The effect of ocean acidification on carbon storage and sequestration in seagrass beds; a global and UK context

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ABSTRACT

Ocean acidification will have many negative consequences for marine organisms and ecosystems, leading to a decline in many ecosystem services provided by the marine environment. This study reviews the effect of ocean acidification (OA) on seagrasses, assessing how this may affect their capacity to sequester carbon in the future and providing an economic valuation of these changes. If ocean acidification leads to a significant increase in above- and below-ground biomass, the capacity of seagrass to sequester carbon will be significantly increased. The associated value of this increase in sequestration capacity is approximately £500 and 600 billion globally between 2010 and 2100. A proportionally similar increase in carbon sequestration value was found for the UK. This study highlights one of the few positive stories for ocean acidification and underlines that sustainable management of seagrasses is critical to avoid their continued degradation and loss of carbon sequestration capacity.

1. Introduction

Ecosystem services can be defined as "the aspects of ecosystems utilized (actively or passively) to produce human well-being" (Fisher et al., 2009). As the importance of understanding how the natural world affects human health, wealth, and well-being is recognized, research into ecosystem services has risen exponentially (Fisher et al., 2009). An ISI Web of Knowledge search into the number of papers referring to the term 'ecosystem services' found 41 in 1995, whilst 2020 were published in 2013, highlighting the increase in interest in this area of science. The marine environment provides a number of ecosystem services, which are essential for human health and well-being, such as provision of food, coastal protection, water purification, and climate regulation (Liquete et al., 2013). Anthropogenic carbon emissions, which cause climate change, are a concern, as climate change may weaken the provision of some ecosystem services by the natural environment (Schröter et al., 2005).

Anthropogenic CO_2 release primarily comes from two sources: (1) emissions from fossil-fuel combustion and industrial processes and (2) the CO_2 flux from land-use changes (especially forest clearing) (Raupach et al., 2007). The first source is of particular concern as this releases over five times the quantity of CO_2 as the latter (7.9 Gt C y^{-1} versus 1.5 Gt C y^{-1}), and emissions are accelerating rapidly (Raupach and Canadell, 2007). The concentration of CO_2 in the atmosphere has risen from 280 ppm in preindustrial times to levels of 390 ppm in 2010, an increase of approximately 40%. In 2013 levels of 400 ppm were measured at Mauna Loa volcano for the first time in recorder history, the highest levels found on earth in millions of years (Showstack, 2013). If CO_2 emissions continue under the 'business as usual' scenario then levels are expected to increase to over 900 ppm by the end of this century (IPCC, 2013).

Increasing CO_2 is of concern as it is a greenhouse gas and alters the energy budget of the earth by changing the net balance of incoming solar radiation and outgoing infrared radiation between the troposphere and the stratosphere, leading to changes in temperature, humidity, clouds and circulation, termed radiative forcing (Kamae and Watanabe, 2013). Greenhouse gases reduce the amount of energy leaving the atmosphere leading to a warming effect (Estrada et al., 2013). Other climatic effects from the increase of these gases include increased intensity of tropical cyclones (Krishnamurti et al., 1998) and increased frequency of El Niño like conditions (Timmermann et al., 1999), alongside conditions of greater precipitation or drought (IPCC, 2007).

The ocean contributes to the key ecosystem service of climate regulation, one aspect of which is the absorption of CO_2 from the atmosphere, acting as a carbon sink. In 2010 it was thought to have absorbed approximately 155 Gt C (Khatiwala et al., 2013), almost

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30% of the anthropogenic CO_2 released into the atmosphere since the pre-industrial times (Doney et al., 2009; Sabine and Feely, 2007). A portion of the CO_2 absorbed by the oceans is stored in living biomass or sequestered in sediments, whilst a large amount remains in its inorganic form. The increase in inorganic carbon stored in the oceans has led to a decrease in pH and associated changes to seawater chemistry, and has been termed ocean acidification (OA) (Doney et al., 2009). Since the Industrial Revolution (approximately 250 years ago), the pH of ocean surface waters has dropped by 0.1 units from 8.2 to 8.1, representative of a 30% increase in hydrogen ion concentration (Guinotte and Fabry, 2008). To try and predict future climate change and associated changes to ocean chemistry, a number of potential scenarios have been developed, and pH is expected to drop to anywhere between 8.05 and 7.6 by the end of this century (Caldeira and Wickett, 2003; IPCC, 2007, 2013; Prinn et al., 2008, 2011).

Ocean acidification is a ubiquitous stressor which is likely to lead to negative consequences for marine organisms (Kroeker et al., 2010), ecosystems (Fabry et al., 2008), and ecosystem service provision (Cooley et al., 2009) in the future. For example the Pacific oyster (*Crassostrea gigas*) is one of the most cultivated molluscs in the world, being extensively cultured or fished in Europe, North America, Asia and Oceana. In 2011 over 650,000 tonnes were harvested, primarily through cultivation (FAO, 2014). In the UK Pacific oyster cultivation was valued at 10.137 million in 2011/12 (Herbert et al., 2012). Research has shown that ocean acidification will have deleterious effects on this species (e.g. Barton et al., 2012; Kurihara et al., 2007), which may lead to a reduction in food provision, and employment potential in the future in relation to this species.

