Manuscript Number: OCMA-D-11-00008R1

Title: Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies

Article Type: SI: Blue Carbon

Keywords: coastal, seagrass meadows, carbon sinks, climate change, mitigation

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Order of Authors: Carlos Duarte; Hilary Kennedy; Núria Marbà; Iris Hendriks

1 Cover Letter

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Victor N de Jonge
Editor-in-Chief
Ocean & Coastal
Management

Ref. Ms. No.: OCMA-D-11-00008

Dear Dr. de Jonge,

Attached, please find a revised version of the ms. "*Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies*" to be reconsidered for publication in "*Ocean & Coastal Management*".

We received one review,where the reviewer stated that "The manuscript should prove very useful to workers in the field and I consider it definitely worth publishing", but recommends that the language be improved and some additional comments addressed before the manuscript be accepted for publication.

We have not spared any efforts in revising the manuscript to accomodate the reviewer's suggestions and improve the style, clarity and language. We have also included a discussion of recent manuscripts and developments that were published after the manuscript was submitted, thereby improving the manuscript further. Below, please find a detailed account of the changes made in response to the reviewer's comments.

As a result of these changes the manuscript is much improvied and we hope that you will now find it acceptable for publication in "*Ocean & Coastal Management*".

Sincerely,

Carlos M. Duarte

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Changes made to address the reviewer's comments

Reviewer #1: However, in some parts the language is not good, and there are a number of other things that needs to be addressed before the manuscript can be accepted for publication.

Action: We agree and have thoroughly revised the manuscript to improve the style, clarity and language, as well as to improve the manuscript where deficiencies were noted.

Reviewer #1: In the end of the Introduction (page 4) the author's states:
"Here we provide a synthesis of recent research addressing both these gaps and identify additional elements required to formulate a robust strategy for climate change mitigation based on the role of seagrass meadows as intensen carbon sinks."
However, while the synthesis of recent research in the manuscript is excellent, the gap analysis and strategies appears to be rather hastily written. Sometimes they are even hard to understand because of poor language. This part of the manuscript would benefit greatly from a thorough revision (more details below).

Action: We agree and have greatly (an additional 1.5 pages) expanded the discussion of gaps and uncertainties, which is now far more clear than it was in the original manuscript.

Reviewer #1: Also, it would be good if the authors could comment on a current paper:
Mcleod et al 2011 "A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2". Frontiers in Ecology and the Environment doi:10.1890/110004).
Which I believe was not published when this manuscript was submitted. This paper has a broader scope than the submitted manuscript, and I think that the overlap is not that big. However, some estimations like the "estimates of carbon burial rates" on page 13 and the rate of seagrass losses are quite different from what is given in the McLeod paper, and it would be good if the authors could include some discussion on this.

Action: Indeed Mcleod et al. was not published - nor accepted - when the ms. was submitted. We now cite Mcleod et al. (2011) where appropriate and comment on the agreement between the estimates cited here and those reported here.

Reviewer #1: On page 15 the authors write (in a very very long and complicated sentence): "Despite these advances in our knowledge on the role of seagrass meadows as carbon sinks, a number of uncertainties remain that

need be dissipated to provide the robust support required to implement climate change mitigation strategies based on
the conservation and recovery of seagrass meadows. These include:"

the list that follows appears to be appropriate and sound recommendations, however it is poorly written, and sometimes are the recommendations not motivated.
For example, the first sentence reads: " Improved knowledge of global seagrass cover, currently limited by insufficient coverage of some regions and poorly constrained, by a factor of two, estimates of surface area covered by seagrasses" I have problems understanding what the authors really mean, are the estimated coverage underestimated by a factor of two, or...?

Action: We agree, and have improved clarity and use of English language (here and throughout the manuscript), and expanded the discussion on the uncertainties and gaps.

Reviewer #1: The next sentence reads " Improved estimates of regional and global estimates", please rephrase, you can't ask for estimates of estimates.

Action: Done.

Reviewer #1: The next again sentence: "Major regions requiring investigation include Indonesia, Malaysia, Borneo, Bahamas and the Bahamas bank, Africa and South America" I agree with the authors, but please motivate WHY you think that these areas should have priority.

Action: We have done so. The text now reads: "*Research effort, including mapping, on seagrass ecosystems in the coast of Africa and South America has been rather limited, and present estimates of the area covered by seagrass meadows in these regions are likely to be severely underestimated"*.

Reviewer #1: Next: " Improved models assessing suitable seagrass areas from environmental characteristics" For what purpose? Explain WHY you think this is important!

Action: We agree. The text now reads: "*Improved models to identify suitable areas for seagrass growth. Mitigation strategies based on seagrass carbon sinks include efforts to conserve seagrass meadows and efforts to restore seagrass meadows. The success of seagrass restoration projects depends critically on the choice of adequate sites to support seagrass growth. However, guidelines on the environmental requirements conducive to successful restoration efforts are still lacking. The light requirements to support seagrass growth have been sufficiently documented as to allow delineation of areas receiving adequate light to support seagrass growth (e.g. Gattusso et al. 2006).*

However, more comprehensive guidelines are needed, including consideration of adequate sediment characteristics and dynamics (e.g. Cabaço et al. 2009), wave and energy environment and even biotic requirements to support adequate seagrass growth".

Reviewer #1: Fifth bullet: "Identification of the factors responsible for variability carbon sink capacity" insert an "in" so that it reads: Identification of the factors responsible for variability in carbon sink capacity.

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***Detailed Response to Reviewers**

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***2 Title Page with all author info**

Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies

Carlos M. Duarte[1,2, *], Hilary Kennedy[3] , Núria Marbà[1], and Iris Hendriks[1]

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Abstract

Seagrass meadows support high primary production rates and their canopies are efficient at filtering particles out of their water column as well as in preventing resuspension of the sediments. In addition, decomposition rates in seagrass sediments are slow, because of low nutrient concentration in seagrass detritus and low oxygen concentration in seagrass sediments. These characteristics result in high carbon burial rates in seagrass meadows, which have the capacity to accumulate large stores of carbon in their sediments, raising the seafloor. Carbon fingerprinting techniques allow to calculate both the age of these deposits and, therefore, the rate of carbon burial and identify the contribution of carbon produced by the seagrass. Yet, data on the regional cover and carbon stocks in seagrass meadows is sparse for some regions, particularly the Indo-Pacific, Africa and South America. In addition, our understanding of the factors regulating the variability in carbon sink capacity among seagrass meadows is limited. These gaps limit the capacity to formulate strategies to mitigate climate change based on the carbon-sink capacity of seagrass meadows. A research strategy needs be formulated to address these gaps and provide the necessary protocols to ensure the accountability of mitigation actions involving the conservation and restoration of seagrass meadows.

