Spatial and temporal variability of carbon stocks within the River Colne Estuary

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Abstract

Saltmarshes are one of the most significant blue carbon sinks but there is a paucity of information regarding saltmarsh carbon stocks globally, consequently these habitats are not included in the global carbon budget. The aim of this study is therefore to better understand the spatial and temporal variation of saltmarsh sediment total organic carbon (TOC) content. Therefore, three saltmarshes along the salinity gradient of the Colne Estuary were studied. The effect of the study sites' locations along the estuary, higher plant species distribution, above-ground biomass and aerobic respiration on TOC content was investigated. The spatial and temporal variation of sediment TOC content was investigated by monthly sampling from two habitats and three zones at each study site. There was a significant spatial variation in plant species distribution which could be due to zonation and the location of the sites along the estuary. Saltmarsh plants were the important driver of spatial and temporal variations in sediment TOC content. The sediment TOC content at the study sites in the lower (Colne Point) and the mid (Brightlingsea) estuary was significantly higher than the upper estuary (Wivenhoe) ($P < 0.001$, range: 9-25 Kg C m^{-2}). The range of sediment TOC content of the studied saltmarshes was between 88% - 290% higher than other UK studied saltmarshes and between 4% -169% higher than the majority of the studied marshes in the Northern Hemisphere. Therefore, if the sediment carbon content of the similar saltmarshes to the Colne estuary were taken into account it would suggest that the UK and global saltmarsh sediment TOC estimate would increase. It will take possibly about 100 years for the realignment saltmarshes at Essex to reach the carbon storage capacity of Colne Point. Therefore, the Colne Point natural saltmarsh is a very significant carbon reservoir that has been overlooked.

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1. Chapter one - Introduction

1.1 Introduction

Between 1750 and 2011 cumulative anthropogenic CO_2 emissions of 2040 ± 310 gigatons (GT) CO_2 have been added to the atmosphere (IPCC 2014). CO_2 is one of the major greenhouse gases (GHG) (Solomon et al., 2007; Baer and Mastrandrea, 2006; Sarmiento et al., 2004) which, with other GHGs (e.g. CH_4 and N_2O) is continuously increasing (IPCC 2014; Murray et al., 2011). The two major sources of anthropogenic CO_2 emission are; deforestation (and land use change) and fossil fuel combustion (Canadell and Raupach, 2008; Jackson et al., 2008; Olander et al., 2007; Baer and Mastrandrea, 2006; Sarmiento and Gruber, 2002). However, about 60% of the CO_2 emitted between 1750 and 2011was removed from the atmosphere by terrestrial and aquatic natural carbon sinks (IPCC 2014). The remainder of the CO_2 that has not been absorbed by these natural sinks has remained in the atmosphere leading to atmospheric CO_2 concentrations of 880 ± 35 GT (IPCC 2014).

The equilibrium climate sensitivity (ECS) is defined as the change in global mean near surface- air temperature which would be due to constant doubling of atmospheric CO_2 equivalent concentration (IPCC 2013). There is a likelihood of between 66-100% that the range of ECS predicted by climate models is between 1.5°C to 4.5°C (IPCC 2013). However, based on the IPCC 2014 assessment, the target ECS is still 2°C. As scientific consensus is that to avoid or moderate the detrimental impacts of climate change it is essential to keep the global temperature increases below 2 °C (IPCC 2014; Kollmuss et al., 2008; Olander et al., 2007; Baer and Mastrandrea, 2006). To achieve that, the atmospheric CO_2 concentration should be kept below 450 ppm by reducing global emissions in the next decade to 80% below of the levels seen in 1990

(Kollmuss et al., 2008; Olander et al., 2007; Baer and Mastrandrea, 2006). In May 2014, the atmospheric CO_2 concentration passed 400 ppm (Vale and Vale, 2017; Givens and Jorgenson, 2015). Since natural carbon sinks have absorbed 60% of the emitted anthropogenic CO_2, one cost-effective way to mitigate climate change and reduce carbon emissions is to protect and enhance terrestrial and oceanic carbon sinks (Yee 2010; Canadell and Raupach, 2008; Baer and Mastrandrea, 2006).

1.2 Coastal blue carbon

Carbon is captured and stored in vegetated coastlines all around the world (Pendleton et al., 2012; Murray et al., 2011). These coastal carbon reservoirs are increasingly referred to as “coastal blue carbon” and include seagrass meadows, mangrove forests and saltmarshes (Pendleton et al., 2012; Gordon et al., 2011; Murray et al., 2011). Coastal blue carbon ecosystems are significant natural sinks for anthropogenic carbon (Murray et al., 2011; Nellemann et al., 2009; Laffoley and Grimsditch, 2009; Chmura et al., 2003 and 2001). Sediment is the most important carbon sink in mangrove forests and saltmarshes (Murray et al., 2011; Nellemann et al., 2009; Laffoley and Grimsditch, 2009; Chmura et al., 2003 and 2001). The organic carbon content of the first top metre of sediment in these ecosystems is: 917 t CO_2e/ha for saltmarshes, 1060 t CO_2e/ha for estuarine mangroves and approximately 1800 t CO_2e/ha for oceanic mangroves (Murray et al., 2011; Nellemann et al., 2009). In general, carbon stored in sediment in saltmarshes and mangrove forests is between 95 to 99% and 50 to 90% of the total carbon in those ecosystems, respectively (Murray et al., 2011; Nellemann et al., 2009). Saltmarshes and mangrove forests store significantly more carbon in their below-ground and above-ground carbon pools than tropical rain forests (Murray et al., 2011; Nellemann et al., 2009; Laffoley and Grimsditch, 2009; Chmura et al., 2003 and 2001, Figure 1-1). In addition, the long-term rate of carbon accumulation within tidal saltmarsh sediment (210 g C m^{-2} y^{-1}) can be greater than that of tropical forests soil (2.3 – 2.5 g C m^{-2} y^{-1}, Pidgeon 2009). Despite this, the focus of climate change and global warming researchers and policy-makers to date has been on the terrestrial carbon reservoirs, while coastal carbon sinks such as saltmarshes have been overlooked as significant carbon sinks (Murray et al., 2011; Lyster, 2010; Laffoley and Grimsditch, 2009; Nellemann et al., 2009; Maderia, 2008).

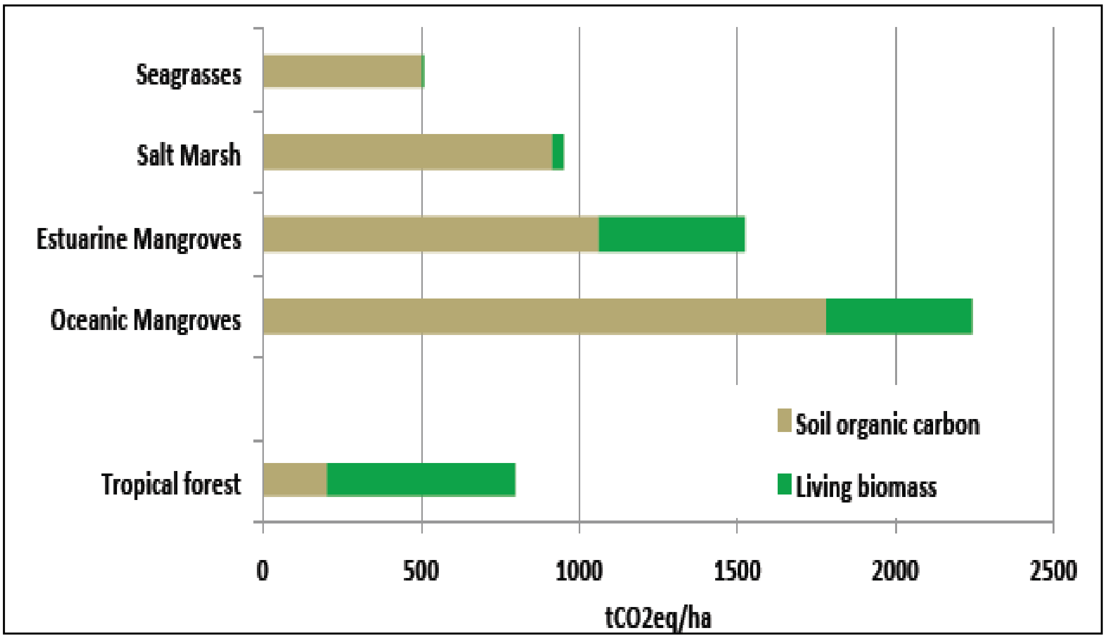

Figure 1-1 A summary of averages of carbon stored (in soil organic carbon and living biomass) in focal coastal habitats. The average of carbon stored in saltmarshes was based on based on extrapolation of studies of saltmarshes in America, Canada and Mexico. Tropical forests are included for comparison. Only the top metre of soil is included in the soil carbon estimates. Obtained from Murray et al. (2011).

The concept of blue carbon was identified and promoted by the Blue Carbon Coalition in 2009 (Murray et al., 2011). The Blue Carbon Coalition is a global coalition between more than 100 conservation groups and stakeholders, and over 150 scientists from 43 different countries (Murray et al., 2011). In December 2010, this coalition, leading up to COP 16 (16th Conference of the Parties) prepared an open statement calling on the UNFCC (United Nations Framework on Climate Change) to consider the conservation and restoration of coastal blue carbon and the inclusion of these sinks in national REDD+[1] strategies and carbon market (Murray et al., 2011). One of the main points that the Blue Carbon Coalition emphasised was the lack of information and the significant data gap on carbon storage and carbon sequestration of coastal and marine vegetation habitats (Murray et al., 2011). An estimate of the amount of carbon stored in each blue carbon sink is presented in Table 1-1.

Table 1-1 The coastal blue carbon sinks and their carbon sequestration rate. This table presents the total amount of carbon that is presented in the top meter of the sediment in the following habitats.

Habitat type	Global extend (km^2)	Annual carbon sequestration (Tonne $C/km^2/year$)	Total carbon stored in living biomass (Tonne C/km^2)	Total carbon stored sediment (Tonne C/km^2)
Salt marsh	22000-400000[a]	163.49[b*]	327-1634[c*]	24986[c*]
Mangrove forest	137000-170000[c]	217.98 [b]	6458-15341[c]	38965[c]
Seagrass	300000-600000[c]	108.99[b]	11-499[c]	13624[c]

Sources: (a) Chmura et al., 2011 & Nelleman et al, 2009 (b) Lewis et al., 2009 (c) Murray et al., 2011, (*) these estimates are based on studies in North America, Canada and Mexico, therefore they are not global figures (Murray et al, 2011).

Saltmarsh is one of the significant costal blue carbon sinks (Murray et al., 2011; Laffoley and Grimsditch, 2009), which accumulate more carbon within their

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[1] Reduction Emission from Deforestation and Degradation. REDD+ is the key mechanism to mitigate climate change, maintaining terrestrial carbon stores by creating financial incentives such as carbon credit for forest conservation (Lyster 2010; Maderia 2008).

sediments in response to climate change and rising sea levels (Kirwan et al., 2012). However, the knowledge gap concerning the factors affecting carbon sequestration in saltmarshes (Saintila and Williams, 2013), and uncertainty about the global and regional carbon storage in saltmarshes (Pidgeon 2009), hinders their effective assessment as global carbon sinks (Saintila and Williams, 2013). This thesis focuses on carbon accumulation in salt marshes.

1.2.1 Saltmarsh

1.2.1.1 Ecology and global distribution

Saltmarshes are globally distributed (Figure 1-2) and extensively occur in temperate areas (Murray et al., 2011; Green et al., 2009). The view that saltmarshes are the temperate equivalent of mangrove forests (Green et al., 2009) is frequently expressed (Adam 2002). However, saltmarshes are also found in the tropics, normally in the vicinity of mangroves (Adam 2002; Saintilan and Williams, 1999).

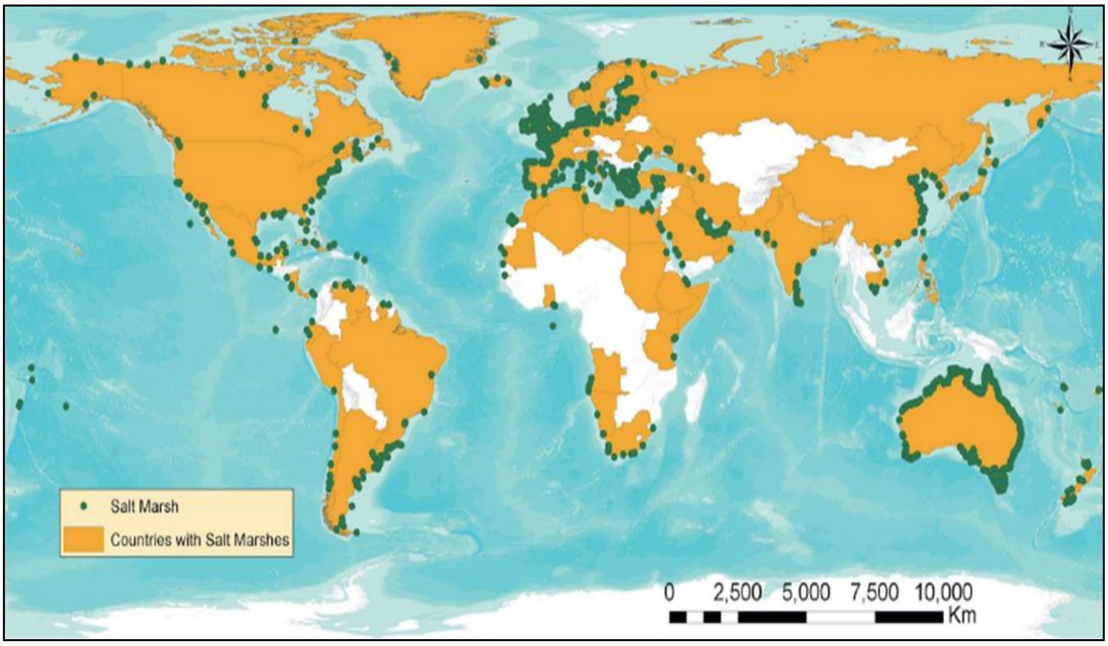

Figure 1-2 Global distribution of saltmarshes. Obtained from Murray et al. (2011) with UNEP-WCMC data.

Saltmarshes occur on sheltered, low coastlines (Adam 2002; Chmura et al., 2001; Adam1993) due to interaction between vegetation, water and sediment (Isacch et al., 2006; Adam 2002). Although, the initial colonisers of the deposited sediment in coastlines are microalgae (Adam 2002; Underwood 2000), the vegetation on the saltmarsh play an important role as ecosystem engineers by trapping sediment (Jones et al., 2010) and developing the marsh (Laffoley and Grimsditch, 2009; Adam 2002). These habitats occur between highest astronomical tides (HAT) and rarely below mean high water neap (MHWN) (Adam 2002). Estuarine and coastal lagoon saltmarshes are also linked with barrier islands, spits, embayment and open shores exposed to low wave energy (Laffoley and Grimsditch, 2009; Adam 2002). These ecosystems are exposed to the full range of tidal regime from microtidal to macrotidal (Murray et al., 2011; Laffoley and Grimsditch, 2009; Adam 2002). They are complex systems where the main vegetated surface is divided into sections by creeks (Laffoley and Grimsditch, 2009; Adam 2002). Spatial variations in saltmarsh vegetation can be observed at the small-scale in an individual marsh to the global scale across multiple marshes (Adam 2002). The small-scale vegetation distribution within each saltmarsh is called zonation (low, mid and high marsh, Barbier et al., 2011; Laffoley and Grimsditch, 2009; Adam 2002 & 1993). A combination of physical process such as elevation, salinity, flooding, nutrient availability, determine zonation and subsequent effects on plant distribution along saltmarshes (Barbier et al., 2011; Laffoley and Grimsditch, 2009; Wood and Hine, 2007; Adam 2002; Levine et al., 1998; Adam 1993). Furthermore, within each zone there is also spatial variation in plant distribution which is based on a small difference in topography (lower than 1cm) within every zone (Adam 2002). For example, Gray and Scott (1977) in a study of saltmarsh plant distribution at Morecambe observed that where *Puccinellia maritima* and *Agrostis stolonifera* occurred together, *Puccinellia maritima* grew in small hollows whereas *Agrostis stolonifera* was observed on the higher elevations. Hence, different species cover in saltmarshes could be the indication of different environmental conditions (Wood and Hine, 2007; Levine et al., 1998; Adam 1993). Therefore, the extrapolation of findings from one specific area to another is problematic and might not be valid (Adam 2002; Bouchard and Lefeuvre 2000).

The global classification of saltmarshes is based on their vegetation cover and is presented in Table 1-2. The West Atlantic type (which is found on the North American Atlantic and Gulf of Mexico coast) occupies the largest area (Adam 2002). The main difference between the West Atlantic types of saltmarsh to the other temperate types of marshes is their extensive dominance by a single species, *Spartina alterniflora* (Adam 2002; Bouchard and Lefeuvre 2000). These saltmarshes are the most extensively studied saltmarshes globally (Adam 2002). In addition, the current estimates of saltmarsh carbon sequestration are mainly based on studies of these marshes (Murray et al., 2011).

Table 1-2 Summary of distinguishing features of major types of saltmarsh (obtained from Adam 2002).
Saltmarshes in Europe, West North America, Japan, Australia and South Africa are classified as temperate marshes.

Distribution		Characteristic
Arctic		Species poor, Lowest zone dominated by *Puccinellia phryganodes*
Boreal		More species rich than Arctic marsh. *Triglochin maritima* and *Salicornia europea* widespread. Often brackish, with extensive *Carex* dominated communities
Temperate		Lower zone (prior to spread of *Spartina anglica*) dominated by *Puccinellia maritima*
	Europe	Upper- marsh dominated by *Juncus martimus*. Widespread occurrence of *Atriplex portulacoides*
	Western North America	*Distichlis spicata*, *Carex lynbei* in brackish sites
	Japan	*Zoysia sinica* dominant mid marsh grass
	Australasia	*Sarcocornia quinqueflora* dominant in low marsh, *Juncus kraussii* in upper marsh
	South Africa	*Sarcocornia spp* in lower marsh *Juncus kraussii* in upper marsh *Spartina maritima* present

Distribution	Characteristic
West Atlantic	Extensive dominance by *Spartina alterniflora*. Gulf of Mexico and Atlantic coasts of North America
Dry coast	Open vegetation, dominated by dwarf shrubs, (including *Sarcocornia spp*, *Suaeda spp*, *Limoniastrum spp* and *Frankenia spp*
Tropical	Very species poor. Extensive *Sporobolus virginicus* and *Paspalum vaginatum* grasslands. *Batis maritima*, *Sesuvium portulacastrum* and *Cressa cretica*

1.2.1.2 Ecosystem services

Ecosystem services are defined as aspects of ecosystems that provide services to human well-being (Fisher et al., 2009; Boyd and Banzhaf, 2007). Saltmarshes are among the most beneficial ecosystems to humans (Barbier et al., 2011; Chmura et al., 2001; Vernberg 1993). The services provided by saltmarshes include raw materials, food, coastal protection, erosion control, water purification, maintenance of fisheries by providing nursery habitats, tourism recreation, education and research, biodiversity support and carbon sequestration (Barbier et al., 2011; Laffoley and Grimsditch, 2009; Zedler and Kercher,2005). Carbon sequestration is one of the important saltmarsh ecosystem services that has been overlooked (Koch et al., 2009; Chmura et al., 2003). The mechanism of carbon sequestration within saltmarshes is explained in detail in the following section.

1.2.1.3 Carbon sequestration and storage

Sediment stores between 95 to 99% of the carbon in saltmarsh habitats (Murray et al., 2011; Nellemann et al., 2009). Globally, these habitats store 430 Tg carbon in the upper 50 cm of their sediment (Chmura et al., 2003). The rate of carbon accumulation within saltmarsh sediment is between 18 to 1713 g C m^{-2} yr^{-1} (Chmura et al., 2011) which is far higher than terrestrial forests at 0.7 to 13.1 g C m^{-2} yr^{-1} (Wegscheidl et al., 2015; Mcleod et al., 2011). Considering the global area of saltmarshes presented in Table 1-1, these habitats could be storing 4.8 to 87.2 Tg C yr^{-1} (Chmura et al., 2011). Saltmarshes are significant and effective carbon sinks for atmospheric CO_2 (Chmura et al., 2011 & 2003) due to their carbon accumulation and sequestration mechanisms (Mcleod et al., 2011). These habitats sequester and accumulate carbon over decades through primary productivity, and million years through accumulating organic carbon within deposited sediment (Mcleod et al., 2011).

Saltmarsh plants trap sediment from the water column (Chmura et al., 2011). The deposited sediment on the saltmarsh is a source of carbon and nutrients for saltmarsh plants (Barbier et al., 2011; Laffoley and Grimsditch, 2009; Chmura et al., 2003 and 2001). By binding the deposited sediment with their roots, salt marsh plants protect the deposited sediment and sediment carbon from being released into the water system (Feagin et al., 2009). Saltmarsh plants also remove CO_2 from the atmosphere through their photosynthetic activity (Chmura et al., 2011; Mcleod et al., 2011; Chmura et al., 2003; Kostka et al., 2002; Choi et al., 2001). The root to shoot ratio of saltmarsh plants is from 1.4 to 50 (Chmura et al., 2003; Kostka et al., 2002; Choi et al., 2001), which is higher than the ratio in other ecosystems such as tropical moist forest plantation (0.092 - 0.253) or tropical dry woodland (0.292 - 0.548) (Mokany et al., 2006). Therefore, root biomass contributes to sediment organic carbon in saltmarshes (Chmura et al., 2003; Kostka et al., 2002; Choi et al., 2001). In addition, the vertical deposition of organic carbon through below-ground biomass decomposition and sediment deposition, can extend up to 8 m deep (Chmura et al., 2003). Furthermore, the absence of oxygen in deep sediments, contributes to low decomposition rates and as a result the carbon accumulated within saltmarsh sediment remains locked away from the carbon cycle for over a million years (Pendleton et al., 2012). Due to the presence of sulphate in sea water, the emission of CH_4 from saltmarsh sediment can be low which means these habitats are very effective carbon sinks for anthropogenic CO_2 (Chmura et al., 2003).

CO_2 and CH_4 are produced as the result of aerobic and anaerobic respiration (Le Mer and Roger, 2001). The aerobic and the anaerobic mineralization and sediment respiration occur in distinctive biogeochemical zones (oxic, suboxic, postoxic, and anoxic zone) within saltmarsh sediments (Jørgensen and Kasten, 2006). In the oxic zone, where aerobic respiration occurs, oxygen is the main electron acceptor (Jørgensen and Kasten, 2006; Jørgensen and Bak, 1991). The anaerobic respiration occurs in the suboxic (postoxic) and the anoxic zone of the saltmarsh sediment (Jørgensen and Kasten, 2006). Nitrate reduction, manganese reduction and iron reduction occur in the suboxic zone, and sulphate reduction, anaerobic respiration of methane and methanogenesis (methane production) occur in the anoxic zone of the sediment (Jørgensen and Kasten, 2006; Jørgensen and Bak, 1991). Due to plant root respiration, water inundation time and organic matter concentration in the sediment, the depth of each of the mentioned biogeochemical zones varies among marine and coastal sediments (Jørgensen and Kasten, 2006; Jørgensen and Bak, 1991). In the anoxic zone in saltmarshes, sulphur is the main electron acceptor which has two forms, one soluble in pore water (HS^- and SO_4^{-2}) and the other being solid form in sediment (FeS_2 or pyrite) (Lord and Church, 1983). Sulphate reducing bacteria in saltmarsh sediment out-compete methanogenic bacteria for available electron donors, such as hydrogen or acetate, resulting in negligible amounts of methane production (Livesley and Andrusiak, 2012; Balderston and Payne, 1976). Smith et al. (1983) and Feijtel et al. (1985) measured CH_4 emission from Louisiana saltmarshes. The annual rate of CH_4 emission from fresh water marsh, brackish marsh and coastal saltmarsh were 14 mg C m^{-2}, 4.8 mg C m^{-2} and 1.3 mg C m^{-2} respectively. The converse relationship between salinity and CH_4 emission (Feijtel et al., 1985) could be due to presence of sulphate in sea water (Chmura et al., 2003) which prevents CH_4 production.

1.2.1.4 Comparison between saltmarshes in Europe and saltmarshes in America

The saltmarsh sediment organic carbon estimates presented in Figure 1-1 and Table 1-1 are mainly based on extrapolation of studies of saltmarshes in America, Canada and Mexico with different measurement methods (Murray et al., 2011). For example, one of the main cited references for producing Figure 1-1 and Table 1-1 was Chmura et al. (2003). Chmura et al. (2003) reviewed literature and extrapolated carbon accumulation and carbon sequestration for saltmarshes by extrapolating data from 107 well studied marshes. Out of that 107 only 13 sites were saltmarshes in Europe, the rest were marshes in USA, Canada and Mexico (Chmura et al., 2003). In addition, these extrapolated estimates, only included coastal saltmarshes and did not include estuarine saltmarshes (Murray et al., 2011). Yet it was assumed that all saltmarshes sequester or accumulate a similar amount of organic carbon. There are differences between saltmarshes in Europe and saltmarshes in America. For instance, the plant species that cover saltmarshes in Europe are different to the plant species covering saltmarshes in America (Table 1-2; Möller, 2006; Adam 2002; Bouchard and Lefeuvre, 2000). The studied saltmarshes in America were dominated by either single species *Spartina alterniflora* or two species, *Spartina alterniflora* and *Spartina patens* (Morris 2007; Choi and Wang, 2004; Valéry et al., 2004; Connor et al., 2001; White et al., 1978). Furthermore, most of the saltmarshes in Europe are in the upper most intertidal zones and are submerged only during spring tide (Lefeuvre et al., 2000; Bouchard and Lefeuvre, 2000). Conversely, the saltmarshes in North America are situated in intertidal areas and inundated during each tide (Lefeuvre et al., 2000). The variation in plant species between saltmarshes in Europe and saltmarshes in America together with the differences in tidal exposure could indicate differences in environmental conditions (Wood et al., 2007; Levine et al., 1998; Adam, 1993). Therefore, the assumption that saltmarshes in Europe accumulate similar amounts of carbon to the saltmarshes in the USA may not be valid.

1.2.1.5 Saltmarshes sink or source of carbon?

Teal (1962) reviewed studies which were conducted in the 1940s looking at saltmarsh primary productivity, and concluded that 45% of saltmarsh carbon production was removed by tidal water before being used by the organisms inhabiting the marsh (Nixon 1980). Odum in 1968 developed the outwelling paradigm based on Teal’s statement (Lefeuvre et al., 2000). Based on the outwelling paradigm, it was concluded that saltmarshes globally were sources of carbon and exported 100 to 200 g m^{-2} yr^{-1} to other nearby ecosystems (Odum 2002; Nixon 1980). The outwelling paradigm was open to criticism because it was based on the export of organic matter in the form of plant detritus from saltmarshes to the coastal water during rain or storm events (Odum 2002; Nixon 1980). Another criticism of this paradigm was its generalisation to saltmarshes globally, yet in the 1960s and 1970s nutrient export from European saltmarshes had not been studied (Lefeuvre et al., 2000). Another concern was that the results of some studies contradicted with outwelling paradigms even for saltmarshes in America. For instance, the amount of carbon exported through particulate carbon from Maryland coastal marshes was 7.3 g m^{-2} yr^{-1}, which was negligible (Heinle et al., 1976). It later appeared that the nutrient and organic material budget of each saltmarsh was highly dependent on the geomorphological character, plant community, tidal amplitude and latitude of each system (Lefeuvre et al., 2000). Smith et al. (1983) and DeLaune et al. (1983) measured carbon accumulation and gas fluxes (CO_2 and CH_4) in marshes in Louisiana with different salinities (Table 1-3). Smith et al. (1983) concluded that a significant proportion of organic carbon in saltmarshes was stored in their sediments and negligible amount of it is exported to adjacent ecosystems during storms.

Table 1-3 Carbon accumulation and gas fluxes over marshes in Louisiana with different salinities.

	Fresh water marsh	**Brackish marsh**	**Saltmarsh**
CO_2 emission (g C m^{-2} yr^{-1})	618[b]	180 [b]	418 [b]
CH_4 production (g C m^{-2} yr^{-1})	160 [a]	73 [a]	4.3 [a]
Sediment C accumulation (g C m^{-2} yr^{-1})	224 [b]	296 [b]	183 [b]

Sources: (a) DeLaune et al., 1983 (b) Smith et al., 1983.

1.2.1.6 The methods applied for measuring above-ground primary productivity in saltmarshes

Above-ground net primary productivity (ANPP) plays an imperative roll in the carbon cycle of a diverse range of ecosystems including saltmarshes (Daoust and

Childers, 1998). ANPP in saltmarshes has been measured with destructive (harvesting) and non-destructive methods (Morris 2007).

Destructive methods: One of the common methods for measuring saltmarsh ANPP is by applying one of several harvesting techniques (Morris 2007). Harvesting methods include: Wiegert-Evans, Milner and Hughes's (Morris 2007) and Smalley's method (Morris 2007; Smalley 1958). Wiegert-Evans' method involves the clipping of above-ground biomass from 1 m^2 permanent paired quadrats (Cronk and Fennessy, 2001). In this method, the disappearance rate of plant litter production is also accounted for while estimating ANPP (Cronk and Fennessy, 2001). ANPP in the Milner and Hughes's method is estimated based on positive changes of standing biomass between the sampling intervals (Morris 2007; Linthurst and Reimold, 1978). The Milner and Hughes method underestimates ANPP by not considering stem and leaf turnover, and only measuring live standing biomass (Morris 2007; Linthurst and Reimold, 1978). Smalley (1958) attempts to correct the Milner and Hughes method by compensating for changes in live and dead standing biomass (Morris 2007).

Linthurst and Reimold (1978) measured ANPP of three saltmarshes along the north Atlantic Ocean, by using three different harvesting methods; Milner and Hughes, Smalley and Wiegert-Evans (Table 1-4). The ANPP estimated by the Milner and Hughes method was lower than the other two methods (Linthurst and Reimold, 1978, Table 1-4). Above-ground biomass and primary productivity in saltmarshes is affected by nitrogen availability, soil drainage, soil aeration and redox potential, sulphide concentration and temperature (De Leeuw et al., 1990). Some of these factors such as temperature and soil salinity fluctuate in a course of a year (De Leeuw et al., 1990). Others, such as redox potential, fluctuate monthly due to spring tide (Armstrong et al., 1985), so long gaps between sampling intervals could cause uncertainty in the ANPP estimation (Morris 2007). Linthurst and Reimold (1978) concluded that the Smalley method and the Wiegert-Evans method are suitable methods for estimating ANPP in saltmarshes. In addition, any harvesting method in saltmarshes need to be chosen based on criteria such as species morphology, local and general environmental conditions (Linthurst and Reimold,1978).

Table 1-4 Comparison of measuring ANPP with three different methods of saltmarshes at north east Atlantic Ocean coast.
Source: Linthurst and Reimold (1978) measured ANPP of the most dominant species at three different sites. However, as the emphasis here is on the applied method and not the species, the range of ANPP at each site are presented.

	Milner and Hughes (g m^{-2} yr^{-1})	**Smalley** (g m^{-2} yr^{-1})	**Wiegert-Evans** (g m^{-2} yr^{-1})
Maine saltmarshes	244-912	562-3523	616-5833
Delaware saltmarshes	522-1319	884-1501	1540-2753
Georgia saltmarshes	220-1866	316-278	1387-6039

Scarton et al. (2002) measured the above-ground biomass of *Sarcocornia fruticose* and *Phragmites australis* in the southern Venice Lagoon saltmarshes. ANPP was estimated using the Smalley and the Wiegert-Evans method on 5 separate months. The maximum above-ground biomass of *S. fruticose* was late summer, over September (1112 g m^{-2}) whereas maximum above-ground biomass of *P. australis* was in August (1095 g m^{-2}, Scarton et al., 2002). The ANPP of *P. australis* estimated by the Smalley method and the Wiegert-Evans method was 876 g d w m^{-2} and 705 g d w m^{-2} respectively (Scarton et al., 2002). It was concluded that the Smalley method was more accurate for estimating ANPP in saltmarshes than the Wiegert-Evans method (Scarton et al., 2002; Giroux and Bédard, 1988; Linthurst and Reimold, 1978). The Wiegert-Evans method was established to measure ANPP in grassland where the vegetation litter collection was not mobile (Linthurst and Reimold, 1978). Yet, in saltmarshes, ANPP estimation based on the Wiegert-Evans method could be complicated due to litter removal by tidal water (Scarton et al., 2002; Giroux and Bédard, 1988; Linthurst and Reimold, 1978).

Non-destructive methods: ANPP in saltmarshes can be estimated by allometric equations (Trilla et al., 2009; Dai and Wiegert, 1996). These equations are driven by the relationship between plant biomass and its morphometric parameters like height or diameter (Trilla et al., 2009; Komiyama et al., 2008; Clough 1992; Dickerman et al., 1986). Allometric equations are highly location and species-specific, therefore these equations need to be assessed prior to being applied (Alongi 2009; Komiayama et al., 2008; Clough et al., 1997). In addition, allometric equations are not suitable methods for estimating primary productivity of saltmarshes with more than one dominant species (Dickerman et al., 1986). Producing allometric equations are labour intensive and time consuming (Trilla et al., 2009). However, due to minimum marsh disturbance, applying allometric equations for measuring ANPP over several years, is preferred (Morris 2007).

Trilla et al. (2009) measured *Spartina alterniflora's* ANPP in the Bahı´a Blanca Estuary, Argentina using an allometric equation. The ANPP was 627 ± 94 g m^{-2} yr^{-1}along all the sites without any spatial and temporal variation (Trilla et al., 2009). It was concluded that due to high salinity resulting from the El Niño/Southern Oscillation (ENSO) period over 2006- 2007, the primary productivity of the marsh was hindered (Trilla et al., 2009).

1.2.1.7 The methods applied for measuring carbon stock in saltmarshes

Some of the papers that were used by Chmura et al., (2003) and Murray et al., (2011) for estimating carbon sequestration by saltmarshes have been reviewed here (Table 1-5). Studies have shown that organic matter accumulation is the main contributor to vertical accretion in tidal marshes (Yu and Chmura, 2009). Hence, sediment accretion, organic matter accumulation and organic carbon accumulation within saltmarshes have been studied either by radioisotope methods (Smith et al., 1983) or by loss on ignition (LOI) (Bryant and Chabreck, 1998; smith et al., 1983). Chmura et al. (2003) converted the organic matter measured in saltmarsh sediments to organic carbon using the following commonly-used equation:

$$\text{Percent of organic carbon} = (0.04)\,\text{LOI} + (0.0025)\,\text{LOI}^2$$

Radioisotope methods: The distribution of ^{137}Cs and ^{120}Pb in soil or sediment is related to sediment organic carbon distribution (Szmytkiewicz and Zalewska, 2014). Therefore, these two isotopes have been used for measuring sediment accretion and carbon accumulation within sediments (Szmytkiewicz and Zalewska, 2014; Mudd et al., 2009; Smith et al., 1983). Johnson et al. (2007) measured percentage organic carbon (% OC) using isotope analysis of one 3 m sediment core which was divided into 10 cm sections for isotope analysis. It was concluded that the Phippsburg Maine saltmarsh sequestration rate was 40 g C m^{-2} yr^{-1} for the last 2500 years. Based on isotope analysis it became apparent that plant community in the saltmarsh had shifted in response to sedimentation and rising sea levels over time.

Loss on ignition: Loss on ignition (LOI) is the method that will be used in this study to measure organic carbon within saltmarsh sediments. This method is based on different thermal analysis (Santisteban et al., 2004). To estimate the global range of carbon storage in saltmarsh sediment, Chmura et al. (2003) extracted data from literature where sediment organic carbon and sediment organic material were measured by LOI (Table 1-5). The variation in LOI results among studies is due to difference in temperature and durations of combustion (Konen et al., 2002). For example, when samples are burned at 550 °C, dissimilarity in sample weight, exposure time, and the position of samples in the furnace, results in variability in measurements (Heiri et al., 2001). However, the result of LOI method when samples are combusted for 2h in 950 °C, are smaller values with less variability between different laboratories result (Heiri et al., 2001). Murray, et al. (2011) stated that the variation in methods measuring sediment carbon content in saltmarshes limits the comparison between the results of these studies and contributes to variability in the reported values. In some of the studies presented in Table 1-5, sediment organic matter was estimated based on only two replicates per marsh (Anisfild et al., 1999; Bryant and Chabreck, 1998). Due to the vast spatial variability in the saltmarsh environment (Adam 2002), two replicates per site might not be adequate to make any conclusions.

Table 1-5 Examples of the studies used for estimating global carbon sequestration in saltmarshes.

Study sites	Measured parameter	Replicate number	LOI measurement applied method	Result (g m^{-2} yr^{-1})	OC reported by Chmura et al., 2003. (g m^{-2} yr^{-1})	Reference
Long Island Sound	OM[a]	2 cores per study site (6 study sites)	480°C for 8 hours	230 -340	72-204	Anisfild et al., 1999
Marsh Island Refuge, natural marsh, La	OM	2	480°C for 8 hours	1716	763	Bryant and Chabreck, 1998
Marsh Island Refuge, impounded marsh, La	OM	2	480°C for 8 hours	794	318	Bryant and Chabreck,1998

Study sites	Measured parameter	Replicate number	LOI measurement applied method	Result (g m^{-2} yr^{-1})	OC reported by Chmura et al., 2003. (g m^{-2} yr^{-1})	Reference
Rockefeller, Refuge, unit14, natural marsh, La	OM	2	480°C for 8 hours	1030	448	Bryant and Chabreck,1998
Rockefeller, Refuge, unit14, impounded marsh, La	OM	2	480°C for 8 hours	736	337	Bryant and Chabreck,1998
Rockefeller, Refuge, unit15, natural marsh, La	OM	2	480°C for 8 hours	1643	657	Bryant and Chabreck,1998

Study sites	**Measured parameter**	**Replicate number**	**LOI measurement applied method**	**Result (g m^{-2} yr^{-1})**	**OC reported by Chmura et al., 2003. (g m^{-2} yr^{-1})**	**Reference**
Rockefeller, Refuge, unit15, impounded marsh, La	OM	2	480°C for 8 hours	816	349	Bryant and Chabreck,1998
Sabine National Wild life, natural marsh, La	OM	2	480°C for 8 hours	4265	1713	Bryant and Chabreck,1998
Sabine National Wild life, impounded marsh, La	OM	2	480°C for 8 hours	1595	714	Bryant and Chabreck,1998

Study sites	Measured parameter	Replicate number	LOI measurement applied method	Result (g m^{-2} yr^{-1})	OC reported by Chmura et al., 2003. (g m^{-2} yr^{-1})	Reference
Fina La Terre, managed marsh, La	OM	31	375 °C after 16 hours	20 ± 6[e]	18	Cahoon 1994
Fina La Terre, unmanaged marsh, La	OM	31	375 °C after 16 hours	150 ± 40[e]	136	Cahoon 1994
Rockefeller, Refuge, managed marsh, La	OM	36	375 °C after 16 hours	20 ± 6[e]	27	Cahoon 1994

Study sites	Measured parameter	Replicate number	LOI measurement applied method	Result (g m^{-2} yr^{-1})	OC reported by Chmura et al., 2003. (g m^{-2} yr^{-1})	Reference
Rockefeller, unmanaged marsh, La	OM	40	375 °C after 16 hours	670 ± 100[e]	309	Cahoon 1994
Mexico	OM	6 cores per site (4 study sites)	400 °C [b]	333.4 – 413	178	Callaway et al. 1997
The Bay of Fundy, Low marsh	OC	5	Two stage combustion; first 350°C then 550°C [b]	68	f	Connor et al., 2001

Study sites	**Measured parameter**	**Replicate number**	**LOI measurement applied method**	**Result (g m^{-2} yr^{-1})**	**OC reported by Chmura et al., 2003. (g m^{-2} yr^{-1})**	**Reference**
The Bay of Fundy, High marsh	OC	5	Two stage combustion; first 350°C then 550°C [b]	340	f	Connor et al., 2001
Dorchester County, Maryland,	OC	2 samples per site (9 sites)	High temperature combustion with infra-red detector	130-366 g kg^{-1}	f	Hussein et al, 2004

Study sites	Measured parameter	Replicate number	LOI measurement applied method	Result (g m^{-2} yr^{-1})	OC reported by Chmura et al., 2003. (g m^{-2} yr^{-1})	Reference
Los Angles	OC	29	Total combustion technique	39 ± 4.1	f	Brevik et al., 2004

(a) Organic matter (b) Duration not specified (c) Three elevations were considered, low marsh, mid marsh and high marsh (e) The rate is per 6 months. (f) Turning to the data as its stated in the original papers.

