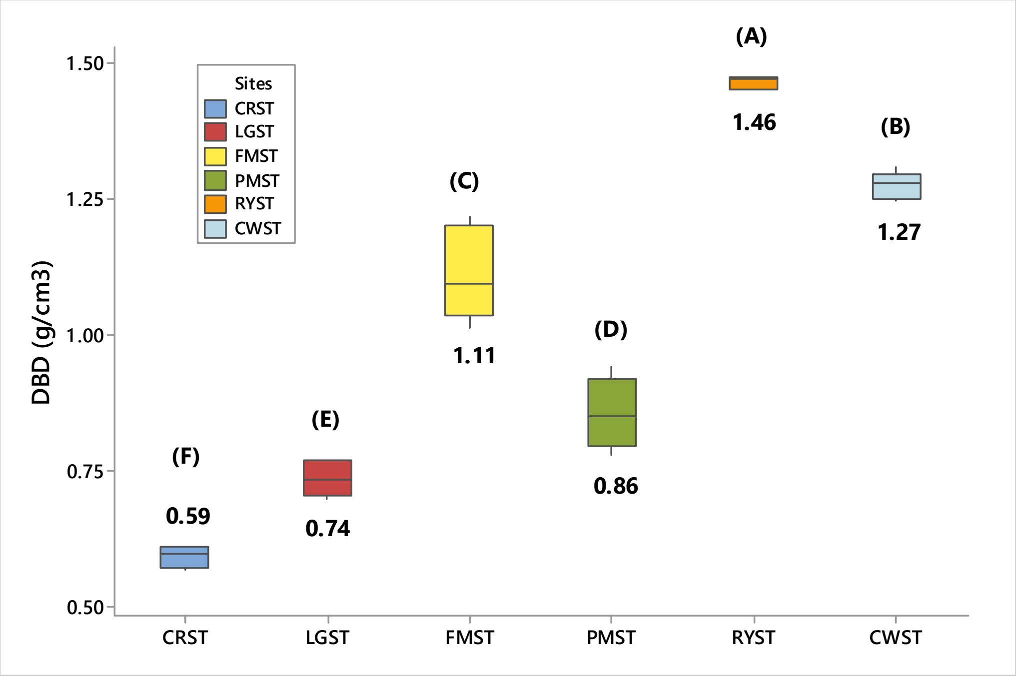


Figure 4.7: Distribution of dry bulk density (DBD) values on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

No significant relationship was found between dry bulk density and below-ground biomass for seagrass sediments when analysed with Pearson's correlation test (r=-0.333; p=0.072). However, there was a negative, statistically significant, strong correlation between DBD and above-ground biomass, (r=-0.750; p= 0.000) (figure 4.8). This association shows that sites with lower sediment DBD, like Creek Rythe and Hayling Island, had higher above-ground biomass, than the sites in the Isle of Wight, Ryde and Cowes, with higher sediment DBD (figure 4.8).

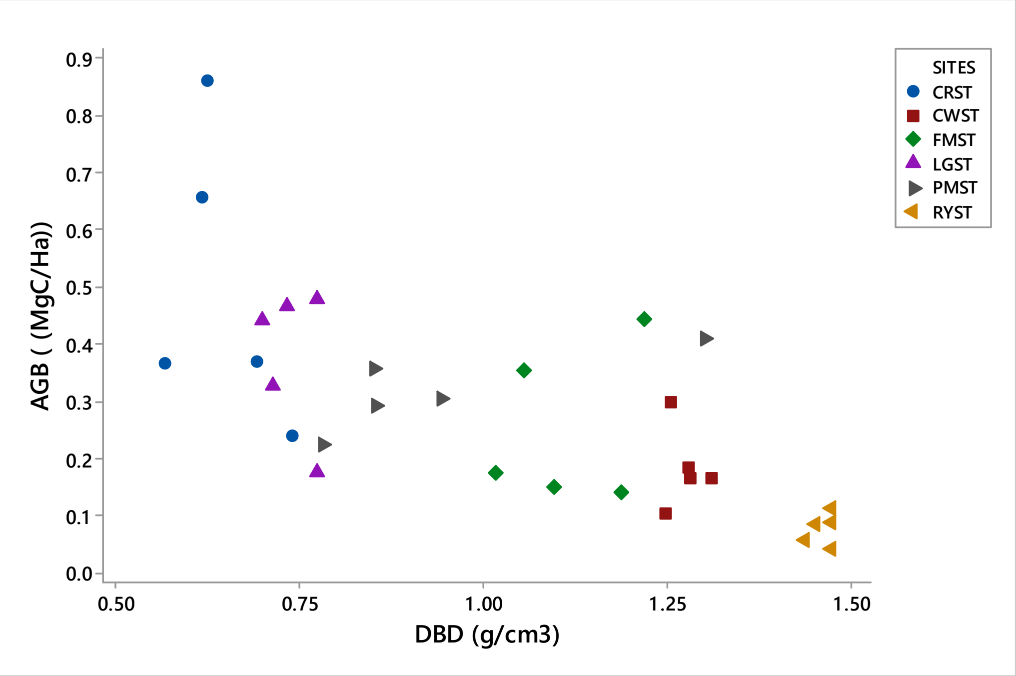


Figure 4.8: Above-ground biomass (AGB) and Dry bulk density (DBD) values for all sites: Creek Rythe (CRST), Hayling Island (LGST), Farlington Marshes (FMST), Porchester (PMST), Ryde (RYST) and Cowes (CWST).

4.4.4 Particle Size Analysis

Ryde had 99% of its particles within fine sand classes (125 - 205 μm) according to the Wentworth (1922) classification scale. Conversely, silt (3.9 - 63μm) particles represented the majority (>50%) of total sediment volume in, 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 the ones in 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), median particle size D50 (μm) and sorting coefficient (φ) 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 (figure 4.9 and table 4.2). 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 (figure 4.9).

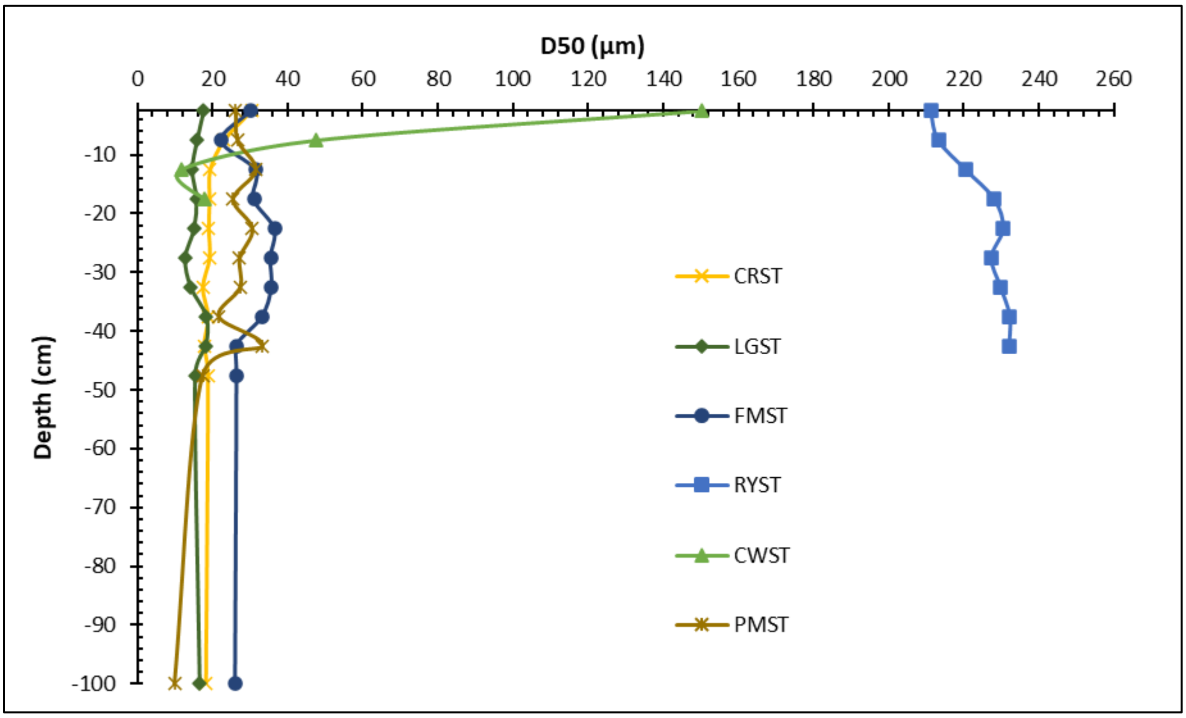


Figure 4.9: Down-core profile of median particle sizes D50 (µm) for all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST.

Creek Rythe and Hayling Island were had very poorly sorted sediment particles throughout the depth profile, according to Folk and Ward's (1957) degree of sorting classification. Sediment particles from all other sites were poorly sorted, apart from Ryde which was moderately sorted. Pearson's correlation tests showed that there was a strong and statistically significant positive relationship between D50 and DBD (r = 0.767; p= 0.000) (figure 4.10), 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).

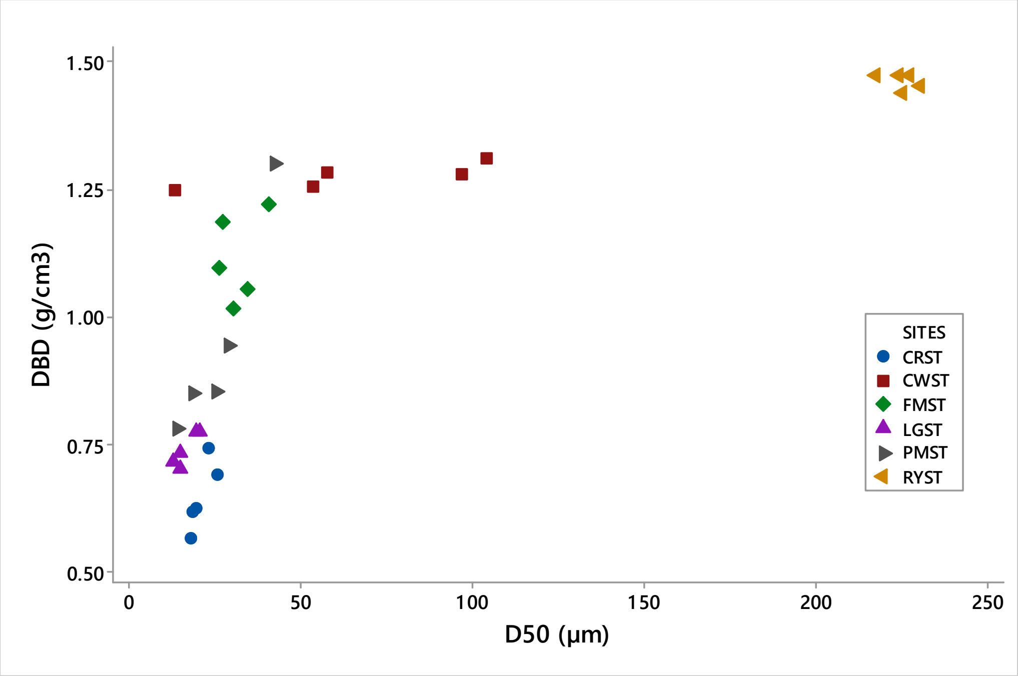


Figure 4.10: Median particle size D50 and dry bulk density (DBD) values for all sites CRST, LGST, FMST, PMST, RYST and CWST.

4.4.5 Sediment Carbon Stocks

4.4.5.1 Organic Matter Content (%OM)

Organic matter content (%OM) was analysed up to 1m deep for cores on all sampling sites except Cowes where the maximum core depth was 20cm, where refusal happened due to the gravely aspects of the sediment below that depth limit. Creek Rythe had the highest %OM with 6.82 ±1.01 % of dry weight while Ryde the lowest %OM, representing 0.84 ± 0.07 % of dry weight (table 4.2). There were significant differences in seagrass sediment %OM between sampling sites (n=30) (table 4.1), with Tukey's post hoc test showing that Creek Rythe had significantly higher %OM values than all other sites, apart from Hayling Island, while values of %OM from Hayling Island were significantly higher than Farlington Marshes, Cowes, and Ryde. Additionally, Ryde's %OM values were significantly lower than all other sites, apart from Cowes (figure 4.11).

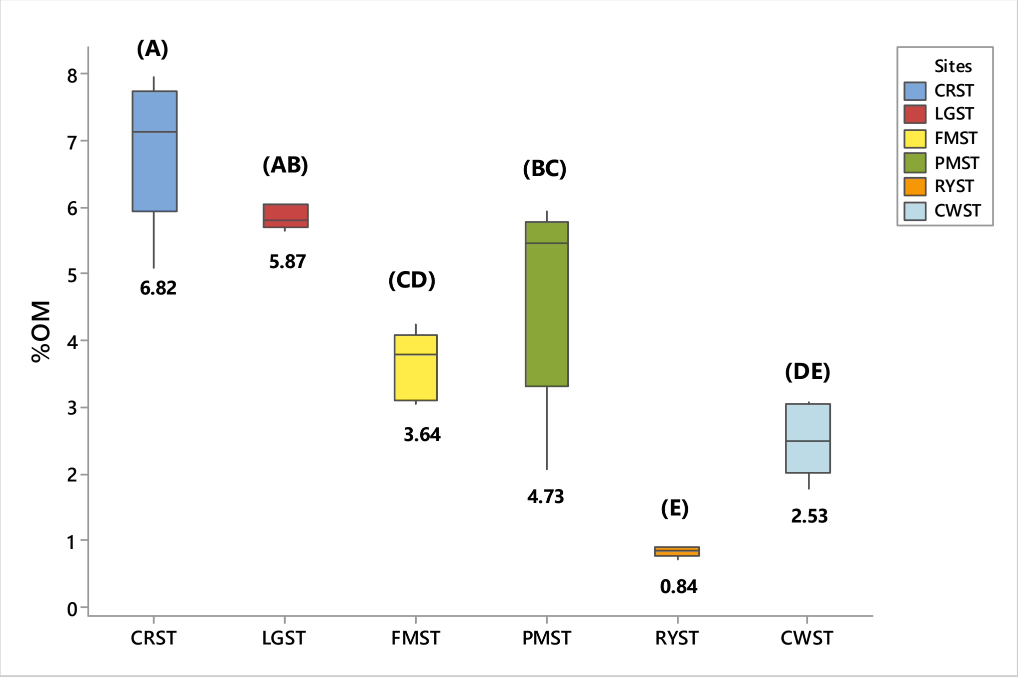


Figure 4.11: Distribution of %OM values between sampling sites, CRST, LGST, FMST, PMST, RYST and CWST, including Tukey's grouping analysis results, same letters correspond to statistically similar means Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

4.4.5.2 Organic Carbon Content (%Corg)

The relationship between %OM, derived by LOI, and $\%C_{org}$ determined by elemental analysis was assessed by a regression model, using $\%C_{org}$ values, from Creek Rythe, Hayling Island and Porchester, and $\%C_{org}$ corrected (after removal of carbonates - %IC) from Ryde, Farlington Marshes and Cowes, (equation 12, figure 4.12).

Equation 12: $\%C_{org} = 0.2133\ \%OM + 0.279$

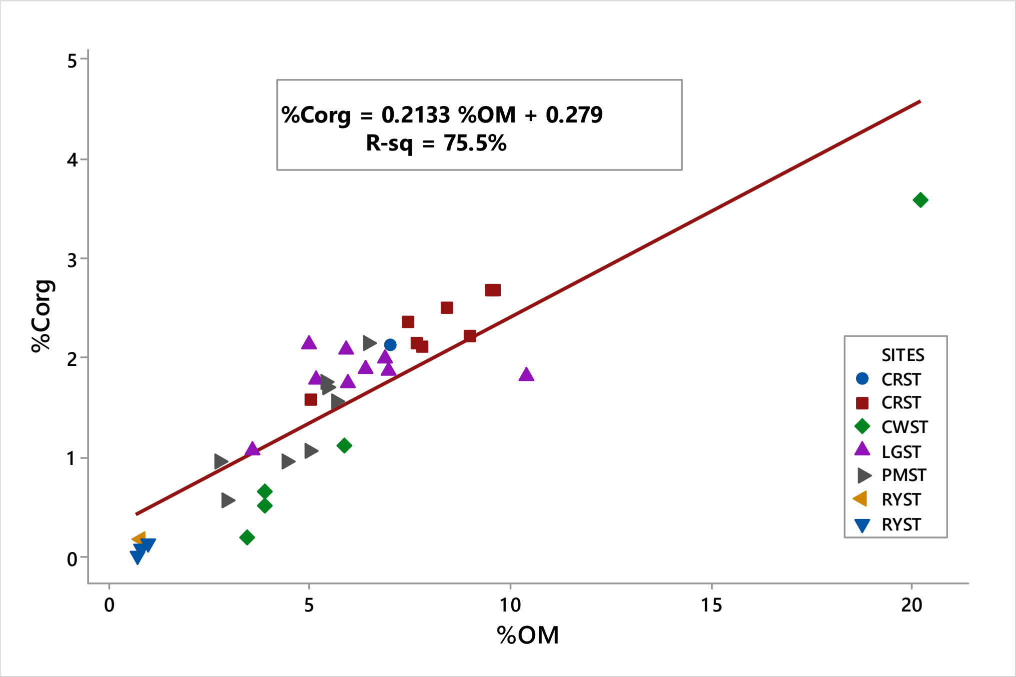


Figure 4.12: Relationship between sediment organic carbon %C$_{org}$ derived from elemental analysis and organic matter %OM calculated via loss on Ignition (LOI), for all sites CRST, LGST, FMST, PMST, RYST and CWST. Model equation and R-sq value included.

The model provided an adequate, and statistically significant (p = 0.00), fit to the data. However, the relationship established by the formulated regression equation was not as strong as the one derived from global literature (R^2 = 0.76 vs R^2 = 0.96, respectively) (Fourqurean *et al.*, 2012). To determine the accuracy of the equation, %C$_{org}$ values, derived from %OM, were calculated using both the developed linear equation (equation 12) and the ones proposed by Fourqurean *et al.*, (2012) (equations 6 and 7) and compared for statistical differences using a paired t-test.

The paired t-test (n=327) showed statistically significant differences (p = 0.00) between %C$_{org}$ values, with lower mean values obtained from equation 12 (1.35 ± 0.54%) than the ones derived from equation 6, used in global literature (1.83 ± 1.06%). When comparing results for %C$_{org}$ calculations within individual sites, only Cowes presented no statistically significant differences (p= 0.342), even though mean %C$_{org}$ values calculated by the developed regression equation were higher than the ones derived from the global literature, 0.83 ± 0.20% and 0.78 ± 0.41% respectively.

%C$_{org}$ values obtained from the regression equation (equation 12) were also compared against %C$_{org}$ equations from a recently published study assessing blue carbon stocks from *Z. marina* meadows in the southwest coast of the UK (equation 13, Green *et al.*, 2018), using a paired t-test (n=327).

$$\textbf{Equation 13}: \%C_{org} = 0.3708\ \%OM + 0.3732$$

Results from this test also showed statistically significant differences between mean $\%C_{org}$ calculated by both equations (p=0.00), with values obtained using Green *et al.*, (2018) significantly higher than the ones reported above (2.23 ± 0.93%). Therefore, analysis for $\%C_{org}$ in this study were based on equations 6 and 7, derived from the literature (Fourqurean *et al.*, 2012), to provide reliable and comparable results to other studies worldwide. Mean $\%C_{org}$ values were significantly different between sites, ranging from 0.13 ± 0.08% of dry weight in Ryde to 3.06 ± 0.4% of dry weight in Creek Rythe (figure 4.13 and table 4.2).

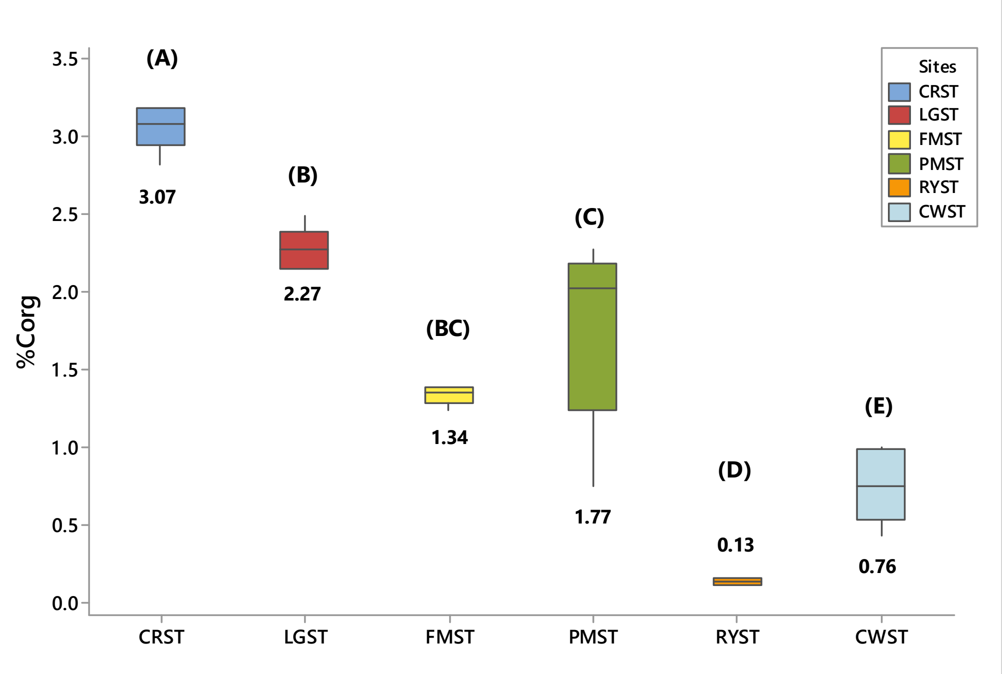


Figure 4.13: Distribution of $\%C_{org}$ values between sampling sites before $Log_{10}(X)$ transformation, including Tukey's grouping results, where the same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range. CRST, LGST, FMST, PMST, RYST and CWST.

Down-core profiles in $\%C_{org}$ displayed variable trends (figure 4.14), with some sites showing general declines in $\%C_{org}$ with depth, such as, Ryde, Farlington Marshes, Porchester and Hayling Island. However, Cowes, with only 20cm deep cores, and Creek Rythe, displayed an overall increase in $\%C_{org}$ with depth from 1.84% at the surface layer, up to 3.35% between 50-100cm deep (figure 4.14). Furthermore, the largest down-core decrease in $\%C_{org}$ was observed in Farlington Marshes, dropping from 2.32% at the surface layer down to 0.67% at 50-100cm deep. For all sites, apart from Cowes, down-core distribution in $\%C_{org}$ was not monotonic, showing alternative increase and decrease with depth.

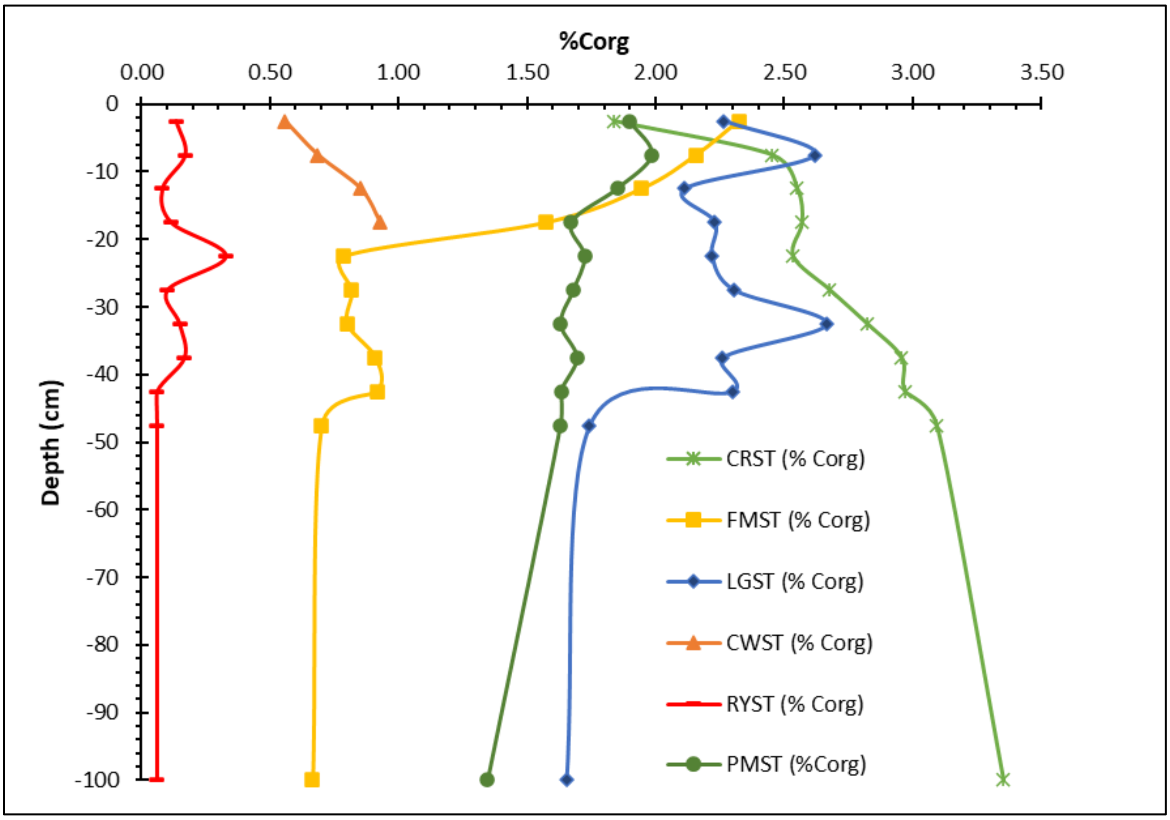


Figure 4.14: Down-core profile of average $\%C_{org}$ for all sampling sites (n=6), CRST, LGST, FMST, PMST, RYST and CWST. All sites had 1m deep cores, apart from Cowes with 20cm deep cores. Each core was divided into 5 cm subsamples, down to 50cm deep, and one larger 50cm subsample between 50 and 100cm deep. Adding to 11 subsamples, per 1m deep core, 5 cores per site.

4.4.5.3 Sediment Carbon Content (C_{stock})

Mean sediment organic carbon content (C_{stock}), including below-ground biomass, for the top metre of soil (or until refusal at Cowes) varied significantly between sampling sites, ranging from 10.09 ± 2.27 MgC ha^{-1} to 181 ± 16.24 MgC ha^{-1} between Ryde and Creek Rythe, respectively (table 4.2; figure 4.15). Mean sediment C_{stock} between all studied sites was 103.12 ± 71.48 MgC ha^{-1} (n=30). Creek Rythe presented significantly higher C_{stock} values than all other sampling sites, while both sites at the Isle of Wight, Cowes and Ryde, presented sediment C_{stock} values approximately ten times lower than all other sampling sites.

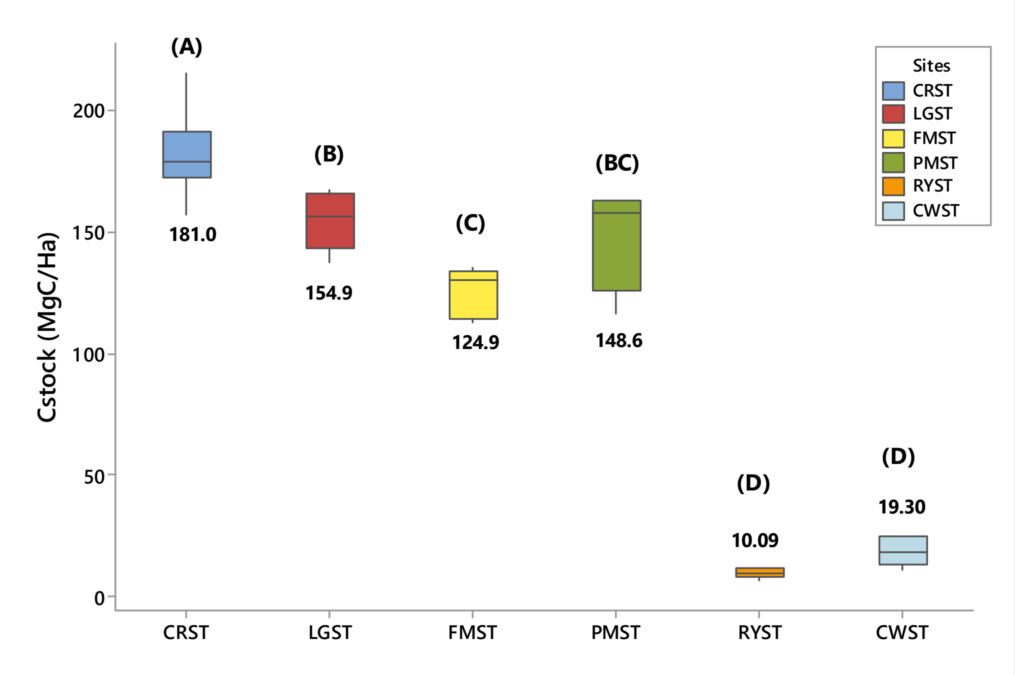


Figure 4.15: Distribution of sediment organic carbon content C_{stock} values for all sampling sites CRST, LGST, FMST, PMST, RYST and CWST, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

Results from correlation tests showed that there was a strong negative correlation between mean particle size (μm) and C_{stock} (r= -0.762; p= 0.000), further investigated in chapter 5. However, no significant relationships were found between sediment carbon content and below or above-ground biomass, and leaf density.

A regression model was developed to determine if C_{stocks} could be predicted from DBD values. The regression analysis was a good fit to the data (R^2 = 86.8%, p=0.000), demonstrating the negative relationship between C_{stock} and DBD (figure 4.16) values could be described by the following equation (equation 14):

Equation 14: $C_{stock} = 317.9 – 209.4*DBD$

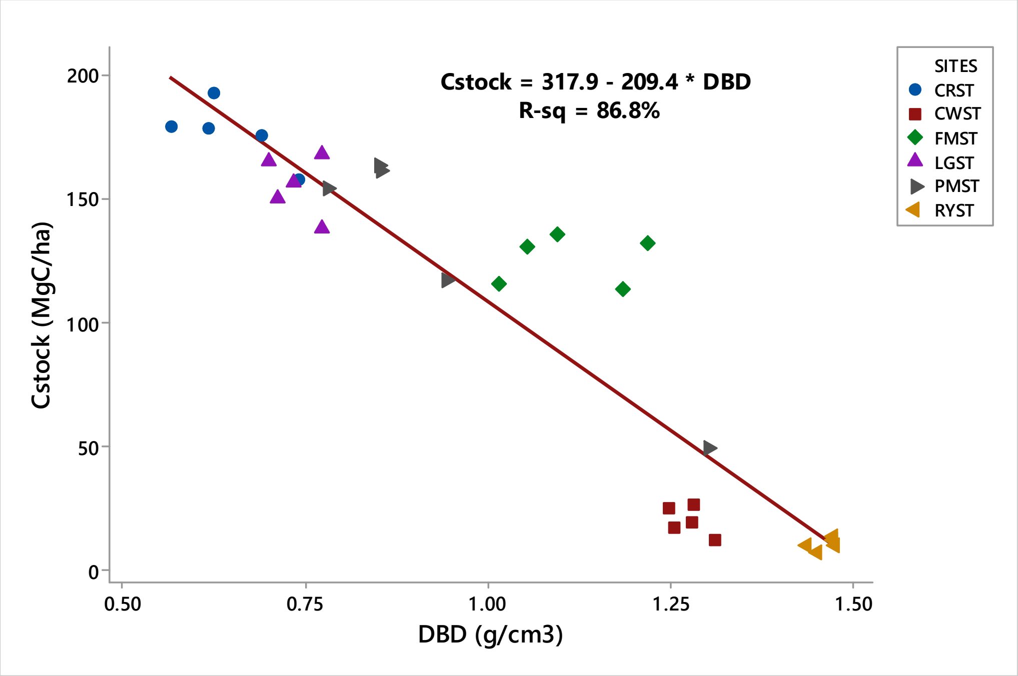


Figure 4.16: Relationship between Dry bulk density (g cm^{-3}) and C_{stock} (MgC ha^{-1}) for all sites, CRST, LGST, FMST, PMST, RYST and CWST. Model equation and R-sq value included.

4.4.6 Comparison between seagrass and un-vegetated sediment organic matter and carbon content

Average %OM was significantly higher in sediment cores from un-vegetated sampling points than ones within seagrass beds for all sampling sites, apart from Hayling Island and Porchester (table 4.3). Un-vegetated 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 un-vegetaded sediments (table 4.3, figure 4.17).

Table 4-3: Summary of statistical results for T-Test between %OM (Mean ± standard deviation) from sediment cores on seagrass and un-vegetated 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	0.00
	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	8	-0.97	0.36
	Un-vegetated	5.58 ± 1.15	5			
Ryde (RYST)	Seagrass	0.84 ± 0.08	5	7	-7.31	0.000
	Un-vegetated	7.14 ±1.96	4			

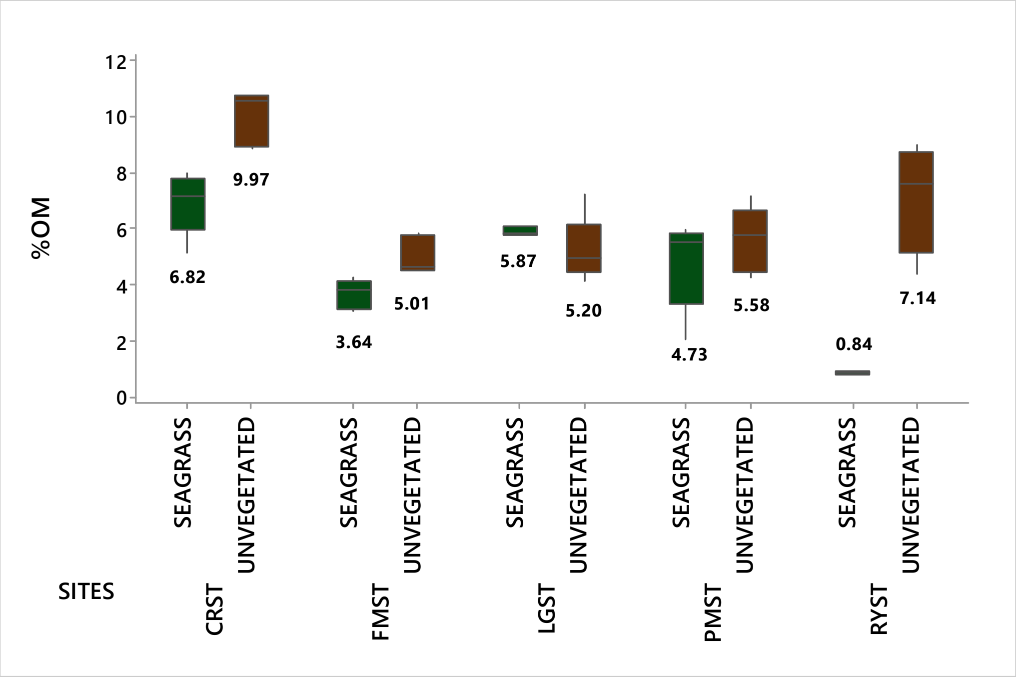


Figure 4.17: Average %OM from seagrass and adjacent mudflat sediment cores for the sampling sites, CRST, LGST, FMST, PMST, RYST and CWST, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

Similarly, to %OM, mean %Corg was significantly higher on un-vegetated sediment cores from Creek Rythe, Farlington Marshes and Ryde (table 4.4, figure 4.18). Un-vegetated sediment cores from Creek Rythe also had the highest %Corg out of all sites, of 3.96 ± 0.42%, followed by Ryde 2.42 ± 0.67%, which showed the highest difference in %Corg between seagrass and un-vegetated sediments, of 2.29% (table 4.4, figure 4.18).

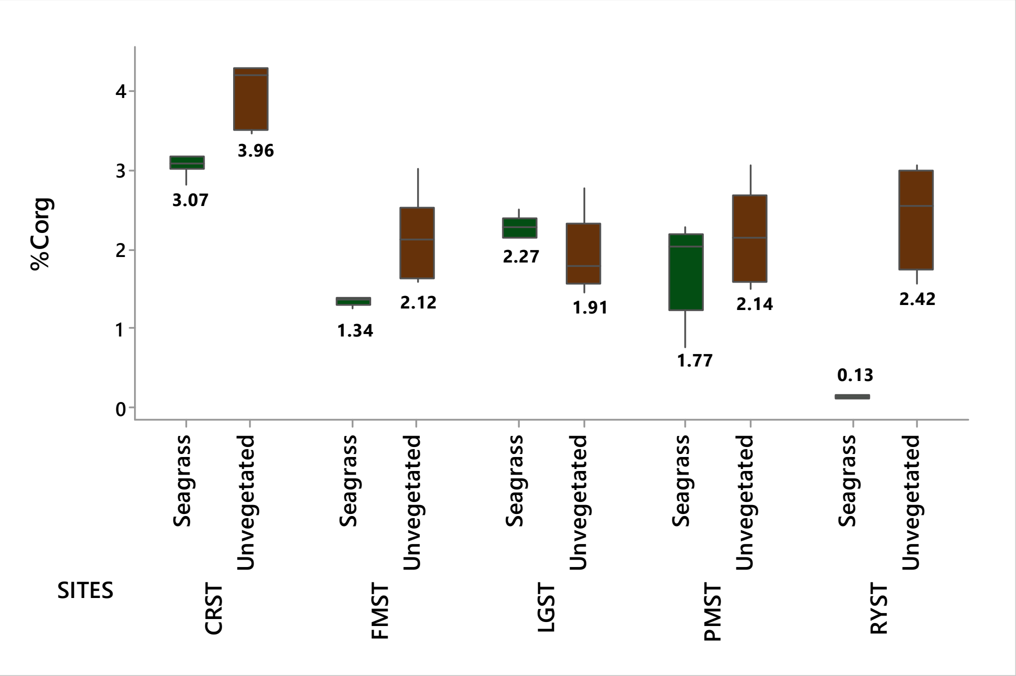


Figure 4.18: Average %C_{org} from seagrass and adjacent mudflat sediment cores for the sampling sites, CRST, LGST, FMST, PMST, RYST and CWST, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

Table 4-4: Summary of statistical results for T-Test between %Corg (Mean ± standard deviation) from sediment cores on seagrass and un-vegetaded 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	2.71 ± 0.39	10	13	-5.72	0.00
	Un-vegetated	3.96 ± 0.42	5			
Hayling Island (LGST)	Seagrass	2.27 ± 0.14	5	8	1.54	0.162
	Un-vegetated	1.91 ± 0.50	5			
Farlington Marshes (FMST)	Seagrass	1.34 ± 0.06	5	12	-3.74	0.005
	Un-vegetated	2.12 ± 0.49	9			
Porchester (PMST)	Seagrass	1.77 ± 0.61	5	8	-0.95	0.371
	Un-vegetated	2.14 ± 0.61	5			
Ryde (RYST)	Seagrass	0.13 ± 0.02	5	7	-7.79	0.000
	Un-vegetated	2.42 ± 0.67	4			

4.5 Discussion

The main results from this chapter contribute to global blue carbon research by reporting the first direct assessment of sediment carbon stocks in the top metre of temperate, intertidal, seagrass meadows in the U.K. Results showed that seagrass meadows from the Solent form significant carbon stocks, on average 103.12 ± 71.45 MgC ha^{-1}, comparable to other global regions (Fourqurean *et al*., 2012a). Additionally, this chapter also demonstrates the variability in sediment carbon stocks, sediment characteristics, above-ground biomass, leaf density, and below-ground biomass, in the form of roots and rhizomes, between sampling sites within the Solent estuarine system. Furthermore, this chapter provides, a comparison between sediment carbon stocks within seagrass meadows and adjacent, un-vegetated, sampling points contributing to the knowledge of seagrass meadows export of organic matter to neighbouring ecosystems.

4.5.1 Living Biomass

Marsden and Chesworth's (2015) inventory identified the first records for seagrasses in the study sites: Portsmouth Harbour 1886; Chichester Harbour 1915; Langstone Harbour 1956; Ryde 1977; and Cowes 1979. The fact that the sampling sites on Chichester Harbour, Hayling Island and Portsmouth Harbour, reported as the oldest meadows, presented higher above-ground biomass values than the younger sites from the Isle of Wight, conform with results obtained by Serrano *et al*. (2016), showing a tendency for high-biomass, persistent and 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 above-ground biomass from the studied seagrass meadows was 0.28 ± 0.0.08 MgC ha^{-1}, 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). Variability among seagrass species, have been reported as a factor that can affect carbon storage potential, with species-habitat interactions likely to strongly impact the storage of C_{org} in both the sediment and living biomass (Lavery *et al*., 2013). For example, 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 (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 (force exerted by water on the sediment) by up to 90% (Hansen and Reidenbach, 2012). Even though above-ground biomass only contributes to 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). This could explain the significant difference in sediment carbon density between Farlington Marshes and the Isle of Wight sites, Ryde and Cowes, when considering the former's higher above-ground biomass values. These results suggest that seagrass canopy and above-ground biomass could be one of the factors influencing the variability of organic carbon stocks in the Solent region.

The lack of a significant relationship between number of leaves and above-ground biomass, can be explained by the high standard deviation in plant density found in some of the sites, like Ryde, suggesting a less uniform cover and patchness, even though quadrats were sampled from areas with a high percentage of plant coverage (e.g. within 10m from the edge of the meadow). The average leaf density across all sites was 394 ± 268 leavess/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 patchness, 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 recognised in Calshot was *Z. marina*, unlike the intertidal meadows analysed in this study, where *Z. angustifolia* was found in all sampling 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 also found in Creek Rythe and Hayling Island, in small mixed patches. Cowes was the only sampling site with predominance of *Z. marina*, with a mean leaf density of 346 ± 247 leaves/m^2, still higher than the ones 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).

A recent assessment of the environmental health of seagrass ecosystems in the British Isles showed that most seagrass sites are subject to some level of anthropogenic disturbance, such as mooring and anchoring, as well as high levels of turbidity (Jones and Unsworth, 2016). As well as anthropogenic disturbance, the extent of seagrass meadows in the UK has also been reduced due to natural disasters, such as wasting disease episodes (Muehlstein *et al*., 1988; Davison and Hughes, 1998; Garrard and Beaumont, 2014; Marsden and Chesworth, 2015; Jones and Unsworth, 2016). These disturbances promote the increase in sediment organic matter mineralisation, which can also be directly proportional to increases in below-ground biomass, related to the input of fresh carbon sources into the system (Villa and Bernal, 2017). Results from this study, however, do not support this theory, as the higher values for below-ground biomass were found in Hayling Island, considered one of the most pristine of the sites.