Introduction.

Seagrass are a group of about 60 angiosperm species adapted to life in the sea, whether permanently or temporarily submerged (Hemminga and Duarte 2000). Seagrass are clonal, rhizomatous plants that develop, largely through clonal growth, large ecosystems termed seagrass meadows, often monospecific but that can include up to 12 species in the tropics (Hemminga and Duarte 2000). Seagrass meadows occur along the shores of all continents, to maximum depths of up to 50 m, depending on water transparency, except Antarctica (Hemminga and Duarte 2000). Whereas there is no comprehensive inventory of the area covered by seagrasss globally, different estimates are available. The documented seagrass area is 177,000 Km^2 (Green and Short 2003), but this is an acknowledged underestimate of the total area covered by seagrass meadows, since many regions with large seagrass meadows (e.g. Indonesia and Bahamas) have not been fully charted. Hence, the estimates most commonly used in the literature use a low estimate of 300,000 Km^2 and a high estimate of 600,000 Km^2 (Duarte et al. 2005a, Nellemann et al. 2009, Mcleod et al. 2011), with the global area potentially suitable to support seagrass growth estimated at 4,320,000 Km^2 (Gattusso et al. 2006).

Seagrass meadows are highly productive ecosystems (Duarte and Chiscano 1999) and play a key role as habitats supporting high biodiversity (Hemminga and Duarte 2000). In addition, they are characterised by their capacity to sequester and store considerable amount of carbon in their carbon-rich sediments (Duarte et al. 2005b), being responsible for 20 % of the global carbon sequestration in marine sediments despite occupying 0.1 % of the ocean surface (Duarte et al. 2005b, Kennedy et al. 2010). Regrettably, seagrass meadows are being lost globally at fast rates, of about 5% $year^{-1}$, and at least 1/3 of the area present has been lost since

World-War II (Orth et al. 2006, Waycott et al. 2009), which represents the loss of an important carbon sink (Mcleod et al. 2011).

Realisation of the important carbon sink capacity of seagrass meadows has recently led to the proposal that seagrass meadows, along with salt-marshes and mangrove forests, could be used to support strategies to mitigate climate change (Nellemann et al. 2009, Laffoley et al. 2009, Mcleod et al. 2011). These strategies would be based on both the conservation and reforestation of seagrass meadows. However, the development of management schemes based on the role of seagrass meadows as intense carbon sinks has been precluded to-date by limitations in current knowledge on the mechanisms conducive to their high carbon sink capacity and the rates of carbon burial they do support. Here we provide a synthesis of recent research addressing both these gaps and identify additional elements required to formulate a robust strategy for climate change mitigation based on the role of seagrass meadows as intense carbon sinks. We believe that the knowledge presented here, largely based on papers published within the past 5 years, provides a solid underpinning to launch carbon mitigation strategies based on the conservation and restoration seagrass meadows.

Mechanisms of carbon burial in seagrass communities.

Metabolic C capture

Seagrasses rank amongst the most productive populations on the biosphere (Duarte and Chiscano 1999). On average, net primary production per unit of area of seagrass populations, when considering that of leaves, rhizomes and roots, is about 1012 g DW m^{-2} yr^{-1} (Duarte and Chiscano 1999), equivalent to 404 g C m^{-2} yr^{-1} or 14.8 ton CO_2 ha yr^{-1}, with a ratio aboveground: belowground production of 16.4 ±

8.5 (Duarte and Chiscano 1999). The most productive seagrass meadows are multispecies meadows in the Indo-Pacific region, those of *Phyllospadix* spp. in the North American Pacific coast and those of *Posidonia oceanica* in the Mediterranean Sea (Duarte and Chiscano 1999). Despite the small global extension of seagrass populations, their net primary production accounts for about 1 % of the global net marine primary production (Duarte and Cebrián 1996). The production of seagrass species accounts for most of the primary production of seagrass communities, which includes contributions by epiphytic communities. The leaves and rhizomes of seagrasses are colonised by epiphytic autotrophic and heterotrophic organisms. Net primary production of seagrass autotrophic epiphytes, comprising microscopic and macroscopic algae, has been quantified for a few seagrass communities (Hemminga and Duarte 2000). Net primary production of seagrass autotrophic epiphytes ranges from 13.8 g DW m^{-2} yr^{-1} to 755 g DW m^{-2} yr^{-1}, and it typically accounts for 20-60 % of total seagrass aboveground productivity (Hemminga and Duarte 2000). Therefore, the photosynthetic activity of seagrass meadows contributes a significant amount of marine organic carbon.

Carbon accumulation in seagrass meadows

Whereas seagrass meadows support an important biomass, this represent a minor component of the carbon stocks in seagrass meadows, which are - by far - dominated by the sedimentary pool. Seagrass sediments are organic-rich, with an average organic concentration of 4.1 % (Kennedy et al. 2010). Seagrass meadows occupy coastal environments over millenary time scales and are able to form thick carbon deposits, raising the seafloor by about 1 mm per year (Kennedy et al. 2010). The thickest documented sedimentary deposit has been reported at 11 m thick for the

Posidonia oceanica meadow at Port Lligat, Spain, corresponding to an accumulation of about 0.18 tons C m^{-2} over 6,000 years of seagrass growth at that site (Lo Iacono et al. 2008). Thick seagrass deposits, several meters in thickness, have been reported for other sites, including other sites in the Spanish Mediterranean, Shark Bay (W. Australia) and Florida Bay (cf. Kennedy et al. 2010).

Hence, seagrass meadows combine a high metabolic capacity to act as carbon sinks with the capacity to accumulate large carbon pools in the sediments over millenary time scales. The long retention times of carbon in sedimentary deposits in seagrass meadows is quite unique and renders seagrass meadows some of the most carbon-rich ecosystems in the Biosphere. Understanding the reasons for the high capacity of seagrass to capture and store carbon is fundamental to manage these ecosystems in support of strategies to mitigate climate change.