The majority of OA research has focussed on the effect of a decrease in pH on calcifying species (Brennand et al., 2010; Courtney et al., 2013; e.g. Gazeau et al., 2007; Iglesias-Rodriguez et al., 2008). The process of calcification is particularly susceptible to a reduction in pH (Fabry, 2008), due to the decrease in carbonate availability and subsequent decrease in calcite and aragonite saturation states. Although non-calcifying photosynthetic organisms are seen as a lesser priority, the ability of marine ecosystems and species to store and sequester carbon in marine sediments under changes in pH and carbonate chemistry is of paramount importance if we are to understand how the ability of the ocean to act as a carbon sink may change under future OA scenarios.

Seagrass beds cover less than 0.2% of the ocean surface, and yet they contribute to a disproportionate amount of marine net primary productivity (NPP) (1%), and are responsible for approximately 15% of carbon storage in the oceans (Kennedy and Bjork, 2012). Seagrasses play an important role in carbon sequestration, partially due to their ability to filter particulate carbon from the water column (Greiner et al., 2013), and to the fact that their belowground component of higher plants is nutritionally poor, unpalatable, and often found in anoxic sediments, so prevents efficient decomposition (Duarte and Cebrian, 1996). The carbon stored in living biomass or sequestered in sediments by seagrasses, alongside salt marsh plants and mangroves, has been termed 'blue carbon' (Nelleman et al., 2009), and the importance of conserving these habitats is increasingly recognised (Laffoley and Grimsditch, 2009; Luisetti et al., 2013; Nelleman et al., 2009).

Carbon storage and sequestration is an imperative component of climate regulation, as this carbon is locked away for either short (living biomass) or long (carbon buried within sediments or in the deep sea) periods of time (e.g. Lo Iacono et al., 2008; Mateo et al., 1997; Passow and Carlson, 2012), rendering it inert. Our definition of marine carbon sequestration has been modified from the OECD definition for biological carbon sequestration (OECD, 2001), to apply to marine environments. Marine carbon sequestration is defined as 'a biochemical process by which carbon dioxide is fixed by living organisms, including phytoplankton, seagrasses and salt marsh plants, and involving the storage of carbon in sediments, or the deep sea, with the potential to reduce atmospheric carbon dioxide levels'. Without the ability of the oceans to sequester this carbon, atmospheric CO_2 concentrations would be higher, leading to climate change occurring at a more rapid pace.

This study aims to detail both current carbon storage and sequestration in seagrass beds, and also how this may change in the face of OA from both a global and UK perspective. The UK has been used as a case study due relatively good data availability, and also to fulfil a real need of the UK's Marine Management Organisation, to inform marine planning in line with the requirements of the UK marine policy statement. A review of the evidence of OA impacts on seagrass will be summarised, alongside a review of current and potential future carbon storage and sequestration of seagrasses. Calculations of standing stock (tC ha^{-1} yr^{-1}) and carbon sequestration (tC ha^{-1} yr^{-1}) have been used to assess these parameters.

2. Carbon storage and sequestration by global and UK seagrass

2.1. Global carbon storage and sequestration by seagrass

Seagrass meadows are estimated to cover between 170,000 and 600,000 km^2 globally (McLeod et al., 2011). They are generally net autotrophic, therefore acting as global carbon sinks (Duarte et al., 2010) This is partially due to their ability to filter sediments and particulate organic carbon from the water column (sestonic particles), through a reduction in flow, wave action and turbulence (Hendriks et al., 2008). Denser meadows trap sediments more effectively than less dense meadows or bare sediment (Greiner et al., 2013), and sediment accumulation in seagrasses is greater than saltmarsh plants (Couto et al., 2013). Carbon storage also comes from a build-up of seagrass necromass (dead roots and rhizomes). Necromass can build-up within the sediment to extremely high volumes, without decomposing, as sediments where seagrasses are found are generally anoxic and therefore prevent efficient decomposition (Romero et al., 1992). Carbon sequestration in seagrass beds ranges from 0.45 to 1.9 tC ha^{-1} yr^{-1} (mean 1.38 tC ha^{-1} yr^{-1}) (McLeod et al., 2011). Approximately 40% of sediment organic carbon comes from seagrass and its associated epiphytes, whilst sestonic particles contribute the other 60% (Gacia et al., 2002). This highlights the importance of seagrass beds in sediment deposition and sequestration of allochthonous inputs of carbon. Increased decay rates occur at higher temperatures (Chmura et al., 2003), therefore carbon sequestration potential may be greater in polar and temperate coastal zones than tropical and sub-tropical zones.

Whilst seagrass carbon sequestration potential and standing stock (quantity of carbon stored within living biomass) is high, it is generally lower than the standing stock and carbon sequestration potential of salt marshes and mangroves, although, due to the higher values of their predicted extent around the globe, their global capacity to store and sequester carbon is comparable (Table 1). Some species of seagrass have a much higher standing stock than others. For example the Mediterranean seagrass *Posidonia oceanica* has a much greater standing stock than smaller seagrass species such as *Zostera noltii* and *Zostera marina*, which have a wide distribution in the Atlantic (Duarte and Chiscano, 1999). Seagrass above: below-ground ratio is variable between species, although a data set comprising of 30 species showed an average balanced distribution between above: below-ground biomass, and *Z. marina* has a 2:1 above: below-ground biomass (Duarte and Chiscano, 1999).

2.2. UK carbon storage and sequestration by seagrass

Whilst mangroves are limited to tropical and sub-tropical zones, salt marshes and seagrass beds provide significant carbon

Table 1
Estimates of global and UK standing stock and carbon burial of 'blue carbon' habitats.