Seagrass rhizomes and roots have important roles in binding and stabilising the sediment, however, while many studies focus on estimating sediment carbon stocks and above-ground biomass linked to net primary production, less attention has been given on below-ground biomass and carbon stocks in seagrass roots and rhizomes (Tomlinson, 1974; 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 (Sand-Jensen, 1975; Jacobs, 1979; Kirkman *et al*., 1982; Kenworthy and Thayer, 1984; Wittman, 1984; Dennison *et al*., 1987). This corroborates the results from temperate seagrass meadows in the Solent dominated by *Zostera* spp., where most of the biomass was found above-ground, rather than in roots and rhizomes.

Average below-ground biomass from the Solent'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 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 living seagrass biomass globally is buried in their soil as rhizomes and roots, which contradicts results found for the temperate species studied in this chapter. In the Solent, highest below-ground biomass was found in carbon rich sites, 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 below-ground biomass/ sediment carbon stocks ratio of 0.084 ±0.062 %. Furthermore, due to the overall low contribution of root and rhizome biomass to below-ground carbon stocks (<1%), it is safe to quantify sediment carbon stocks for temperate seagrass meadows in the Solent without removing roots and rhizomes.

4.5.2 Particle size and sediment density

It has been suggested 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 above-ground biomass, have sediments with a larger mean grain size and moderately sorted. 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 contains a greater amount of carbon (Armitage and Fourqurean, 2016). This would explain why the Isle of Wight sites, Ryde and Cowes, with predominantly sand sediments, showed the lowest organic carbon storage among the studied sites. The strong relationship between sediment silt content and C_{stocks} show that the physical properties of the particle sizes can be determining factors for carbon storage in seagrass systems. These relationships are discussed further in chapter 5.

Dry bulk density, 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 dry bulk density for all sediment cores analysed was 1.01 ± 0.32 g/cm^3, in accordance with the reported global seagrass mean dry bulk density of 1.03 ± 0.02 g/cm^3 (Fourqurean *et al*., 2012a). Moreover, dry bulk density 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). The significant positive relationship between median grain size and dry bulk density reported in this chapter, explains why sites with less sediment compaction and higher median grain size, and more sand particles, like Ryde, have lower %C$_{org}$.

These results support the hypothesis 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 tend 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, sand, particles, and lower compaction and larger interstitial spaces, results in remineralisation of stored carbon, and lower sediment C$_{stocks}$, as at Ryde and Cowes (Serrano *et al*., 2016, Serrano *et al*., 2018; Gullström *et al*., 2018). These relationships between compaction and remineralisation of stored carbon explain how dry bulk density values could be safely used as a proxy to determine C$_{stocks}$ from the sediment of seagrass meadows in the Solent, using the linear equation established in this chapter (Equation 14).

4.5.3 Sediment C$_{stock}$

The mean sediment carbon stock value for the top metre of sediment of 103.13 ± 71.45 MgC ha^{-1} found in this study falls below Green *et al*. (2018) estimations from subtidal *Z. marina* meadows from the West coast of the UK (table 4.5). 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 from extrapolated 30cm cores, which could 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). 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. Moreover, when using the seagrass meadows areal extent reported by Marsden and Chesworth's (2015) survey, the total organic carbon stock in the top metre of sediment at the studied sites, including below-ground biomass, was 54.7 x 10^3 MgC ha^{-1}. 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. Therefore, based on these values, the amount of carbon stored in the Solent's seagrass meadows sediments is ten times higher than the reported estimated average for sediment blue carbon in UK's seagrass meadows.

Table 4.5 shows seagrass sediment C_{stocks} reported in previous studies, from different parts 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*., 2017b) These results show that seagrass sediment carbon stocks in the Solent region, UK are comparable to results from tropical sites, especially in Australia and Indonesia. The mean value of sediment organic carbon content stored in the Creek Rythe site at 181 ± 16.24 MgC ha^{-1}, is comparable to the suggested global mean range of 165.6 MgC ha^{-1} (table 4.5).

Table 4-5: 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 the present study (in bold). * represent studies where C_{stocks} down to 1metre 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)
Multispecies	**Central Southern England, UK**	**0-100 (or to refusal)**	**103.13 ± 71.45**	**Present Study**

The results of this study show that sheltered sites with older meadows like Creek Rythe in Chichester Harbour have significantly higher C_{stocks} than disturbed and younger sites like Farlington Marches in Langstone Harbour and Porchester in Porstmouth Harbour, even though they have similar sedimentary environments. The most recently recorded sites, with the greatest wave exposure (Ryde and Cowes), had a significantly lower amount of organic carbon stored in their sediments. It is also important to highlight that the sediment cores from Cowes were the shortest amongst all other sites, 20cm deep, which suggests a lower ability to store sediment C_{stocks} as well as the other study sites.

Carbon sequestration rates in restored meadows are expected to be lower than mature meadows, although increasing gradually over time, which could directly affect the depth of seagrass carbon pools, as well as their storage potential (Garrard and Beaumont, 2014). Villa and Bernal (2017), also 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).

It is important to note the observed difference in $\%C_{org}$ down-core trends between the study sites. 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 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). The age of the sediment layers, as well as sediment accretion rates, will be further analysed and discussed in chapter 6.

In addition, 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; Mazarrasa *et al*., 2017b). However, the fate of allochthonous carbon on 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). To address this, this study provided a comparison between %OM and %C_{org} from cores within un-vegetated sampling points, neighbouring seagrass meadows, and the ones within seagrass meadows. Sediment cores from un-vegetated sampling points had significantly higher %OM and %C_{org} values than sampling points within seagrass meadows on Creek Rythe, Farlington Marshes and Ryde (tables 4.3 and 4.4). Furthermore, Creek Rythe, the site with the highest reported seagrass meadow areal extension, of 100.24 ha, and highest mean seagrass sediment C_{stock} of 181.0 ± 16.24 MgC ha^{-1}, also presented the highest %OM (9.97 ± 0.98%) and %C_{org} (3.96 ± 0.42 %) from neighbouring un-vegetated sediment cores. Conversely, Ryde presented the second largest %OM (7.14 ± 1.96%) and %C_{org} (2.42 ± 0.67 %) within un-vegetated sampling points, even though Ryde's seagrass meadows sediment C_{stock} was the lowest between all sampling sites, of 10.09 ± 2.27 MgC ha^{-1}.

Serrano *et al*. (2016) reported that seagrass meadows and un-vegetated sediments in environments conducive for depositional processes (i.e., estuaries) accumulated up to 400% more mud compared to other coastal ecosystems. This would explain the higher or similar %OM found in un-vegetated sediments compared to seagrass sediment cores, for most sampling sites in the Solent. 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*., 2017b). Serrano *et al*. (2016) also concluded that in estuarine seagrass ecosystems, sediment C_{org} originated from both mud inputs linked to allochthonous C_{org} via deposition from upstream transport and seagrass inputs. Similarly, 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 un-vegetated areas and deeper ocean zones, based on a review from 65 published reports. Kennedy *et al*., (2010) compared the organic carbon isotope signatures between seagrass sediments and those in un-vegetated sediments adjacent to the meadows, concluding that the relative contribution of seagrass to the C_{stock} was similar between seagrass and adjacent un-vegetated sediments. This suggests that the footprint of seagrass meadows on sediment C_{stocks} extends beyond the boundaries of the meadows (Duarte and Krause-Jensen, 2017). 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, un-vegetated reference sites. Even so, they also report a higher variability in sediment C_{stocks} within the meadows then the ones found in this chapter, which could explain their results (Colarusso *et al*., 2016).

4.6 Conclusions

Results from this chapter contribute to gaps in the existing global database on seagrass meadow carbon stocks, which currently lack information from seagrass species in UK 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 representative sediment C_{stocks}. Even though there were significant differences in carbon storage between sites, seagrass meadows in the UK have important carbon sink potential, even comparable with some tropical regions. These results confirm the importance of seagrass ecosystems as CO_2 sinks and the need to protect these large carbon pools in order to avoid remineralisation and resultant GHG emissions.

Furthermore, comparisons between $\%C_{org}$ calculated by different methods, LOI or elemental analyses, as well as comparisons between $\%C_{org}$ calculations using different regression equations based on %OM values, provide important insights on the need to review and update global literature and methods to estimate carbon stocks in seagrass meadows. Results from this chapter also show that the temperate intertidal seagrass meadows of the Solent and adjacent harbours play an important role in carbon cycling and sediment dynamics within the ecosystem, as suggested by the comparisons between organic matter in seagrass and un-vegetated 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 worldwide, in order to accurately assess and quantify their environmental 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, some of which are further discussed in chapter 5.

5 Environmental factors as predictors of carbon stocks in seagrass sediments

5.1 Preamble

Results from this chapter have been published on December 2019, as a paper entitled: 'Environmental drivers of sediment carbon storage in temperate seagrass meadows', on Hydrobiologia's special issue, Trends in Aquatic Ecology III, DOI: https://doi.org/10.1007/s10750-019-04153-5, with first authorship. Other authors added editorial contributions to the paper. It has been established that seagrass ecosystems have great carbon storage potential, acting as important global carbon sinks. However, many researchers have been focusing their studies on a limited range of aspects that could influence seagrass's carbon storage potential, leaving gaps in knowledge as to which factors could be acting in conjunction to regulate carbon uptake. This chapter provides an evaluation of the relationship between a range of variables and carbon storage potential in seagrass meadows. By establishing relationships and trends between variables, this study provides important information on the main environmental factors affecting seagrass carbon storage potential, including those that could be useful in restoration projects. Statistical analysis included tests for analysis of variance, followed by a post hoc test to identify which factors significantly differed between sites. Multiple regression and a Principal Components Analysis were used to aggregate and summarise highly correlated variables and establish their relationship to sediment carbon storage.

5.2 Introduction

Seagrass meadows have a large global extent (17.1 – 60 million ha), with a wide latitudinal distribution, from the arctic to tropical regions, found in widely varied settings, from sheltered estuaries to exposed shores, from intertidal zones down to 90m deep in the ocean (Duarte, 1991; Hemminga & Duarte, 2000, Chmura *et al*., 2003, Carruthers *et al*., 2007; Mazarrasa *et al*., 2018). This variation in distribution and setting, is responsible for the highly variable estimations 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*., 2017b). Recent studies have reported the influence of environmental characteristics on sequestration and storage of C_{org} in seagrass sediments, evidencing the risks of extrapolating regional and global estimates based on limited data sets represented by only a few species and habitats (Nellemann *et al*., 2009; Fourqurean *et al*., 2012a; Lavery *et al*., 2013; Garrard & Beaumont, 2014; Serrano *et al*., 2014; Samper-Villarreal *et al*., 2016; Serrano *et al*., 2016; Mazarrasa *et al*., 2018). The variability of seagrass carbon stocks must be considered for implementation of blue carbon projects with the aim of climate change mitigation, as well as to identify areas with potential to become future CO_2 sources (Herr and Landis, 2016; Herr *et al*., 2017). For this reason, it is essential to promote research to improve understanding of the principal factors that influence carbon sequestration and storage in seagrass sediments, as well as those that may cause disturbance, resulting in CO_2 emissions through remineralisation of sediment carbon deposits (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 biomass); the retention of allochthonous carbon into the sediment; and carbon burial efficiency in seagrass sediments (Mazarrasa *et al*., 2018). These mechanisms have been reported to be positively related to anoxic conditions within the sediments, the proportion of fine particles, and refractory, molecularly complex, carbon being stored (Mateo *et al*., 2006; Serrano *et al*., 2016; Mazarrasa *et al*., 2018).

Seagrass sediment's organic carbon content (C_{stock}), may remain deposited for millennia, constituting a long-term carbon sink (Duarte, 2010). Carbon accumulated within seagrass sediments can be derived from autochthonous sources, including the living below-ground biomass (i.e. roots and rhizomes) and plant detritus, and allochthonous sources ingrained in the sediment matrix mainly deposited from the water column (e.g. sestonic carbon) (Gacia *et al*., 2002; Mateo *et al*., 2006; Kennedy *et al*., 2010). However, between these two sources, autochthonous C_{stocks} from living above-ground biomass, which may be exposed to aerobic conditions and herbivory, is considered a short-term carbon sink with little contribution to seagrass meadows' total C_{stocks} (Enriquez *et al*., 1993; Mateo *et al*., 2006; Fourqurean *et al*., 2012b; Mazarrasa *et al*., 2018).

Seagrass meadows have been experiencing a global decline estimated at 7% per year, which exposes sediment C_{stock} to erosion and aerobic conditions, potentially leading to CO_2 emissions (Waycott *et al*., 2009; Marbà *et al*.,2014; Serrano *et al.*, 2016; Lovelock *et al*., 2017; Mazarrasa *et al*., 2018). This decline in seagrass C_{stocks} has been driven by a range of anthropogenic disturbances related to eutrophication (e.g. organic matter and nutrient loading in coastal waters), shading, shoreline erosion, warming, and physical removal by trawling and anchoring, particularly during the last century (Duarte, 2002; Orth *et al*., 2006; Ralph *et al*., 2006; Macreadie *et al*., 2012; Marbà *et al*., 2013; Duarte, 2014).

Several studies have reported a negative relationship between increased turbidity and seagrass meadow survival, as a result of eutrophication (Short and Wyllie-Echeverria, 1996; Waycott *et al*., 2009; Jones and Unsworth, 2016). Conversely, other studies have shown that eutrophication and nutrient loading might favour the accumulation of allochthonous carbon (e.g. microalgae and epiphyte bloom) in the 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). Other studies have shown that despite increasing carbon accumulation rates, organic deposits derived from allochthonous sources are chemically weaker (labile), and more prone to remineralisation triggered by microbial activity, when compared with autochthonous, seagrass derived, carbon deposits (Enriquez *et al*., 1993; Macreadie *et al*., 2012).

Other drivers of degradation, such as climate change, also aggravate seagrass decline, as a result of multiple impacts including ocean acidification, and increases in sea surface temperature (SST) rise and sea level (Short and Neckles, 1999; Jordą *et al*., 2012; Saunders *et al*., 2013; Valle *et al*., 2014). Even though global trends of SST rise will not be uniform, with regional, seasonal and annual differences, the Intergovernmental Panel on Climate Change (IPCC) expect a mean increase between 2.6 °C− 4.8 °C until 2100 (IPCC's 8.5 RCP scenario) (IPCC 2013; Repolho *et al*., 2017). Over the same period, global average ocean pH is expected to decrease 0.13–0.42 units by the end of this century, falling to between 8.05 and 7.6, depending on the divergent concentration pathways reported in IPCC scenarios (IPCC, 2013; Garrard and Beaumont; Repolho *et al*., 2017).

Increases in ocean temperature have been linked with disturbance in seagrasses growth and distribution, with direct effects on the rate of photosynthesis and consequent nutrient uptake (Lee *et al*., 2007; Koch *et al*., 2013; Thomson *et al*., 2015; Repolho *et al*., 2017). Higher temperatures may promote an initial increase in photosynthesis rates but this is likely to be followed by a rapid decline after optimum enzymatic temperatures are reached, and accompanied by faster growth and respiration rates, which leads to a net negative carbon balance (Lee *et al*., 2007; Dhir, 2015; Repolho *et al*., 2017).

Additionally, ocean acidification has been linked to increases in photosynthetic rates due to the increase in the concentration of aqueous CO_2 as a primary carbon source, and dissolved inorganic carbon as bicarbonate ions (Garrard and Beaumont, 2014; Repolho *et al*., 2017). However, the effect of ocean acidification on the sequestration of autochthonous C_{org} and seagrass biomass still needs to be clarified, with some studies suggesting increases in sequestration rates under acidic conditions (Palacios and Zimmerman, 2007; Hall-Spencer *et al*., 2008; Fabricius *et al*., 2011; Russell *et al*., 2013; Garrard and Beaumont, 2014; Mazarrasa *et al*., 2018) and others reporting substantial decrease (Martínez-Crego *et al*., 2014; Repolho *et al*., 2017).

Sea level rise will lead to changes in water depth, which could result in a reduction in submarine irradiance, caused by the increase in water depths coupled with the potential increase in concentration of suspended particles, washed in by coastal erosion (Mazarrasa *et al*., 2018). This increase in turbidity will presumably reduce seagrass net primary production and consequent C_{org} sequestration in deeper waters, but, in contrast, possibly enhance C_{org} sequestration in intertidal meadows in regions where the rise will be more pronounced in low tides, reducing dry periods (Short and Neckles, 1999; Saunders *et al*., 2013). Sea level rise could also cause changes in salinity levels, due to saltwater intrusion, resulting in the movement of seagrasses towards landward edges, into areas formerly covered by mangroves or saltmarshes (Saunders *et al*., 2013; Valle *et al*., 2014).

Nevertheless, it is clear that anthropogenic and climatic changes in the ocean's physical and chemical properties are expected to disturb organisms' biological and physiological homeostasis, and negatively impact marine ecosystems (Fabry *et al*., 2008; Rosa *et al*., 2014; Repolho *et al*., 2017). Thus, understanding the response of seagrass ecosystems to climate change and anthropogenic stress has become a priority for the development of effective conservation, management and protection within blue carbon projects (Brierley and Kingsford, 2009; Hoegh-Guldberg and Bruno, 2010; Valle *et al*., 2014). It is vital to draw attention to the potential that environmental stressors can act in synergy and effects will be driven by seagrass species' abilities to tolerate and adapt to different scenarios (Ralph, 1999; Sunda and Cai; 2012; Repolho *et al*., 2017).

The high sensitivity of seagrasses to environmental change and disturbance, evidenced by their reported global decline, confirms the need to protect their habitat, and to understand the environmental thresholds that could threaten their role as long term carbon sinks (Marbà *et al*., 2013; Cullen-Unsworth *et al*., 2014; Jones and Unsworth, 2016; Mazarrasa *et al*., 2018). Therefore, assessments of environmental quality have been increasingly incorporated into ecosystem management, including monitoring programs based either directly or indirectly on seagrass responses to environmental disturbance (Martínez-Crego *et al*., 2008; Montefalcone, 2009; Roca *et al*., 2016). For example, the European Union (EU) Water Framework Directive (WFD) includes the monitoring of these ecosystems as a reference for the ecological status of coastal areas, by using characteristics such as shoot density, percentage 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, 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 impacted 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 environmental factors are geographically biased, being concentrated in tropical and Mediterranean regions, as well as focusing 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*., 2017b; 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*., 2017b), and others comparing between meadows from different geographical regions (Lavery *et al*., 2013; Miyajima *et al*., 2015; Dahl *et al*., 2016; Gullström *et al*., 2018; Rohr *et al*., 2018), which could make a reliable assessment of variability harder. To date, understanding of the interaction between these factors, and their level of influence on the regulation of seagrass sediment C_{stocks}, is still very limited (Serrano *et al*., 2016).

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 different 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 date, no study has evaluated the interaction between environmental factors and seagrass sediment carbon storage at the intermediate (estuary) scale, incorporating different habitat characteristics, and mixed species meadows. Therefore, this chapter reports the results of a study aiming at identifying the key environmental factors influencing carbon storage in intertidal seagrass sediments from different sites within the Solent estuarine complex and adjacent harbours, by providing a comprehensive analysis of the relationships between environmental variables and seagrass sediment carbon storage capacity. The objectives are: 1) to determine the variation between variables across sampling sites. 2) to determine which variables act as drivers for sediment carbon storage in the top 30cm seagrass sediment layer. 3) to establish relationships between each individual variable and carbon stock in seagrass sediments.

Thus, this chapter contributes to global seagrass research by identifying and highlighting the main environmental variables affecting carbon storage in seagrass sediments, further contributing to the understanding of which components need to be taken into account when producing regional (temperate) or global estimations of sediment C_{stocks} in seagrass meadows.

5.3 Study Sites and Methodology

5.3.1 Study Sites

The same six fieldwork sites studied in chapter 4 were revisited during the summer (June-August) of 2018, namely Creek Rythe (CRST) (figure 3.3) in Chichester Harbour, Hayling Island (LGST) (figure 3.4) and Farlington Marshes (FMST) (figure 3.5) in Langstone Harbour, Porchester (PMST) (figure 3.6) in Portsmouth Harbour, and Cowes (CWST) and Ryde (RYST) (figure 3.7) on the Isle of Wight. 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 noltii*, *Zostera angustifolia*, and *Ruppia spp.* meadows (figure3.1) (Marsden & Chesworth, 2015).

However, even though seagrass meadows are present in the region, studies have been reporting water quality issues in the area (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 (figure 3.1), have been classified as eutrophic or at risk of eutrophication (when a water body becomes highly enriched with nutrients such as nitrate and phosphate) 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 Solent estuaries 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).

The EU-WFD describes Chichester Harbour’s estuary as a transitional waterbody, with a wide variety of marine sediment habitats including extensive estuarine mudflats, and intertidal areas often supporting *Zostera* spp. and green algae and saltmarshes (Velegrakis, 2000; Marsden and Chesworth, 2015; Environment Agency, 2016a). Some of the many ecosystem services provided by Chichester

Harbour include: provision of nesting and feeding grounds for birds, residency for common seal colonies, and nursery areas for many species of juvenile fish such as bass (Nelson, 2016; SeaView, 2017). However, levels of dissolved Inorganic Nitrogen (DIN) in Chichester harbour are described as 'Moderate' by the Environment Agency Catchment Data Explorer, with excessive algal growth also being monitored as part of the Nitrates Directive (Environment Agency, 2016a; 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). Recent models indicate that approximately 54% of the total nitrogen load in Chichester Harbour comes from offshore coastal background sources, while nitrogen inputs from freshwater diffuse sources (agricultural and urban) account for approximately 34% of that total (Environment Agency, 2016a).

Similarly, Langstone Harbour was designated as Polluted Water (Eutrophic) under the Nitrates Directive in 2008, with a Nitrate Vulnerable Zone (NVZ) established in its catchment (Environment Agency, 2016a). At the time of the designations there was clear evidence that Langstone Harbour was eutrophic, based on the widespread growth of the opportunistic macroalgae *Enteromorpha spp.* and *Ulva spp*., covering up to 33% of the intertidal area (Environment Agency, 2016a). Available evidence from recent models indicates that the proportion of nitrogen in Langstone Harbour from offshore coastal background sources is approximately 40% of the total nitrogen load; with all nitrogen inputs from freshwater agricultural diffuse sources accounting for 43% of this total (Environment Agency, 2016a).

Likewise, Portsmouth Harbour has dual designation as both a Sensitive Area (Eutrophic) and Polluted Water (Eutrophic) (Environment Agency, 2016a). Macroalgal surveys undertaken in 2009 and 2011, indicate that between 389 and 567 ha of Portsmouth Harbour's intertidal area was covered in macroalgae (density 25 to 100%), representing between 43 and 63 % of the available intertidal area (Environment Agency, 2016a). The nutrient budget for Portsmouth Harbour shows that approximately a quarter of the nitrogen comes from combined freshwater diffuse agricultural sources, with coastal background sources accounting for about two thirds of the nitrogen load and only a small amount of nitrogen coming from sewage works (Environment Agency, 2016a).

On the Isle of Wight, The Eastern Yar (Bembridge Harbour) was also designated as a Polluted Water under the Nitrates Directive in 2008, and a Nitrate Vulnerable Zone (NVZ) (Environment Agency, 2016b). Macroalgal surveys undertaken in 2012 and 2015 indicated that macroalgae covered between 28% and 42% of the available intertidal area (Environment Agency, 2016b). The nutrient budget for Bembridge Harbour showed that diffuse riverine sources of nitrogen from the Eastern Yar dominated (51%) total nitrogen load, while approximately a quarter of this total came from offshore coastal background sources (Environment Agency, 2016b).

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). This supports the idea that the Solent acts as a single estuarine cell, with tidal flows creating complex systems of clockwise re-circulating tidal eddies that direct strong currents primarily towards the Isle of Wight shore (Bray and Cottle, 2003). 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. Langstone Harbour and Porchester have 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 algal mats (Marsden & Chesworth, 2015). At the Isle of Wight sites, Cowes has a MLWS and MHWS tidal range between 0.8-4.2m, while Ryde has a MLWS and MHWS tidal range of 0.2-3.1m, respectively.

Therefore, this chapter analysed relationships between seagrass carbon stocks, sediment and biological factors, from each of the sampling sites, to determine environmental drivers of C_{stocks}. Sediment factors comprised 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 in relation to mean sea level and biological parameters including leaf density, presence of single or mixed species meadows, and patchiness, were also included.

5.3.2 Field Methods

This chapter investigated the effects of environmental factors on seagrass carbon stocks in the top (rhizosphere) layer of sediment from the selected sampling sites (Methods, section 3.2.4). The same five sampling plots used in chapter 4 were revisited during June-August of 2018, for all six sampling sites following the GPS location recorded in 2017 (Methods, section 3.2.2).

One 30cm deep sediment core, or until refusal, was sampled from within the same five 0.25 m^2 quadrats used in chapter 4, providing a total of five sediment cores per site, 30 in total, for pore-water analyses (figure 3.8) (Methods – section 3.2.4). Cores were collected using a Russian corer, with a 5cm diameter. Each core was divided in the field into 5cm depth subsamples, with 6 subsamples per core (Howard, *et al*., 2014). Each subsample was then transferred into individual bags, labelled with location, date, plot, and sample number. Post collection, the sediment subsamples were kept in a cold storage room at 4ºC at the University of Brighton's sediment analysis lab, for < 48 hours prior to analysis. In addition, values from the sediment cores collected in 2017, analysed in chapter 4, for sediment carbon stock, dry bulk density, and particle size, were also used, curtailed to 30cm deep. Above-ground biomass and leaf density values were also derived from data collected in 2017. Seagrass species were identified, and a visual assessment of meadow landscape classifying very patchy (< 20%), patchy (20 ≤70%) or dense (> 70%) cover, was conducted with a walkover of the sites.

Organic matter stored in marine sediments is closely related to mineral surfaces, with finer particles providing more binding sites for sediment C_{org}, whilst also reducing redox potential and remineralization rates (Keil *et al*., 1993; Burdige *et al*., 2007; Pedersen *et al*., 2011; Serrano *et al*., 2016). Mud content, including clay and silt particles (< 63 μm), has been appointed as a better representative fraction of seagrass bulk sediment and their C_{stocks}, rather than solely using clay particles (< 4 μm), as previously suggested by a few studies (De Falco *et al*., 2004; Burdige *et al*., 2007; Pedrosa-Pamies *et al*., 2013; Serrano *et al*., 2016). Therefore, for the analyses performed in this chapter, %mud (4 - 63 μm) has been selected as a factor potentially influencing C_{stocks} in seagrass meadows within the Solent, UK.

5.3.3 Laboratory methods

5.3.3.1 Ion Chromatography

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).

Sediment subsamples were analysed for nutrients within 48h of collection, to prevent organic decomposition (Michalski and Kurzyca, 2006; EPA, 2007). Samples were preserved in a cold room before being prepared for Ion Chromatography (IC) analysis in the laboratory to determine concentration of nitrogen species and sulphate in the pore water.

IC analysis (Thermo Scientific™ Dionex™ AS-DV Autosampler) was conducted using an AS-23 column and sodium carbonate (Na_2CO_3) and sodium bicarbonate ($NaHCO_3$) eluents. The AS-23 carbonate eluent anion-exchange column is particularly recommended to measure oxyhalides in drinking water, ground water, wastewater, and other diverse sample matrices, due to its high capacity and selectivity which facilitate the determination of ions at low-µg/L levels and in the presence of high concentration of chloride, sulphate and carbonate (Thermo Scientifc, 2013).

IC is used for speciation analysis, separating ions based on their charge and retention time, with the possibility of simultaneous detection of anion and cations (Jackson, 2000; Buchberger, 2001; Michalski and Kurzyca, 2005). 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 nitrite (NO_2^-) and sulphate (SO_4^{-2}) peaks were clearly detected (using dilution factor of 2), and the concentration of both anions was converted from mg/L into μM prior to analysis, following the equations below:

Equation 15: (**X***2*1000)*1/46.01 – Where 2 represents the dilution factor and 46.01 the molar mass of NO_2^-.

Equation 16: (**X***2*1000)*1/96.06 - Where 2 represents the dilution factor and 96.06 the molar mass of SO_4^{-2}.

5.3.3.2 pH and Salinity

Salinity (super saturated solution) and pH (super saturated solution) of each pore water subsample was measured in the laboratory, following the 2:5 ratio proposed by Head's (2006) manual. Approximately 3g of dry sediment sample were 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 a mean 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, and calibration was always tested between every 30 samples.

Supernatants from the same (previously stirred) samples used for pH analysis were used to determine salinity levels. Small droplets were applied to a Bellingham + Stanley™ Eclipse Hand Held Refractometer 45-63, to measure sea water content ($^0/_{00}$), corresponding to Practical Salinity Units (PSU). Three replicates of each reading were measured and a mean was calculated. The refractometer was calibrated periodically, by taking a reading using distilled water and checking if the boundary line read "0".

5.3.4 Statistical Analyses

Statistical analyses performed in this chapter included: Anderson-Darling test for normality, ANOVA, Tukey's post hoc test, Pearson's or Spearman's rho's correlations, linear regression model tests, and PLS and PCA multivariate analyses (Methods – section 3.2.1). Normality probability plots and histogram frequency of residuals were tested using the theory-driven Anderson-Darling method for each of the 11 variables (Anderson and Darling, 1954): sediment C_{stock}, dry bulk density (DBD), mean grain size, sorting coefficient, %mud, pH, salinity, nitrite (NO_2^-), sulphate (SO_4^{-2}), elevation and leaf density. When assumptions of normality were not met, variables were transformed using Log_{10} (X) and retested for normality (table 5.1). Site differences between each variable were tested using ANOVA and post-hoc Tukey's test was used to identify significantly different means for each variable, when present [Methods, section 3.2.1 (ii)].

Pearson's correlation tests were used to analyse the relationship between sediment C_{stocks} and: sorting coefficient, pH, salinity, elevation and leaf density. Spearman's rho tests were used to assess the relationship between sediment C_{stocks} and: mean grain size, %mud, nutrients (NO_2^- and SO_4^{-2}). 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) [Methods, section 3.2.1 (iv)].

In addition, a Partial Least Square (PLS) regression and a Principal Component Analysis (PCA) were conducted to test the influence of edaphic, environmental and seagrass-related factors on sediment organic carbon content (mean C_{stock} for the top 30 cm of sediment) [Methods, section 3.21 (v)]. The coding scheme applied to perform the PLS analysis was (-1, 0, +1), which is used to estimate the difference between each component level mean and the overall mean (Minitab, 2017). The model was performed with no cross-validation, so the cumulative fraction (R-sq) of all ten predictors was assessed, to determine which ones had a higher influence in variation of sediment C_{stocks}.

For better analysis and comparability, all graphs have been standardised to show sites from left to right on an East to West geographical direction, starting with inland sites (CRST-LGST-FMST-PMST), followed by the sites on the Isle of Wight (RYST-CWST).

5.4 Results

Of all 11 variables, mean grain size, dry bulk density, %mud, and concentrations of NO_2^- and SO_4^{-2}, failed to meet the assumption of normality of residuals when tested with Anderson-Darling and were transformed prior to analysis of variance (table 5.1). Furthermore, all variables were significantly different between sampling sites, apart from leaf density and concentration of nitrites (tables 5.1 and 5.2).

Table 5-1: 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 ($p<0.05$), n=30.

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	9.57	0.000	0.5504	0.47	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

Table 5-2: Seagrass sediment and vegetation data, including location and elevation of each sampling site. Sites are presented in decreasing order of sediment C_{stock}. Values are presented as mean (± SD), n=30 for all variables, including Tukey's grouping results following ANOVA, where the same letters correspond to statistically similar means for each variable.

Study sites	Coordinates	Meadow extent (ha)*	C_{Stock} (30cm) ** $(MgCha^{-1})$	Vegetation	Leaf density (m^{-2})	Above-ground Biomass $(MgC\ ha^{-1})$	Elevation in relation to msl (m)	Dry bulk density (gdm^{-3})	Mean grain size (µm)	Sorting coefficient (φ)	% Mud	pH	Salinity (‰)	NO_2^- $(µmolL^-)$	SO_4^{-2} (µmolL-)
Hayling Island	50°47'54"N, 0°59'48"W	70.1	51.13 ± 7.84 (A)	*Z. marina / Z. angustifolia / Z. noltii / 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)	2.34 ± 0.31 (A)	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	100.24	45.31 ± 3.53 (A)	*Z. marina / Z. angustifolia / Z. noltii / 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)	2.18 ± 0.53 (A)	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. noltii* 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)	1.23 ± 0.36 (BC)	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)	2.18 ± 0.22 (A)	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. noltii* Very patchy	346 ± 247	0.18 ± 0.07 (BC)	-1.82 ± 0.05 (E)	1.27 ± 0.02 (A)	72.40 ± 36.91 (B)	1.81 ± 0.77 (AB)	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)	0.84 ± 0.04 (C)	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.**

5.4.1 Sediment carbon content (C_{stock})

The mean sediment C_{stock} in the 30cm of seagrass sediment across all six sites was 33.80 ± 18.40 MgCha^{-1} (n=30). However, ANOVA indicated a significant variance in the mean sediment C_{stock} between sampling sites, with Tukey's pairwise comparison showing that Cowes and Ryde had significantly lower sediment C_{stock} values than all other sites, but were not significantly different between themselves. The highest values for sediment C_{stock} within the top 30 cm layer was found in Hayling Island with a mean value of 51.13 ± 7.84 MgCha^{-1} (table 5.2, figure 5.1).

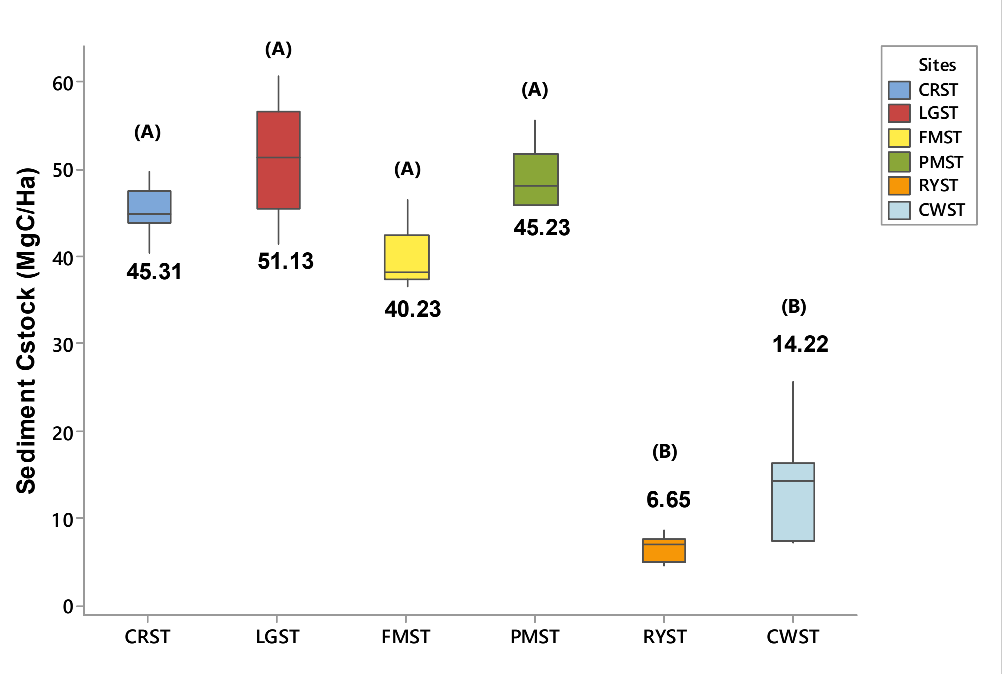


Figure 5.1: Distribution of sediment C_{stocks} values on all sampling sites, Creek Rythe (CRST), Hayling Island (LGST), Farlington Marshes (FMST), Porchester (PMST), Ryde (RYST) and Cowes (CWST), including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

5.4.2 Dry bulk density

The mean dry bulk density (DBD) (g/cm^3) values across all sites was 0.99 ± 0.03 g/cm^3 (n=30), with Ryde and Cowes having significantly higher DBD values than all other sites, above the calculate average (table 5.2). Creek Rythe had significantly lower DBD values than all other sites, apart from Hayling Island. Likewise, Hayling Island's DBD values were significantly lower than Farlington Marshes, Cowes and Ryde (table 5.2, figure 5.2).

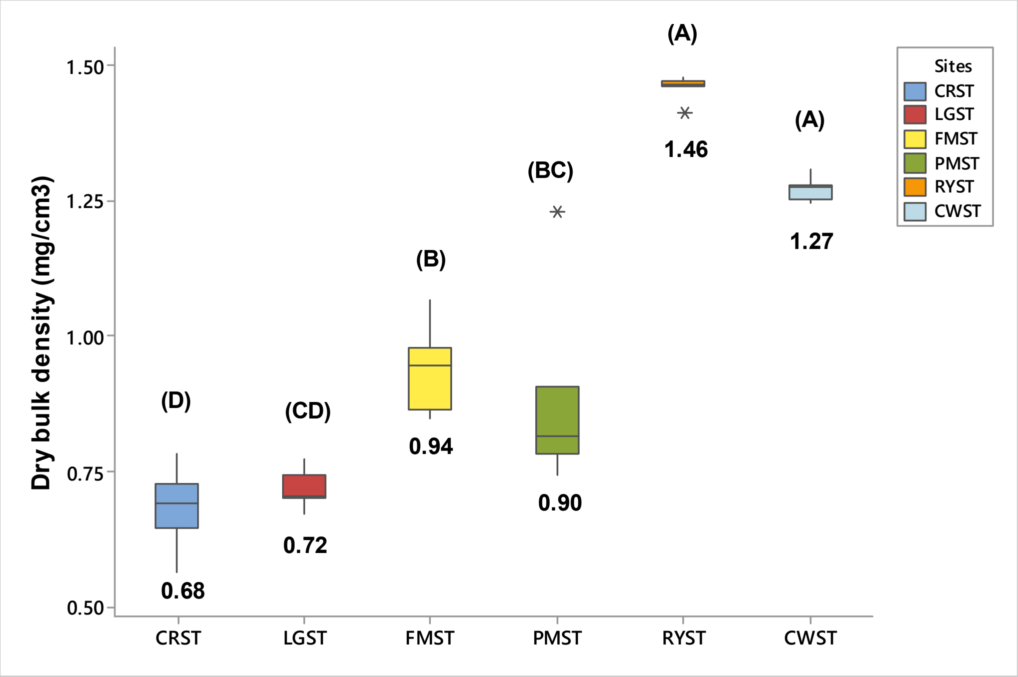


Figure 5.2: Distribution of dry bulk density (DBD) on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST, before transformation, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

5.4.3 Particle size analyses

5.4.3.1 Mean grain size

There were significant differences between the mean grain size (μm from the top 30cm sediment layer of the sampling sites, with Ryde's average sediment particles being significantly larger (225.01 μm) than all other sites (table 5.2 and figure 5.3). Conversely, Hayling Island and Creek Rythe had the finest average grain size values (20.37) across all sites, significantly lower than Cowes and Ryde (table 5.2 and figure 5.3). In addition, all sites were classified as muddy, silt rich, sediments according to the Wentworth scale (1922), apart from the ones in the Isle of Wight, Cowes and Ryde, which contained average grain size (μm) within the class of very fine and fine sand respectively, both significantly different than all other sites.

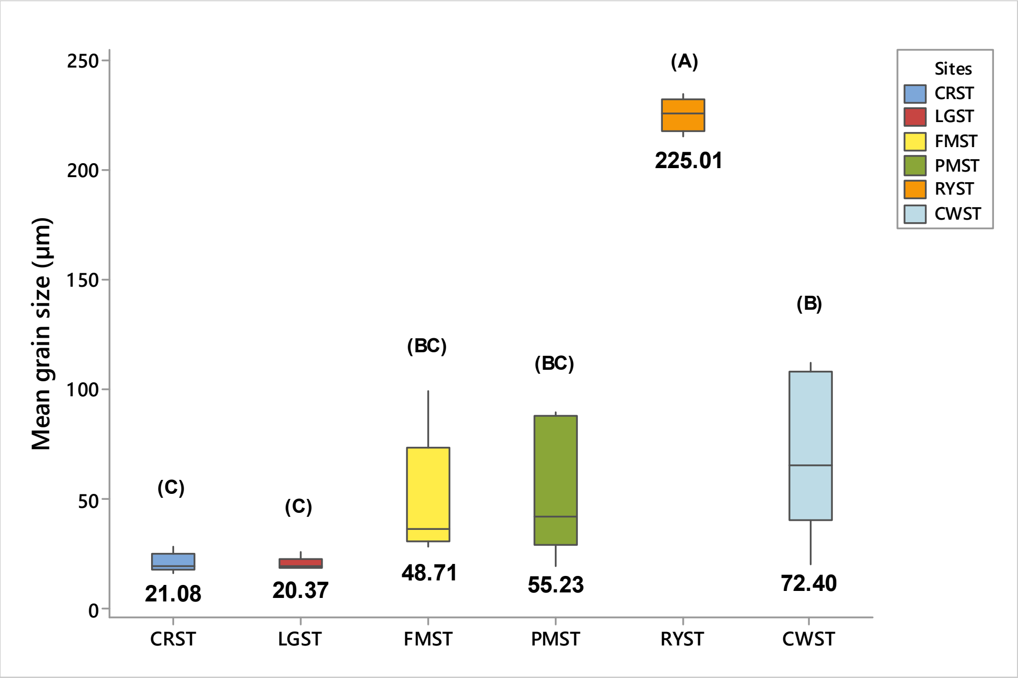


Figure 5.3: Distribution of grain size (μm) on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST, before transformation, including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

5.4.3.2 Degree of Sorting

The degree of sorting from sediment particles from Ryde was significantly lower than all other sites apart from Porchester, being the only one within the moderately sorted class (table 5.2). Hayling Island, Creek Rythe and Farlington Marshes presented the highest sorting coefficients respectively, all being classified as very poorly sorted using Folk and Ward's (1957) classification (methods, section 3.2.3; table 5.2).