Understanding the high capacity for carbon burial in **seagrass meadows**

The high primary production of seagrass communities is matched by high rates of organic matter consumption through respiration (Duarte et al. 2010), largely derived by the contribution of heterotrophic organisms, such as benthic animals and sediment bacteria, present with high biomass in these ecosystems. Yet, more than 80 % of seagrass production is not consumed by herbivores (Duarte and Cebrián 1996), and decomposition rates of seagrass detritus are slow when compared with those of other organisms, because of the low nutrient (nitrogen and phosphorous) concentration in their tissues (Enríquez et al 1993). Hence, a fraction of the organic carbon produced by seagrass communities is not consumed by heterotrophs, resulting in a tendency for seagrass ecosystems to be generally autotrophic communities acting as carbon sinks (Duarte and Cebrián 1996, Duarte et al. 2010). Whereas organic matter consumption (respiration) may exceed production (gross primary production) during some periods of the year (Hemminga and Duarte 2000), the vast majority of metabolic estimates of seagrass communities available at annual time scales reveal that they are autotrophic, and hence act as CO_2 sinks (Duarte et al. 2010). The excess organic carbon produced by seagrass ecosystems is exported or buried (Duarte and Cebrián 1996).

Particle trapping: the role of seagrass meadows as filters.

Seagrass meadows develop lush canopies that affect the water flow above them, thereby acting as ecosystem engineers modifying their abiotic environment (Jones et al. 1997). The presence of seagrass canopies at the benthic boundary layer alters the roughness of the bottom (Granata et al. 2001; Nepf and Vivoni 2000) and thereby the vertical flow profile over the sediments and the associated turbulence structure (Ackerman and Okubo 1993; Fonseca et al. 1982; Gambi et al. 1990; Koch et al. 2006; Koch and Gust 1999), especially when canopy height represents more than 10 % of the height of the water column (Nepf and Vivoni 2000). Depending on shoot density and seagrass species, flow reduction resulting from current deflection by the canopy ranges from 2- to more than10 -fold compared to water flow outside the seagrass bed (Ackerman 1986; Gambi et al. 1990; Hendriks et al. 2008). Seagrass canopies also have a dampening effect on waves (Bouma et al. 2005; Fonseca and Cahalan 1992). When waves enter the near shore region, they encounter the friction (shear stress) of the seagrass canopy and become shallow water waves. This leads to wave-induced transport in a process referred to as Stokes drift, which may be of considerable impact in many coastal environments. Although wave attenuation is maximal when the meadow occupies a large portion of the water column (Fonseca and Cahalan 1992), reduction in wave energy and orbital velocity occurs even when beds are located at 5-15 m depth and the plants occupy a small portion of the water column (Granata et al. 2001). However, the capacity of seagrasses to trap sediment might be lost under extreme flow conditions in wave-exposed environments (Fonseca and Bell 1998; Koch and Gust 1999).

Apart from the direct effect of dampening of waves and currents by seagrass canopies leading to increased sediment deposition (Gacia and Duarte 2001; Gacia et al. 1999; Hendriks et al. 2008) and decreased resuspension (Lopez and Garcia 1998; Terrados and Duarte 2000), seagrass can also directly intercept suspended sediment particles with their canopies. Seagrass canopies increase the effective benthic surface by as much as twenty times thereby providing a large surface for sediment deposition and the probability of contact. The collision of suspended particles with seagrass leaves increases particle path length and causes momentum loss (Hendriks et al. 2008), which results in increased deposition. Field estimates indicate that the potential for particle contact with leaf surfaces sometimes approaches 100 % in *Zostera marina* canopies (Ackerman 2002). In addition, exopolymeric substances secreted by epiphytes can bind sediment particles to seagrass leaves (Agawin and Duarte 2002). Epiphytic layers on seagrass leaves may also contribute to the trapping of particles in seagrass beds by increasing the roughness of the canopy and increasing the velocity gradient layer on the leaf surface (Koch et al. 2006). The capacity of seagrass meadows to trap particles can be quite high, and, for instance, Barrón et al. (2004) calculated, using carbon budgets across seagrass patches of different age, that the input of carbon originating elsewhere, trapped into sediments of *Cymodocea nodosa* patches in a Mediterranean lagoon, must be about 157 mmol C m^{-2} day^{-1}.

Hence, seagrass meadows act as filters trapping and retaining particles suspended in the water column, which drives an additional carbon flow contributing to carbon sequestration in seagrass sediments (Kennedy et al. 2010).

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High carbon preservation in seagrass sediments

High metabolic carbon sink capacity and high carbon trapping capacity supports a large flow of carbon to seagrass sediments. However, in order for seagrass meadows to be effective as carbon sinks this carbon must be effectively preserved in the sediments for centuries to millennia, as can be the case. The mechanisms conducive to high carbon preservation rates in seagrass sediments include (1) low nitrogen and phosphorus content in seagrass tissues (Duarte 1990), which renders seagrass detritus a poor substrate to support microbial growth and results in low decomposition rates (Enriquez et al. 1993); (2) low oxygen concentration in seagrass sediments. Seagrass sediments are often anaerobic, which leads to inefficient microbial metabolism and enhances seagrass preservation; (3) the fact that a fraction of seagrass production (up to 50%), that of roots and rhizomes, is placed directly into the sediments, often at depths of tens of centimetres (Duarte et al. 1998), contributing to the high preservation efficiency for these tissues; (4) the fact that being underwater, seagrass sediments are free of fires, which are responsible for the emission as CO_2 of much of the organic carbon accumulated in forest soils on land, and (5) the dissipation of waves and turbulence by seagrass canopies prevents sediment resuspension and increases the retention of sediments and the associated carbon. The combination of all these factors leads to high carbon preservation in seagrass sediments, which together with high metabolic inputs and particle trapping rates explain the role of seagrass meadows as intense carbon sinks in the biosphere.