	Area	Standing stock		Carbon burial		Notes
Global	10^{12} m^2	Mean t C ha^{-1}	Global tC × 10^6	Mean tC ha^{-1} yr^{-1}	Global tC × 10^6 yr^{-1}	
Seagrass	0.177–0.6	2.52 (0.001–23.38) N = 251	44.6–151.2	1.38 (0.45–1.90) N = 123	24.4–82.8	a
Mangroves	0.138–0.181	156.6 (39.7–271.5) N = 19	2161–2834	2.26 (20–949) N = 34	31.2–40.9	b
Salt marshes	0.022–0.4	6 (1.9–13) N = 3	13.2–240	2.18 (0.18–17.13) N = 96	4.8–87.2	c
Total blue carbon habitats	0.337–1.181		2218.8–3225.2		60.4–210.9	
UK	10^6 m^2	Mean t C ha^{-1}	UK tC × 10^3	Mean tC ha^{-1} yr^{-1}	UK tC × 10^3 yr^{-1}	
Seagrass	50–100	1.61	8.05–16.1	0.524	2.62–5.24	d
Salt marsh	453	4.4	199.3	1.41 (0.64–2.19)	63.9	e

A Standing stock and carbon burial were calculated by the minimum and maximum area multiplied by the mean standing stock and mean carbon burial rates.

a Area and carbon burial from McLeod et al. (2011), standing stock from Fourqurean et al. (2012).

b Area from Chmura et al. (2003) and Bouillon et al. (2009), carbon burial rates from McLeod et al. (2011), standing stock calculated from biomass Komiyama et al. (2008) and % carbon content of mangroves Bouillon et al. (2008).

c Area from Chmura et al. (2003) and Duarte et al. (2005), carbon burial rates from Chmura et al. (2003), and standing stock from Bouchard and Lefeuvre (2000).

d Area from Davison and Hughes (1998), the Biodiversity Information Reporting Group (2008), and Luisetti et al. (2013), carbon burial rates from Cebrian et al. (1997), standing stock calculated from biomass Duarte and Chiscano (1999) and % carbon content of Z. marina (36%: Duarte, 1990).

e Area from Boorman (2003), carbon burial from Cannell et al. (1999), standing stock calculated from biomass Burden et al. (2013), % wet: dry weight ratio (18%: Mitsch et al., 2006) and % carbon content of saltmarshes (35%: Hemminga et al., 1996).

storage and sequestration potential around the UK (Table 1). There are four species of seagrass found in the UK: *Zostera marina*, *Zostera noltii*, *Ruppia maritima* and *Ruppia cirrhosa*. *Z. marina* is the most abundant species, whilst *R. maritima* and *R. cirrhosa* are uncommon. Previously *Z. marina* was described as two species: *Z. marina* and *Z. angustifolia*, although *Z. angustifolia* is now thought to be a conspecific of *Z. marina* (Davison and Hughes, 1998). Previously seagrass beds were abundant around the UK, but their extent has been drastically reduced by disease. In the 1930s a 'wasting disease' destroyed over 90% of *Z. marina* populations on the Atlantic coasts of Europe and the USA (Muehlstein, 1989). Since this time some recovery is evident, although *Zostera* beds are considered scarce in the UK (Davison and Hughes, 1998).

Z. marina and *Z. noltii* have been recorded along many parts of the UK coastline (Fig. 1), although the aerial extent of meadows is uncertain. The biodiversity information group (BRIG, 2008) estimated that between 16 and 100 km^2 of seagrass beds occurred around the UK. Luisetti et al. (2013) calculated that 48.87 km^2 of *Z. marina* beds had been mapped, whilst Davison and Hughes (1998) give a total of 52.8 km^2 of known *Zostera* beds. It must be noted that the aerial extent of seagrass beds has only been quantified for some special areas of conservation (SACs), whilst the extent in other sites is unknown. It is expected that the cover of seagrass beds around the UK may be at least double this. As a conservative estimate, a cover of 50–100 km^2 of seagrass beds around the UK has been used for this study.

As *Z. marina* (including *Z. angustifolia* conspecific) is the most abundant species of seagrass found around the UK, measurements of standing stock and carbon burial rates have been used for this species. It must be taken into consideration that standing stock and burial rates of *Z. noltii* are thought to be substantially less (Cebrian et al., 1997; Duarte and Chiscano, 1999), although this should not impact on calculations as the mapped extent of *Z. marina* is almost 49 km^2 (Liquete et al., 2013), therefore the actual extent of this species alone should easily fall within 50–100 km^2. The carbon sequestration rates of *Z. marina* are largely unstudied. Cebrian et al. (1997) reported a sequestration rate for *Z. marina* of 0.52 tC ha^{-1} yr^{-1} in a Spanish Bay, whilst Greiner et al. (2013) reported a sequestration

rate of 0.37 tC ha^{-1} yr^{-1} in a 10 year-restored *Z. marina* meadow on the East coast of the USA. No carbon sequestration rates have been recorded for *Z. marina* around the UK. As the carbon sequestration rates in the restored bed were shown to be increasing annually and expected to be less than the burial rates of a mature meadow (Greiner et al., 2013), the burial value for Spanish Bay was used to calculate the carbon sequestration potential. Whilst the standing stock and carbon sequestration potential of seagrasses around the UK is lower than the standing stock and carbon sequestration potential of saltmarshes (Table 1), they still have the potential to store and sequester a significant amount of carbon (store: 8050–16,100 tC, sequester: 2620–5240 tC yr^{-1}).