5.4.3.3 Mud content (%Silt and Clay)

%Mud (4 - 63 µm) included both silt and clay fractions on all sampling sites (table 5.2). Hayling Island had the highest mean %mud (93.85%), followed by Creek Rythe (87.50%). Both sites had significantly higher %mud than Cowes and Ryde. Ryde had the lowest mean %mud in the top 30cm layer of sediment and was significantly different than all other sites (1.14%) (figure 5.5).

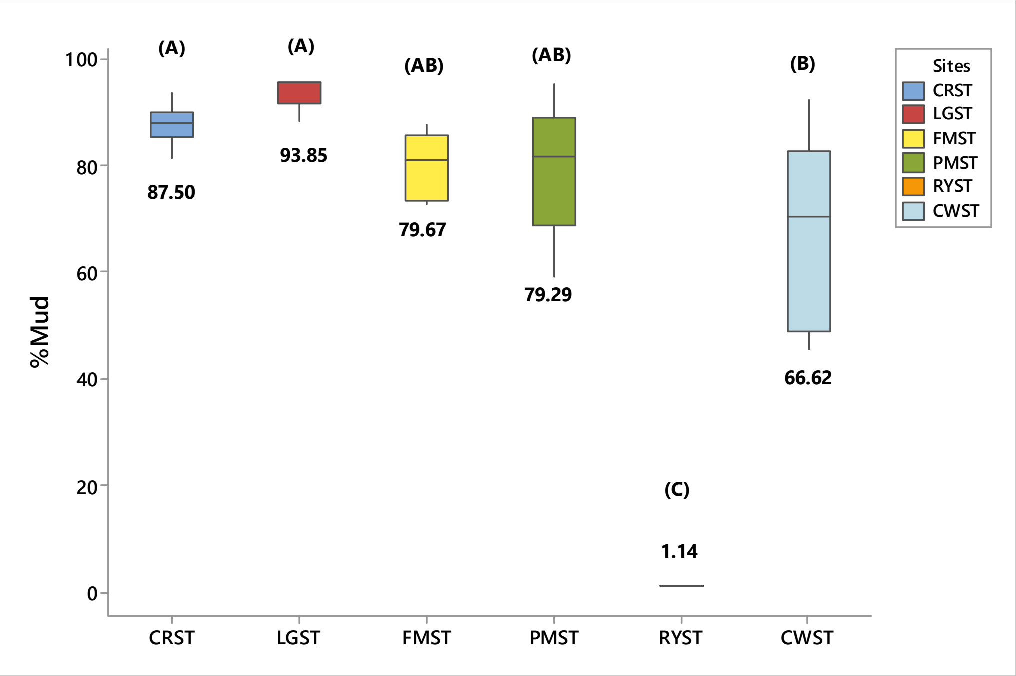


Figure 5.5: Distribution of %Mud values on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST before transformation, including Tukey's grouping analysis of transformed values after ANOVA, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

5.4.4 Pore water pH and Salinity

The average pore water pH values across all sites was 7.28 ± 0.28 (n=30) (table 5.2). Ryde had the highest mean pH value across all sampling sites (7.65 ± 0.33), significantly higher than Creek Rythe, Porchester and Hayling Island (table 5.2, figure 5.6). Moreover, Hayling Island presented the lowest mean pH value (7.07 ± 0.1) across all sites, significantly lower than Ryde and Farlington Marshes (table 5.2, figure 5.6).

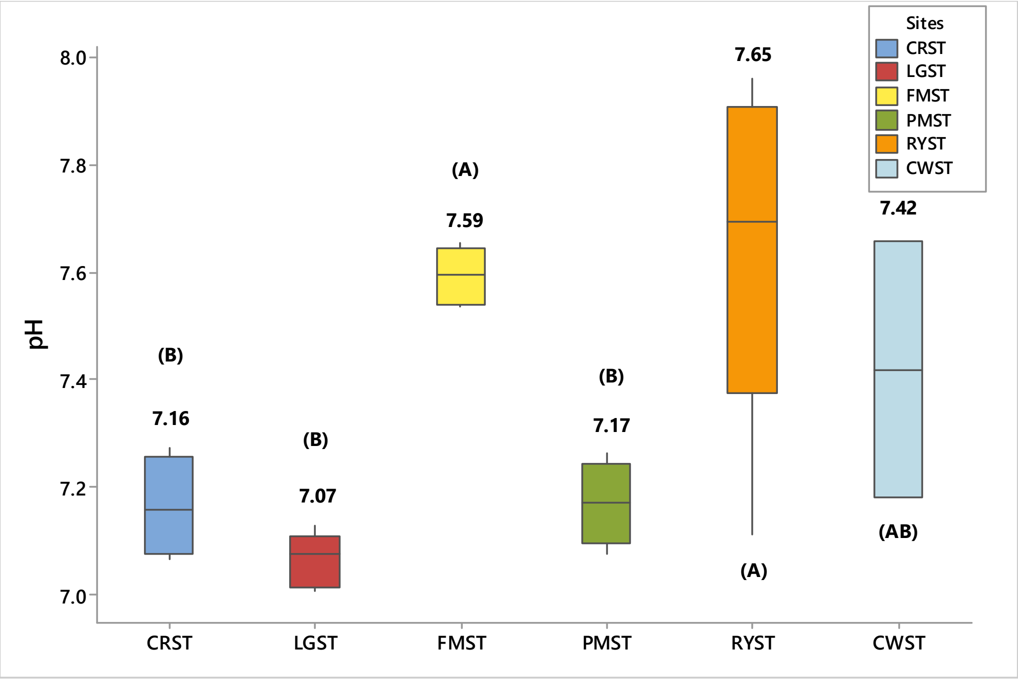


Figure 5.6: Distribution of pH values on all sampling sites CRST, LGST, FMST, PMST, RYST and CWST, including Tukey's grouping analysis after ANOVA, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

Variation in mean salinity levels between sites was examined, with significantly lower levels found in the Isle of Wight's sites when compared against all others (table 5.2, figure 5.7). Ryde had the lowest pore water salinity levels (1.4 ± 0.55 ‰), significantly similar to Cowes (2.0 ± 0.0 ‰), with both Isle of Wight sites having significantly lower salinity levels than Hayling Island, which presented the highest salinity values across all sites (15.6 ± 0.89 ‰) (table 5.2, figure 5.7).

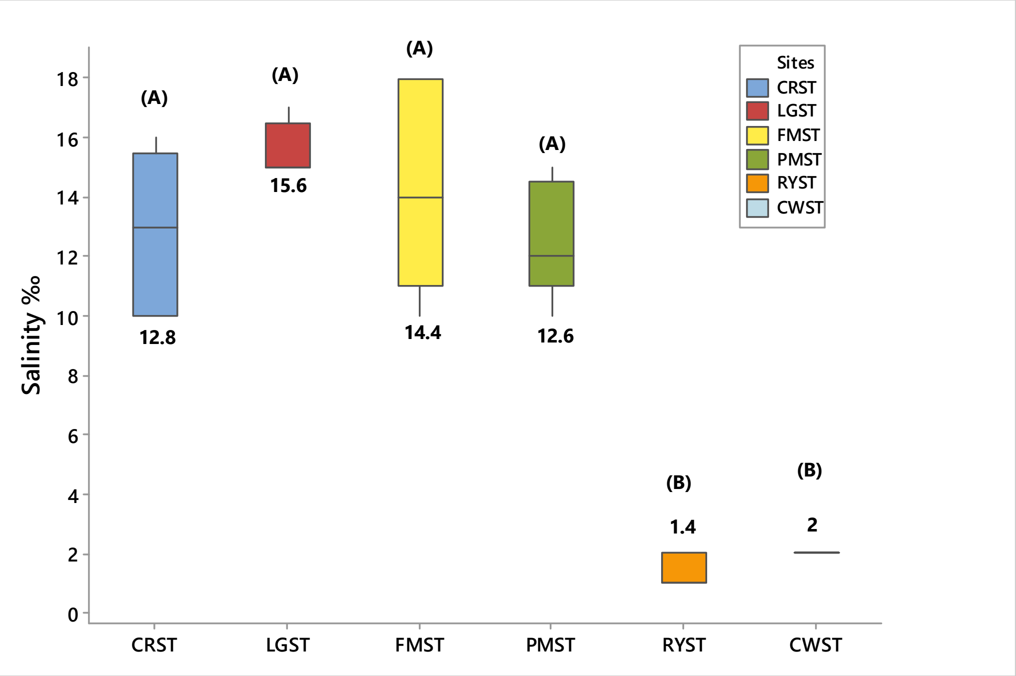


Figure 5.7: Distribution of Salinity levels (‰) on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST, including Tukey's grouping analysis after ANOVA, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

5.4.5 Pore water Nutrients

Mean pore water concentrations of nitrites NO_2^- (μM) and sulphates SO_4^{-2} (μM) in the first 30cm layer of seagrass sediments from the sampling sites showed no significant differences between sites (table 5.2). 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 sediment layers, Cowes to 10cm and Ryde to 15cm depth (figure 5.8). 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 5.8). 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 5.8).

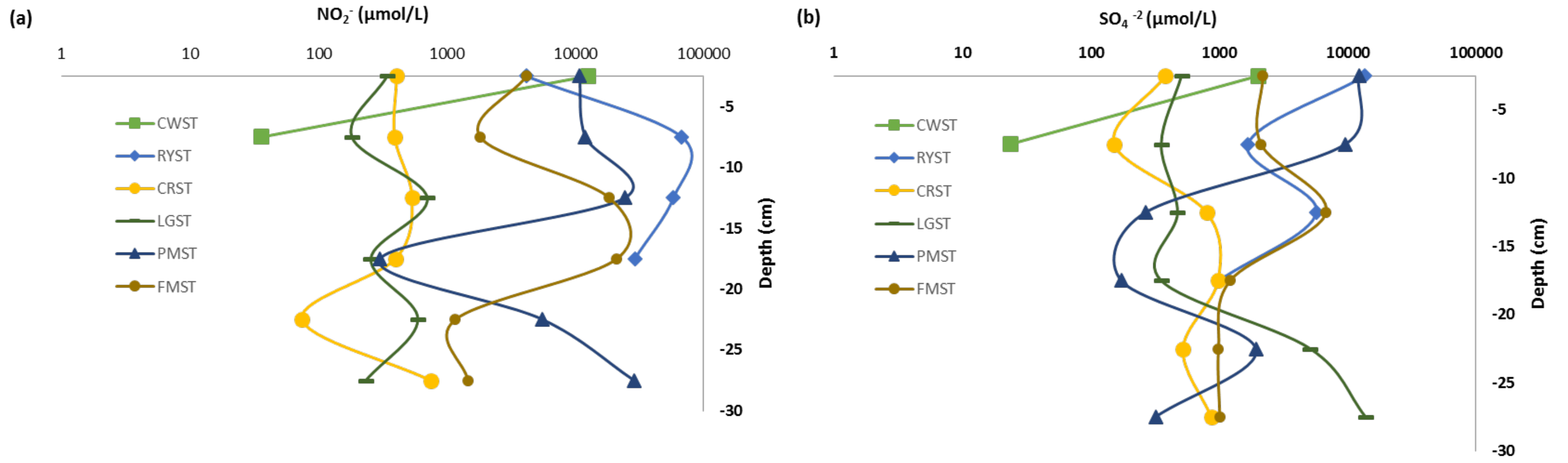


Figure 5.8: Concentrations of nitrites NO_2^- (a) and sulphates SO_4^{-2} (b) $(\mu M)/L$ down-core for all sample sites: CRST, LGST, FMST, PMST, RYST and CWST. Pore water extracted from 30cm sediment cores for all sites, apart from Cowes (20cm). Nutrients concentrations were only detected down to 15cm in Ryde and 10cm deep in Cowes.

5.4.6 Elevation in relation to mean sea level

Seagrass meadows at Cowes were located at a significantly lower elevation in relation to mean sea level than all other sites, at -1.82 ± 0.05m (table 5.2, figure 5.9). Of all the sites, only Farlington Marshes and Creek Rythe were located above mean sea level, which was significantly different than all other sites, at 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 5.2, figure 5.9).

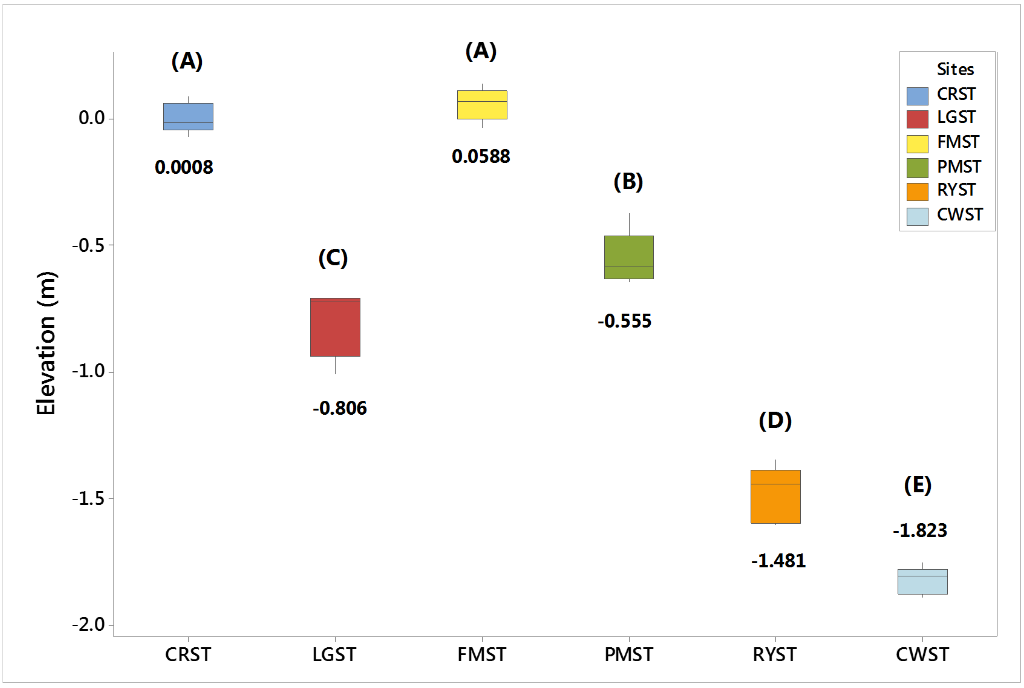


Figure 5.9: Distribution of mean elevation above sea level on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

5.4.7 Vegetation

Average leaf density across all sites was 394 ± 268 leaves/m^2 (n=30) (table 5.2). There was no significant difference in leaf density between sampling sites, but large variations around the means were recorded (table 5.2, figure 5.10). Farlington Marshes presented the widest range of distribution in leaf density values, followed by Ryde and Cowes, contributing to the large variation on the average leaf density across all sites (figure 5.10). Moreover, sites like Creek Rythe, Hayling Island and Porchester seemed to have a more uniform distribution in leaf density between cores (figure 5.10).

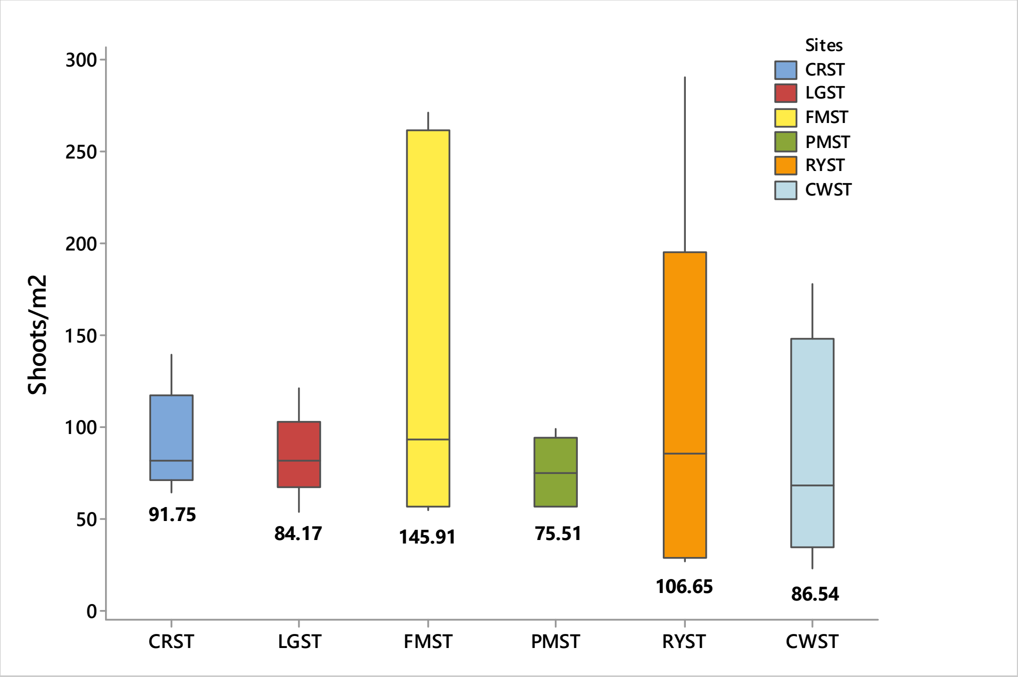


Figure 5.10: Distribution of leaf density values on all sampling sites, CRST, LGST, FMST, PMST, RYST and CWST. Mean values in bold, n =30. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

Z. angustifolia was the predominant species identified in Farlington Marshes and Ryde, and was present at all sites apart from Cowes (table 5.2). The four remaining sites were mixed species meadows, representing greater canopy complexity (table 5.2). At Farlington Marshes and Cowes, seagrass meadows presented very patchy landscape patterns, with un-vegetated sediment between 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 and very little un-vegetated space in between (table 5.2).

5.4.8 Relationships between environmental variables and sediment C_{stock}

5.4.8.1 Sediment Parameters

A regression model was developed to determine if C_{stocks} could be predicted from DBD values. The regression analysis was a good fit to the data ($R^2 = 87.7\%$, $p = 0.00$), demonstrating that the negative relationship between C_{stock} and DBD from the top 30cm sediment layer (figure 5.11) could be described by the following equation (equation 17):

Equation 17: $C_{stock} = 90.95 - 57.44*DBD$

The correlation plot showed that with Ryde, Cowes and Farlington Marshes mostly formed individual groups, with higher DBD and lower sediment C_{stock}, while Creek Rythe, Hayling Island, and Porchester were grouped closer together, displaying lower values for DBD but higher sediment C_{stocks} (figure 5.11).

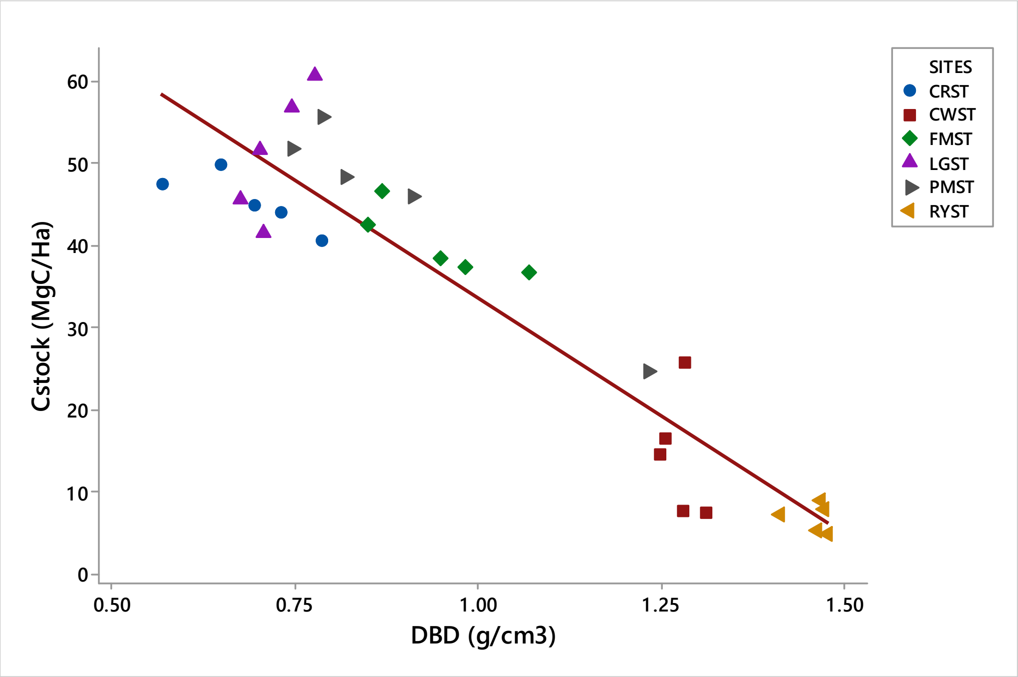


Figure 5.11: Relationship between sediment C$_{stocks}$ (30cm) and dry bulk density (DBD) including linear regression line and equation, R^2 and n values for all sites: CRST, LGST, FMST, PMST, RYST and CWST.

Similarly to dry bulk density, there was a significant negative relationship between mean grain size and sediment C$_{stock}$ (r = -0.712 and p = 0.000) (figure 5.12), but a positive relationship between C$_{stock}$ and sroting coefficient (r = 0.391 and p = 0.033) (figure 5.13). Sites like Ryde, with significantly bigger mean grain particle size and higher sorting coefficient, had the lowest values of sediment C$_{stock}$. However, contrarily to the other sediment parameters analysed, there was a significant positive correlation between %mud and sediment C$_{stocks}$ (r = 0.761, p = 0.004) (figure 5.14). Ryde had the lowest values for %mud across all sites, and the lowest sediment C$_{stocks}$.

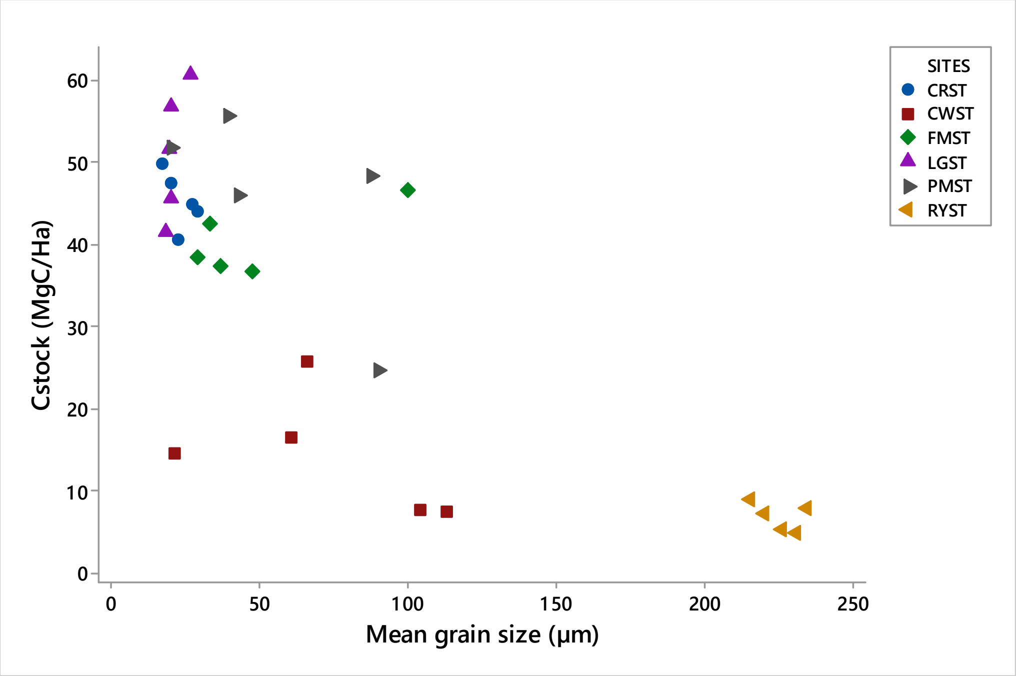


Figure 5.12: C$_{\text{stocks}}$ and mean grain size values from the top 30cm sediment layer for all sites: CRST, LGST, FMST, PMST, RYST and CWST.

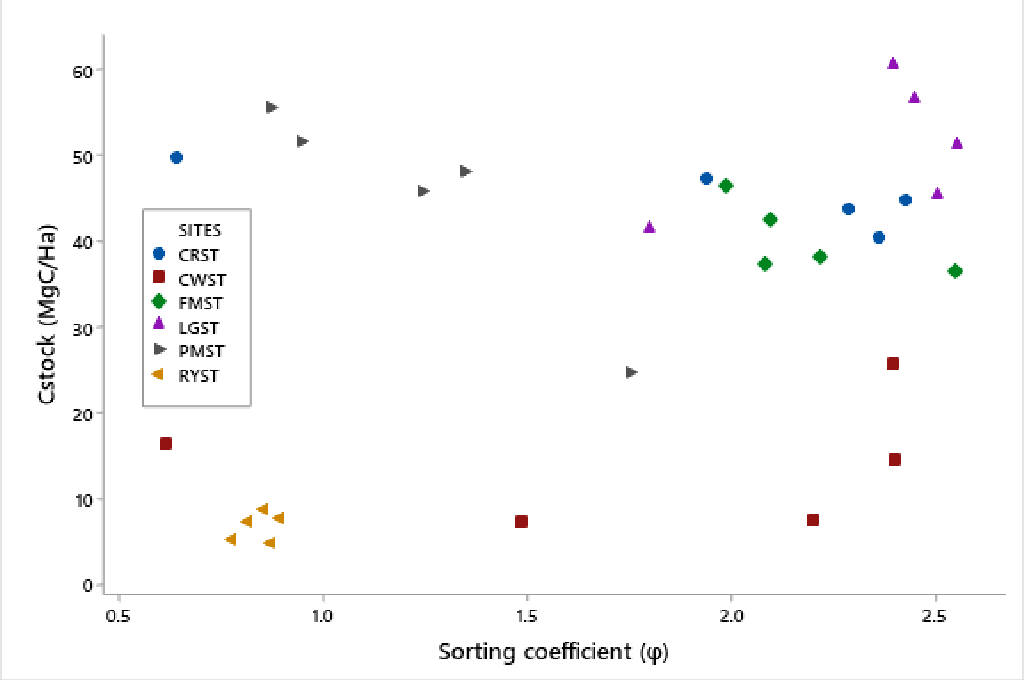


Figure 5.13: C$_{\text{stocks}}$ and sorting coefficient values from the top 30cm sediment layer for all sites: CRST, LGST, FMST, PMST, RYST and CWST.

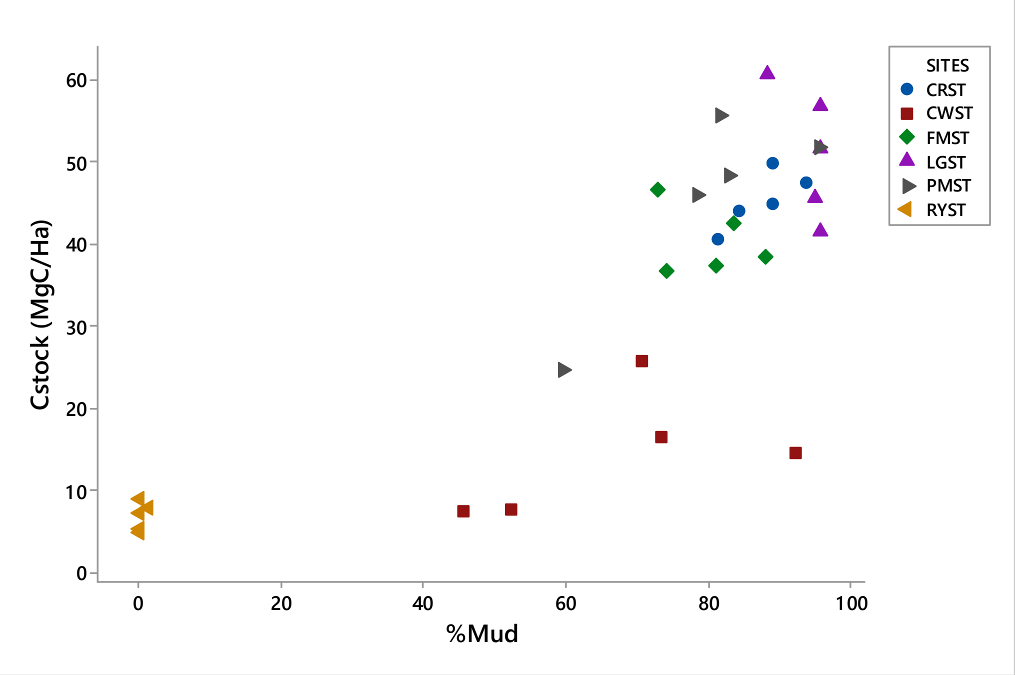


Figure 5.14: C_{stocks} and %mud values from the top 30cm sediment layer for all sites: CRST, LGST, FMST, PMST, RYST and CWST.

5.4.8.2 Pore water parameters

The association between pH levels and sediment C_{stock} showed a statistically significant moderate negative relationship (r = -0.545; p = 0.003). Sites with higher (more alkaline) pore water pH levels, like Ryde, Cowes and Farlington Marshes, formed individual clusters, and had lower C_{stocks} (figure 5.15). There was also a significant positive relationship between sediment C_{stocks} and salinity (r = 0.876; p = 0.000). Sites with significantly lower salinity levels, like Ryde and Cowes, grouped together in the correlation plot, presenting the lowest sediment C_{stock} values (figure 5.16).

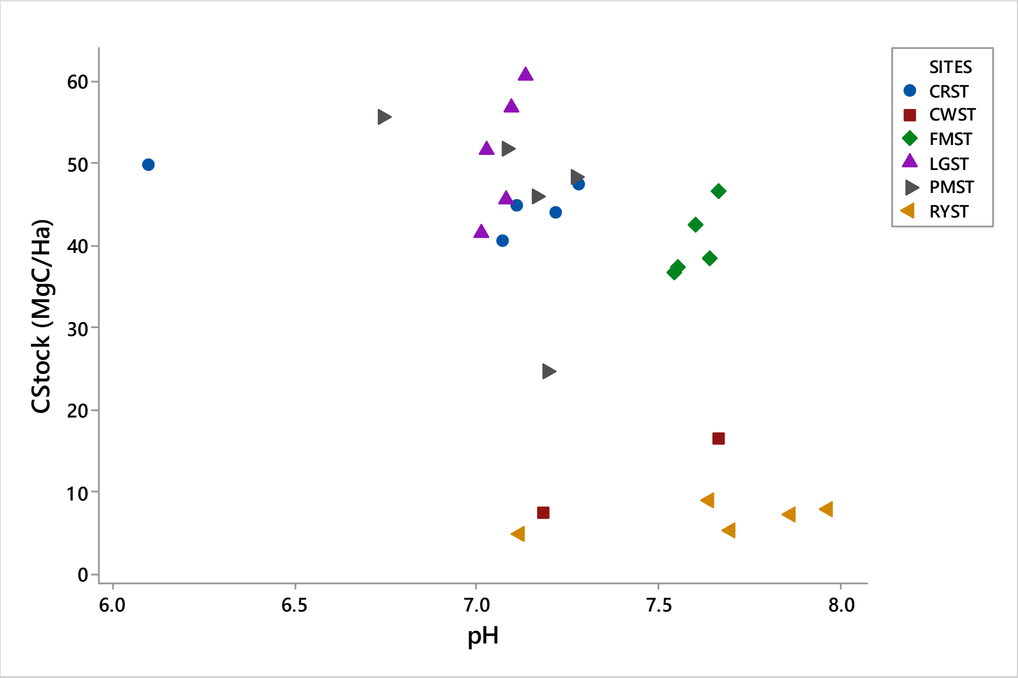


Figure 5.15: C$_{stocks}$ and pore water pH levels from the top 30cm sediment layer for all sites: CRST, LGST, FMST, PMST, RYST and CWST.

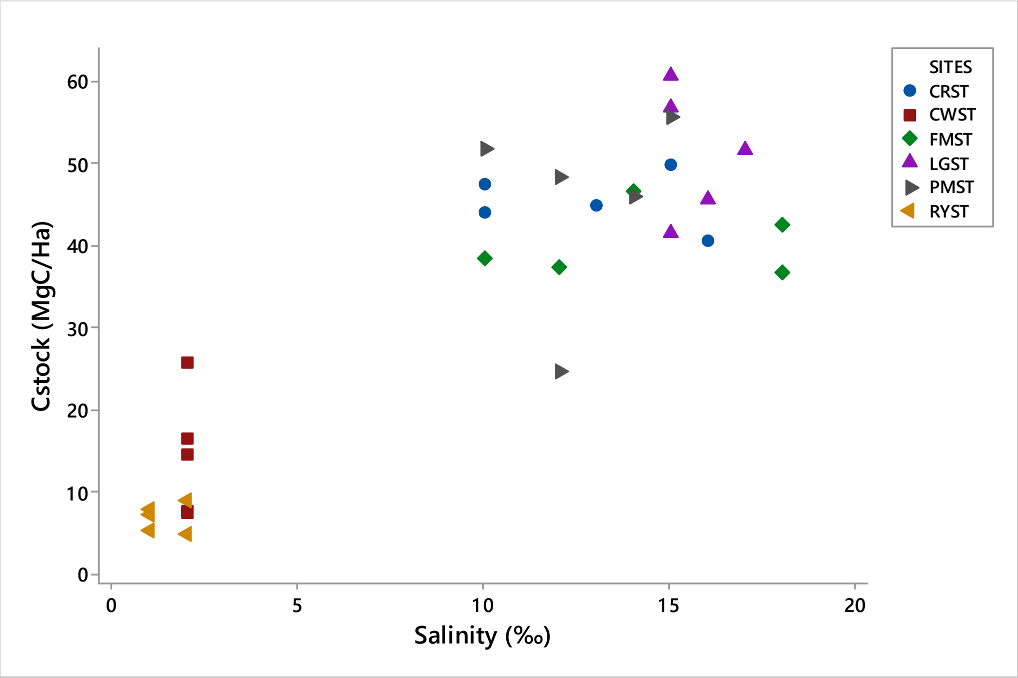


Figure 5.16: C$_{stocks}$ and pore water salinity levels from the top 30cm sediment layer for all sites: CRST, LGST, FMST, PMST, RYST and CWST.

The concentration of sulphates was significantly negatively correlated with sediment C_{stock} (r = -0.522, p = 0.004), where sites with higher concentration of sulphates, like Ryde, presented lower sediment C_{stocks} (figure 5.17). However, concentration of nitrites was only moderately significantly correlated to sediment C_{stock} (r = -0.423, p = 0.031) (figure 5.18).

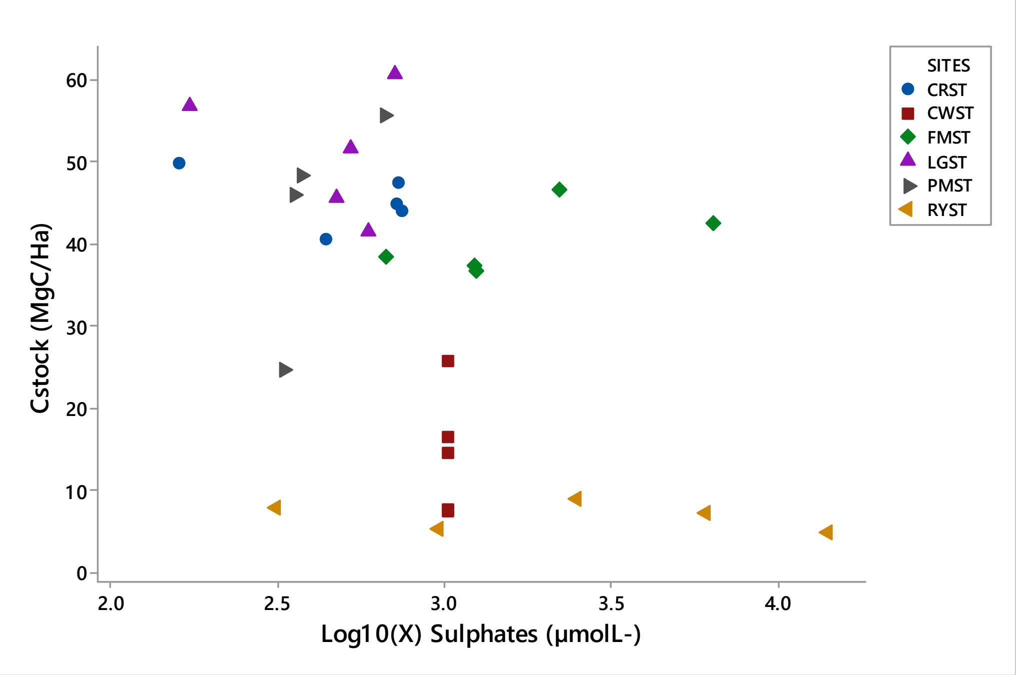


Figure 5.17: C_{stocks} and concentration of sulphates from the top 30cm sediment layer: for all sites, CRST, LGST, FMST, PMST, RYST and CWST. Concentrations of sulphates are represented by $Log_{10}(X)$ values.

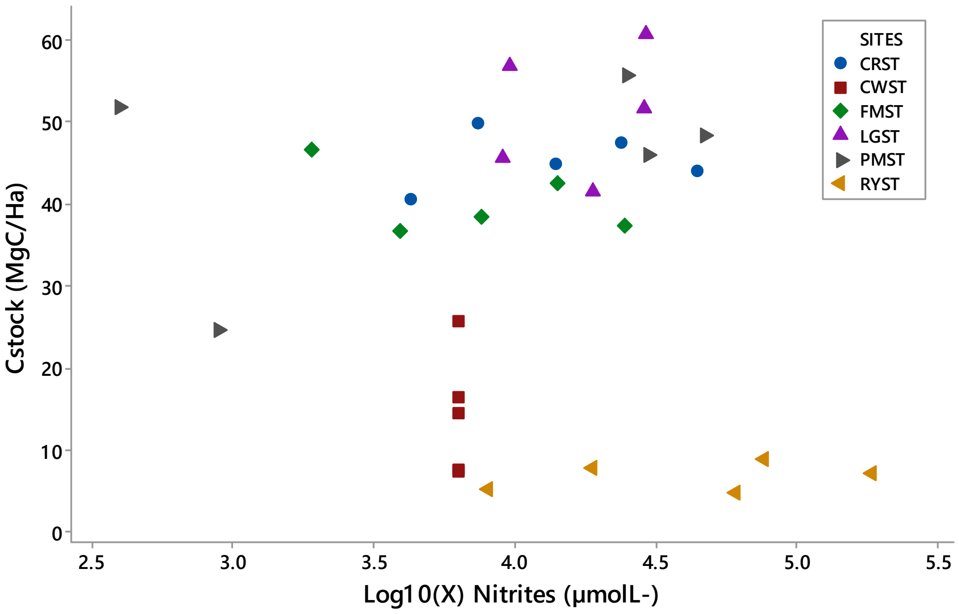


Figure 5.18: C_{stocks} and concentration of nitrites from the top 30cm sediment layer: for all sites, CRST, LGST, FMST, PMST, RYST and CWST. Concentrations of sulphates are represented by $Log_{10}(X)$ values.

5.4.8.3 Elevation above mean sea level

There was a significant positive relationship between elevation above mean sea level and sediment C_{stock} ($r = 0.719, p = 0.000$; n = 30), with sites located at lower elevation above sea level, like those at the Isle of Wight, Ryde and Cowes, supporting significantly less sediment C_{stock} (figure 5.19).

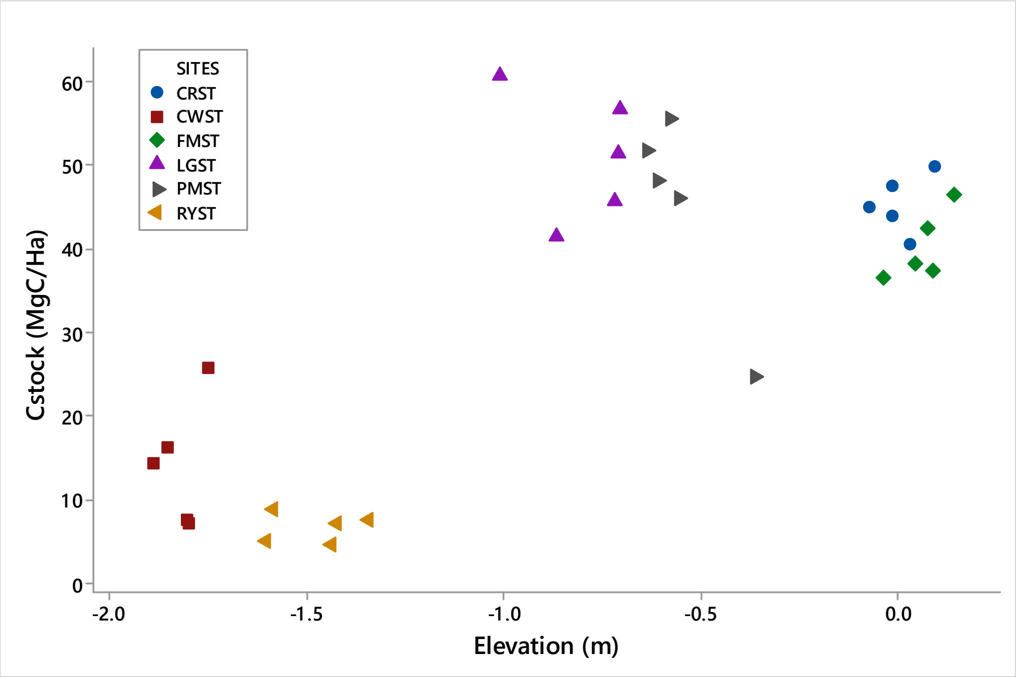


Figure 5.19: C_{stocks} from the top 30cm sediment layer and elevation above mean sea level for all sites, CRST, LGST, FMST, PMST, RYST and CWST.

5.4.8.4 Vegetation

There was no significant relationship between C_{stock} from the top 30cm layer of sediment and leaf density (*r* = -0.095, *p* = 0.616).

5.4.9 Multivariate Analyses

5.4.9.1 Partial Least Square (PLS)

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 are responsible for explaining 90% of the variation in the model data (table 5.3).

Table 5-3: Model selection for C_{stock} Partial Least Square analysis. Where X variance represents the amount of variance in the terms that is explained by the model and R-sq the percentage of variation in the response that is explained by the model.