Assessing seagrass carbon burial

Assessment of the net community metabolism of seagrass meadows

Available estimates of seagrass community metabolism, described by gross primary production, respiration and net community production, have been recently reviewed and synthesised to quantify the role of seagrass meadows as carbon sinks (Duarte et al 2010). Most seagrass metabolic estimates have been derived from changes in oxygen concentration in incubation chambers deployed *in situ* and from diel oxygen concentration curves measured in the field (Duarte et al 2010). However, metabolic rates of seagrass communities have been also calculated from changes in CO_2, ^{14}C uptake and incubations of sediment cores, containing seagrass communities, in the laboratory. Since year 1956, seagrass community metabolism has been quantified for 155 sites. These estimates are unevenly distributed, with most of them (67 %) assessing the metabolism of tropical and subtropical seagrass meadows and more than one forth that of Mediterranean ones (Duarte et al 2010). There is a substantial gap of information on community metabolic rates for seagrass meadows along the coasts of the Southern Hemisphere and North and West Pacific regions (Duarte et al 2010).

The synthesis of available estimated revealed that gross primary production (GPP) of seagrass communities averages 224.9 ± 11.1 mmol O_2 m^{-2} day^{-1} and tends to exceed respiration (R, average ± standard error = 187.6 ± 10.1 mmol O_2 m^{-2} day^{-1}) for most meadows (Duarte et al 2010). This indicates that seagrass meadows tend to be autotrophic ecosystems, with an average net community production (NCP) of 27.2 ± 5.8 mmol O_2 m^{-2} day^{-1} (Duarte et al 2010). Two-thirds (63%) of the seagrass meadows examined acted as CO_2 sinks. Seagrass community metabolic rates vary across geographical regions and species, with tropical seagrass meadows tending to have lower (although not significantly) NCP than temperate ones (Duarte et al 2010). Meadows of fast-growing seagrass species have the highest GPP, and together with those of *Thalassia testudinum*, the highest R (Duarte et al 2010). GPP and R are positively related, but seagrass meadows tend to be net autotrophic ecosystems (i.e. GPP/R > 1) when GPP exceeds 186 mmol O_2 m^{-2} day^{-1} (Duarte et al 2010), and seagrass meadows tend to act as CO_2 sinks when average aboveground biomass exceeds 41 g DW m^{-2} (Duarte et al 2010).

The average net metabolic capture of carbon by seagrass communities (9.9 ± 2.22 mol C m^{-2} yr^{-1}, Duarte et al 2010) is more than five times the C sink capacity of that of North American wetlands and the net carbon captured by the 10% seagrass meadows with the largest carbon sink capacity is well above the rates of carbon sink in undisturbed Amazonian forests, assumed to be the largest terrestrial carbon sinks (Duarte et al 2010). Considering a global area of seagrass meadows ranging from 300,000 km^2 to 600,000 km^2 and the average (± SE) NCP per unit of area, seagrass meadows would bury, only through their metabolic activity, between 20 and 50 Tg C $year^{-1}$ using the low estimate of global seagrass extension and between 41 and 101 Tg C $year^{-1}$ using the high estimate of seagrass cover. These estimates confirm that seagrass meadows rank amongst the strongest CO_2 sinks in the biosphere, and that despite their small global extension (less than 0.1 % of ocean surface) they bury about 20 % of the total carbon buried in the global ocean.

Assessment of carbon storage

The extent to which seagrass organic matter accumulates in the sediment can be determined in a number of ways (Table 1). In studies examining the fate of organic carbon, estimates of losses due to herbivory, decomposition and export can be compared with seagrass primary production to determine how much carbon is unaccounted for and hence is assumed to accumulate in the sediment. Duarte and Cebrian (1996) compiled the available data and estimated that, on average, 16% of seagrass primary production accumulates in the sediment. There are limitations to this technique as it generally provides only an indirect estimate of carbon accumulation. In addition, data compilations may have a mismatch between the amount of data available for primary production relative to that available for herbivory, decomposition and export. The data provided are also average values and do not therefore identify the relative importance of different seagrass species, which may be substantial. For example, Cebrian et al. (1997) followed the fate of carbon in four Mediterranean seagrass species and found that *Posidonia oceanica* had about 23 times higher capacity to accumulate organic carbon stocks than *Zostera noltii.* This kind of carbon budgeting provides short-term (annual) estimates of carbon accumulation in seagrass meadows. A more direct approach to studying short-term carbon accumulation is provided by sediment traps. Sediment traps are instruments that can be deployed in seagrass meadows to measure the quantity of sinking particles (Gacia et al. 1999). The traps can be deployed on a weekly or monthly basis and the organic (and inorganic) content of collected particles determined. As yet, there is little data available that uses this technique (Table 1).

Analyses of radioactive components of sediments coupled with estimates of carbon concentration can provide longer term estimates of carbon accumulation. The two most common techniques use the naturally occurring radioactive isotopes of lead (^{210}Pb) and carbon (^{14}C). Both techniques rely on the radioactive decay of these isotopes, the rate of which is well known. The ^{210}Pb has a half-life of 22.3 years, which means that after 22.3 years, only half of the original amount is undecayed. If the sediment layers are undisturbed, then as the sediment ages it slowly loses its radioactivity. The age of a sediment layer can therefore be determined by how much ^{210}Pb it contains. For ^{14}C, its half-life of 5730 years and so the age of much older sediments can be dated. This radiocarbon dating can be used to estimate the age of carbon containing materials up to about 58,000 to 62,000 years. In sediments the ^{14}C of refractory seagrass organic matter such as roots and rhizomes is commonly measured (Table 1).

Estimates of the short-term carbon storage in sediments (years) averages about 53 g C m^{-2} yr^{-1} and compares well with direct estimates of longer term carbon burial, averaging 58 g C m^{-2} a^{-1} (Table 1). The data sets used in these calculations are, however, from a restricted geographical area and represent meadows of only a few of all seagrass species.

Isotopic fingerprinting and accountability of seagrass carbon burial

Organic matter sources that contribute and accumulate in the sediments of seagrass meadows have different, and identifiable, organic carbon stable isotope signatures that can be tracked and quantified. Besides the seagrass tissues themselves, other potential sources of organic carbon are plankton, (usually collected as suspended particulate organic matter), seagrass epiphytes, microphytobenthos, macroalgae and terrestrial organic matter, including that of mangroves. All these organic matter sources have isotopic signatures that are generally different from those of seagrass tissues (Moncreiff and Sullivan 2001). So by measuring the stable isotopic signature of organic carbon (δ^{13}C) in seagrass sediments the proportions of seagrass and other organic matter sources that have accumulated can be estimated. Kennedy et al. (2010) compiled a data set containing 219 analyses of the organic carbon stable isotopic signature of seagrass sediments which have been collected at 88 locations around the world and showed that 50% of the organic matter that accumulates is derived from the seagrass tissues, with the other 50% of the organic matter that accumulates was derived from the trapping of phytoplankton and terrestrially derived particles by the seagrass canopy.