3. The impact of ocean acidification on seagrasses

The global ocean pH is expected to fall to between 8.05 and 7.6 by the end of this century (IPCC, 2013; Prinn et al., 2011). This wide range of predicted values are built on scenarios of future development which make assumptions of the speed and shape of future political and technical changes, how human activities will change and natural resource availability (Prinn et al., 2011). As research on the effect of OA on seagrass beds is limited, it was not possible to separate out the impact of different scenarios, and therefore experiments using pH levels that fell between pH 7.9 and 7.6 are reported. This covers pH levels described for the IPCC 'business as usual' scenarios within the IPCC 4th and 5th assessments (IPCC, 2007, 2013).

Photosynthetic rates increased in seagrass species subjected to short-term (6 months or less) acidification (Alexandre et al., 2012; Invers et al., 2001; Jiang et al., 2010; Thom, 1996), but this increase was not apparent in seagrasses subjected to long-term (>1 year) acidification (Garrard, 2013; Hall-Spencer et al., 2008). Some seagrasses showed an increase in leaf growth rate, although this response was only apparent for those exposed to acidification that lasted for days (Jiang et al., 2010; Thom, 1996), rather than months or years (Alexandre et al., 2012; Campbell and Fourqurean, 2013; Hall-Spencer et al., 2008). Increased vegetative growth/density
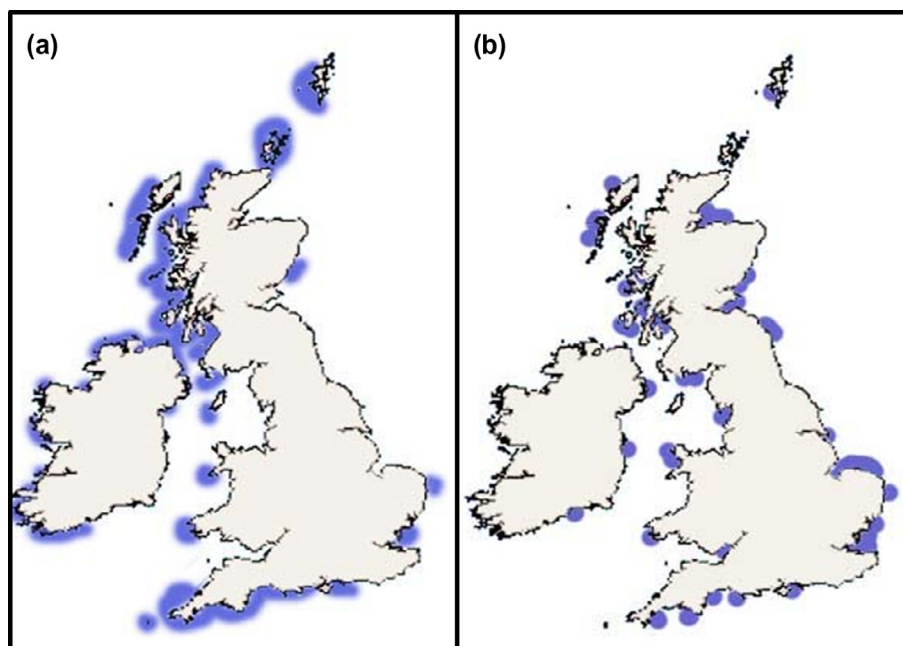
Fig. 1. Recorded distribution of (a) *Zostera marina*, and (b) *Zostera noltii* around the coast of Britain and Ireland (from www.marlin.ac.uk).

was observed for all seagrasses exposed to long-term acidification, both in a laboratory setting (Palacios and Zimmerman, 2007), and in observations of CO_2 vents in tropical (Fabricius et al., 2011; Russell et al., 2013) and Mediterranean climates (Garrard, 2013; Hall-Spencer et al., 2008). At pH levels expected for the end of this century under the 'business as usual' scenario (pH 7.6–7.9), shoot density increased by 200% at the vents in Papua New Guinea (Fabricius et al., 2011), increased by 60–100% in Ischia, Italy (Garrard, 2013; Hall-Spencer et al., 2008), and almost doubled in a laboratory setting (Palacios and Zimmerman, 2007). Shoot density at very low pH vent sites (pH 6.8–7.0) increased 4-fold (Russell et al., 2013).

Whilst it appears that an increase in above-ground biomass, through an increase in shoot density, is a response to OA, an even greater response appears to be the increase in below-ground biomass. In long-term experiments below-ground biomass increased in all species tested (Fabricius et al., 2011; Palacios and Zimmerman, 2007; Russell et al., 2013), whilst in short-term experiments the concentration of below-ground non-structural carbohydrates increased (Campbell and Fourqurean, 2013; Jiang et al., 2010). This suggests an increase in translocation of photosynthate into below-ground compartments, in response to OA (Campbell and Fourqurean, 2013; Jiang et al., 2010; Russell et al., 2013), which leads to an increase in the growth of roots and/or rhizomes. Below-ground biomass increased by 25% per shoot in *Z. marina* in response to pH 7.8 (Palacios and Zimmerman, 2007), whilst below-ground biomass (g m^{-2}) increased by over 300% in *Cymodocea* sp. in response to pH levels expected for the end of this century (pH 7.6–7.9).