Predictors	X Variance	R-sq
Dry bulk density (g dm^{-3})	0.42	0.77
Sorting coefficient (φ)	0.51	0.86
%Mud	0.58	0.89
pH	0.72	0.89
Sulphates SO_4^{-2} ($\mu molL^{-}$)	0.78	0.89
Nitrites NO_2^{-} ($\mu molL^{-}$)$^{-}$	0.84	0.90
Elevation (m)	0.89	0.90
Salinity (‰)	0.92	0.90
Above-ground Biomass (Mg C Ha^{-1})	0.94	0.90
Leaf density (leaf/m^{-2})	0.99	0.91

The PLS model also determined individual coefficients to each predictor, where higher coefficient values indicated a higher influence in sediment C_{stock}. According to the regression model, the most important factors responsible for the variation in sediment C_{stocks} were dry bulk density (DBD), followed in a ranked order by %mud, SO_4^{-2}, pH, NO_2^-, sorting coefficient, salinity, above-ground biomass, elevation, mean grain size and leaf density (figure 5.20).

Additionally, DBD, sorting coefficient, SO_4^{-2}, and leaf density showed negative relationships with sediment C_{stocks} (negative coefficient values), while %mud, pH, NO_2^-, elevation, salinity, above-ground biomass and grain size were positively related to sediment C_{stocks} (positive coefficient values).

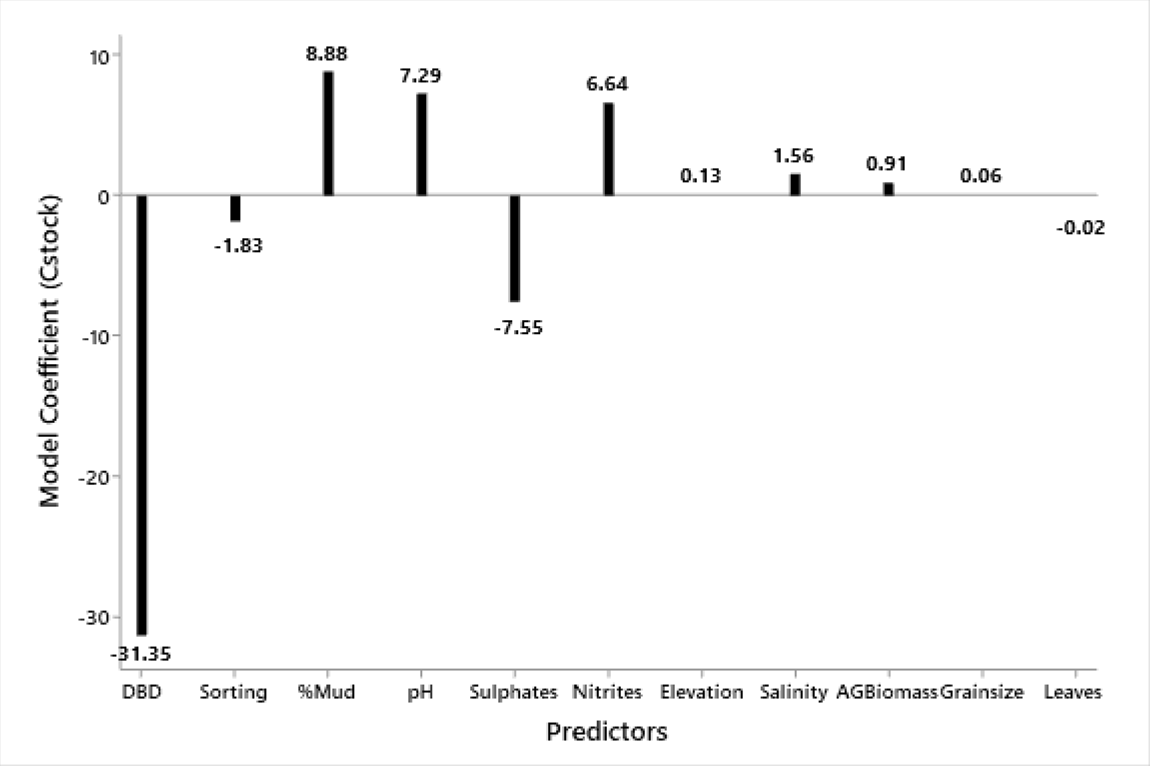


Figure 5.20: Partial least square regression model coefficient plot. The model assesses the relative influence of different predictors for sediment C_{stocks}. Predictors are dry bulk density (DBD), sorting coefficient, %mud, pH, sulphates (SO_4^{-2}), nitrites (NO_2^-), elevation, salinity, above ground biomass, mean grain size, and leaf density, ranked by level of importance from left, most important, to right, least important

5.4.9.2 Principal Components Analysis (PCA)

The five predictors appointed by PLS as main drivers for variation in sediment C_{stocks} (coefficient>5), were selected for PCA analysis (Dry bulk density, %mud, pH, nitrites and sulphates). The first two principal components cumulatively explained 77.5% of the variation in the data, with eigenvalues > 1 (figure 5.21). The first principal component (PC1) explained 60.1% of the variation, with 17.4% being explained by the second principal component (PC2).

Sediment characteristics showed the largest influence on PC1, with DBD with positive loadings on the component, closely related to sediment C_{stock} and %mud with negative loadings (table 5.4). PC2 was mainly and negatively influenced by the concentration of nitrites (table 5.4).

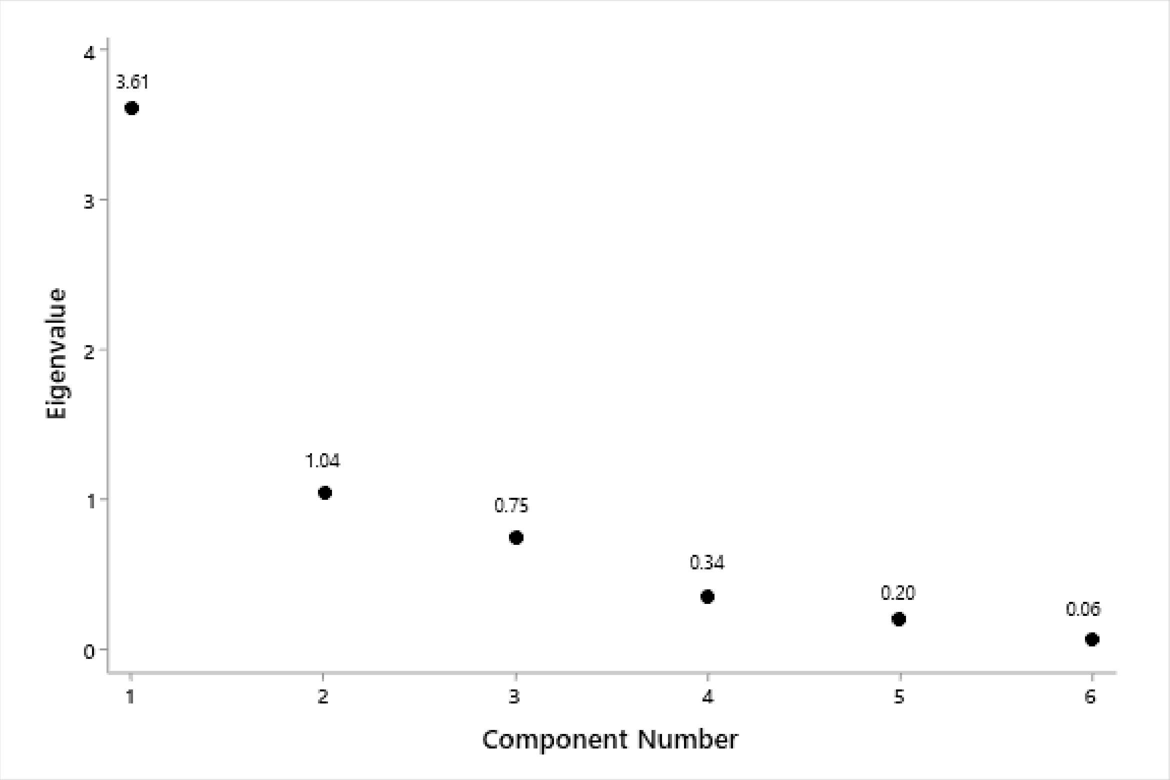


Figure 5.21: Scree plot of PCA analysis, showing eigenvalues for each component.

Table 5.4: Loading values of each variable on the first two principal components. The larger the absolute value of the loading coefficient, the more important the corresponding variable is in calculating the component.

Variables	Loadings	
	PC1	PC2
Sediment C_{stock} (Mg C Ha^{-1})	-0.469	-0.148
Dry bulk density (g dm^{-3})	0.479	0.161
Nitrites NO_2^- (µmolL^-)$^-$	0.152	-0.916
Sulphates SO_4^{-2} (µmolL^-)	0.412	0.100
pH	0.391	0.183
%Mud	-0.453	0.265

Most points for Creek Rythe and Hayling Island had low values for both PC1 and PC2, representing sites with highest C_{stock}, high %mud and lowest DBD. Most points from Ryde were located away from both PC1 and PC2, representing the site with lowest C_{stock}, lowest %mud, highest DBD, and higher concentration of both pore water nutrients (nitrites and sulphates) (figure 5.22). Cowes and Farlington Marshes had mostly positive relationships with both principal components, representing sites with similar pH levels. However, Cowes had higher values for PC1, while points from Farlington Marshes was grouped closer to the centre of both axis (figure 5.22).

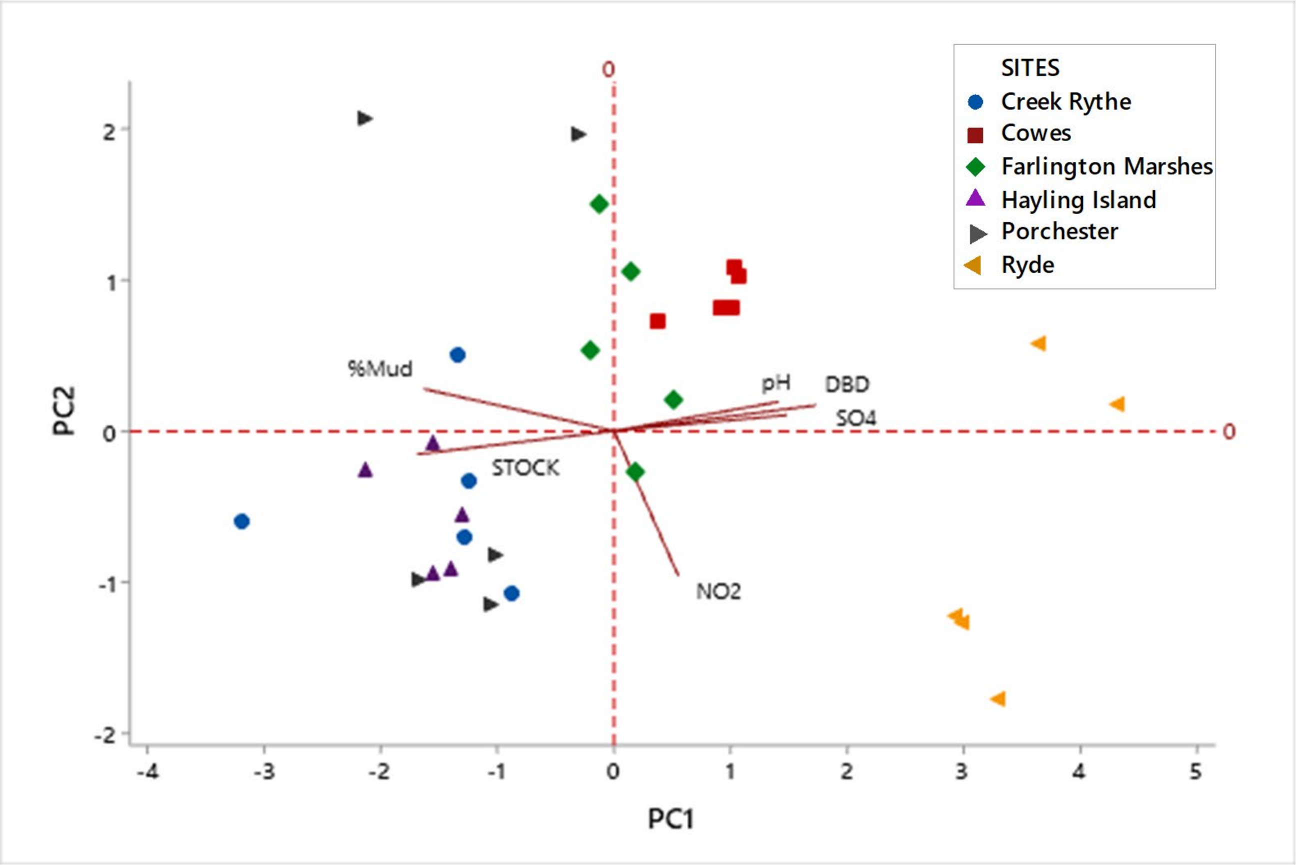


Figure 5.22: Principal component analysis (PCA) showing the six seagrass study sites CRST, LGST, FMST, PMST, RYST and CWST, related to the five most relevant predictor variables, dry bulk density (DBD), %mud, pH, nitrites (NO_2^-) and sulphates (SO_4^{-2}) (Figure 5.20) in terms of sediment C_{stocks} as the response variable.

5.4.10 Discussion

Results from this study provide valuable insights into the environmental factors driving sediment carbon storage in temperate seagrass ecosystems, specifically from intertidal seagrass meadows in the Solent region, England. Sediment C_{stock} from the top 30cm layer of the cores collected in 2018 were comparable to the ones collected from the same quadrats in 2017 (chapter 4), showing no temporal variation, which was expected given the short-term characteristic of this study. Seagrass meadows within the same geographic region and estuarine system complex, but 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: were dry bulk density (DBD), followed in a ranked order by %mud, SO_4^{-2}, pH, NO_2^-, sorting coefficient, salinity, above-ground biomass, elevation, mean grain size and leaf density. Biological factors have not been included in this study at this point. Indeed, dry bulk density can be used as a predictor for sediment C_{stocks} as indicated by the regression equation reported in this study. However, when the combined association of factors was analysed, dry bulk density, proportion of mud, pH, nitrites and sulphates showed the greatest influence on sediment C_{stocks}. Moreover, sediment characteristics such as dry bulk density and proportion of mud, acted in conjunction to explain most of the variation in sediment C_{stocks}.

5.4.10.1 Sediment characteristics

Sites with a higher % mud and lower mean grain size, characterized as muddy, and better sorted sediment particles with lower dry bulk density, had higher amounts of organic carbon stored in their sediments (Creek Rythe, Hayling Island and Porchester). It has been reported that sediment grain size influences the aggregation of organic particles, with finer grain size being related to higher organic matter content of sediments in coastal environments (Mayer, 1994; Rohr *et al*., 2016; Serrano *et al*., 2016; Dahl *et al*., 2016). Recent studies have assessed the role of environmental parameters in determining seagrasses' carbon sink potential, 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). These studies corroborate the results of this research, showing that high sediment

C_{stocks} are strongly linked to a high percentage of fine grain sizes and low dry bulk density, suggesting that seagrass meadows situated in areas with such sediment characteristics have a higher potential to act 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 rates 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 processes, thus promoting high carbon storage (Serrano *et al*., 2016).

Higher proportions of fine grain size (%mud), with higher sediment surface areas, also contribute to the preservation and accumulation of organic matter (Mayer, 1994; Dahl *et al*., 2016; Mazarrassa *et al*., 20185; Rohr *et al*., 2018). Sites with lower mean grain size, like Hayling Island and Creek Rythe, are likely to have lower permeability and highly 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 values of sediment C_{stocks} (Hedges, 1995; Wilson *et al*., 2008; Dahl *et al*., 2016). This is because amongst other factors, like temperature, higher levels of oxygen in sediments can increase bacterial organic matter degradation rates by up to 100 times more than in anoxic sediments (Sahm *et al*., 1999; Dahl *et al*., 2016; Mazarrasa *et al*., 2018).

However, even though sediment grain size has been described as a strong predictor for carbon storage in saltmarshes and some seagrass sites, in others it seems to be less relevant (Samper-Vilarreal *et al*., 2016; Rohr *et al*., 2016; Kelleway *et al*., 2016; Dahl *et al*., 2016). The relationship between carbon storage and sediment characteristics is more evident in meadows with low seagrass biomass and a high proportion of finer particle sizes, such as the ones studied in this chapter, while in Mediterranean meadows dominated by seagrass species with a greater biomass, e.g. *Posidonia spp*., the amount of autochthonous carbon seems to be more influential for carbon storage than mud and silt content (Serrano *et al*., 2016).

Mean grain size is directly linked to sediment porosity and density, and it has been previously demonstrated that sediment density has a negative relationship with sediment organic carbon, affirming the results encountered for the variance in dry bulk density (DBD) between sites in this study, with sites with lower DBD (and therefore higher porosity) having higher sediment C_{stocks}, e.g. Creek Rythe and Hayling Island (Dahl *et al.*, 2016).

In combination with particle size, the degree of exposure to hydrodynamic forces such as waves, tides and currents, is also a determinant factor for the sedimentation patterns and erosion in coastal areas (Mazarrasa *et al*., 2018). Meadows situated in more exposed areas could result in a high export of autochthonous organic matter, leading to a low carbon storage potential of the area (Rohr *et al*., 2016; Dahl *et al*., 2016). The level of exposure in seagrass meadows is usually reflected by 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 around the Isle of Wight, at Ryde and Cowes, which are more exposed to tidal influence and wave activity, and present lower sediment C_{stocks} than the mainland sites.

The degree of sorting is also used as a proxy to determine physical exposure related to movement of water masses, with better sorted particles representing slower deposition levels driven by stable hydrodynamic conditions (Folk and Ward, 1957; Mazarrasa *et al*., 2017b; Rohr *et al*., 2018). Conversely, sites with higher C_{stock} presented very poorly sorted particles according to Folk and Ward's (1957) scale. These results disagree with those obtained by Rohr *et al*., (2018), where the level of exposure from meadows in the Baltic Sea was an important driver for sediment C_{stock} in *Z. marina* meadows, with high exposure leading to lower sediment C_{stock} levels due to the potential export of carbon to other adjacent ecosystems.

It has been shown that sediment characteristics are significant for determining the carbon storage potential in seagrass sediments with low biomass species, e.g. *Zostera spp*. and *Ruppia spp*, as analysed in this study. Other factors related to sedimentation processes have previously also shown to be relevant, such as water depth, meadow productivity, sedimentation rate, trapping of fine-grained sediment and organic matter, and biological factors (Mazarrasa *et al*., 2018). Although these factors were not been investigated in this study, they may also be determinant in areas of high carbon storage potential (Serrano *et al*., 2016; Dahl *et al*., 2016; Mazarrasa *et al*., 2018).

Furthermore, there is typically a negative relationship between proportion of fine sediments and hydrodynamic energy, with smaller grain sizes found in sheltered embayments compared to exposed outer coastal regions (Samper-Villarreal *et al*., 2016; Santos *et al*., 2019; Prentice *et al*., 2019). Studies also suggest that higher flow velocities greatly increase the loss of C_{stocks} from seagrass sediments (Dahl *et al*., 2018; Prentice *et al*., 2019; Santos *et al*., 2019). 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.

5.4.10.2 Pore water parameters

Rohr *et al*., (2018) suggest an increase in salinity leads to lower production rates in seagrass meadows, influencing the storage of sediment C_{stocks}. Other studies suggest the negative influence of physical conditions from brackish environments, with lower salinity levels than marine environments, on plant growth and meadow productivity *(Salo et al., 2014;* Dahl *et al*., 2016*;* Mazarassa *et al., 2018; Rohr et al., 2018).* Furthermore, Hemminga and Duarte (2000) report that hyposaline ($5^{0}/_{00}$) or hypersaline ($45^{0}/_{00}$) conditions can promote stress and consequent loss of seagrass meadows. Levels of salinity in the top 30cm of seagrass sediment in this study varied from 1.4 $^{0}/_{00}$ in Ryde to 15.6 $^{0}/_{00}$ in Hayling Island. Salinity followed the same trends in variation between sites as %mud, being higher on sites with lower dry bulk density and mean grain size, e.g. Creek Rythe and Hayling Island, and thus being associated with higher sediment C_{stocks}.

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 relationship with seagrass sediment carbon storage. Sites with higher sediment carbon stocks had lower pore water pH, including Hayling Island and Creek Rythe, than sites with less sediment carbon stored, such as Ryde. This relationship is corroborated by Invers's *et al*. (1997) findings of a decrease in photosynthetic rates of between 20-75% when pH increased by 0.6 units for *Posidonia oceanica* and *Cymodocea nodosa*, and 0.8 units for *Zostera noltii*. 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. On a wider scale, studies suggest an increase in seagrass productivity and consequent carbon storage in acidic scenarios, with Garrard 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%.

Repolho *et al*. (2017) indicate that ocean acidification benefits photosynthesis and growth rates of primary producers in general, but particularly for seagrass species that follow facultative photosynthetic pathways under low dissolved CO_2 conditions, such as *Z. noltii*, and could benefit from higher concentrations of dissolved CO_2 (Koch *et al*., 2013; Mercado *et al*., 2003). However, the benefits of ocean acidification to seagrass carbon storage and sequestration potential are based on assumptions regarding the conservation of existing seagrass meadows in a climate changing future, and do not take into account the potential loss of other ecosystem services, such as the impact of lower pH levels on associated fish and invertebrate species (Garrard and Beaumont, 2014).

Other factors such as nutrient availability should also be taken into account when investigating seagrass carbon sink potential, and even though concentrations of nitrites and sulphates in the pore water of the top 30cm layer of seagrass sediment did not differ between study sites, they may play an important role in the carbon storage and sequestration process for seagrass meadows (Armitage and Fourqurean, 2016; Mazarassa *et al*., 2018). It has been suggested that the amount of organic carbon in the sediment can be positively linked to above and belowground plant productivity, with seagrass productivity being sensitive to nutrient (e.g., nitrogen or phosphorus) input, often decreasing substantially as a result of light limitation during macro- or microalgal 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).

Studies show that the concentration of ammonium, nitrate, nitrite and phosphate is higher in seagrass sediments than in bare substrate, and nitrogen fixed in the sediments can be found in seagrass leaves within hours (Perry and Dennison, 2000). This is related to the anoxic sediment conditions surrounding seagrass roots and rhizomes, which favour the association of nitrogen-fixing bacteria (Kuo, 1993; Perry and Dennison, 2000). However, it has also been suggested that sulphate reducing bacteria might be responsible for nitrogen fixation in anaerobic sediments, also being associated with input of phosphorous to the sediment by remineralisation of organic detritus (Caraco *et al*., 1989).

Therefore, it is clear that nutrient availability in seagrass sediments is closely related to microbial activity in their rhizosphere, associated with the release of oxygen by seagrasses' rhizomes into the sediment, 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 concentration of oxygen with depth, decreasing microbial activity (Mazarrasa *et al*., 2018).

5.4.10.3 Elevation above mean sea level

Intertidal seagrass meadows are particularly vulnerable to multiple daily stressors, such as air exposure, temperature range, 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 anthropogenic pressure and elevated levels of nutrients from industrial and agricultural waste, which not only affect meadows' health, but increases epiphyte productivity (Short and Willie-Echeverria, 1996; Ye *et al*., 2003).

The sites in the Isle of Wight, Ryde and Cowes, were located at the lowest elevations above mean sea level relative to the other sites, and also presented the lowest amounts of sediment C_{stocks}. Even though all sites are intertidal, differences in elevation can relate 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, different studies have identified increased desiccation stress as a factor that slows recovery time in intertidal seagrass beds growing on higher elevations, indicating higher vulnerability to extreme weather events due to global warming, like sea level rise (de Fouw *et al*., 2016; El Hacen *et al*., 2018).

5.4.10.4 Vegetation

There was no significant difference in leaf densities between sampling sites, but meadows with mixed species (*Z. marina / Z. angustifolia/ Z. noltii / Ruppia spp*), and dense and continuous beds, namely Creek Rythe, Hayling Island and Porchester, had higher amounts of sediment C_{stocks} than sites with beds of single species, such as Farlington Marshes and Ryde, or were very patchy like Cowes. Mazarrasa *et al*., (2018) suggest that mixed species and continuous meadow landscapes can act as favourable indicators of enhanced carbon storage potential for seagrass meadows. Higher species diversity increases seagrass' efficiency in reducing currents and consequent sediment resuspension, therefore contributing to organic matter deposition, especially in blade-like leaf species like *Zostera spp*. and *Thalassia spp*., forming muddy, organic rich sediments (Verduin and Backhaus, 2000; Koch *et al*., 2006; Peralta *et al*., 2008; Hendricks *et al*., 2008, Mazarrasa *et al*., 2018). Additionally, continuous and dense meadows are efficient in retaining autochthonous carbon, such as leaf detritus, and accumulate finer sediment particulates, consequently enhancing their carbon storage and sequestration capacity (Miyajima *et al*., 2017; Oreska *et al*., 2017; Ricart *et al*., 2017; Mazarrasa *et al*., 2018). Moreover, Dahl *et al*. (2016) listed canopy complexity as one of the most influential factors in seagrass carbon storage, but they also highlight that seagrass biomass and cover are generally highly dynamic and act on a shorter time-scale than the sedimentary carbon storage processes, therefore are not fully representative over decades or centuries. However, Prentice *et al*. (2019) found no clear relationship between seagrass canopy complexity and sediment C_{stocks} content from *Z. marina* meadows on the coast of British Columbia, Canada, suggesting that canopy complexity was a poor predictor for sediment C_{stocks}.

5.4.10.5 Environmental drivers of variation in sediment C_{stock}

According to the PLS regression model analysis, dry bulk density, concentration of nutrients, pH, elevation, salinity and grain size were the main factors influencing C_{stocks} in the top 30cm of sediment in the studied sites. In a similar analysis, Dahl *et al*. (2016) listed sediment density and porosity, and amount of fine grain size particles, as the main drivers for sediment carbon storage, whereas seagrass-associated variables, like species, had a minor influence, therefore these variables have not been included in this study. Rohr *et al*. (2018) identified three sediment variables (mud content, sediment density, and degree of sediment sorting), and two environmental variables (water depth and salinity) as the main indicators of carbon storage variability in *Z. marina* seagrass meadows from sampling sites across 13 countries. These results from the few studies to date to evaluate the effects of multiple drivers on seagrass carbon storage show that across different global regions and study sites, sediment features, especially related to particle size and proportion of fine particles, are likely to be highly relevant features contributing to seagrass carbon sink potential.

5.5 Conclusions

In conclusion, this study showed that seagrass meadows within the same climatic region, and even estuarine complex, do not share the same potential for long-term sediment carbon storage, and that environmental characteristics strongly influence this service. Dry bulk density was a good proxy for sediment C_{stocks}. Larger stocks were associated with meadows located in sheltered bays, with high sediment mud content and well sorted particles. Conversely, exposed meadows under intense anthropogenic impacts 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}.

The wide variability between and within seagrass meadows, related to species composition, and carbon sequestration and storage potential, has been suggested as one of the main limitations in the inclusion of seagrass meadows within marine protected areas or when selecting cost-effective areas for seagrass restoration projects to be used in climate change mitigation schemes. This research indicates that the most influential factors driving temperate seagrass sediment C_{stocks}, namely dry bulk density 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. All seagrass environments, including those with lower carbon sequestration and storage capacity, may play important roles in maintaining biodiversity and should be valued for a range of ecosystem services such as coastal protection, nursery habitats, and sediment stabilization. However, results presented in this study indicate that there are key factors that should be considered, individually or ideally in combination, when developing and implementing conservation or restoration projects, and climate change mitigation strategies, using seagrass ecosystems. Thus, at least for the purpose of developing blue carbon projects, grouping seagrass into bioregions is not a useful way to discuss similarities or differences in carbon sink potential.

Given the significant influence of sediment characteristics on seagrass carbon storage potential, it is important to consider sediment dynamics, including accretion rates, when developing blue carbon projects in these ecosystems as well as biological aspects, including meadows recovering states. Moreover, in the face of climate change, it is important to understand how events such as sea level rise, increased frequency of storm surges, and floods would impact sediment accretion and carbon sequestration rates in seagrass meadows, as further discussed in chapter 6.

6 Impacts of weather events on carbon sequestration and geochronology

6.1 Preamble

Sediment accretion rates for the studied sites were analysed using ^{210}Pb dating techniques. These were then used to determine carbon sequestration rates, which have not previously been assessed for seagrass meadows in the UK. The relationship between carbon sequestration rates, sediment accretion rates, and weather variables were established using correlation analysis. Additionally, a comparison of sediment accretion and carbon sequestration rates between periods with reported extreme weather events was conducted, producing novel insights on the influence of climate events on seagrass carbon sequestration potential. This information is vital to understand and predict potential consequences of climate change to coastal blue carbon ecosystems worldwide.

6.2 Introduction

6.2.1 Carbon sequestration rates in seagrass meadows

Vegetated coastal environments, including seagrass meadows, have high potential plant productivity, which coupled with the low rates of organic matter decomposition in their anoxic and mineral rich sediments, has been increasingly recognised as an important climate change mitigation ecosystem service (Bjork *et al*., 2008; Nellemann *et al*., 2009; Emmer *et al*., 2015; Poppe and Rybczyk, 2018). Carbon sequestration in vegetated coastal environments is further enhanced by their ability to trap particles from the water flow and store them in the soil (Kennedy *et al*., 2010; Duarte *et al*., 2013). It has been reported that on average seagrasses, salt marshes and mangroves accumulate organic matter and mineral particles at rates exceeding 10 cm per century, 30-50 times greater than accumulation rates from terrestrial forests soils (McLeod *et al*., 2011; Duarte *et al*., 2013). Moreover, seagrass and other vegetated coastal environments also provide coastal protection by dissipating wave energy through increasing drag, reducing near-bed flow velocity, and elevating the bottom boundary layer (Bryan *et al*., 2007; Duarte *et al*., 2013). Therefore, their contribution to bathymetric changes through sediment accretion (Mazarrasa *et al*., 2013) and shoreline accretion, is key to their role in coastal protection (Potouroglou *et al*., 2017).

Global carbon sequestration in seagrass beds has been reported to range from 0.45 to 1.9 MgC ha^{-1} year^{-1} (mean 1.38 MgC ha^{-1} year^{-1}) (Garrard and Beaumont, 2014), or 83 X 10^{-6} Mg C m^{-2} year^{-1}, translating to global sequestration rates of between 27 and 40 x 10^{18} Mg C year^{-1} (Kennedy and Björk, 2009). Fourqurean *et al.* (2012a), estimated seagrass to capture 27.4 x 10^{18} Mg C year^{-1}, which could result in up to approximately 19 x 10^{21} Mg of carbon currently being stored within seagrass plant biomass and the top metre of sediment. Moreover, recent estimates show an average carbon storage of 140 Mg C ha^{-1} in the top metre of seagrass meadow sediments, corresponding to 520 Mg of carbon dioxide equivalence per hectare (Mg CO_2eq ha^{-1}) (Pan *et al.,* 2011; Pendleton *et al*., 2012). Thus, the potential impact of loss of seagrass ecosystems to global CO_2 budgets is relevant, reinforcing the importance of establishing the magnitude of the C_{org} pools, including biomass and sediment storage. However, there has been little attempt to assess “blue carbon” sequestration and storage capacity in seagrass meadows, connected to climate change and sea level rise in these ecosystems (Duarte *et al*., 2010; Duarte *et al*., 2011; Fourqurean *et al*., 2012a; Garrard and Beaumont, 2014; Jones and Unsworth, 2016).

For vegetated coastal environments to be included in climate change mitigation policies, and potentially in voluntary carbon markets, accurate estimates of carbon stocks and sequestration rates are essential (Emmer *et al*., 2015; Howard *et al*., 2017). However, despite the growing focus on blue carbon ecosystems, carbon sequestration processes by seagrasses remains the least studied or published of all vegetated coastal environments (Grimsditch *et al*., 2013). The few studies quantifying carbon sequestration (C_{seq}) rates from seagrass sediments report a highly variable range of results, mainly attributed to variability among species and habitats (Duarte *et al*., 2010, Kennedy *et al*., 2010, Grimsditch *et al.,* 2013, Lavery *et al*., 2013, Rozaimi *et al*., 2013). Other studies suggest that the variability in C_{seq} rate estimations, ranging from 45 to 190 g C m^{-2} year^{-1}, may be attributed to difficulties in obtaining reliable long-term accretion rates from these environments (Chmura *et al*., 2003; Green and Short 2003; Mcleod *et al*., 2011; Schile *et al*., 2017; Poppe and Rybczyk, 2018). Most existing studies are mainly focused on *Zostera marina* meadows or tropical and subtropical species, like *Posidonia oceanica* (Green and Short 2003; Duarte *et al*., 2010, Kennedy *et al*., 2010; Grimsditch *et al*., 2013; Lavery *et al*., 2013; Rozaimi *et al*., 2013; Poppe and Rybczyk, 2018).

Tomasko *et al*. (2017) emphasize the importance of increasing the confidence in carbon sequestration estimates for seagrass meadows, by deriving multiple and site-specific sequestration rates based on calculations that include relevant pathways (burial and/or bicarbonate) if applicable, rather than using values based on literature. Similarly, Marba *et al*., (2015), highlight the need to design robust models to understand the consequence of seagrass habitat loss, and the efficiency of restoration projects for seagrass carbon sequestration capacity. Degradation and loss of seagrasses lead to diminution and loss of their associated ecosystem services, which may occur rapidly, for example immediate loss of fisheries habitat provision, or delayed, for example carbon may remain stored below-ground for some time after degradation, before being remineralised (Macreadie *et al*., 2014). This temporal relationship between seagrass degradation and loss, and ecosystem services is currently unknown (Potouroglou *et al*., 2017), highlighting the need for studies including historical evaluations of fluctuations in C_{seq} rates, such as the one reported in this chapter.

6.2.2 Effects of climate change on seagrass ecosystems

The impacts of climate change on seagrass communities have not been well-studied until relatively recently, in comparison to terrestrial plant communities (Overpeck *et al*., 1990; Bradley *et al*., 1999; Menzel *et al*., 2001; Walther *et al*., 2002; Gottfried *et al*., 2012; Côté-Laurin, 2017; Shields *et al*., 2018). Recently, studies have attempted to demonstrate the trends and effects of current and future climate change related factors on seagrass productivity and distribution (Short and Neckles, 1999; Jordà *et al*., 2012; Lefcheck *et al*., 2017; Shields *et al*., 2018). However, the detection of changes in seagrass distribution patterns related to climate change may prove difficult, especially when seagrass sites are already impacted by other anthropogenic pressures (Bjork *et al*., 2008; Amone-Mabuto *et al.,* 2017; Macreadie *et al*., 2019).

Global climate change may impact seagrasses through: increasing storm frequency and intensity; changes in the distribution of storm occurrences; rising water temperatures; reduced light levels due to sea-level rise; and rising CO_2 levels in coastal waters, all of which can cause direct and indirect impacts, including physical disturbance (Preen *et al*., 1995; Moncreiff *et al*., 1999; Wanless *et al*., 1988; Brierley and Kingsford 2009; Nakamura, 2010; Hyndes *et al*., 2016; Cote-Laurin *et al*., 2017; Arias-Ortiz *et al*., 2018b; Macreadie *et al*., 2019). Responses to changes in environmental conditions have also been reported, including shifts in the structure and function of seagrass meadow ecosystems by localised species invasions and extinctions (Bjork *et al*., 2008; Hyndes *et al*., 2016; Mellin *et al*., 2016). Moreover, the accelerating trend in global decline and degradation of seagrass meadows could have major impacts on the stability of coastal sediments and coastal geomorphology (Orth *et al*., 2006; Waycott *et al*., 2007; Waycott *et al*., 2009; Potouroglou *et al*., 2017). Furthermore, since 95% of carbon in seagrass meadows is stored below-ground in the sediments, decreases in sediment stabilisation and elevation functions are likely to affect carbon sequestration potential (Potouroglou *et al*., 2017).

Sediment accretion in coastal ecosystems could respond to climate change through feedbacks that involve increased plant growth and production, through more efficient sediment trapping as a result of increased CO_2 levels (Langley *et al*., 2009) and sea-level rise (Fourqurean *et al*., 2012). Indeed, recent models, based on salt-marsh research, indicate that climate change may increase sediment carbon sequestration and accretion rates in the first half of the twenty-first century (Donato *et al*., 2011; Duarte *et al*., 2013; Leonardi *et al*., 2018). This long-term preservation and continuous accretion of carbon in the soil of vegetated coastal environments related to sea-level rise could lead to the development of carbon deposits several metres thick (Mateo *et al*., 1997; Donato *et al*., 2011).

Nonetheless, the risks of accelerated sea-level rise could be enhanced by associated increases in the frequency of extreme sea levels, wave activity, and the magnitude of storm surges (Menendez and Woodworth, 2010), resulting in a higher intensity and frequency of flooding and erosion of vulnerable coastal areas (Duarte *et al*., 2013). Studies have shown that significant wave-height variations are clearly linked to climate models, with reported increases in wave heights in the North Pacific, North Atlantic and Southern Ocean during the past century (Izaguirre *et al*., 2010; Menendez *et al.,* 2008; Hemer *et al*., 2010; Young *et al*., 2011). Increased wave heights have been shown to be directly related to wind (strength and direction) and storminess, linked to climate change, resulting in flooding and erosion that threaten coastal environments (Seneviratned *et al*., 2012; Duarte *et al*., 2013). Therefore, a substantial shift in suitable habitat for seagrasses may occur, in response to rising sea levels, with intertidal, or shallow subtidal, meadows migrating shoreward where accommodation space is available, and subtidal meadows could be at risk of decline due to reduced light availability (Short and Neckles, 1998; Bjork *et al*., 2008; Potouroglou *et al*., 2017; Macreadie *et al*., 2019). Consequently, estuaries in southeast England are most in danger from the cumulative effects of sea level rise and land subsidence (Robins *et al*., 2016). The long-term climate impacts that UK estuaries have been facing include a decline in water quality, and habitat conversion, negatively impacting their ecological integrity (Robins *et al*, 2016). In addition, changes in GMSL might also reduce intertidal areas, outpacing the accretion rates of marshes, decreasing habitat availability and promoting a shift in species distribution (Wong *et al*., 2014).

fThus, active monitoring and management of seagrass ecosystems is required to improve the understanding of their ecology at a range of spatial and temporal scales in response to climate change forcing (Orth *et al*., 2006; Amone-Mabuto *et al*., 2017; Shields *et al*., 2018). It is important that existing legislation and directives include not only mitigation programs but also adaptive and responsive mechanisms that address current and projected impacts of climate change on coastal environments, including seagrass meadows (Nachmany *et al*., 2014; Frost *et al*., 2016; Unsworth *et al*., 2019). To make this possible, robust predictive model of future seagrass habitat distributions must be provided, including monitoring reports on indicators that provide an early warning of reduced resilience, and imminent shifts in distribution (Unsworth *et al*., 2018b; Macreadie *et al*., 2019).

6.2.3 Use of ^{210}Pb dating in vegetated coastal sediments

Reliable measurements of sediment accretion rates can be used in conjunction with carbon density data to produce accurate estimates of C_{seq} rates for seagrass ecosystems (Arias-Ortiz *et al*., 2018a). Other factors that could be considered when estimating C_{seq} rates for seagrass meadows are frequency of submergence of the habitats and the effects of water and soil chemistry in the carbon remineralisation processes, where applicable (Villa and Bernal, 2017). Therefore, measurements of C_{seq} rates can be obtained in one of two ways: by measuring the concentration of C_{org} in sediments and ascribing dates to either the entire profile of interest or to specific intervals; or by directly estimating sediment accretion rates (Arias-Ortiz *et al*., 2018a).

Sediment accretion rates and elevation change in seagrasses meadows worldwide have been determined by various methods that consider historical and recent changes. Mapping techniques (with e.g. Altus altimeter, Stanley compulevel, topographic surveys, Bos *et al*., 2007; Ganthy *et al*., 2013; Paquier *et al*., 2014) are used to provide estimates of large scale and long-term changes in elevation and coverage, but lack the precision needed to track annual elevation changes, whereas sediment traps (Gacia and Duarte, 2001) measure sedimentation over shorter periods of days to a few months, but ignore root contributions to sediment binding (Potouroglou *et al*., 2017). Alternatively, radionuclide dating methods using lead (^{210}Pb), carbon (^{14}C), as well as the artificial radionuclide Cesium (^{137}Cs), and other isotopes are used to date marked depths (Mateo *et al*.,1997; Macreadie *et al*., 2012, Orem *et al*., 1999; Lo Iacono *et al*., 2008; Serrano *et al*., 2012; Serrano *et al*., 2014; Miyajima *et al*., 2015; Serrano *et al*., 2016) providing estimations of sedimentation rates from decades to centuries and up to millennia (Villa and Bernal, 2017). Sediment radionuclide dates are then coupled with the amount of C_{stock} per dated section, to assess carbon sequestration rates, and provide long term accretion data (Duarte *et al*., 2011; Arias- Ortiz *et al*., 2018a).

The decay rates of radionuclides are well known, with half-lives ((t½) - time for half of the original amount to be undecayed) of ^{210}Pb and ^{14}C established at 22.26 and 5730 years, respectively (Duarte *et al*., 2011). Therefore, ^{210}Pb dating is the most widely utilised method for more recent (~150 years) sediment profiles, providing a time frame compatible with recorded management actions and enabling the determination of fluctuations in carbon sequestration rates related to natural or human impacts (Koide *et al*., 1972; Wise,1980; Thompson *et al*., 2001; Marland *et al*., 2001; Teasdale *et al*., 2011 Duarte *et al*., 2011; Ward *et al*., 2014; Arias-Ortiz *et al*., 2018a; Poppe and Rybczyk, 2018). When sediment accretion rates in marine ecosystems are primarily associated with build-up of autochthonous organic and inorganic material, ^{210}Pb is known to be deposited mainly from atmospheric fallout, at a steady state, with little post-depositional mobility except for physical or biological mixing of the sediments (Alongi *et al*., 2004; Cochran *et al*., 1998; Marbà *et al*., 2015). It is impostant to state that it is a challenge to resolve event-based impacts using a chronological approach that like ^{210}Pb dating, since sampling resolution might have great implications on the ages profile.

This chapter presents an assessment of carbon sequestration rates from intertidal seagrass meadows in central Southern England, an assessment not previously undertaken for any UK seagrasses. The objectives were to: 1) analyse sediment accretion rates for the studied sites, using ^{210}Pb dating techniques; 2) use the established dating horizons to evaluate carbon sequestration rates; 3) establish a relationship between dated horizons, carbon storage, sequestration and historical meteorological data; 4) use an exploratory approach to provide a better understanding of the potential impacts of future climate change related events like sea level rise and occurrence of storms and floods on carbon sequestration and storage.