Using the range of organic carbon accumulation rates reported for seagrass meadows as between 83 to 133 g C m^{-2} y^{-1} (Duarte et al. 2005b), and combining this with the estimate that 50% of this organic matter is derived from seagrass tissues, it can be calculated that between 41 and 66 g C m^{-2} y^{-1} of the organic matter produced by seagrasses become buried in the sediment (Kennedy et al. 2010). The burial rate of seagrass-derived organic matter can be now compared with the net amount of organic matter produced in seagrass meadows (net community production) of around 120 g C m^{-2} y^{-1} (Duarte et al. 2010) to conclude that the amount buried represents 30-50% of the net community production. The organic matter not retained in seagrass sediments could have been exported away from the seagrass meadows to be decomposed or stored elsewhere. Overall, the total organic carbon sink sustained by seagrass meadows is the sum of their net community production and the non seagrass derived carbon that has been trapped and accumulates in their sediments. The sum of these two terms gives a range of between 160 to 186 g C m^{-2} y^{-1} , comparable to other recent estimates (e.g. 138 ± 38 g C m^{-2} y^{-1} in Mcleod et al. 2011), and further demonstrates the importance of seagrass meadows for carbon sequestration.

Limitations in the assessment of seagrass carbon sink capacity

The initial calculations by Duarte et al. (2005a) that seagrass meadows act as intense carbon sinks and contribute a significant fraction of all carbon sequestered in marine sediments allowed the formulation of climate change mitigation strategies based on the conservation and recovery of seagrass meadows (Nellemann et al. 2009, Lafoley et al. 2009). Parallel research, improved our understanding of the processes conducive to the role of seagrass meadows as carbon sinks (e.g. Hendriks et al. 2008) and delivered improved estimates of the carbon pools stored in seagrass sediments (Lo Iacono et al. 2008). The adoption of climate change mitigation strategies based on the conservation and recovery of seagrass meadows requires that current uncertainties be resolved. This need prompted recent synthesis assessing the metabolic capacity of seagrass meadows to act as carbon sinks (Duarte et al. 2010) and the identification of sources of carbon to seagrass sediments (Kennedy et al. 2010).

Our knowledge on the role of seagrass meadows as carbon sinks has improved rapidly in the past years. However, substantial uncertainties and gaps remain. These uncertainties need be addressed to provide the robust underpinnings required to implement climate change mitigation strategies based on the conservation and recovery of seagrass meadows. The actions require to address current uncertainties include:

1. Improved estimates of global seagrass cover. Present estimates of global seagrass are based on extrapolations and a canonical estimate of seagrass cover is lacking, largely due to difficulties in resolving seagrass cover using remote sensing tools. As a result, current estimates of global seagrass cover range two fold (see above). This uncertainty results from insufficient mapping of seagrass meadows in some regions, including Indonesia, Malaysia, Borneo, Bahamas and the Bahamas bank, Africa and South America. Some of these regions (Indonesia, Malaysia, Borneo, Bahamas and the Bahamas bank) have extensive carbonate platforms, suitable to support seagrass meadows, but have not been mapped. Research effort, including mapping, on seagrass ecosystems in the coast of Africa and South America has been rather limited, and present

estimates of the area covered by seagrass meadows in these regions are likely to be severely underestimated. Robust estimates of global and regional estimates of CO_2 sequestration by seagrass meadows require reliable estimates of the area they cover. Moreover, seagrass cover is a dynamic property, as meadows are declining worldwide (Orth et al. 2006, Waycott et al. 2009). Hence, global estimates need also be revised regularly to account for losses and, where present, gains.

2. A more comprehensive investigation of carbon stocks and burial rates over different time scales, including estimates of the thickness of sediments deposits under extant seagrass meadows. Current estimates of carbon stocks and burial rates in seagrass sediments are remarkably few, representing an insufficient basis to estimate carbon stocks accumulated in seagrass sediments.
3. Elucidation of the fate of the carbon exported from seagrass meadows. About 50% to 70% of the net community production of seagrass meadows is exported and could be buried elsewhere, as suggested recently (Kennedy et al. 2010). Assessing burial rates of seagrass-derived carbon in sediments with distance from seagrass beds will help resolve the size of the footprint of seagrass burial, since existing evidence indicates that seagrass carbon can be found buried in sediments at least tens of meters away from seagrass meadows (Kennedy et al. 2010). Hence, assessing carbon pools in seagrass sediments alone underestimates the carbon sink capacity of seagrass meadows. Resolving the footprint of seagrass meadows for carbon sequestration is essential to ensure the accountability of carbon removal by seagrass meadows in mitigation strategies based on conservation and restoration of seagrass meadows.

4. Identification of the factors responsible for variability in seagrass carbon sink capacity. Seagrass meadows range greatly, over an order of magnitude in their capacity to act as carbon sinks (e.g. Duarte et al. 2010). Whereas this variability is partially associated with changes in the biomass and species composition of the meadows (Duarte et al. 2010), models to predict the carbon sink capacity of seagrass meadows are still lacking. Yet, understanding of the factors controlling the carbon sink capacity of seagrass meadows will be fundamental to underpin the development of sound management strategies to maximise carbon sink capacity by, for instance, giving priority to the conservation of meadows with high carbon sink potential or managing the environment to maximise carbon removal by seagrass meadows.
5. Improved models to identify suitable areas for seagrass growth. Mitigation strategies based on seagrass carbon sinks include efforts to conserve seagrass meadows and efforts to restore seagrass meadows. The success of seagrass restoration projects depends critically on the choice of adequate sites to support seagrass growth. However, guidelines on the environmental requirements conducive to successful restoration efforts are still lacking. The light requirements to support seagrass growth have been sufficiently documented as to allow delineation of areas receiving adequate light to support seagrass growth (e.g. Gattusso et al. 2006). However, more comprehensive guidelines are needed, including consideration of adequate sediment characteristics and dynamics (e.g. Cabaço et al. 2009), wave and energy environment and even biotic requirements to support adequate seagrass growth.