Differences in response to short- and long-term acidification (Table 2) highlight the importance of long-term experimentation in OA studies. To predict changes to the carbon storage and sequestration potential of seagrasses only results from long-term experiments have been used (Table 3). Seagrass above- and below-ground biomass are important factors in determining the carbon storage and sequestration potential. Whilst values of changes in above-ground biomass were sparse for long-term studies, the change in seagrass density was measured for all long-term studies (Fabricius et al., 2011; Garrard, 2013; Hall-Spencer et al.,

Table 2

The effect of ocean acidification on photosynthesis, growth and biomass of seagrasses exposed to short- and long-term acidification to pH 7.6–7.9 (Alexandre et al., 2012; Data reported from: Beer and Koch, 1996; Campbell and Fourqurean, 2013; Fabricius et al., 2011; Garrard, 2013; Hall-Spencer et al., 2008; Invers et al., 2001; Jiang et al., 2010; Palacios and Zimmerman, 2007; Thom, 1996).

Effect of OA on:	Short term	Long term
Photosynthesis	↑	↔
Leaf growth rate	↑/↔	↔
Shoot density/vegetative growth	↔	↑
Aboveground NSC	↔	↔
Belowground NSC	↑	?
Aboveground biomass	↔	↑/↔
Belowground biomass	?	↑

2008; Russell et al., 2013; Zimmerman et al., 1997). As seagrass density and above-ground biomass values are inextricably linked, changes in seagrass density can be used as a proxy for changes in above-ground biomass (Marba and Duarte, 2003). Seagrass density has also been shown to be an important influence on particle deposition rate (Hendriks et al., 2008). Whilst below-ground biomass was not measured for all studies, it is an important factor in carbon sequestration, as a large portion of the carbon sequestered comes from burial of dead roots and rhizomes.

3.1. Quantifying the impact of ocean acidification on seagrass carbon sequestration

Particle deposition increases linearly with increasing shoot density of the seagrass *Posidonia oceanica*, except at high current velocities (Hendriks et al., 2008). Although only tested for this species, it is expected that this relationship will hold true for other species. If we use this linear relationship to calculate changes to carbon deposition from the seston, an increase in seagrass density of 60% (Garrard, 2013) should lead to a 60% increase in organic carbon deposition. If belowground biomass increases by 125% (Palacios and Zimmerman, 2007) then a 125% increase in carbon sequestration from plant material is expected. Carbon deposition from sestonic particles represents 60% of carbon sequestration, whilst

Table 3
Increases in shoot density and belowground biomass in response to long-term (>1 year) acidification to pH 7.6–7.9.

Species	Shoot density (%)	Belowground biomass (per unit area)	Source
Zostera marina	80[a]	125%[a,b]	Palacios and Zimmerman (2007)
Cymodocea sp.	0–200	300%	Fabricius et al. (2011) and Russell et al. (2013)
Posidonia oceanica	60–100	?	Garrard (2013) and Hall-Spencer et al. (2008)

[a] It must be noted that an increase in shoot density or belowground biomass was not observed for plants grown under light limited conditions (5% surface irradiance).
[b] Biomass (per unit area) for *Z. marina* calculated by the increase in biomass per shoot, multiplied by the increase in density.

burial of dead roots and rhizomes (necromass) is thought to account for approximately 40% of carbon sequestration (Gacia et al., 2002). From these values we can calculate the potential change in carbon sequestration of seagrasses in response to ocean acidification at pH levels expected for 2100. For this exercise we have assumed that the cover of seagrass remains the same.

The increase in both above- and below-ground biomass in response to OA will have significant positive implications for the carbon sequestration capacity of seagrass beds in the future. Our results suggest that annual carbon sequestration may increase by 86% on both a local (UK) and global scale by 2100. This may lead to a global increase in annual seagrass carbon sequestration of up to 71.4 million tC annually and a potential increase of up to 4500 tC in the UK (Table 4).

3.2. Quantifying the impact of ocean acidification on seagrass carbon storage

At pH values expected for the end of this century, shoot density increased in four of the five studies, with an increase of between 60% and 200% (Fabricius et al., 2011; Garrard, 2013; Hall-Spencer et al., 2008; Palacios and Zimmerman, 2007). Shoot density has been used as a proxy for above-ground biomass, as this parameter was not measured in the aforementioned studies. Changes to below-ground biomass were only calculated for two studies (Fabricius et al., 2011; Palacios and Zimmerman, 2007) and increased by between 125% and 300%. If we take the average above: belowground ratio of seagrasses globally (1:1.1) and that of *Zostera marina* (2:1) (Duarte and Chiscano, 1999), alongside the conservative values of an increase of 60% in shoot density (and therefore above-ground biomass) (Garrard, 2013) and an increase of 125% for below-ground biomass (Palacios and Zimmerman, 2007), we can calculate the potential change in the global and UK standing stock of seagrasses in response to ocean acidification at pH levels expected for 2100 if seagrass cover remains stable over this time period.

At present day coverage of seagrass, the standing stock of seagrass is expected to significantly increase in response to OA by the end of this century (Table 5). The global ratio of above: below-ground biomass of seagrasses is expected to decrease from 1:1.1 to 1:2.3 by the end of this century. Similarly, the ratio of above: below-ground biomass of *Z. marina* is expected to decrease from 2:1 to 1.4:1 by the end of this century. Global standing stock is expected to increase by 94%, whilst the standing stock in the UK is expected to increase by 82%. This increase will be driven by increases in above- and below-ground biomass of seagrass.