1.3 Colne estuary

The coast of Essex comprises 10% of the remaining UK saltmarsh (Green et al., 2009). These Essex saltmarshes are classified as lowland marshes which are associated with low-lying geographic areas (Boorman 2003), and are either estuarine or coastal marshes. Estuarine marshes within Essex are formed along the rivers Stour, Colne, Blackwater, Roch, Crouch and Thames. In addition, coastal marshes are located on the Dengie Peninsula and Hamford Water (Nedwell et al., 2016; Green et al., 2009).

This research was conducted at three separate saltmarshes along the Colne Estuary (Figure 1-3). The Colne is a shallow river (Kocum et al., 2002) with the depth range from 1.5 m to greater than 15 m from the head of the river to the river mouth respectively (Nedwell et al., 2016). The Colne Estuary is 16 km long (Nedwell et al., 2016) having a 90-km shore-line due to the river's five tidal arms branching into the main river channel (Kocum et al., 2002). The Colne estuary is a macro-tidal estuary (Kocum et al., 2002). The depth of water column during high tide increases from the upper estuary towards the mouth of the estuary (Kocum et al., 2002). The depth of the water column during high tide at the Hythe, Wivenhoe and Brightlingsea is 3m, 5m and 14 m respectively (Kocum et al., 2002). The estuary exhibits a strong salinity gradient with the range of 0.5 ppm at the head of the estuary to >30 ppm at the mouth of the estuary (Figure 1-3, Nedwell et al., 2016).

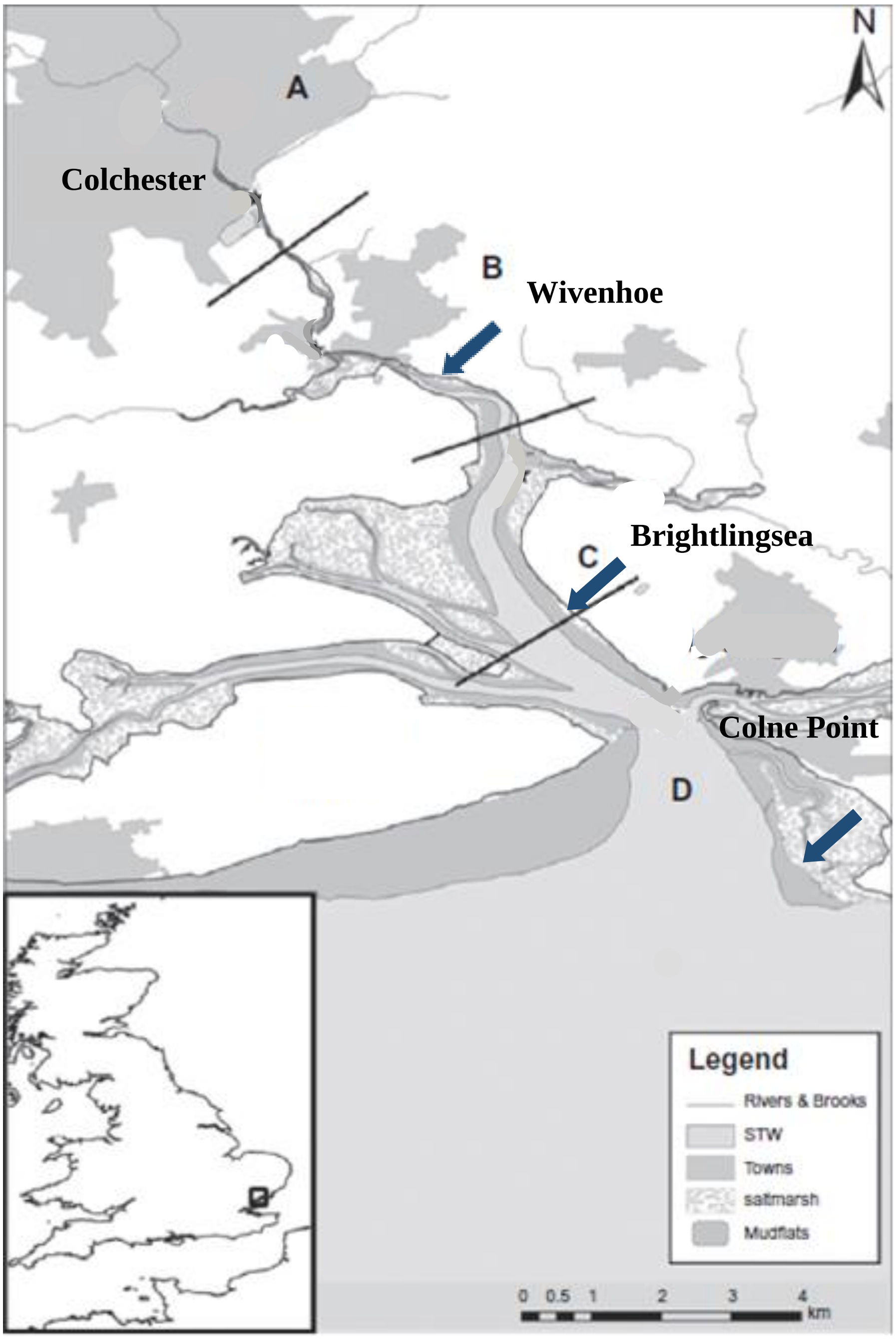

Figure 1-3 The location of the estuary in the UK, and the study sites within the estuary. Major salinity regions of the estuary are marked as zones A-D: A, 0.5–5 ppm; B, 5–18 ppm; C, 18–30 ppm; D, >30 ppm. The navy-blue arrows on the map point to the locations of the study sites along the estuary. The map was adopted from Nedwell et al., (2016.)

The Colne River catchment is approximately 350 km^2 with a population of 216000 (Nedwell et al., 2016). One of the major activities along the Colne Estuary is agriculture (Nedwell et al., 2016). The Colne river estuary is eutrophic with the two main nutrient loads being agricultural run-off and the Colchester sewage treatment plant (Nedwell et al., 2016). According to the E.U. Water Framework Directive (WFD) ground water and estuarine water are categorised into five ecological status classes, ranking from 0 to 1: bad, poor, moderate, good and high (Krause-Jensen et al., 2005; Andersen et al., 2004). The reference sites for WFD assessment are pristine or having a minor deviation from the undisturbed status due to anthropogenic activity (Krause-Jensen et al., 2005; Andersen et al., 2004). Under WFD, the Colne Estuary has been classified as a moderate status estuary (Nedwell et al., 2016).

The extent of the saltmarsh habitat around the river channel is about 900 ha (Nedwell et al., 2016). Parts of the estuary and its saltmarshes are protected as a Site of Special Scientific Interest (SSSI), a National Nature Reserve, a Special Protected Area, a Special Area of Conservation, a Ramsar Site and a Marine Conservation Zone (Nedwell et al., 2016; Green et al., 2009). In this study, three saltmarshes along the estuary were chosen as the study sites: upper estuary (marsh close to Wivenhoe), mid estuary (saltmarsh near Brightlingsea) and low estuary (Colne Point, Figure 1-3). These study sites were chosen to investigate the effect of saltmarsh location along the estuary on saltmarsh higher plant distribution, sediment total organic carbon (TOC) content and sediment respiration. These study sites are described in detail in chapter 2 (see 2.5.2.1).

1.4 The importance and novelty of this research

Clearly temperate saltmarshes can be extremely important natural sink for anthropogenic CO_2 (Mcleod et al., 2011). However, the significant knowledge gap regarding the carbon sequestration potential of these saltmarshes, particularly those within Europe, prevents them from being included in the global carbon budget (Murray et al., 2011). In addition, detailed information on the key environmental and biological drivers of variation in carbon accumulation and carbon sequestration within these ecosystems is unclear (Mcleod et al., 2011). This study therefore examines the spatial and temporal variation in above-ground primary productivity, sediment organic carbon content and sediment aerobic respiration to investigate the link between these ecosystem functions in one of the most studied estuaries in the northern hemisphere (Nedwell et al, 2016). Furthermore, in this research due to intensive and monthly sampling from the above-ground biomass and sediment, the precise spatial and temporal variability have been captured. Therefore, the data generated from this study are more robust compared to the studies presented in Table 1-5. Murray et al. (2011) highlighted the knowledge gap of sediment carbon content of European saltmarshes and estuarine saltmarshes. Two out of the three study sites in this research are estuarine saltmarshes and the other site is a coastal saltmarsh. The two estuarine saltmarshes are exposed to the gradient of anthropogenic activities. Therefore, this research provides a clear understanding of how a combination of anthropogenic activities and the location of the marsh along the estuary, could impact sediment carbon content in estuarine saltmarshes. These findings could fill some of the existing knowledge gap. In addition, the findings of this research will highlight the importance of the studied saltmarshes as important carbon sinks and create an increased incentive to protect them from degrading. In summary, this study provides a better understanding of spatial and temporal variation of sediment carbon stock in the Colne river estuary. For the first time the sediment TOC content, aerobic respiration and ANPP are measured along the Colne estuary.

1.5 Thesis hypothesis, aims and objectives

The main aim of this thesis is to explore the distribution of sediment TOC content and the relationships between sediment organic carbon content, sediment respiration, above-ground biomass and higher plant species richness within the study sites.

The hypotheses that will be examined throughout this thesis are as follows:

Hypothesis$_1$: There will be significant spatial and temporal variation in higher plant above-ground biomass, ANPP, sediment TOC content, and sediment respiration between saltmarshes in the upper estuary (Wivenhoe), mid estuary (Brightlingsea) and lower estuary (Colne Point).

Aim$_{1:}$ To investigate the spatial and temporal differences in ANPP, sediment TOC content and sediment respiration between saltmarshes at upper, mid and lower estuary.

Objective $_1$: To measure higher plant above-ground biomass, ANPP, sediment TOC content and sediment respiration at the three above mentioned sites monthly, and analyse the results.

Hypothesis$_2$: There will be significant difference in higher plant above-ground biomass, ANPP, sediment TOC content and sediment respiration within each study site between zones (low marsh, mid marsh and high marsh).

Aim$_{2:}$ To explore the differences in higher plant above-ground biomass, ANPP, sediment TOC content and sediment respiration within each study site between low marsh, mid marsh and high marsh.

Objective $_2$: To measure higher plant above-ground biomass, ANPP, sediment TOC content and sediment respiration at the three mentioned zones within each study monthly and analyse the results.

Hypothesis$_3$: There will be a link between saltmarsh vegetation characteristics (such as ANPP, saltmarsh plant species richness, saltmarsh plant above-ground biomass and stem density) and sediment TOC content at all the study sites (Colne Point, Brightlingsea and Wivenhoe, saltmarshes).

Aim$_{3:}$ To investigate the association between the measured saltmarsh vegetation characteristics and the measured sediment TOC content at Colne Point, Wivenhoe and Brightlingsea.

Objective $_3$: The association between saltmarsh vegetation characteristics and sediment TOC content will be investigated by linear regression analysis.

2. Chapter two - General Methodology

2.1 Introduction

In this chapter, the common methodology to all the results chapters are described, as well as site descriptions, the habitat types and zonation definitions. These definitions as well as that of season are the same in Chapters 3, 4 and 5 of this thesis. The sediment sample collection strategy described in this chapter is only part of Chapters 4 and 5 (no sediment samples were collected as part of the studies presented in Chapter 3).

2.2 Spatial variability

2.2.1 Site description

The Essex coastline includes one of the largest concentrations of tidal mudflats and saltmarshes in North West Europe (Harmsworth and Long, 1986, see Chapter 1 section 1.3).

Research presented within this thesis was conducted on saltmarshes located along the Colne Estuary. The Colne Estuary is macro-tidal estuary with a tidal range of 5.2 m at Brightlingsea (Takuechi 2006; Kocum et al., 2002). This estuary is a funnel shaped estuary which is very wide at its mouth and very narrow at the upper estuary (Essex and South Suffolk Shoreline Management Plan 2, 2010). Due to its shape and its high tidal range this estuary is dominated by ebb currents and has a tidal water amplitude that increases as waves move up stream (Essex and South Suffolk Shoreline Management Plan 2, 2010). The Colne estuary is about 16 km long (Underwood et al., 1998) and is branching with five tidal arms flowing into the main river channel

(Essex and South Suffolk Shoreline Management Plan 2,2010; Boorman, 2003). Under the EU Water Framework Directive, the Colne Estuary Ecosystem has been assigned a moderate quality status (Nedwell et al., 2016, see Chapter one - Introduction, section 1.3). The Colne Estuary is defined by steep channel sides except for low lying areas at the mouth of the estuary (Essex and South Suffolk Shoreline Management Plan 2, 2010).

Due to its geomorphology and its hydrodynamics, including the existing tidal arms, mudflats and saltmarshes (Murray et al.,2002; Meire et al., 2005), the Colne is representative of a large proportion of temperate estuaries internationally (Nedwell et al.,2016). Consequently, this estuary is one of the most comprehensively studied estuaries in the Northern hemisphere (Nedwell et al., 2016).

In this study, three saltmarshes located in different parts of the Colne estuary, were chosen as study sites. These sites were on the same side of the Colne Estuary (Eastern side) downstream of the Colne Barrier, where the natural tidal flow of the river is not disturbed (Dale et al., 2014). Chmura et al. (2003) stated that the main source of TOC to saltmarshes is sedimentation, and saltmarshes with higher sedimentation rates have higher sediment TOC content. According to Essex and South Suffolk Shoreline Management Plan 2 (2010) the funnel shape of the Colne estuary causes sediment to be removed from the upper estuary and deposited in the lower estuary so sedimentation is not homogenous. Hence a site at the upper estuary (Wivenhoe), a site at the mid estuary (Brightlingsea) and a site at the lower estuary (Colne Point, Figure 2-1 & Table 2-2) were selected in order to capture the spatial distribution of TOC in saltmarsh sediments.

The saltmarshes at Brightlingsea and Colne Point are part of the Colne Estuary National Nature Reserve (Ratcliffe 1977). The first study site was Colne Point (see Table 2-1 for location). This site is located between a shingle ridge and a sea wall. The shingle ridge protects this marsh from the North Sea and the sea wall separates the marsh from the adjacent agricultural land. This site is situated at the low-lying part of the estuary where it is completely submerged during high tide (Essex and South Suffolk Shoreline Management Plan 2, 2010). This site has been described as in a natural state for at least the few last centuries (Aziz and Nedwell, 1986). This marsh is also one of the designated SSSI sites along the Colne Estuary (Ratcliffe 1977) and a permit from Natural England was obtained for sampling this site (Figure 2-1). Colne Point was located approximately 16.8[2] Km downstream of the East Hill Bridge (the upper part of the estuary where is tidal) at the top of the estuary (Purdy et al., 2002; Takuechi 2006). The ratio of vegetated habitat to creek habitat at this site was 10.55:1[3].

The second site selected was Brightlingsea. This site was approximately 1.85km north of Brightlingsea Creek within the main river Colne system. Brightlingsea marsh was located mid-estuary (Nedwell et al., 2016; Essex and South Suffolk Shoreline Management Plan 2, 2010). This site had well-developed reeks and salt pans. Brightlingsea marsh was about 11.14 km downstream of the East Hill Bridge. The site was located approximately 5.6 km upstream of Colne Point. At Brightlingsea, the Colne River joins the North Sea where the river salinity increases from 18 ppt to 30 ppt (Nedwell et al., 2016; Underwood et al., 1998). At the location of the marsh,

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[2] And [3] The creek and the vegetated habitat area, the distance between each site and the distance of each site from the top of the estuary was estimated by satellite image analysis for this thesis.

which is only submerged during high tide (O’Connor, 2009), the salinity was approximately 30 ppt (Nedwell et al., 2016; Underwood et al., 1998). A small sewage treatments work at Brightlingsea is a source of allochthonous nutrient inputs to the Colne River (Ogilvie et al., 1997). The ratio of the vegetated habitat to the creek habitat in this marsh was 2.5:1 (see Table 2-1).

Wivenhoe was the third sampling site selected, approximately 6.4 km downstream of the East Hill Bridge, 0.25km downstream from the Colne Barrier and 4.75km upstream of the Brightlingsea site. Here the creek system is less developed and the creeks are only few cm deep and the vegetated habitat is fragmented. Wivenhoe is a small marsh system. The ratio of the vegetated habitat to the creek habitat at Wivenhoe marsh was 45:1 (see Table 2-1). The salinity ranges from 5 and 18 (Underwood et al., 1998, Figure 2-1).

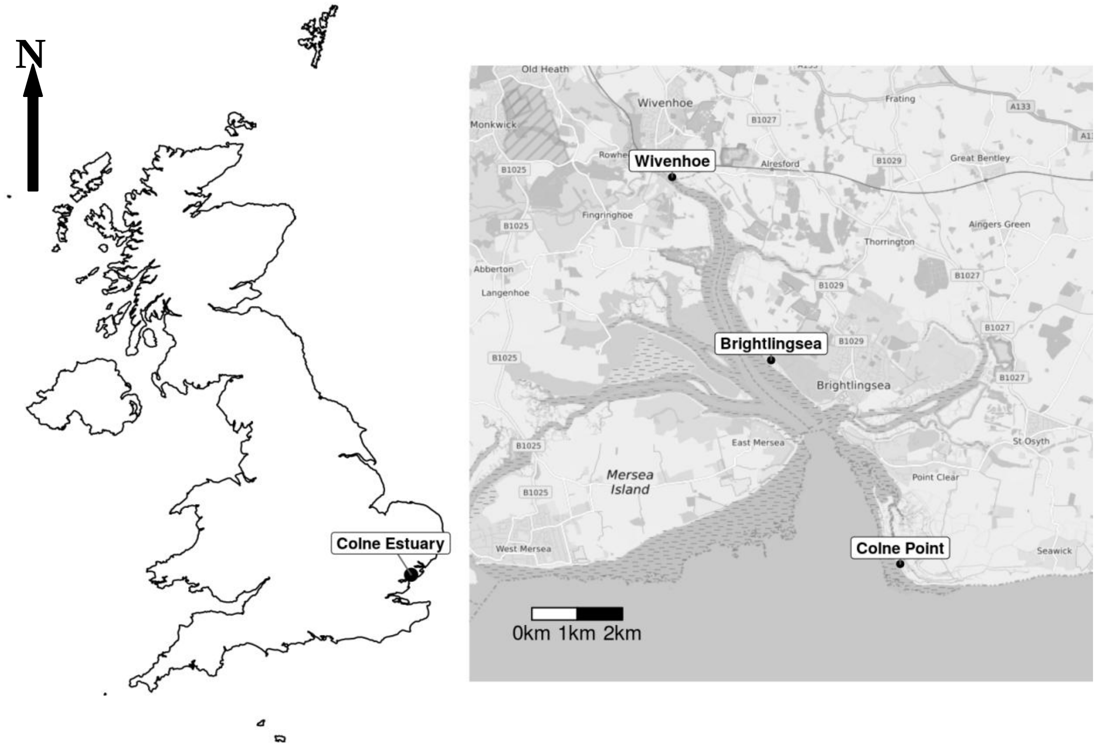

Figure 2-1 The map of the Colne Estuary in the UK and the study sites at the Colne Estuary.

This map was produced in R environment by Dr. David Clark for this thesis.

Table 2-1 Latitudes and longitudes (unit degrees/min/sec), the sampling area and the habitat types surface area (in hectares) of study sites.

	Colne Point	Brightlingsea	Wivenhoe
Latitude	51°46'49.80"N	51°48'56.50"N	51°51'6.76"N
Longitude	1° 2'28.19"E	0°59'47.36"E	0°57'58.79"E
The study site area	1.27	2.36	0.46
The vegetated habitat area at the study site	1.16	1.68	0.45
The creek habitat area at the study site	0.11	0.68	0.01

2.2.1.1 Habitat types within studied saltmarshes

The two common features of saltmarshes are vegetated areas and tidal creeks (Green et al., 2012 and 2009; Pethick, 1984; Chapman, 1974). The tidal creeks irrigate the saltmarsh vegetation and provide nutrients and sediment to the marsh (Wood and Hine, 2007). In this study vegetated and creek are considered as two different habitat types within each sampling site.

2.2.1.2 Zone determination

The higher plant species distribution within the saltmarsh is the result of interaction between physical and chemical characteristics of the saltmarsh sediment (saltmarsh height from chart datum and saltmarsh salinity) and plant community (Langlois et al., 2003). Thus, sampling sites were divided into 3 zones (low, mid and high marsh) based on the elevation of each zone from chart datum (see Table 2-2) coupled with dominant plant species. A preliminary botanical survey was carried out to record the percentage of the saltmarsh higher plants along the sites. At the same time, the height of each zone above chart datum was measured using theodolite and ranging pole during low tide. The area of the marsh with the lowest height from the chart datum (ranging between 5.13 – 5.40 m above CD) was dominated by *Spartina maritima* or *S. maritima* along with *Puccinellia maritima* (as in Langlois et al., 2003). At higher points on the marsh the dominance of *S. maritima* decreased and another species such as *Aster tripolium* and *Limonium vulgare* were present. At the three sites, the vertical distance between low and mid-marsh ranged between 3 to 8 cm (herein classified as mid-marsh, see Huiskes et al., 1995; Boorman 1967). The highest stand of marsh was dominated by either *Atriplix portulacoides* or *P. maritima* and ranged in vertical height from the mid marsh by 6 to 16 cm depending on the exact position of sampling (herein defined as High marsh, see Huiskes et al., 1995).

Table 2-2 The height of the low marsh, mid marsh and high marsh at Colne Point, Brightlingsea and Wivenhoe from chart datum (m).

	Low marsh	**Mid marsh**	**High marsh**
Colne Point	5.14	5.16	5.19
Brightlingsea	5.24	5.26	5.31
Wivenhoe	5.46	5.51	5.56

2.3 Temporal variability

There were two sampling campaigns in this study; one-year sediment sample collection (Table 2-4) and one-year (from June 2014 to July 2015, see Table 2-3) vegetation sample collection. Sampling was separated by season during each year.

The season division in this research, is compatible with the growth and biological activity observed for saltmarsh plants within the northern hemisphere with spring representing the start of the growth season (March, e.g. Caçador et al., 2000), maximum growth occurring in mid-summer (July, e.g. Valiela et al., 1975) and growth decline and subsequent zero growth occurring during Autumn (October) and mid-winter (December) respectively (Valiela et al., 1975).

2.4 Sampling strategy

In this study, two types of samples were collected. One set of samples collected was above-ground biomass (including higher plant species and biomass survey). The other set of samples were collected below-ground (within the sediment) and included total organic carbon, sediment chlorophyll *a* concentration, bulk density, moisture content and sediment respiration. The sampling strategy for each set of collected samples is presented in Table 2-5.

2.4.1 Above-ground vegetation survey and biomass

The above-ground vegetation survey and the biomass collection, for each site was carried out on the same day. The monthly above-ground vegetation study started in July 2014 and finished in June 2015. The sampling dates from each site over the sampling period are presented in Table 2-3.

Table 2-3 The sampling dates of monthly vegetation sample collection for each site.

	Summer	Autumn	Winter	Spring
Colne Point	17/07/2014	7/10/2014	05/01/2015	16/04/2015
	20/08/2014	26/11/2014	26/02/2015	20/05/2015
	18/09/2014	19/12/2014	23/03/2015	16/06/2015
Brightlingsea	03/07/2014	29/10/2014	23/01/2015	13/04/2015
	07/08/2014	NA	19/02/2015	09/05/2015
	26/09/2014	05/12/2014	25/03/2015	17/06/2015
Wivenhoe	30/07/2014	20/10/2014	30/01/2015	20/04/2015
	27/08/2014	20/11/2014	27/02/2015	27/05/2015
	24/09/2014	10/12/2014	18/03/2015	29/06/2015

2.4.1.1 Botanical survey

Monthly vegetation surveys were carried out for one year using 12 × 1 m^2 quadrats (Ford et al., 2016; Isacck et.al., 2006) at each of the zones of the sampling sites (and therefore consistent with biomass sampling). The percentage cover of higher plants and bare soil were recorded. The stem density and the stem height of the plants were also determined in areas in smaller quadrats (0.01 m^2, n = 4) within each larger quadrat (i.e. 1 m^2). Those measurements were carried on in the field. The number of stems or the stem density was measured by counting the stems in the smaller quadrats. The stem height was also measured within the smaller quadrats using a ruler, with one end of the ruler was touching the ground. Then the average canopy height was recorded as the small quadrat’s stem height. The flowering plants were identified mainly during summer based on species description and specification in Rose and O’Reilly (2006).

Plant species richness (S), was estimated (Morris et al., 2014) as follows:

> S = number of the species present at each zone within each study site in this current research.

2.4.1.2 Above-ground biomass sampling

The Wiegert-Evans method (cited in Cronk and Fennessy, 2001) was followed for sampling above-ground biomass. At each zone within each study site, three locations were randomly chosen. At each chosen location, two quadrats (1 m^2) were paired and placed permanently. Thus, at each zone within each study site, there were three paired quadrats (9 paired quadrats per study site). Each one of the 1 m^2 quadrats was divided into 100 smaller quadrats (0.01m^2). A gridded map of each segmented 1 m^2 quadrat was prepared and used to randomly locate successive sampling ensuring that no specific area was sampled more than once. All plant biomass was sampled (clipped from ground level in each 0.01m^2). Each paired 1 m^2 quadrat was sampled ($n = 4\times$ 0.01 m^2 quadrats) alternatively to ensure at least one month recovery between every sampling event.

2.4.1.3 Daily temperature measurement

At each study site, two Onset HOBO loggers were placed at the mid marsh to measure daily temperature every 30 minutes. At the end of the sampling year, the average of daily temperature per season was estimated.

2.4.2 Below-ground sampling collection strategy (sediment samples)

Sediment samples were collected monthly from each habitat type in each zone within each site during low tide. Sampling occurred from January to December 2013 (Table 2-4). Sediment samples were collected using PVC cores with a 6.5 cm internal diameter. The depth of the cores varied as follows: For TOC analysis, the cores were inserted to a depth of 20 cm and for sediment mineralization measurements it was 10 cm. In addition, PVC cores with a 1 cm internal diameter were used to collect sediment samples to a maximum depth of 2 cm for measuring sediment chlorophyll *a* concentration.

Each sampling site was divided into plots of 5 m width, with each such plot containing the three zones and the two habitat types. On every sampling date, one plot that was not sampled the previous month would be selected. At the selected plot, three locations for taking samples within each habitat type at each zone were randomly selected and a 2 m distance between each spot was maintained. All the randomly selected sampling locations were on a line parallel to the shore. At each location, three cores were taken: one for TOC analysis, one for sediment mineralization analysis and one of sediment chlorophyll *a* measurement as described in the paragraph above. Therefore, to measure each of the mentioned variables, every month, three samples were collected from vegetated and creek habitat in each zone, within each station (the total number of samples collected monthly for measuring each variable from Colne Point, Brightlingsea and Wivenhoe were 15, 18 and 15 respectively). To facilitate sampling in the vegetation habitat, the plant cover at each sampling point was clipped prior to the collection of sediment cores. The sampling strategy and number of replicates were presented in Table 2-5.

Table 2-4 The sampling dates of monthly sediment sample collection for each site.

	Spring	Summer	Autumn	Winter
Colne Point	27/01/2013	16/04/2013	10/07/2013	23/10/2013
	23/02/2013	18/05/2013	14/08/2013	19/11/2013
	14/03/2013	05/06/2013	21/09/2013	None due to flooding
Brightlingsea	13/01/2013	23/04/2013	31/07/2013	16/10/2013
	20/02/2013	21/05/2013	07/08/2013	16/11/2013
	16/03/2013	25/06/2013	28/09/2013	19/12/2013
Wivenhoe	10/01/2013	25/04/2013	24/07/2013	09/10/2013
	06/02/2013	22/05/2013	21/08/2013	09/11/2013
	28/03/2013	26/06/2013	18/09/2013	17/12/2013

Table 2-5 The below-ground sampling strategy within each zone (low, mid and high marsh) at the study sites (Colne Point, Brightlingsea and Wivenhoe).

Within each zone at every study site, there were two habitat types (vegetated and creek, excluding Colne Point low marsh and Wivenhoe high marsh). At any sampling event 3 replicates for measuring each of the variables were collected; sediment TOC content, bulk density, moisture content, respiration, chlorophyll *a* concentration.

	Colne Pont	Brightlingsea	Wivenhoe
Low marsh	Creek: <none> Vegetated: 3	Creek: 3* Vegetated: 3	Creek: Vegetated: 3
Mid marsh	Creek: 3 Vegetated: 3	Creek: 3 Vegetated: 3	Creek: 3 Vegetated 3
High marsh	Creek: Vegetated: 3	Creek: 3 Vegetated 3	Creek: <none> Vegetated: 3

2.5 Sample analysis

2.5.1 Above-ground biomass

In the laboratory, on the same day that samples were collected, samples were washed to remove the mud and visible microalgae attached. The samples were then air dried overnight. The vegetation samples then were divided into dead and live biomass, based on their physical appearance and tissue water content as determined by weight before and after drying (Willis et al., 2016). Water content was determined by drying specimens (n = 4 per 1 m^2 quadrat) at 60°C until a constant weight was reached.

2.5.1.1 Above-ground net primary productivity (ANPP) calculation

The Smalley method (Smalley, 1959) for estimating aboveground net primary productivity (ANPP) was followed (also see Cronk and Fennessy, 2001; Santos et al., 2004). The difference between standing live biomass (Δ^{live}) and standing dead biomass (Δ^{dead}) for each 1 m^2 quadrat was calculated between each sampling intervals (days) to calculate production rates as follows:

- when $\Delta^{live} > 0$, $\Delta^{dead} > 0$ then $ANPP = (\Delta^{live} + \Delta^{dead}) \div$ (sampling interval)
- when $\Delta^{live} < 0$, $\Delta^{dead} < 0$ then $ANPP = 0$
- when $\Delta^{live} > 0$, $\Delta^{dead} < 0$ then $ANPP = \Delta^{live} \div$ (sampling interval)
- when $\Delta^{live} < 0$, $\Delta^{dead} > 0$ then $ANPP = 0$

For each season, the ANPP for each month (therefore n = 3) was summed to obtain a total biomass value as used in other studies (e.g. Bouchard et al., 1998, Cronk and Fennessy, 2001).

2.5.2 Below-ground sample analysis (sediment samples)

2.5.2.1 Sediment total organic carbon (TOC) content, bulk density and sediment water content

The total number of cores collected for measuring sediment TOC content is presented in Table 2-6.

Table 2-6 Number of sediment cores collected across all habitat types and zones within each site during each season (from Jan – Dec 2013).

	Spring	Summer	Autumn	Winter
Colne Point	36	43	27	43
Brightlingsea	50	53	48	54
Wivenhoe	38	42	45	39

Differences in the number of samples taken (as displayed in Table 2-6) was due to the absence of creek habitat at Colne Point Low marsh and Wivenhoe High marsh, and lack of access to the Colne Point site during late autumn 2013 because of local flooding. In addition, a few samples were lost during transition or were not able to be taken from the field due to shallow sediment deposition). After transferring the samples to the laboratory, they were stored in a cold room at 4°C until processed (within 24 hrs). Following extraction from the PVC cores sediment samples were initially divided into 3 sections: 0-2 cm, 2-10 cm and 10-20 cm. The wet weight of the samples was also recorded and then samples were dried at 60°C until a constant weight[4].The bulk density and the sediment water content of the samples were calculated using the following equations (see Chambers et al., 2011):

Sediment bulk density = sample dry weight ÷ fresh sample volume (g cm^{-3})

Sediment water content (%) = [(sample wet weight – sample dry weight) ÷ (sample wet weight)] ×100

The dry sediment samples were then ground finely with a pestle and mortar, vegetation roots were not removed from the samples. Samples were then acidified in small crucibles using 2 M HCl solution to remove inorganic carbon in the sediment (as per McKew et al., 2011 and Chambers et al., 2011) and oven dried. TOC concentration was measured on 0.1 g of the acidified sediment using a Schimadzu 5000 TOC analyser (Schimadzu, Japan), the oven temperature was at 900 $^{\circ C}$ and the CO_2 evolved was measured on an infrared detector.

To calculate the total organic carbon (TOC) the initial weight of the sediment sample was recorded. The total organic carbon content (as mg g^{-1} of sample and as also as a percentage of the original sample weight) was determined (as per McKew et al., 2011). Carbon density and total sediment TOC content were calculated as per Avelar (2017) using equation 1 and 2 respectively:

1) Carbon density (g C.cm^{-3}) = TOC% × BD

2) Sediment TOC content (g C cm^{-2}) = Carbon density (g C.cm^{-3}) × H

Where TOC % (g g^{-1}) is the percentage of organic carbon in the sample; BD is the Bulk density (g cm^{-3}); and H (cm) is the wet sediment sample height (here the core sample was always 20 cm). The sediment carbon stock measured in this research was

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[4] Following the initial analysis of the sediment TOC content of 0-2 cm, 2-10 cm and 10-20 cm of collected samples, no difference was observed so those sections of the core were pooled together.

presented as sediment TOC content throughout the thesis and in the figures. Sediment organic carbon percentage and sediment carbon density were used to compare the values generated by this research to the relevant studies.

2.5.2.2 Chlorophyll *a*

Sediment samples for chlorophyll *a* (chl *a*) measurement were collected (see Table 2-5) from the top 2 cm of cores which were dominated by the microphytobenthic algae. In the field samples were immediately placed in clean glass universal vials, wrapped in foil and put in a cold box containing dry ice to prevent chl *a* degradation. In the laboratory, these samples were kept in the dark and in -20°C until processing.

Samples were frozen for a minimum of 24 hours, and then freeze-dried overnight, homogenised and ground in pestle and mortar. Chl *a* was extracted from sediment samples with methanol (99.5%) buffered with $MgCO_3$ (see Jensen et al., 1978) before being used for pigment extraction.

100 mg of each freeze-dried sample was placed into centrifuge tubes and 4 ml of buffered methanol was added to each sample. Then samples were incubated in the dark at 4° C for 24 h. The samples were then mixed and centrifuged for 15 min at 4000 G.

A 1 ml of the buffered methanol was used as blank. Samples absorbance was measured at 665 nm and 750 nm wavelengths (Stal et al., 1984) by a Genesys 10SUV-VIS spectrophotometer. Immediately after measuring the absorbance, samples were acidified with a drop of 10% HCl and left for 5 minutes. Again, absorbance was measured in the same wavelengths as before (Lorenzen 1967). The phaeopigment-corrected chl *a* concentration was calculated (mg g^{-1} dry weight of sediment) using the following equations (Stal et al., 1984):

3) $((A_n - A_a) \times V \times 1320) \div (74.5 \times W) = \mu g\ CHL\ a\ g^{-1}$

4) $((4.14 \times A_a) \times A_n) \times V \times 1286) \div (74.5 \times W) = \mu g\ phaeo\ g^{-1}$

V= volume of solvent in ml; W= Weight of freeze dried sediment in g; A_n = the absorbance at 665 nm before acidification minus absorbance at 750 nm before acidification A_a = the absorbance at 665 nm after acidification minus the absorbance at 750 nm after acidification (Stal and De Brouwer, 2003).

2.5.2.3 Sediment respiration

For sampling strategy and replicate numbers see Table 2-4. During sample collection sediment temperature was measured using an electronic thermometer (which subsequently determined the temperature at which respiration rates were calculated back in the laboratory).

Soil basal respiration (BAS) is the constant rate of respiration due to the mineralization of organic matter within the soil (Pell et al., 2006; Creamer et al., 2014), and is estimated by measuring either CO_2 production or O_2 uptake (e.g. Creamer et al., 2014). Here BAS was measured by the titration method (Pell et al., 2006; Bridgham and Richardson, 1992). The CO_2 produced through sediment microbial respiration is trapped in a sodium hydroxide solution based on the following formula:

$$CO_2 + 2\ NA^+ + 2\ OH^- \rightleftharpoons CO_3^{-2} + 2\ NA^+ + H_2O$$

Since CO_2 is produced and there is OH^- in the alkaline solution, the reaction moves to the right (Pell et al., 2006; and Richardson, 1992). At the end of the incubation the amount of CO_2 produced is estimated indirectly by titrating the un-reacted OH^- in the alkaline solution with an acid such as hydroxide acid (Pell et al., 2006).

2.5.2.3.1 Chemicals and solutions needed for measuring sediment basal respiration

Water used to prepare the following solutions was boiled to remove CO_2 (Pell et al., 2006). The list of the chemicals and solutions were as follows (Pell et al., 2006):

The 0.1 M sodium hydroxide solution which was made by dissolving 4 g NaOH in 1 litre deionised water. The second solution was 0.05 M hydroxide acid (HCl) which was made by dissolving 4.3 ml of 36% HCL in 250 ml deionised water initially and then the volume was adjusted to 1 litre by adding more deionised water. To make the third solution, 0.05 M barium chloride ($BaCl_2$), 10.41 g $BaCl_2$ was added to 1 litre deionised water. Finally, the Phenolphthalein indicator solution was made by adding 0.1 g Phenolphthalein to 100 ml 60% (v/v) ethanol (60ml ethanol in 40 ml deionised water).

2.5.2.3.2 BAS measurement procedure

Samples collected from the field were kept in a cold room (4°C) for a maximum of 24 hours before processing (as a standard practise – see Creamer et al., 2014). Each core was horizontally divided into two sections i.e. 0-2 cm and 2-10 cm. Each section was sampled (exact weight measured but always between 15-30 grams and representing approximately 75 % of the upper section and between 17-25% of deeper sediment samples) for BAS assessment. The roots were kept within the sediment samples collected from the vegetated habitat. Without homogenising, samples were placed in 150 ml Drechsler bottles. The remaining portions of samples were weighed, and dried at 60°C until constant weight was reached (equation 5). The estimated dry weight of samples was used to normalise respiration rates (equation 6). Approximately half of sediment respiration is aerobic (and within the top 5 cm of sediment, Kostka et al., 2002) whilst the remainder is anaerobic (Thamdrup el al., 1998). In this thesis respiration rates were determined at a standardised sediment depth (0-2 cm) and should therefore be considered a conservative although standardised approach to estimating BAS.

To measure sediment BAS 4 ml of 0.1 M NaOH solution was pipetted into 10 ml test tubes that were then suspended into the Drechsler bottle containing sediment samples. To correct the estimation of measured BAS for CO_2 in the air, 4 ml of 0.1 M NaOH solution was also placed into three Drechsler bottles which did not have any sediment inside. The 0.1 M NaOH in these three Drechsler bottles was titrated at the end of the incubation and used as a blank in the BAS calculation (2.5.2.3.3). Afterwards all the Drechsler bottles were gas tight sealed with red turnover stoppers and placed in an incubator for 8 hours at the average ambient temperature on the sampling day (for number of samples see Table 2-6).