6. Assessments of the impacts of seagrass loss on the fate of the carbon deposits stored by the seagrass meadow. The accelerated decline of seagrass meadows represents a loss of carbon sink capacity and is, therefore, an issue of concern. However, seagrass meadows also protect, by dissipating wave energy and reducing resuspension the massive sedimentary stocks of organic carbon accumulated over time. Current understanding of the functioning of seagrass meadows suggest that the loss of seagrass cover may, therefore, render the associated sedimentary carbon deposits vulnerable to be lost through erosive and resuspension processes. If seagrass decline rendered sedimentary carbon stocks vulnerable conservation strategies would be even more needed, since the consequences for carbon cycling will not be limited to the loss of carbon sink capacity but may include the remobilisation and eventual emission as CO_2 of carbon stocks accumulated over millennia. However, the fate of sedimentary carbon stocks following seagrass loss is as yet unknown, and resolving this unknown is, therefore, a matter of urgency.

Future strategies

The uncertainties listed above need be articulated into a research agenda conducive to a robust understanding of seagrass carbon burial to underpin climate change mitigation programs based on the conservation and restoration of seagrass meadows. These programs also require the development of reliable protocols for the cost-effective measurement of carbon sequestration ensuring the accountability of the carbon sequestered by seagrass meadows.

Whereas the benefits of conservation programs to preserve the carbon sink capacity of seagrass meadows can be readily evaluated, those of seagrass restoration programs involve greater uncertainties. Seagrass restoration programs are costly and have typically shown limited success at the time scales at which they have tested, typically two to four years. However, models show that the clonal nature of seagrasses leads to an exponential growth (Sintes et al. 2005, 2006), where seedlings or patches containing a few shoots may grow after a few decades to millions of shoots extending over significant areas, as documented in some field studies (e.g. Duarte and Sand-Jensen 1990). The explosive clonal growth of seagrasses offers a distinct advantage relative to reforestation projects on land, as the larger initial planting costs may be offset by the explosive clonal growth coupled with the distinct carbon-sink intensity of seagrass meadows. There is, therefore, a need to develop and validate models to predict the cumulative carbon sink associated with seagrass restoration projects and to evaluate their cost efficiency.

Acknowledgements

This is a contribution to the MEDEICG project, funded by the Spanish Ministry of Science and Innovation (number CTM2009-07013). We thank G. Grimsditch for the encouragement to write this paper. I.H. was supported by a Juan de la Cierva fellowship from the Spanish Ministry of Research and Innovation.

References

Ackerman, J.D., 1986. Mechanistic implications for pollination in the marine angiosperm Zostera marina. Aquat. Bot. 24, 343-353.

Ackerman, J.D., 2002. Diffusivity in a marine macrophyte canopy: Implications for submarine pollination and dispersal. Aquat. Bot. 89, 1119-1127.

Ackerman, J.D., Okubo, A.m 1993. Reduced Mixing in a Marine Macrophyte Canopy. Funct. Ecol. 7, 305-309.

Barron, C., Marba, N., Terrados, J., Kennedy, H., Duarte, C.M., 2004. Community metabolism and carbon budget along a gradient of seagrass (*Cymodocea nodosa*) colonization. Limnol. Oceanogr. 49, 1642–1651.

Belperio, A.P., Hails, J.R., Gostin, V.A., Polach, H.A., 1984 The stratigraphy of coastal carbonate banks and Holocene sea levels of northern Spencer Gulf, South Australia. Mar. Geol. 61, 297-313.

Bouma, T.J., et al. 2005. Trade-offs related to ecosystem engineering: a case study on stifness of emerging macrophytes. Ecology 86, 2187-2199.

Cabaço, S., Santos, R., Duarte, C.M., 2008. The impact of sediment burial and erosion on seagrasses: a review. Estuar. Coastal Shelf Sci. 79, 354–366.

Cebrian J., Duarte, C.M., Marba, N., Enriquez S., 1997. Magnitude and fate of the production of four co-occurring western Mediterranean seagrass species. Mar. Ecol. Progr.-Ser. 159, 308-308.

Denny, M.W., 1988. Biology and the Mechanics of the Wave-Swept Environment. Princeton University Press, Princeton, New Jersey.

Duarte, C.M., ySand-Jensen, K., 1990. Seagrass colonization: Patch formation and patch growth in *Cymodocea nodosa*. Mar. Ecol. Progr.-Ser. 65, 193-200.

Duarte, C.M., Chiscano, C.L., 1999. Seagrass biomass and production: a reassessment. Aquat.Bot. 5, 159-174

Duarte, C.M., Cebrián, J., 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41, 1758-1766

Duarte, C.M., Marba, N., Gacia, E., Fourqurean, J.W., Beggins, J., Barron C., Apostolaki, E.T., 2010. Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. Global Biogeochem. Cycles, 24, GB4032, doi:10.1029/2010GB003793.

Duarte, C.M., Cebrián, J. , 1996. The fate of marine autotrophic production, Limnol. Oceanogr. 41, 1758- 1766.

Duarte, C.M., Borum, J., Short, F.T., Walker, D.I., 2005a. Seagrass Ecosystems: Their Global Status and Prospects. In: Polunin NVC (ed) Aquatic Ecosystems: Trends and Global Prospects, Cambridge Univ. Press.

Duarte, C.M., Middelburg, J.J., Caraco, N., 2005b. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences 2: 1-8.

Duarte, C.M., 1990. Seagrass nutrient content. Mar. Ecol. Progr.-Ser. 67, 201-207.

Duarte, C.M., 2002. The future of seagrass meadows. Environ.l Conserv. 29, 192-206

Duarte, C.M., Merino, M., Agawin, N.S.R., Uri, J., Fortes, M.D., Gallegos, M.E., Marbá, N., Hemminga, M., 1998. Root production and belowground seagrass biomass. Mar. Ecol. Progr.-Sre. 171, 97-108.

Enríquez, S., Duarte, C.M., Sand-Jensen, K. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94, 457-471.

Enríquez, S., Duarte, C.M., Sand-Jensen, K., 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94, 457-471.

Fonseca, M.S., Cahalan, J.A., 1992. Preliminary evaluation of wave attenuation by four species of seagrass. Estuar. Coastal Shelf Sci. 35, 565-576.