6.3 Methods

6.3.1 Study Sites

Carbon sequestration rates were calculated for four study sites, Creek Rythe (CRST) in Chichester Harbour (figure 3.3); Hayling Island (LGST) (figure 3.4) and Farlington Marshes (FMST) (figure 3.5) in Langstone Harbour; and Porchester (PMST) (figure 3.6) in Porstmouth Harbour. The two Isle of Wight sites (Cowes and Ryde) (figure 3.7), discussed in chapters 4 and 5, have been excluded from this analysis, due to very low, or zero, detection of ^{210}Pb in their sediment cores via gamma spectrometry. This could be related to the low fraction of clay particles in these sediments, as reported in chapter 4, reducing affinity with ^{210}Pb, which facilitates its mobility by wave and tidal activity or by recent erosion resulting in surface sediment loss (Cundy and Croudace, 1996).

Portsmouth, Langstone and Chichester harbours are characterised by low energy coastal environments, which combined with a micro/meso-tidal range, and the presence of estuaries and natural harbours, has promoted the widespread development of saltmarshes and mudflats since the late Holocene (Waller and Long, 2003). Moreover, this region has some of the most complex tidal regimes in the U.K., caused by its natural coastal configuration and the proximity of a semi-diurnal tidal node in conjunction with historical natural and anthropogenically-driven changes in water depth and coastal morphology, which has led to a distortion of the tidal curve (Cundy and Croudace, 1996). As a result, patterns of sediment transport in the region have been described as more complicated than other coastal regions along the UK, with fluvial and cliff erosion inputs, and transport driven by tides, wave activity and littoral drift, generally moving from east to west (Dyer, 1971; Bray *et al*., 1995, SCOPAC, 2003) (figure 6.1).

Figure 6.1: Location of seagrass study sites, from west to east: PMST, FMST, LGST, and CRST. Coloured arrows show the patterns of sediment input and transport according to SCOPAC (STS), (2012).

6.3.2 Field Methods

During the summer of 2017 (June- August), two 50cm deep (or until refusal) 7.5 cm diameter PVC sediment cores were extracted from each of the four study sites (figure 3.8), resulting in a total of eight cores (labelled CRST1, CRST 2, FMST1, FMST2, LGST1, LGST2, PMST1 and PMST 2). This depth was expected to cover the last 150 years of sediment accretion, which is the maximum detection limit for ^{210}Pb dating (Appleby, 1992).

PVC sediment cores used for carbon sequestration analyses were carefully collected, to allow minimum compression (<10%) (Ward *et al*., 2014). This was done by measuring the height difference between the depth to which the core tube was inserted in the sediment, and the top sediment layer inside the core, to avoid the “nail effect”. Whereby the core penetrates the sediment as a solid rod or nail, disturbing the sediment horizons, potentially skewing sediment carbon analyses results (Howard *et al*., 2014). Therefore, cores were carefully removed by digging around and capping at the bottom, then immediately packed, labelled and sealed with industrial cling film and duct tape, to prevent remobilisation, degradation and contamination.

6.3.3 Laboratory methods

All cores were stored in freezers at -26°C at the University of Brighton, prior to preparation for laboratory analysis. Each frozen core barrel was then extruded from the PVC tubes, by allowing the outer core surface to thaw and then forcing the frozen sediment out. Sediment compaction was then re-assessed by measuring the length of the core section before and immediately after extrusion (Ward *et al.,* 2014). Each sediment core was cleaned, logged, and sliced into 1 cm depth increment subsamples, to be analysed for ^{210}Pb, and ^{137}Cs radionuclides, organic matter (converted to total organic carbon), sediment particle size and soil bulk density (Cundy *et al*., 2000; Mizugaki *et al*., 2006) (figure 6.2).

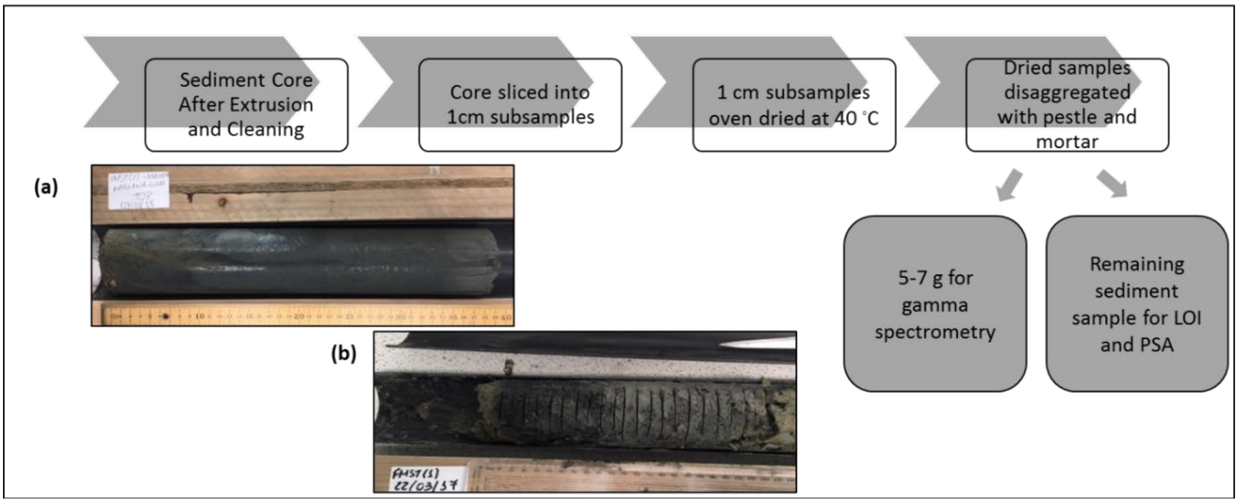


Figure 6.2: Flow-chart of methods used in this chapter, including image of a sediment core after extrusion (a) and a sediment core being sliced into 1cm sub-samples (b).

Each 1 cm subsample was oven dried at 40 ºC prior to gamma spectrometry analysis, until constant weight was achieved, to determine soil moisture content and dry bulk density (Ward *et al*. 2014). Dried subsamples were then prepared for analysis by gently disaggregating the material using a pestle and mortar. Approximately 5-7 g of dried sediment from each subsample was carefully weighed into cylindrical plastic vials for determination of $^{210}\text{Pb}_{\text{total}}$, and ^{137}Cs down core activities via gamma spectrometry (Ward *et al*., 2014). The remaining dried sediment from each sample was separated to be analysed for organic matter content and particle size.

6.3.3.1 Gamma spectrometry

Each cylindrical plastic vial containing sediment sub samples was placed in a Canberra well type ultra-low background HPGe gamma ray spectrometer to determine the activity of the ^{137}Cs (661.65 keV), ^{214}Pb (351.92 keV) and ^{210}Pb (46.54 keV). The spectra were recorded using a 16k channel integrated multichannel analyser. Spectral analysis was conducted using the Genie 2000 system. Energy and efficiency calibrations were carried out using bentonite clay spiked with a mixed gamma-emitting radionuclide standard, QCYK8163, and checked against an IAEA certified sediment reference material (IAEA 135). Detection limits of radionuclides are dependent on age, radionuclide gamma energy, count time and sample mass. To achieve maximum quality of data within a minimum time period the samples were left counting until detection error was ≤5% for all the relevant radionuclides. Typically, each sample count time was between 48 and 96 hours.

6.3.3.2 Organic matter content analysis

In order to determine organic matter content for each 1cm core subsample, the loss on ignition (LOI) method was used [methods, section 3.2.2 (ii)], using the calculations described and tested in chapter 4 (Equations 3, 4, 6 and 7). Following removal of organics, samples were analysed for particle size.

6.3.3.3 Particle size analysis

The same method described in chapter 4 was used to determine particle size distribution in each 1cm core subsample. A Malvern 2000 Laser Particle Size Analyser, graded according to the Wentworth scale, was used to identify the silt and clay fractions to determine % mud content (< 63 µm). Median grain size (D50) and sorting coefficients (equation 11) were also calculated, as described on chapter 4 and in methods – section 3.2.3.

6.3.3.4 Radioisotope dating and sediment accretion rates

Excess (unsupported) ^{210}Pb was calculated as the difference between total ^{210}Pb and supported ^{210}Pb, to distinguish between excess ^{210}Pb deposited at the sediment surface, and supported ^{210}Pb that has decayed in-situ. For the purpose of this study, ^{214}Pb levels have been used as a baseline to calculate supported ^{210}Pb. Cores were analysed in alternate 1-cm sections from the surface to the depth at which the excess ^{210}Pb concentration declined to zero. However, where greater resolution was required, all 1cm samples were used. Generally, ^{210}Pb dates can be validated using artificial radionuclide ^{137}Cs profiles as date markers, when the ^{137}Cs profiles are well preserved, enabling identification of high activity peaks in the soil profile (Ward *et al*., 2014; Villa and Bernal, 2017).

In this study, long-term sediment accretion rates were determined for each core using the down-core distribution of ^{210}Pb with both the Constant Flux: Constant sedimentation (CF:CS) model and the constant rate of supply (CRS) model, as well as ^{137}Cs impulse dating method for comparison and validation (Krishnaswamy *et al*., 1971; Appleby and Oldfield 1978; Appleby and Oldfield, 1992; Appleby, 2001) (methods section 3.2.6).

6.3.3.5 Constant Flux: Constant sedimentation (CF:CS) model

In this model, the ^{210}Pb specific activity at the surface is assumed to be constant and decreases exponentially with cumulative mass and the depth of burial is related to the elapsed time since burial through the rate of sedimentation [methods, section – 3.2.6 (i)]. Moreover, this model is to some degree able to cope with temporal variations in mass accretion rates, like mixing at the surface layers (Arias-Ortiz *et al*., 2018a). Average accretion rates can be calculated based on the gradient of the line of least squares regression of the natural logarithm of ^{210}Pb excess against depth. In order to calculate supported ^{210}Pb, lowest values of ^{210}Pb in all samples down the core were calculated, to be used as equilibrium baseline. The base level of ^{210}Pb was removed from the total ^{210}Pb to leave the unsupported $^{210}\text{Pb}_{\text{excess}}$ in the sediment, which was used to date the sediment.

The CF:CS method involves calculating average sediment accretion rates for the sediment cores by dividing the decay constant of ^{210}Pb by the gradient of the log normal line of the excess ^{210}Pb down the sediment core. In order to calculate the gradient of the line, a least squares regression analysis was used. Sediment accretion rates were derived from the calculation below (Krishnaswamy *et al*., 1971):

Equation 18: $\text{Sediment accretion rates (cm/year)} = (\text{Decay constant 210Pb})/$
$(\text{Gradient of Ln line of the unsupported } {}^{210}\text{Pb in the soil})$; **where decay constant of ^{210}Pb = 0.03114.**

6.3.3.6 Constant Rate of supply (CRS)

The CRS model assumes a constant flux of ^{210}Pb to the sediments over time [methods, section 3.2.6 (i)] (Breithaupt *et al*., 2014; Andersen, 2017). The initial specific activity is variable and inversely related to sediment accretion rates, as higher rates lead to lower $^{210}\text{Pb}_{\text{excess}}$ specific activity and vice versa. Dating is based on a comparison of $^{210}\text{Pb}_{\text{excess}}$ inventories below a given depth with the overall $^{210}\text{Pb}_{\text{excess}}$ inventory in the sediment core (Arias-Ortiz *et al*., 2018a). The accurate determination of the $^{210}\text{Pb}_{\text{excess}}$ inventories is of critical importance and required for the application of the CRS model (Appleby, 2001). Therefore, the CRS method was used to calculate accretion rates at specific dates. These were then linked to fluctuations in sediment supply by examination of available climate and hydrological data from the time period established by the calculated dates.

The age of sediment at depth x was calculated using the formula below. The inventory of each sediment subsample was calculated using ^{210}Pb excess within the sample, multiplied by the dry bulk density of the sample. Ages and hence sediment accretion rates were then calculated using equation 19 (Appleby and Oldfield, 1978; Appleby, 2001):

Equation 19: $\text{Age at depth x} = x\ ln\ (\frac{\text{unsupported inventory at depth x}}{\text{unsupported inventory at entire core}})$

6.3.3.7 Sediment accretion rate derivation for ^{137}Cs impulse dating

Equation 20, for estimating sediment accretion rates, uses the number of years since a known ^{137}Cs input event occurred and measures the amount of sediment that has accumulated following that event (Robbins and Edgington, 1972):

Equation 20: $\frac{\text{Depth of surface 137Cs actitity maximum (mm)}}{\text{Date sample taken} - \text{date of known 137Cs production event}}$

Two events were used for these cores, pre-1963 weapons testing and the Chernobyl nuclear reactor meltdown in 1986, which previous studies have shown are respectively the second highest and highest ^{137}Cs input events in northern Europe (Callaway *et al*., 1996; Rosen *et al*., 2009). However, ^{137}Cs profiles from central southern England might contain additional ^{137}Cs from AEE Winfrith nuclear plant discharges, produced during fuel-rod inspections 1973-1977, which could potentially mask 1963's maximum fallout values (Cundy and Croudace, 1996). Error values are calculated using the depths either side of the main event. The resultant sediment accretion rates can be used to independently verify the ^{210}Pb dating methods (Cundy and Croudace, 1996). Although, it should be noted that the 1963 peak is becoming obsolete as a result of its age (Drexler *et al*., 2018).

6.3.3.8 Carbon sequestration rates

Sediment accretion rates calculated by the CRS model were used to calculate carbon sequestration rates, as a factor of dry bulk density (DBD), soil organic carbon (C_{org}), and sedimentation rate (SR) (Villa and Bernal, 2017):

Equation 21: $C_{Seq}\ (\mathrm{g\ m^2\ year^{-1}}) = (\mathrm{DBD}\ (\mathrm{g\ cm^{-3}}) \times (C_{org}(\%)/100) \times (\mathrm{SR}\ (\mathrm{mm\ year^{-1}})/10))*10^4$

6.3.4 Climate Data

Historical climate data for the Solent region was obtained from the MET office archives, covering the period between 1900 and 2017 for daily maximum and minimum temperatures, wind speed and precipitation. Daily values of maximum and minimum temperature, wind speed and precipitation were summed and used to calculate a mean for each year of interest. Monthly sea level data were collected from the Permanent Service for Mean Sea Level (PSMSL) database for the Portsmouth station; data were available between 1955 and 2017. Monthly sea level values were also summed to calculate a yearly mean. The relationships between minimum and maximum temperature, wind speed, precipitation, sea level, and sediment C_{Seq} rates (g m^2 year^{-1}), were then analysed.

The occurrence of historical weather events that impacted the region were assessed from a collection of reports from the MET office, classified as 'extreme' weather events, and data collected from coastal flooding events classified as level 3 by

SurgeWatch2.0 (Haigh *et al*., 2017). An example is the Burn's day storm on 25 January 1990, with strong winds reported over parts of southern England and Wales, and recorded maximum gusts of 80 knots in the Solent (McCallum, 1990; MET, 2016). Events were divided into three categories, flood, storm, and strong wind gusts, as reported by each respective source, and grouped into five years periods, in order to account for possible errors in sediment dating and sediment accretion rates calculated by the CRS method (table 6.1).

Table 6-1: Five-year period used to calculate mean sediment accretion rates (mm year^{-1}) and C_{Seq} rates (g m^{2} year^{-1}) corresponding to the listed extreme weather events in the Solent, in chronological order, with respective sources. Weather events were classified as flood, storm and strong wind gusts.

	Extreme Weather Events	
Period (5 Years)	**Reported Event**	**Sources**
1914-1918	1916 – Flood	Zong & Tooley (2003); Haigh *et al.* (2017)
1929-1933	1931 – Flood	Met Office (1931); Lamb (1991); Hickey (1997); Eden (2008); Haigh *et al.* (2017)
1951-1955	1953 – Storm	Met Office (1953); Lamb (1991); Hickey (1997); Zong & Tooley (2003); Eden (2008); Haigh *et al.* (2015); Haigh *et al.* (2017)
1977-1981	1979 – Storm	Met Office (1978); Lamb (1991); Hickey (1997); Zong & Tooley (2003); Eden (2008); Ruocco *et al.* (2011); Haigh *et al.* (2015); Haigh *et al.* (2017)
1978-1982	1981 – Flood	Met Office (1981); Eden (2008); Ruocco *et al.* (2011); Haigh *et al.* (2015); Haigh *et al.*, (2017)
1985-1990	1987 – Storm	Burt and Mansfield (1988)
1987-1991	1989 – Flood	Met Office (1989); Davison *et al.* (1993); Hickey (1997); Eden (2008); Ruocco *et al.* (2011); Haigh *et al.* (2015); Haigh *et al.* (2017)
1988-1992	1990 – Storm	McCallum (1990); MET Office (2016)
1991-1995	1993 – Flood	Davison *et al.* (1993); Met Office (1993); Eden (2008); Ruocco *et al.* (2011); Haigh *et al.* (2015); Haigh *et al.* (2017)
1996-2000	1998 – Flood	Ruocco *et al.* (2011); Haigh *et al.* (2017)
2000-2005	2002 – Strong Winds	Eden (2008); Ruocco *et al.* (2011); Haigh *et al.* (2015); Haigh *et al.* (2017)
2002-2006	2004 – Flood	Met Office (2004); Eden (2008); Haigh *et al.* (2015); Haigh *et al.* (2017)
2005-2009	2007 – Flood	Eden (2008); Haigh *et al.* (2015); Haigh *et al.* (2017)
2006-2010	2008 – Flood	Wadey *et al.* (2013); Haigh *et al.* (2015); Haigh *et al.* (2017)
2010-2014	2012 – Flood	Met Office (2012); Haigh *et al.* (2017)
2011-2015	2013 – Strong Winds	Met Office (2014)
2012-2016	2014 – Strong winds	Met Office (2014); Haigh *et al.* (2015); Haigh *et al.* (2017)

6.3.5 Statistical analyses

Statistical analyses performed in this chapter included: Spearman's Rho correlation, Anderson-Darling test for normality, ANOVA, and Tukey's post hoc tests (Methods – section 3.2.1).

Spearman's Rho Correlation tests were used, due to non-normal distribution of data, to assess the relationship between estimated C_{Seq} rates (g m^2 $year^{-1}$) and the following variables: %mud, D50 (µm), sorting coefficient (φ) minimum and maximum yearly average temperatures (°C), precipitation (mm), average wind speed (kn), and sea level (mm).

The difference in sediment accretion rates (mm $year^{-1}$) and C_{Seq} rates (g m^2 $year^{-1}$) between periods with reported extreme weather events classified as storms, floods, strong wind gusts, and periods with no reported events, were tested using a series of ANOVA to identify significant differences between time periods (Conover and Iman, 1981). Both sediment accretion and C_{seq} rates met the assumption of normality of residuals when tested with Anderson-Darling so no transformation of data was needed prior to analysis of variance.

6.4 Results

6.4.1 Radionuclide dating

$^{210}Pb_{excess}$ activity profiles generally decreased with depth for all cores apart from LGST 1, which showed possible signs of sediment mixing (figure 6.3). Core CRST 1 (figure 6.3a) presented the highest surface count values of $^{210}Pb_{excess}$, of 128.76 Bq/Kg, with a count value of supported ^{210}Pb equilibrium established at 11.28 Bq/Kg, similar to the one established at CRST 2 (figure 6.3b), of 11.61 Bq/Kg. Farlington Marshes cores presented the lowest count values of supported ^{210}Pb equilibrium, established at 7.84 and 7.24 Bq/Kg, for FMST 1 and FMST 2 respectively (figures 6.3c and 6.3d). FMST1 core also presented the lowest surface $^{210}Pb_{excess}$ count, of 32.39 Bq/Kg (figure 6.3c). The maximum $^{210}Pb_{excess}$ activity detection depth was at 45 cm on LGST cores (figures 6.3e and 6.3f), with LGST 1 (figure 6.3e) presenting the second highest surface count value 78.10 Bq/Kg. Both Porchester cores presented the highest count values of supported ^{210}Pb equilibrium, of 18.20 and 18.06 Bq/Kg for PMST 1 and PMST 2, respectively (figure 6.3g and 6.3h).

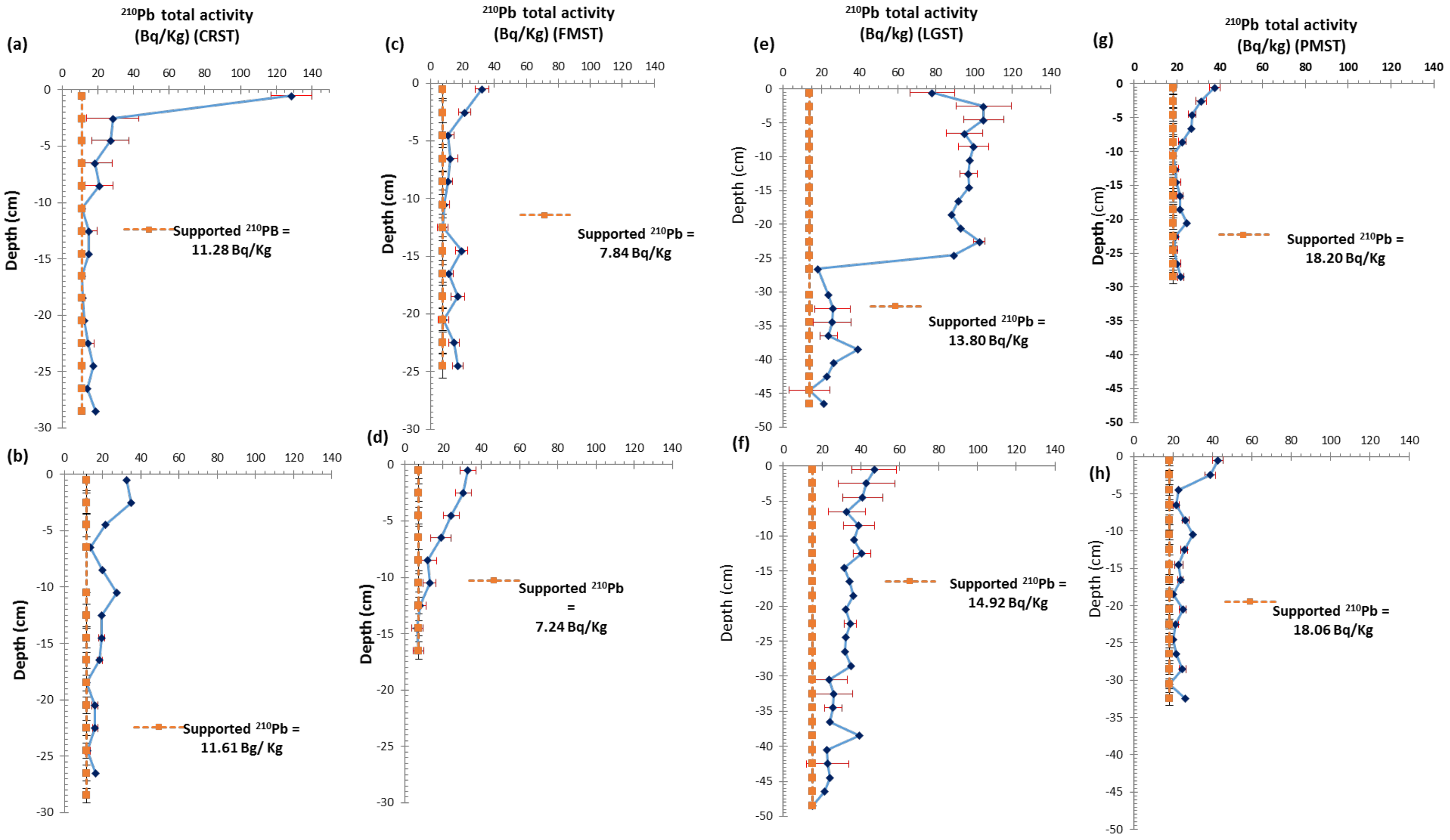


Figure 6.3: Total activity down-core for ^{210}Pb (a) CRST 1 (b) CRST 2, (c) FMST 1, (d) FMST 2, (e) LGST 1, (F) LGST 2, (g) PMST 1 and (h) PMST 2 represented by blue lines (diamond markers), with error calculations (5%) shown in red. Supported ^{210}Pb values represented by orange (square markers) lines on all graphs.

6.4.2 Sediment accretion rates

Calculated regression equations for each core are shown below (figures 6.4 and 6.5). The regression analysis between sediment accretion rates and depth, calculated by the CF:CS model, showed that the model was a good, and statistical, fit to the data on all cores ($p < 0.05$), with R^2 values ranging from 0.55 (PMST 2) to 0.94 (PMST 1) (figures 6.5c and 6.5d).

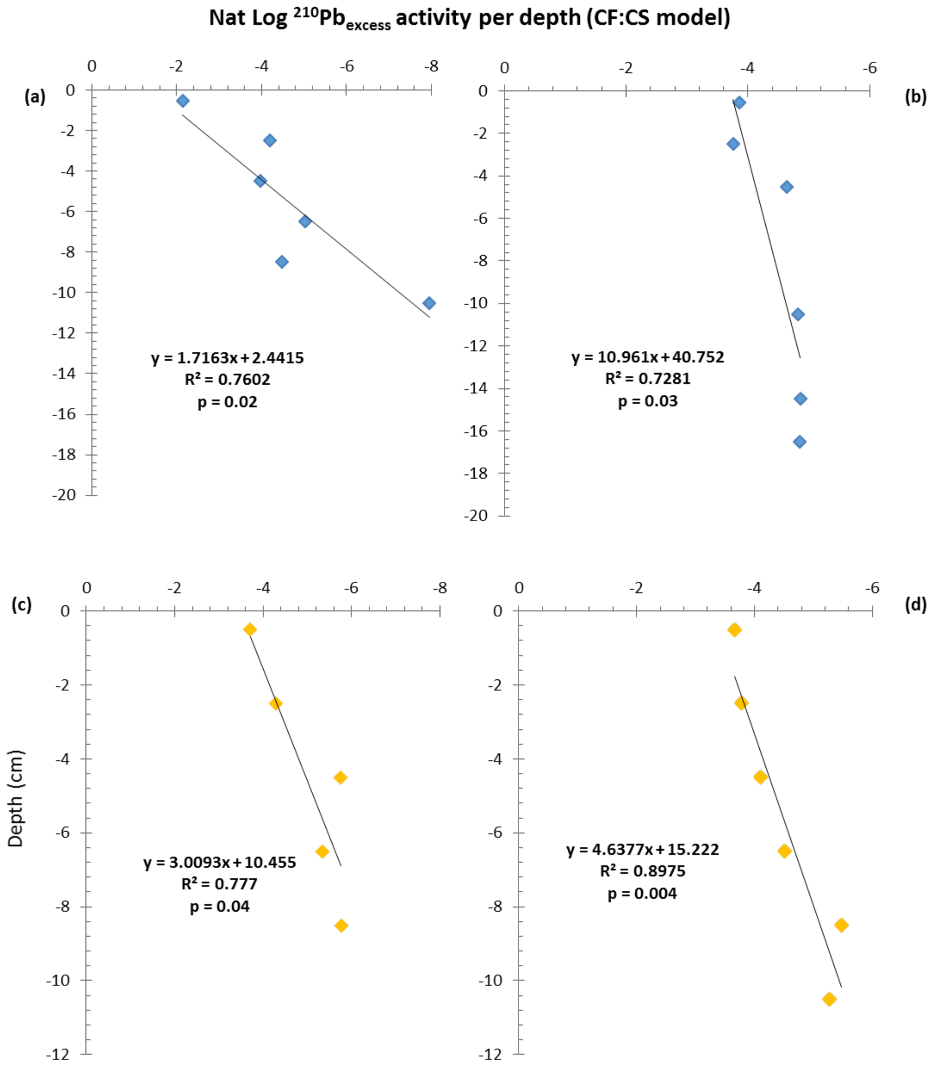


Figure 6.4: Natural Log (Ln) of $^{210}Pb_{excess}$ per depth (using the CF:CS model) with regression line and calculated regression equation, including R^2 and p values, for (a) CRST 1, (b) CRST 2, (c) FMST 1 and (d) FMST 2.

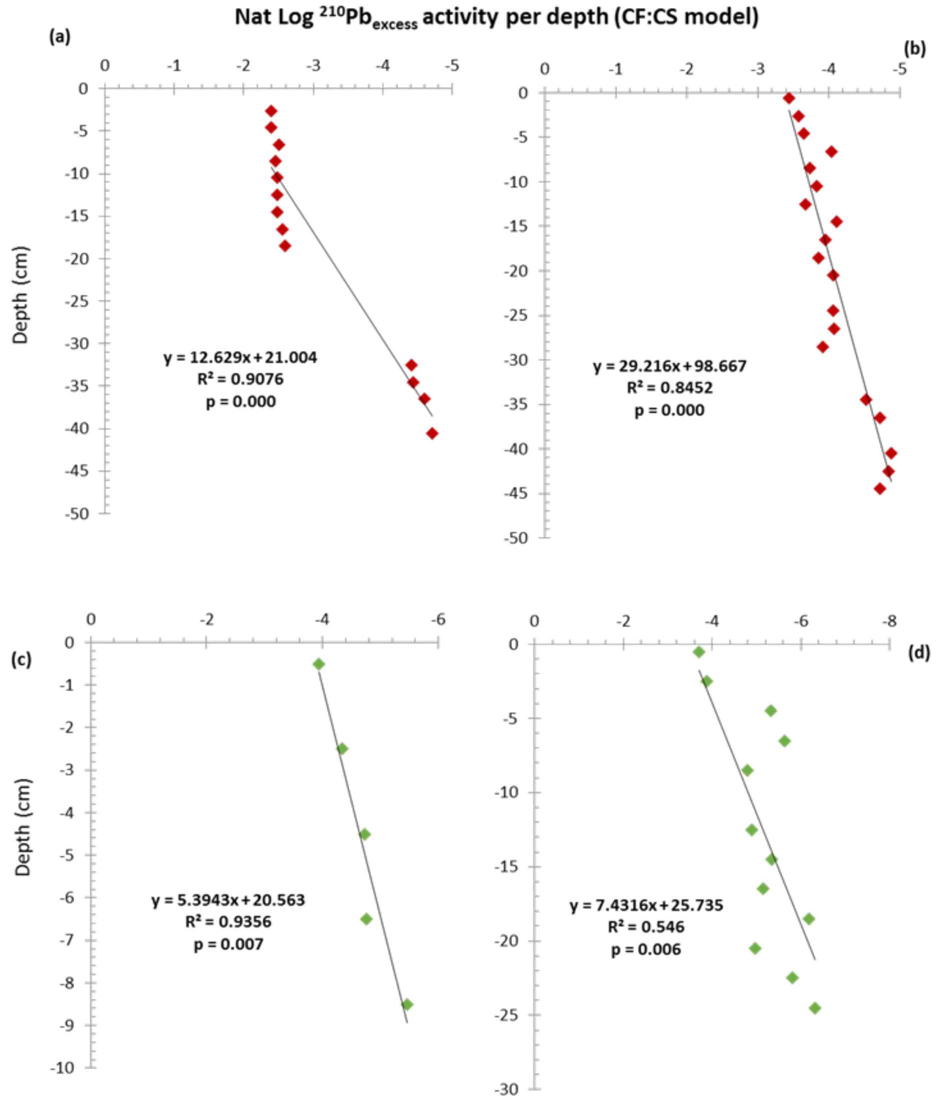


Figure 6.5: Natural Log (Ln) of ^{210}Pb $_{excess}$ per depth (CF:CS model) with regression line and calculated regression equation, including R^2 and p values, for (a) LGST 1, (b) LGST 2, (c) PMST 1 and (d) PMST 2.

The ^{210}Pb profiles indicated steady accretion due to their log-linear nature on all cores. Mean sediment accretion rates calculated using the CF:CS model ranged between 1.2 mm/year (CRST 1 and FMST 1) and 10.8 mm/year (LGST 2) (table 6.2). Mean sediment accretion rates calculated by the CRS model were the same as those found using the simple, CF:CS, model for the CRST 1 and FMST 1 cores, but higher than the CF:CS model for the PMST 2 core (table 6.2). All other cores had lower average sediment accretion rates calculated by the CRS method, than CF:CS (table 6.2). Similarly, to the CF:CS method, CRS calculated sediment accretion rates were the lowest for the CRST 1 and FMST 1 cores, of 1.2 mm/year, and the highest for the LGST 2 core, of 6.3 mm/year (table 6.2).

Table 6-2: Comparison between the average sediment accretion rates for the Creek Rythe CRST 1 and CRST 2, Farlington Marshes FMST 1 and FMST2, Hayling Island LGST 1 and LGST 2, and Porchester PMST 1 and PMST 2. Cores calculated using the simple method (CF:CS) from the regression line of the ^{210}Pb in the core profile over time, and from the CRS model. The CRS method does not provide upper and lower values, representing 5% error. Maximum depth of ^{210}Pb $_{excess}$ activity included.

			Sediment accretion rates (mm/year)		
Core	**Maximum ^{210}Pb excess activity (cm)**	**Method**	**Lower**	**Average**	**Upper**
CRST 1	15	CF:CS	0.6	1.2	2.4
		CRS	-	1.2	-
CRST 2	19	CF:CS	2.5	4.7	6.8
		CRS	-	3.6	-
FMST 1	11	CF:CS	0.6	1.2	7.6
		CRS	-	1.2	-
FMST 2	13	CF:CS	1.1	1.6	3.0
		CRS	-	1.2	-
LGST 1	43	CF:CS	3.6	4.3	5.5
		CRS	-	3.4	-
LGST 2	45	CF:CS	8.8	10.8	13.8
		CRS	-	6.3	-
PMST 1	11	CF:CS	1.2	1.8	3.5
		CRS	-	1.7	-
PMST 2	25	CF:CS	2.6	4.2	11.9
		CRS	-	4.3	-

Even though ^{137}Cs was detected on all sites, historical peaks related to 1963 and 1986 were not clearly identifiable. There was also evidence of ^{137}Cs activity at depths below the age of its introduction in the environment in the 1950's on LGST 1, LGST 2, PMST 1 and PMST 2 cores (figure 6.6). Therefore, the ^{137}Cs method was not used to calculate sediment accretion rates for this study.

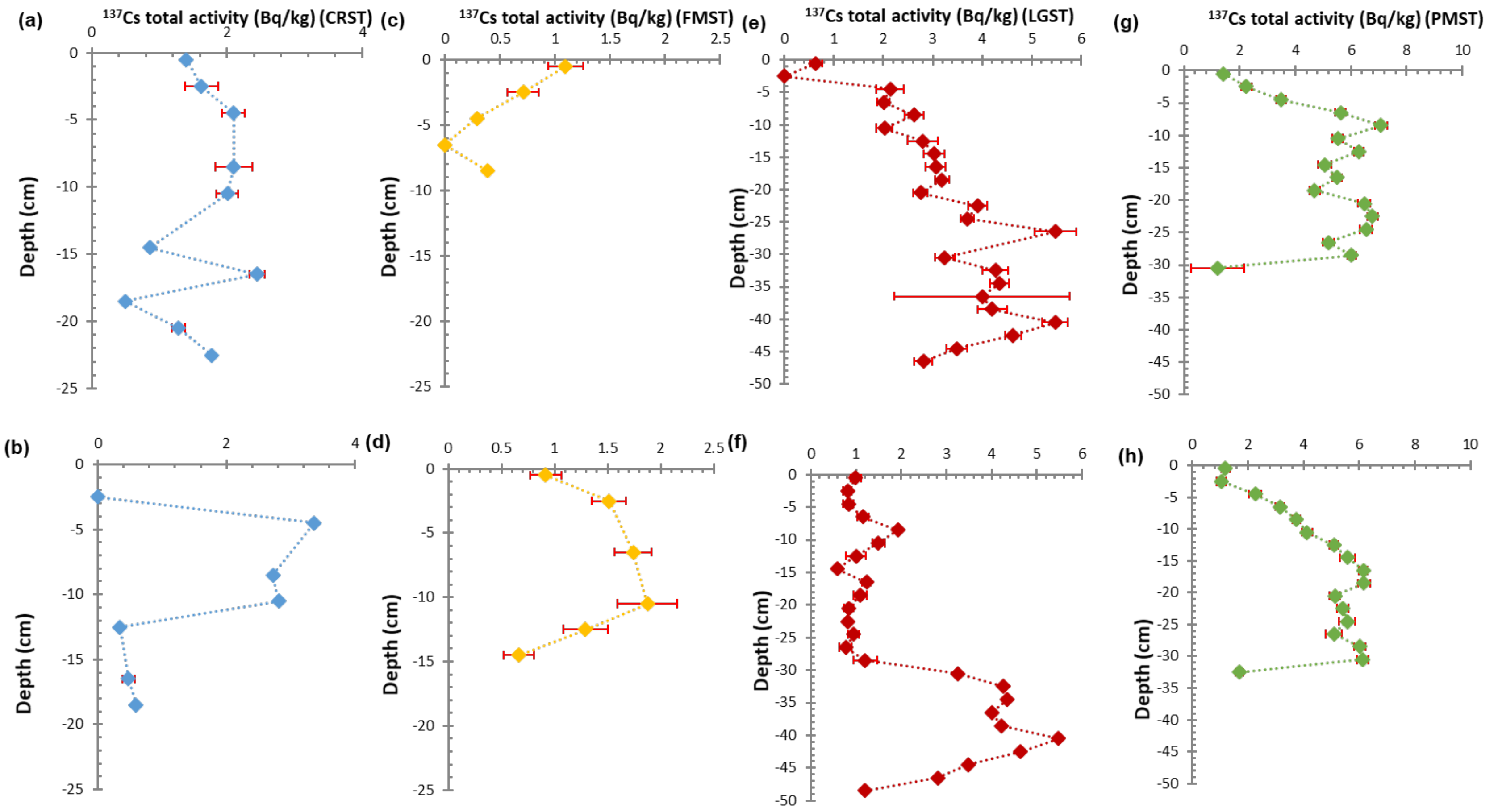


Figure 6.6: ^{137}Cs activity down the core profile, with identified 1963 and 1986 markers from (a) CRST 1, (b) CRST 2, (c) FMST 2, (d) LGST 1, (e) LGST 2, (f) PMST 1 and (g) PMST 2. Horizontal red bars show error margins in activity (5%).

6.4.3 Carbon sequestration rates

Since the ^{210}Pb CRS method can determine sediment accretion rates by depth and respective age, these values were used to calculate carbon sequestration rates down core for all sampling sites. The highest C_{seq} rates were found in one of the cores from Hayling Island (LGST 2) of 106.05 ± 49.09 (g m^2 $year^{-1}$), and lowest values were found in Farlington Marshes (FMST 1), of 19.91 ± 10.72 (g m^2 $year^{-1}$) (table 6.3). The average C_{seq} rate for all cores was 67.91 ± 32.39 (g m^2 $year^{-1}$) (table 6.3). The average mud fraction (silt + clay) between cores was 86.80 ± 9.89 %, with 22.73 ± 7.96 (µm) median particle size and 1.97 ± 0.32 sorting coefficient, indicating muddy sediments with predominantly fine and poorly sorted particles (table 6.3).

Daily temperature data recorded for 12 hours, between 09:00 in the morning and 09:00 in the evening were used to evaluate the temporal relationship between temperature and carbon sequestration rates. The reported maximum and minimum yearly temperature across the studied time period averaged 14.83 ± 0.23 (°C) and 7.53 ± 0.25 (°C), respectively (table 6.3). Precipitation level data recorded during the same 12 hours period daily were also used in the analysis, with yearly averages of 2.18 ± 0.18 (mm) per day across all sites (table 6.3). Maximum wind speed was measured daily, through the whole 24h period, averaging 9.69 ± 0.44 (kn) (table 6.3). The mean reported sea level for the studied years was 7074.01 ± 19.98 (mm) (table 6.3).

Table 6-3: Depth and age of all collected cores, with respective carbon sequestration rates, %mud, median grain size (D50), degree of sorting, and climate data including maximum and minimum temperature ranges, precipitation levels and wind speed (MET office archives), as well as mean sea level (Permanent Service for Mean Sea Level (PSMSL) database - Portsmouth station). Values are presented as mean (± SD) for all variables.

SITES	Core	Core Depth (cm)	Core Age	Carbon sequestration rate (g m^2 year^{-1})	%Mud	D50 (μm)	Sorting coefficient (ϕ)	Temp max (0900-0900) (°C)	Temp min (0900-0900) (°C)	Precipitation (0900-0900) (mm)	Windspeed (0100-2400) (kn)	Sea level (mm)
Creek Rythe (CRST)	1	12.5	1906-2016	24.56 ± 19.42	92.49 ± 5.61	23.64 ± 10.10	1.93± 0.75	14.71 ± 0.34	6.99 ± 0.51	2.22 ± 0.34	8.16 ± 2.42	7082.0 ± 50.91
	2	16.5	1947-2016	86.22 ± 98.82	83.31 ± 11.74	27.60 ± 11.77	2.41 ± 0.21	14.90 ± 0.45	7.41 ± 0.66	1.83 ± 0.31	10.26 ± 1.16	7066.1 ± 37.91
Farlington Marshes (FMST)	1	*8.5*	1950-2017	19.91 ± 10.72	94.29 ± 3.44	16.64 ± 4.52	2.19 ± 0.22	15.10 ± 0.72	7.95 ± 1.20	2.39 ± 0.15	10.13 ± 1.06	7083.0 ± 39.64
	2	10.5	1939-2017	51.07 ± 27.55	67.31 ± 13.18	37.54 ± 10.64	1.66 ± 0.17	14.89 ± 0.49	7.49 ± 0.61	2.27 ± 0.37	8.83 ± 2.01	7078.5 ± 24.72
Hayling Island (LGST)	1	*36.5*	1901-2017	82.74 ± 84.25	96.28 ± 3.47	12.95 ± 1.50	2.42 ± 0.21	14.51 ± 0.87	7.17 ± 0.87	2.26 ± 0.58	9.57 ± 0.25	7067.5 ± 39.31
	2	44.5	1921-2017	106.05 ± 49.09	86.26 ± 7.50	21.03 ± 5.96	2.48 ± 0.06	14.87 ± 0.73	7.36 ± 0.74	2.07 ± 0.42	9.85 ± 0.78	7054.8 ± 37.94
Porchester (PMST)	1	*8.5*	1972-2017	76.70 ± 95.08	79.72 ± 12.09	26.68 ± 7.74	1.24 ± 0.36	14.51 ± 0.62	7.50 ± 0.58	2.12 ± 0.30	9.81 ± 1.03	7062.5 ± 33.93
	2	*24.5*	1954-2017	96.05 ± 51.78	94.79 ± 0.85	15.77 ± 1.54	1.42 ± 0.58	14.76 ± 0.73	7.51 ± 0.62	2.13 ± 0.58	9.55 ± 0.52	7061.7 ± 41.77
Mean				**67.91 ± 32.39**	**86.81 ± 9.81**	**22.73 ± 7.96**	**1.97 ± 0.32**	**14.78 ± 0.20**	**7.42 ± 0.28**	**2.16 ± 0.17**	**9.52 ± 0.70**	**7069.5 ± 10.43**

For the CRST 1 core, the oldest sediments assessed using ^{210}Pb dating by the CRS method were laid down around 1906 (figure 6.7a). However, the CRST 2 core showed different patterns of sediment accretion per year, with the oldest sediments assessed using ^{210}Pb dating by the CRS method laid down around 1947 (figure 6.7b).