Due to toxicity of $BaCl_{2,}$ the titration was carried out in a fume cupboard. Then, 4 ml of 0.05 M $BaCl_2$ was pipetted into the solution to precipitate the carbonate ions (as $BaCO_3^-$). Three or four drops of phenolphthalein were added to the solution which turns the solution pink indicating free and non-reacted OH^-. The remaining OH^- was then titrated with 0.05 M HCl to the point that the indicator turns colourless. The HCl volume used for titration was used in equation 6 (see section 2.5.2.3.3) to calculate respiration.

2.5.2.3.3 Sediment BAS calculation

To estimate sediment BAS rate the dry weight of sediment samples (S_{dw}) was calculated as:

5) $S_{dw} = (A / B) \times C$

Where A is the dry weight of the sub-sample (g); B is the wet weight of the sub-sample (g) and C is weight of the sample (g).

The BAS rate unit is µg CO_2-C g^{-1}DW h^{-1} and was calculated with the following equation (Pell et al., 2006):

6) $$BAS= \frac{(M_C \times (V_b - V_a) \times (0.05 \times 1000))}{S_{dw} \times t \times 2}$$

Where M_C is carbon molecular weight; V_b is the volume (ml) of the 0.05 M HCl needed to titrate the trap solution from the empty flasks (blank) to the end point; V_a is the volume (ml) of the 0.05 M HCl needed to titrate the trap solution from the flasks with samples (blank) to the end point; 0.05 ×1000 is the normality of the acid in mill equivalents; S_{dw} is the sediment sample dry weight; t is incubation time (h), the result of the equation is multiple by two because per each trapped CO_2 molecule, 2 OH^- are consumed.

As stated above, the surface area of each sample before incubation was measured. To present the BAS variable by surface area, the S_{dw} of each sample was divided by its surface area which the product in g cm^{-2}. Then the BAS calculated rate was multiplied by g cm^{-2} and multiply by 10^{-1} thus the unit of the BAS presented in this chapter was mg CO_2-C m^{-2} h^{-1}.

2.6 Statistical analysis

Data were analysed using the statistical package R version 3.1.2 (Crawley 2002). The distribution of all the measured variables and presented in this thesis were examined using a Shapiro-Wilk test. The Shapiro-Wilk test found that the saltmarsh higher plant species diversity, above-ground biomass and ANPP, sediment TOC content, sediment bulk density, sediment chl *a* concentration, and sediment respiration variables were not normally distributed. Therefore, each set of variables, were transformed using logarithmic transformation, natural logarithmic transformation, square root and arcsine transformation. The skewness of the transformed variables from normal distribution was examined. The statistical analysis was carried on the transformed variables with the smaller skewness and the least deviation from normality (Osborn 2010, see the appendixes). The Shapiro-Wilk found that the transformed variables were not normally distributed. The Shapiro-Wilk test becomes extremely powerful with high number of observations (n >300, i.e. replicates, Kim 2013). In the current thesis, the number of replicates were higher than 300, for instance total replicates for TOC were 518, for respiration and chl *a* measurement 566. This results in the test returning a significant result even with a slight deviation from normality making it nearly impossible to distinguish the true distribution of the data (Kim 2013). However classical ANOVA and ANOVA based models become more powerful, especially with non-normally distributed data when the power (replication) is increased (Zuur et al., 2010). Therefore, general linear models were used throughout this thesis apart from the saltmarsh higher plant species diversity variable, the rest of the named variables were transformed and statistical analysis was carried on the transformed variables as explained below.

2.6.1 The spatial and temporal variation of saltmarsh higher plant species diversity

The spatial and temporal variation of saltmarsh plant species composition in this study was analysed by applying package Vegan (Oksanen et al., 2007) within statistical package R version 3.1.2 (Crawley 2002). Since this variable was not normally distributed, non-metric multidimensional scaling (NMDS) was used to visualise the similarities in composition as determined through Bray Curtis Similarity index for each sites, zones and season. The determent stress (or the distance between 2-dimensions) for the produced Shepard plots was > 0.1 which indicated great representation in reduced dimensions (Crawley 2002). The spatial and temporal variation of saltmarsh plant species composition was analysed by PERMNAOVA to determine significance of the effect of the different factors (season, site and zone, as per Anderson 2001).

2.6.2 Above-ground and below-ground variables analysis

The above-ground and the below-ground variables distribution was examined by Shapiro-Wilk test. Shapiro-Wilk test found that above-ground biomass and ANPP, sediment TOC content, sediment chl *a* concentration, and sediment respiration variables were not normally distributed. Therefore, every listed variable was transformed applying different transformation. The skewness for each data transformation was estimated by applying e1071 package (Dimitriadou et al., 2005). For each variable, the least skewed transformation was chosen for statistical analysis. As it explained above, due to the power of ANOVA analysis for high number of observation (e.g. replicates), the minor heterogeneity of the transformed variable did not impact the statistical analysis result (McDonald 2014; Zuur et al., 2010). Due to the hierarchy of the spatial factors, the transformed variables were analysed with nested ANOVA to identify significant differences among the mean values of measured variables of each spatial factor, temporal factor and the interaction between them (Zuur et al.,2009; Zuur etal.,2007). The transformed above-ground biomass and ANPP variables were analysed with this model:

1) Measured variable ~ season/site/zone

The rest of the variables (below-ground measured variables) were analysed by these two models:

2) Measured variables ~ season/site/habitat

3) Measured variables ~site/habitat/zone

The models validation was presented in the appendixes of the thesis. Where ANOVA results were significant, a Tukey-Kramer post hoc test in package lsmeans in R (Lenth 2016) was applied to identify the pairs of groups that were significantly different to each other.

The measured variables were presented by mean value ± 95% confidence intervals in figures and the text in this thesis (95% CI, see McDonald 2009; Cumming et al., 2007; Altman et al., 2005). To produce the figures, first summary tables of the transformed variable including mean value and 95% CI were calculated applying Rmisc package in R (Hope 2013). Before back transforming the summary table for each figure the upper limit and lower limit of the measured variable was calculated by adding and deducting the 95% CI to the mean values of each group (McDonald 2009). The figures were produced using the back transformed summary table and applying package ggplot2 in R Studio (Wickham 2009).

2.6.3 The relationship between measured variables

The standard linear regression is a very frequently applied test in biology (Dytham 2011). To examine the cause and effect relationship between the measured variables, standard linear regression analysis was applied. Due to the assumption of linear regression test, the y or the dependant variables were transformed while the predictor or the x variables were not (see Dytham 2011). The residuals of each regression line were also examined.

3. Chapter three - The Temporal and Spatial Variation of Saltmarsh Higher Plants

3.1 Introduction

Saltmarsh formation is due to the interaction between water, sediment and vegetation (Isacch et al., 2006). The drivers of higher plant species distribution along saltmarshes (known as zonation, see Pennings et al., 2005) are marsh elevation, frequency of tidal inundation, salinity, nutrient limitation and competition between the species (Pennings et al., 2005; Kiehl and Trenberth 1997, Pennings and Callaway 1992), and the physical environment (Pennings et al., 2005). Saltmarsh zonation, plant species diversity, species percentage cover, above-ground biomass and above-ground net primary productivity are saltmarsh properties (Minden and Kleyer 2011) which impact the ecosystem services that these habitats provide (Ford et al., 2016; Koch et al., 2009; Valery et al., 2004; Burke et al., 2002). For instance, Ford et al. (2016) demonstrated that saltmarsh plant diversity had a positive correlation with the ecosystem services that saltmarshes provide, such as sediment stabilization and preventing sediment erosion. Other ecosystem services that these habitats provide are wave attenuation and coastal zone protection (Möller et al., 2014; Koch et al., 2009; Moeller et al., 1996). Koch et al. (2009) demonstrated that higher above-ground plant biomass in saltmarshes contributes to a higher wave attenuation and consequently better coastal zone protection.

The main emphasis of this current research is carbon accumulation and storage in saltmarshes (Chapter 4). Saltmarsh plants contribute to autochthonous carbon accumulation within these ecosystems, through root and litter production (Curcó et al., 2002; Kostka et al., 2002; Hemming and Buth et al, 1991). Other studies in saltmarshes highlighted that some of the saltmarsh plant community characteristics, such as plant stem height and stem density, contribute to higher carbon accumulation within the saltmarsh sediment (Bos et al., 2007; Bouma et al., 2007; Zedler and Callaway 1999) by trapping material suspended in the water column (Bos et al., 2007; Klemm et al., 2006; Bouma et al., 2005). For example, in the saltmarsh pioneer zone, *S. maritima* due to its leaf shape and its above-ground morphology, is one of the most effective species in trapping sediment from the water column and reducing saltmarsh erosion (Curado et al., 2012; Sanchez et al, 2001). Valery et al. (2004) showed that marshes at Mont Saint-Michel, where *Elymus athericus* was the dominant species, had higher organic carbon within its sediment than the plant community with different dominant species. The slow decomposition rate of litter produced by *E. athericus,* and this species' ability to trap sediment is believed to be the reason for high sediment carbon content in Mont Saint-Michel marshes (Valery et al., 2004). Variation in species may play different roles in sediment accumulation, it is important to quantify the spatial and temporal variability in the above-ground biomass of saltmarsh plants. This chapter focuses on examining the higher plant assemblage, richness, stem density, above-ground biomass and above-ground net primary productivity at the study sites. The three study sites are situated at a different salinity gradient of the estuary (see 2.2.1). Therefore, it is expected that the species composition at each study site might be different. To compare the temporal variability, vegetation surveys and above-ground biomass (live and dead standing biomass) collection were collected monthly. The amount of carbon accumulated in the sediment of each site will be presented in Chapter 4.

3.2 Hypothesis, aims and objective

Hypothesis $_1$: The plant diversity at the upper estuary (Wivenhoe) will be lower than mid and low estuary (Brightlingsea and Colne Point). In addition, the distribution of species will vary across the different zones (low, mid and high marsh) within each site.

Aim$_1$: To determine whether saltmarsh higher plant diversity differs between the three zones at each study sites and between the study sites.

Objective $_1$: To conduct monthly surveys of the saltmarsh higher plant species abundance at the three zones (Low, mid and high marsh) of the three study sites (Colne Point, Brightlingsea and Wivenhoe).

Objective $_2$: To investigate the spatial variation in saltmarsh higher plant species abundance within the study sites at the three zones using R-studio statistical software.

Hypothesis $_2$: There will be a significant spatial difference in live and dead standing above-ground biomass at the study sites (Colne Point, Brightlingsea and Wivenhoe).

Aim $_2$: To determine the live and dead above-ground biomass at the study sites.

Objective $_3$: Quantify above-ground live and dead standing biomass from three permanent quadrats at each zone (low, mid and high marsh) within each site monthly.

Hypothesis $_3$: There will be a temporal variation in the live and dead above-ground biomass of saltmarsh plants at all sites with the highest live above-ground biomass being present during spring and summer.

Aim $_3$: To investigate the seasonal variation in live and dead standing biomass within each study site using the data collected in aim two. Use data in aim two to quantify live and dead above ground biomass.

Objective $_4$: To quantify the above-ground biomass (live and dead standing biomass) at each site for each season.

Hypothesis $_4$: There will be a significant seasonal difference in saltmarsh higher plant primary productivity between sites (Colne Point, Brightlingsea and Wivenhoe).

Aim $_4$: To determine the difference in the rate of saltmarsh higher plant primary productivity at each site.

Objective $_5$: To estimate the rate of saltmarsh higher plant primary productivity for each site and season using monthly changes of above-ground live and dead biomass.

3.3 Methodology

For site and zone description, see Chapter 2 (section 2.2.1.2). The sampling design, sample collection, replication and dates of sample collection are presented in section 2.4.1 of Chapter 2. Due to the observed data distribution, the data were transformed and analysed using a nested ANOVA. If another test was used to analyse the data, it is stated in this chapter. The mean values and 95% confidence intervals of the data were calculated before back transformation. The presented data in this chapter, both in the figures and text, are in the form: mean ± 95% confidence intervals (CIs, back transformed). Tukey test was applied for post hoc analysis. For examining the association between the variables due to the assumption of linear regression test, the y or the dependant variables were transformed before examining the association (see

Dytham 2011). Whereas, the predictor or the x variables were not transformed (see Dytham 2011).

3.4 Results

3.4.1 Saltmarsh higher plant characteristics

A total of 16 species of saltmarsh higher plants were identified across all sites and zones. The higher saltmarsh plant species at each zone within each site with their percentage cover during the sampling year were presented in Figure 3-1, Figure 3-2 & Figure 3-3.

3.4.1.1 Species composition and percentage cover

Colne Point: At Colne Point low marsh, 28% (95% CI, 18-43%) of the marsh was covered by *Spartina maritima* and another 18% (95% CI, 13-26%) of it was covered by the second most dominant species, *Puccinellia maritima*. The higher saltmarsh plant species at Colne Point low marsh that each covered between 1 to 2 % of the marsh were: *Limonium vulgare*, *Salicornia europaea*, *Triglochin maritima* and *Plantego maritima*. Two species covered less than 1% of low marsh namely, *Armeria maritima* and *Spergularia maritima* (Figure 3-1A).

The dominant species changed from *Spartina maritima* at low marsh to *Puccinellia maritima* at the mid marsh, where it covered 65% (95% CI, 55- 77%) of the mid marsh. The percentage cover of *Spartina maritima* at mid marsh reduced to less than 1%. *Suaeda maritima* and *Atriplex portulacoides* each covered less than 3% in the mid marsh at Colne Point. Other saltmarsh higher plant species that grow at Colne Point covered less than 2 % of this zone and these were: *Spergularia maritima*, *Salicornia europaea*, *Plantego maritima*, *Cochlearia angelica* and *Agrostis stolonifera* (Figure 3-1B).

Atriplex portulacoides with 58 % (95% CI, 51-66%) coverage was the dominant species at Colne Point high marsh. The percentage cover of *Puccinellia maritima* was 14% (95% CI, 8-26%) which is lower than its percentage cover at the low marsh and the mid marsh at Colne Point. Other saltmarsh higher plant species such as *Juncus Maritimus, Aster tripolium*, *Suaeda maritima*, *Salicornia europaea*, *Elymus pycnanthus* and *Agrostis stolonifera* had a percentage cover at high marsh between 1-2% each. In addition, other species such as *Cochlearia anglica*, *Plantego maritima* and *Spergularia maritima* were also present at high marsh with less than 1% cover each (Figure 3-1C).

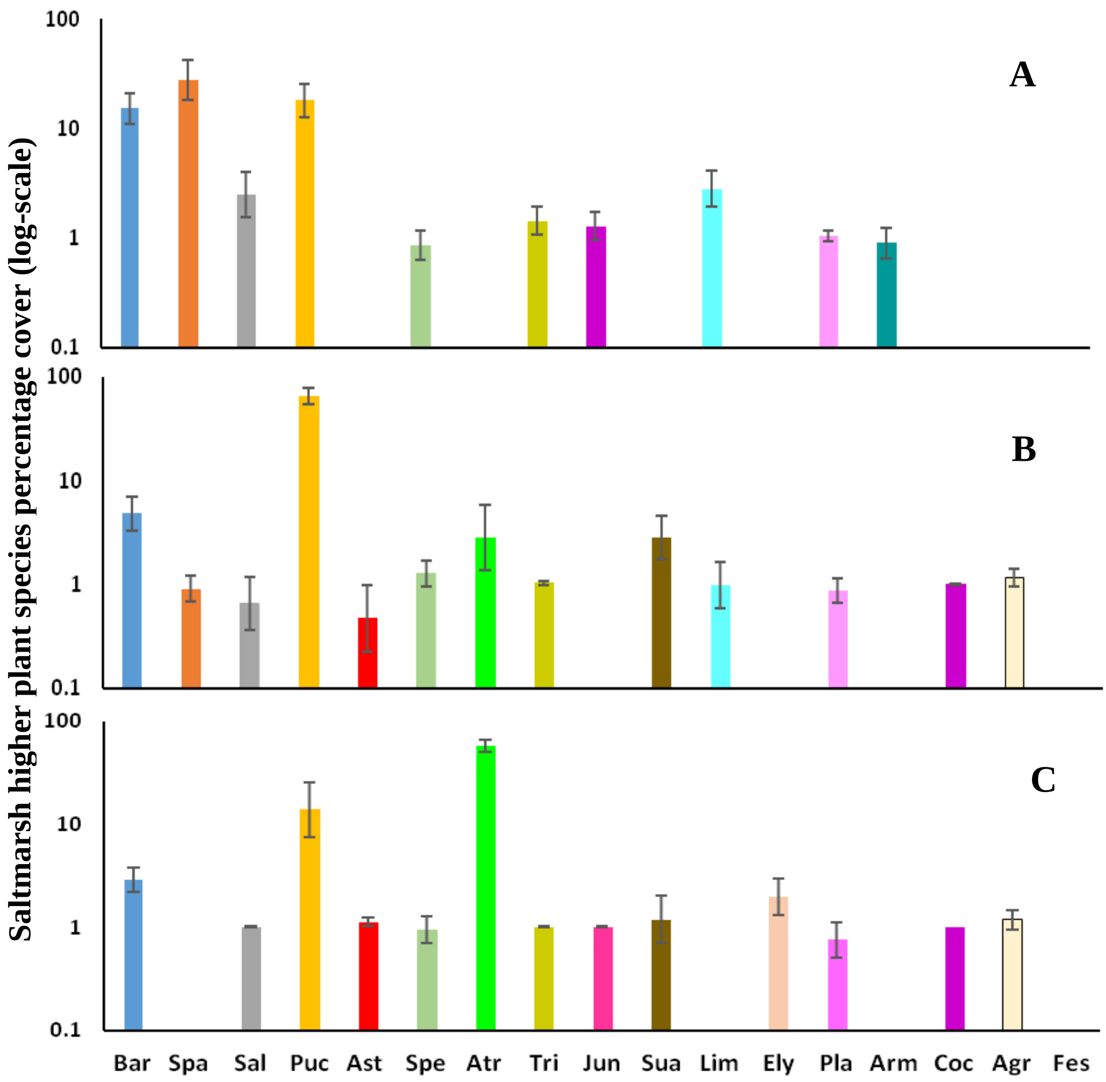

Figure 3-1 The spatial distribution of the saltmarsh higher plant species at Colne Point low, mid and high marsh. The values are log-10 scale of seasonal species percentage cover mean ± 95% confidence interval (back transformed).
Figure **A**, **B** and **C** illustrate low, mid and high marsh respectively. There were not enough replicates for the columns without error bars. Number of quadrats per zone: Colne Point; low marsh=30, mid marsh=34 and high marsh=32. Bar=bare sediment, Spa=*Spartina maritima*, Sal=*Salicornia europaea*, Puc=*Puccinellia maritima*, Ast=*Aster tripolium*, Spe=*Spergularia maritima*, Atr=*Atriplex portulacoides*, Tri=*Triglochin maritima*, Jun=*Juncus maritimus*, Sua=*Suaeda maritima*, Lim=*Limonium vulgare*, Ely=*Elymus pycnanthus*, Pla=*Plantego maritima*, Arm=*Armeria maritima*, Coc=*Cochlearia anglica*, Agr=*Agrostis stolonifera*, Fes=*Festuca rubra*.

Brightlingsea: At Brightlingsea low marsh, *Puccinellia maritima*, with 29 % (95% CI, 18- 50%) cover, was the dominant plant species. After *Puccinellia maritima*, *Spartina maritima* with 14 % (95% CI, 9-19%) cover and *Limonium vulgare* with 7 % (95% CI, 3 -15%) were the most abundant species. Other species such as

Salicornia europaea, *Aster tripolium*, *Atriplex portulacoides*, *Suaeda maritima*, *Spergularia maritima*, *Triglochin maritima* and *Plantego maritima* were also recorded at this zone with less than 3% cover each (Figure 3-2A). At Brightlingsea mid marsh, like the Colne Point mid marsh, the dominant species was *Puccinellia maritima* with 50% (95% CI, 44-57%) cover. In this zone, *Atriplex portulacoides* with 37% (95% CI, 29- 48%) cover was the second most abundant species. The percentage cover of *Spartina maritima*, *Aster tripolium*, *Spergularia maritima*, *Juncus Maritimus*, *Limonium vulgare* and *Suaeda maritima* was lower than 1% (Figure 3-2B). At Brightlingsea high marsh, the dominant species was *Puccinellia maritima* with 52% (95% CI, 43-62%) cover. The percentage cover of *Atriplex portulacoides* and *Limonium vulgare* was less than 4% in that zone. The other species at Brightlingsea high marsh were *Salicornia europaea*, *Aster tripolium*, *Juncus maritimus* and *Plantego maritima* which covered between 1 to 2% of the high marsh (Figure 3-2C).

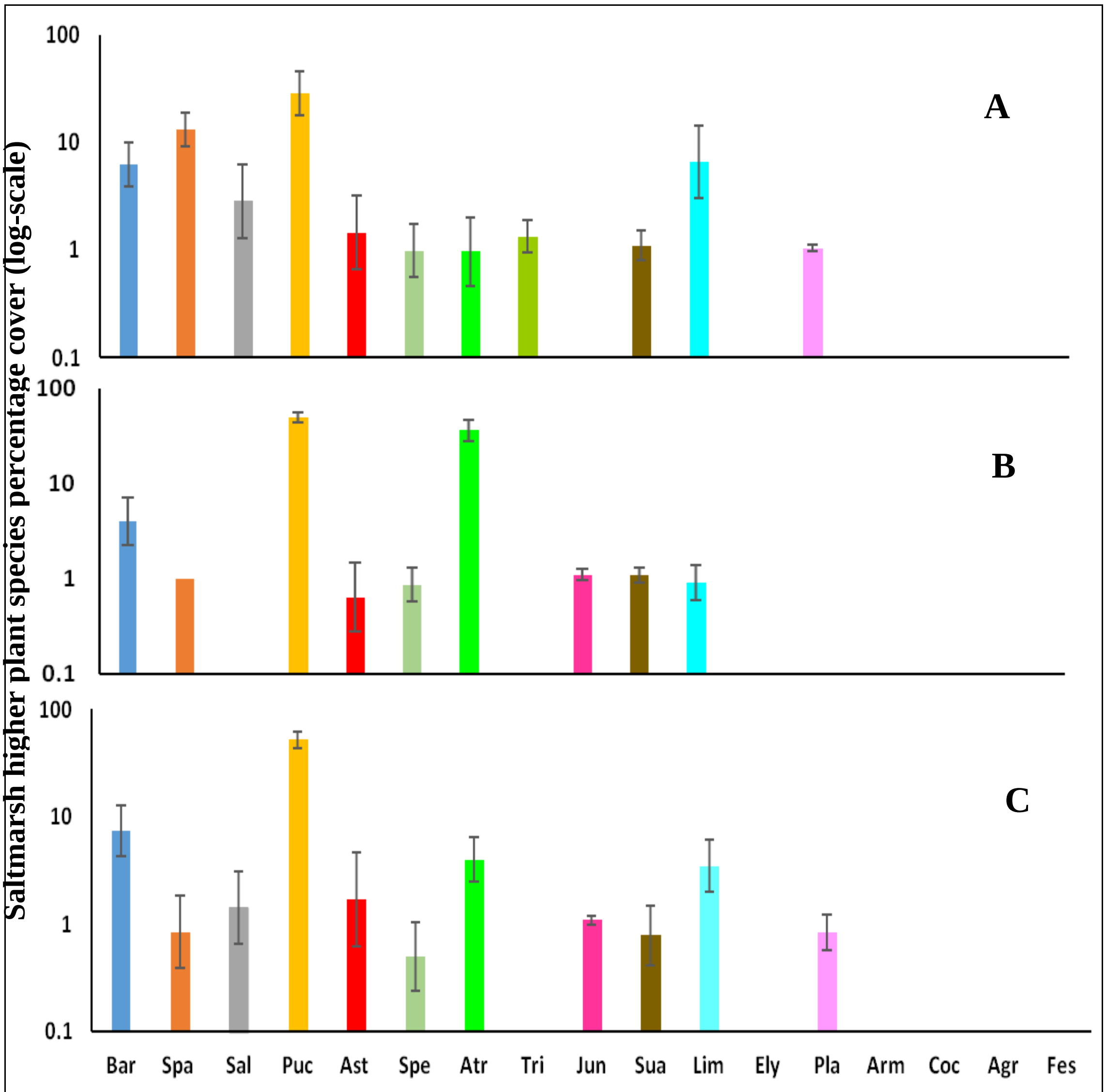

Figure 3-2 The spatial distribution of the saltmarsh higher plant species at Brightlingsea low, mid and high marsh. The values are log-10 scale of seasonal species percentage cover mean ± 95% confidence interval (back transformed).
Figure **A**, **B** and **C** illustrate low, mid and high marsh respectively. There were not enough replicates for the columns without error bars. Number of quadrats per zone; low marsh=27, mid marsh=27 and high marsh=27. Bar=bare sediment, Spa=*Spartina maritima*, Sal=*Salicornia europaea*, Puc=*Puccinellia maritima*, Ast=*Aster tripolium*, Spe=*Spergularia maritima*, Atr=*Atriplex portulacoides*, Tri=*Triglochin maritima*, Jun=*Juncus maritimus*, Sua=*Suaeda maritima*, Lim=*Limonium vulgare*, Ely=*Elymus pycnanthus*, Pla=*Plantego maritima*, Arm=*Armeria maritima*, Coc=*Cochlearia anglica*, Agr=*Agrostis stolonifera*, Fes=*Festuca rubra*.

Wivenhoe: At Wivenhoe, low marsh, *Spartina maritima* with 50% (95% CI, 44-57%) cover was the dominant species. The other species in that zone were *Salicornia europaea*, *Aster tripolium*, *Puccinellia maritima* and *Spergularia maritima* with less than 2% cover for each species (Figure 3-3A). Like the mid marshes at Colne Point and Brightlingsea, at Wivenhoe mid marsh the dominant species was *Puccinellia maritima* with 28% (95% CI, 20-40%) cover. In that zone the second most abundant species was *Aster tripolium* which covered 17% (95% CI, 11-24%) of the zone. The mid marsh at Wivenhoe had the highest percentage cover of *Aster tripolium* among the mid marshes of the study sites. *Salicornia europaea* and *Atriplex portulacoides* cover less than 2% of the mid marsh and *Spartina maritima*, *Spergularia marina*, *Juncus maritimus* and *Suaeda maritima* cover less than 1% each at the Wivenhoe mid marsh (Figure 3-3B). The Wivenhoe high marsh was like the high marsh at Brightlingsea where *Puccinellia maritima* with 43% (95% CI, 27-69%) coverage was the dominant species. *Aster tripolium* with 3 % (95% CI, 2 -4%) cover was the second most abundant species at Wivenhoe high marsh. *Spartina maritima*, *Triglochin maritima*, *Suaeda maritima* and *Festuca rubra* only covered 1% of this zone. *Salicornia europaea, Spergularia maritima* and *Atriplex portulacoides* were also present at this zone but covered less than 1% of the marsh (Figure 3-3C).

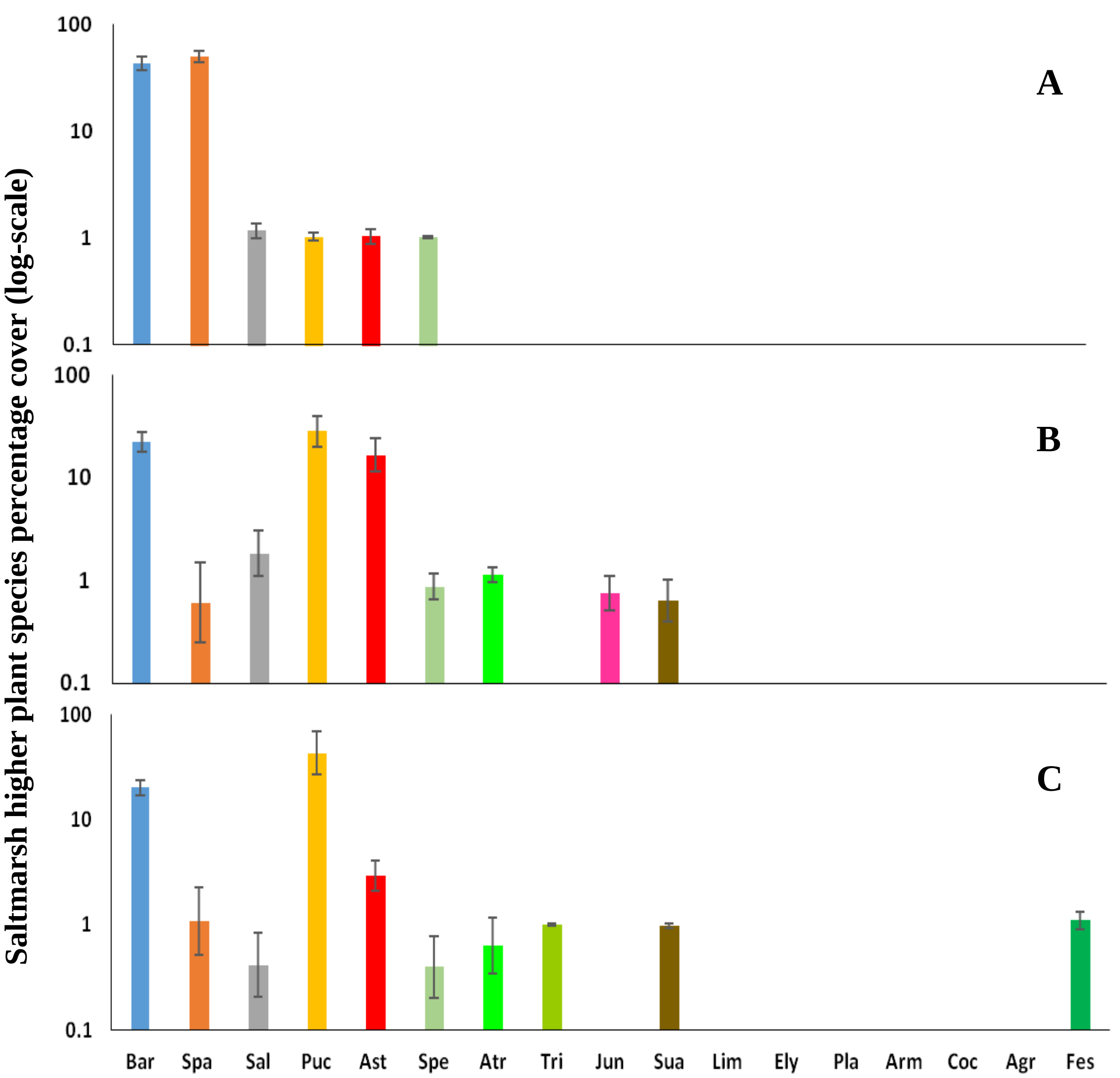

Figure 3-3 The spatial distribution of the saltmarsh higher plant species at Wivenhoe low, mid and high marsh. The values are log-10 scale of seasonal species percentage cover mean ± 95% confidence interval (back transformed).
Figure **A**, **B** and **C** illustrate low, mid and high marsh respectively.
Number of quadrats per zone; low marsh=30, mid marsh=32 and high marsh=30. Bar=bare sediment, Spa=*Spartina maritima*, Sal=*Salicornia europaea*, Puc=*Puccinellia maritima*, Ast=*Aster tripolium*, Spe=*Spergularia maritima*, Atr=*Atriplex portulacoides*, Tri=*Triglochin maritima*, Jun=*Juncus maritimus*, Sua=*Suaeda maritima*, Lim=*Limonium vulgare*, Ely=*Elymus pycnanthus*, Pla=*Plantego maritima*, Arm=*Armeria maritima*, Coc=*Cochlearia anglica*, Agr=*Agrostis stolonifera*, Fes=*Festuca rubra*.

P. maritima has been identified as a key species for trapping and stabilizing sediment in European saltmarshes (Langloise et al., 2003; Andresen et al., 1990) therefore, its spatial variation between the study sites was investigated. There was a significant difference in *P. maritima* percentage cover between the sites ($F_{2, 267} = 11.60$, $P < 0.001$). *P. maritima* percentage cover was significantly lower at Wivenhoe than Colne Point and Brightlingsea (Tukey test, $P < 0.05$, Figure 3-1, Figure 3-2 & Figure 3-3).

3.4.1.2 The spatial and temporal pattern of species distribution

There was a significant spatial variation in saltmarsh higher plant species (PERMANOVA: $F_{2, 265} = 88.250$, $P < 0.001$, Figure 3-4A). As presented in Figure 3-4A, the saltmarsh higher plant species distribution at the three study sites was highly influenced by saltmarsh zonation and as explained previously, some of the plant species were only found in a specific zone at the three study sites (Figure 3-1, Figure 3-2 & Figure 3-3).

There was significant variation in saltmarsh higher plant species composition between the sampling sites (PERMANOVA: $F_{2, 265} = 47.01$, $P < 0.001$, see Figure 3-4B). However, as described in 3.4.1.1, species distribution overlapped between the study sites. Some of the species were found in the three sites whereas few species were only recorded at one site. Therefore, the clusters in Figure 3-4B were less clear than Figure 3-4A.

In addition to the spatial variation in saltmarsh higher plant species distribution, there was significant seasonal variation in species distribution at the study sites (PERMANOVA: $F_{3, 265} = 5.87$, $P < 0.001$, see Figure 3-4 C). The species diversity clusters in Figure 3-4C (seasonal diversity) were less clear than Figure 3-4A and Figure 3-4B. Saltmarsh higher plant species such as *Spergularia maritima*, *Plantego maritima* and *Cochlearia angelica* were mainly observed during spring and summer. However, species such as *Atriplex portulacoides*, *Puccinellia maritima* and *Spartina maritima* were recorded throughout the sampling year.

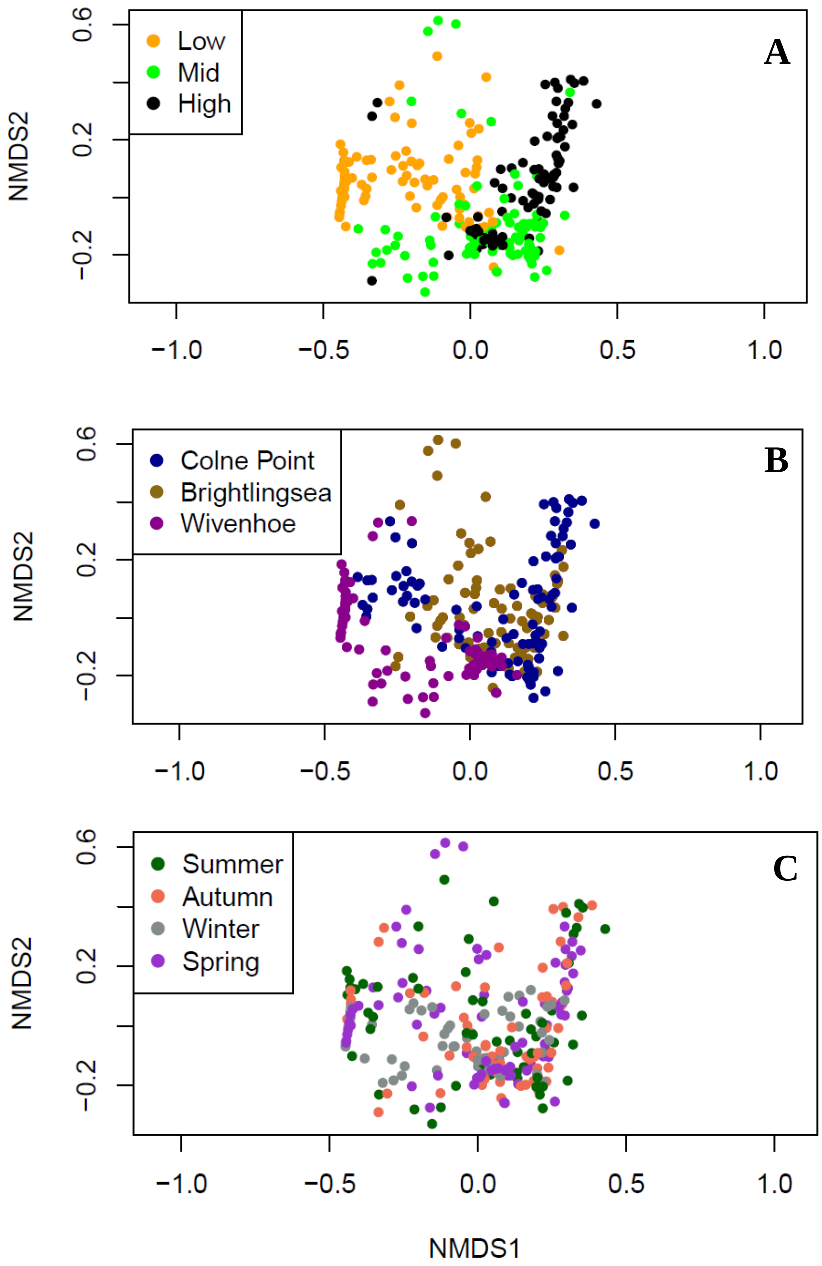

Figure 3-4 The saltmarsh higher plant species distribution within each zone, each site and seasonal distribution of saltmarsh higher plant species.

NMDS (non-metric multidimensional scaling) was used to graphically illustrate how the composition of samples was close to one another. The axes are the non-parametric multidimensional analysis scores. Each circle in above figures, represents one quadrat (N=324). **A)** (stress = 0.17), the orange, green and black circles are quadrats in low, mid and high marsh respectively. **B)** (stress = 0.16), dark blue, gold and fuchsia circles are quadrats at Colne Point, Brightlingsea and Wivenhoe respectively. **C)** (stress = 0.16), green, coral, grey and purple circles represent summer, autumn, winter and spring respectively.

3.4.1.3 Species richness, stem density and stem height

The other characteristics of the higher plant communities such as species richness and stem density per m^{-2} for each zone within each study site were also measured throughout the sampling year and analysed (Table 3-1).

Species richness: There was a significant difference in species richness (*S*) between sites ($F_{2, 214}$= 16.1, $P < 0.001$, see Table 3-1) and there was a significant site zone interaction ($F_{6, 2014}$ = 4.24, $P < 0.001$). The mean *S* at Brightlingsea was 5 species m^{-2} (4 – 5 species m^{-2}) and was significantly higher than Colne Point and Wivenhoe where there were 3 species m^{-2} (Tukey test, $P < 0.01$). There was no significant difference in *S* between Colne Point and Wivenhoe. At Colne Point and Wivenhoe there were no significant differences in *S* between zones. At Brightlingsea, however, *S* did vary at each zone with the high marsh having the lowest species richness (Tukey test, $P < 0.05$, Table 3-1).

Stem Density: There was significant difference in stem density between the sites ($F_{2,784}$ = 41.1, $P < 0.001$, see Table 3-1) and there was a significant site zone interaction ($F_{6,784}$ = 55.32, $P < 0.001$). Stem density at Brightlingsea (2800 per $m^{2,}$ 95% CI, 2500-3100 m^{-2}) was significantly higher than Colne Point (1700 m^{-2}, 95% CI ,1600 -2100 m^{-2}, Tukey test, $P <0.05$). In addition, stem density at Wivenhoe (1400 m^{-2}, 95% CI, 1100-1600 m^{-2}) was the lowest among the study sites (Tukey test, $P < 0.05$). Stem density at low, mid and high marsh was compared between the sites. Low marsh at Brightlingsea and low marsh Wivenhoe had the lowest stem density among the sites (Tukey test, $P < 0.001$). Colne Point mid marsh had the highest stem density whereas Wivenhoe mid marsh had the lowest stem density (Tukey test, $P < 0.001$, see Table 3-1). The stem density at Wivenhoe high marsh was the highest and Wivenhoe low marsh has the lowest stem density among the sites (Tukey test, $P < 0.001$, Table

3-1). Therefore, Wivenhoe had the biggest difference in stem density between the zones of any sites.