Fonseca, M.S., Fisher, J.S., Ziemann, J.C., Thayer, G.W.,1982. Influence of the seagrass, *Zostera marina,* L. on current flow. Estuar. Coastal Shelf Sci.15, 367-380.

Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Mar. Ecol. Progr.-Ser. 171, 109-121.

Gacia, E., Duarte, C.M., Granata, T., 1999. An approach to the measurement of particle flux and sediment retention within seagrass (Posidonia oceanica) meadows. Aquat. Bot. 65, 255-268.

Gacia, E, Duarte, CM, Middelburg, JJ., 2002. Carbon and nutrient deposition in a Mediterranean seagrass (Posidonia oceanica) meadow. Limnol. Oceanogr. 47, 23-32.

Gacia, E., Duarte, C.M., 2001. Sediment Retention by a Mediterranean *Posidonia oceanica* Meadow: The Balance between Deposition and Resuspension. Estuar. Coastal Shelf Sci. 52, 505-514.

Gacia, E., Granata, T.C., Duarte, C.M., 1999. An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. Aquat. Bot. 65, 255-268.

Gambi, M.C., Nowell, A.R.M., Jumars, P.A., 1990. Flume Observations on Flow Dynamics in *Zostera marina* (Eelgrass) Beds. Mar. Ecol. Progr.-Ser. 61, 159-169.

Gattuso, J.-P., Gentili, B., Duarte, C.M., Kleypas, J.A., Middelburg, J.J., Antoine, D., 2006. Light Availability in the Coastal Ocean: Impact on the Distribution of Benthic Photosynthetic Organisms and their Contribution to Primary Production. Biogeosciences 3, 489–513.

Granata, T.C., et al. 2001. Flow and particle distributions in a nearshore seagrass meadow before and after a storm. Mar. Ecol. Progr.-Ser. 218, 95-106.

Green, E. P. , Short, F. T., 2003. World Atlas of Seagrasses, California University Press, 310 pp.

Hemminga, M.A., Duarte, C.M., 2000. Seagrass Ecology. Cambridge Univ. Press, Cambridge.

Hendriks, I.E., Sintes, T., Bouma, T.J., Duarte, C.M., 2008. Experimental assessment and modeling evaluation of the effects of seagrass (Posidonia oceanica) on flow and particle trapping. Mar. Ecol. Progr.-Ser. 356, 163-173.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946-1957.

Kennedy, H., Beggins, J., Duarte, C.M., Fourqurean, J.W., Holmer, M., Marbà, N., and Middelburg JJ. 2010. Seagrass sediments as a global carbon sink: Isotopic constraints. Global Biogeochemical Cycles 24, doi:10.1029/2010GB003848.

Kennedy, H., Beggins, J., Duarte, C.M., Fourqurean, J.W., Holmer, M., Marbà, N., Middelburg, J.J., 2010 Seagrass sediments as a global carbon sink: Isotopic constraints. Global Biogeochem. Cycles 24, doi:10.1029/2010GB003848.

Koch, E.W., Gust, G., 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. Mar. Ecol. Progr.-Ser. 184, 63-72.

Koch, E.W., Ackerman, J.D., Verduin, J., van Keulen, M., 2006. Fluid dynamics in seagrass ecology - from molecules to ecosystems. In: Larkum, A.W.D., Orth, R.J., Duarte, C.M. (eds.), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, The Netherlands, pp. 193-225.

Laffoley, D.d'A., Grimsditch, G., 2009. The management of natural coastal carbon sinks. IUCN, Gland, Switzerland. 53 pp.

Lo Iacono, C., Mateo, M.A., Gracia, E., Gasch, L., Carbonell, R., Serrano, L., Danobeitia, J., 2008. Very high-resolution seismo-acoustic imaging of seagrass meadows (Mediterranean Sea): Implications for carbon sink estimates. Geophysical Res. Lett. 35, L18601, doi:10.1029/2008GL034773

Lopez, F., Garcia, M., 1998. Open-channel flow trhough simulated vegetation: Suspended sediemnt transport modeling. Water Resour. Res. 34, 2341-2352.

Mateo, M.A.,Cebrian, J., Dunton, K., Mutchler, T., 2006. Carbon flux in seagrass ecosystems. In Larkum, W.D., Orth, R.J., Duarte, C.M. (eds). Seagrasses: Biology, Ecology and Conservation. Springer 567-593.

Mateo, M.A., Romero, J., Pérez, M., Littler, M.M., Littler, D.S., 1997 Dynamics of Millenary Organic Deposits Resulting from the Growth of the Mediterranean Seagrass Posidonia oceanica. Estuar. Coastal Shelf Sci. 44, 103-110.

Mcleod, E,, Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B. 2011. A Blueprint for Blue Carbon: Towards an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Frontiers Ecol. Environ. doi:10.1890/110004

Moncreiff, C.A., Sullivan, M.J., 2001. Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. Mar. Ecol. Progr.-Ser. 215, 93-106.

Nellemann, C., Corcoran, E., Duarte, C.M., Valdés, L., De Young, C., Fonseca, L., Grimsditch, G., 2009. Blue Carbon. A Rapid Response Assessment. United Nations Environment Programme, GRID-Arendal.

Nepf, H.M., Vivoni, E.R. 2000. Flow structure in depth-limited, vegetated flow. J. Geophys. Res. 105, 28547-28557.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L. Jr., Hughes, A. R., Kendrick, G.A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., Williams, S.L., 2006. A Global Crisis for Seagrass Ecosystems. Bioscience 56, 987-996.

Sintes, T., Marbà, N., Duarte, C.M., Kendrick, G., 2005. Non-linear processes in Seagrass Colonisation Explained by Simple Clonal Growth Rules. Oikos 108, 165 –175.

Sintes, T., Marbà, N., Duarte, C.M. 2006. Modeling non-linear seagrass clonal growth: Assessing the efficiency of space occupation across the seagrass flora. Estuaries Coasts 29, 72–80.

Terrados, J., Duarte, C.M. 2000. Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L.) meadow. J. Exp. Mar. Biol. Ecol. 243, 45-53.

Waycott, M., Duarte, C.M., Carruthers, T. J.B., Orth, R.J.,. Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L. Jr., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Nat. Acad. Sci. USA (PNAS) 106, 12377-12381

Table 1. Summary of estimates of sediment accumulation and carbon burial rate in seagrass meadows.