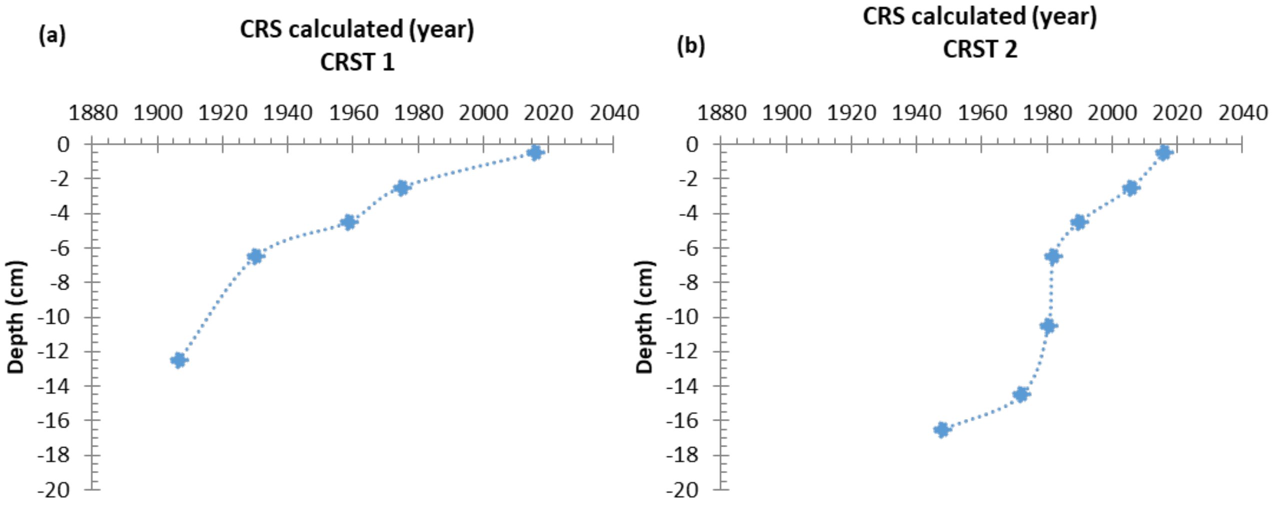


Figure 6-7: CRS calculated age of each depth for the (a) CRST 1 core, and (b) CRST 2 core for the Creek Rythe site.

The data showed higher accretion rates around 1906 (2.6mm/yr), and 1975 (1.2mm/yr) for the CRST 1 core. %mud increased with age, from 82.6% in 2016 to 93.9% in 1975, the highest value was found in 1930 with 96.4 % (figure 6.8a). More recent sediments were better sorted than older ones, but they were still within the poorly sorted classification, according to Folk and Ward (1957) (figure 6.8b). Sediment accretion rates were calculated over time using the CRS method (figure 6.8c), showing accretion rates varied between 0.5-2.6mm/yr between 1906 and 2016. C_{seq} rates were the highest during 1930, of 35.68 g m^2 $year^{-1}$, and the lowest in 2016, at 10.3 g m^2 $year^{-1}$ (figure 6.8d).

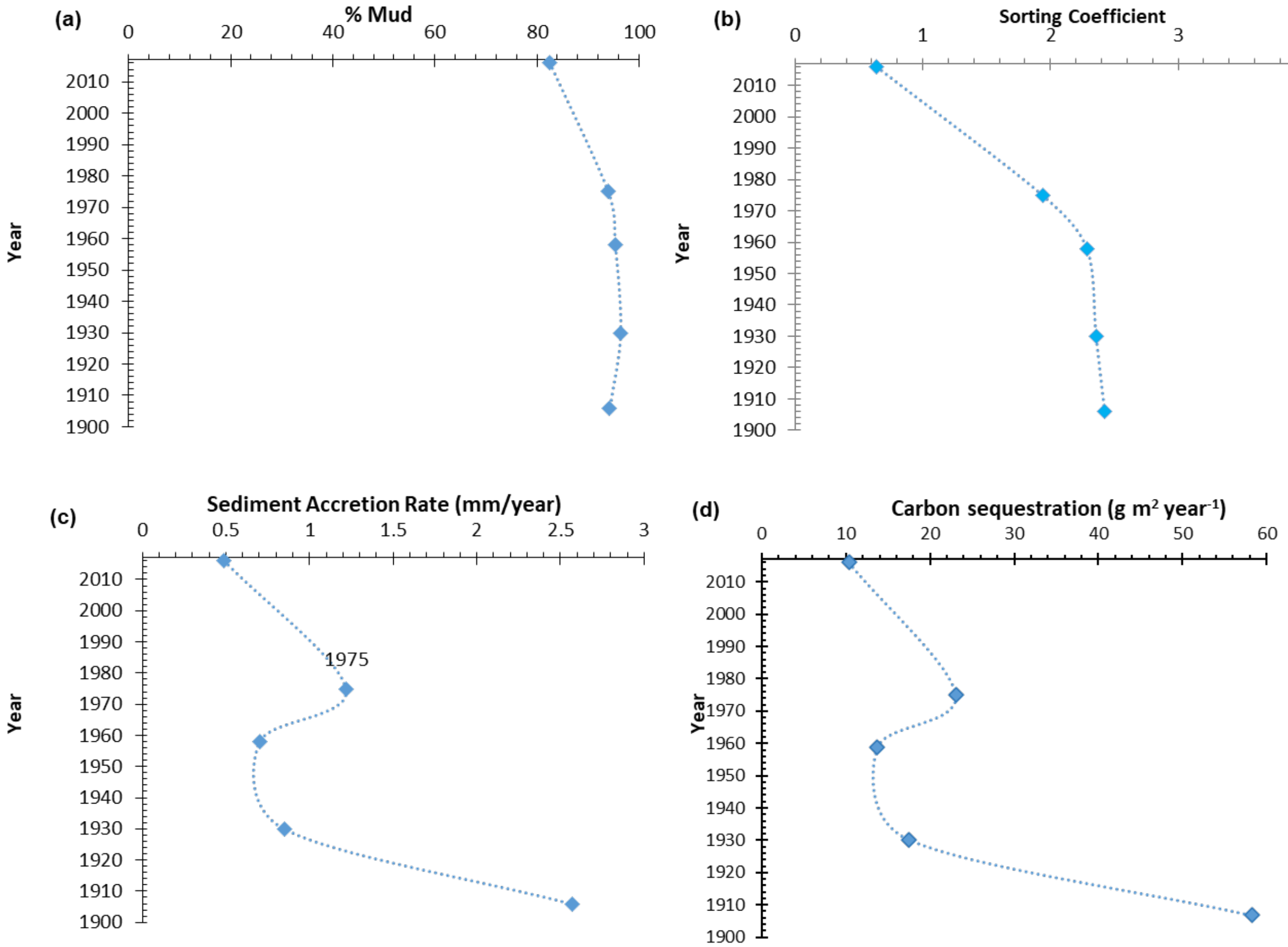


Figure 6-8: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d), with age, for the CRST 1 core.

Similar to CRST 1, %mud increased with age, from 72.8% in 2016 to 96.6% in 1980, the highest value for the CRST 2 core (figure 6.9a). Degree of sorting remained steady with age for this core, apart from a small increase in the late 1970s, related to an increase in sediment accretion rate. All particles were within the very poorly sorted classification, according to Folk and Ward (1957) (figure 6.9b). Sediment accretion rates varied between 0.76-1.99mm/yr between 1947 and 2016. Higher accretion rates happened around 1982 (12.1mm/yr), and 1980 (4.9mm/yr) (figure 6.9c). C_{seq} rates were the highest during 1982, at 296.5 g m^2 $year^{-1}$, and the lowest in 1947, at 18.6 g m^2 $year^{-1}$ (figure 6.9d).

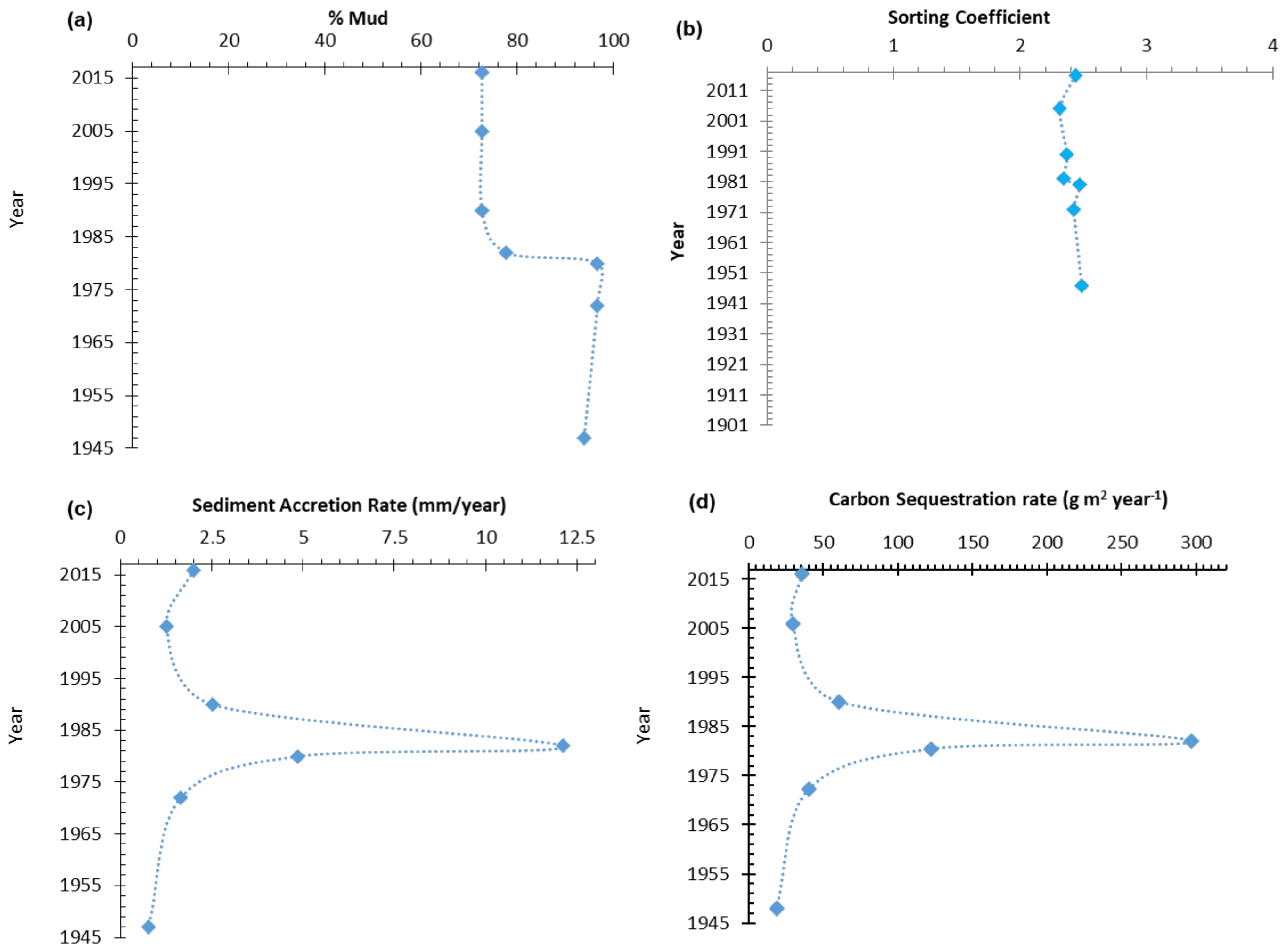


Figure 6-9: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d) with age, for the CRST 2 core.

The FMST 1 core had its oldest sediments assessed using ^{210}Pb dating by the CRS method, laid down around 1950 (figure 6.10a). Whereas, the FMST 2 core had older dated sediments than FMST 1, laid down around 1939, when assessed using ^{210}Pb dating using the CRS method (figure 6.10b).

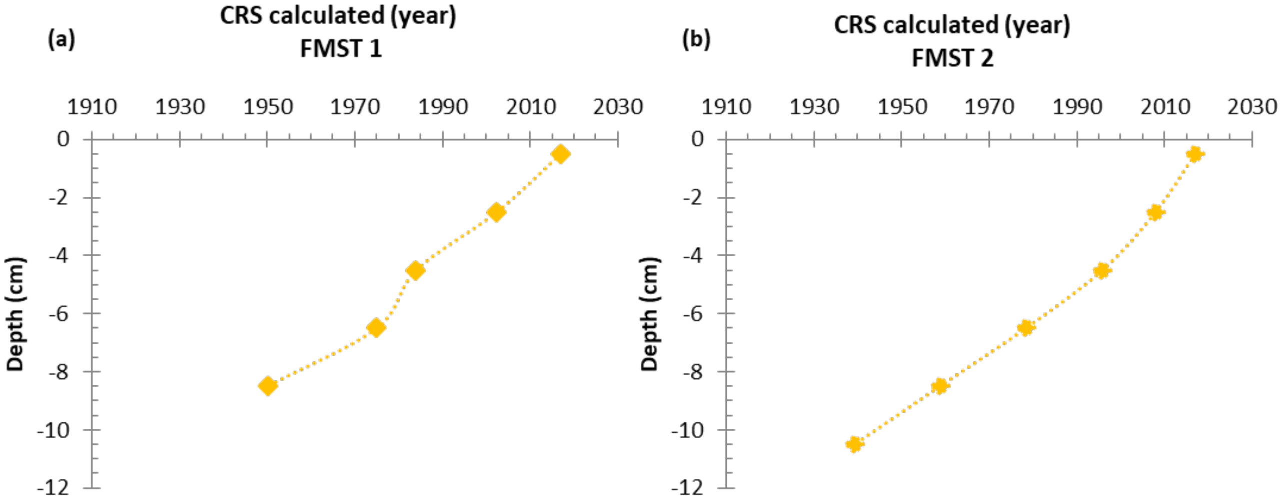


Figure 6-10: CRS calculated age of each depth for the (a) FMST 1 core, and (b) FMST 2 core for the Farlington Marshes site.

For the FMST 1 core, higher accretion rates were noted around 1984 (2.22mm/yr). Similarly to the CRST cores, %mud increased with age, from 91.78% in 2017 to 98.06% around 1950, the highest value (figure 6.11a). There was a slight decrease in the degree of sorting around the 1990's, probably related to the peak in sediment accretion rates around that time, and changes in elevation. All particles were within the very poorly sorted classification, according to Folk and Ward (1957) (figure 6.11b). Sediment accretion rates varied between 0.43-1.37mm/yr between 1950 and 2017 (figure 6.11c). C_{seq} rates were the highest around 1984, of 35.38 g m^2 year^{-1}, and the lowest around 1950, at 7.31 g m^2 year^{-1} (figure 6.11d).

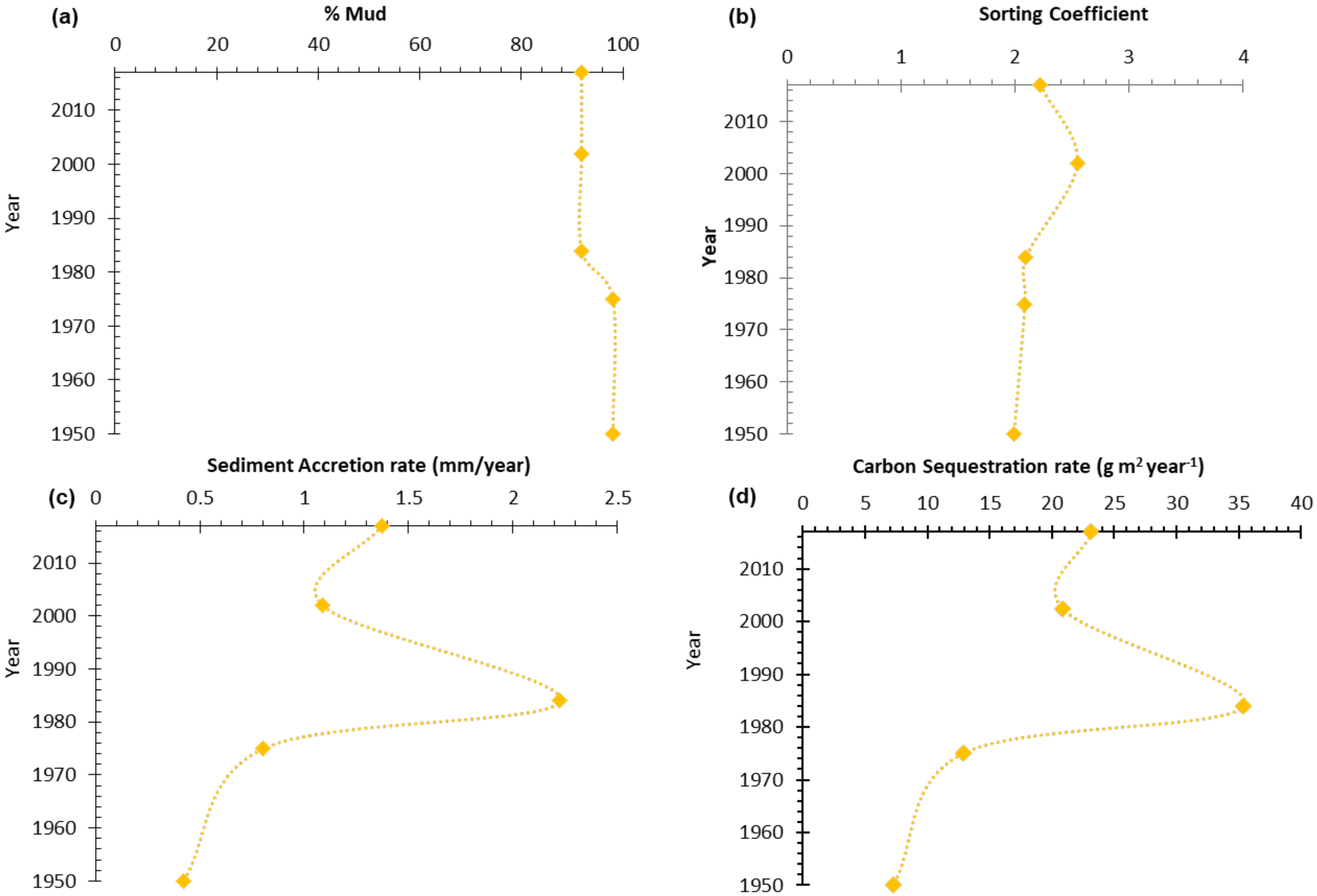


Figure 6-11: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d) with age, for the FMST 1 core.

For thr FMST 2 core, sediment accretion rates showed an overall trend of increase over time, with a stall between the 1950's and 1990's. Higher accretion rates are noted around 2017 (2.21mm/yr) and 2007 (1.65mm/year). Similarly to FMST 1, %mud increased with age, from 57.35% in 2017 to 63.79% around 1939, and the highest values were found around 1958 and 1978, both with 84.01% (figure 6.12a). There was a decrease in the degree of sorting in the newest sediments, although all particles were within the poorly sorted classification, according to Folk and Ward (1957) (figure 6.12b). Sediment accretion rates varied between 0.32-2.21mm/yr between 1939 and 2017 (figure 6.12c). C_{seq} rates did not follow the same pattern as sediment accretion rates in this core, with highest values around 1958, of 81.03 g m^2 $year^{-1}$, and the lowest around 1939, at 12.36 g m^2 $year^{-1}$, with large fluctuations over the dated time period (figure 6.12d).

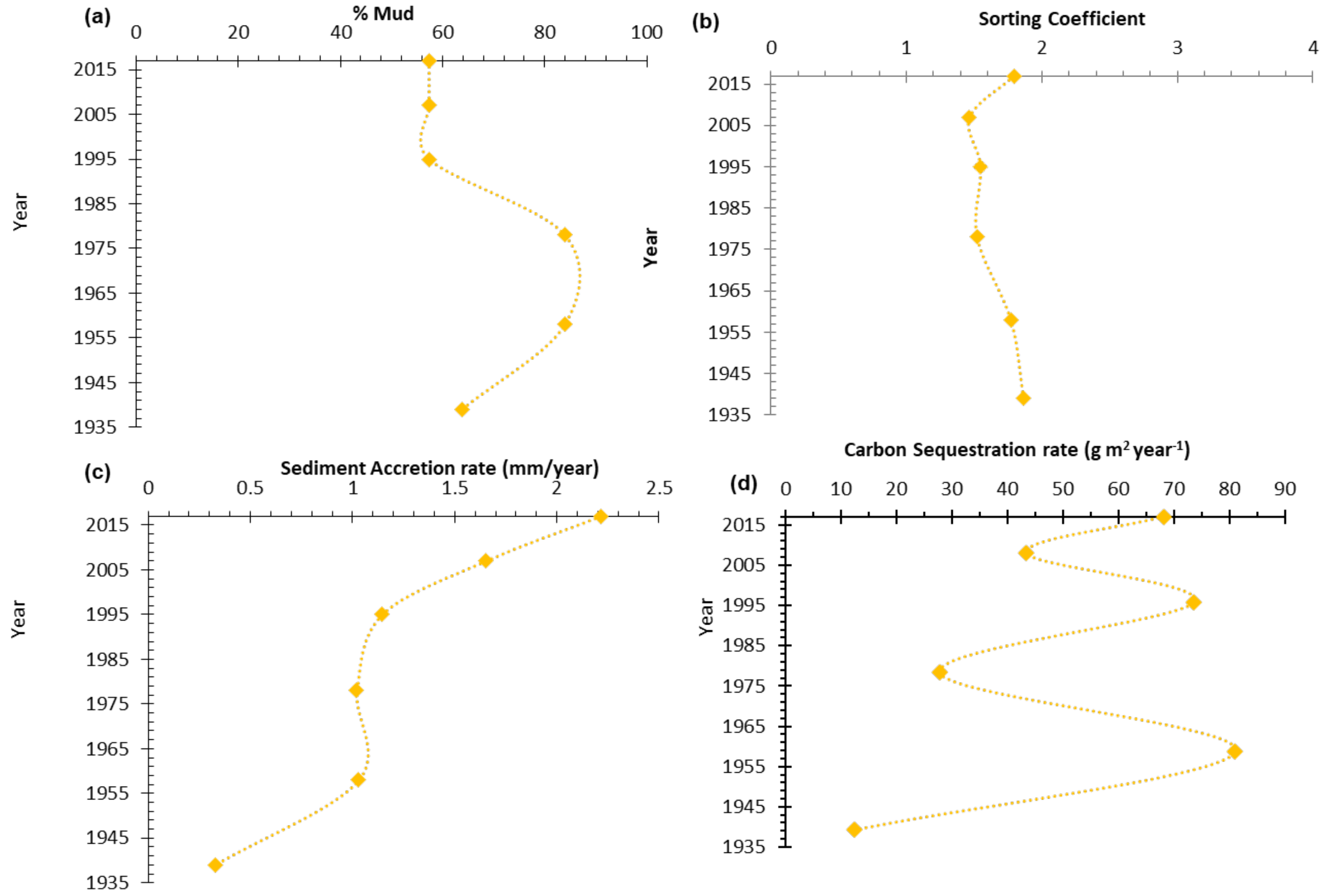


Figure 6-12: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d) with age, for the FMST 2 core.

The LGST 1 core provided the oldest dateable horizon of all sites, at 1901, with deeper $^{210}Pb_{excess}$ activity down-core (table 6.3 and figure 6.13). The LGST 2 core, had its oldest dateable horizon at 1921, assessed using ^{210}Pb dating by the CRS method (figure 6.13b).

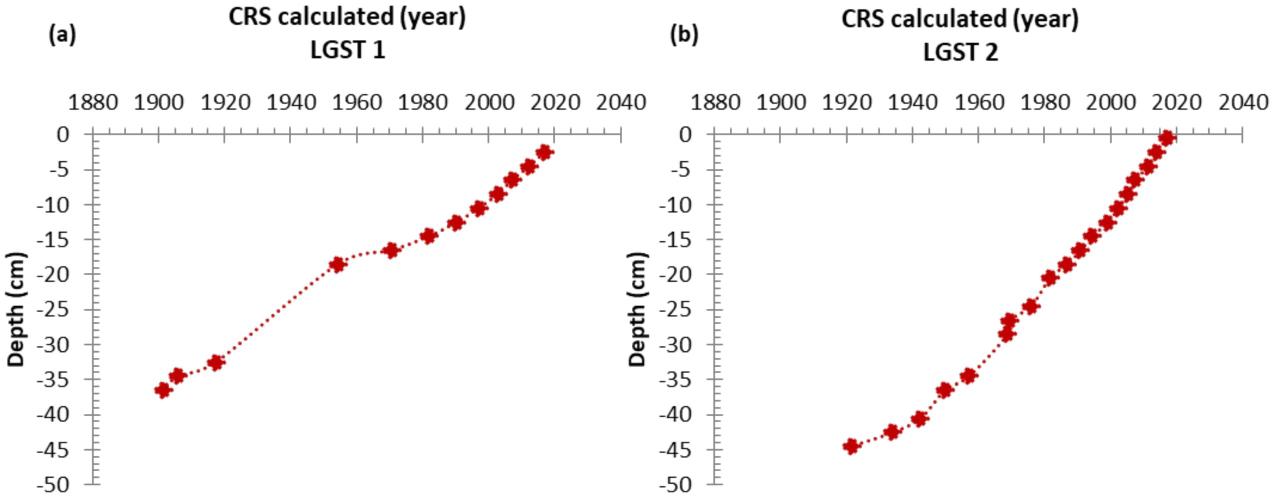


Figure 6-13: CRS calculated age of each depth for the (a) LGST 1 core, and (b) LGST 2 core for the Hayling Island site.

For the LGST 1 core, higher accretion rates were recorded around 1917 (12.18mm/yr). Similarly to the previous sites, %mud showed a general trend of increase with age, from 88.99% in 2017 to 98.62% in 1901 (figure 6.14a). The degree of sorting increased over time within this core, with particles varying from poorly to very poorly sorted classification, according to Folk and Ward (1957) (figure 6.14b). Sediment accretion rates varied between 1.22-4.27mm/yr between 1901 and 2017 (figure 6.14c). C_{seq} rates showed an increase between the 1920's and 1970, not following sediment accretion rates patterns, with highest values during that period around 1954, of 318.22 g m^2 $year^{-1}$, and lowest in 1970, at 14.33 g m^2 $year^{-1}$ (figure 6.14d).

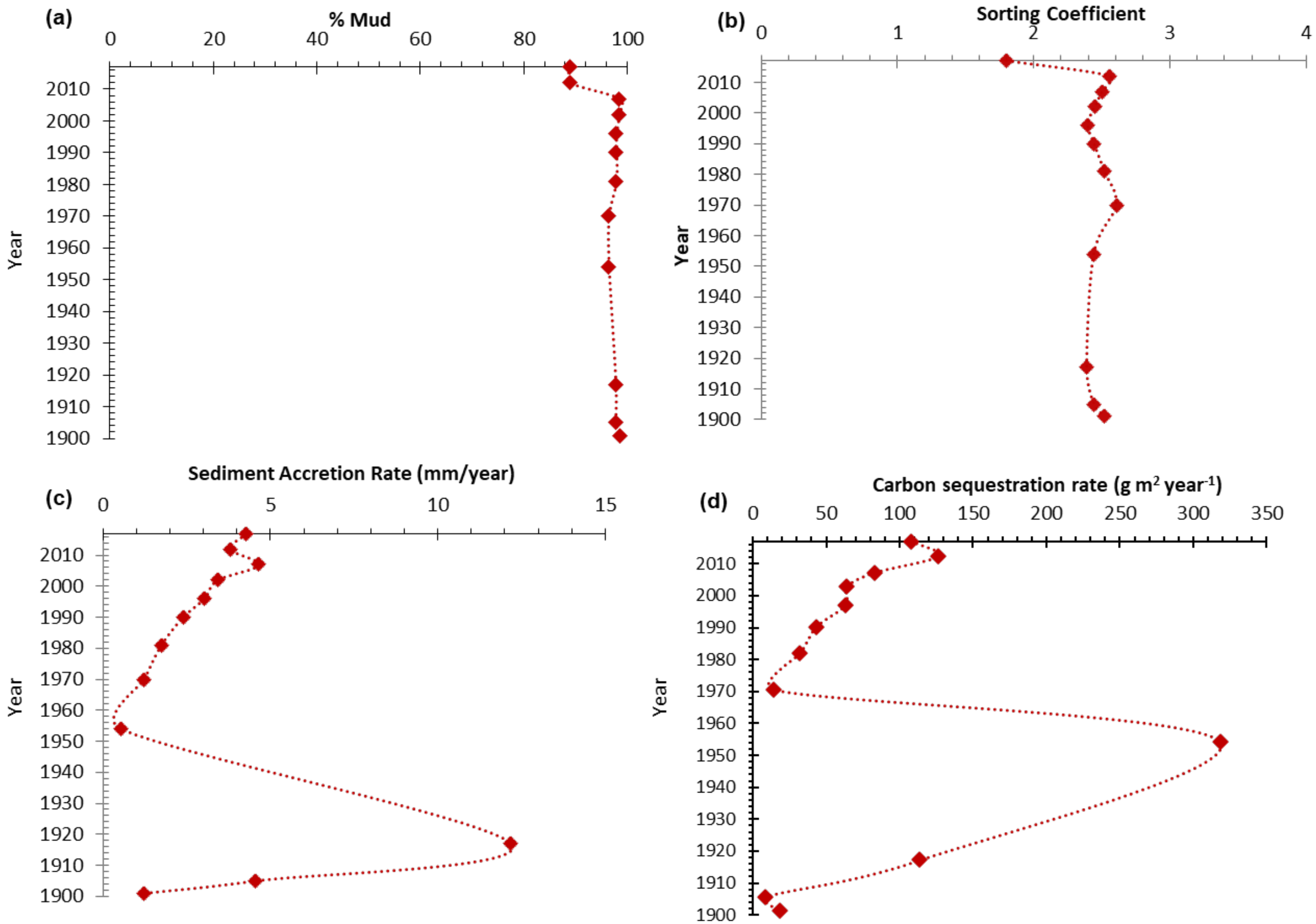


Figure 6-14: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d) with age, for the LGST 1 core.

%mud for the LGST 2 core showed a greater variation with age for this core than all other cores, changing from 77.78% in 2017 to the highest values of 94.25% around both 1994 and 1999 (figure 6.15a). The degree of sorting followed the same patterns of change over time as %mud, although all particles were within the very poorly sorted class, according to Folk and Ward (1957) (figure 6.15b). Higher accretion rates were recorded around 1970 (30.07mm year^{-1}) (figure 6.15c), with similar patterns of relative peaks in %mud and sorting coefficient around that period (figures 6.15 a and b). Sediment accretion rates varied between 0.77-6.50mm/yr between 1921 and 2017 (figure 6.15c). C_{seq} rates for this core showed contrasting patterns to sediment accretion rates, with highest values around 1956, of 184.80 g m^2 year^{-1}, and the lowest around 1921, at 15.57 g m^2 year^{-1} (figure 6.15d).

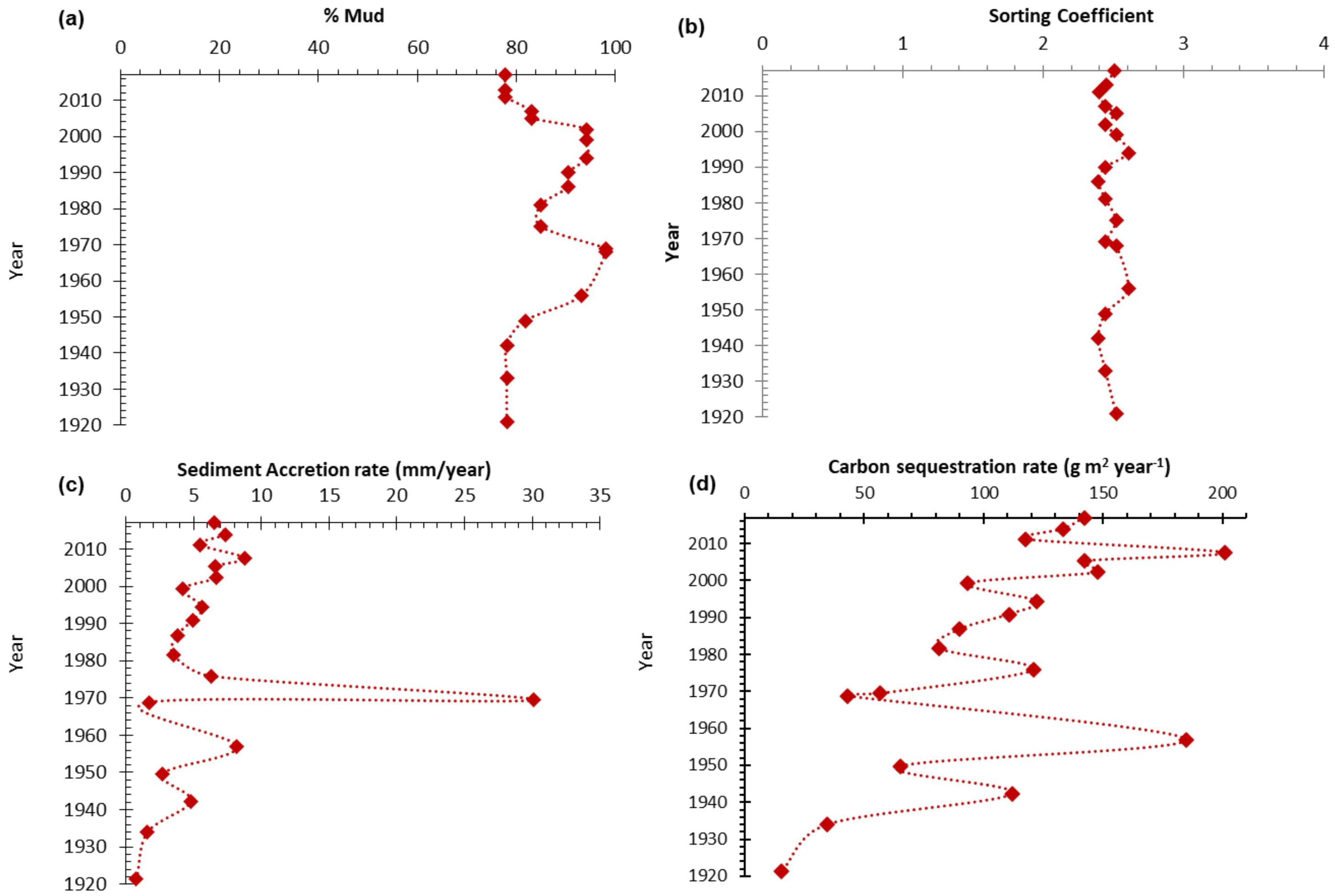


Figure 6-15: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d) with age, for the LGST 2 core.

The PMST 1 core was dated to a maximum of 1972 (table 6.2), while the PMST 2 core, was dated to a maximum age of 1954 (figure 6.16b).

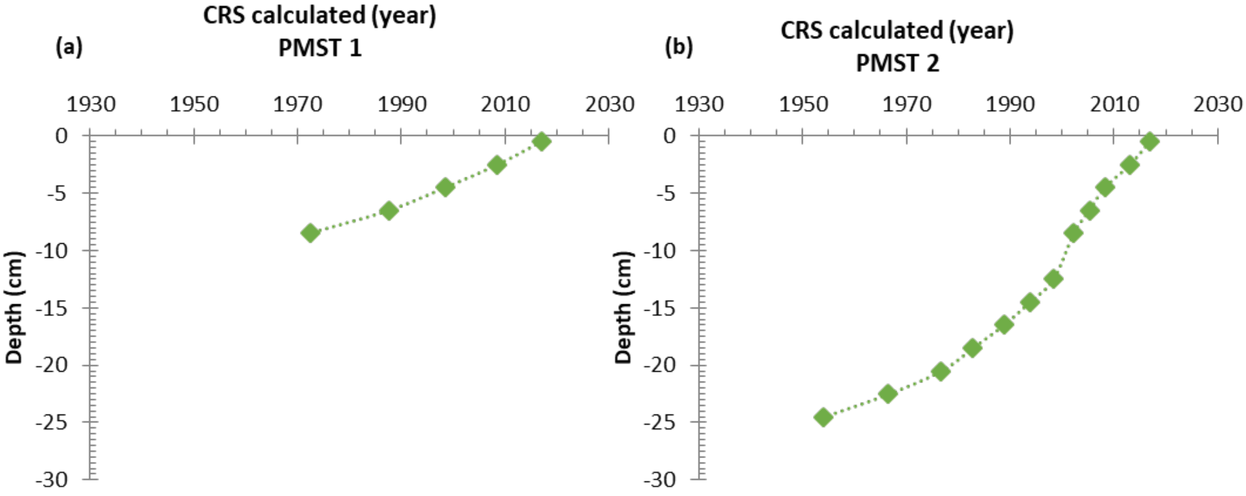


Figure 6-16: CRS calculated age of each depth for the (a) PMST 1 core, and (b) PMST 2 core for the Porchester site.

Similar to the previous sites, %mud increased with age, from 70.88% in 2017 to 92.96% in 1972, the highest value (figure 6.17a). The degree of sorting followed similar patterns of change with age as %mud, with older particles, with higher %mud, showing sorting coefficient values within the very poorly sorted class, according to Folk and Ward (1957) (figure 6.17b). Sediment accretion rates varied between 0.82-2.37 mm/yr between 1972 and 2017 (figure 6.17c), showing a general trend of decrease with age. C_{seq} rates also decreased with age, showing a greater decrease during recent years, up to 2010, than sediment accretion rates. C_{seq} rates were the highest during 2017, of 246.08 g m^2 year^{-1}, and lowest around 1972, at 22.02 g m^2 year^{-1} (figure 6.17d).

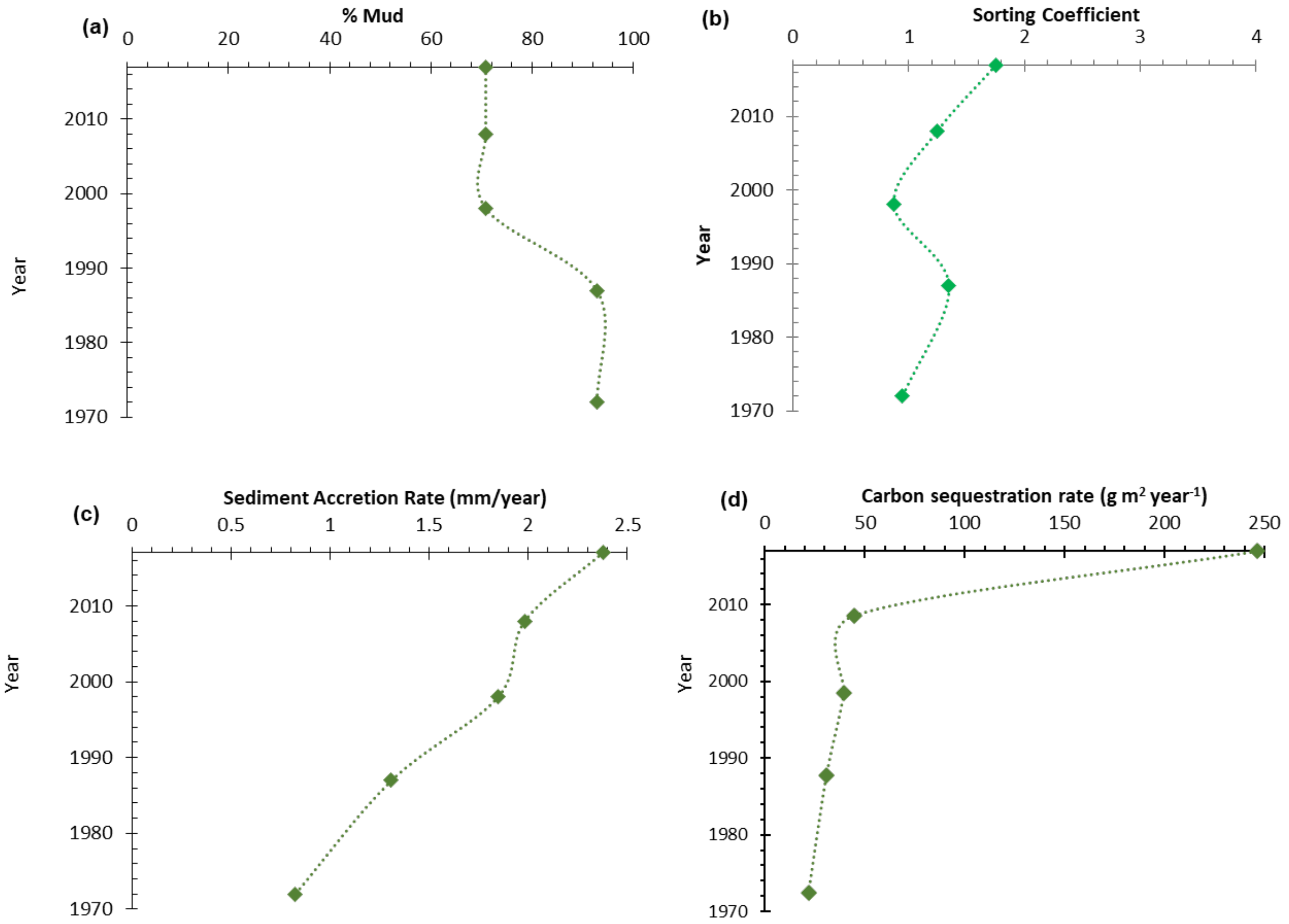


Figure 6-17: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d) with age, for the PMST 1 core.