At Colne Point, mid marsh had higher stem density than the other two zones (Tukey test, $P < 0.001$). At Brightlingsea there was no significant difference in stem density between the zones.

Stem height: There was a significant site zone interaction ($F_{6, 206} = 18.96$, $P < 0.001$, see Table 3-1). Colne Point, high marsh had the tallest plants in that site (Tukey test, $P < 0.05$). At Brightlingsea, plants at low marsh were shorter than plants at mid marsh and high marsh (Tukey test, $P < 0.001$). At Wivenhoe, unlike Colne Point, the plants at high marsh were the shortest (Tukey test, $P < 0.001$, see Table 3-1).

Table 3-1 The higher plant community composition characteristics at each zone (low, mid and high marsh) of the study sites (Colne Point, Brightlingsea and Wivenhoe).
Low, mid and high stand for low marsh, mid marsh and high marsh. S stands for plant species richness. The values are mean ± 95% CI. Presented in the Number of the quadrats per each zone within each site is the same as Figure 3-1, Figure 3-2 & Figure 3-3.

Site	Zone	S (species m^{-2})	Stem density (per m^{-2})	Stem height (cm)
Colne Point	Low	4 (3- 4)	1200 (1000-1400)	20 (18-23)
	Mid	3 (3- 4)	4200 (3500-5000)	28 (25-31)
	High	3 (3- 4)	1300 (1000-1700)	39 (33-46)
Brightlingsea	Low	5 (4- 6)	3300 (2900-3800)	17 (14-21)
	Mid	5 (4-6)	2800 (2400-3200)	33 (29- 38)
	High	3 (2- 3)	2400 (1900 - 2900)	37.5 (33-42.5)

Site	**Zone**	**S (species m^{-2})**	**Stem density (per m^{-2})**	**Stem height (cm)**
Wivenhoe	Low	1 (1-1.32)	400 (300- 400)	30 (27- 35)
	Mid	3 (3-4)	1300 (1000-1700)	29 (23-37)
	High	4 (3-4)	4200 (3400-5200)	16 (12-21)

3.4.2 Above- ground biomass

There was a significant difference in standing biomass between the sites ($F_{2, 612}$ = 52.489, *P* < 0.001, Figure 3-5). There was also a significant site zone interaction ($F_{6, 612}$ = 16.23, *P* < 0.001). Standing biomass included live standing biomass and dead standing biomass (Figure 3-5). Live standing biomass at Colne Point, Brightlingsea and Wivenhoe was 300 g m^{-2} (95% CI, 258 -348 g m^{-2}), 305 g m^{-2} (95% CI, 260-359 g m^{-2}) and 131 g m^{-2} (95% CI, 107-162 g m^{-2}), respectively. Dead standing biomass at Colne Point, Brightlingsea and Wivenhoe was 135 g m^{-2} (95% CI, 111 - 163 g m^{-2}), 173 g m^{-2} (95% CI, 149 -201 g m^{-2}) and 84 g m^{-2} (95% CI, 70.0 -101 g m^{-2}), respectively. The live standing biomass at Colne Point, Brightlingsea and Wivenhoe was 55%, 43% and 36% higher than the dead standing biomass, respectively (Tukey test, *P* < 0.001, Figure 3-5).

There was no significant difference between live standing biomass at Colne Point and Brightlingsea. The live standing biomass of these two sites was significantly higher than the live standing biomass at Wivenhoe (Tukey test, *P* < 0.001). The dead standing biomass at the three sites followed the same pattern as live standing biomass (Figure 3-5).

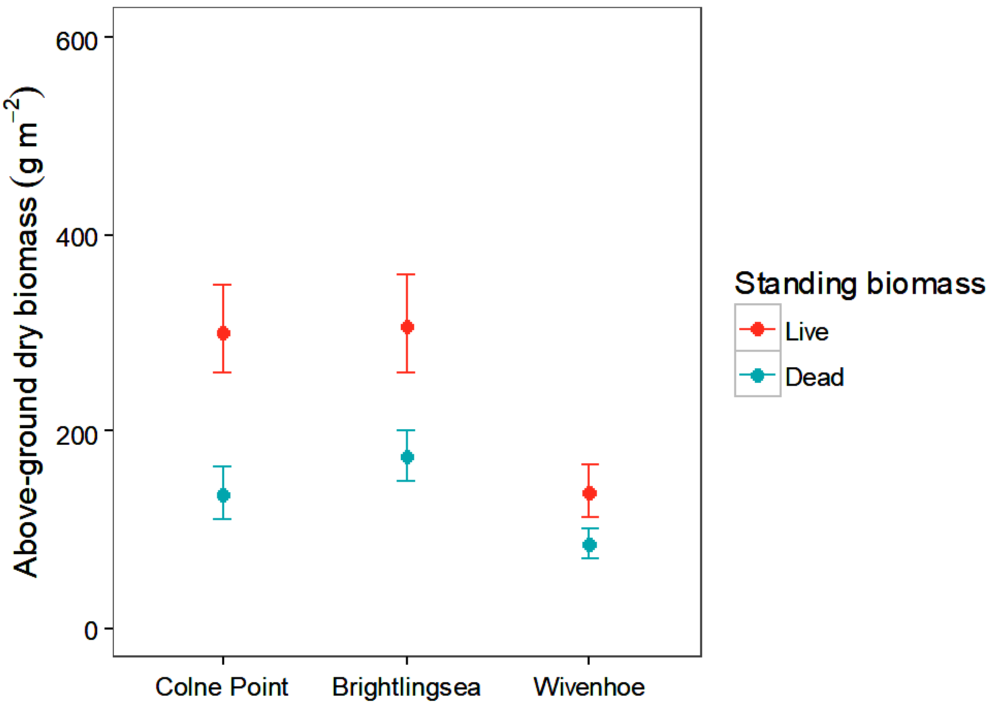

Figure 3-5 Above-ground live and dead standing biomass at Colne Point, Brightlingsea and Wivenhoe. Values are mean value ± 95% confidence interval (back transformed).
Each circle represents the mean result of seasonal sampling (4 seasons) from one site with three zones, high, mid and low marsh, with three replicates per zone at each sampling event. Colne Point; N live standing biomass = 108, N dead standing biomass = 108. Brightlingsea; N live standing biomass = 99, N dead standing biomass = 99. Wivenhoe; N live standing biomass = 108, N dead standing biomass = 108.

3.4.2.1 Spatial variation of live and dead standing biomass

Colne Point: There was no significant difference in live standing biomass between low, mid and high marsh at Colne Point (Figure 3-6A).Unlike live standing biomass, dead standing biomass at Colne Point high marsh (76 g m$^{-2,}$ 95% CI, 51 -113 g m^{-2}) was between 68% lower than dead standing biomass at mid marsh (240 g m$^{-2,}$ 95% CI, 202-285 g m^{-2}, Tukey test, $P < 0.001$, see Figure 3-6B).

Brightlingsea: Unlike Colne Point, live standing biomass at mid marsh (383 g m^{-2}, 95% CI, 309 - 475 g m^{-2}) and high marsh (427 g m^{-2}, 95% CI, 74 -123 g m^{-2}) was between 53-54 % higher than the live standing biomass at the low marsh (174 g m^{-2}, 95% CI, 135 – 225 g m^{-2}, Tukey test, $P < 0.01$,Figure 3-6A). At this site, there was no significant spatial variation in dead standing biomass (Figure 3-6B).

Wivenhoe: At Wivenhoe, there was no significant difference in live standing biomass between low marsh (96 g m^{-2}, 95% CI, 74 – 123 g m^{-2}) and high marsh (129.3 g m^{-2}, 95% CI, 94 – 177 g m^{-2}). However, the amount of live standing biomass at mid marsh was 54 % higher than the live standing biomass at the low marsh in Wivenhoe (Tukey test, $P < 0.01$, see Figure 3-6A). At this site, the mid marsh had 53% higher dead standing biomass (140 g m^{-2}, 95% CI, 108 -183 g m^{-2}) than the low marsh and the high marsh (Figure 3-6B).

Comparison of live and dead standing biomass between the sites: The live standing biomass at Colne Point low marsh was 53.5% higher than the live standing biomass at Wivenhoe low marsh (Tukey test, $P < 0.01$). There was no significant difference in live standing biomass at mid marsh between the three sites (Figure 3-6A). Whereas, the live standing biomass at Colne Point and Brightlingsea high marsh was 62% and 70% higher than live standing biomass at Wivenhoe high marsh (Tukey test, $P < 0.001$, Figure 3-6A).

Dead standing biomass at Colne Point low marsh was about 53% higher than the dead standing biomass at Wivenhoe low marsh (Tukey test, $P < 0.05$, see Figure 3-6B). There was no significant difference in dead standing biomass at the mid marsh of the study sites (Figure 3-6B). Nevertheless, at Brightlingsea high marsh, dead standing biomass (196 g m^{-2}, 95% CI, 153 -250 g m^{-2}) was significantly higher than the dead standing biomass at Colne Point and Wivenhoe high marsh (Tukey test, $P < 0.01$, see Figure 3-6B).

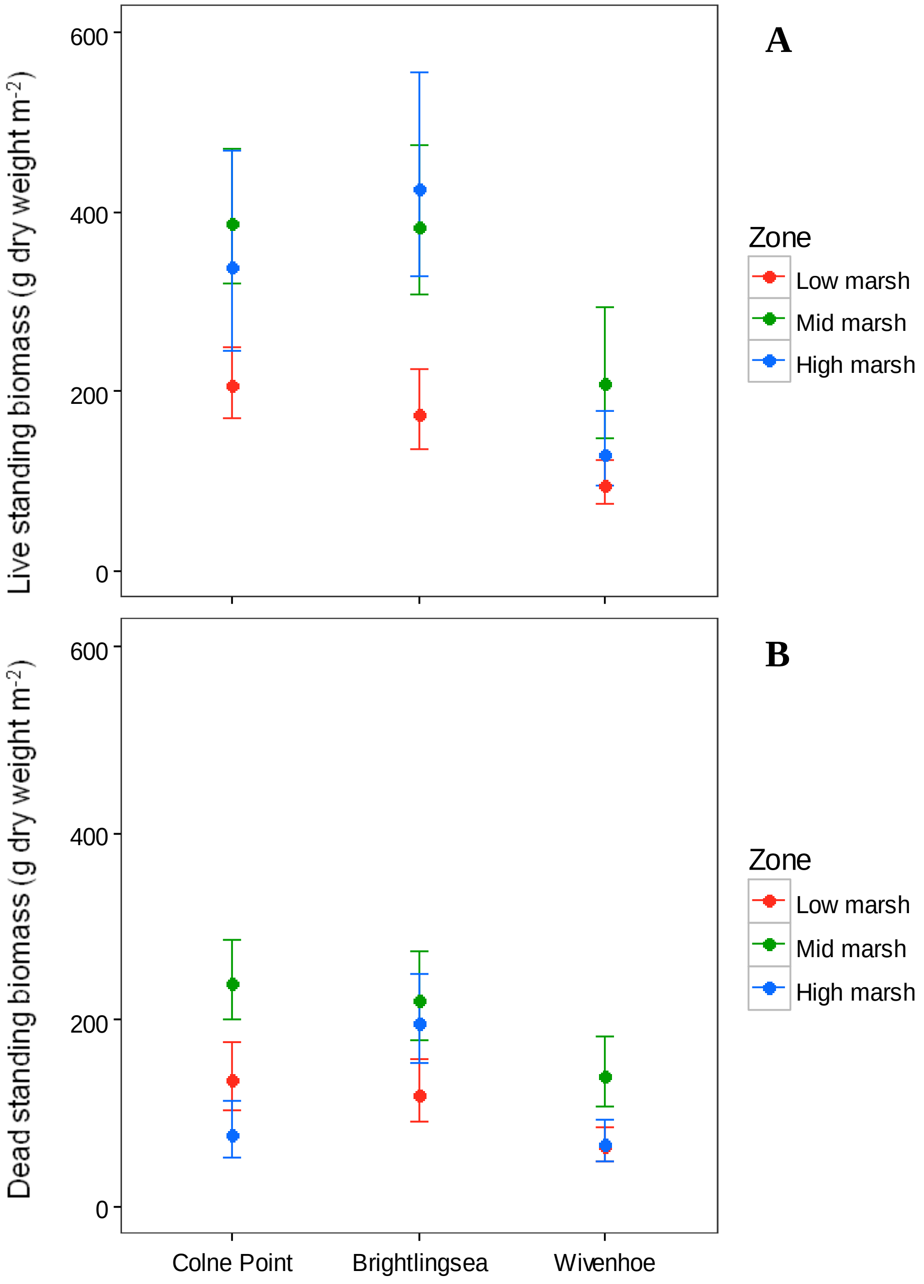

Figure 3-6 Spatial changes of live and dead standing biomass at Colne Point, Brightlingsea and Wivenhoe. Values are mean value ± 95% confidence interval (back transformed).
Figures A and B are live and dead standing biomass, respectively. Each circle represents the mean result of seasonal sampling (4 seasons) from one site, with three replicates per zone at each sampling event. Colne Point; N low marsh = N mid marsh = N high marsh = 36. Brightlingsea; N low marsh = N mid marsh = N high marsh = 33. Wivenhoe; N low marsh = N mid marsh = N high marsh = 36.

3.4.2.2 Temporal variation of live and dead standing biomass

There was a significant seasonal change in live standing biomass at the sampling sites ($F_{3,\,606}$= 28.36, $P < 0.001$, Figure 3-6B). There was also a significant interaction between season and sites ($F_{8,\,606}$= 12.33, $P < 0.001$) which means that live standing biomass in each site changed differently to another site at the same season (Figure 3-7A).

Colne Point: At Colne Point, there was no significant difference in live standing biomass between summer (356 g $m^{-2,}$ 95% CI, 284 – 448 g m^{-2}) and autumn (271 g $m^{-2,}$ 95% CI, 213 – 345 g m^{-2}). However, it significantly increased from winter (174 g m^{-2} , 95% CI, 122 – 248 g m^{-2}) to spring (483 g m^{-2}, 95% CI, 392 – 596 g m^{-2}) by 178.4% (Tukey test, $P < 0.01$, see Figure 3-7A).

Brightlingsea: At Brightlingsea, unlike Colne Point, the live standing biomass decreased significantly from summer (425 g $m^{-2,}$ 95% CI, 345 – 523 g m^{-2}) to autumn (164 g $m^{-2,}$ 95% CI, 101– 266 g m^{-2}) by 61.47% (Tukey test, $P < 0.05$). It then remained stable throughout the rest of the year (Figure 3-7A).

Wivenhoe: At Wivenhoe, unlike Brightlingsea, there was no significant difference in live standing biomass between summer (182 g $m^{-2,}$ 95% CI, 140 – 237 g m^{-2}) and autumn (90 g $m^{-2,}$ 95% CI, 61 – 133 g m^{-2}). Nevertheless, it then increased significantly from winter (93 g m^{-2} , 95% CI, 69 – 126 g m^{-2}) to spring (233 g m^{-2} , 95% CI, 158 – 343 g m^{-2}) by 150% (Tukey test, $P < 0.01$, see Figure 3-7A).

Comparison of live standing biomass between the sites: Due to the lack of significant differences in live standing biomass between Colne Point and Brightlingsea over the four sampling seasons, it appeared that lower live standing biomass at Wivenhoe was the driver of the significant seasonal differences. For instance, over summer, the live standing biomass at Brightlingsea was 57% higher than the live standing biomass at Wivenhoe (Tukey test, $P < 0.05$, Figure 3-7A). In addition, live standing biomass at Colne Point was about 49% higher than the live standing biomass at Wivenhoe over summer (Tukey test, $P < 0.05$, Figure 3-7A). Over autumn, the live standing biomass at Colne Point was 67% more than the live standing biomass at Wivenhoe (Tukey test, $P < 0.01$, Figure 3-7A). Furthermore, over winter live standing biomass at Brightlingsea was 53% higher than live standing biomass at Wivenhoe (Tukey test, $P < 0.05$, Figure 3-7A).

There was no significant seasonal difference in the dead standing biomass at the three study sites (Figure 3-7B).

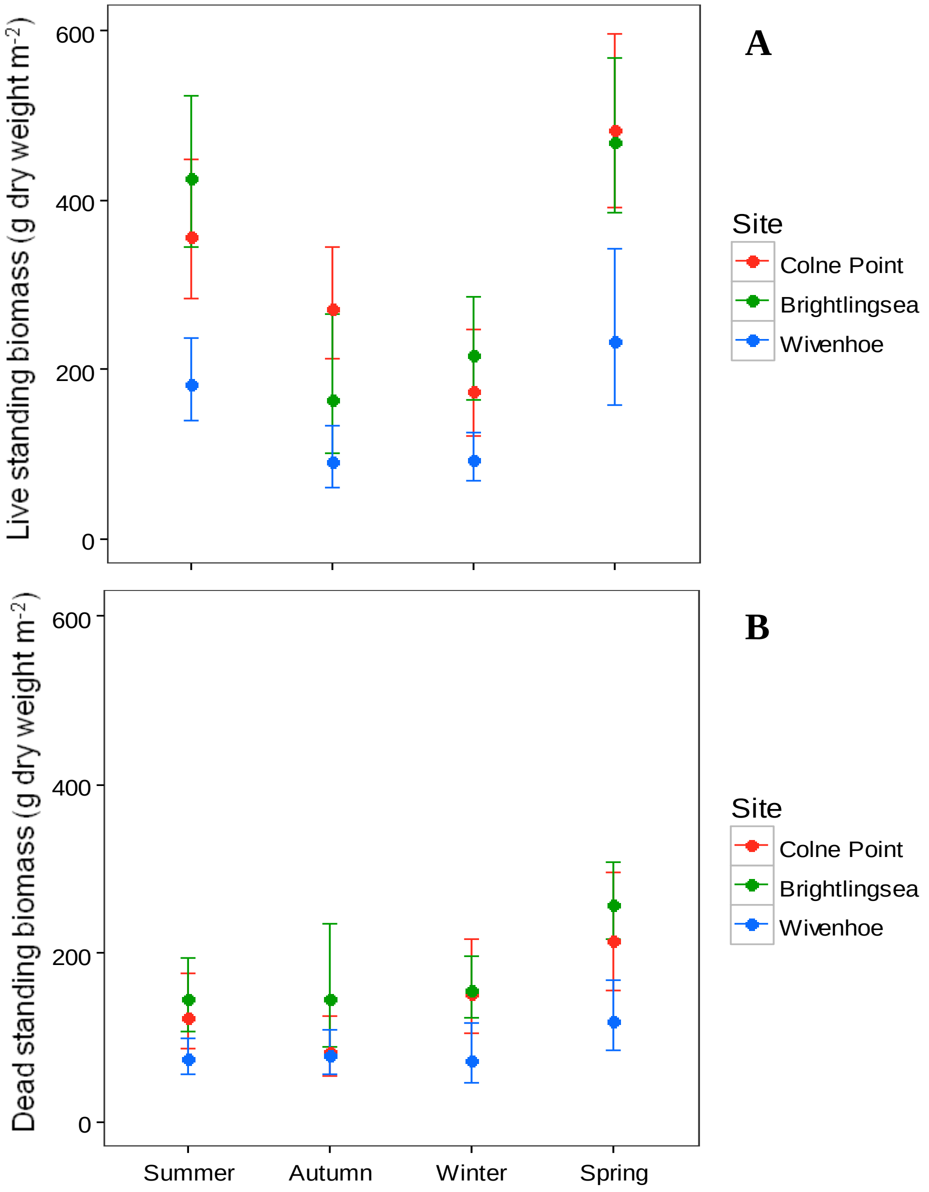

Figure 3-7 Temporal changes of live and dead standing biomass at Colne Point, Brightlingsea and Wivenhoe. Values are mean value ± 95% confidence interval (back transformed). Figures A and B are live and dead standing biomass, respectively**.** Each circle represents the mean result of seasonal sampling from 3 zones, with three replicates per zone at each sampling event. Colne Point; N summer = N autumn = N winter = N spring = 27. Brightlingsea; N summer = 18, N autumn = N winter = N spring = 27. Wivenhoe; N summer = N autumn = N winter = N spring = 27.

3.4.3 Above - ground net primary productivity (ANPP)

There was no significant difference in ANPP between low marsh, mid marsh and high marsh at the three study sites (Figure 3-8A). There was a significant seasonal difference in ANPP ($F_{3, 252} = 12.81$, $P < 0.001$, see Figure 3-8B). The ANPP was higher during summer (4.5 g m^{-2}, 95% CI, 3-6 g m^{-2}) and spring (5 g m^{-2}, 95% CI, 4-7 g m^{-2}) than autumn (2 g m^{-2}, 95% CI, 1-2g m^{-2}) and winter (2 g m^{-2}, 95% CI, 2-3 g m^{-2}) at the study sites. At Colne Point and Brightlingsea, there was no significant seasonal difference in ANPP within each site (Figure 3-8B). The only significant difference in ANPP was at Wivenhoe, the ANPP increased significantly from winter (2 g m^{-2} day^{-1}, 95% CI, 1-2.5 g m^{-2} day^{-1}) to spring (5 g m^{-2} day^{-1}, 95% CI, 3-9 g m^{-2} day^{-1}, Tukey test, $P < 0.05$, see Figure 3-8B). The total ANPP at Colne Point, Brightlingsea and Wivenhoe were 2227 g m^{-2} y^{-1}, 1565 g m^{-2} y^{-1} and 1772 g m^{-2} y^{-1}, respectively.

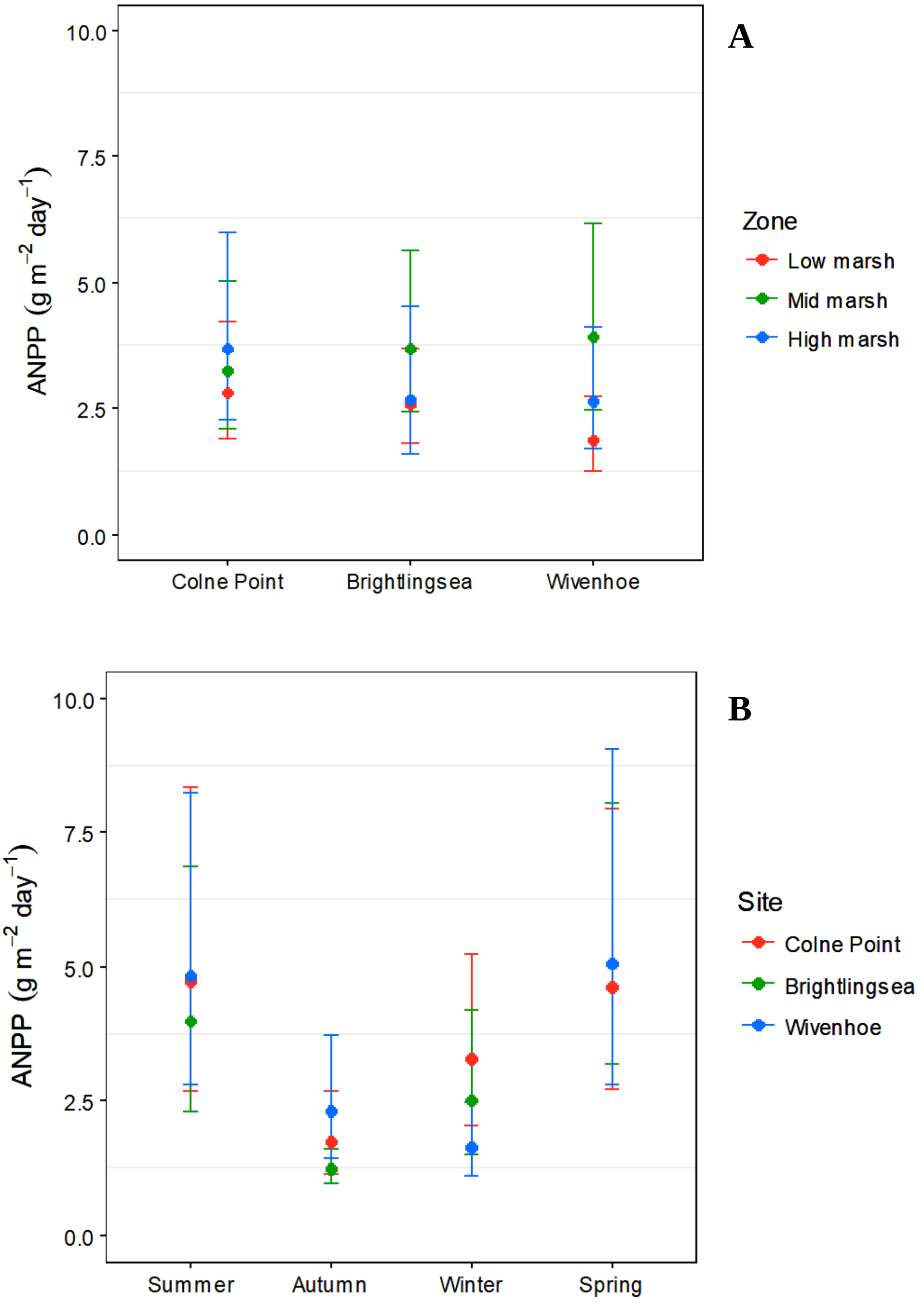

Figure 3-8 Spatial and seasonal variation of above-ground net primary productivity at Colne Point, Brightlingsea and Wivenhoe. Values are mean value ± 95% confidence interval (back transformed).
A) Each circle represents the mean result of seasonal sampling (4 seasons) from one site, with three replicates per zone and site. Colne Point; N low marsh = N mid marsh = N high marsh = 33. Brightlingsea; N low marsh = N mid marsh = N high marsh = 30. Wivenhoe; N low marsh = N mid marsh =N high marsh = 33. **B)** Each circle represents the mean result of seasonal sampling from 3 zones with three replicates per season zone and site. Colne Point; N summer = 18, N autumn = N winter = N spring = 27. Brightlingsea; N summer = N autumn = 18, N winter = N spring = 27. Wivenhoe; N summer = 18, N autumn = N winter = N spring = 27.

3.4.4 The association between saltmarsh higher plant characteristics, above-ground biomass and ANPP

There was a significant positive association between above-ground biomass and stem density (regression analysis, $F_{1, 154} = 27.83$, $P < 0.001$, Figure 3-9A). It means the quadrats with higher above-ground biomass were more likely to have higher stem density. There was also a weak significant positive association between above-ground biomass and stem height (regression analysis, $F_{1, 154} = 5.61$, $P <0.05$, Figure 3-9B). In addition, there was a significant positive association between and above-ground biomass and species richness (regression analysis, $F_{1, 154} = 21.5$, $P <0.001$, see Figure 3-10B). It means that the quadrats with higher above-ground biomass were more likely to have higher species richness. However, there was no association between ANPP and species richness (Figure 3-10A).

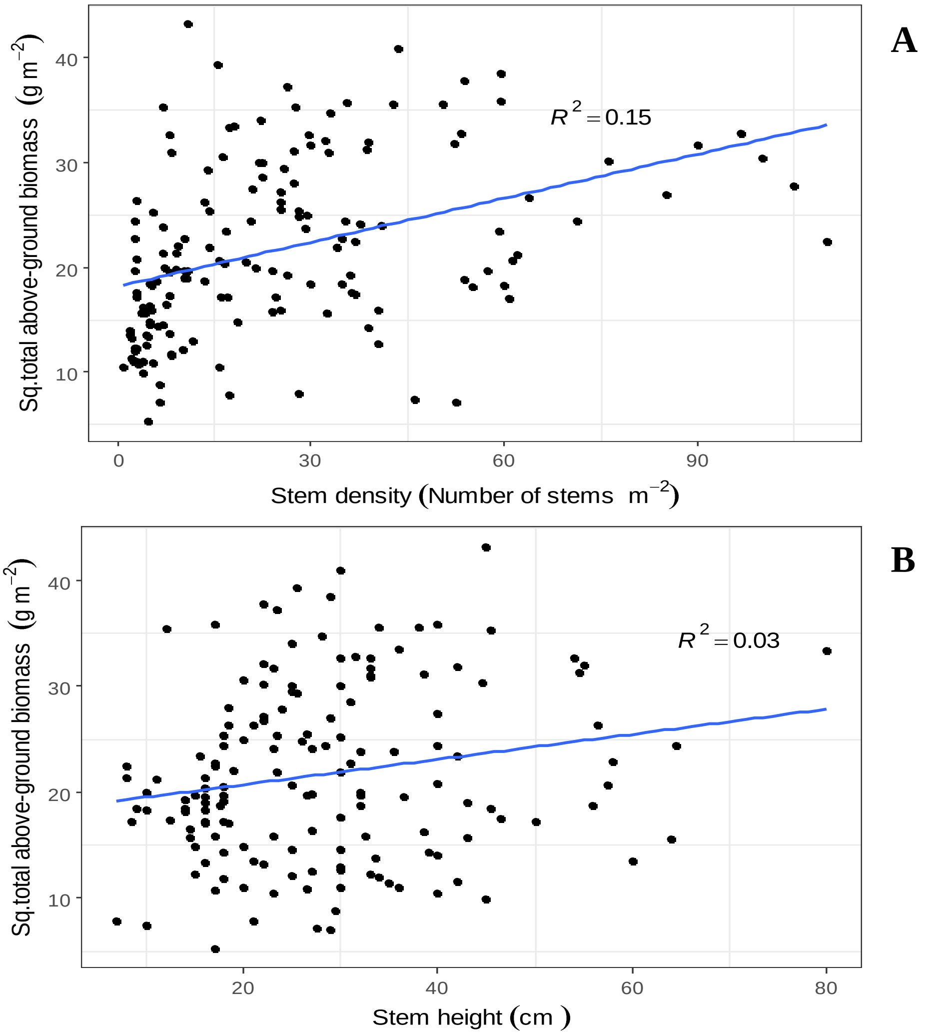

Figure 3-9 The association between square root transformed total above-ground biomass (above-ground live plus above-ground dead biomass), saltmarsh higher plant stem density and stem height.
A) The association between transformed total above-ground biomass and stem density. **B)** The association between transformed total above-ground biomass and stem height.

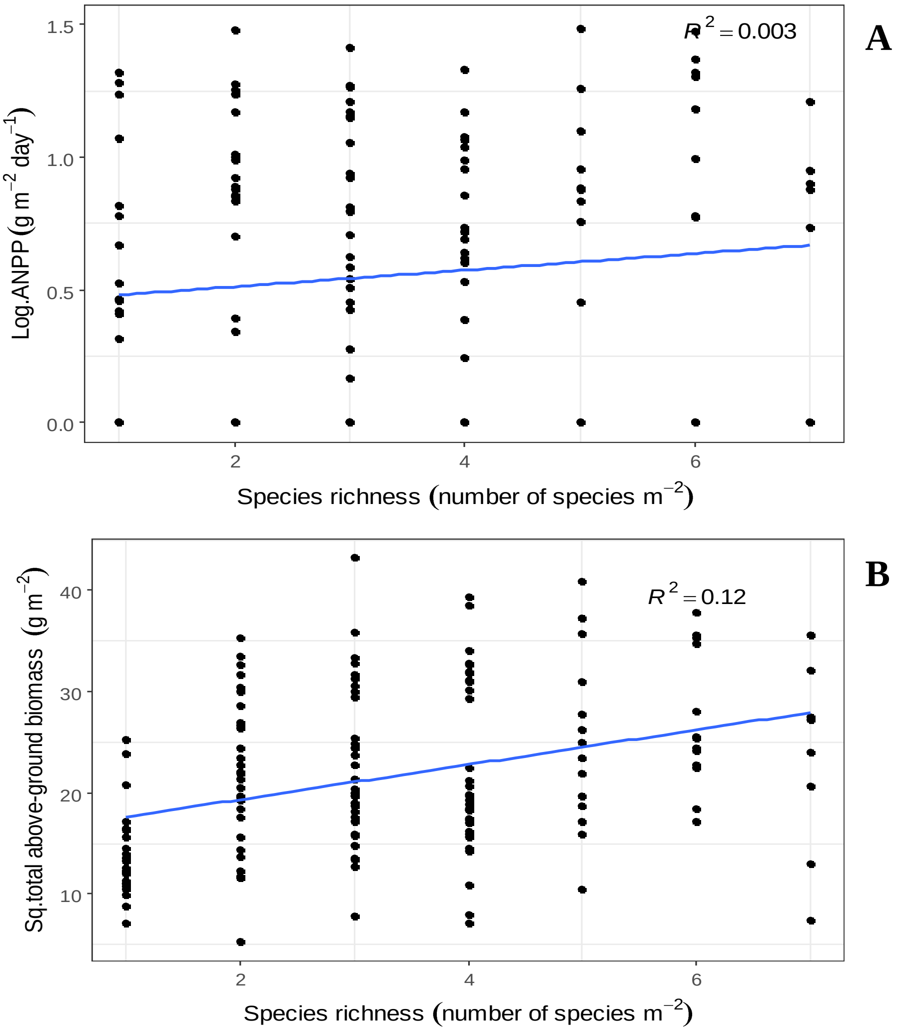

Figure 3-10 The association between transformed above-ground biomass, above-ground primary productivity and species richness.
A) The association between square root transformed above-ground biomass and species richness. **B)** The association between was no log transformed ANPP and species richness.

3.4.5 Seasonal daily temperature variation

There was a significant seasonal variation in daily temperature ($F_{3,\ 522}$= 187, *P* <0.001, Figure 3-11). Summer was significantly the warmest season over the sampling period (June 2014-July 2015) (19 °C , 95% CI, 18.8-20.1°C, Tukey test, P < 0.001) and winter the coldest (7.3 °C , 95% CI, 6.2 – 8.5 °C, Tukey test, P < 0.001). There was no significant difference in daily temperature between autumn and spring (Figure 3-11).

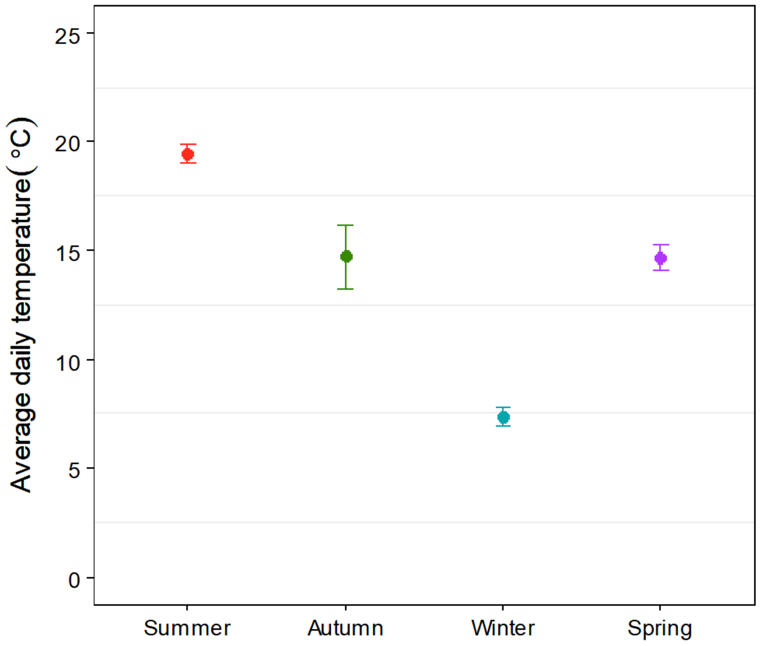

Figure 3-11 The average daily temperature during sampling period (June 2014-July 2015) at the three study sites. Values are mean value ± 95% confidence interval.
Number of the samples per season were similar and equal to 523 per season.

3.5 Discussion

In this section, first the saltmarsh higher plants diversity, their distribution at the three study sites, and the possible factors that impacted the observed plant distribution patterns are discussed. The higher saltmarsh plants distribution of the study sites in this research are also compared with the saltmarshes around Europe. The spatial and temporal above-ground biomasses, and the measured ANPP in this study, are also discussed.

3.5.1 Saltmarsh higher plant distribution

The distribution of the identified plants within saltmarshes are influenced by various factors such as salinity, inundation and plant root waterlogged tolerance, sediment characteristics and nutrient availability (Wood and Hine, 2007; Levine et al., 1998;

Adam 1993). Although these factors were not measured in this study, they could have influenced the saltmarsh higher plant distribution at the three study sites.

Spartina maritima was one of the dominant pioneer species at the low marsh at all the study sites. *S. maritima* was first recorded in Essex saltmarshes in 1666 by Merrett (Hubbard 1965). This pioneering species successfully grows at the low marsh due to its physiological characteristics (Reboreda and Caçador 2008). *S. maritima* root grows up to 45 cm deep in the sediment which allows this plant to establish itself at low marsh where exposure to tidal energy and immersion is highest (Reboreda and Caçador 2008; Yannic et al., 2004). *S. maritima* also has well developed aerenchyma (Reboreda and Caçador 2008) which facilitate oxygen transformation from the upper part of the plant to its root, thus this plant tolerates immersion longer than other saltmarsh plants (Reboreda and Caçador 2008). The bacteria living on the root of *Spartina maritima* by fixing nitrogen, facilitates the growth of this species in this harsh environment (Reboreda and Caçador 2008). *Spartina maritima* is important for saltmarsh formation because it traps, stabilizes and oxygenates the sediment and facilitates colonization by other saltmarsh plant species (Castillo et al., 2008; Yannic et al., 2004). Another key pioneering species found throughout the study sites is *Salicornia europaea* which is known to tolerate high salinity and inhabits saltmarshes across Europe (Ungar et al., 1979). *Salicornia europaea* accumulates sodium salt, mainly NaCl, in its tissues. Therefore, for osmoregulation, it absorbs and accumulates water in its lower leaves (Moghaieb et al., 2004).

Puccinellia maritima is also one of the key species that traps sediment in the UK and European salt marshes (Wolters, et al., 2005) which inhibits soil erosion at low marsh, mid marsh (Hughes 2004; Bouma et al., 2001; Esselink et al., 2000; Rozema 1996; Grey and Scott 1977) and sometimes high marsh (Ford et al., 2016). *P.*

maritima was common along the Colne river estuary. *P. maritima* also tolerates water-logged sediments and its roots produce a network within the sediment that bio stabilises the marsh, thus reduces erosion (Cooper 1982). The percentage cover of *P. maritima*, at Brightlingsea and Colne Point was higher than Wivenhoe. Wivenhoe is located at the upper Colne Estuary where the salinity is lower and the nitrogen concentration is higher than the mid (Brightlingsea) and lower estuary (Colne Point) (Nedwell et al., 2016). *P. maritima* is adapted to grow under high salinity (Cooper 1982) and its abundance decreases under high nitrogen concentration (Kiehl et al., 1997; Olff et al., 1997). Therefore, its higher abundance at Colne Point and Brightlingsea could be due to the suitable salinity and nutrient concentration at these two marshes.

Unlike *S. maritima* and *P. maritima*, *Atriplex portulacoides* cannot tolerate water-logging conditions due to its undeveloped aerenchyma and root systems that present up to 15 cm within the saltmarsh sediment (Bockelmann et al., 1999). Therefore, *A. portulacoides* is only found in relative high abundance within the upper marsh which experiences less inundation (Crook et al., 2002). *A. portulacoides* was a common species of Colne Point and Brightlingsea high marshes.