4. Valuing the carbon sequestration component of climate regulation by seagrass, between present day and 2100

Understanding the extent and mechanisms of carbon storage and sequestration by seagrass, and how this will change with increasing ocean acidification, is clearly valuable from a natural resource management perspective. However, monetary valuation of this service further enables the debate, making the potential costs and benefits transparent and comparable to other impacts of ocean acidification. Carbon sequestration is an important component of climate regulation and the benefits of this are a stable and equable climate (NEA, 2011). These benefits can be valued in monetary terms using a carbon price as a proxy. Carbon prices can be determined using a number of different methods, including market, abatement or mitigation costs and social costs (DECC, 2011; Defra, 2007; Stern, 2006; Tol, 2005). Part of the case study here is UK based so a UK price is used, specifically the currently advised DECC central non-traded carbon price (DECC, 2011).

4.1. Valuing carbon sequestration by global and UK seagrass beds

Combining the mid DECC (2011) CO_2 price with the sequestration rates derived in Section 3, a £/ha/yr value can be calculated for global and UK CO_2 sequestration by seagrasses (Table 6). CO_2 values are calculated by multiplying carbon values by 3.67.

Table 4
Estimates of carbon sequestration, in tC/ha/yr, for seagrass globally and in the UK in response to ocean acidification.

	Seston, tC/ha/yr	Necromass, tC/ha/yr	Total sequestration, tC/ha/yr	Sequestration, tC/area/yr (Global area = 17.7–60 * 106 ha: McLeod et al., 2011) (UK area = 5000–10,000 ha: BRIG, 2008; Davison and Hughes, 1998; Luisetti et al., 2013)
Global				
Current	0.83[a]	0.55[a]	1.38	24.4–82.8 * 10[6]
2100 OA scenario[d]	1.33[b]	1.24[c]	2.57	45.5–154.2 * 10[6]
Change	0.5	0.69	1.19	21.1–71.4 * 10[6]
UK				
Current	0.31[a]	0.21[a]	0.52	2600–5200
2100 OA[d] scenario	0.5[b]	0.47[c]	0.97	4850–9700
Change	0.19	0.26	0.45	2250–4500

[a] Carbon deposition from sestonic particles represents 60% of carbon sequestration, whilst burial of dead roots and rhizomes (necromass) is thought to account for approximately 40% of carbon sequestration (Gacia et al., 2002).
[b] Particle deposition increases linearly with increasing shoot density (Hendriks et al., 2008), therefore an increases in seagrass density of 60% should lead to a 60% increase in organic carbon deposition (*1.6).
[c] If belowground biomass increases by 125% then a 125% increase in carbon sequestration from plant material is expected (*2.25).
[d] OA scenario using pH levels between 7.6 and 7.9.

Table 5
Estimates of standing stock (above- and below-ground biomass), in tC/ha, for seagrass globally and in the UK in response to ocean acidification.

	Above ground biomass, tC/ha	Below ground biomass, tC/ha	Total standing stock, tC/ha	Standing stock, tC (tC/ha * area) (Global area = 17.7–60 * 106 ha: McLeod et al., 2011) (UK area = 5000–10,000 ha: BRIG, 2008; Davison and Hughes, 1998; Luisetti et al., 2013)
Global				
Current[a]	1.2	1.32	2.52	44.6–151.2 * 10^6
2100 OA scenario	1.92[b]	2.97[c]	4.89	86.6–293.4 * 10^6
Change	0.72	1.65	2.37	42.0–142.2 * 10^6
UK				
Current[d]	1.07	0.54	1.61	8100–16,100
2100 OA scenario	1.71[b]	1.22[c]	2.93	14,700–29,300
Change	0.64	0.68	1.32	6600–13,200

[a] Global seagrass ratio of above: belowground biomass = 1:1.1 (Duarte and Chiscano, 1999).
[b] At 2100 pH levels shoot density increased 60–200%. We take the conservative values of an increase of 60% in shoot density (and therefore above-ground biomass) *1.6.
[c] At 2100 pH levels below-ground biomass increased 125–300%. We take the conservative values of an increase of 125% in below-ground biomass *2.25.
[d] The ratio of above: below-ground biomass for *Z. marina* = 2:1 (Duarte and Chiscano, 1999).

Table 6
Current and future carbon sequestration value with and without OA.

	Current day	2100 without OA	2100 with OA
Global			
Sequestration rate (tCO$_2$/ha/yr)[a]	5.06	5.06	9.43
Carbon value (£/tCO$_2$)	55	284	284
Value (£/ha/yr)	278.3	1437.04	2678.12
Total value (£ million/global/yr)[b]	4926–16,698	25,436 –86,222	47,402 –160,687
UK			
Sequestration rate (tCO$_2$/ha/yr)[a]	1.91	1.91	3.56
Carbon value (£/tCO$_2$)	55	284	284
Value (£/ha/yr)	105.05	542.44	1011.04
Total value (£ million/UK/yr)[b]	0.53–1.05	2.71–5.42	5.06–10.11

[a] As calculated in Table 4.
[b] Calculated from the minimum and maximum area (Table 1) multiplied by CO$_2$ sequestration value.