%mud for the PMST 2 core remained relatively consistent over time, with variation from 94.70% around 2017 and 93.76% around 1954 (figure 6.18a). The degree of sorting followed similar patterns as C_{seq} and sediment accretion rates, with most particles within the poorly sorted class, according to Folk and Ward (1957) (figure 6.18b). Sediment accretion rates varied between 1.15-5.26 mm/yr between 1954 and 2017, with the highest accretion rates recorded around 1998 (8.70 mm/yr) (figure 6.18c). C_{seq} rates showed a similar pattern as sediment accretion rates up to around 1995, with highest values around 1998, of 206.59 g m^2 $year^{-1}$, and lowest around 1954, at 28.99 g m^2 $year^{-1}$ (figure 6.18d).

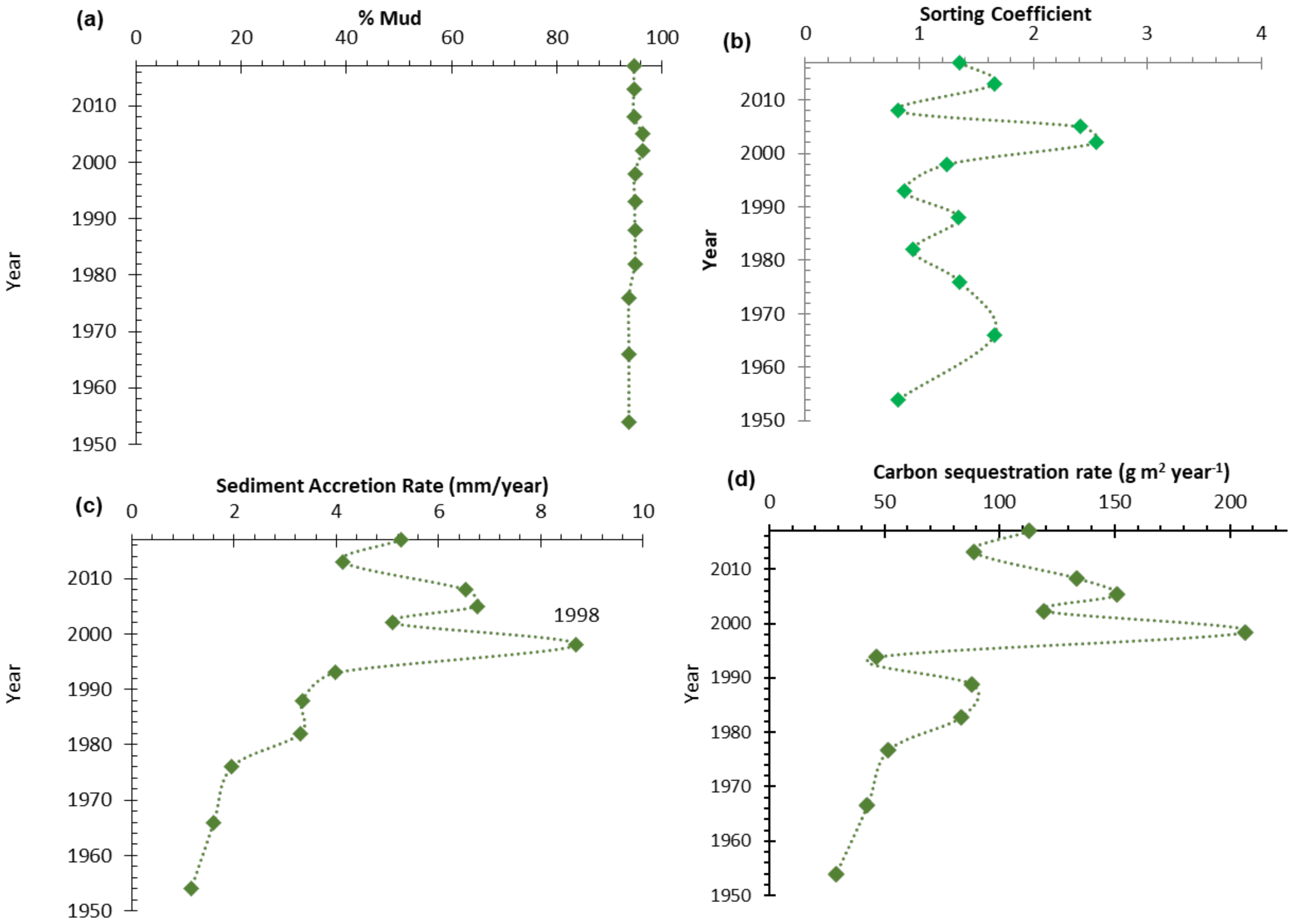


Figure 6-18: Distribution of % mud (a), Degree of sorting (b), ^{210}Pb CRS method derived sediment accretion rates (c), and Carbon sequestration rates (d) with age, for the PMST 2 core.

6.4.4 Relationships between environmental variables and Carbon sequestration rates

C_{seq} rates from Creek Rythe (CRST) showed a strong significant relationship with wind speed ($r_s = 0.720$; $p < 0.05$), suggesting that for the cores from this site C_{seq} rates increased during periods of higher wind speeds (table 6.4). C_{seq} rates from both Farlington Marshes (FMST) cores, were strongly and significantly correlated to sediment characteristics, showing negative relationships with %mud ($r_s = -0.656$; $p < 0.05$), and a positive relationship with median grain size (D50) ($r_s = 0.656$; $p < 0.05$) (table 6.4). C_{seq} rates from the Porchester (PMST) cores showed a significant relationship with %mud ($r_s = 0.483$; $p < 0.05$), and strong positive associations with maximum average temperature ($r_s = 0.514$; $p < 0.05$) and minimum average temperature ($r_s = 0.650$; $p < 0.01$), suggesting that variations in temperature, may affect carbon sequestration processes on this site (table 6.4). Hayling Island's (LGST) cores showed a significant negative relationship between C_{seq} rates sorting coefficient ($r_s = -0.373$; $p < 0.05$) (table 6.4).

Table 6-4: Spearman's correlation coefficients (r_s) between carbon sequestration rate and environmental variables for all study sites Statistically significant relationships are in bold, represented by * when p < 0.05 and ** when p <0.01.

ENVIRONMENTAL VARIABLES / SAMPLING SITES	%MUD	D50 (µm)	Sorting coefficient (ϕ)	Temp max (0900-0900) (°C)	Temp min (0900-0900) (°C)	Precipitation (0900-0900) (mm)	Wind speed (0100-2400) (kn)	Sea level (mm)
Creek Rythe (CRST)	-0.074	-0.060	0.455	-0.018	0.188	0.383	**0.720***	-0.084
Farlington Marshes (FMST)	**-0.656***	**0.656***	-0.518	0.389	0.353	-0.100	-0.536	-0.072
Hayling Island (LGST)	-0.332	0.266	**-0.373***	0.101	0.264	0.287	0.02	0.251
Porchester (PMST)	**0.483***	-0.319	0.470	**0.514***	**0.650****	0.163	-0.108	0.243

6.4.5 Relationships between weather events and sediment accretion and C_{seq} rates

Table 6-5: Summary of statistical results for ANOVAs, including values of df, F, p and n, for C_{seq} and sediment accretion rates, between periods of no reported climate events and periods of reported storms, strong wind gusts and flooding. Where Df represents the degree of freedom, and significance value for ANOVA α = 0.05. AD (p) is Anderson- Darling test for normality, normal result (p > 0.05).

Variable	df	F	p	n	AD (p)	Normality
C_{Seq} rates (g m^2 $year^{-1}$)	3	4.76	0.004	89	0.596 (0.119)	Normal
Sediment Accretion Rate (mm $year^{-1}$)	3	7.40	0.000	85	0.571 (0.134)	Normal

Results showed that the sediment accretion rates calculated by the ^{210}Pb CRS method were significantly higher in multiyear periods with occurrence of flood events (4.26 ± 2.28 mm/year, n = 16) and strong wind gusts (3.89 ± 2.44 mm/year, n = 43), than in periods with no reported climate events (1.28 ± 0.68 mm/year, n = 15) (table, 6.5 and figure 6.19). Mean sediment accretion rates from periods related to storm events (2.64 ± 1.25 mm/year, n = 11) showed no statistically significant differences compared to periods with other weather events, or periods with no events reported (table 6.5 and figure 6.19).

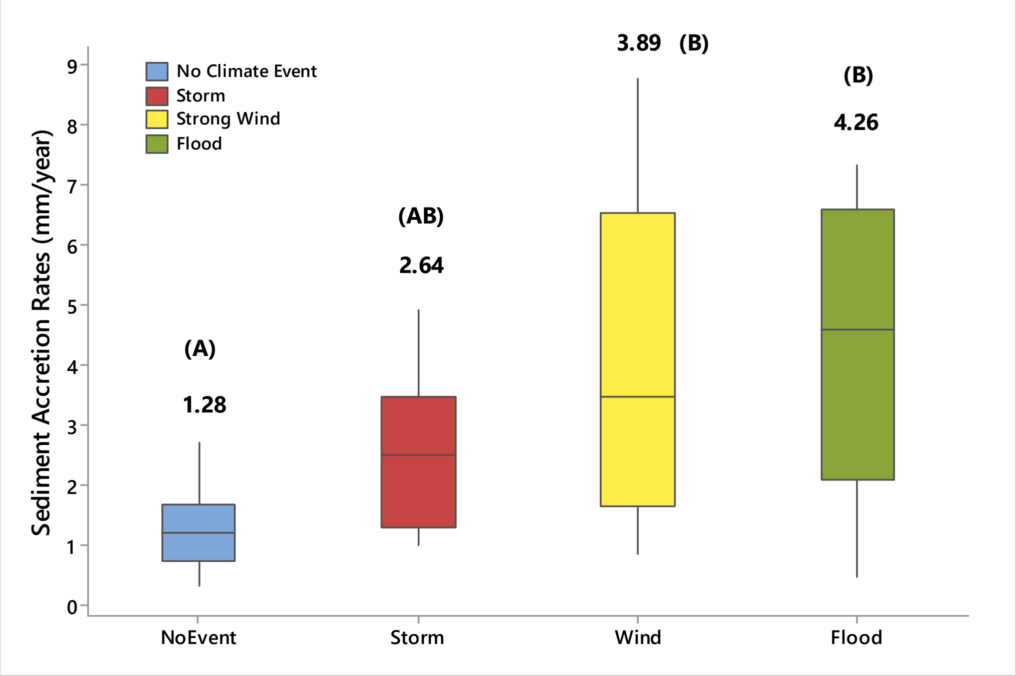


Figure 6-19: Distribution of sediment accretion rates for the four classes of weather: no event (n=15), storm (n=11), wind (n=43) and floods (n=16), including Tukey's grouping analysis results, where the same letters correspond to statistically similar means. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

Average C_{seq} rates were also significantly higher in periods when strong wind gusts (105.5 ± 61.5 g m^2 $year^{-1}$; n = 16) and flood events were reported (85.61 ± 54.34 g m^2 $year^{-1}$; n = 28), than periods with no reported extreme climate events in the Solent (46.69 ± 36.58 g m^2 $year^{-1}$; n = 19) (table 6.5 and figure 6.20). Mean C_{seq} rates from periods related to storm events (62.01 ± 30.56 g m^2 $year^{-1}$, n = 11) also showed no statistically significant difference to periods with other weather events, or periods with no events reported (table 6.5 and figure 6.20).

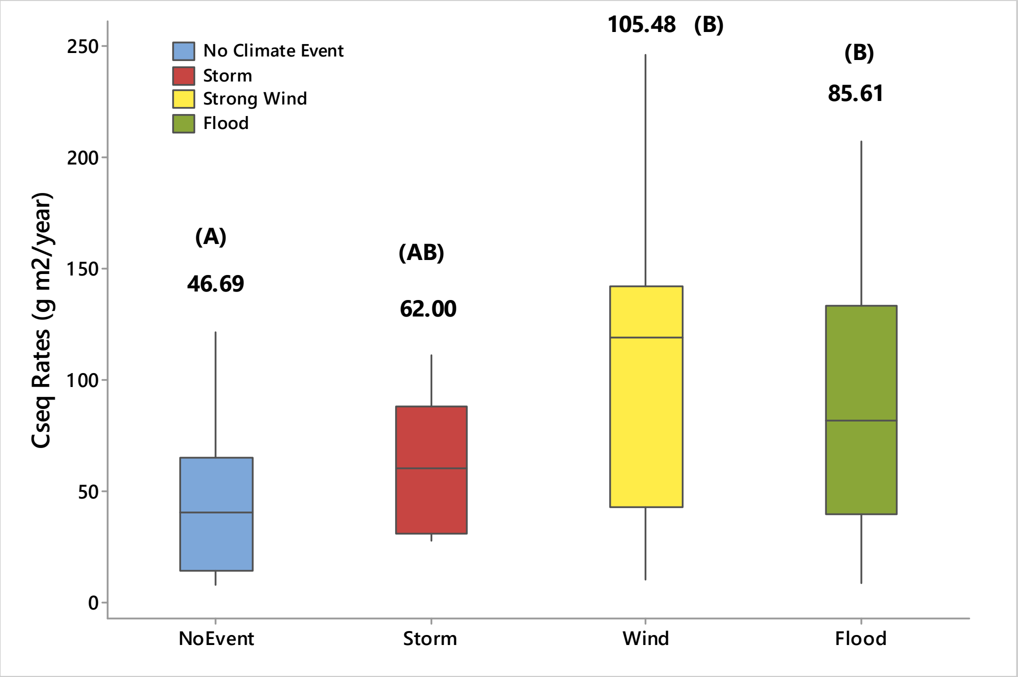


Figure 6-20: Average carbon sequestration rates for the four classes of weather: no event (n=19), storm (n=11), wind (n= 16) and floods (n=43), including Tukey's grouping analysis results, same letters correspond to statistically similar means. Mean values in bold. Median line represented in the 50% interquartile boxes, and whisker lines representing lower and upper 25% values range.

6.5 Discussion

Results from this chapter show that ^{210}Pb activity can be used to determine sediment accretion rates from seagrass sediment cores in the Solent, U.K. This is indicated by the comparable sediment accretion rates measured by both the CF:CS and CRS methods, for all cores. However, there were differences in maximum depth of ^{210}Pb$_{excess}$ detection, sediment accretion rates, and C$_{seq}$ rates, between cores from the same study sites, evidencing the importance of direct measurement of C$_{seq}$ rates, to be used in blue carbon budgets, rather than using global or regional estimations. Even though ^{137}Cs was detected in all cores, peaks related to the historical 1986 and 1963 fallouts were not easily distinguished. Furthermore, there was some evidence of down-core leaching shown by detection of ^{137}Cs below the main 1963 activity peak, at pre-1950 dates, i.e. prior to its large-scale introduction into the environment, as seen in other studies (Cundy and Croudace, 1996; Ruiz-Fernandez and Hillaire-Marcel, 2009; Ward *et al*., 2014; Drexter *et al*., 2018). Therefore, sediment accretion rates based on ^{137}Cs activity were not calculated in this study.

Relationships between environmental variables and C$_{seq}$ rates were not uniform between sites, with wind speed being the most influential on C$_{seq}$ rates from Creek Rythe, while C$_{seq}$ rates from Farlington Marshes showed strong relationships with sediment characteristics (%mud and D50). Conversely, C$_{seq}$ rates from Porchester showed relationships with %mud and fluctuations in minimum and maximum temperatures, while C$_{seq}$ rates from Hayling Island were significantly influenced by the degree of sorting. Additionally, the significantly higher sediment accretion rates and C$_{seq}$ rates during periods with extreme weather events suggest that future climate change related events, mainly an increase in frequency and strength of storms with strong wind gusts and floods in south central England, can impact intertidal seagrass meadows and their role as blue carbon sinks.

6.5.1 The use of ^{137}Cs to assess sediment accretion rates in the Solent

Transient markers such as ^{137}Cs are one of the most commonly used options to independently validate ^{210}Pb chronologies in vegetated coastal sediments (Lynch *et al*., 1989; Sanders *et al*., 2010; Aria-Ortiz, *et al*., 2018). ^{137}Cs can be used as a chronometer in sediments either by assuming that the peak in activity corresponds to the fallout peak in 1963 or 1965 in the Northern and Southern Hemisphere, respectively, and/or that the depth of its first detection corresponds to the onset of fallout in the mid-1950s (Ribeiro Guevara and Arribére, 2002; Stupar *et al*., 2014; Arias-Ortiz *et al*., 2018a). Moreover, in sediment cores from Europe, ^{137}Cs can display a peak of elevated activity, corresponding to emissions caused by the Chernobyl accident in 1986 (Callaway *et al*., 1996; Cundy and Croudace, 1996).

The use of ^{137}Cs as a marker for vegetated coastal sediments may, however, have some limitations. ^{137}Cs activity released in the atmosphere from above ground nuclear weapons testing in the 1950s and early 1960s is now one third of that recorded in the 1960's rendering the identification of peaks and their correspondence to this time period mid-more difficult to determine (Drexel *et al*., 2018; Arias-Ortiz, *et al*., 2018a). This might explain the cause of no detection of identifiable ^{137}Cs 1963 peaks for the CRST 2 and PMST 2 cores.

Furthermore, it has been reported that ^{137}Cs has a high solubility in seawater, and that the presence of sands and carbonates, common in seagrass sediments, could be listed as conditions that do not favour the adsorption of ^{137}Cs and may lead to its down core mobility (Bruland, 1983; Davis *et al*., 1984; He and Walling, 1996; Koch, 2001). This could explain the lack of detectable peaks from the Farlington Marshes cores, which had the lowest %mud. This solubility effect could be intensified in the intertidal zone, which is not permanently submerged, being inundated by the tide to different extents depending on location (Arias-Ortiz, *et al*., 2018a), as in sites utilised in this study in central southern England. High organic matter content can also affect the distribution of ^{137}Cs in sediments as it is preferentially accumulated in leaf litter and may be absorbed by living roots. (Davis *et al*., 1984; Olid *et al*., 2008) Thus, the decomposition of this organic phase in organic-rich sediments, like the ones studied here, may cause ^{137}Cs down core mobility (Staunton *et al*., 2002).

Furthermore, the potential for erroneous ^{137}Cs profiles, can also be attributed to large increases in sand-sized particles, uptake by vegetation, biological activity, and/or diffusion of ^{137}Cs (Drexler *et al*., 2018). Profiles with missing peaks, multiple peaks, or extremely broad peaks, which are unsuitable for dating, were mainly constrained to particular environments such as wetlands with highly erosional or depositional geomorphology, and oceanic or high nutrient environments in which there is high cation exchange, such as the study sites investigated in this thesis (Milan *et al*., 1995; Iurian *et al*., 2015; Drexler *et al*., 2018).

Cundy and Croudace (1996) evaluated the use of ^{137}Cs activity peaks to date sediment layers, suggesting that to obtain reliable accretion rates, mineralogical corrections should be applied. These corrections should be followed by an assessment and consideration of possible time lags between atmospheric fallouts and sediment deposition, due to erosion and depositional processes, estimated at between 6-12 months for small watersheds (Ritchie *et al*., 1973; Cundy and Croudace, 1996). Another important factor to be considered is post-depositional mixing, as a consequence of physical reworking, bioturbation and chemical remobilisation, which may redistribute ^{137}Cs within the profile and make it harder to detect evident peaks (Cundy and Croudace, 1996).

Moreover, the ^{137}Cs peak related to the Chernobyl incident is not as high in southern England as in sediments from other areas of Europe, particularly the north of the UK, Scandinavia and the Baltic States, due to low rainfall over the area during the passage of the Chernobyl 'plume', which could explain the lack of evident 1986 peaks in the studied sediment cores (Cambray *et al*., 1987, Kempe & Nies, 1987; Petersen *et al*., 1990, Cundy and Croudace, 1996). This was also corroborated by Cundy and Croudace's (1996) salt marsh sediment cores from the Solent, which had very weak, and often absent, 1986 ^{137}Cs peaks and were recorded over 20 years ago when activity levels were higher. Where an upper peak does occur, the presence of ^{134}Cs could be used to confirm a Chernobyl peak, however, due to radioactive decay in the seven years after the Chernobyl incident, the ^{134}Cs activity can be too low to be quantified accurately, since ^{134}Cs half-life = 2·06 years, and so a ^{134}Cs/^{137}Cs ratio cannot be determined (Cundy and Croudace, 1996). Hence, these factors together may compromise the use of ^{137}Cs to validate ^{210}Pb geochronologies in seagrass ecosystems, including those in south central England (Arias-Ortiz, *et al*., 2018a).

6.5.2 Sediment accretion and C_{seq} rates from the Solent

The measured supported ^{210}Pb ranged from 7.24 Bq kg^{-1} in Farlington marshes FMST 2 core to 18.20 Bq kg^{-1} in Porchester (PMST 1). Cundy and Croudace (1996), reported an average supported ^{210}Pb inventory of 12.2 Bq kg^{-1} for the Solent, in a comprehensive study of salt marshes within the region. An observed ^{210}Pb inventory lower than expected might imply that the site has low sediment deposition, and the apparent long-term accretion rate could be attributed to bioturbation, while a higher than expected inventory could imply that the site is depositional, and the apparent long-term accretion rate reflects both accretion and bioturbation (Baskaran and Santschi 2002, Bentley and Kahlmeyer 2012, Muhammad *et al*. 2008; Poppe and Rybczyk, 2018). These assumptions support the results from this study, with the lower sediment accretion rates found in Farlington Marshes (FMST 2), of 1.6- and 1.2-mm year^{-1}, than the ones found in Porchester (PMST 1), of 4.2- and 4.3-mm year^{-1}, using both CF:CS and CRS methods, respectively. Even though both sites receive fluvial sediment input, Farlington Marshes is more exposed to tidally driven sediment mixing than Porchester, which could explain the lower sediment accretion rates, due to sediment flushing (figure 6.1, SCOPAC, 2003).

Duarte *et al.* (2013) described an average accretion rate for seagrass meadows, based on a global review of 12 studies, of 2.02 ± 0.44 mm year^{-1}, with accretion rates ranging from 0.61 - 6 mm year^{-1}. Average sediment accretion rates for all cores analysed in this study, calculated by both the CF:CS and CRS methods, fell within this reported global range, apart from the LGST 2 core in Hayling Island, which produced average accretion rates of 10.8 mm year^{-1} using the CF:CS method and 6.3 mm year^{-1} using the CRS method. An analysis of the CRS accretion rates per calculated date for that core showed a large peak in accretion around 1970-1980, which did not correspond to a similar peak in C_{seq} rates (figures 6.11c and 6.11d). This suggests that there was a large input of mineral sediment during that period, possibly due to coastal erosion from a reported storm (1979), recorded coastal flood events (1981), and natural littoral drift in the area (SCOPAC, 2003 and Haigh *et al*., 2017).

Based on a classification system reported by Arias-Ortiz (2018a), the sediment cores from Hayling Island possibly showed $^{210}Pb_{excess}$ specific activities that correspond to mixing attributed to higher rates of sediment accretion and sediment resuspension (Gardner *et al*., 1987; Cearreta *et al*., 2002; Haslett *et al*., 2003; Swales and Bentley, 2015; Jankowska *et al*., 2016; Serrano *et al*., 2016). However, similarly high mean sediment accretion rates, of 8.9 ± 7.0 mm year^{-1} have been reported for *Thalassia testudinum* meadows in Florida Bay (Orem *et al*., 1999).

In general, mean sediment accretion rates calculated in this study using the CF:CS and the CRS methods, were higher than those reported by Marba *et al*. (2015), of 0.67 ± 0.03 mm year^{-1} for *P. australis* meadows in Western Australia, and by Miyajima *et al.* (2015), of between 0.32–1.34 mm year^{-1} for temperate, sub-tropical and tropical multi-species seagrass meadows along East and Southeast Asia. Sites like Creek Rythe, Farlington Marshes and Porchester, had cores with calculated sediment accretion rates similar to those reported by Poppe and Rybczyk (2018) (1.9 ± 0.1 mm year^{-1}) and Jankowska *et al*. (2016) (1.3 ± 0.2 mm year^{-1}) for *Z. marina* meadows. However, Creek Rythe and Porchester also had cores with higher mean sediment accretion rates, comparable to those reported by Serrano *et al.* (2014) of between 2.4 - 4.2 mm year^{-1} from *Posidonia oceanica* meadows in the Mediterranean, demonstrating the variability in sediment accretion within sites.

Both cores from Creek Rythe showed very similar patterns of sediment accretion and C_{seq} rates over time, with peaks around the 1980's. These could be related to periods of high wind speeds reported around this time, and there was a relationship between wind speed and C_{seq} rates for this site found in this study, as well as the occurrence of storms and floods during this period (Haigh *et al*., 2017). However, cores from the other sites showed variations in this pattern, for example one of the cores from Farlington Marshes (FMST 2), showed two peaks in C_{seq} rates around 1995 and 1955, even though sediment accretion rates were declining during these periods. The correlation analyses performed showed that Farlington Marshes's C_{seq} rates are strongly and significantly associated with sediment characteristics, therefore, these fluctuations could be related to the increase in %mud recorded for the same period, around 1995, preceded by a decrease around 1955, with closely related sorting patterns (Figures 6.9 a, b, c and d). Moreover, the LGST 1 core from Hayling Island, showed a large peak in sediment accretion rate around the 1910's, but a peak in C_{seq} rates only around the 1950's, which is likely to represent a period when seagrass meadows from this site covered larger areas and presumably had higher plant density and biomass, than in preceding years. This would also corroborate the notion that seagrass meadows in central southern England are still in a recovery phase and have not attained the levels of canopy density and carbon storage capacity recorded prior to the 1950's global dieback (Jankowska *et al*., 2016). Porchester's PMST 1 core showed a steep increase in C_{seq} rates over the last decade, which is likely to be related to the higher %mud found in the top layers of the core and an increase in allochthonous organic matter input by anthropogenic activities and urban development.

Mean C_{seq} rates from seagrass meadows in the studied sites were high, 67.91 g m^{-2} year^{-1}, compared to other global regions, due to high long-term accretion rates and carbon density, even if the latter is lower than estimated global averages (table 6.6).

This result falls within the estimated range of C_{seq} rates from 45 to 190 g m^{-2} $year^{-1}$, reported by Mcleod *et al*. (2011) in a review of seven studies summarising a total of 123 sites, with a mean rate of 138 ± 38 g m^{-2} $year^{-1}$. Furthermore, the mean C_{seq} rates from the Solent's seagrass meadows are comparable to those reported by Jankowska *et al*. (2016), when analysing sediment from *Z. marina* meadows in the Baltic sea (table 6.6).

Table 6-6: C_{seq} rates (g m^{-2} $year^{-1}$) for different geographic regions as reported by literature and the present study, including depth of sediment cores and mean ± st.dev, when available.

Region	Sediment Layer (cm)	Carbon sequestration rate (g m^{2} $year^{-1}$)	Reference
Global	-	83	Duarte *et al*. [2005]
Global	-	138 ± 38	McLeod *et al*. [2011]
Virginia, Atlantic coast	0 -10	37 ± 3	Greiner *et al*. [2013]
Dongsha Island, South China Sea	0 - 5	33	Huang *et al*. [2015]
Oyster Harbour, Western Australia	0 - 15	26 ± 1	Marbà *et al.* [2015]
Oyster Harbour, Western Australia	0 - 150	3	Rozaimi *et al*. [2016]
Inner Puck Bay, South Baltic Sea	0 - 10	3.9 ± 1	Jankowska *et al*., 2016
Inner Puck Bay, South Baltic Sea	10 - 60	41 ± 27	Jankowska *et al.,* 2016
Outer Puck Bay, South Baltic Sea	0 - 10	0.8 ± 0	Jankowska *et al.,* 2016
GS, South Baltic Sea	0 - 10	2.78 ± 0	Jankowska *et al*., 2016
Red Sea	0-100	6.77	Serrano *et al*., 2018
Padilla Bay, Washington	0 - 20	9.14 ± 0.59	Poppe and Rybczyk, 2018
Central southern England	**0 - 50**	**67.91 ± 32.39**	**Present Study**

Another potential reason for the low C_{seq} rates reported by Poppe and Rybczyk (2018) and Jankowska *et al*. (2016) is the shorter, up to 20cm, cores collected (table 6.6). It is also important to consider that existing reviews of C_{seq} rates, have been mainly dominated by well-studied species, such as *Posidonia oceanica*, despite *Zostera marina* being the most widespread seagrass species in the northern hemisphere (Green and Short 2003; Poppe and Rybczyk, 2018). *P. oceanica* has an exceptional capacity for carbon storage and sequestration because of its thick, dense mat of roots and rhizomes, and as a result is not representative of all seagrass species (Gacia *et al*., 2002, Mateo *et al*., 1997, Serrano *et al*., 2012).

Moreover, studies assessing restored seagrass sites usually report an increase in C_{seq} rates over time (Greiner *et al*., 2013; Marba *et al*., 2015). For example, Marba *et al*. (2015) reported an increase in C_{seq} rate from 16.2 ± 2.4 to 25.2 ± 4.7 g m^{-2} $year^{-1}$, between 6 year and 18 year restored seagrass sites from Oyster Harbour, Australia. This increase in C_{seq} rates after revegetation could explain the high C_{seq} rates recorded for the seagrass meadows in this study, which are likely to still be in recovery phase after reported dieback caused by wasting disease (Muehlstein, *et al*., 1988; Marsden and Chesworth, 2015).

High variability in net production by seagrasses, including variability among species and habitats, has been identified as one of the factors that can contribute to the wide range in estimated carbon sequestration rates by these ecosystems (Duarte *et al*. 2010, Kennedy *et al*. 2010, Grimsditch *et al*. 2013, Lavery *et al*. 2013, Rozaimi *et al*. 2013). Other studies suggest that the variability in carbon sequestration rates may be attributed to difficulties in obtaining reliable long-term accretion rates in these environments, with existing reviews being dominated by tropical and subtropical species like *Posidonia oceanica* and *Zostera marina* (Green and Short 2003; Poppe and Rybczyk, 2018). Additionally, despite the growing focus on blue carbon ecosystems, carbon sequestration processes by seagrasses remains the least studied or published of all vegetated coastal systems (Grimsditch *et al*., 2013).

Moreover, results from this study suggest that environmental variables had different degrees of influences on C_{seq} rates between sampling sites. Sediment particles had a significant relationship to C_{seq} rates on cores from Farlington Marshes and Porchester, although weaker on the latter (table 6.4). Furthermore, C_{seq} rates were related to variations in temperature on Porchester, and wind speed on Creek Rythe (table 6.4).

6.5.3 Influence of climate change on C_{seq} rates

Anthropogenic or natural disturbance of seagrass meadows may decrease canopy height and density by damaging plants, as well as uprooting plants in some parts of the bed, resulting in fragmentation of the meadow into patches (Nakamura, 2010). After an intense storm, it is typical to find dead seagrasses piled up in extensive wrack lines along the shore (Eleuterius and Miller, 1976; Green and Short, 2003). Seagrass loss also results from smothering by sediments and light limitation due to increased turbidity from suspended sediments (Preen *et al*., 1995; Moncreiff *et al*., 1999; Wanless *et al*., 1988). These dieback events, promoted by extreme weather, can temporarily enhance sediment C_{seq} rates, due to the increase in organic matter from seagrass decay within the meadow and neighbouring areas (Duarte *et al*., 2013). In contrast, if disturbances are too intense or prolonged, seagrass fragments may keep decreasing into smaller units until they disappear completely (Horinouchi *et al*., 2009). This short-term increase in C_{seq} rates following disturbance could explain the significantly higher sediment accretion and C_{seq} rates reported in this study around historical periods of extreme weather events. However, it is important to note that this was an exploratory study, and the data is not robust enough to resolve for temporal availability, given the fact that sample resolution plays an important role in the ^{210}Pb sediment dating approach. It does however set a benchmark for future studies, to further analyse possible correlations between historical changes in C_{seq} and sediment accretion rates and disturbances caused by extreme weather events.

Several studies have reported evidence of climate induced shifts in the seasonal growing pattern of marine primary producers (Preen *et al*., 1995; Heck *et al*., 1996; Tilmant *et al*., 1994; Fourqurean and Rutten, 2004; Byron and Heck, 2006; Amone-Mabuto *et al., 2017; Shields et al, 2018; Arias-Ortiz et al*., 2018b*)*. This would be increasingly probable if a cyclone or severe storm passed over already highly fragmented seagrass beds (Anton *et al*., 2009; Pihl *et al*., 2006; Horinouchi *et al*., 2009; Nakamura, 2010; Cote-Laurin *et al*., 2017). Shields *et al.* (2018) related this shift to an increase in the length of the stressful summer season, impacting the timing of *Z. marina's* growth and decline periods. Fluctuations in temperature and C_{seq} rates were found to be significantly correlated at Porchester, with both maximum and minimum temperatures showing positive correlations with C_{seq} rates. Higher temperatures increase rate of photosynthesis and primary production, which could promote seagrass growth, increasing meadow extent therefore trapping more suspended particles, increasing C_{seq} rates (Lee *et al*., 2007; Collier and Waycott, 2014; Egea *et al*., 2018; George *et al*., 2018). Conversely, lower temperatures could negatively impact seagrass growth rate, promoting diebacks during wintertime which could then increase C_{seq} rates by increasing the input of autochthonous carbon (Collier and Waycott, 2014; Hughes *et al*., 2018; Burkholz *et al*., 2019). However, the consequences of extreme climate change events on seagrass communities are extremely difficult to monitor due to the unexpected nature and unpredictable occurrence of such events (Amone-Mabuto *et al*., 2017). For example, Cyclone Sandy in the Gulf of Carpinteria, Australia, uprooted 70% of the seagrass meadow with 12 m waves generated by 220 km h^{-1} winds (Poiner *et al*., 1989). However, extreme weather events do not always have negative impacts, such as the category 4 Hurricane Andrew that passed over South Florida in 1992, with negligible impacts on seagrasses despite its intensity (Tilmant *et al*., 1994).

Bjork *et al*. (2008) discussed the impacts of flooding on seagrass ecosystems, which resulted in decreased irradiance both because of increased water depth and the increased turbidity and smothering by rapid sedimentation. Also, heavy rains may adversely affect seagrasses as a result of increased freshwater inputs decreasing salinity, as noted after an extreme rain event in Venezuela, which delayed recovery of *Thalassia testudinum* in seagrass beds in the region (Chollett *et al*., 2007). Another example was the sharp decline in seagrass species richness and leaf biomass in the Philippines and Thailand when the silt and clay content of the sediment exceeded 15%, due to increased terrestrial run off near estuaries during periods of high precipitation (Terrados *et al*., 1998).

Extreme flooding events, increasingly common in Eastern Africa, have been shown to cause large-scale losses of seagrass habitats (Bandeira and Gell 2003), while some 1,000 km^2 of seagrasses in Queensland, Australia, were lost by uprooting and/or sediment disturbances after two major floods and one cyclone within three weeks (Preen *et al*., 1995). Similarly, seagrasses in Queensland were lost in a catastrophic flooding event, and it took three years for them to recover (Campbell and McKenzie 2004).

There have been reports of climate change being responsible for increases in intensity and possibly frequency of tropical storms, although there is uncertainty in these predictions and limited scientific consensus at present (Trenberth 2005; IPCC

2007; Bjork *et al*., 2008; Lyddon *et al*., 2019). Such storms in coastal areas may cause massive sediment movements, in accordance with the significantly higher sediment accretion rates during periods of storm events found in this study, which could have disastrous effects on seagrass meadows by uprooting or burying the plants (Short *et al*., 2006) or conversely provide resilience to sea level rise through positive surface elevation change (Potouroglou *et al*., 2017). However, the patterns of sediment accretion rates have not been uniform between cores from the same study site, which suggests that other variables might have acted in conjunction to the meteorological events identified, e.g. anthropogenic activities, potentially playing a role in these results. Increased turbidity caused by storms can remain long after the storm subsides, decreasing light availability, while increases in rainfall and discharges from rivers can increase sediment loading, which may also result in decreased light levels or smothering of seagrasses (Bjork *et al*., 2008). Therefore, it is very important to monitor seagrass meadows regularly to measure their status and record short and long-term trends and possible effects of disturbance on these ecosystems (Unsworth *et al*., 2018b; Macreadie *et al*., 2019).

6.6 Conclusions

High carbon sequestration rates were recorded from seagrass meadows in central south England, which combined with the high reported carbon stocks (chapter 4), establish the importance of these ecosystems as blue carbon sinks, comparable to other global, including tropical, regions. However, it is clear that sediment characteristics, as well as climate variables such as wind speed and temperature, are associated with changes in seagrasses carbon sequestration rates. These variables can be possibly related to the frequency of occurrence of storms bringing strong wind gusts and flood events, which directly impact sediment accretion and carbon sequestration rates in UK seagrass meadows, shown for the first time in this chapter. The increased nutrient loading from inland and marine sediments, brought by these climate events, could benefit seagrass growth and sequestration rates in the short term. However, there is likely to be a tipping point that is not yet predictable, in which increased levels of turbidity caused by higher sedimentation rates would be damaging to these ecosystems. Furthermore, the difference in $^{210}Pb_{excess}$ activity profiles from the studied sites, and consequent sediment accretion rates, highlight the variability in carbon sequestration rate potential between meadows, and the need for direct measurements to be reported, rather than extrapolations based on reported values for other areas. In conclusion, monitoring of the health and extent of seagrass meadows in the UK and elsewhere is of paramount importance, especially in the face of the predicted increased frequency and magnitude of climate change related events (IPCC, 2018).

7 General Discussion

7.1 Preamble

The main results from this study provide crucial information on the state of the UK's intertidal seagrass meadows, being the first to directly assess carbon stocks and sequestration rates, while also establishing the main environmental and climate related factors that influence these systems. These analyses were performed using sediment cores to 1m deep, from mixed species meadows within the Solent region, therefore providing reliable data on the sediment C_{stocks} within these ecosystems. These results contribute to global blue carbon research by showing that intertidal temperate seagrass meadows, which have thus far been comparably understudied, have a large carbon sink potential. However, this study also highlights the variability in sediment C_{stocks}, accretion, and C_{seq} rates within and between sites, suggesting there are large uncertainties regarding the use of proxies and estimations, based on extrapolations, in blue carbon research. Moreover, this study provides further knowledge on the main drivers of carbon storage on seagrass meadows from the studied sites, as well as reporting how climate related events in the form of storms, wind gusts and floods, have historically impacted these ecosystems. Therefore, results from this study provide crucial information for the inclusion of seagrass ecosystems in protection and conservation programs, with the aim of climate change mitigation.

7.2 Current state of seagrass meadows from the study sites

Seagrass meadows from the studied sites are currently classified as being of high ecological status by the EU WFD, but are also within designated Nitrate vulnerable zones (NVZ), due to signs of eutrophication (Environment Agency, 2016a/b). Results from this thesis have established the importance of seagrass meadows from the studied sites as carbon sinks, being able to store large amounts of carbon in their sediments, comparable to global estimations (Chapter 4). However, historical evidence collected by Tubbs (1999) suggested more extensive subtidal and intertidal *Zostera spp.* meadows in Portsmouth, Langstone and Chichester Harbours, and on the north east and north-west coasts of the Isle of Wight, prior to a wasting disease outbreak, which would suggest that the meadows investigated in this study are still in a state of recovery.

Moreover, Macreadie *et al*. (2019) relates the uncertainty regarding mechanisms of control of C_{stocks} in blue carbon ecosystems, and more specifically the significant variation in sediment C_{stocks} observed within seagrass meadows (chapter 4), to complex canopy-hydrodynamic interactions that are not yet fully understood. The hydrodynamic interactions with canopy density can potentially affect the spatial and temporal patterns in carbon sequestration rates, especially in restored meadows, therefore better understanding of these processes must be sought to confidently design stock and sequestration assessments, and to predict the temporal development of stocks following management actions (Marba *et al*., 2015; Tomasko *et al*., 2017; Macreadie *et al*., 2019). This could explain the high variability in C_{seq} rates within and between study sites found in this study (chapter 6).

This highlights the need for protection and conservation of these sites, not only to maintain the blue carbon stored in their sediments, but also to maintain important ecosystem services linked to these environments, such as: critical feeding grounds for birds; important nursery areas for seabass; and supporting threatened runs of migratory salmon and sea trout on their way to and from spawning grounds, as well as migration routes for eels to spawn at sea (Jackson *et al*., 2001; Hiscock *et al*., 2005; Bertelli and Unsworth, 2014; Lilley and Unsworth, 2014; Harding *et al*., 2016; Jones *et al*., 2018). However, to date, conservation programs are rarely based on the explicit consideration of local threats and drivers for a specific seagrass meadow, and instead focus on conserving seagrass as part as a broader management plan incorporating other specific habitats or species (Jones *et al*., 2018). One way to improve this would be to include conservation and protection of seagrass ecosystems in financing mechanisms involving reduction of CO_2 emissions (Wylie *et al*., 2016; Herr *et al*., 2017; Howard *et al*., 2017). Yet, in order to effectively include seagrass ecosystems in climate regulation policy making programmes, a comprehensive understanding of the factors that control C_{stocks}, as described in chapter 5, and sequestration rates, as described in chapter 6, are urgently required.

To date, the market value of blue carbon ecosystems can be assessed by the costs involved in avoiding damage through protection programmes, or by the costs required to replace ecosystems services lost from degradation (Campagne *et al*., 2015; Cole and Moksnes, 2016). For example, the total extent of vegetated coastal ecosystems in Europe, ~ 3 billion ha, represents 1.5-4% of the total global blue carbon extent and has been valued at US$ 180 billion, with current degradation trends representing an economic loss of up to US$ 1 billion by 2060 (Luisetti *et al*., 2013). However, even though seagrass meadows in the UK and northern Europe have been directly or indirectly included in conservation law and agendas, studies suggest that these programs might not have been effective in protecting and preserving these ecosystems, with declines being consistently reported (Harding *et al*., 2016; Jackson *et al*., 2016; Jones and Unsworth, 2016; Jones *et al*., 2018; Green *et al*., 2018; Smale *et al*., 2019).