Aster tripolium was another observed species at the three study sites. Although *A. tripolium* is a halophyte, its growth is reduced under high saline conditions and it grows more rapidly under freshwater conditions (Geissler et al., 2009). *A. tripolium* can also grow in saline conditions by storing NaCl in its lateral roots and tissues that do not photosynthesise (Geissler et al., 2009). When salinity increases, it is also able to accumulate NaCl in its leaves and it closes the stomata to prevent water evaporation (Geissler et al., 2009). Under these conditions its growth decreases as does its competitive ability (Geissler et al., 2009). This reduced productivity may drive its differential distribution across the three sites with the highest abundance and stem height recorded at Wivenhoe.

The difference in the saltmarsh plant species variation between the study sites could be due to their locations along the estuary with different salinity and nutrient gradients. The concentration of N at the Colne Estuary can reach up to 1mM nitrate, which is high especially at the upper estuary due to overflow from the sewage treatment work (STW) near the Hythe Bridge (Nedwell et al., 2016). The nutrient concentration in the water column decreases from the upper estuary towards the mouth of the estuary which is due to daily mixing of sea water with the river water (Nedwell et al., 2016). *P. maritima* distribution along the Colne estuary could be an example of the impact of nutrient and salinity impact on plant species distribution at the study sites.

The Colne river salinity at Colne Point, Brightlingsea and Wivenhoe are: >30 ppt, 18-30 ppt and 5-18 ppt, respectively (Nedwell et al., 2016). *A. tripolium* had the highest percentage cover with the tallest stems at Wivenhoe, which has the lowest salinity of the study area. High water salinity inhibits *A. tripolium* growth and abundance (Geissler et al., 2009) as explained earlier.

Comparison between the study sites: There were species that were observed only in one study site. For example, *Cochlearia anglica* is a saltmarsh plant species that was only recorded at Colne Point high marsh. This species mainly grows on sandy substrate (Hepburn 1943). Colne Point is a coastal saltmarsh along the Colne Estuary. Generally coastal saltmarshes are exposed to relatively high wave energy and sandy sediment deposition (Dalrymple et al., 1992). It is possible that the localised hydrodynamics result in a habitat type, in particular a substratum that enables *C.*

anglica to successfully compete. Another species that was only observed at Colne Point was *Elymus pycnanthus*. *E. pycnanthus* grows at high marsh together with *A. portulacoides* in the saltmarshes of the Westerschelde estuary, SW Netherland (Rozema 1996; De Leeuw et al., 1990) and coastal saltmarshes in Italy (Landi and Angiolini, 2013). This species grows in coastal marshes where the substrate is sandy (Doing 1997). Therefore, *E. pycnanthus* inhabits at Colne Point possibly for the same reason as *C. anglica*.

One species that was limited to only one of the sites investigated was *Festuca rubra* which was only observed at Wivenhoe high marsh. The root system of this species cannot tolerate water-logged conditions which otherwise inhibits its growth (Cooper 1982). Due to the shape of the estuary (see the general methodology section 2.2.1.2), it is likely that the Wivenhoe marsh would be water-logged for a shorter time than Colne Point and Brightlingsea and therefore *F. rubra* is only able to exist in the site with least immersion.

Comparison with other studies: The higher plant species observed at the study sites along the Colne estuary, also inhabit in other estuaries in Europe. For example, Lefeuvre et al. (2000) and Bouchard and Lefeuvre (2000), studied the saltmarsh plant species diversity at the Mont Saint-Michel bay, France. The recorded saltmarsh plant species at Mont Saint-Michel bay, except from few species, were like those observed along the Colne Estuary in this study. However, the species distribution along the study sites of the Colne estuary was different to the Mont Saint-Michel marsh. The dominant species at Mont Saint-Michel low marsh was *P. maritima* and other species such as *A. tripolium*, *A. portulacoides*, *Salicornia spp*. and *Spartina anglica*[5] were also observed with significantly lower abundance (Lefeuvre et al., 2000; Bouchard

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[5] This species was not observed at the study sites along the Colne estuary.

and Lefeuvre, 2000). Similarly, at Colne Point and Brightlingsea low marsh *P. maritima* was also the dominant species.

Unlike the study sites along the Colne estuary, the mid marsh at Mont Saint-Michel was only dominated by *A. portulacoides* and the Mont Saint-Michel high marsh was covered by *Elytrigia aetherica* and *F. rubra* (Lefeuvre et al., 2000; Bouchard and Lefeuvre, 2000). The difference in species distribution at the study sites along the Colne Estuary and saltmarsh at Mont Saint-Michel could be due to the possible variation in the hydrology. For instance, Colne Point saltmarshes are subject to inundation twice per day (Nedwell et al., 2004) whereas at Mont Saint-Michel low, mid and high marsh inundation frequency decreased from 25 to 0.2% (Lefeuvre et al., 2000). This means that the saltmarshes at Mont Saint-Michel are occasionally inundated and also not all the saltmarshes from low marsh to high marsh are covered with tidal water.

The species richness measured at Colne Point, Brightlingsea and Wivenhoe were similar to what Ford et al. (2016) measured at the other Essex saltmarshes such as Abbotts Hall, Tillingham and Fingringhoe Wick (3.8-4.7 m^{-2}). The species richness and diversity of saltmarshes is influenced by tidal inundation, salinity and nutrient availability in the estuaries (Bernhardt et al., 2003). Abbotts Hall and Tillingham marshes are located at Blackwater Estuary which is a macro-tidal estuary with a similar salinity gradient to the Colne Estuary (Möller and Spencer, 2002). Fingringhoe Wick marsh is located within the Colne Estuary and it is therefore not surprising that the species richness and composition was within the same range as reported within this thesis. The mid-estuary peak in wetland plant species richness theory (Engels et al., 2010; Sharpe and Baldwin, 2009) could be a compatible theory for species richness at Colne Estuary study sites. Based on this theory, mid estuary has the optimal growth condition for most of the plant species in the estuary. Therefore, higher species richness at Brightlingsea (mid estuary) then the other two study sites could be explained by this theory.

The relationship between species richness and both ecosystem function and services such as ANPP and above-ground biomass are ambiguous (Hillebrand et al., 2008; Sullivan et al., 2007). Lefeuvre et al. (2000) and Gough et al. (1994) found a reverse relationship between above-ground biomass and species richness which is not compatible with the findings in this thesis. The highest species richness was at Brightlingsea. Above-ground biomass at this site was also higher than Wivenhoe (upper estuary). It is possible that the environmental conditions at Brightlingsea support both plant species richness and plant above-ground biomass production. Although the higher plant species richness at lower estuary was the same as the upper estuary, however the above-round biomass at low estuary site (Colne Point) was higher than the above-ground biomass at the site at the upper estuary. Therefore the reason for positive correlation between species richness and above-ground biomass in this study is unknown.

3.5.2 Above-ground biomass and ANPP

Spatial variation: In frequently submerged habitats such as saltmarshes, sediment plays an important role in providing nutrients for vegetation, because it is the primary source of N, P, Fe, Mg and other nutrients (Xie et al., 2007). According to Essex and Suffolk Shoreline Management Plan (2010), sedimentation at low (Colne Point) and mid estuary (Brightlingsea) is higher than upper estuary (Wivenhoe). Higher biomass at Colne Point and Brightlingsea may therefore result from the relative positions in the estuary and increased nutrient loading through sedimentation. Saltmarshes that are exposed to higher amount of sedimentation and higher tidal range have also higher above-ground biomass (Lefeuvre et al., 2000).

At Colne Point, the reason for the lack of spatial variation in above-ground biomass is not known. Unlike Colne Point, it appeared that the vegetation properties such as vegetation stem length and vegetation stem density, could be the drivers of spatial variation in above-ground standing biomass at Brightlingsea and Wivenhoe. For instance, at Brightlingsea, shorter vegetation cover at low marsh than mid marsh and high marsh could be the driver of lower above-ground standing biomass at this zone. Lower stem density results in less live standing above-ground biomass (Jackson et al, 1986). Therefore, the lower live standing biomass at Wivenhoe low marsh than other zones in that study sites, could be due to a lower stem density of grass, *S. maritima* than the vegetation cover at the two other zones. Curcó et al. (2002) concluded that woody vegetation cover at mid marsh contributed to higher live standing above-ground biomass. Therefore, in this study, higher live standing above-ground biomass at Wivenhoe mid marsh than the other zones in this site could be due to long and woody *A. tripolium* stems.

Seasonal variation: The seasonal changes of live above-ground biomass at the study sites were similar to previous work (Bouchard and Lefeuvre 2000; García et al., 1993; Hopkinson and Schubauer, 1984; Schubauer and Hopkinson, 1984), with higher amounts of live above-ground biomass over spring (Colne Point and Wivenhoe) or summer (Brightlingsea) followed by reduction over either autumn (Brightlingsea) or winter (Colne Point and Wivenhoe). The variation in above-ground biomass at saltmarshes are controlled by the physical condition (such as geographical location, location of the marsh along the coast or estuary and exposed tidal range) and nutrient availability (Laffoley and Grimsditch, 2009; Silliman et al, 2002), light, temperature

(Piao et al., 2015; Bauerle et al., 2012; Naidoo and Naicker, 1992) and plant phenology (Naidoo and Naicker, 1992). In temperate regions, after a cold winter plants need to accumulate heat to start leaf production in spring (Piao et al., 2015). Therefore, above-ground biomass increase from winter to spring could be due to the temperature rise in spring. Light regulates the plant growth and carbon sequestration by plant leaf in the northern hemisphere (Bauerle et al., 2012). In temperate regions of the northern hemisphere, the photoperiod decreases from summer to autumn (Bauerle et al., 2012). The shorter photoperiod during autumn, contributes to lower biomass production by plants (Bauerle et al., 2012). Therefore, the reduction of above-ground production over autumn, in this study here, could be due to shorter day length over autumn. The driver of different temporal variation in above-ground biomass between the study sites remains unknown.

Comparison with other sites: The ratio of live to dead above-ground biomass in this study was between 1.5:1 and 2.2:1, which was significantly higher than some other studies such as Schubauer and Hopkinson (1984), where this ratio was 0.24:1. Schubauer and Hopkinson (1984) measured live and dead above-ground biomass at a saltmarsh in Georgia (USA) where the study area was not covered by tidal water periodically, and thus organic matter, nutrients and minerals were not supplied to the marsh frequently (Schubauer and Hopkinson, 1984). Conversely, the Colne Estuary is a macro-tidal estuary where the study sites might be covered by tidal water frequently which could encourage substantial above-ground biomass and primary productivity (Lefeuvre et al., 2000).

The ANPP and above-ground biomass of study sites at Colne Estuary were higher than the literature (Table 3-2) which could be due to hyper-nutrification of the Colne estuary (Nedwell et al., 2016; Kocum et al., 2002; Ogilvie et al., 1997). The higher concentration of nutrients available to saltmarsh plants encourages increase in above-ground biomass and higher ANPP (Deegan et al., 2012; Darby and Turner, 2008; Morris et al., 2002).

The measured above-ground biomass of the current study was also higher than the above-ground biomass measured by Ibañez et al. (2000) (Table 3-2). The study sites of Ibañez et al. (2000) were located at micro-tidal lagoons where the marsh was not completely covered by tidal water. In addition, high soil salinity contributed to low above-ground biomass production in those marshes (Ibanez et al., 2000). Connor (1995) also measured the above-ground biomass and ANPP, applying peak standing biomass over May, July and October (Table 3-2). Due to the method used for measuring primary productivity, the ANPP and above-ground biomass at the Bay of Fundy measured by Connor (1995) were underestimated. In this thesis the above-ground biomass was measured monthly for a year. Therefore, the estimate of the above-ground biomass in this thesis could be more accurate than the listed studies above.

Table 3-2 The above-ground biomass and net above-ground primary productivity of other related studies.

AGB: Above-ground biomass; ANPP: above-ground net primary productivity: low, mid, high and upper high represent low marsh, mid marsh, high marsh and upper high marsh; DNA: data not available.

Location	species	AGB (g m^{-2})	ANPP (g $m^{-2} y^{-1}$)	Method for measuring AGB	Method for measuring ANPP	reference
Spain (Guadalquivir delta)	DNA	12.8 - 1268	DNA	Harvesting	DNA	García et al.,1993
France (Mont Saint- Michel) low	*Puccinellia maritima and Suaeda maritima*	580-780	1080	Harvesting	Smalley	Lefeuvre et al., 2000
France (Mont Saint- Michel) mid	*Atriplex portulacoides*	DNA	1000-2000	Harvesting	Smalley	Lefeuvre et al., 2000
France (Mont Saint- Michel) high	*Atriplex portulacoides*	DNA	1990	Harvesting	Smalley	Lefeuvre et al., 2000
France (Mont Saint- Michel) upper high	*Salicornia spp*	DNA	200-500	Harvesting	Smalley	Lefeuvre et al.,2000
Italy (Po Delta)	*Arthrocnemum macrostachyum*	683	DNA	DNA	DNA	Ibañez et al. 2000
Spain (Ebro Delta)	*Arthrocnemum macrostachyum*	190	DNA	DNA	DNA	Ibañez et al. 2000

Location	**species**	**AGB (g m^{-2})**	**ANPP (g $m^{-2} y^{-1}$)**	**Method for measuring AGB**	**Method for measuring ANPP**	**reference**
Spain (Ebro Delta)	*Arthrocnemum macrostachyum*	840	DNA	DNA	DNA	Ibañez et al. 2000
Spain (Ebro Delta)	*Salicornia fructosia*	580	DNA	DNA	DNA	Ibañez et al. 2000
Canada (Bay of Fundy)	*Plantago maritima*	465	296	Harvesting	Peak standing biomass	Connor 1995
Canada (Bay of Fundy)	*Spartina patens*	525	500	Harvesting	Peak standing biomass	Connor 1995
Canada (Bay of Fundy)	*Spartina alterniflora*	803	718	Harvesting	Peak standing biomass	Connor 1995
Colne Pont	See section 1.3.1.1	3172.9	2227	Harvesting	Smalley	This study
Brightlingsea	See section 1.3.1.1	3355.4	1565	Harvesting	Smalley	This study
Wivenhoe	See section 1.3.1.1	1995.2	1772	Harvesting	Smalley	This study

3.6 Conclusions

In total 16 higher plant species were identified across the three study sites. The saltmarsh higher plant compositions between the zones within the study sites were distinctively different. In addition, there was different in saltmarsh higher plant composition between the study site at upper, mid and low estuary. Furthermore, there were species of higher plants which were only recorded either at low estuary site or upper estuary site. It appeared that the location of the study site along the estuary and plant physiological characteristics to tolerate inundation, root water-logged condition, different salinity range and substrate features and nutrient, could be the driver of higher plant spatial variation between the sites and within each zone.

The species richness at the mid estuary (Brightlingsea) was higher than the low and upper estuary which could be explained by the mid-estuary peak theory.

The spatial variation in above-ground biomass between the study sites could be due to variation in sedimentation rate which requires further investigation. The location of the study site along the estuary and the vegetation characteristics such as plant height and stem density could be the drivers of spatial variation in above-ground biomass within each study sites. In addition, higher abundance of *P. maritima* at Colne Point and Brightlingsea than at Wivenhoe could be one of the drivers of higher above-ground biomass at these two sites than Wivenhoe. The variation in temperature and possibly photoperiod could have resulted in temporal changes in above-ground biomass within each study site.

The ANPP along the Colne estuary changed seasonally which could be due to variation in temperature and probably variation in photoperiod during the sampling year. The seasonal temperature increases from winter to spring, which encourages the plant root production which itself is essential for above-ground biomass production. During spring and summer, due to the longer photoperiod, plants will photosynthesise more than autumn and winter .Therefore, ANPP over spring and summer will be higher than the rest of the year.

4. Chapter four - Bio-Physiochemical characteristics and the standing organic carbon biomass of below- ground saltmarsh sediment

4.1 Introduction

Saltmarshes provide a variety of ecosystem services. These ecosystems act as natural coastal defences (Barbier et al., 2011; Bos et al., 2007). Saltmarsh plants root form networks that hold the saltmarsh sediment together therefore reducing coastal erosion (Callaway et al., 2012; Barbier et al., 2011; Bos et al., 2007; Kostka et al., 2002; Schubauer and Hopkinson, 1984). In addition, saltmarsh vegetation reduces the tidal water energy and contributes to coastal zone protection (Barbier et al., 2011; Bos et al., 2007). However, one of the ecosystem services that saltmarshes provide, which has been largely over looked, is their significant role as natural carbon sinks (Chmura et al., 2003).

Based on studies of the saltmarshes in north America, the total amount of carbon in the upper 50 cm of saltmarsh sediment is estimated to be 430 Tg (or 430 x 10^{12}g C) globally (Murray et al., 2011; Chmura 2009). As explained in Chapter 1 (1.2.1.3), it is believed that this figure is an underestimate of the carbon stored in the saltmarsh sediment (Chmura 2009) due to the following reasons; the depth of sediment storing carbon in saltmarshes is higher than 50 cm and could be up to 8 m (Chmura et al., 2003). Furthermore, due to the slow decomposition rate within saltmarsh sediment, the amount of organic carbon in the sediment does not change with sediment depth (Chmura 2009). In addition, the amount of carbon stored in saltmarshes in North

America was the main source for this estimation (Murray et al., 2011; Laffoley and Grimsditch, 2009). The European coastal zone has the highest concentration of saltmarshes globally (Murray et al., 2011). The saltmarshes in Europe are covered by different saltmarsh plant species to saltmarshes in North America which is due to different environmental condition between these systems (Adam 2002). Therefore, the sediment TOC content in saltmarshes in Europe and America could be different. However due to insufficient information regarding their sediment carbon content, European saltmarshes were not included in the estimation of global carbon stock (Murray et al., 2011). To estimate the total carbon stored in saltmarshes, it is essential to know their area cover (Murray et al., 2011). However, the aerial extent of saltmarshes is not documented in all the regions around the world (Murray et al., 2011; Chmura 2009). Therefore, the amount of carbon accumulated in the sediment of these habitats could not be estimated with high confidence (Laffoley and Grimsditch, 2009).

One of the important features of saltmarshes as carbon sinks is their feedback to climate change (Murray et al., 2011; Chmura 2009). One of the consequences of climate changes is sea level rise (SLR, see Kirwan et al., 2016; Kirwan and Guntenspergen, 2012; Simas et al., 2001). Due to SLR, saltmarsh inundation periods will increase as will sediment trapping (Kirwan et al., 2016; Kirwan and Guntenspergen, 2012; Simas et al., 2001). Sediment that contains nutrients and minerals encourages saltmarsh plant growth which results in higher carbon sequestration (Kirwan and Mudd, 2012). In addition, longer inundation periods also promote root production by saltmarsh plants (Kirwan and Guntenspergen, 2012; Kostka et al., 2002) and therefore increase the sediment organic carbon content within saltmarshes (Kirwan and Guntenspergen, 2012; Kostka et al., 2002) and increase bio stabilisation of entrapped sediment (Chen et al., 2012). Historically saltmarshes have not been detrimentally affected by SLR due to their vertical accretion (Kirwan and Guntenspergen, 2012). Studies of different SLR scenarios combined with physiobiological responses of saltmarshes to SLR, have highlighted that saltmarshes (apart from saltmarshes around Gulf of Mexico and Venice lagoon) will not submerge (Kirwan et al., 2016; Kirwan and Megonigal, 2013). Therefore, saltmarshes will continue to remain as significant natural carbon sinks (Kirwan and Mudd, 2012) unlike some other carbon sinks such as peatlands.

Saltmarshes absorb 210 g C m^{-2} y^{-1} which equals to 770 g CO_2 m^{-2} y^{-1} (Chmura 2009) compared to 20-30 g C m^{-2} y^{-1} absorption by Northern peatlands (Turunen et al., 2002, 2004; Gorham et al., 2003; Vitt et al., 2000; Gorham 1991). Northern peatland includes boreal and subarctic peatland (Gorham 1991). Boreal peatlands contribute to ~20% of methane emission to the atmosphere through anaerobic respiration (Olefeldt et al., 2017), while in contrast, saltmarshes produce negligible amounts of methane (Chmura 2009; Chmura et al., 2003). Because of the predicted temperature increases it is thought that the water content of peatlands will reduce (Pastor et al., 2003), causing a shift from anaerobic to aerobic respiration (Olefeldt et al., 2017). Consequently, due to aerobic respiration, the carbon stored in peatlands will be released into the atmosphere as CO_2 (Pastor et al., 2003). Therefore, due to climate change, including temperature rise, peatlands could convert from significant natural carbon sinks to considerable sources of CO_2 (Olefeldt et al., 2017; Pastor et al., 2003).

When the feedback of saltmarshes and peatlands to climate change are compared, the significance of the saltmarshes as natural carbon sinks and their importance to climate change adaptation is further highlighted. Therefore, it is important to measure the amount of carbon stored within saltmarshes precisely. At the international level, filling this knowledge gap is important because the amount of carbon accumulated in the saltmarshes is not yet included in the global carbon budget (Murray et al., 2011; Laffoley and Grimsditch, 2009). As the UK government has set a target of zero emission by 2050 (Osmani and O'Reilly, 2009), the knowledge of the amount of carbon accumulated in any natural carbon sinks within The UK such as saltmarshes, is important. In addition, the data generated in this thesis can be used to add to the international data base on sediment carbon content in saltmarshes.

4.2 Hypothesis, aims and objectives

Hypothesis $_1$: There will be a significant spatial variation in sediment TOC content within every study site due to the presence of two habitat types (vegetated and creek) and three zones (low marsh, mid marsh and high marsh).

Aim$_{1:}$ To investigate the difference in sediment TOC content within the two habitat types at each zone at each study site.

Objective$_1$: Samples will be collected from 3 zones (low, mid and high marsh) and with two habitat types (vegetated and creek) monthly for a year (see Chapter 2, sections 2.2.1.1 & 2.2.1.2).

Hypothesis$_2$: There will be a significant seasonal and spatial variation in the total organic carbon (TOC) content of the top 20 cm of sediment at study sites between the upper estuary (Wivenhoe), mid estuary (Brightlingsea) and lower estuary (Colne Point) with the highest sediment TOC content during summer.

Aim$_{2:}$ To measure the TOC content in the top 20 cm of sediment of all the three sites seasonally.

Objective$_2$: Sediment samples up to 20 cm depth will be collected monthly for a year, from Colne Point, Brightlingsea and Wivenhoe using PVC cores. After removing the inorganic carbon from the sediment samples, the TOC content of the collected samples will be measured by loss on ignition.

Objective$_3$: After sediment TOC been measured, the result will be then analysed to investigate the variation between the study sites.

Hypothesis$_{3:}$ There will be a significant spatial variation in the physiochemical characteristics of the sediment in the top 20 cm between Colne Point, Brightlingsea and Wivenhoe.

Aim$_{3:}$ To compare the spatial variation in the sediment bio-physiochemical characteristic in the top 20 cm of sediment between Colne Point, Brightlingsea and Wivenhoe.

Objective$_5$: Chlorophyll *a* content is one of the sediment biological characteristics. Consequently, during each monthly sampling effort, sediment samples will be collected to measure sediment chlorophyll *a* content of the top 0-2 cm of the sediment.

Objective$_6$: The chlorophyll *a* will be extracted by methanol from the 0-2 cm depth collected samples. The chlorophyll *a* content of every extracted solution will be measured by spectrophotometry.

4.3 Methodology

Study sites, zones and habitats are described in Chapter 2 section 2.2.1. The sampling design, sample collection, replication and sample date of collection are presented in sections 2.3 and 2.4.2 of Chapter 2, The measured variables in this chapter were not normally distributed. Therefore, the data were transformed to be analysed using a nested ANOVA. If any other test was used to analyse the data, it is mentioned in this chapter. The mean values and 95% confidence intervals of the data were calculated before back transformation. The presented data in this chapter, both in the figures and text, are in the form: mean ± 95% confidence intervals (CI, back transformed). In examining the association between the variables due to the assumption of linear regression test, the y or the dependant variables were transformed while the predictor or the x variables were not (Dytham 2011). The sediment carbon stock measured in this research was presented as sediment TOC content throughout the thesis and in the figures. Sediment %TOC and sediment carbon density were used to compare the values generated by this research to the relevant studies. The sediment TOC content is presented in Kg C m^{-2} through this chapter. However, to compare the measured values in this thesis with other studies, the measurement unit were changed to a suitable unit where applicable.

4.4 Results

4.4.1 TOC distribution at the three sites along the Colne Estuary

The sediment TOC content of the vegetated habitat at Colne Point (20 Kg C m^{-2}, 95% CI, 18-22 Kg C m^{-2}) and Brightlingsea (23 Kg C m^{-2}, 95% CI, 20-25 Kg C m^{-2}) was significantly higher than sediment TOC content of the vegetated habitat at Wivenhoe (13 Kg C m^{-2} , 95% CI, 12-14 Kg C m^{-2}, Tukey test, $P < 0.001$, see Figure 4-1).

In addition to vegetated habitat, there was a spatial variation in sediment TOC content in the creek habitat among the study sites. The sediment TOC content of the creek habitat at Brightlingsea (16 Kg C m^{-2}, 95% CI, 15-18 Kg C m^{-2}), was significantly higher than the sediment TOC content of the creek habitat at Colne Point (12 Kg C m^{-2}, 95% CI, 11-13 Kg C m^{-2}, Tukey test, $P < 0.001$) and Wivenhoe (10 Kg C m^{-2}, 95% CI, 9-10 Kg C m^{-2}, Tukey test, $P < 0.001$). The sediment TOC content in the Colne Point creek habitat was also significantly higher than the same habitat at Wivenhoe (Figure 4-1, Tukey test, $P < 0.05$).

At all the three sites, the sediment TOC content of the creek habitat was significantly lower than the vegetated habitat ($F_{5, 505} = 49.71$, $P < 0.001$). At Colne Point, sediment TOC content of the vegetated habitat was 41% higher than the creek habitat, at Brightlingsea, it was 29%, and at Wivenhoe it was 25% higher than the sediment TOC content of the creek habitat (Figure 4-1).

Due to the consistent differences of sediment TOC content between these two habitat types at the three sites, it was decided to investigate the seasonal and spatial variation of sediment TOC content by habitat type.

Figure 4-1 The sediment TOC content of the vegetated and the creek habitat within each site (Colne Point, Brightlingsea and Wivenhoe) along the Colne Estuary in the top 20 cm of sediment. Values are mean values ± 95% confidence interval (back transformed).
Each circle represents the result of seasonal sampling (4 seasons, spring, summer, autumn and winter) from one site with three zones, with three replicates. Colne Point; N vegetated habitat =94, N creek habitat = 55. Brightlingsea; N vegetated habitat = 102, N creek habitat =103.Wivenhoe; N vegetated habitat= 97, N creek habitat=67.

4.4.1.1 The seasonal and spatial variation of sediment TOC content in the vegetated habitat

In this section first the seasonal (Figure 4-2A) and then the spatial (Figure 4-2B) variation in sediment TOC content in the vegetated habitat of the three sites, are described.

Seasonal variation in sediment TOC content: In the vegetated habitat at Colne Point and Brightlingsea, there was significant seasonal variation in sediment TOC content throughout the year (Figure 4-2A, Tukey test, $P < 0.001$).

The sediment TOC content in the Colne Point vegetated habitat increased from spring (16 Kg C m^{-2}, 95% CI, 14-18 Kg C m^{-2}) to summer (29 Kg C m^{-2}, 95% CI, 24-35 Kg C m^{-2}, Tukey test, $P < 0.001$) and did not change between summer and autumn (Figure 4-2A).

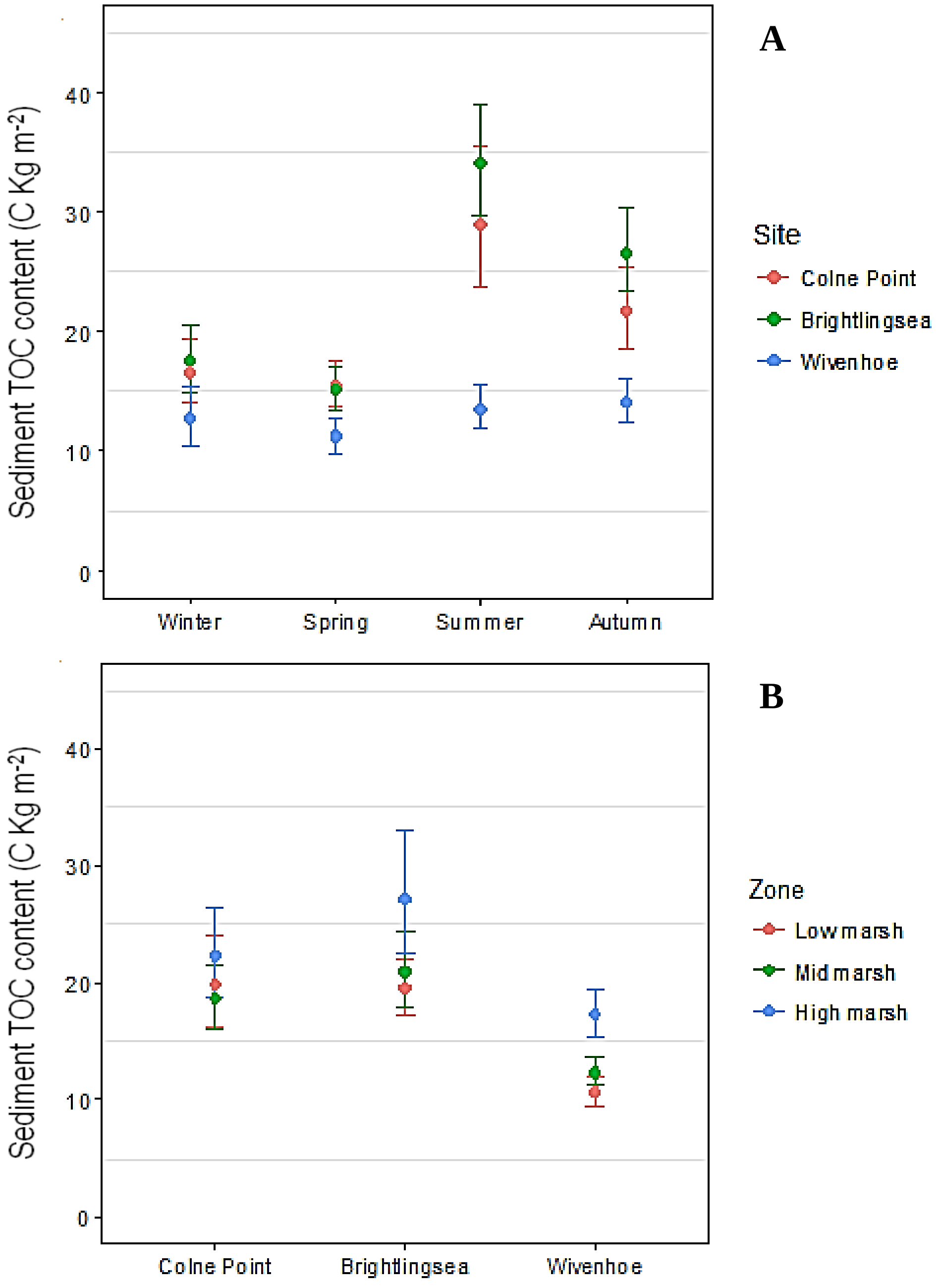

Figure 4-2 The seasonal and spatial variation of sediment TOC content of the vegetated habitat in the top 20 cm of the sediment of the three sampling sites (Colne Point, Brightlingsea and Wivenhoe). Values are mean values ± 95% confidence interval (back transformed).
A) Each circle represents number of seasonal samples (3 months) at each site with three zones, with three replicates. Colne Point; N spring=23, N summer=27, N autumn=18 and N winter= 26. Brightlingsea N spring=25, N summer=26, N autumn=24 and N winter= 27. Wivenhoe N spring=21, N summer=25, N autumn=28 and N winter= 23. **B)** Each circle represents number of 12-month sampling of sediment at the vegetated habitat at each zone within each site, with three replicates. Colne Point; N low marsh=30, N mid marsh=33, N high marsh=31. Brightlingsea N low marsh=36, N mid marsh=30, N high marsh = 36. Wivenhoe, N low marsh=34, N mid marsh=34 and N high marsh = 29.

At Brightlingsea, like Colne Point, sediment TOC content in the vegetated habitat increased from spring (15 Kg C m^{-2}, 95% CI, 13-17 Kg C m^{-2}) to summer (34 Kg C m^{-2}, 95% CI, 30-39 Kg C m^{-2}, Tukey test, $P < 0.001$) and did not change significantly from summer to autumn (Figure 4-2A).

Sediment TOC content at Wivenhoe vegetated habitat did not change seasonally (Figure 4-2A) ranging from 10 Kg C m^{-2} to16 Kg C m^{-2}.

Over summer, the sediment TOC content in the vegetated habitats at Colne Point (29 Kg C m^{-2} , 95% CI, 24-35 Kg C m^{-2}) and Brightlingsea (34 Kg C m^{-2} , 95% CI, 30-39 Kg C m^{-2}) were 52% and 59% higher than the sediment TOC content in the vegetated habitat at Wivenhoe (14 Kg C m^{-2} , 95% CI, 12-16 Kg C m^{-2}, Tukey test, $P < 0.001$) respectively (Figure 4-2A).

Furthermore, during autumn, sediment TOC content in the vegetated habitat at Colne Point (22 Kg C m^{-2}, 95% CI,18.5-25 Kg C m^{-2}) and at Brightlingsea (27 Kg C m^{-2}, 95% CI, 23-30 Kg C m^{-2}) was 53% and 88% higher than the sediment TOC content of the vegetated habitat at Wivenhoe, respectively (14 Kg C m^{-2}, 95% CI, 12.5-16 Kg C m^{-2}, Tukey test, $P < 0.001$).

The spatial variation in sediment TOC content within the vegetated habitat: In the vegetated habitat, there was a significant site and zone interaction ($F_{10, 502} = 5.05$, $P < 0.001$) which implies that the sediment TOC content changes in each zone at each study site, was different to the same zone at the other study site (Figure 4-2B).

The spatial variation in sediment TOC content in the vegetated habitat within each site was examined first. In the Colne Point vegetated habitat, there was no spatial variation in sediment TOC content (Figure 4-2B). At Brightlingsea high marsh (27 Kg C m^{-2}, 95% CI, 22-33 Kg C m^{-2}) sediment TOC content was higher than the low marsh (20 Kg C m^{-2}, 95% CI, 17-22 Kg C m^{-2}, Tukey test, $P < 0.05$).

At Wivenhoe, similar to Brightlingsea, sediment TOC content in the vegetated habitat high marsh (17 Kg C m^{-2} , 95% CI, 15-19 Kg C m^{-2}) was significantly higher than in the low marsh (11 Kg C m^{-2} , 95% CI, 9.5-12 Kg C m^{-2}) and the mid marsh (12 Kg C m^{-2} , 95% CI, 11-14 Kg C m^{-2}, Tukey test, $P < 0.001$, Figure 4-2B).

For the next level of the analysis, sediment TOC content of the low marsh, mid marsh and the high marsh were compared across the sites. In the vegetated habitat, sediment TOC content in the low marsh at Wivenhoe (11 Kg C m^{-2}, 95% CI, 9.5-12 Kg C m^{-2}) was 85% lower than the sediment TOC content of the low marsh at Colne Point (20 Kg C m^{-2} , 95% CI, 16-24 Kg C m^{-2}, Tukey test, $P < 0.001$) and the low marsh at Brightlingsea (20 Kg C m^{-2} , 95% CI, 17-22 Kg C m^{-2}, Tukey test, $P < 0.001$).

Furthermore, in the same habitat, sediment TOC content of the mid marsh at Wivenhoe (12 Kg C m^{-2} , 95% CI, 11-14 Kg C m^{-2}) was 50.6% lower than the sediment TOC content at the mid marsh at Colne Point (16 Kg C m^{-2} , 95% CI, 19-21 Kg C m^{-2}, Tukey test, $P < 0.001$) and 73% lower than Brightlingsea mid marsh (21 Kg C m^{-2} , 95% CI, 18-24 Kg C m^{-2}, Tukey test, $P < 0.001$, Figure 4-2B).

In addition, the sediment TOC content of the vegetated habitat, at Brightlingsea high marsh (27 Kg C m^{-2}, 95% CI, 22-33 Kg C m^{-2}) was 35.5% higher than the sediment TOC content at Wivenhoe high marsh (17 Kg C m^{-2}, 95% CI, 15-19 Kg C m^{-2}, Tukey test, $P < 0.001$).

4.4.1.2 The seasonal and spatial variation of sediment TOC content in the creek habitat

In this section, as in the previous section, first the seasonal variation in sediment TOC is described then the spatial variation in sediment TOC content in the creek habitat.

Seasonal variation of sediment TOC content in the creek habitat: At Brightlingsea, sediment TOC content of the creek habitat increased by 56% from spring (11Kg C m^{-2}, 95% CI, 10-13 Kg C m^{-2}) to summer (25 Kg C m^{-2}, 95% CI, 21-30 Kg C m^{-2}, Tukey test, $P < 0.001$). It then dropped by 31.5% from summer to autumn (17 Kg C m^{-2}, 95% CI, 15-19 Kg C m^{-2}, Tukey test, $P < 0.05$, Figure 4-3A).

The seasonal variation of sediment TOC content across the sites was also investigated (**Error! Reference source not found.**). Over summer, creek habitat sediment TOC content at Brightlingsea (25 Kg C m^{-2} , 95% CI, 21-30 Kg C m^{-2}) was higher than sediment TOC content at Colne Point (15 Kg C m^{-2} , 95% CI, 12-18 Kg C m^{-2}), Tukey test, $P < 0.01$) and Wivenhoe (10 Kg C m^{-2} , 95%CI, 10-11 Kg C m^{-2}, Tukey test, $P < 0.001$, Figure 4-3A).

During autumn, the sediment TOC content in the creek habitat at Brightlingsea (17 Kg C m^{-2} , 95% CI, 15-19 Kg C m^{-2}) was 60% higher than the sediment TOC content at Wivenhoe (10 Kg C m^{-2} , 95% CI, 9-11.5 Kg C m^{-2}, Tukey test, $P < 0.001$, Figure 4-3A).

The spatial variation in the creek habitat sediment TOC content: The sediment TOC content of the creek habitat at Brightlingsea low marsh (17 Kg C m^{-2}, 95% CI, 15-19 Kg C m^{-2}) was 47% higher than the sediment TOC content at Wivenhoe low marsh (9 Kg C m^{-2}, 95% CI, 8 to 9 Kg C m^{-2}, Tukey test, $P < 0.001$).

The sediment TOC content in the creek habitat at Brightlingsea high marsh (17 Kg C m^{-2}, 95% CI, 14-21 Kg C m^{-2}) was 33.5% higher than the sediment TOC content at Colne Point high marsh (11 Kg C m^{-2}, 95% CI, 10-13 Kg C m^{-2}, Tukey test, $P < 0.05$, Figure 4-3B).