Combining these £/ha/yr rates with the seagrass areas detailed in Section 2 a global (£/global/yr) and UK (£/UK/yr) value for annual carbon sequestration by seagrass can be calculated. In the OA scenario, the increase in value is due both to the increased CO$_2$ sequestration rate and also to the increasing CO$_2$ price; the central non-traded value is £55 in 2010 rising to £284 in 2100 in Real £2011 (DECC, 2011). In the non-OA scenario the increase in value is solely due to the increase in CO$_2$ price.

The monetary value of carbon sequestered by seagrasses increases with time, although the increase in seagrass density and belowground biomass will lead to an almost doubling of value of seagrass carbon sequestration in 2100, increasing 'blue carbon' sequestration capacity and to some extent mitigating the negative effects of ocean acidification. This increase in value strengthens the argument to maintain these seagrass habitats into the future.

4.2. Long term values of carbon sequestration by global and UK seagrass beds

Annual values, such as those presented in Table 6, do not provide a true indication of the long term value of this ecosystem service in this habitat. As comparisons may be made to long term development options (e.g. harbour development) it is critical that long term values for this service are also provided. As such, the Net Present Value (NPV) of carbon sequestration is also calculated. We explore two scenarios, firstly one with sequestration increasing linearly over time with increasing ocean acidification, and secondly a scenario with no OA and a constant carbon sequestration rate (Table 7). We assume that seagrass cover remains stable within the predicted range and no meadow degradation and loss occurs. We also assume that the annual carbon sequestered by the

seagrasses is permanent. The DECC (2011) central non-traded carbon price is again applied to calculate the values of CO$_2$ sequestration under the two scenarios. As recommended by the HM Treasury Green Book (2011), and line with UK policy we apply a discount rate of 3.5% diminishing over time.

5. Discussion

This study has investigated the potential change to carbon storage and sequestration by seagrass beds in response to ocean acidification. It must be taken into consideration that the benefit of increased carbon storage and sequestration by seagrass beds in response to ocean acidification is unlikely to outweigh the negative impact on other ecosystem services provided by the ocean. Many other marine ecosystem services may be negatively impacted by a decrease in pH, most notable of which may be provisioning services such as wild fisheries and aquaculture (Cooley et al., 2009). Ocean acidification has been shown to have negative impacts on the behaviour of fish (Dixson et al., 2010; Munday et al., 2014), whilst early life histories and calcification have been impaired in many species of commercially harvested molluscs and crustaceans (Arnold et al., 2009; Gazeau et al., 2010, 2007). Fisheries and aquaculture were worth $217.5 billion in 2010 (FAO, 2012), a value 13–44 times the value of carbon sequestration capacity of seagrass beds, therefore negative impacts of OA on fisheries and aquaculture alone will likely outweigh the increase carbon sequestration capacity of seagrass, leading to loss of employment and indirect revenue costs (Cooley and Doney, 2009).

Furthermore, seagrass beds provide numerous other ecosystem services such as nursery habitat, food provision, coastal protection and water purification (Barbier et al., 2011). The effect of ocean acidification on these other services has not been evaluated in this

Table 7
Estimation of long term CO_2 sequestration by global and UK seagrass habitats, 2010–2100, under two OA scenarios, and associated monetary values, expressed as Net Present Value (NPV) UK£ 2011 real prices. The HM Treasury Green Book (2011) discount rate of 3.5% diminishing over time has been applied.

	UK seagrass	Global seagrass
Without OA		
CO_2 sequestered, million tonnes	0.9–1.7	8149–27,652
Value of CO_2 sequestered (£million)	43–87	406,468–1,379,324
With OA		
CO_2 sequestered, million tonnes	1.2–2.5	17,909–39,575
Value of CO_2 sequestered (£million)	61–123	879,667–1,957,365

paper, and it is unknown whether ocean acidification may lead to more negative consequences for other ecosystem services provided.

This paper highlights perhaps one of the few positive stories for ocean acidification. Seagrasses are important carbon sinks and are responsible for approximately 15% of carbon storage in the oceans (Kennedy and Bjork, 2012). A reduction in the pH of ocean surface waters is expected to lead to an increase in both above- and below-ground biomass, leading to an 82–94% increase in the carbon storage and sequestration potential of this group of taxa, potentially increasing ocean storage of carbon by 12–14%. Currently, mean carbon burial in seagrass beds is lower than in mangroves and saltmarshes (1.38 tc ha^{-1} yr^{-1} in comparison to 2.18–2.26 tc ha^{-1} yr^{-1}), although the increase in carbon burial expected in response to future OA would increase mean carbon sequestration rates to a rate higher than the mean value for saltmarshes and mangroves (2.57 tc ha^{-1} yr^{-1}). This will increase the conservation value of this habitat, and if seagrass cover remains stable, by the end of this century an extra 21.1–74.4 million tonnes of carbon could be sequestered annually by seagrasses per year. This equates to an extra 77.4–270.0 million tonnes CO_2. The average annual CO_2 emissions per capita in the UK in 2010 were 7.9 t CO_2 (World Bank, 2014). This increase equates to sequestration of between 10 and 34 million of the UK populations emissions in 2010. This increase in sequestration rates will add a net present value of between approximately £500 and 600 billion to carbon sequestration in seagrass beds between 2010 and 2100. In the UK, carbon sequestration by seagrass beds is expected to increase by 2250–4500 tonnes carbon per year or 8258–16515 tonnes CO_2 equivalent. This will lead to a net present value of carbon sequestration in seagrass beds in the UK between 2010 and 2100 by approximately £18–36 million between 2010 and 2100.