The combined area of the seagrass meadows from the six study sites investigated in this thesis is 406.03 ha, according to Marsden and Chesworth's (2015) survey, accounting for nearly 10% of the reported intertidal seagrass meadows in the whole of the UK. Studies estimated a total UK areal coverage of 9 X 10^3 ha for *Zostera spp.*, with half, 4.5 X 10^3 ha, located in England and Wales (Dickie *et al*., 2014). More specifically, mapped *Z. marina* meadows account for 4.9 X 10^3 ha, i.e. approximately 50% of the total seagrass area in the UK (Luisetti *et al*., 2019). This would suggest that the other half of the estimated areal cover for UK seagrass is composed of intertidal mixed species meadows, including *Z. noltii*, *Z. angustifolia* and *Ruppia spp.* such as the sites investigated in this study. However, Jones and Unsworth (2016), investigated the status of eleven seagrass meadows across the UK, ten located within European protected areas, reaching the conclusion that they are currently in a perilous state, based on morphometric and ratio bio-indicators. Jones *et al*. (2018) also found nitrogen levels in seagrass leaf tissue that suggested eutrophication, probably due to contamination from urban sewage and livestock effluent, in numerous *Z. marina* meadows across the UK, including within conservation areas. In addition, results from this thesis show that pore water nutrient levels linked to eutrophication, in the form of sulphates and nitrites, act in conjunction to influence sediment carbon storage on the studied sites, with concentration of sulphates specifically being negatively related to sediment C_{stock} (chapter 5).

These results lead to questions regarding the effectiveness of conservation and environmental protection laws for seagrass meadows and highlight the need for further research, to examine and understand factors that influence meadow extent, quality and function and develop effective conservation objectives (Jackson *et al*., 2016). Current programs are mainly focused on the restoration of degraded seagrass meadows globally, with low rates of success (37% on average) (Leschen *et al*.,2010; Cunha *et al*., 2012; Orth *et al*., 2012; Katwjik *et al*., 2015; Macreadie *et al*., 2015; Marba *et al*., 2015; Infantes *et al*., 2016, Moksnes *et al*., 2016; Moksnes *et al*., 2018). This is because once ecosystem loss or degradation occurs, thresholds are reached, which may promote irreversible regime shifts that make it hard to restore meadows to favourable states (Maxwell *et al*., 2017; Flindt *et al*., 2016; Moksnes *et al*., 2018). Even when restoration is successful, the carbon sink potential of restored meadows might never return to pristine conditions, even after decades (Marba *et al*., 2015; Moksnes *et al*., 2018).

Identifying and understanding the prevalence of both direct and indirect 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). Results from this thesis showed the variability in carbon storage, above and below-ground biomass (chapter 4) and sedimentation rates (chapter 6) between studied sites, which can potentially contribute to the implementation of more relevant regional policymaking, by identifying areas with highest potential for carbon sequestration (chapter 5), with the aim of mitigating eutrophication and offsetting atmospheric CO_2 emissions, under changing climate scenarios (chapter 6).

7.3 Environmental and climatic variables influencing carbon stocks and sequestration

In 2015, the United Nations (UN) developed a set of 17 Sustainable Development Goals (SDGs) as part of the 2030 Sustainable Development Agenda, with SDG14 “Life below water”, specifically targeted at the conservation and sustainability of oceans, seas and marine resources (United Nations, 2015). Indeed, to achieve sustainability, long-term management plans need to be based on the understanding of the social-ecological characteristics and the human environment interactions of the systems under consideration, including seagrass meadows (Folke *et al*., 2005; Levin *et al*., 2009; Ruiz-Frau *et al*., 2019). Thus, the biology, ecology, and the effects of impacts on seagrass habitats need to be well understood, and information on the anthropogenic factors that influence these ecosystems are needed in order to design effective management plans (Hemminga and Duarte, 2000). Especially since, as other coastal marine ecosystems, seagrasses are threatened by anthropogenic pressures at different spatial scales (Duarte *et al*., 2008; Grech *et al*., 2012; Ruiz-Frau *et al*., 2019).

Therefore, results from this study provide valuable insights into the environmental factors driving sediment carbon storage in temperate seagrass ecosystems, specifically from intertidal seagrass meadows in the South-central region, UK. Chapter 4 showed that there were significant differences in %C_{org} between seagrass and un-vegetated sediment cores, suggesting that sediment C_{stocks} in seagrass meadows might be influenced not just by meadow productivity and filtering capacity, but also environmental factors such as sediment characteristics (chapter 5). Understanding the factors that promote carbon storage in seagrass sediments is important to identify regional and global blue carbon hotspots to be included in conservation and protection programs. Seagrass degradation and recovery are affected by both current and historical environmental conditions, and feedbacks between seagrass and local biotic and abiotic factors (O'Brien *et al*., 2018). Hence, restoration approaches should be exclusive and tailored to particular sites, therefore understanding the requirements and suitable approaches for each region is needed to ensure efficient use of funds (Jackson *et al*., 2016). It has been proposed that healthy carbon stores and seagrass growth rates can act as a buffer against adverse conditions, reducing the amplitude of damage and impact and promoting fast recovery under ideal conditions (Collier *et al*., 2010). Therefore, identifying environmental factors that positively influence sediment carbon storage, like the ones listed in chapter 5, is of upmost importance.

Ruiz-Frau *et al*. (2019) evaluated current perceptions of seagrass meadows by stakeholders as a guide to improve management efforts and prioritise areas of action, highlighting the need to identify the importance of these ecosystems and associated services (chapter 4). Secondly, their study also suggests the need for an evaluation of current and future pressures, and their associated causes (chapter 5 and chapter 6) in order to contribute to a more effective focus of management efforts (Ruiz-Frau *et al*., 2019). Similarly, Unsworth *et al*. (2019) identified the main challenges for seagrass conservation and policy responses, listing amongst them the need for up-to-date information on status and condition (chapter 4), as well as identifying indicators that provide early warnings of seagrass global change impacts (chapter 6). Therefore, important factors driving sediment C_{stocks} in the studied sites (chapter 5), should be identified and monitored in seagrass ecosystems, including elevation in relation to mean sea level, pore water sulphates, pH and salinity; and grain size, proportion of mud and dry bulk density. Furthermore, studies using seagrass transplantation techniques as a method for restoration showed that sheltered locations, with finer sediment particles, were essential for long-term survival of transplanted seagrass plots (van Katwijk *et al*., 2009; Valle *et al*., 2015). This would suggest that sheltered sites with fine sediment particles such as Chichester and Langstone harbours would be well suited for seagrass transplantation programmes in unvegetated mudflat areas. Moreover, sediment characteristics such as dry bulk density and proportion of mud, acted in conjunction to explain the bulk of the variation in sediment C_{stocks} (chapter 5), suggesting that seagrass ecosystems with finer sediment particles provide important climate change mitigation services and should therefore be the focus of protection measures for climate mitigation programmes in the region.

Thus, it is important to note that relationships between environmental factors and carbon storage may not be consistent for all seagrass systems, being influenced by many potential interactions among environmental factors, as shown by the results in this study. Therefore, the mechanisms that regulate spatial variability in carbon stocks and accumulation rates in seagrass meadows require continued investigation (Mazarrasa *et al*., 2018; Santos *et al*., 2019; Prentice *et al*., 2019). For example, most of the estimated carbon sequestration studies for seagrass meadows have focussed on the process of the burial of fixed carbon in their sediments, as a rate of sediment accretion over time, and the quantified organic carbon content of those same sediments. (Duarte *et al*., 2010; Fourqurean *et al*., 2012; Greiner *et al*., 2013; McLeod *et al*., 2013). However, results from recent studies have suggested that seagrass meadows can assimilate a much greater amount of carbon than that sequestered by burial alone (Tomasko *et al*., 2017). Alternative theories propose that: the vast majority of carbon assimilation by seagrass meadows might not be sequestered at all, being recycled back into the water column or exported elsewhere instead, as noted for *Syringodium filiforme* by Zieman and Wetzel (1980); or carbon can be sequestered by alternative pathways to burial alone, like the bicarbonate pathway, first described by Smith (1981) (Rau and Caldeira 1999, Rau *et al.* 2001, Isobe *et al*. 2002, Harvey 2008, Unsworth *et al*., 2012).

In addition, there is still little knowledge on the fate of carbon lost from seagrass meadows following degradation, even though global rates of the seagrass loss have been increasing (Macreadie *et al*., 2013; Marba *et al*., 2015; Moksnes *et al*., 2018; Macreadie *et al*., 2019). The rate, sources and fate of exported carbon remain unclear for many seagrass species and geographical regions, although carbon produced in any blue carbon ecosystem may also contribute significantly to the C_{stocks} of adjacent ecosystems (Duarte & Krause- Jensen, 2017; Krause-Jensen *et al*., 2018; Huxham *et al*., 2018). Therefore, findings in this study demonstrate the necessity of considering spatial variability when assessing regional or national sediment stocks and provide guidance into which seagrass meadows may be included into blue carbon and conservation projects.

7.4 Future climate change

Climate change has been reported as one of the major threats to coastal ecosystems potentially impacting their carbon stocks (Macreadie *et al*., 2019). However, the level of impact will depend on the frequency and intensity of climate change related events, as well as the degree of exposure, sensitivity and resilience of the ecosystems, which are still highly uncertain (IPCC, 2018). Seagrass ecosystems, like the ones from this study, are particularly sensitive to sea level rise, which could promote the loss of deep-water seagrass due to low light penetration, or landward migration in areas where seawater floods the land (Kirwan and Megonigal, 2013; Lovelock *et al*., 2015; Macreadie *et al*., 2019). Tidal simulations for the UK suggest that a mean sea level change greater than ~ 1m would have a substantial impact on tidal amplitude, increasing the risk of coastal flood events (Palmer *et al*., 2018; MET, 2019). Furthermore, current predictions for the UK show an increase in coastal flood risk over the 21st century, and beyond, under all RCP climate change scenarios (Palmer *et al*., 2018). This means both an increase in the frequency and magnitude of extreme water levels around the UK coastline, with projections to 2300 suggesting that sea levels in London and southern England will continue to rise over the coming centuries under all RCP climate change scenarios, ranging from 0.5 - 2.2m, 0.8 - 2.6m and 1.4 - 4.3m for RCP2.6, RCP4.5 and RCP8.5, respectively (Palmer *et al*., 2018).

This predicted rise in global and regional sea level, associated with climate change models, poses a threat to seagrass ecosystems in the Solent region and adjacent harbours (IPCC, 2013; POST, 2017). For example, it has been reported that sea level rise and increased vertical sediment accretion can promote seagrass loss, followed by ecosystem shifts that make it hard to successfully restore these ecosystems back to favourable states (Maxwell *et al*., 2017; Flindt *et al*., 2016; Moksnes *et al*., 2018). At local scales, the impacts of coastal sea level change in the UK typically arise primarily from regional extreme water level events, often associated with storm surges and extreme wave conditions combined with the local tide (UKCP, 2019).

However, studies suggest that past storm surge incidents in the UK were mainly driven by extreme water levels related to a rise in mean sea-level, rather than an increase in storminess (Woodworth *et al*., 2009; Menendez and Woodworth, 2010; Robins *et al*., 2016). Regardless, the predicted increase in mean sea-level rise will change the dynamics of storm surge generation and propagation, increasing the risk of low-lying coastal flood risk and inundation, posing the greatest flood risk to estuaries and harbours, like the ones investigated in this thesis (McInnes *et al*., 2003; Robins *et al*., 2016; Palmer *et al*., 2018; UKCP, 2019). In addition, Macreadie *et al*. (2019) suggest that the occurrence of storms could cause the erosion of seagrasses and loss of C_{stocks}, while flood events, associated with extreme rainfall, may result in mortality, but could also increase sediment accretion and C_{seq} rates, agreeing with the results found in this study (chapter 6).

Climate change predictions for the UK also include high impact changes in precipitation patterns, especially within estuarine ecosystems, with potential habitat loss and deterioration in water quality caused by storm clusters and consequent eutrophication (Robins *et al.,* 2016). This is particularly important since studies show that in the past few decades there has been an increase in annual average rainfall over the UK as well as high intensity episodic rainfall events (Palmer *et al*., 2018). Even though results from this study showed no significant relationship between historical precipitation and C_{seq} rates for the studied sites, future predictions for UK precipitation patterns expect significant changes in the trends of winter and summer precipitation by 2100 (Jenkins *et al*., 2018; UKCP, 2019). For example, winters in the UK, for the most recent decade (2009-2018), have been on average 5% wetter than 1981-2010 and 12% wetter than 1961-1990, while summers in the UK have also been wetter, by 11% and 13% respectively. (UKCP, 2019) This seasonal variation in precipitation patterns could promote diebacks of seagrass species, related to difficulties in adaptation to physiological responses, and the survivability of early life stages (both seeds and spores), under inconsistent environmental pressures (Duarte *et al*., 2018).

Moreover, Githaiga *et al*. (2019) suggested that disturbance to seagrass ecosystems may need to be large scale (in time and/or space) before an effect is found. This assumption was based on a comparison between sediment C_{stocks} from intact and degraded sites, performed by Macreadie *et al*. (2015) in Australia, where seismic testing in the 1960s damaged a range of *Posidonia australis* meadows, leading to a loss of 72% of sediment C_{stocks}. Additionally, these environmental changes could also affect the symbiotic relationships between microbiome communities and macrophytes, impacting trophic levels and organisms feeding on seagrass derived organic matter, including reduced energy transfer due to reduced carbon fixation (Duarte *et al*., 2018). However, no climate change policy mechanisms are currently in place for seagrass meadows in the UK, although there is growing interest in incorporating blue carbon habitats into natural climate solutions in other countries (Hejnowicz *et al*., 2015; Sutton- Grier and Moore 2016; Griscom *et al*., 2017; Howard et al., 2017; Neelemann *et al*., 2018).

This thesis demonstrates how sediment C_{stocks} and accretion rates responded to past weather-related events, increasing during periods with strong wind gusts and flood events (chapter 6). Thus, results from this thesis provide crucial insights on the future impacts of climate change related weather events on seagrass ecosystems, which have been suggested as one of the main uncertainties regarding blue carbon research on these ecosystems (Macreadie *et al*., 2019). It is therefore important to include regional climate change predictions, especially regarding sea level rise, and related storm surges and flooding event, when planning and promoting the conservation and managements of existing meadows, to preserve their long-term carbon storage capacity (Hejnowich *et al*., 2015; Duarte *et al*., 2017; Moksnes *et al*., 2018; Mazarassa *et al*., 2018).

7.5 Recommendations for management

Results from this thesis highlight the importance of assessing C_{stocks} in seagrass meadows where favourable conditions for C_{seq} exist, to explore and develop efficient conservation and restoration programmes within these regions and understand the potential consequences of global change to these ecosystems. The high variability in C_{stocks} (chapter 4) and C_{seq} rates (chapter 6) found in this study, are not uncommon to other seagrass meadows located in temperate regions (Hodgson and Spooner 2016; Jankowska *et al*., 2016; Röhr *et al*., 2016, 2018; Kindeberg *et al*., 2018; Poppe and Rybczyk 2018;Prentice *et al*., 2019). However, this variability in global and regional C_{stock} values, along with the lack of data on meadow extent, present the main challenges for including seagrasses in effective national and international blue carbon policies (Hejnowicz *et al*. 2015; Green *et al*. 2018; Neelemann *et al*. 2018).

Thus, even though seagrass meadows in the UK and northern Europe have been directly or indirectly included in conservation law and agendas, studies suggest that these programs might not have been completely effective in protecting and preserving these ecosystems, with declines being consistently reported (Harding *et al*., 2016; Jackson *et al*., 2016; Jones and Unsworth, 2016; Jones *et al*., 2018; Green *et al*., 2018; Smale *et al*., 2019). This could be due to poor coastal water quality related to eutrophication and release of pollutant, one of the main factors impacting seagrass abundance and distribution across de British Isles, which may have contributed to the outbreak of wasting disease in the early 1930's (Butcher, 1933; Short and Wyllie-Echeverria, 1996; Davison and Hughes, 1998; Jones *et al*., 2018). Since then, recovery of UK's *Z. marina* meadows has been slow and inconsistent, with losses still being recorded and this recovery is likely in an ongoing state (Bertelli *et al*., 2017; Short, 2018).

A recent report from the UK's Marine Management Organisation (MMO1135), aiming to identify suitable sites for marine habitats restoration and creation, included seagrass meadows as potential habitats of interest (MMO, 2019). The UK's seagrass meadows, have been included as habitat and protected features of Marine Conservation Zones (MCZs), mainly due to their high biodiversity support, and are a named component of "Lagoons and Shallow Sandbanks" within the European Union Habitats Directive (Jackson *et al*., 2016; Smale *et al*., 2019). More specifically, seagrass meadows are listed as a Priority Marine Feature in Scotland, as a priority habitat on the Natural Environment and Rural Communities Act 2006 in Wales, and as Features of Conservation Importance (FOCI) for the proposed Marine Conservation Zones (MCZs) and Reference Areas (RAs) under the Marine and Coastal Access Act in England (JNCC, 2014; Jackson *et al*., 2016). However, monitoring of seagrass in the British Isles happens around a six yearly reporting cycle, and focuses on monitoring the status of the features, such as meadow extent, rather than meadow resilience and possible causes of pressure, like the ones identified in this study (chapter 5 and chapter 6) (Jackson *et al*., 2016).

Understanding possible impacts of eutrophication and global change on seagrass meadows' health and carbon sink potential is important, especially since current preservation and management efforts have been reported as ineffective (Jones *et al*., 2018). For example, all sampling sites selected for this study are within areas of protection, with the two sampling sites on the Isle of Wight, Cowes and Ryde, part of The Solent and Isle of Wight Lagoons', which consists of coastal lagoons priority habitats. While the other four sampling sites, are included in two of the three designated Special Protection Areas (SPAs) in the Solent, namely: Porchester, in the Portsmouth Harbour SPA, Creek Rythe, Hayling Island and Farlington Marshes, in the Chichester and Langstone Harbours SPA. Furthermore, there are two Special Areas of Conservation (SACs) in the Solent estuarine system: the Solent and Isle of Wight Lagoons, and The Solent Maritime (Harding *et al*., 2016). Both regions were selected as SACs due to the presence of habitats of special interest, including the seagrass sampling sites investigated in this thesis (Harding *et al*., 2016). However, results showed that sites like Farlington Marshes, Ryde and Cowes, with lower sediment C_{stocks} (chapter 4), showed signs of eutrophication and patchy seagrass distribution, even though they are currently within protection zones (chapter 5).

This is because, despite this statutory recognition, there are still many uncertainties regarding the health, structure, distribution and temporal scales of these meadows, with few studies on UK's seagrass meadows, and even less aimed at their role as blue carbon sinks, like the one in this thesis (chapter 4 and chapter 6) (Lefebvre *et al*. 2009; Peters *et al*., 2015; Jackson *et al*., 2016; Jones and Unsworth, 2016; Bull and Keyton, 2016; Green *et al*., 2018; Smale *et al*., 2019). In Europe, even though the EU Habitats Directive (92/43/EEC) includes protection of European seagrass meadows, it only affords protection to habitats within designated Special Areas of Conservation (SACs), or indirectly, under EU water quality law, namely the Urban Wastewater Treatment Directive (91/271/EEC) and the WFD (2000/60/EC) (Jones *et al*., 2001; Jones *et al*., 2018). At the scale of the North-East Atlantic, seagrasses are on the OSPAR list of threatened and/or declining species and habitats, being identified as a priority for the conservation and protection of marine biodiversity, under annex V of the OSPAR Convention (OSPAR, 2003; Tullrot, 2009).

Recently, a new project named Seagrass Ocean Rescue has been developed with the aim of restoring seagrass meadows in the UK, by planting one million *Z. marina* seeds on a designed two-hectare area in Dale, West Wales (Unsworth *et al*., 2019). However, lead researchers in the project listed proximity to the intertidal zone or presence of mobile sandy substrate as some of the main reasons for failed attempts in the past (Unsworth *et al.*, 2019). These highlight the need for better knowledge of suitable environmental conditions, in order to choose ideal sites to achieve successful seagrass restoration projects, like the ones reported in this study (van Katwijk *et al*., 2015; Unsworth *et al*., 2019). Furthermore, Unsworth *et al*. (2019) also concluded that in order to potentially facilitate such large-scale seagrass restoration projects, methods must be developed to ensure that the large quantity of seeds planted are not rapidly washed away from the restoration site, and can successfully germinate and grow. Therefore, studies aiming to understand the impacts of weather events on seagrass meadows and their carbon storage and sequestration potential, like the one in this thesis (chapter 6), should be developed to better identify sites across global regions where restoration and conservation efforts would be successful, especially under the threat of future climate change.

Even though seagrass restoration has been conducted for nearly 70 years, since the middle of the last century (e.g., Addy, 1947), the vast majority of seagrass projects have been of limited extent (<0.5 ha), often experimental and almost exclusively in sheltered estuarine waters (van Katwijk *et al*., 2015; Paulo *et al*., 2019). Restoration attempts in more wave exposed coasts, like the one proposed by Seagrass Ocean Rescue, are still few, with open coast large-scale, non-experimental restoration only been attempted in Western Australia, to date (Fonseca *et al*., 1998; Paling *et al*., 2003; Bull *et al*., 2004; van Katwijk *et al*., 2009; Katwijk *et al*., 2015). Generally, restoration projects including seagrass meadows represent an attempt to induce a change in ecological state, from a condition of low structural complexity (typically unvegetated) to a more complex system (vegetated), usually driven by environmental thresholds, such as the ones listed on chapter 5 (Carr *et al*., 2010; Maxwell *et al.*, 2015; Maxwell *et al*., 2017; Moksnes *et al*., 2018; Paulo *et al*., 2019).

Paulo *et al*. (2019) agree that the challenge in implementing seagrass restoration projects in physically dynamic coastal environments, is to create a resilient seagrass habitat before perturbations occur, and critical environmental thresholds are crossed, which could revert the system back to the bare substrate condition; i.e., failure of the restoration effort. As the ecosystem is altered from its previous stable state, it is likely that a combination of different factors, such as human-induced disturbances, storms and grazing, could act as antagonistic feedback mechanisms preventing recovery and restoration of seagrass ecosystems (Moksnes *et al*., 2018). Therefore, if seagrass restoration is viewed as an effort to catalyse a state shift (from an unvegetated to a vegetated state), factors limiting this transition must be understood as a basis for setting realistic restoration goals and expectations, such as the relationships between C_{stocks} and C_{seq} rates and environmental and climatic variables established in this thesis (chapter 5 and chapter 6).

8 General Conclusions

The major focus of this thesis was to provide an overview of the role of temperate intertidal seagrass meadows from central southern England as carbon sinks, as well as elucidating the main factors driving variability in carbon stocks between sites. Additionally, this thesis also quantified sediment accretion and carbon sequestration rates for the same seagrass meadows, to understand how they have fluctuated related to past extreme weather events. The results can be used in management and conservation policies, including protection and restoration of seagrass meadows regionally and globally. The aim of this study was to assess how carbon sequestration and storage in Southern England's intertidal seagrass ecosystems have been influenced by recent (up to 100 years) weather events, in order to contribute towards global knowledge on the role of seagrasses as carbon sinks, and a better understanding of blue carbon regulating processes under a changing climate. To address this aim, three objectives were proposed:

1. Establish a regional carbon storage profile by determining aboveground and belowground biomass, and carbon content of the sediment, to determine total carbon stocks.
2. Establish relationships between carbon storage and environmental factors to promote the understanding of features that influence seagrass carbon sink potential.
3. Establish a geochronology to identify how organic carbon sequestration has fluctuated over time in relation to reported precipitation, storminess, and sea level.

8.1 Key findings

1) Results from this study contribute to global blue carbon research by reporting the first direct assessment of sediment carbon stocks in the top metre of temperate, intertidal, seagrass meadows in the U.K. Results showed that seagrass meadows form the Solent form significant carbon stocks, on average 103.12 ± 71.45 MgC Ha^{-1}, comparable to other global regions (165.6 MgC Ha^{-1}). Moreover, this study has shown that dry bulk density can be confidently used as a proxy to determine sediment C_{stock} values in intertidal seagrass meadows. An analysis of methods used

to derive sediment %C_{org} from %OM values showed that caution must be taken when assessing C_{stocks} using literature-derived equations and estimations, due to the significant difference found in values calculated using different equations in this study. In addition, this study also demonstrates the variability in sediment carbon stocks, sediment characteristics, above-ground biomass, shoot density, and below-ground biomass, in the form of roots and rhizomes, between sampling sites within the same region, highlighting the need for site-specific assessment. Furthermore, a comparison between sediment carbon stocks within seagrass meadows and neighbouring, un-vegetated, sampling points suggest that seagrass meadows export, or catchment, of organic matter to adjacent unvegetated ecosystems.

2) This study provides valuable insights into the relationship between environmental factors and sediment carbon storage in temperate seagrass ecosystems, specifically from intertidal seagrass meadows in the UK. Results showed that seagrass meadows within the same geographic region, but with different species composition, showed significantly different sediment C_{stocks}, dry bulk density, sorting coefiicient, mean grain size, proportion of mud and pore water pH and salinity. Overall, the main factors significantly related to seagrass sediment C_{stocks} were: elevation in relation to mean sea level, pore water sulphates, pH and salinity, grain size, proportion of mud and dry bulk density. Indeed, dry bulk density can also be used as a predictor for sediment C_{stocks} up to 30cm deep, as indicated by regression analysis. When the combined association of factors was analysed, dry bulk density, proportion of mud, pH, NO_2^- and SO_4^{-2} showed the highest influence on sediment C_{stocks}. Moreover, sediment characteristics such as dry bulk density and proportion of mud, can be grouped as the factors that act in conjunction to mainly explain variation in sediment C_{stocks}. Therefore, these findings demonstrate the necessity of considering spatial variability and environmental variables, mainly sediment characteristics, when assessing regional or national sediment stocks with the aim to incorporate seagrass meadows into effective blue carbon and conservation projects.

3) Results from this study show that ^{210}Pb activity can be used to estimate C_{seq} rates from intertidal seagrass sediment cores in central southern England. The mean rate of C_{seq} from seagrass meadows in this study was 67.91 g m^{-2} $year^{-1}$, higher than some other global regions and within the estimated global range of C_{seq} rates from 45 to 190 g m^{-2} $year^{-1}$, reported for seagrass meadows. However, there were

substantial differences in maximum depth of $^{210}Pb_{excess}$ detection, sediment accretion rates, and C_{seq} rates, between cores from the same study sites, evidencing the importance of direct measurement of C_{seq} rates, to be used in blue carbon budgets, rather than using global or regional estimations. Even though relationships between environmental variables and C_{seq} rates were not uniform between sites, sediment accretion rates and C_{seq} rates were apparently higher during periods with extreme weather events, suggesting that future climate change related events, are likely to impact intertidal seagrass meadows and their role as blue carbon sinks. This study has shown that the Solent's seagrass meadows as essential providers of carbon storage benefits, and that spatial and temporal aspects, mainly retaled to extreme weather events, must be considered when implementing conservation and restoration projects in the area. Therefore, these results contribute to the development of effective governance and management of these ecosystems.

4) Results from this thesis have established that temperate intertidal seagrass meadows from central southern England as important carbon sinks. This highlights the need to incorporate these ecosystems in more effective conservation programmes, tailored exclusively to protect and restore these seagrass meadows, rather than being included in general programmes within their regions. Important results on the factors that possibiy regulate and influence carbon storage in these ecosystems have also been described, providing insights on some of the abiotic features that should be monitored and could be used as proxies to identify blue carbon hotspots and priority regions for conservation. This thesis also reported the first C_{seq} rates for seagrass meadows from central southern England, providing vital knowledge on how sediment accretion rates have fluctuated over time. Understanding these dynamics is important to the development of effective management and protection programs that aim to mitigate future climate change impacts in the region.

8.2 Recommendations for further study

The current study was limited to assessing organic C_{stocks} and sequestration rates within intertidal seagrass meadows from central southern England. An area of further study could incorporate an analysis of inorganic carbon stocks within these meadows, considering carbon stored as carbonates, to promote a better understanding of the role of these ecosystems as carbon sinks (Gallagher *et al.*, 2019). The study also assessed total carbon stocks within multispecies meadows, future research can therefore consider phenology of the individual species, and their contribution to carbon storage as well as assessing the state of the meadow's ecological health and adaptation potential (Duarte *et al*., 2018). Assessing carbon stocks in the subtidal areas of these study sites can be also considered, to assess carbon storage within all seagrass meadows in the region.

Furthermore, to date, there has been little attempt to assess greenhouse gas emission fluctuation connected to climate change and sea level rise in these ecosystems (Duarte *et al*., 2010; Duarte *et al*., 2011; Fourqurean *et al*., 2012a; Garrard and Beaumont, 2014; Jones and Unsworth, 2016). Therefore, further studies could incorporate the difference between total carbon stocks at two different periods in time to be used as a proxy for CO_2 emissions to the atmosphere. Conversely, direct flux measurements could be employed to assess other gases that don't accumulate in the system, such as methane (CH_4) and nitrous oxide (N_2O). To achieve these measurements, CO_2 and CH_4 fluctuations could be analysed using a static flux chamber method, to evaluate daily fluctuations, over 24h periods, and seasonal fluctuations, within a year, or longer periods of time (Bahlman *et al*. 2015).

Additionally, seagrass monitoring methods have primarily used in situ approaches including scuba/snorkeling surveys (Gotceitas *et al*., 1997), ground-based, on foot, sampling (Moore *et al*., 2000), and hovercraft-based mapping (McKenzie, 2003). More recently, active and passive remote sensing approaches have been introduced to estimate the coverage and quality of seagrass habitats (Duffy *et al*., 2018). Other methods, such as active acoustic remote sensing using side scan sonars, have also been deployed to quantify seagrass meadows coverage (Barrell *et al*., 2015; Hossain *et al*., 2014), whilst passive spectral sensors on-board platforms such as satellites or light aircraft have proven useful to quantify seagrass meadow dynamics (e.g. Baumstark *et al*., 2016 and Cunha *et al*., 2005). Thus, remote sensing technologies, including advanced sensors, such as Synthetic Aperture Radar (SAR) and LiDAR, videography, and airborne data (including unmanned aerial vehicles - UAVs), could be used in conjunction with ground-based surveys, to provide more robust assessments and monitoring of seagrass meadows' areal extent (Dat Pham *et al*., 2019; Unsworth *et al*., 2019).

The information acquired by high spatial resolution maps, using optical sensors, such as multispectral and hyperspectral datasets, can be used to provide invaluable information about the current health status of seagrass meadows, for better management of protected areas, and improve understanding of biodiversity, functioning, services, and future sustainability of seagrass ecosystems, particularly in areas with reported decline, such as the ones investigated in this study (Qiu *et al*., 2019; Giardino *et al*., 2019). For example, freely available multi-spectral Landsat data have been used to detect changes in seagrass meadow extent, as well as fluctuations in biomass (Knudby *et al*., 2010; Misbari and Hashim, 2016). Moreover, finer spatial resolution optical and infra-red satellite data from systems such as IKONOS and Quickbird (with a spatial resolution finer than 4 m) have also been used to generate useful biomass estimates for multiple seagrass species (Duffy *et al*., 2018).

Duffy *et al*. (2018) demonstrated the potential of low-cost, flexible, drone-based data collection techniques for monitoring intertidal seagrass meadows, like the ones in this thesis. The use of these technologies over traditional ground approaches can provides advantages such as the flexibility in deployment and the utility of data, especially regarding time series monitoring for management purposes, to better understand seagrass meadows dynamics and differentiate between natural variation and human induced changes (Cunha et al., 2005; Duffy *et al*., 2018). Furthermore, better understanding of within-meadow seagrass heterogeneity, provided by the use of lightweight drones, can be a complementary approach to more traditional boundary mapping, which has often been conducted using satellite and airborne imagery, providing useful estimations of seagrass coverage, biomass and species composition (e.g. Phinn *et al*., 2008 ; Duffy et al., 2018).

In recent years, ecological niche modelling has also been used to predict the effects of climate change on seagrass ecosystem distributions (Valle *et al*., 2014; Davis *et al*., 2016; Chefaoui *et al*., 2018), the potential distributions of certain seagrass-associated species (March *et al*., 2013; Chefaoui *et al*., 2016; Jayathilake and Costello, 2018) and seagrass conservation priorities (Valle *et al*., 2013; Adams *et al*., 2016). Ecological modelling can be a useful and promising tool for seagrass restoration programs, as it is used to determine the most favourable environmental conditions for species growth, by collecting large scale datasets within seagrass meadows, including variables including: light intensity; seagrass coverage and biomass; sediment accretion rates; water velocity; sediment parameters and porewater nutrients (Valle *et al*., 2011; Adams *et al*., 2016; Stankovic *et al*., 2019). It would be interesting to test these ecological models in the studied sites, especially to provide comparisons between C_{stocks} from sub-tidals and intertidal meadows where present, like in Cowes, Creek Rythe, and Hyaling Island. Therefore, in future, the combination of remote sensing technologies and additional information regarding greenhouse gas emissions, could be coupled with the results from this thesis to develop habitat suitability models in order to provide a baseline for site selection for seagrass restoration within the studied region.

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Appendix I

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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 of different seagrass species. Therefore, understanding the drivers for sediment C_{stocks} variation is crucial to developing effective conservation and restoration projects for seagrass ecosystems. This study analyses the influence of environmental factors on the variation in sediment C_{stocks} for six intertidal seagrass meadows within the Solent region, in southern England. There were significant differences between sites for all variables, except leaf density, and concentrations of the sediment pore water nutrients. Sediment dry bulk density, mean grain size, sorting coefficient, % mud, elevation above sea level, and pore water salinity showed high 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 greatly influenced C_{stock}. Moreover, sediment characteristics acted in conjunction to explain most of the variation in C_{stock} among sites. Therefore, sediment characteristics should be considered as important indicators for carbon storage potential in intertidal temperate seagrass meadows.

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 accumulation 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 accumulation 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 accumulation 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_{stocks}) 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). 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). 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 favour 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). 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; Marbà *et al*., 2018). The effects of ocean acidification on the accumulation of autochthonous C_{org} in seagrass sediments and biomass still need to be clarified, with some studies suggesting increases in accumulation 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). In addition, 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 the factors that 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 influence C_{stock} 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 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 within seagrass vegetation can also affect their carbon storage potential, with species-environment interactions likely to strongly impact the storage of sedimentary carbon (Lavery *et al.*, 2013). Furthermore, previous studies have suggested that C_{org} accumulates at twice the rate in estuaries, compared to coastal environments (Nellemann *et al.*, 2009). Serrano *et al.*, (2016) suggested that C_{org} accumulation in estuaries is enhanced by their highly depositional nature, with inputs of fine-grained particles, such as silt and clay sediments, retaining more C_{org} than sands (Keil and Hedges, 1993; Burdige, 2007); and preserving sediment stored C_{org} by reducing redox potentials and remineralisation rates (Hedges and Keil, 1995; Dauwe et al., 2001; Burdige, 2007; Pedersen et al., 2011).

To 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. Further understanding of these relationships would benefit global seagrass research, conservation and restoration programs for climate change mitigation, and the use of seagrass as an 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 are identified. It was hypothesised that sediment characteristics most strongly influence carbon storage within the studied temperate intertidal seagrass meadows.

Methods

Study Sites

The Solent (including Southampton Water and the Isle of Wight), together with the adjacent large interconnected harbours of Portsmouth, Langstone and Chichester, is considered one of the most important coastal regions 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 why this region has been selected as a Special Area of Conservation (SAC) (McLeod *et al*., 2005). Tidal amplitudes are not uniform in the region, with the eastern end (Chichester) having almost double the tidal range of the western end (Hurst Point), providing longer inundation periods (Dyer & King, 1975). Studies have been reporting water quality issues in the region (Harding *et al*., 2016; Environment Agency 2016a; 2016b). The increase in nutrient levels can cause algal blooms, promoting the growth of benthic algae which can potentially smother seabed habitats, including seagrass meadows (Harding *et al*., 2016). Therefore, the estuaries and harbours in the region 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).

Six study sites with known seagrass meadows, were selected within the region, in central southern England, following an assessment of the most recent seagrass distribution inventory (Marsden and Chesworth, 2015) (**Table 1**). Selected sites were Creek Rythe in Chichester Harbour, Hayling Island and Farlington Marshes in Langstone Harbour, Porchester in Portsmouth Harbour, and Cowes and Ryde on the Isle of Wight (**Figure 1**). Seagrass meadows from all sites are 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*, *Zostera noltei*, *Zostera angustifolia*, and *Ruppia spp.* meadows (Marsden & Chesworth, 2015), which represent the most common seagrass characteristics in England. 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*, 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 algal mats (Marsden & Chesworth, 2015). At the Isle of Wight sites, Cowes is characterised by gravel and soft to firm sandy sediments, with 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 1**). Sediment variables comprised 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 in relation to mean sea level and the biological parameters leaf density and above-ground biomass were also recorded. Degree of sorting, calculated as the sorting coefficient from the different sediment grain size fractions, was used with elevation with reference to mean sea-level as a proxy for degree of exposure of the site (see Folk & Ward, 1957). Through this paper, elevation in relation to mean sea level has been referred to as elevation. 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, giving 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, samples were collected during the summer (June-August) of 2017 including: 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 in relation to 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). Elevation data were recorded to take into account inundation frequency and duration. 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 classifying very patchy (<20%), patchy (20 ≤70%) or dense (> 70%) cover, was conducted with a walkover of the sites. Above-ground biomass and leaf density were 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). Sediment 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 components (Howard, *et al.*, 2014). Seagrass species were recorded and whole leaves (stem to tip) were counted from each sample to determine leaf density. Filamentous macroalgae and invertebrates were removed from seagrass biomass during the washing procedure, however, any microalgae epiphytic load, when found, was not scraped from the leaves, to prevent loss of vegetative organic matter. Plant biomass was determined by oven-drying it to a constant weight (72 h at 60 ºC) (Howard, *et al.*, 2014). The 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; Wood, 2015). Samples were cooled at room temperature in a desiccator for at least one hour after LOI, 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:

$$\text{Equation 1: } Pd = (1 - \varphi) * Ps$$

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, 2007). 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, 1967). 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). Dry sediment sample was weighed and 3g 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 17. 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. Relationships between each variable and pooled carbon stocks (30cm deep) were assessed by calculating mean values per core, within the sampled quadrats, with 30 (5 per site) samples in total. 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, 1986; Marin-Guirao *et al*., 2005). All results assume a significance of $p < 0.05$.

Results

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 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 1).** The mean DBD values for all sites was 0.99 ± 0.03 g/cm^3 (n=30). The mean DBD values at Ryde and Cowes were significantly higher than all other sites **(Table 1).** All sites were classified as muddy, silt rich, sediments according to the Wentworth scale, apart from Cowes and Ryde, which contained average grain sizes (µm) within very fine and fine sand classes respectively. The sorting coefficient at Ryde was significantly higher than all other sites **(Table1).** 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%), which were both significantly higher than Cowes and Ryde (**Table 1**).

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 1**). Mean salinity levels were significantly lower in the Isle of Wight 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 1)**. Mean pore water concentrations of nitrites and sulphates showed no significant differences between sampling sites **(Table 1)**. 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**).

Seagrass meadows at Cowes were located at a significantly lower elevation in relation to mean sea level than all other sites, at -1.82 ± 0.05m. **(Table 1)**. Of all the sites, only Farlington Marshes and Creek Rythe were located above mean sea level, which was significantly different than all other sites, at 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 1).**

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 1)**. *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 than the other study sites, while Hayling Island and Creek Rythe supported dense beds with continuous seagrass meadows **(Table 1)**. There were significant differences in above-ground biomass between sampling sites, with Creek Rythe presenting significantly higher above-ground biomass values, of 0.497 ± 0.25 MgCha^{-1} (n=5), than both sites on the Isle of Wight **(Table 1).** Ryde had the lowest biomass values amongst all sites, at 0.07 ± 0.03 MgCha^{-1} (n=5), significantly lower than Creek Rythe and Hayling Island **(Table 1)**.

Relationships between environmental variables and sediment C_{stock}

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 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_{stock} (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}.

The six predictors indicated by PLS as main drivers for variation in sediment C_{stocks}, with a coefficient > 5, were selected for inclusion in a 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 for Ryde, Cowes and Farlington Marshes grouped separately from other sites, while points for Creek Rythe, Hayling

Island and Porchester were closer together **(Figure 5)**. Points for Creek Rythe and Hayling Island had low values for both PC1 and PC2, representing sites with highest C_{stock}, high %mud and lowest DBD. Ryde was the site with the lowest C_{stock}, lowest %mud, highest DBD, highest degree of sorting and a 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 axes. This could be explained by the higher values for C_{stock} and lower DBD in Farlington Marshes **(Figure 5).**

Discussion

Results from this study provide important insights into the environmental factors driving sediment carbon storage in temperate seagrass ecosystems. Intertidal seagrass meadows in the Solent region, England, 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, and 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 reported in 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 most 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 accumulation 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). Therefore, 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; Mazarrasa *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 less energetic depositional environments 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 greater exposure leading to lower sediment C_{stock} due to the potential export of carbon to other adjacent ecosystems. Furthermore, Ryde and Cowes, which were located at the lowest elevations in relation to mean sea level, had the lowest values of sediments C_{stocks}. Differences in elevation are related to varying periods of emersion and desiccation between low and high tide, which impacts carbon accumulation 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). 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}, asrdnd 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*. In addition, 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 Garrard 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 accumulation potential, potentially increasing ocean storage of carbon by 12–14%.

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 level was 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 accumulation 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 sediment characteristics most strongly influence carbon storage within temperate intertidal seagrass meadows. However, seagrass meadows within the same climatic region, do not share the same potential for long-term sediment carbon storage, and numerous environmental characteristics strongly influence this ecosystem service. Therefore, while seagrass research at global, and continental, scales are 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 ecosystem generally, and highlight the need for the consideration of multiple environmental features and their interactions in seagrass blue carbon research. In the central southern England region, larger carbon stocks were associated with meadows located in sheltered harbours, with high mud content and well sorted sediment 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 and increased storminess. 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. We encourage an evaluation of the relationship between seagrass sediment C_{stocks} and environmental variables across different global regions, including the variables used in this study and others, if applicable, i.e. leaf height; stable isotopes of carbon and nitrogen (^{13}C and ^{15}N); particulate organic nitrogen; and measurements of sediment phosphorous concentration.

List of figures

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, white lines represent roads.

Fig. 2 Concentrations of (a) nitrites NO_2^- (µmol/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.

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.

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.

Fig. 5 Principal component analysis 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}) (see Figure 4) in terms of sediment C_{stocks} as the response variable.

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