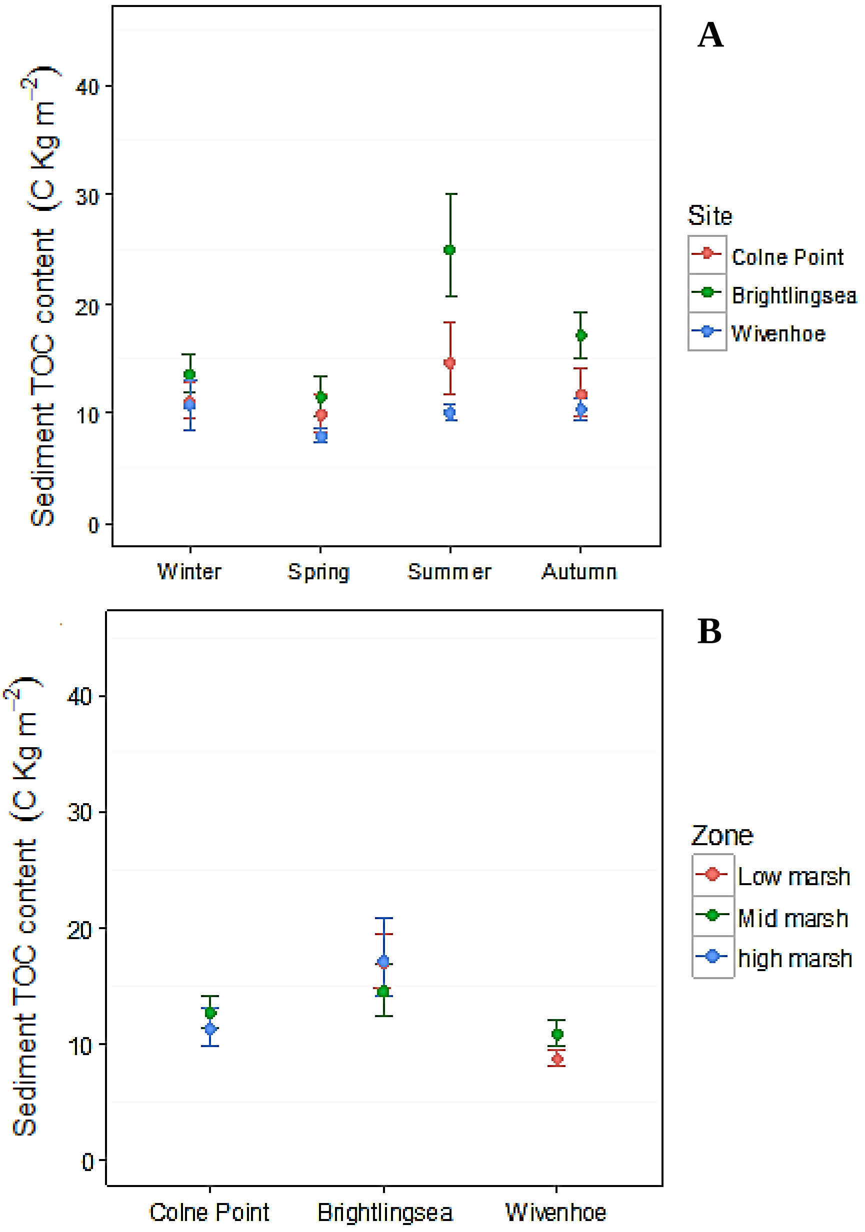

Figure 4-3 The seasonal and spatial variation of sediment TOC content of the creek habitat the in the top 20 cm of the sediment of the three sampling sites (Colne Point, Brightlingsea and Wivenhoe). Values are mean values ± 95% confidence interval (back transformed).
A) Each circle represents number of seasonal sampling (3 months) at each site with three zones, sampling and three replicates. Colne Point; N spring=13, N summer=16, N autumn=9 and N winter= 17. Brightlingsea N spring=25, N summer=27, N autumn=24 and N winter= 27. Wivenhoe N spring=17, N summer=17, N autumn=17 and N winter= 16.**B)** Each circle represents number of 12-month sampling of sediment at the creek habitat at each zone within each site, with three replicates. Colne Point; N mid marsh=28, N high marsh=27. Brightlingsea N low marsh=33, N mid marsh=35, N high marsh = 35. Wivenhoe, N low marsh=33and N mid marsh=34.

4.4.2 Bio-Physiochemical sediment characteristics along the Colne Estuary

Apart from sediment TOC content, other sediment properties such as the chlorophyll *a* content of the 0-2cm of the sediment profile and bulk density of the 0-20 cm sediment depth were measured. The spatial and temporal variation of sediment chlorophyll *a* content is presented below.

4.4.2.1 The chlorophyll *a* content of the 0-2 cm of the sediment profile

There was a significant site and habitat interaction ($F_{12, 494}$=3.96, $P < 0.001$) in chlorophyll *a* content (Figure 4-4). The sediment chlorophyll *a* (chl *a*) content in the creek habitat at Colne Point (30 µg chl *a* g^{-1} sediment DW, 95% CI, 25-36 µg chl *a* g^{-1} sediment DW) and Brightlingsea (29 µg chl *a* g^{-1} sediment DW, 95% CI, 26-33 µg chl *a* g^{-1}sediment DW) was 33% and 22% higher than chl *a* of the vegetated habitat of both stations (19 µg chl *a* g^{-1} sediment DW, 95% CI, 16-22 µg chl *a* g^{-1} sediment DW) and (23 µg chl *a* g^{-1}sediment DW, 95% CI, 20-27 µg chl *a* g^{-1} sediment dry weight respectively, Tukey test, $P < 0.05$, Figure 4-4).

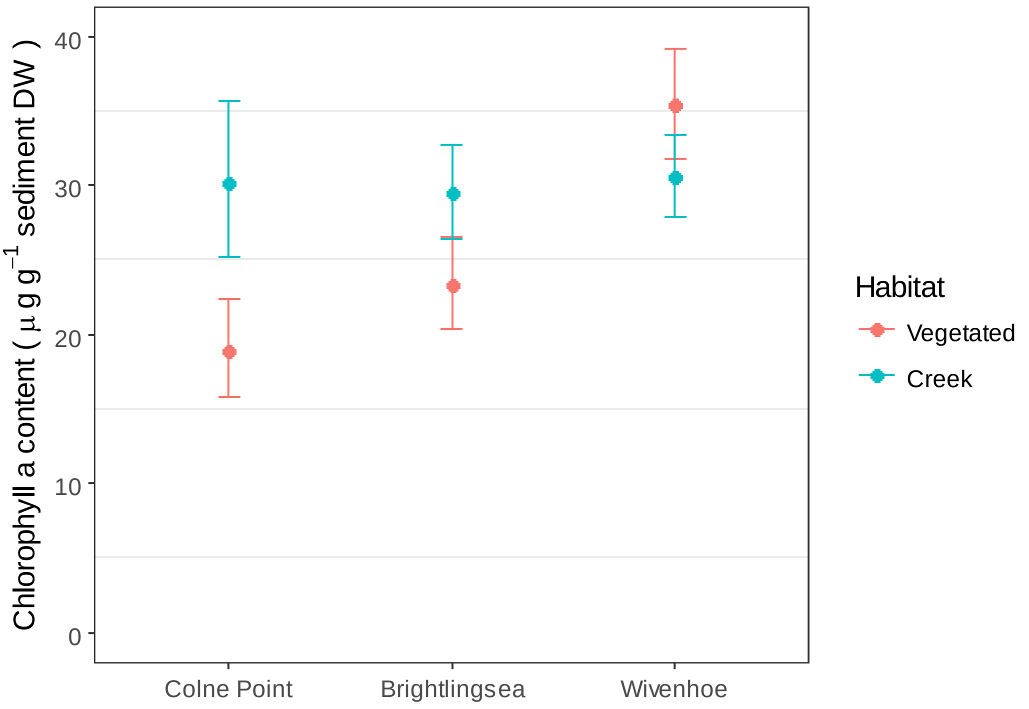

Figure 4-4 The chlorophyll *a* content of the top 0-2 cm of the vegetated and the creek habitat (back transformed).
Each circle represents the result of seasonal (3 months) sampling from each site with three zones, and with three replicates. Colne Point; N vegetated habitat =94, N creek habitat = 55. Brightlingsea; N vegetated habitat = 102, N creek habitat =103.Wivenhoe; N vegetated habitat= 97, N creek habitat=67.

There was no seasonal variation in sediment chlorophyll *a* content within the two habitat types at any of the study sites.

4.4.2.2 The association between sediment TOC content and chlorophyll *a*

The association between sediment TOC content and chlorophyll *a* content was examined (Figure 4-5). There was no significant relationship between sediment TOC content and chlorophyll *a* content.

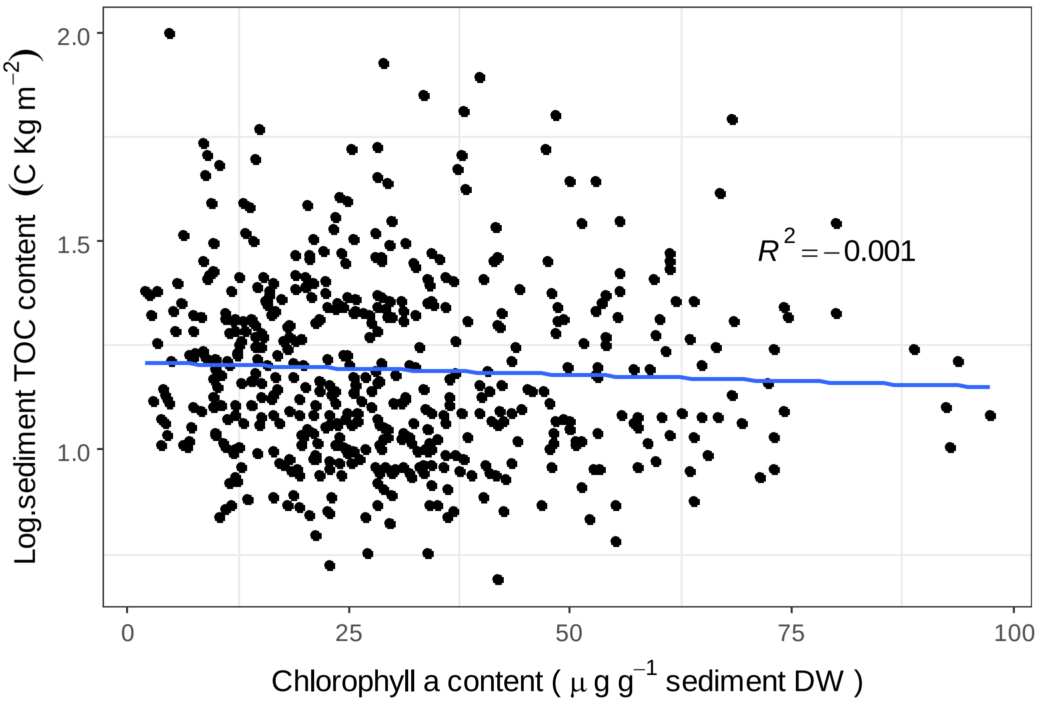

Figure 4-5 The association between transformed values of sediment TOC content and sediment chlorophyll *a* content.

4.5 Discussion

Comparison between the two habitat types: In this study, the sediment TOC content in the vegetated habitat was consistently higher than the creek habitat. This is likely due to the significant role of saltmarsh plants as sources of primary productivity (Howes et al, 1980; Valiela et al., 1976). The sediment TOC content within saltmarshes is due to allochthonous and autochthonous sources (Saintilan et al., 2013). Saltmarsh plants and biofilm communities contribute to the autochthonous sources of sediment TOC content through primary productivity (Callaway et al., 2012; McKew et al., 2011; Choi et al., 2001; Ember et al., 1987). In addition, biofilm communities contribute to sediment TOC through the production of extracellular polymeric substance (EPS), and saltmarsh plants by their root system (Middelburg et al., 1997; Gerdol and Hughes, 1994). In addition, saltmarsh plant roots (during growth after being decomposed) add TOC to saltmarsh sediment (Kostka et al., 2002). Furthermore, plant root systems and the EPS produced by biofilm communities on saltmarsh sediment, reduce saltmarsh sediment shear stress, which reduces saltmarsh erosion and consequently protects accumulated TOC within the saltmarsh sediment (Middelburg et al., 1997; Gerdol and Hughes, 1994). Saltmarsh plant litter when being decomposed is buried in sediment as another source of autochthonous TOC (Callaway et al., 2012; Curcó et al., 2002; Choi et al., 2001; Middelburg et al., 1997; Hemming et al, 1991; Ember et al., 1987). Saltmarsh plants also reduce the tidal water velocity and hydrodynamic energy, increasing sediment trapping from the water column (Bos et al., 2007). The sediment trapped from the water column by the marsh vegetation is one of the allochthonous sources of TOC in the vegetated habitat (Yang et al, 2008). In addition, the sediment TOC that is accumulated in the vegetated habitat sediment is less susceptible to being removed from the marsh surface by wave action (Kostka et al., 2002). Therefore, saltmarsh plants are likely to be the key influence on sediment TOC content in the vegetated habitat. All the above factors could help explain the higher sediment TOC content at the vegetated habitat than the creek habitat. Although there was no significant correlation between sediment chlorophyll *a* content and sediment TOC content in this study, the contribution of biofilm to nutrient cycle and saltmarsh plant retention (Aspden et al., 2004) cannot be ignored.

Sediment TOC content spatial variation: The sediment TOC content in the two habitat types at Wivenhoe was significantly lower than sediment TOC content in these habitat types at Colne Point and Brightlingsea. This is likely to be due to the location of the sites within the Colne Estuary. The Colne estuary is a macro-tidal and a funnel shape estuary (Essex and South Suffolk Shoreline Management Plan 2, 2010; Kocum et al., 2002). This estuary is dominated by ebb waves and the currents have higher amplitude towards the upper estuary (Essex and South Suffolk Shoreline Management Plan 2, 2010). Thus, the high-energy waves at the upper estuary remove sediment from that area causing erosion of sediment containing TOC in the upper estuary (Essex and South Suffolk Shoreline Management Plan 2, 2010). Conversely the mouth and the lower estuary experiences accretion which is supported by the sediment load brought to the sheltered areas by wave action (Essex and South Suffolk Shoreline Management Plan 2, 2010). While one of the main source of TOC in saltmarshes is sedimentation (Yang et al., 2008; Nyman et al., 2006; Chmura et al., 2003), it is possible that the higher TOC content in Colne Point and Brightlingsea vegetated and creek habitats than in Wivenhoe was due to sediment accretion at the two lower estuary sites and sediment loss at Wivenhoe. In addition to sedimentation, excess nutrients - especially nitrogen- at the upper Colne estuary (Nedwell et al., 2016) could also contribute to the lower sediment TOC concentration at Wivenhoe saltmarsh. High concentrations of nutrients - especially nitrogen- prevent root formation in saltmarsh plants (Langley et al., 2015). The Colne estuary is a eutrophic estuary with high concentration of nitrate, up to 1 mM in the water (Nedwell et al., 2016). The nutrient concentration decreases from upper estuary towards the lower estuary at the Colne River (Nedwell et al., 2016). Due to the impact of high nutrient concentrations on saltmarsh plant root formation (Langley et al., 2015), it could be possible that root formation at Wivenhoe was lower than Colne Point and Brightlingsea. Therefore, it is possible that plant root formation at Wivenhoe is lower than Colne Point and Brightlingsea. Consequently, the sediment TOC content is lower at Wivenhoe than Colne Point and Brightlingsea (as found by Morris and Bradley 1999).

The spatial variation in sediment TOC content within each study site was likely to be caused by a combination of environmental setting, sedimentation and saltmarsh plant contribution. Within each study site, sediment TOC distribution in respect to zonation was different. This finding highlights the complexity of the saltmarsh ecosystem as mentioned by Adam (2002). Some of the factors that could impact the spatial variation of sediment TOC content within each site could be plant stem density and stem height, which have a positive impact on sediment trapping and consequently sediment TOC content (Bos et al., 2007; Bouma et al., 2007; Zedler and Callaway, 1999). When the tidal water reaches saltmarshes with high stem density and long stems, the architecture of the plants results in velocity gradients which facilitates deposition, accretion and organic carbon accumulation in the vegetated habitat (Bos et al., 2007; Klemm et al., 2006; Bouma et al., 2005). However, the driver or the drivers of the spatial variation in sediment TOC content in the vegetated habitat at each site remains unknown.

Temporal variation in sediment TOC content: Although extensive studies have been conducted on spatial variability of sediment carbon concentration in saltmarshes, the temporal variation of sediment carbon saltmarsh pools remains underexplored (Bauer et al., 2013; Callaway et al., 2012; Zhou et al., 2007). Saltmarsh vegetation clearly is important for sediment TOC content in these ecosystems. As saltmarsh vegetation characteristics (e.g. primary productivity, stem height) changes seasonally, it stands that sediment TOC content might also vary seasonally. The seasonal changes in sediment TOC content in the vegetated habitat at saltmarshes is likely to be due to saltmarsh plant root production (Callaway et al, 2012; Kostka et al, 2002; Schubauer and Hopkinson, 1984). In this thesis, sediment TOC content during spring was at its lowest in the vegetated habitat at Colne Point and Brightlingsea whereas the above-ground standing live biomass was high (Chapter 3). Spring (around mid to late March) is the start of the growth season of the saltmarsh plants, when the above ground production by salt marsh plants is at its highest (Schubauer and Hopkinson,1984) and root production is still low (Darby and Tuner 2007; Schubauer and Hopkinson, 1984). In 2013, it snowed from mid to late March over the study sites. Due to lack of soil insulation, late snow or frost at end of winter or early spring, could result in plant root growth reduction (Bokhorst et al., 2012). Therefore, the maximum below-ground biomass and root formation at the study sites could be over summer (as seen in Darby and Turner 2007). Over summer, root growth increases (Callaway et al, 2012; Darby and Turner 2007; Kostka et al, 2002; Schubauer and Hopkinson, 1984) which results in higher sediment TOC content in the vegetated habitat (Callaway et al, 2012; Kostka et al, 2002). In this study, the root production was not measured directly, however the sediment samples contained saltmarsh plant root biomass when sediment TOC was measured. Therefore, the increase in sediment TOC content from spring to summer at Colne Point and Brightlingsea may have been due to increase in root production between spring and summer.

The sources of sediment TOC content in the creek habitat are marine phytoplankton, the epipelic community, organic carbon distributed from the vegetated habitat and organic carbon particles from freshwater sources (Childers and McKellar, 1987; Ember et al., 1987). In this study, the sediment chlorophyll *a* content did not change seasonally. In addition, it was only at Brightlingsea where the sediment TOC content in the creek habitat changed seasonally. In contrast, the sediment TOC content in the creek habitat at Wivenhoe and Colne Point remained unchanged over the year. Therefore, the driver of seasonal changes of the sediment TOC content in the creek habitat in this study cannot be explained.

Comparison with other studies: To allow a comparison to other studies, the sediment TOC content values obtained in this research are presented in different units only in this section. In a related study, the spatial variation of sediment carbon density in the vegetated habitat of the saltmarshes at the Venice lagoon, Italy, was measured (Roner et al., 2016). The sediment TOC density in Roner et al. (2016) study was 0.044 g C cm^{-3} which was lower than the range of the estimates in this thesis (0.06 - 0.15 g C cm^{-3}). The higher amount of sediment carbon density in the saltmarshes at Colne Estuary may have been due to the estuary tidal regime. The Colne Estuary has a macro-tidal regime (Essex and South Suffolk Shoreline Management Plan 2, 2010; Kocum et al., 2002) whereas the Venice lagoon is a micro-tidal regime (Roner et al., 2016). Micro-tidal regimes do not cover all the marshes thus the tidal water does not provide sediment and nutrients to the whole marsh (Kearny and Turner, 2016). In saltmarshes, sedimentation contributes to marsh vertical accretion (Ganju et al., 2017). In addition, sediment is the main source of N, P, Fe, Mg and other nutrients for saltmarsh plants (Xie et al., 2007). Therefore, in a micro-tidal marsh, where the marsh does not receive as large a sediment load, saltmarsh plants will not grow, or will die due to insufficient available nutrients (Ganju et al., 2017; Xie et al., 2007). Therefore, unvegetated areas develop on the micro-tidal marsh (Ganju et al., 2017). Consequently, due to reduction of vertical accretion and vegetation cover, micro-tidal marshes are susceptible to erosion (Ganju et al., 2017; Kearney and Turner, 2016). Conversely the tides in macro-tidal areas cover all the marsh area (Abril et al., 1999). In addition, saltmarsh in Venice lagoon is an eroding marsh (Kirwan et al., 2016; Kirwan and Guntenspergen, 2012; Day et al., 1999). Sediment TOC content at eroded saltmarshes decreases over time (Mudd and Fagherazzi 2016).

The spatial distribution of sediment carbon density in two reclaimed saltmarshes at the outer bay (0.042 g C cm^{-3}) and upper bay (0.036 g C cm^{-3}) of the Bay of Fundy estuary in the Canada was also previously investigated (Connor et al., 2001). While the Bay of Fundy and the Colne Estuary are both macro-tidal estuaries (Essex and South Suffolk Shoreline Management Plan 2, 2010; Connor et al., 2001), the range of sediment carbon density in the three sites at the Colne Estuary (0.06 - 0.15 g C cm^{-3}) was higher than the sites at the Bay of Fundy. However, the saltmarshes in the Bay of Fundy were reclaimed marshes (Connor et al., 2001) whereas the three sites at Colne Estuary were natural mature marshes (Essex and South Suffolk Shoreline Management Plan 2, 2010). Due to the high nutrient concentration in reclaimed marshes, the carbon storage capacity of the reclaimed marshes is 50% lower than natural salt marshes (Santin et al., 2009). High nutrient concentration in the saltmarsh sediment prevents root production by saltmarsh plants. Saltmarsh plant roots contribute to saltmarsh sediment carbon density (Langley et al., 2015; Kostka et al., 2002). Therefore, less root production by saltmarsh plants in reclaimed land contributes to lower sediment carbon density than natural marsh.

Choi and Wang (2004) studied the spatial distribution of sediment TOC inventories of the upper 50 cm of sediment in coastal saltmarshes within the St. Marks National Wildlife Refuge of north western Florida. The sediment TOC content in low marsh, mid marsh and high marsh in those saltmarshes were 25 $\pm$ 4 Kg C m^{-2}, 10 $\pm$ 5 Kg C m^{-2} and 10 $\pm$ 6 Kg C m^{-2} (Choi and Wang, 2004). The sediment carbon content of the three saltmarshes in the Colne Estuary (10-20 Kg C m^{-2}, 11.5-17 Kg C m^{-2} and 16-21 Kg C m^{-2} in the low marsh, mid marsh and the high marsh respectively) was within the higher range of sediment carbon content in the Choi and Wang (2004) study. This could be because the Colne Estuary is a macro-tidal estuary whereas the studied saltmarshes by Choi and Wang (2004) were not macro-tidal (Choi and Wang, 2004). This study represents data obtained from monthly sampling from two habitat types within three zones at three sampling sites. Therefore, the spatial and temporal variability of sediment TOC content at the studied sites of this research are captured by collecting over 500 sediment cores over a year. Conversely, Choi and Wang (2004) only examined spatial variability of sediment TOC content in Florida saltmarshes with 17 sediment cores. Therefore, it is more probable that the true variability and representative values were obtained in this present research. The spatial variation in the sedimentation rate was the reason for the spatial variation of carbon content across the saltmarshes in Florida (Choi and Wang, 2004). In this present study, sedimentation rate could be the driver of spatial variation in sediment TOC content between the study sites.

The range of sediment organic carbon estimated for Colne Point, Brightlingsea and Wivenhoe saltmarshes (0.06 - 0.15 g C cm^{-3}) was comparable with the results obtained by Chmura et al. (2003) for saltmarshes in Rhone Delta in France (0.073 g C cm^{-3}), Marsh Island Refuge and Rockefeller Wildlife Refuge in Louisiana (0.012-0.190 g C cm^{-3}), and higher than the Dengie Marsh and Hut marsh in the UK (0.041 g C cm^{-3} and 0.027g C cm^{-3} respectively), Skalingen marsh in Denmark (0.021- 0.027 g C cm^{-3}), Scheldt and St. Annalands in the Netherlands (0.020- 0.029 g C cm^{-3} and 0.041 respectively). Consequently, the measured sediment TOC content at the study sites along the Colne estuary was within the range of other studied saltmarshes. However, the estimated average sediment TOC content in the upper 20 cm at Colne Point and Brightlingsea saltmarshes vegetated habitat (20.1 Kg C m^{-2} and 22.33 Kg C m^{-2} respectively) were slightly higher than the average of TOC content in top the 1m of the soil across the UK (18 Kg C m^{-2}, Bradley et al., 2005). This could highlight the importance of saltmarshes at Colne Point and Brightlingsea as significant natural carbon sinks at a national and international scale.

The sediment TOC content in the creek habitats along the three study sites were compared with sediment carbon content of mudflats. Cook et al. (2004) investigated the carbon and nitrogen cycle in two mudflats in the Huon Estuary, Australia. The sediment TOC content within those mudflats was at its highest over autumn (6.5%) and spring (7.5%) at the upper mudflat (Cook et al., 2004). The range of sediment TOC content at the creek habitat of the three sites in the Colne Estuary in this study was found to be 7.81% to 15.35% C DW^{-1} sediment. Because the velocity of the tidal water in the tidal creeks is higher than for mudflats (Palmer and Gusf, 1985) it was expected that sediment TOC % in the mudflat in Cook et al. (2004) to be higher than the creeks in this current thesis. The sources of sediment TOC content at mudflats and tidal creeks are discharge of anthropogenic organic matter, microphytobenthos and biofilm primary productivity (Fernandes and Nayak, 2015; Cook et al., 2004; Childers and McKellar, 1987; Ember et al., 1987), and the organic carbon discharged from plant roots (Childers and McKellar, 1987; Ember et al., 1987). Therefore, the variation in these sources could be drivers of sediment TOC content variation the creek habitat between this study and that of Cook et al. (2004). In addition, the difference in sedimentation between the Huston estuary (a micro-tidal estuary, see Butler 2006) and the Colne estuary (a macro-tidal estuary, see Essex and South Suffolk Shoreline Management Plan 2, 2010; Kocum et al., 2002) could be a driver of the variation in sediment TOC content between the sites.

The sediment TOC % of a mudflat at the upper Bay of Fundy (0.3 -1.5%, see Cammen and Walker, 1986) was lower than the measured sediment TOC % in the creek habitats examined in this thesis (7.81% to 15.35% C DW^{-1} sediment). The intertidal mudflat at the Bay of Fundy is an important habitat for *Corophium voluntator*, an infaunal amphipod (Carriere-Garwood 2014; Pearson and Gingeriest, 2006; Murdoch et al., 1986). *C. voluntator* is a deposit feeder that grazes bacteria and diatoms which consequently reduces the biofilm and chlorophyll *a* content in the mudflat (Smith et al., 1996; Gerdol and Hughes, 1994; Murdoch et al., 1986). The microphytobenthos in biofilm produce EPS which is very important in stabilizing the sediment and in reducing sediment erosion within in mudflat environments (Hagerthey et al., 2002; Smith and Underwood, 1998). Biofilm could be removed from the sediment surface by *C. voluntator* grazing (Smith et al., 1996, Stal et al., 2003). Therefore, the shear strength of the sediment decreases in presence of *C. voluntator* which could contribute to sediment erosion (Gerdol and Hughes, 1994) and consequently, could result in the reduction of sediment TOC content (Mortimer et al., 1999). It was concluded by Cammen and Walker (1986) that the high sediment respiration and low concentration of chlorophyll *a* contributed to the low sediment TOC content in the mudflats at the Bay of Fundy. In the current thesis, *C. voluntator* was rarely found in the creek habitat of any of the study sites which could explain the higher amount of sediment TOC content compared to reported for the Bay of Fundy.

The Bio-Physiochemical sediment characteristics and sediment TOC content at the study sites: Chlorophyll *a* was measured due to its positive correlation to sediment TOC content within sediment (Cole et al., 1988; Underwood and Smith 1998). One of the sources of sediment TOC content is epipelic algae (Smith and Underwood 1998; Learman et al., 2016). Therefore, chlorophyll *a* content, an indicator of epipelic algae biomass, (Underwood and Smith 1998) was measured to investigate the contribution of these algae to sediment TOC content at the study sites. Due to higher chlorophyll *a* content in the creek habitat than the vegetated habitat, it could be suggested that epipelic algae was one of source of sediment TOC content in the creek habitat. This was also suggested by Alexander et al. (2017).

4.6 Conclusion

This is the first study that has measured seasonal and spatial sediment TOC content extensively in the three saltmarshes along the Colne estuary. Sediment TOC content at the vegetated habitat was higher than the creek habitat which could be due to the important saltmarsh vegetation contribution in carbon sequestration and carbon accumulation. The temporal variation in sediment TOC content at the study sites, especially the high sediment TOC content at Colne Point and Brightlingsea over summer could be due to the higher root production from spring to summer.

The spatial variation in sediment TOC content between the study sites along the Colne estuary was possibly dependent on the location of the saltmarsh in the estuary, nitrogen availability in the tidal water, sedimentation and saltmarsh plant characteristics. Brightlingsea and Colne Point marsh sediment stores higher amounts of sediment TOC than Wivenhoe marsh. This may be due to their location at the mid and lower estuary, higher sediment accumulation, lower nitrogen concentration in the tidal water and higher plant root production. The spatial variation of sediment TOC content within each study site was different from one another which highlights the complexity of the saltmarsh system. In addition, the driver(s) of spatial variation in sediment TOC content within each study site remains unknown.

It is suggested that the variation in primary productivity, especially root production by saltmarsh plants, could be a significant driver of seasonal variation of sediment TOC content.

The epipelic algae and the organic carbon exported from the vegetated habitat to the creek habitat could be two important sources of sediment TOC content in this habitat.

5. Chapter five - Metabolism of Sediment Carbon: Respiratory Loss

5.1 Introduction

The amount of carbon that is locked away from the atmosphere and stored in saltmarshes depends highly on the following factors: tidal flow of these ecosystems (microtidal, mesotidal and macrotidal saltmarshes) (Mudd and Fagherazzi, 2016; Guo et al., 2009); the amount of sediment deposition (Chmura et al., 2003); saltmarsh plants primary productivity (Mudd and Fagherazzi, 2016; Guo et al., 2009) saltmarsh sediment respiration (Bu et al.,2015) and nutrient concentration in saltmarshes (Langley et al., 2015). Saltmarsh plants sequester carbon by photosynthesis and store it in their above- and below-ground tissue (Mudd and Fagherazzi, 2016). The spatial and temporal variation of 0-20 cm carbon stock (sediment TOC content) and one of the possible bioengineering mechanisms that contributes to carbon sequestration (saltmarsh plants species distribution, spatial and temporal changes of above-ground biomass and above-ground primary productivity) in the study sites were discussed in the previous chapters. In this chapter one of the ways that organic carbon is lost, sediment aerobic respiration, from the study sites, is discussed.

There are several possible ways that the sediment carbon stock is exported to the adjacent ecosystems. For example, it might be “washed- away” due to precipitation and tidal flooding (Howes et al., 1994). However, loss rates through this mechanism appear negligible (Chalmers et al., 1985). For example, carbon removal from Maryland coastal marshes was 7.3 g m^{-2} yr^{-1} (Heinle and Flemer, 1976). Another way that sediment TOC content is lost from saltmarshes is via its release into the atmosphere through sediment respiration, organic carbon and organic matter mineralization (Bu et al., 2015; Bauer et al., 2013; Guo et al., 2009). Due to climate change and temperature rise, sediment respiration within saltmarshes could increase which could contribute to increased carbon loss from these ecosystems (Van de Broek et al., 2016). Therefore, to understand the fate of carbon within saltmarshes it is important to investigate saltmarsh sediment respiration (Bauer et al., 2013; Guo et al., 2009) in addition to sediment TOC content. In marine sedimentary systems, characterised by high rates of sediment accretion, 50 % of the carbon oxidation occurs through aerobic respiration (Thamdrup et al., 1998) and 50% through anaerobic respiration (sulphate reduction or Fe (III) reduction) (Kostka et al, 2002; Thamdrup et al., 1994; Thamdrup et al., 1998; Canfield et al., 1989). As mentioned in the introduction of this thesis, aerobic respiration occurs in the oxic and suboxic zones of saltmarsh sediment where oxygen is available to act as an electron acceptor (Jørgensen et al., 2006; Jørgensen et al., 1991). Anaerobic respiration occurs in the suboxic (postoxic) and anoxic zone of the saltmarsh sediment (Jørgensen et al., 2006). Due to plant root respiration, marsh inundation and organic matter concentration in the sediment, the depth of each of the mentioned biogeochemical zones varies among marine and costal sediments (Jørgensen et al., 2006; Jørgensen et al., 1991).

Sediment respiration is the sum of heterotrophic (microbes, microphytobenthos and sediment fungus) and autotrophic (root) respiration (Hanson et al., 2000). To investigate the impact of saltmarsh plant root and ambient temperature on sediment CO_2 production, the vegetated and the creek sediment respiration was measured using basal respiration method. Due to the emersion and submerging of saltmarshes with tidal waters it is difficult to measure the sediment respiration directly in the field

(Livesley et al., 2012). Therefore, in this study sediment respiration was measured in laboratory condition. Nedwell et al. (2004) measured anaerobic respiration (sulphate reduction) at four sites along the Colne Estuary, including Colne Point mudflat and saltmarsh. However, there is no information regarding aerobic respiration in saltmarshes along the Colne River Estuary. Therefore, this chapter focuses on spatial and temporal variation in sediment aerobic respiration which results in the release of carbon to the atmosphere. In this thesis, aerobic respiration was measured in the top 2 cm of the saltmarsh sediment collected from the study sites.

5.2 Hypothesis, aims and objectives

Hypothesis$_1$: There will be a significant difference in the sediment respiration, of the top 2 cm of saltmarsh sediment, between the vegetated and the creek habitats[6] in the three zones (low, mid and high marsh) and the three sites (Colne Point, Brightlingsea and Wivenhoe). The sediment respiration in the vegetated habitat will be higher than the creek habitat.

Aim$_1$: To investigate the spatial variation in sediment respiration between the vegetated and the creek habitats at each zone in each of the study sites.

Objective$_1$: Collect sediment samples, up to 2 cm depth, monthly for a year (January-December 2013) from the two habitat types (the vegetated and the creek habitats) at the three zones (low, mid and high marsh) at Colne Point, Brightlingsea and Wivenhoe saltmarsh using PVC cores.

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[6] The habitat types are explained in the general methodology section.

Objective$_2$: Quantify the sediment respiration in samples collected in objective 1. Sediment respiration will be quantified by measuring the sediment basal respiration using a titration method.

Objective$_3$: To analyse variation in the sediment respiration between the two habitat types (the vegetation and the creek) within the three zones at every study site. The result will be analysed applying nested ANOVA in the R-studio statistics package. If there is a significant difference in sediment respiration between the two habitat types, then the spatial variation in this variable between each zone (low, mid and high marsh) within each habitat type will be investigated.

Hypothesis$_2$: Significant seasonal differences will exist in saltmarsh sediment respiration between sites located in the upper estuary (Wivenhoe), the mid estuary (Brightlingsea) and the lower estuary (Colne Point), with the highest rates found during summer for every site.

Aim$_2$: To determine the seasonal (winter. spring, summer and autumn) variation in sediment respiration between the study sites.

Objective$_4$: To analyse the seasonal (winter, spring, summer and autumn, three months per season) variation in respiration in the top 2 cm of salt marsh sediment.

Hypothesis$_3$: The sediment respiration at the upper estuary (Wivenhoe) will be greater than the sediment respiration at the mid estuary (Brightlingsea) and lower estuary (Colne Point).

Aim$_3$: To determine whether there is a significant difference in the sediment respiration in saltmarsh sediment between Wivenhoe, Brightlingsea and Colne Point marsh.

Objective$_5$: To analyse and compare the measured sediment respiration of Wivenhoe, Brightlingsea and Colne Point by applying nested ANOVA in the R-Studio statistical package.

5.3 Methodology

The sampling collection strategy and the date of sample collection, sediment respiration method and data analysis are explained in general methodology sections; 2.4.2, 2.5.2 and 2.6.2 respectively. As in the previous result chapters, the presented variables were analysed using nested ANOVA, unless as otherwise stated. The variables presented in the figures within this chapter, are in the form: mean ± 95% confidence interval (CI, back transformed).

5.4 Results

5.4.1 Spatial variation in sediment respiration

There was no significant difference in sediment respiration between the vegetated and the creek habitat types ($F_{12, 530} = 0.92$, $P > 0.05$, Figure 5-1), consequently it was decided to combine the vegetated and the creek habitat samples to investigate the spatial and seasonal variation in sediment respiration between zones at each of the three study sites (Figure 5-1).

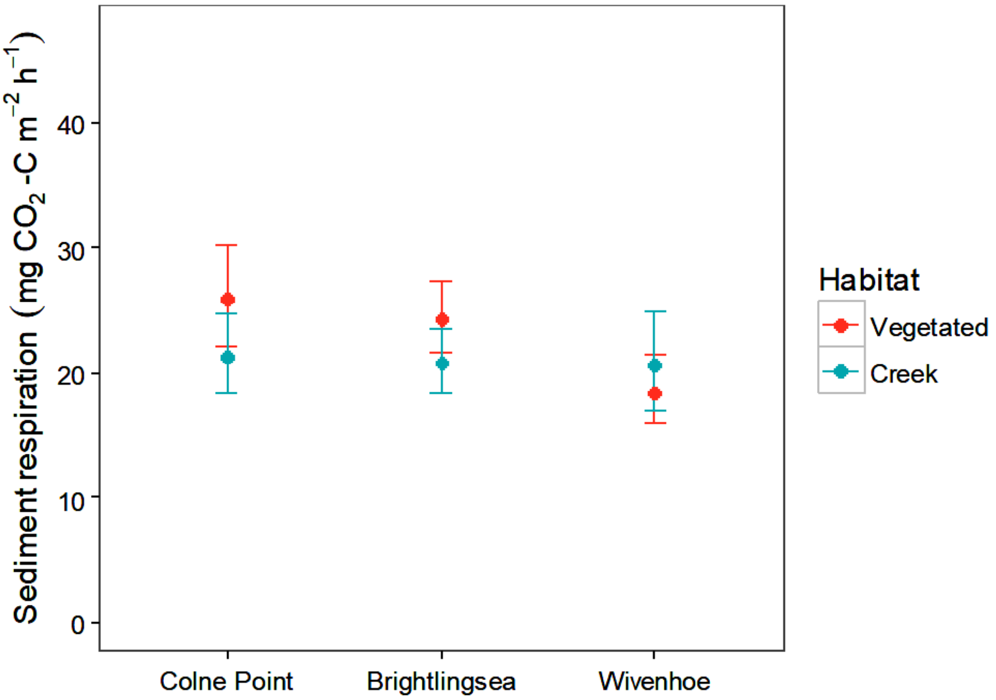

Figure 5-1 The sediment respiration in the top 2 cm of sediment in the two habitat types, vegetation and creek, within each site, Colne Point, Brightlingsea and Wivenhoe. Values are mean value ± 95% confidence intervals (back transformed).

Each circle represents the mean result of seasonal sampling (4 seasons) from one site with three zones, high, mid and low marsh, with three replicates per season, zone and site. Colne Point; N vegetated habitat =99, N creek habitat = 66. Brightlingsea; N vegetated habitat = 108, N creek habitat =108.Wivenhoe; N vegetated habitat= 103, N creek habitat=70.

There was no significant variation in sediment respiration between low marsh, mid marsh and the high marsh within Colne Point, Brightlingsea and Wivenhoe ($F_{6, 545}$ = 1.21, $P > 0.05$).

5.4.2 Seasonal variation in sediment respiration

The seasonal sediment temperature was presented in Table 5-1. There was no spatial variation in sediment temperature between sites. Therefore, the average temperature from the three sites, were pooled together and the average of sediment seasonal temperature is presented below. There was seasonal variation in sediment temperature ($F_{3, 23}$ = 80.38, $P<0.001$, $N_{\text{per season}}$= 36). The temperature increased significantly from winter to spring (Tukey test, P<0.001) and remained stable over spring and summer. It then decreased significantly from summer to autumn (Tukey test, P<0.001).

Table 5-1 Seasonal sediment temperature within the three study sites along the Colne river Estuary in 2013. Values are mean value ± 95% CI.