The values detailed here are the best available current estimates. However, they are dependent on a number of key assumptions and it is recognised that there is considerable uncertainty associated with these values. Key uncertainties and assumptions are discussed below as a starting point for wider discussion of recommendations for future research.

Firstly it assumed that seagrass coverage will remain continuous until the end of this century, however, if current rates of seagrass loss continue this will not be the case as, although the value of each individual hectare of seagrass will increase, much of the benefits of OA on carbon storage and sequestration will be lost. Approximately 30% of seagrass beds are thought to have been lost since the mid-1970s (Waycott et al., 2009). Target 15 of the 2010 Aichi targets of the Convention on Biological Diversity (CBD) is that "by 2020, ecosystem resilience and the contribution of biodiversity to carbon stocks has been enhanced, through conservation and restoration, including restoration of at least 15 per cent of degraded ecosystems, thereby contributing to climate change mitigation and adaptation and to combating desertification". This calls for national and regional policies to implement the protection of both terrestrial and marine carbon sinks, including seagrass beds. Whilst seagrass cover appears to be declining in

many parts of the world (Waycott et al., 2009), evidence of recovery has been seen in some areas (Greening et al., 2011; Reise and Kohlus, 2008), and some seagrass restoration projects have proved successful (Orth et al., 2006; Thorhaug, 1985). If seagrass protection legislation is successfully implemented then this, coupled with ocean acidification, could see an even sharper increase in the carbon storage and sequestration value of seagrass beds in the future. We recommend that improved mapping of current seagrass beds is undertaken, alongside evidence projections for the future under different environmental and management scenarios, to enable improved sustainable management of these habitats.

An additional assumption is made of the permanence of the sequestration. Whilst the dead roots and rhizomes of the seagrass *Posidonia oceanica* are known to form mattes and be stored for millennia (Mateo et al., 1997), the permanence of sequestration for other species of seagrass is unknown. We recommend that carbon dating studies be used to aid in understanding the permanence of carbon sequestration of different seagrass species. Changes to carbon sequestration rates in response to ocean acidification have not been directly measured, and therefore had to be inferred from changes in plant structure and biomass. We used the precautionary principle, taking values from the lower end of the scale on OA induced effects (an increase in density of 60% and increase in belowground biomass of 125%). If future increases in plant density and belowground biomass exceed these values than higher rates of carbon storage and sequestration are expected.

There is uncertainty in both the carbon price and discount rate. A variety of carbon prices and discount rates are available but no single price or rate is ideally suited to environmentally sequestered carbon (Beaumont et al., 2014). Discounting is central to economic theory and yet the discount rate for valuing natural capital has been contested in numerous published studies (Hampicke, 2011; Nordhaus, 2007; Stern, 2007; Weitzman, 2007). Different discount rates can lead to significant variation in economic valuation, and if a lower discount rate was used then the value of carbon storage and sequestration in seagrass beds in response to OA could be orders of magnitude higher. Likewise varying the carbon price also has the potential to significantly change the value of carbon sequestration. Further research is required to develop carbon prices and discount rates which are specifically designed for environmental carbon sequestration, and to better enable the inclusion of associated uncertainty into estimates and more broadly into environmental management considerations.

Inconsistency in seagrass carbon sequestration rates add further conjecture into the question. Only two values could be obtained for carbon sequestration in *Zostera marina*, the primary species which occurs around the UK (0.37–0.52 tC ha^{-1} yr^{-1}: Cebrian et al., 1997; Greiner et al., 2013). These values came from studies in the USA and the Mediterranean and it has not been demonstrated that carbon sequestration rates in the UK are the same. Global seagrass carbon sequestration rates were extremely variable (0.45–1.90 tC ha^{-1} yr^{-1}: McLeod et al., 2011), although the mean rate (1.38 tC ha^{-1} yr^{-1}) of 123 studies was used, which should disguise some of the variation. There is also recognised uncertainty associated with how these carbon sequestration rates will change with OA, but one thing is certain; carbon storage and sequestration by seagrasses in response to future ocean acidification is set to increase, and as such we will see an increase in the value of these systems for regulating our climate.

6. Conclusions

Seagrass beds provide numerous other important ecosystem services such as protection of the coastline, bioremediation of waste, food provision, and maintenance of marine biodiversity (Cullen-Unsworth and Unsworth, 2013; Jackson et al., 2012). These

services have not been investigated in this study, but it must be taken into consideration that whilst the story may be positive for carbon sequestration, other ecosystem services may suffer. Seagrass-associated taxa such as fish and invertebrates are likely to respond negatively to OA (e.g. Dupont and Thorndyke, 2009; Munday et al., 2009), leading to a potential decrease in ecosystem services such as food provision and maintenance of biodiversity.

Seagrass beds are environmentally, socially and economically important habitats and as such their sustainable management is critical to avoid their continued degradation and associated loss of ecosystem services. This paper provides an important step forward with regard to reviewing and synthesising the current evidence base regarding carbon sequestration by seagrass beds and how this is impacted by OA. It has also provided a valuable guide to directing future research in this area by highlighting key data gaps which will need to be filled to enable management of this valuable habitat.

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