	Winter	**Spring**	**Summer**	**Autumn**
Temperature (°C)	2.5 ± 0.76	13.0 ± 0.76	16.0 ± 0.72	9.0 ± 0.77

There was a significant site season interaction ($F_{8,\,530} = 7.34$, $P < 0.001$) which meant the seasonal changes of sediment respiration at one site was different from the seasonal changes of sediment respiration of another study site (Figure 5-2).

Colne Point: At Colne Point, the range of sediment respiration was between 15- 34 mg CO_2-C m^{-2} h^{-1} over the sampling period (from January to December 2013). The sediment respiration in the summer (34 mg CO_2-C m^{-2} h^{-1} ,95% C, 27-42.5 mg CO_2-C m^{-2} h^{-1}) was 47% greater than sediment respiration in the winter (18 mg CO_2-C m^{-2} h^{-1}, 95% CI, 15-23 mg CO_2-C m^{-2} h^{-1}, Figure 5-2, Tukey test, P<0.001).

Brightlingsea: At Brightlingsea sediment respiration in the summer (34 mg CO_2-C m^{-2} h^{-1}, 95% CI, 30-39 mg CO_2-C m^{-2} h^{-1}) was 32% greater than sediment respiration in the winter (23 mg CO_2-C m^{-2} h^{-1}, 95% CI, 21-25 mg CO_2-C m^{-2} h^{-1}, Tukey test, P<0.05). Sediment respiration in the summer also was 62% higher than sediment respiration in the autumn (13 mg CO_2-C m^{-2} h^{-1}, 95% CI, 10-16 mg CO_2-C m^{-2} h^{-1}, Tukey test, P<0.001). Sediment respiration in the autumn was 76% lower than sediment respiration in the winter (Figure 5-2, Tukey test, P<0.001).

Wivenhoe: At Wivenhoe, sediment respiration increased from spring by (17 mg CO_2-C m^{-2} h^{-1}, 95% CI, 14-20 mg CO_2-C m^{-2} h^{-1}) to summer (41 mg CO_2-C m^{-2} h^{-1}, 95% CI, 37-45 mg CO_2-C m^{-2} h^{-1}) by 141 % (Tukey test, $P<0.001$). It then decreased by 61% to 16 mg CO_2-C m^{-2} h^{-1}, 95% CI, 13-19 mg CO_2-C m^{-2} h^{-1}) in the autumn (Figure 5-2, Tukey test, $P<0.001$).

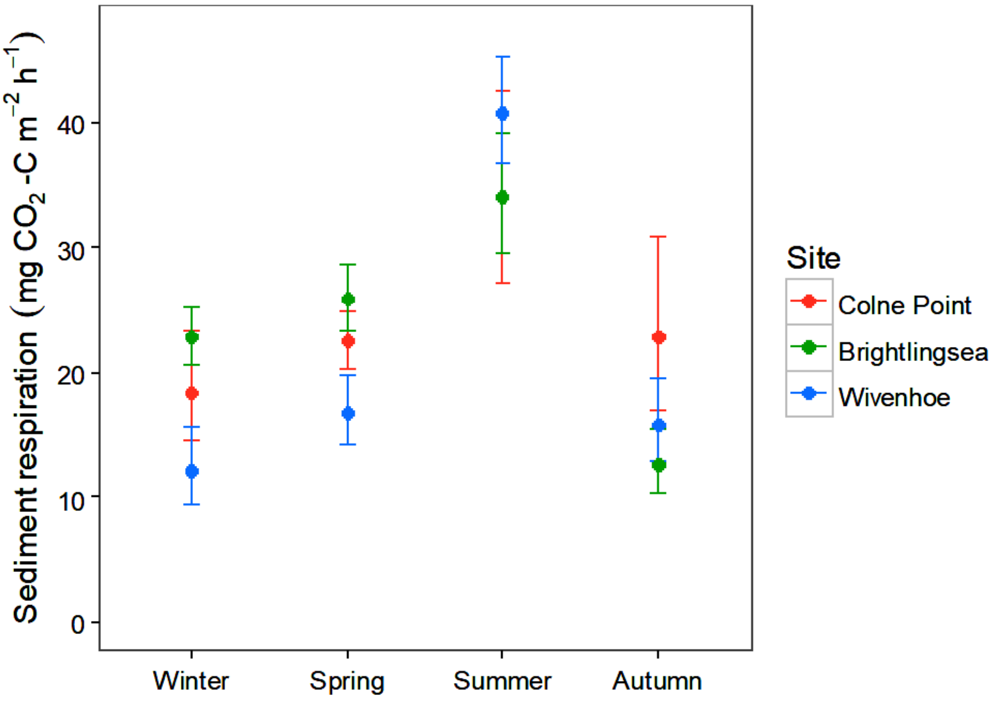

Figure 5-2 The seasonal variation of sediment respiration in the top 2 cm of sediment from the two habitat types (the vegetated and the creek) at the three sampling sites (Colne point, Brightlingsea and Wivenhoe). Values are mean value ± 95% confidence intervals (back transformed)

Each circle represents number of seasonal samples (3 months) at each site with two habitat types and three zones, with three replicates. Colne Point; N winter= 45, N spring= 54, N summer=45, N autumn=30. Brightlingsea N winter =54, N spring=54, N summer=54 and N autumn= 54. Wivenhoe N winter=41, N spring=42, N summer=45 and N autumn= 45.

Comparison between the sites: Sediment respiration at Colne Point during autumn was 43% higher than sediment respiration at Brightlingsea (Tukey test, $P<0.01$). Sediment respiration at Brightlingsea was 46.7% and 35.20% higher than Wivenhoe in the winter and spring, respectively (Figure 5-2).

5.5 Discussion

As mentioned previously, sediment respiration in saltmarshes is due to heterotrophic (microbial and fungi) and autotrophic (root) respiration (Hanson et al., 2000; Vargas et al, 2010; Livesley et al., 2012). The roots of saltmarsh plants act as a conduit to oxygenate the sediment around the plant roots which increases the sediment respiration (Kostka et al., 2002). As the saltmarsh plants roots were not removed from the sediment samples for measuring respiration, it was expected that sediment respiration of the vegetated habitat would be higher than the sediment respiration of the creek habitat. However, in this study, there was no significant difference observed in sediment respiration between the two habitats. In the field, prior to sediment sample collection from the vegetated habitat, the plants shoots were cut at the sediment surface level. Therefore, the shoot and the root of the plants were disconnected from each other. Howes et al. (1984) stated that saltmarsh plant root respiration is not significant when it is separated from its shoot. Therefore, in this study, lack of significant difference in sediment respiration between the two habitat types could be due to insignificant plant root respiration after being disconnected from its shoot. Therefore, sediment respiration measured in this study could be underestimated.

The lack of variation observed in sediment respiration between low marsh, mid marsh and high marsh could not be explained here. However, these findings agree with those of Buchan et al. (2003) who also did not observe spatial variation in sediment respiration at the saltmarsh at Sapelo Island, USA. This was likely due to the lack of spatial variability of the microbial community responsible for sediment respiration and organic matter decomposition at the Sapelo Island saltmarsh (Buchan et al., 2003).

Sediment respiration in saltmarshes is affected by saltmarsh plant productivity, ambient temperature, water table position, nutrient availability (Thamdrup et al., 1998; Magenheimer et al., 1996; Winkler et al., 1996) and sediment TOC content (Kostka et al., 2002; Thamdrup et al., 1998). The correlation between sediment respiration and sediment TOC content will be investigated in Chapter six of this thesis.

As seen in Table 5-1, the average temperature for the three sites over winter was 2.5°C which increased to 13°C, over spring. Jong et al. (1974) demonstrated that increasing temperature from 5°C to 15°C resulted in a two-fold (Apple et al., 2006) increase in sediment respiration. Apple et al., (2006) explained that at lower temperatures bacterial production and bacterial respiration increases with temperature due to the nutrient and organic carbon availability in the ecosystem. The production of enzymes by the sediment microbial community is dependent on available carbon and this process speeds up with increasing temperature (Alison et al., 2010). In this study, temperature increased from winter to spring but the sediment TOC content (Chapter 4) did not increase from winter to spring. At Colne Point and Brightlingsea marsh, however, in summer when the sediment TOC content increased, the sediment respiration also was higher than sediment respiration in the winter. Therefore, it could be suggested that at Colne Point and Brightlingsea, sediment TOC content could be a significant driver of sediment respiration. This suggestion is compatible with the findings of Kostka et al. (2002), Thamdrup et al. (1998) and Howes et al. (1984).

At Wivenhoe, although the sediment TOC concentration remained stable over the year, the sediment respiration did not follow the same pattern and increased in the summer. Wivenhoe saltmarsh is located at the upper estuary where possibly high quantity of nutrients was available in the water column (Nedwell et al., 2016). Thus, it is possible that increased temperature, and available nutrients (Nedwell et al., 2016) caused the elevation of microbial respiration over summer at Wivenhoe. The findings from Wivenhoe marsh were consistent with Nedwell et al. (2004) who also measured sediment respiration (anaerobic sediment respiration) at the upper, mid and lower estuary along the River Colne. Nedwell et al. (2004) concluded that anaerobic respiration at the upper estuary was affected more by a rise in temperature than the lower estuary due to the higher nutrient availability at the upper estuary.

The variation in seasonal changes of sediment respiration at each site could be due to impact of temperature coupled with nutrient concentration at each site. Nedwell et al. (2016) stated that nutrient concentrations in the Colne estuary decrease from the upper estuary towards the mid and lower estuary. Therefore, nutrient concentration at Wivenhoe (upper estuary) might be higher than Brightlingsea (mid estuary) and Colne Point (lower estuary). The possible higher nutrient concentration at Wivenhoe than Colne Point and Brightlingsea, coupled with gradual temperature rise from winter to summer, could be the cause of the higher increase of sediment respiration at this site than the other two sites during the same period. Morris et al. (1999) also concluded that the temperature rise impact on sediment respiration was more significant on sediment respiration at eutrophic saltmarshes than oligotrophic saltmarshes. In addition, sediment respiration at oligotrophic saltmarshes does not increase significantly with temperature (Morris et al., 1999).

A lack of significant difference in sediment respiration over winter, spring and summer between Colne Point and Brightlingsea, could be due to the equal amount of sediment TOC content at these two sites over the same period. A positive correlation between sediment TOC content and sediment respiration in saltmarshes has been stated by other studies (Kostka et al., 2002; Thamdrup et al., 1998; Howes et al., 1984). In this study also, there was a positive association between sediment TOC content and sediment respiration which will be discussed in Chapter 6.

This is the only study where aerobic respiration has been measured in saltmarshes along the Colne estuary. Therefore, the results from this study are not directly comparable with other studies that have measured saltmarsh anaerobic respiration. Nedwell et al. (2004) measured sulphate reduction (one of the pathways of anaerobic respiration, Middleburg et al., 2005) at Colne Point saltmarsh and mudflat. As with this study here, Nedwell et al. (2004) observed seasonal variation in sediment respiration. In addition, comparable to this study, Nedwell et al., 2004 found that sediment anaerobic respiration at the upper estuary was more influenced by temperature than sediment anaerobic respiration at the lower estuary.

5.6 Conclusion

This is the first study that has measured spatial and temporal variation of sediment aerobic sediment respiration in the study sites along the Colne River estuary. In this study, there was no spatial variation in sediment respiration between the zones (low, mid and high marsh), neither between habitat types (the vegetated and the creek). Sediment TOC content and temperature could be two significant drivers of sediment respiration. The sediment respiration over summer was higher than the sediment respiration over winter at the three study sites. However, the important impact of nutrients on sediment respiration should not be ignored. To identify the important factors affecting sediment respiration in saltmarshes, in addition to sediment temperature and sediment TOC content (the two variables that were measured in this study) measuring sediment nutrient concentration is also recommended.

6. Chapter six - General discussion

In recent years, saltmarshes have increasingly been recognized as significant carbon sinks (Chmura et al., 2011). However, the lack of information concerning their global and regional sediment carbon storage (Ouyang and Lee, 2014), means that the carbon stored by these habitats is not considered in global carbon budgets (Murray et al., 2011). Both Murray et al. (2011) and Chmura et al. (2003) published estimates of carbon stocks in saltmarshes globally but used data that were collected with different methods. The work by Murray et al. (2011) was based on data from coastal saltmarshes located in America, Mexico and Canada which did not include estuarine marshes. Chmura et al. (2003) estimated globally carbon stock and carbon sequestration in saltmarshes by extrapolating data from 107 sites of which only 12% were saltmarshes in Europe, highlighting the lack of information on carbon stocks in saltmarshes in Europe. Most of the saltmarshes in Europe are located at the upper intertidal zone and only submerged during spring tide (Lefeuvre et al., 2013; Bouchard and Lefeuvre, 2000), whereas the saltmarshes of North America are mainly situated in intertidal areas and inundated during each tide (Lefeuvre et al., 2013). In addition, saltmarshes in Europe are covered with different marsh plant species compared to saltmarshes in North America which are mainly dominated by one species (Möller et al., 2006; Adam 2002; Bouchard and Lefeuvre, 2000). For example, saltmarshes in the West Atlantic coast of North America are covered mainly by *Spartina alterniflora* (Adam 2002). The variation in species cover is due to different environmental conditions between the two continents (Adam 2002).

Therefore, due to differences between saltmarshes in Europe and saltmarshes in America, extrapolating carbon data from one of these regions and assuming that these systems store similar amounts of carbon in their sediment may not be valid. In addition, saltmarshes are complicated ecosystems with high spatial variation in their environmental conditions (Adam 2002). This spatial variability might also have an impact on the sediment TOC content within saltmarshes.

Therefore, one of the aims of this study was to investigate how spatial variation in environmental condition could impact sediment TOC content in saltmarshes along the Colne Estuary. Consequently, three sites along the length of the Colne river estuary were chosen. The study sites along the estuary were characterised by different environmental conditions such as, location of the study site along the estuary, salinity, nutrient concentrations (Nedwell et al., 2016) and sedimentation rate (Essex and South Suffolk Shoreline Management plan 2, 2010) of the Colne estuary. One of the study sites was coastal saltmarsh and the other two were estuarine saltmarshes. The spatial variation of sediment TOC at each study site due to habitat type (the vegetated and the creek) and zonation (low, mid and high marsh) was also investigated.

In this study, the temporal variation of sediment TOC content, the vegetated characteristic and aerobic respiration were also investigated. In addition, the impact of above-ground saltmarsh plant vegetation, and aerobic respiration on sediment TOC content was also investigated.

There are characteristics that Colne estuary shares with a high proportion of temperate estuaries such as existing tidal arms, and ecosystems such as mudflat and saltmarsh (see Meire et al., 2005; Murray et al., 2002). Therefore, this estuary is typical of a considerable proportion of estuaries in the temperate zone (Nedwell et al., 2016) which makes it a suitable study site to investigate the spatial and temporal variation of sediment TOC content. The spatial variation of the anthropogenic nutrient input within the estuary was investigated over 20 years (Nedwell et al., 2016). This knowledge on anthropogenic nutrient input within Colne estuary facilitates understanding the impact that nutrients might have on the spatial variation of sediment TOC content and the spatial variation of saltmarsh plant species. This study is a unique and the most comprehensive study to investigate the spatial and temporal variation of sediment TOC content within an estuary and coastal saltmarsh system. In addition, for the first time the sediment TOC content of saltmarshes along the Colne River is measured. Consequently, this study fills part of the global and local knowledge gap by investigating sediment TOC in one of the most studied estuaries within the Europe.

6.1 The main findings

Saltmarsh properties: The higher plant species distribution at the study sites within the Colne estuary was zone specific which was highlighted in NMDS plots in Chapter 3. For instance species such as *Spartina maritime* was one of the main species at the low marsh and *Atriplex portulacoides* was found mainly at high marsh. The variation in the saltmarsh higher plant species was very clear even at Wivenhoe marsh which was the smallest study site. This finding highlights that even in small saltmarsh, variation in environmental conditions such as saltmarsh elevation (Chapter 2, page 55) impacts on higher plant species distribution.

In addition, the species composition among the study sites at upper estuary, mid estuary and low estuary was different. This was influenced by a combination of factors such as location of the site along the estuary, gradients in anthropogenic nitrogen concentration (Nedwell et al., 2016) and variation in salinity along the estuary. *Puccinellia maritima* percentage cover was lowest at the upper estuary

(Wivenhoe) then mid (Brightlingsea) and lower estuary (Colne Point). *P. maritima* has been identified as a key species for trapping and stabilizing sediment in European saltmarshes (Langloise et al., 2003; Andresen et al., 1990). In addition, water based sediment deposited on saltmarshes is the main source of sediment TOC content in these ecosystems (Yang et al., 2008; Nyman et al., 2006; Chmura et al., 2003). Lower nitrogen concentration and higher salinity encourages *Puccinellia maritima* growth resulting in higher abundance (Cooper 1982; Kiehl et al., 1997; Olff et al., 1997) at mid and lower Colne estuary sites. Although the significant of the other saltmarsh species in sediment trapping have not been identified, their importance contribution to saltmarsh stabilizing cannot be ignored.

The association of species richness, with above-ground biomass and ANPP was also investigated. There was a positive association between above-ground biomass and species richness in this study which was in contradiction with previous studies such as Lefeuvre et al. (2000) and Gough et al. (1994). The result of this research also suggests that saltmarsh plant species richness might not be a suitable predictor for ANPP. In most plant species, between 30-50% of the carbon fixed by plant above-ground biomass through ANPP is transferred to the root system (Buyanovsky and Wagner, 1997) which in saltmarshes could contribute to sediment TOC content (Kostka et al., 2002).

The highest measured above-ground biomass was either during spring (at Colne Point and Wivenhoe) or summer (at Brightlingsea). The temporal variation in above-ground biomass in saltmarsh is influenced by abiotic factors such as light and temperature (Piao et al., 2015; Bauerle et al., 2012; Naidoo and Naicker, 1992), environmental condition such as location of the marsh along the coast or estuary and exposed tidal range, nutrient availability (Laffoley et al., 2009; Silliman et al, 2002) and plant phenology (Naidoo and Naicker, 1992). The temporal variation of the above-ground biomass was investigated to examine its importance for sediment TOC content temporal variation.

Sediment TOC content: In this study, sediment TOC content of the vegetated habitat was from 25% to 41% higher than sediment TOC content in the creek habitat. In this research, the root production was not measured directly, however saltmarsh plant roots were in the sediment samples throughout the sediment TOC measurements, which is a usual practice. Therefore, the measured sediment TOC variable included root production in the vegetated habitat. Consequently, it is highly possible that the temporal variation of sediment TOC content at Colne Point and Brightlingsea was due to root growth. The sediment TOC content at Colne Point and Brightlingsea was higher during summer than the rest of the year. However, sediment TOC content at Wivenhoe did not change seasonally which is surprising. The higher nutrient concentration at the upper estuary, due to sewage treatment work and agricultural run-off at the upper estuary (Nedwell et al., 2016), might prevent extensive root network formation (Langley et al., 2015). This could contribute to lack of seasonal changes in sediment TOC content at Wivenhoe. Saltmarsh plants and the biofilm community, contribute to sediment TOC content at saltmarshes through primary productivity (Saintilan et al., 2013; Callaway et al., 2012; McKew et al., 2011; Choi et al., 2001; Ember et al., 1987). However, in this study no association was found between sediment chlorophyll *a* content and sediment TOC content. Therefore, chlorophyll *a* content could not be a suitable predictor for sediment TOC content.

The spatial variation of sediment TOC content in respect to zonation, at Wivenhoe and Brightlingsea was different to Colne Point. In addition, these spatial variations could not be explained by the measured variables such as stem density (Table 6-1).

This highlights the complexity of the factors influencing sediment TOC content spatial variation within a small area such as a single study site. However, the spatial variation of sediment TOC content between the sites was due to the shape of the estuary, nutrient concentration and possibly higher percentage cover of *P. maritima* at the mid and lower estuary than the upper estuary.

Sediment aerobic respiration: One of the ways that sediment TOC content is released into the atmosphere from saltmarshes is through sediment respiration. It is most likely that the combination of nutrient concentration and temperature were the drivers of the temporal variation in aerobic respiration. At Wivenhoe, increased temperature and available nutrients (Nedwell et al., 2016) caused the elevation of microbial respiration over summer and high organic carbon turnover. Although Nedwell et al. (2004) measured anaerobic respiration along the Colne estuary, the conclusion of this study is compatible to findings by Nedwell et al. (2004): sediment respiration at the upper estuary was affected more by a rise in temperature than the lower estuary due to the higher nutrient availability in the upper estuary.

The ratio of carbon loss through aerobic respiration to the carbon stock in the study sites in this research is insignificant. Considering the average night[7] length during the sampling period, the measured aerobic respiration for each study site was extrapolated for 2013. In this study carbon emission through aerobic respiration through the top 0-2 cm of the saltmarsh sediment from Colne Point, Brightlingsea and Wivenhoe was estimated to be: 0.407 C g m^{-2} yr^{-1} (0.344 – 0.469 C g m^{-2} yr^{-1}), 0.344 C g m^{-2} yr^{-1} (0.282 – 0.423 C g m^{-2} yr^{-1}) and 0.297 C g m^{-2} yr^{-1} (0.250 – 0.391 C g m^{-2} yr^{-1}), respectively. The percentage of sediment TOC loss through measured aerobic

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[7] It is acknowledged that microbes respire during the day, however the respiration was measured in dark condition to avoid the impact of microbial photosynthesis on measured CO_2 production.

respiration in the study sites was between 0.0001- 0.0003% through both habitat types, which is negligible. However, the aerobic respiration measured in this study was possibly an underestimate of the aerobic respiration, since daytime microbial respiration was not measured. Furthermore, as explained in Chapter 5, due to measurement in vitro, the root respiration was possibly not detected which adds to the uncertainty of the sediment respiration estimate and its contribution to carbon loss.

Associations between measured variables and sediment TOC content: One of the aims of this study was to investigate the association between the measured variables to identify a suitable predictor for sediment TOC content at the study sites (Table 6-1).

The association between sediment TOC content and sediment aerobic respiration is described above.

There was no association between sediment TOC content and ANPP, neither between sediment TOC content and above-ground biomass. There was no association between sediment TOC content and plant species richness (Table 6-1). A lack of association between the above-ground saltmarsh vegetation biomass, ANPP and the sediment TOC content could be due to the one year gap between the sediment sample collection and the vegetation sampling. The two abiotic factors that affect the above-ground biomass and ANPP are light and temperature (Piao et al., 2015; Bauerle et al., 2012; Naidoo and Naicker, 1992) which might be different each year. Therefore, due to a year gap between the above-ground and the sediment TOC content measurements, there was no association between these variables. However, as saltmarsh plant species are relatively stable year-on-year (see Mossman et al., 2012; Wolters et al., 2005), it is not expected that the species richness changes in a year.

Therefore, it could be said with more confidence that there was no significant association between sediment TOC content in the vegetated habitat and saltmarsh plant species richness. Consequently, the saltmarsh plant species richness is not a suitable predictor of sediment TOC content within the study sites.

Table 6-1 The association between log-transformed sediment TOC content and species richness, log-transformed sediment TOC content and above-ground biomass, log-transformed sediment TOC content and sediment respiration. Linear regression analysis was used to examine the associations.

NS, $P > 0.05$, * $P<0.05$, ** $P <0.01$, *** $P<0.001$

	ANPP (g m^{-2})	**Species richness (number of species m^{-2})**	**Above_ ground biomass (g m^{-2})**	**Plant stem density (number of stems m^{-2})**	**Sediment respiration (mg CO$_2$- C m^{-2} h^{-1})**
Sediment TOC content (C Kg m^{-2})	$F_{1, 164}$ =1.4 $R^2 = 0.002$ NS	$F_{1, 164}$ =0.44 $R^2 = - 0.003$ NS	$F_{1, 235}$ =1.4 $R^2 = 0.006$ NS	$F_{1,215} = 0.00$ $R^2 = 0.0002$ NS	$F_{1,244} = 7.14$ $R^2 = 0.074$ ***

Comparison with other sites: In this study, Colne Point and Brightlingsea saltmarsh which are located at the higher salinity side of the Colne Estuary, had higher sediment TOC content that Wivenhoe with the lower salinity.This finding contradicts the findings of Yando et al. (2016). Yando et al. (2016) concluded that sediment carbon density at saltmarshes with higher salinity were lower than the saltmarshes marshes with lower salinity. Yando et al. (2016) measured the sediment carbon density of three subtropical saltmarshes, one each in: central Texas (0.005-0.01 C g cm^{-3}), Louisiana (0.012-0.032 C g cm^{-3}), and Florida (0.02-0.031 C g cm^{-3}). The comparison between this study and Yando et al. (2016) is important because it shows why a conclusion drawn from few sites might not represent sites located in other geographical locations. The sites studied by Yando et al. (2016) are micro-tidal saltmarshes located at subtropical North America. Whereas, the sites in this thesis are located at temperate zone, and exposed to a macro-tidal regime. In a macro-tidal marsh, all areas of the marsh are covered, and so the nutrient and sediment is distributed to all the marsh (Abril et al., 1999). In addition, due to higher salinity, the percentage cover of *P. maritima* increased from the upper estuary to the lower estuary, which could contribute to higher sediment trapping by this species at these sites. As explained above, higher sedimentation in macro-tidal saltmarshes contributes to higher sediment TOC content and higher sediment carbon density. Therefore, it could be concluded that the impact of salinity on sediment carbon content and sediment carbon density within saltmarshes, is different globally.

The carbon density[8] of the study sites at Colne Point (0.06 - 0.15 g C cm^{-3}) was also higher than the carbon density of saltmarshes at Bay of Fundy, Canada (0.036 g C cm^{-3}- 0.042 g C cm^{-3}, see Connor et al., 2001). Although the Bay of Fundy and the Colne Estuary are both macro-tidal estuaries (Essex and South Suffolk Shoreline Management Plan 2, 2010; Kocum et al., 2002; Connor et al., 2001), and are in the temperate zone, the saltmarshes in the Bay of Fundy were reclaimed marshes (Connor et al., 2001) whereas the three sites at Colne Estuary were natural mature marshes (Essex and South Suffolk Shoreline Management Plan 2, 2010). Due to the high nutrient concentration in reclaimed marshes, the carbon storage capacity of the reclaimed marshes is 50% lower than natural salt marshes (Santin et al., 2009). High nutrient concentration in the saltmarsh sediment prevents root production by saltmarsh plants. Saltmarsh plant roots contribute to saltmarsh sediment TOC content (Langley et al., 2015; Kostka et al., 2002). Therefore, less root production by

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[8] In addition to sediment TOC content, sediment carbon density was also calculated in this study to compare the values with other sites.

saltmarsh plants in reclaimed land contributes to lower sediment carbon density in the reclaimed land compared to natural marsh. Therefore, this comparison highlights that even when two saltmarshes exposed to the same tidal regime and are in the same climate zone (such as temperate or subtropical), the amount of carbon stored in the two marshes might not be the same due to the saltmarshes' respective histories.

The sediment carbon density of this study was also higher than sediment carbon density of the saltmarsh in the Venice lagoon, Italy (0.044 g C cm^{-3}, Roner et al., 2016). Saltmarsh in the Venice lagoon is in the Mediterranean climate condition, exposed to a micro-tidal regime and is an eroding saltmarsh (Kirwan et al., 2016; Kirwan and Guntenspergen, 2012; Day et al., 1999). Sediment carbon density and carbon content at eroded saltmarshes decreases over time (Mudd and Fagherazzi 2016). Due to wave action, an eroding saltmarsh loses its sediment containing organic carbon over time. Therefore, an eroding saltmarsh could be a source of carbon and not a carbon sink.

The range of carbon density estimated for Colne Point, Brightlingsea and Wivenhoe saltmarshes (0.06 - 0.15 g C cm^{-3}) was within the higher range of other saltmarshes globally (Table 6-2). In addition, the range of carbon density for the studied marshes along the Colne Estuary was also higher than the carbon density of the managed realignment and natural saltmarshes at Tollesbury (0.011-0.014 g C cm^{-3}, respectively, see Burden et al., 2013) at Blackwaters Estuary in Essex. This comparison is very important because the three study sites along the Colne estuary all natural saltmarshes. Furthermore, Colne Point saltmarsh is a protected natural saltmarsh and is 4280 ± 45 years old (May, 1980). It could be stated that this saltmarsh has possibly been accumulating organic carbon for a very long time. Although the carbon storage capacity of the realignment saltmarshes should not be ignored, however it takes 100 years for these marshes to accumulate as much carbon as a natural saltmarshes (Burden et al., 2013).Therefore, Colne Point is a very significant natural carbon sink that along with other undisturbed UK saltmarshes has not been included in the UK carbon budget.

Table 6-2 The sediment carbon density of saltmarshes. Data obtained from Chmura et al. (2003).

Saltmarsh location	Sediment carbon density (g C cm^{-3})
Rhone Delta in France	0.073
Marsh Island Refuge and Rockefeller Wildlife Refuge (Louisiana, USA)	0.012- 0.190
Dengie Marsh (UK)	0.041
Hut marsh (UK)	0.027
Skalingen marsh (Denmark)	0.021- 0.027
Scheldt (Netherland)	0.020- 0.029
St. Annalands (Netherland)	0.041
Colne Estuary (UK)	0.06 - 0.15

In addition, the estimated average sediment TOC content in the upper 20 cm of the sediment in the Colne Point and Brightlingsea saltmarshes vegetated habitat (20.1 Kg C m^{-2} and 22.33 Kg C m^{-2} respectively) were slightly higher than the average of TOC content in top one metre of the soil across the UK (18 Kg C m^{-2}, see Bradley et al., 2005). This also could highlight the importance of the saltmarshes at Colne Point and Brightlingsea as significant natural carbon sinks at a national and international scale.

Based on the sediment TOC content of the saltmarshes at North America, Canada and Gulf of Mexico, the organic carbon content of the top meter of saltmarsh sediment globally was estimated 917 t CO_2e/ha (Murray et al., 2011; Nellemann et al., 2009). Considering the above comparison, it is apparent that many factors such as saltmarsh condition (reclaimed marsh or natural marsh, eroding or stable marsh) and its type (estuarine marsh or coastal saltmarsh), its tidal exposure (exposed to macro-tidal or micro-tidal regime) affect how much carbon is accumulated in the saltmarsh and if the saltmarsh will be a sustainable blue carbon sink. This conclusion was confirmed by Kirwan et al (2016), Kirwan and Guntenspergen (2012) and Fagherazzi et al. (2012). In this study, although the saltmarshes were located in one estuary, there was significant variation in sediment TOC content among the study sites. In addition, by extrapolating from the site at the lower estuary, it was not possible to predict the sediment TOC content at the upper estuary. At Essex, there was also variation in sediment carbon density between saltmarshes along the Colne estuary and the saltmarshes along the Blackwater estuary. Therefore, by extrapolating the sediment carbon content of Colne Estuary for the saltmarshes at Blackwater estuary, the estimates of sediment TOC content would be higher than the actual measured amount for saltmarshes at Blackwater estuary. Therefore, estimating the global amount of sediment organic carbon at saltmarshes by Murray et al. (2011) which is based on a certain geographical region seems not to be accurate. In addition, Reef et al. (2016) and Kirwan et al. (2012) concluded that eutrophic saltmarshes in Europe, in response to elevated atmospheric CO_2, by increasing plant root production, accumulate more carbon in their sediment. Due to their exposure to macro-tidal regime in a eutrophic estuary, the study sites in this research could be considered as significant carbon sinks.

The criticism of the current global carbon storage estimates of saltmarshes sediments, have been discussed. However it is important to discuss how the sediment TOC content of the saltmarshes along the Colne estuary will impact the global estimate if they are to be included in the extrapolation. The studied saltmarshes along the Colne Estuary contain between 4% to 169% higher amount of organic carbon in their top 20 cm than the top meter of the majority of the Murray et al. (2011) and Nellemann et al. (2009) reference sites which were used for global saltmarsh sediment organic carbon content estimation. In addition, the studied saltmarshes at Colne Estuary hold between 88% to 290% higher amount of sediment TOC content than the rest of the UK sites. Therefore, including the sediment TOC content of the studied saltmarshes along the Colne Estuary within the global and UK saltmarsh sediment organic carbon content will increase the current estimates.

6.2 Future work

To estimate the total organic carbon stock in the study sites, it is important to investigate the depth of organic carbon stored in the study sites. In addition, to identify the source of the carbon, and estimate the accretion rate and the carbon accumulation rate of the studied marshes it is important to conduct isotope analysis.

Due to importance of the studied saltmarshes especially Colne Point as significant carbon sinks, it is important to investigate the way to include them in the national carbon budget. This might also generate incentive to manage and protect the marshes more efficiently.

It is important to study the impact of the increasing temperature and sea level rise (SLR) on carbon storage capacity of the studies marshes. If there is space for saltmarsh species in the land, due to SLR, saltmarsh species will move landward.

Which means that saltmarsh will keep absorbing and storing carbon in its sediment. If there is a sea wall behind saltmarsh which will prevent the saltmarsh plant species to move into the land, then it might be necessary to consider breaking the sea wall. If the saltmarsh will be submerged, it is important to estimate the amount of carbon that will be released into the ocean because of that.

In this study, the daily sediment respiration and plant respiration which contribute to carbon loss from saltmarsh were not measured. Therefore, it is important to measure the mentioned variables *in situ* to estimate the gaseous carbon loss thorough the study sites. This will provide more information about the carbon dynamic in the saltmarshes and also will facilitate estimating of the saltmarsh carbon budget.

6.3 Conclusion

There was a spatial variation in the saltmarsh higher plant distribution among the study sites. This variation could be due to the location of the sites along the estuary, salinity gradients and possibly the gradients of anthropogenic nutrient input to the estuary. In addition, the distribution of saltmarsh higher plants along the Colne Estuary was zone specific, which means at each zone, specific plant species were found.

The higher plant species richness did not impact the above-ground biomass, above-ground primary productivity and the sediment TOC content at the study sites. However, the presence of *Puccinellia maritima* coupled with the sedimentation regime along the estuary, could be an important driver of spatial variation in sediment TOC content between the study sites. Sediment TOC content at the study sites increased from upper estuary to the lower estuary. The temporal variation of the sediment TOC content was possibly due to variation in saltmarsh higher plant root production especially during summer.

Due to the significant amount of sediment TOC content of the study sites along the Colne River estuary and comparing that with the existing literature, it was concluded that saltmarshes along Colne River Estuary, especially Colne Point, are significant carbon reservoirs and should be included in the UK natural carbon sinks budget.

Currently, the global and the UK estimates of the sediment TOC content do not include the studied sites along the Colne Estuary. If these habitats, especially Colne Point, were to be included in these global and UK estimates, these overall estimates would be consequently increased.

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8. Abbreviations

ANPP: Above-ground net primary productivity

CI: Confidence intervals

COP: Conference of the Parties

DIC: Dissolved inorganic carbon

ECS: Equilibrium climate sensitivity

ENSO: El Niño/Southern Oscillation

EPS: Extracellular polymeric substance

GHG: Greenhouse gases

GT: Gigatons (giga=10^9)

HAT: Highest astronomical tide

IPCC: Intergovernmental panel on climate change

LOI: Loss on ignition

MHWN: Mean high water neap

REDD+: Reduction Emission from Deforestation and Degradation

SLR: Sea level rise

Tg: Tera gram (Tera = 10^{12})

TOC: Total Organic Carbon

UNFCC: United Nations Framework on Climate Change

WFD: Water framework directive

SSSI: Site of special scientific interest

A Chapter three Appendix - Analysis of the measured vegetation variables

A.1 Above-ground biomass

A.1.1 Data distribution and transformation

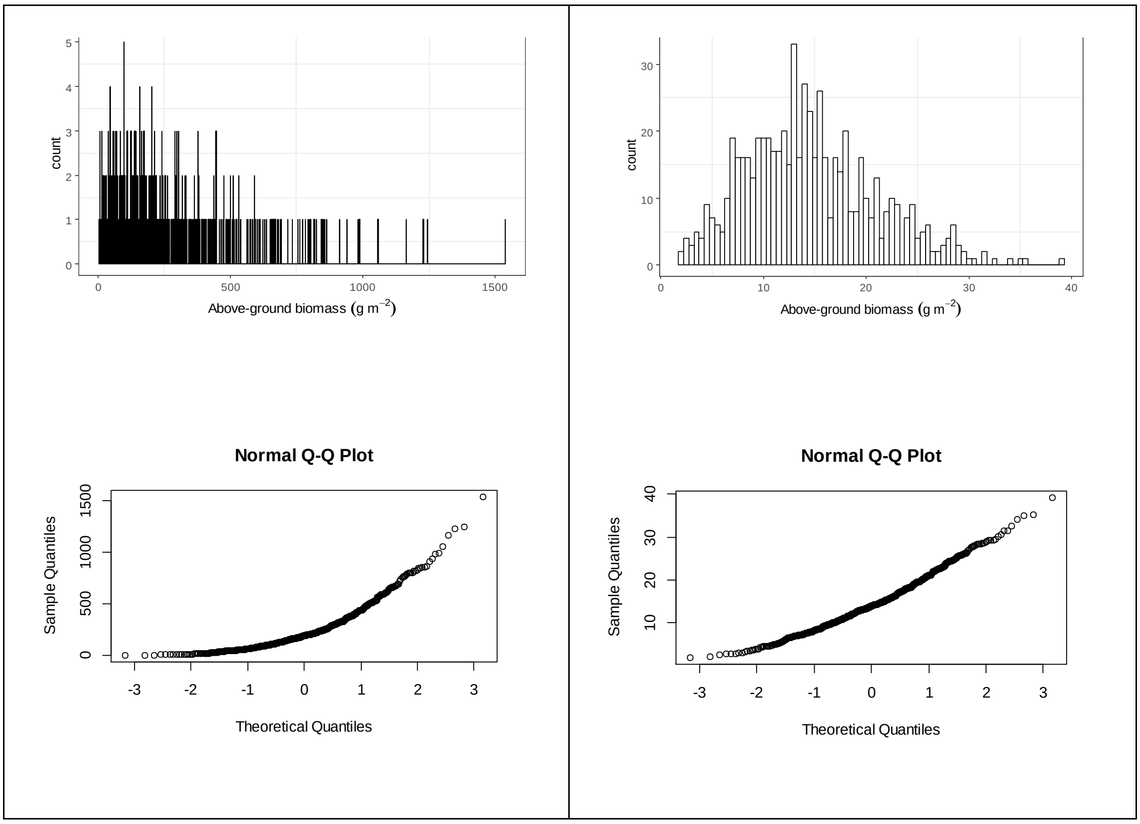


Figure A-1 The distribution of above-ground biomass variable (left), above-ground biomass square root transformed (right) variable.

The two histograms on the top illustrate the distribution of above-ground biomass variable before (top-left) and after square root transformation (top right). The q-q plot distribution of above-ground biomass variable before transformation (bottom- left) and after square root transformation (bottom-right).

A.1.2 Model analysis validation

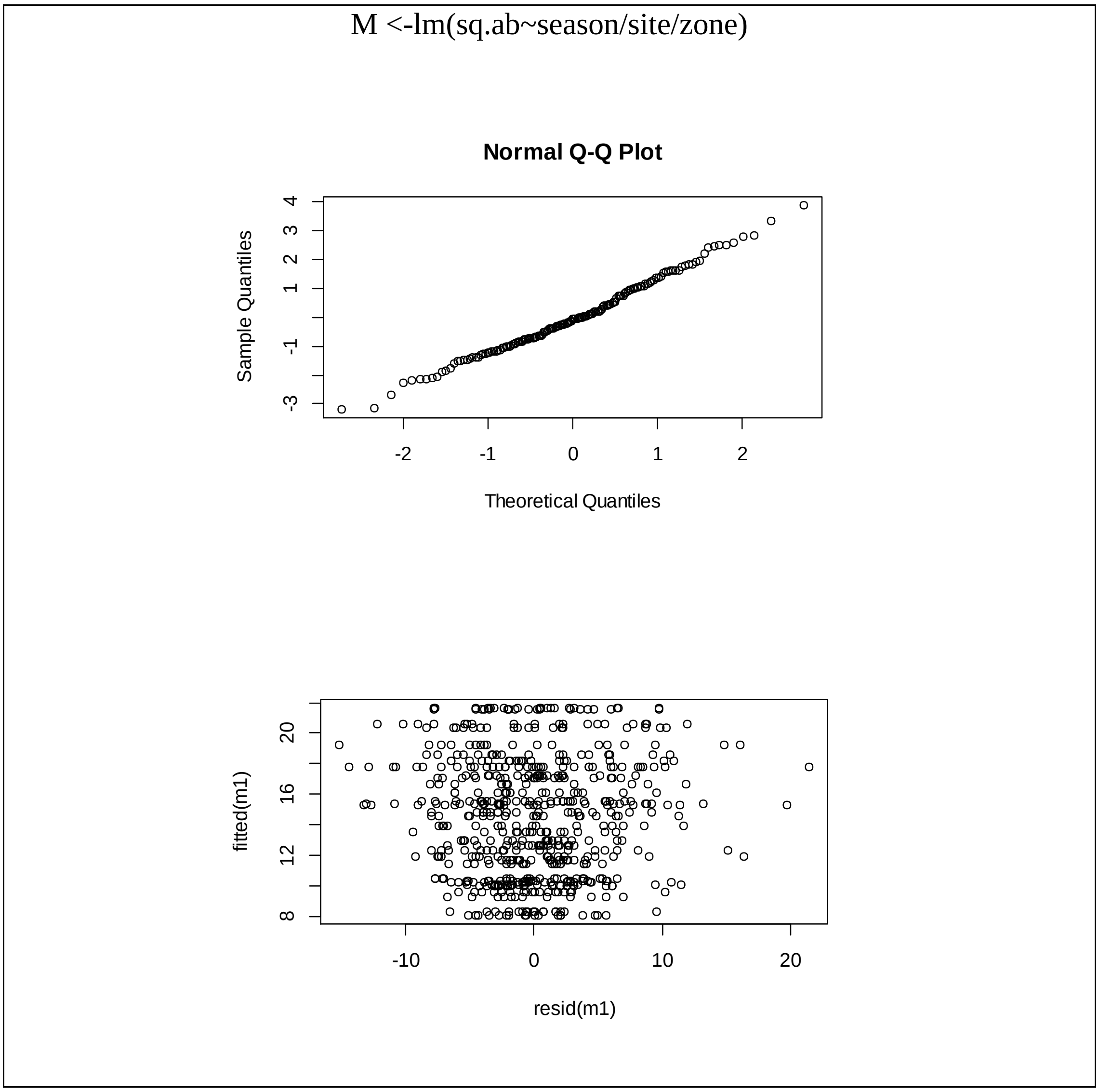


Figure A-2 The residual distribution of the applied regression models for analysing above-ground biomass variable.

The two figures in the left column illustrate the model 1residual distribution (top) and the model 1 residual distribution against the same model (bottom).

A.2 ANPP

A.2.1 ANPP distribution

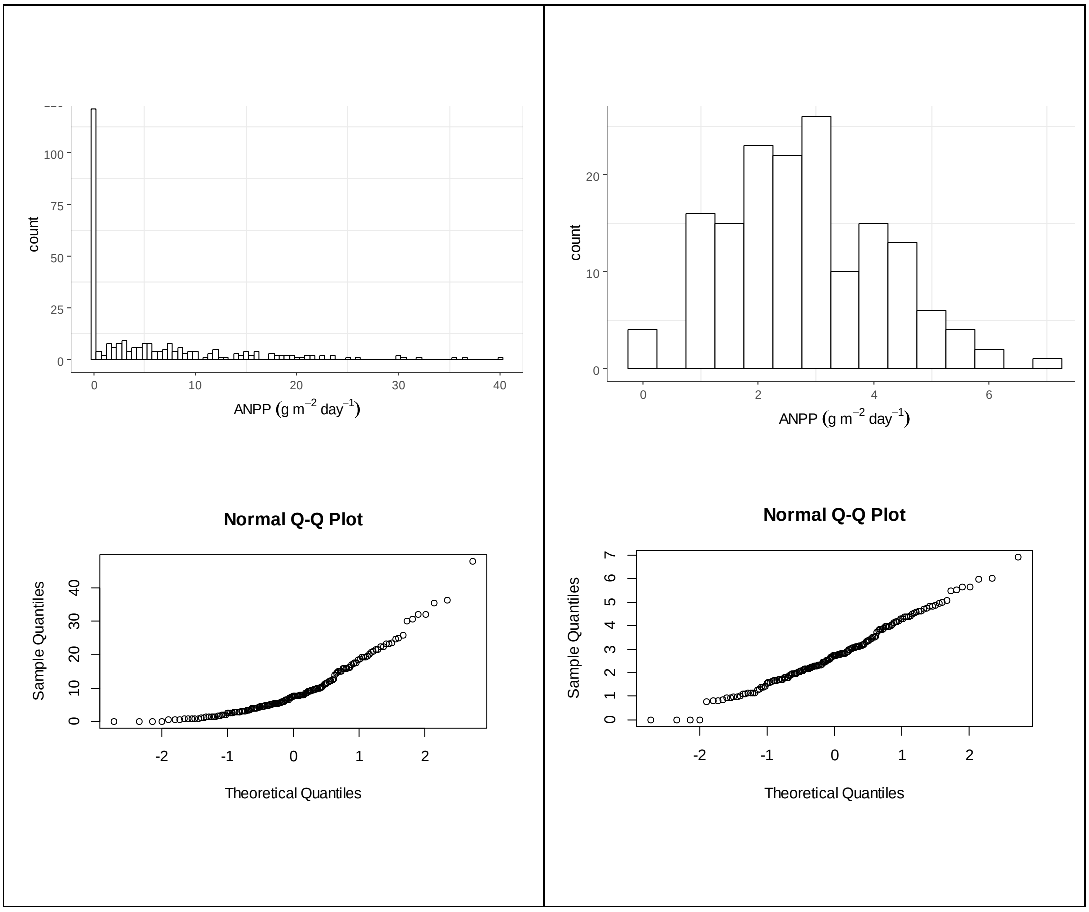


Figure A-3 The distribution of ANPP variable (left), above-ground biomass square root transformed (right) variable.

The two histograms on the top illustrate the distribution of ANPP variable before (top-left) and after square root transformation (top right). The q-q plot distribution of ANPP variable before transformation (bottom- left) and after square root transformation (bottom-right).

A.2.2 Model analysis validation

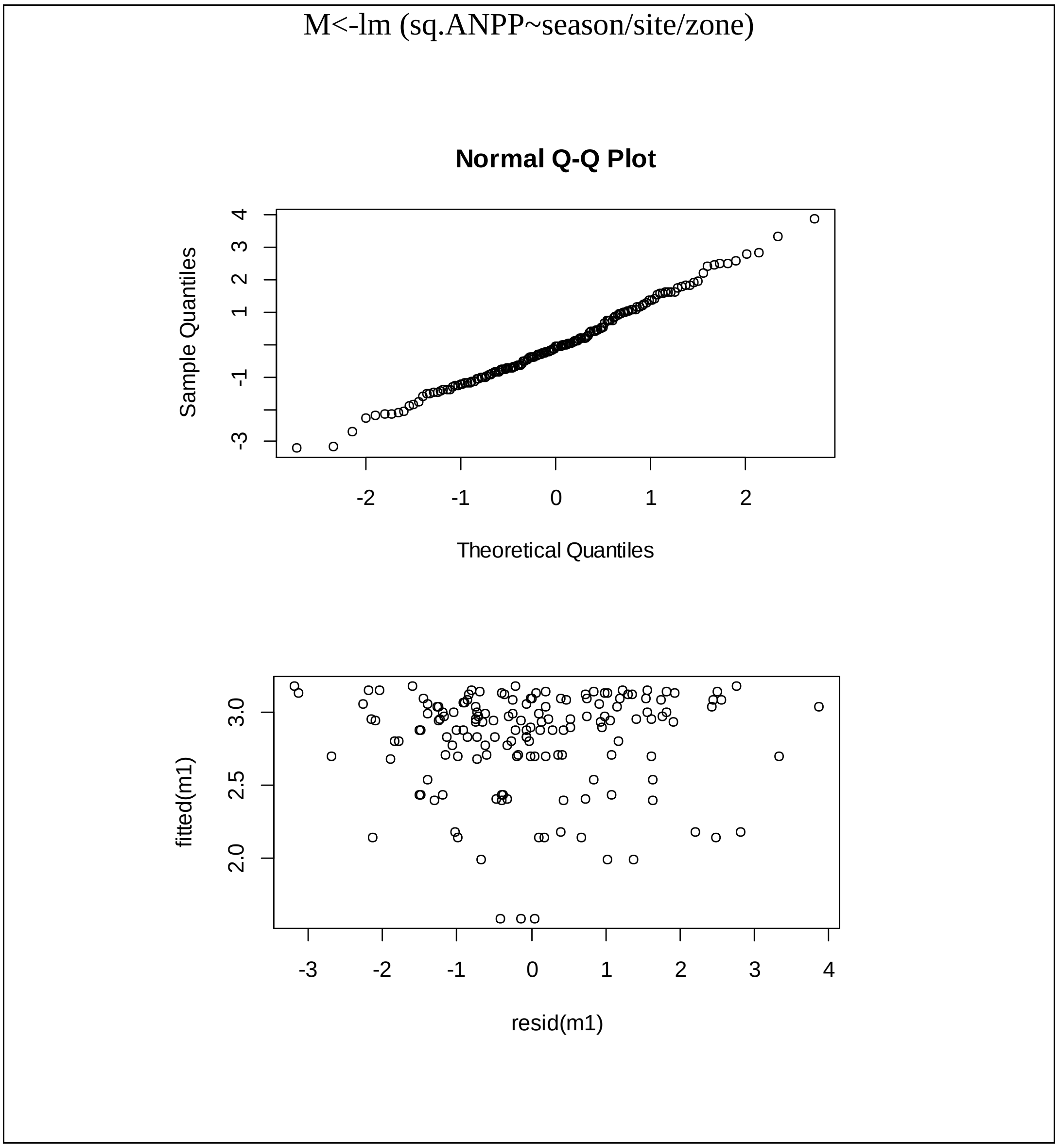


Figure A-4 The residual distribution of the applied regression models for analysing ANPP variable.

The two figures in the left column illustrate the model 1residual distribution (top) and the model 1 residual distribution against the same model (bottom).

A.3 Other vegetation characteristics distribution values

A.3.1 Species richness

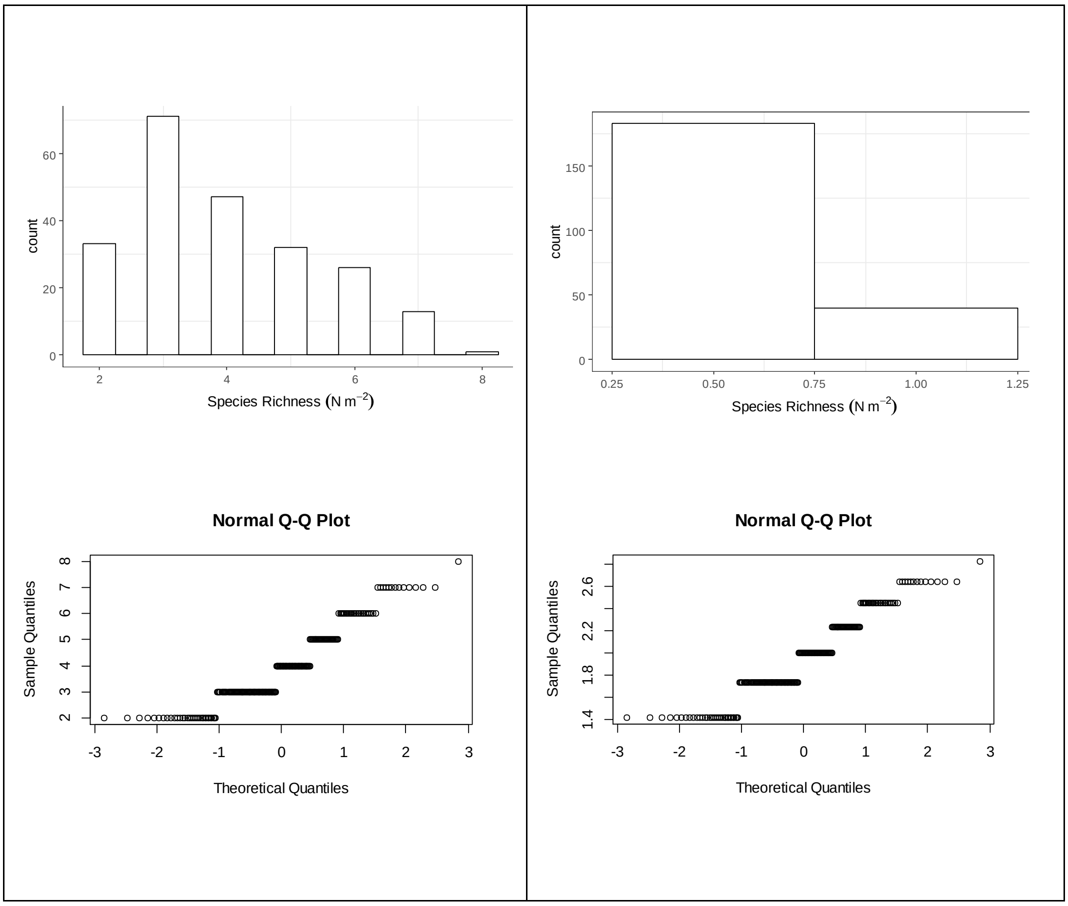


Figure A-5 The distribution of species richness variable (left), species richness biomass square root transformed (right) variable.

The two histograms on the top illustrate the distribution of species richness variable before (top-left) and after square root transformation (top right). The q-q plot distribution of species richness variable before transformation (bottom- left) and after square root transformation (bottom-right).

A.3.2 Stem density

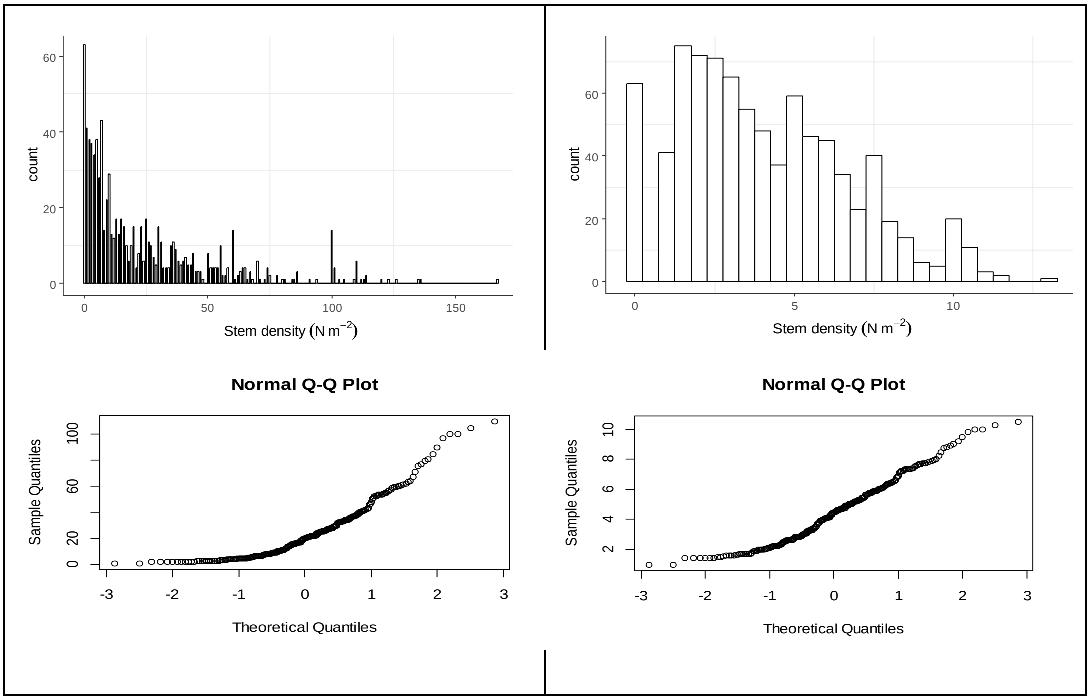


Figure A-6 The distribution of stem density variable (left), stem density square root transformed (right) variable.

The two histograms on the top illustrate the distribution of stem density variable before (top-left) and after square root transformation (top right). The q-q plot distribution of stem density variable before transformation (bottom- left) and after square root transformation (bottom-right).

A.3.3 Stem height

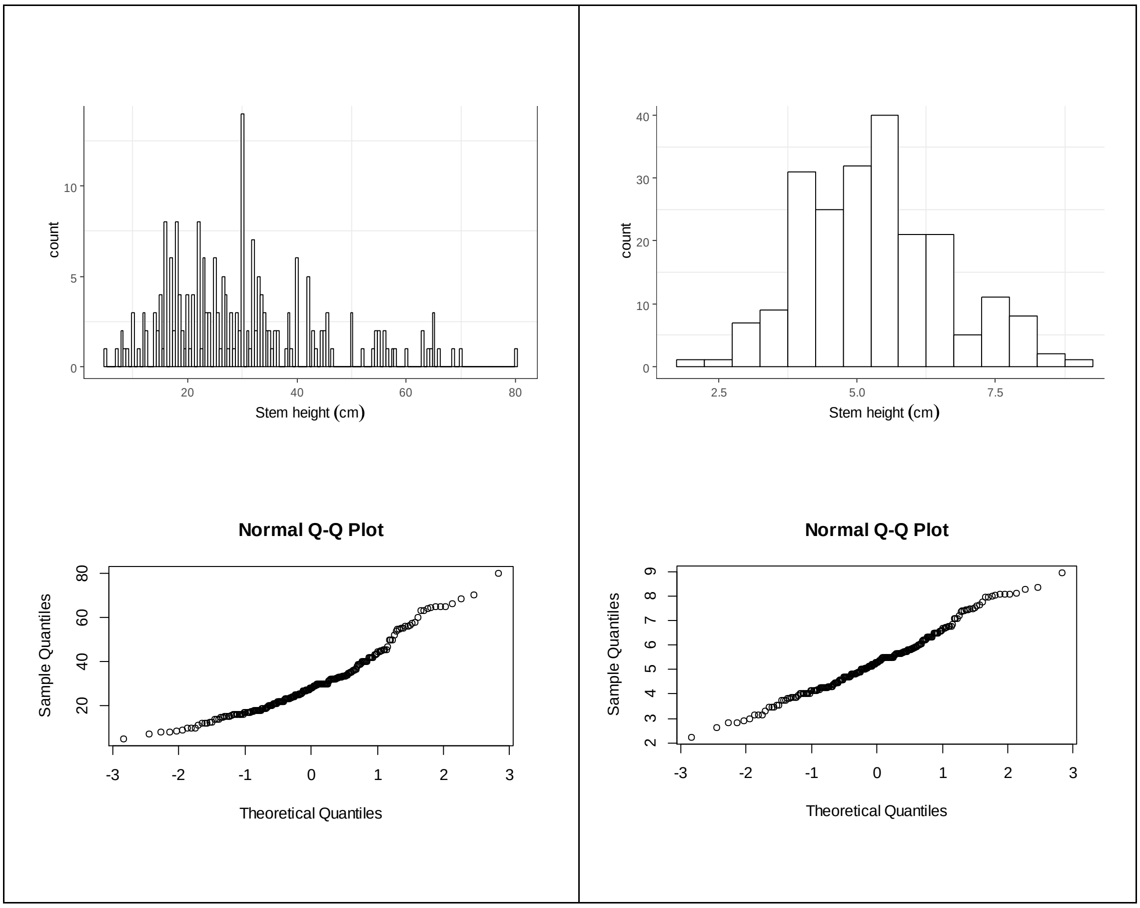


Figure A-7 The distribution of stem height variable (left), stem height square root transformed (right) variable.

The two histograms on the top illustrate the distribution of stem height variable before (top-left) and after square root transformation (top right). The q-q plot distribution of stem height variable before transformation (bottom- left) and after square root transformation (bottom-right).

B Chapter four Appendix - Analysis of the sediment TOC content and chlorophyll a content

B.1 TOC

B.1.1 Data distribution and transformation

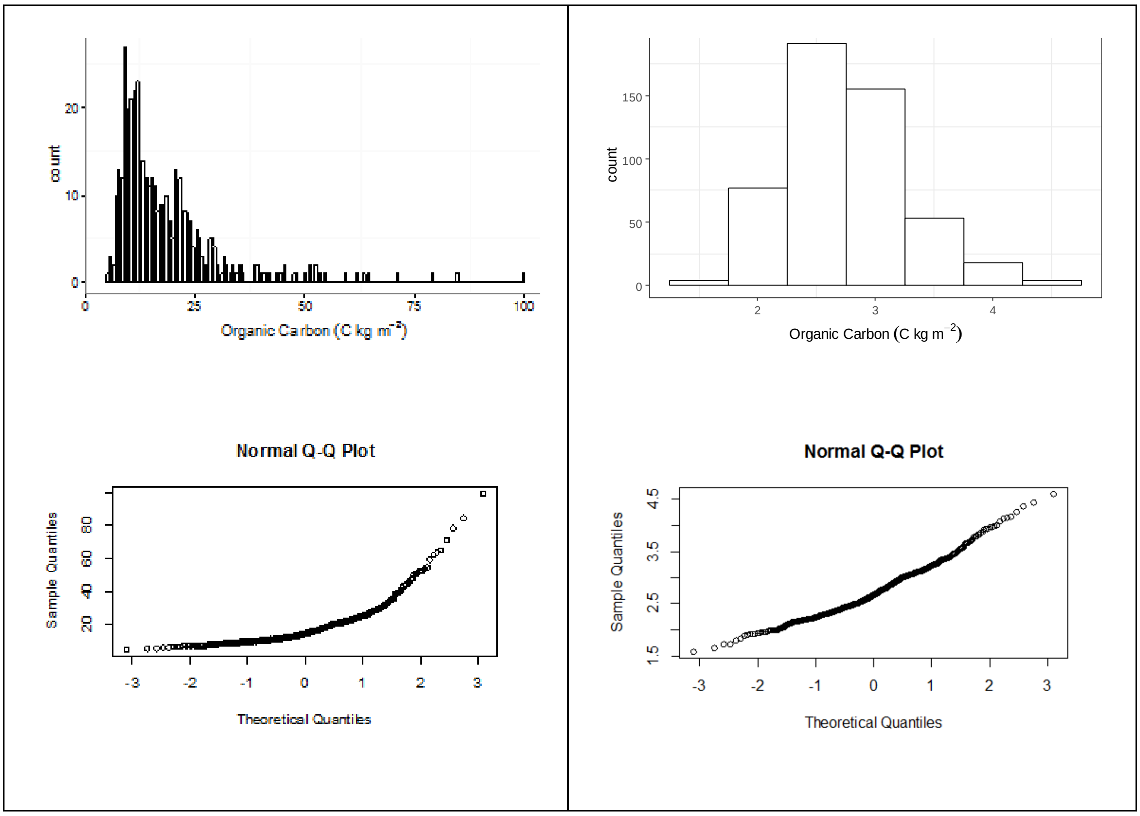


Figure B-1 The distribution of TOC variable and TOC natural log transformed.
The two histograms on the top illustrate the distribution of TOC variable before (top-left) and after logarithmic transformation (top-right). The q-q plot distribution of TOC variable before transformation (bottom- left) and after natural log transformation (bottom-right).

B.1.2 Model analysis validation

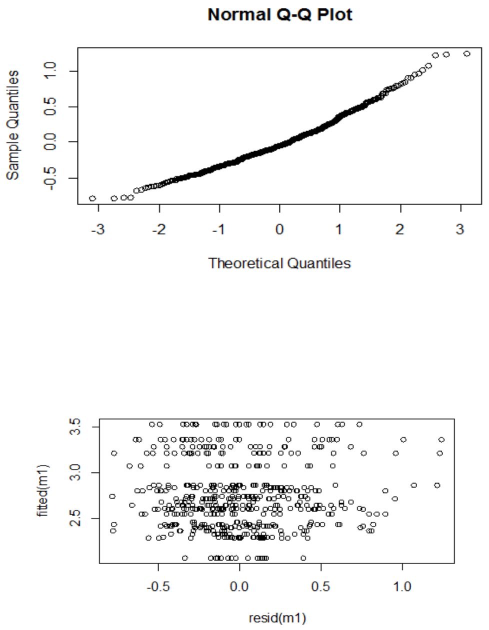
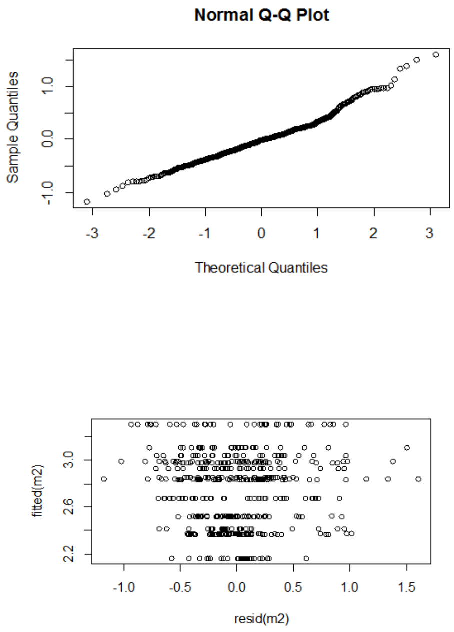
1) lm (log TOC~season/site/habitat)	2) lm (log TOC~site/habitat/zone)
	

Figure B-2 The residual distribution of the applied regression models for analysing TOC variable.

The two figures in the left column illustrate the model 1residual distribution (top-left) and the model 1 residual distribution against the same model (bottom-left). The two figures in the right column illustrate the model 2 residual distribution (top-right) and the model 2 residual distribution against the same model (bottom-right).

B.2 Chlorophyll

B.2.1 Data distribution and transformation

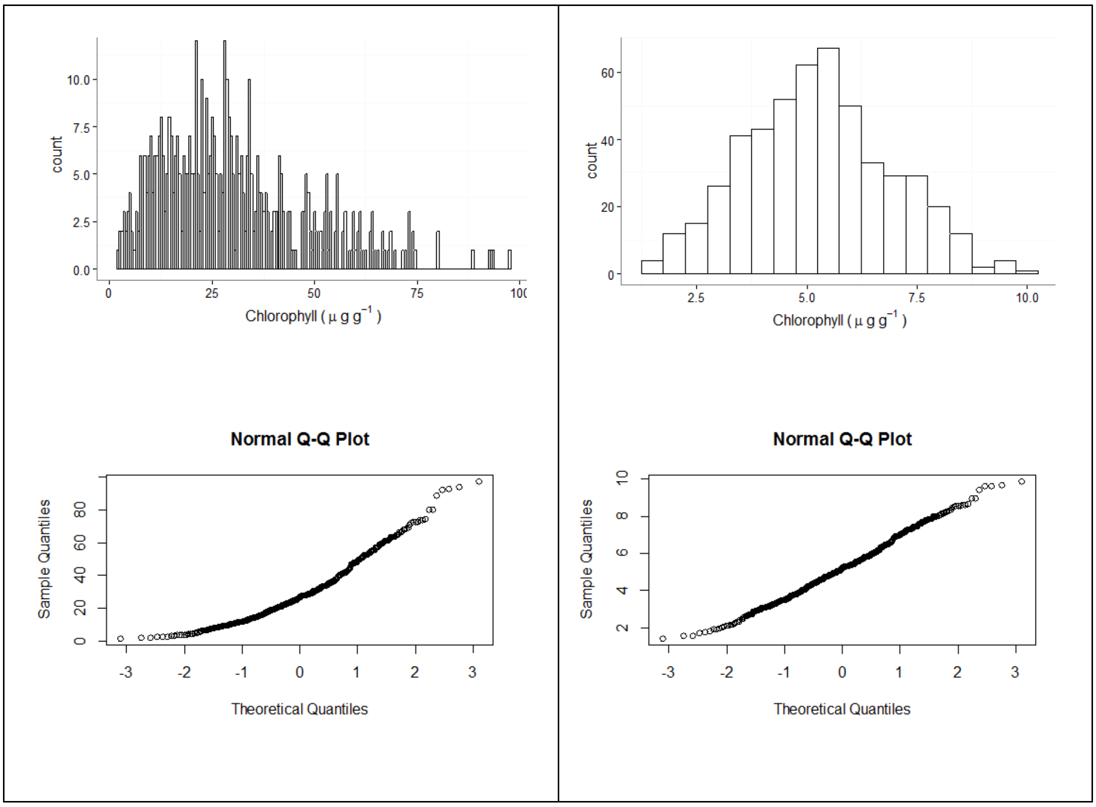


Figure B-3 The distribution of chlorophyll *a* variable (left), chlorophyll *a* square root transformed (right), variable.

The two histograms on the top illustrate the distribution of, chlorophyll *a* variable before (top-left) and after square root transformation (top right). The q-q plot distribution of chlorophyll *a* variable before transformation (bottom- left) and after square root transformation (bottom-right).

B.2.2 Spatial distribution of chlorophyll *a* in the vegetated habitat

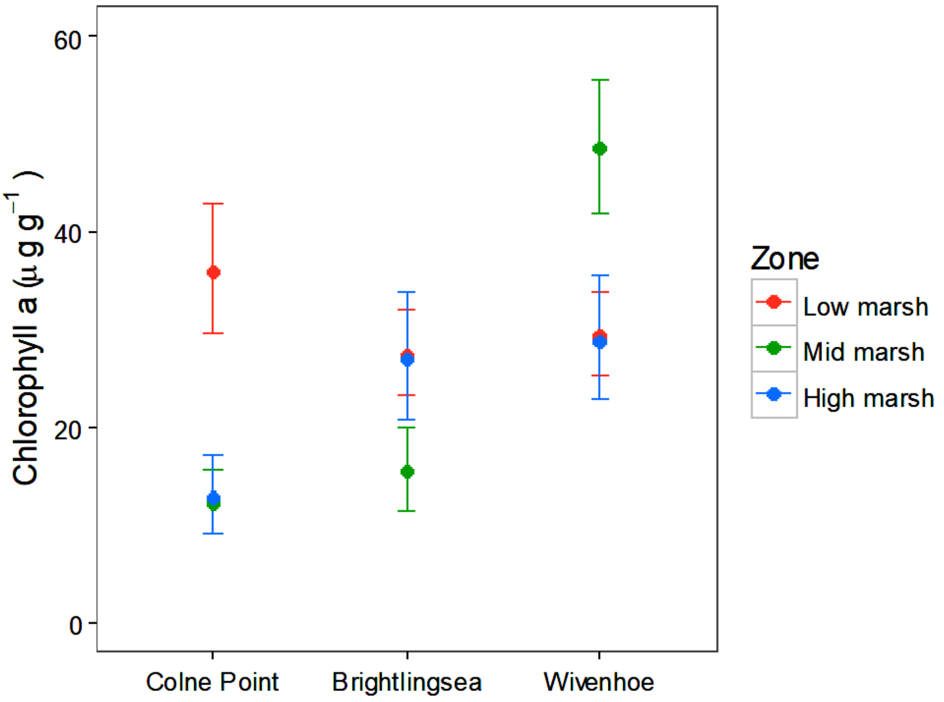


Figure B-4 The spatial distribution of sediment chlorophyll *a* concentration of the vegetated habitat along the Colne River Estuary sampling sites. Values are mean value ± 95% confidence interval (back transformed).
Each circle represents number of 12-month sampling of sediment at the vegetated habitat at each zone within each site, with three replicates. Colne Point; N low marsh=30, N mid marsh=33, N high marsh=31. Brightlingsea N low marsh=36, N mid marsh=30, N high marsh = 36. Wivenhoe, N low marsh=34, N mid marsh=34 and N high marsh = 29.

Table B-1 Pairwise comparison of sediment chlorophyll *a* concentration between zones in vegetated habitat, at each sampling sites.

The result of the post hoc Tukey test.
Region NS P > 0.05, * P <0.05, ** P<0.01, *** P<0.001

	Low marsh -Mid marsh	**Low marsh – high marsh**	**Mid marsh – high marsh**
Colne Point	***	***	NS
Brightlingsea	*	NS	*
Wivenhoe	**	NS	**

Table B-2 The pairwise comparison of sediment chlorophyll *a* concentration in similar zones of the vegetated habitat between sites.
The result of the post hoc Tukey test.
Region NS P > 0.05, * P <0.05, ** P<0.01, *** P<0.001

	Low marsh	**Mid marsh**	**High marsh**
Colne Point - Brightlingsea	NS	NS	*
Colne Point – Wivenhoe	NS	**	**
Brightlingsea -Wivenhoe	NS	**	NS

C Chapter five Appendix - Analysis of the measured sediment respiration

C.1 Sediment respiration data distribution and transformation

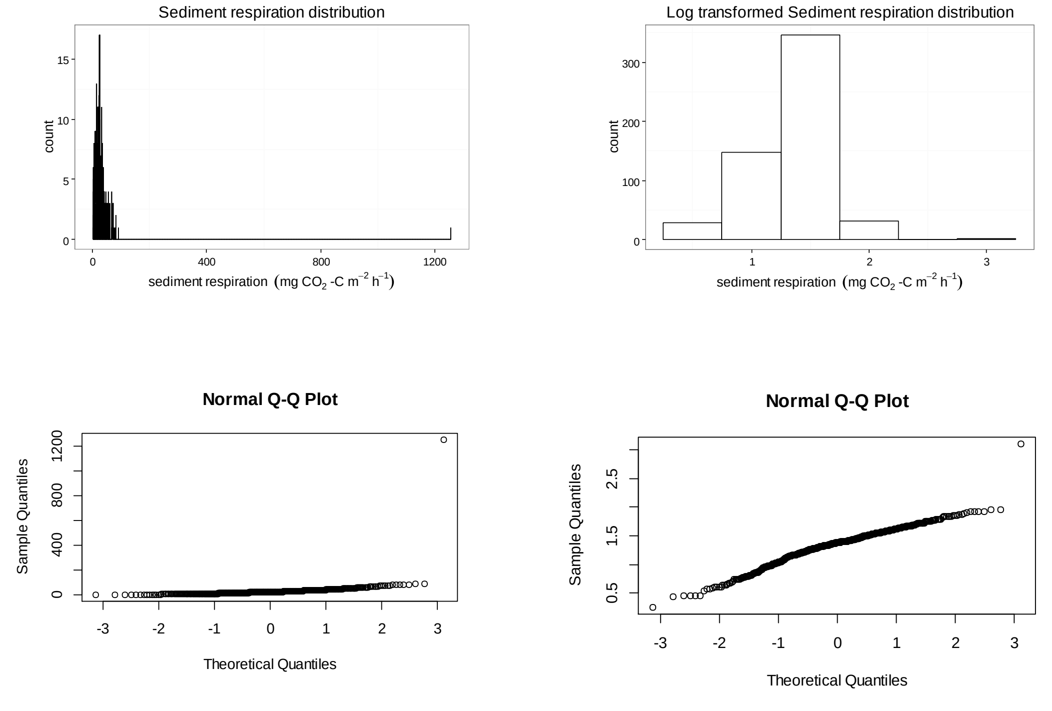


Figure C-1 The distribution of sediment respiration variable and sediment respiration variable log10 transformed.

The two histograms on the top illustrate the distribution of sediment respiration variable before (top-left) and after log10 transformation (top-right). The q-q plot distribution of sediment respiration variable before transformation (bottom- left) and after log10 transformation (bottom-right).

C.2 Model analysis validation

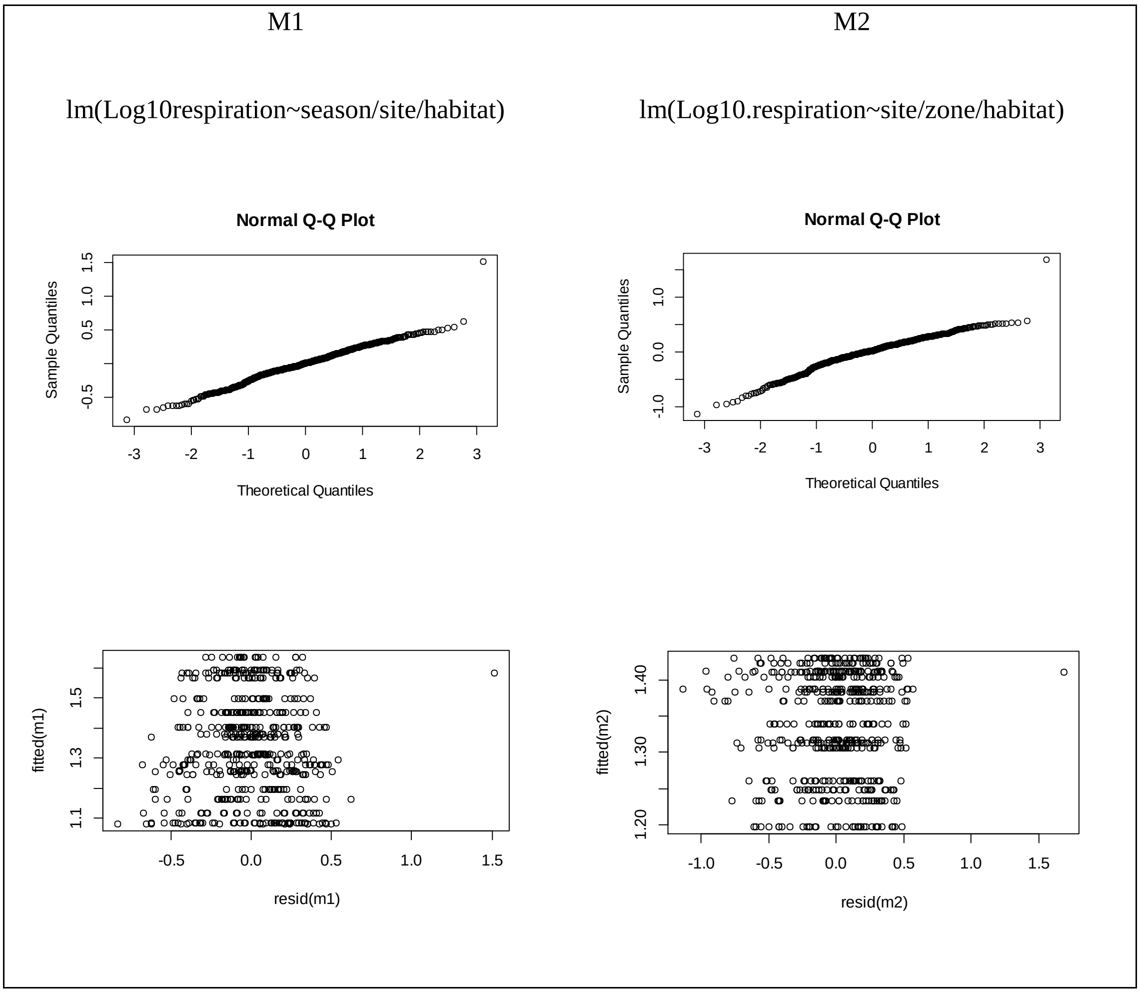


Figure C-2 The residual distribution of the applied regression models for analysing sediment respiration variable.

The two figures in the left column illustrate the model 1residual distribution (top-left) and the model 1 residual distribution against the same model (bottom-left). The two figures in the right column illustrate the model 2 residual distribution (top-right) and the model 2 residual distribution against the same model (bottom-right).