Table

Location	Dating technique	Sediment accumulation rate (mm m^{-2} y^{-1})	Carbon burial (gC m^{-2} y^{-1})	Seagrass	Reference
Fanals point, NW Mediterranean	direct measure of sedimentation rate		198	*P. oceanica*	1
Ischia, NW Mediterranean	Radiocarbon,^{14}C Annual carbon budget	1.65	30 19.5	*P. oceanica*	2 6
Culip, NW Mediterranean	Radiocarbon,^{14}C	0.61	9	*P. oceanica*	2
Port Lligat, NW Mediterranean	Radiocarbon,^{14}C	4.14	75	*P. oceanica*	2
Campello, NW Mediterranean	Radiocarbon,^{14}C	2.03	112	*P. oceanica*	2
Tabarca 1, NW Mediterranean	Radiocarbon,^{14}C	1.14	62	*P. oceanica*	2
Tabarca 2, NW Mediterranean	Radiocarbon,^{14}C	1.88	104	*P. oceanica*	2
Medas, NW Mediterranean	Radiocarbon,^{14}C Annual carbon budget	0.79	12.6 72.5	*P. oceanica*	2 6
Bay of Calvi, Corsica	Annual carbon budget		16.6	*P. oceanica*	6
Spencer Gulf,	^{210}Pb	2 – 2.7		*P. australis*	3

S. Australia					
Spencer Gulf, S. Australia	^{14}C	0.2 – 1.4		*P. australis*	3
Port Lligat, NW Mediterranean	^{14}C	1.1		*P. oceanica*	4
Ebro delta, NW Mediterranean	Carbon content of different aged sand waves.		43.8	*C. nodosa*	5
Cala Jonquet, NW Mediterranean	Annual carbon budget.		52.4	Zostera marina	7
Cala Jonquet, NW Mediterranean	Annual carbon budget.		4.4	Cymodocea nodosa	7
Cala Jonquet, NW Mediterranean	Annual carbon budget.		2.9	Zostera noltii	7
Cala Jonquet, NW Mediterranean	Annual carbon budget.		66.4	Posidonia oceanica	7

1] Gacia et al., 2002; 2] Mateo et al., 1997. 3] Belperio et al., 1984; 4]Iacano C.L. et al., 2008; 5] Barron et al., 6] Mateo et al., 2006; 7] Cebrian et al., 1997

***Research Highlight**

1) Seagrass meadows support high primary production rates and their canopies are efficient at filtering particles out of their water column as well as in preventing resuspension of the sediments.
2) Decomposition rates in seagrass sediments are slow, because of low nutrient concentration in seagrass detritus and low oxygen concentration in seagrass sediments.
3) Seagrass meadows support high carbon burial rates and have the capacity to accumulate large stores of carbon in their sediments, raising the seafloor.
4) Our understanding of the factors regulating the variability in carbon sink capacity among seagrass meadows and its regional variation is limited. These gaps limit the capacity to formulate strategies to mitigate climate change based on the carbon-sink capacity of seagrass meadows.
5) A research strategy needs be formulated to address these gaps and provide the necessary protocols to ensure the accountability of mitigation actions involving the conservation and restoration of seagrass meadows.

Introduction.

Seagrass are a group of about 60 angiosperm species adapted to life in the sea, whether permanently or temporarily submerged (Hemminga and Duarte 2000). Seagrass are clonal, rhizomatous plants that develop, largely through clonal growth, large ecosystems termed seagrass meadows, often monospecific but that can include up to 12 species in the tropics (Hemminga and Duarte 2000). Seagrass meadows occurr along the shores of all continents, to maximum depths of up to 50 m, depending on water transparency, except Antarctica (Hemminga and Duarte 2000). Whereas there is no comprehensive inventory of the area covered by seagrasss globally, different estimate are available. The documented seagrass area is 177,000 Km^2 (Green and Short 2003), but this is an underestimate of the total area covered by seagrass meadows, since many regions with large seagrass meadows (e.g. Indonesia and Bahamas) have not been fully charted. Hence, the estimates most commonly use in the literature use a low estimate of 300,000 Km^2 and a high estimate of 600,000 Km^2 (Duarte et al. 2005a), with the global area suitable to support seagrass growth estimated at (Gattusso et al. 2006).

Seagrass meadows are highly productive ecosystems (Duarte and Chiscano 1999) and are key ecosystems to support coastal biodiversity (Hemminga and Duarte 2000). In addition, they are characterised by their capacity to sequester considerable amount of carbon in their carbon-rich sediments (Duarte et al. 2005b), being responsible for 20 % of the global carbon sequestration in marine sediments despite occupying 0.1 % of the ocean surface (Duarte et al. 2005b, Kennedy et al. 2010). Regrettably, seagrass meadows are being lost globally at fast rates, of about 5% $year^{-1}$, and at least 1/3 of the area present has been lost since World-War II (Orth et al. 2006, Waycott et al. 2009), which represents the loss of an important carbon sink.

Realisation of the important carbon sink capacity of seagrass meadows has recently led to the proposal that seagrass meadows, along with salt-marshes and mangrove forests, could be used to support strategies to mitigate climate change (Nellemann et al. 2009, Lafoley et al. 2009). These strategies would be based on both the conservation and reforestation of seagrass meadows. However, the development of management schemes based on the role of seagrass meadows as intense carbon sinks has been precluded to-date by limitations in current knowledge on the mechanisms conducive of their high carbon sink capacity and the rates of carbon burial they do support. Here we provide a synthesis of recent research addressing both these gaps and identify additional elements required to formulate a robust strategy for climate change mitigation based on the role of seagrass meadows as intensen carbon sinks. We believe that the knowledge presented here, largely based on papers published within the past 5 years, provides a solid underpinning to launch carbon mitigation strategies based on seagrass meadows.

Mechanisms of carbon burial in seagrass communities.

Metabolic C capture

Seagrasses rank amongst the most productive populations on the biosphere (Duarte and Chiscano 1999). On average, net primary production per unit of area of seagrass populations, when considering that of leaves, rhizomes and roots, is about 1012 g DW m^{-2} yr^{-1} (Duarte and Chiscano 1999), with a ratio aboveground: belowground production of 16.4 ± 8.5 (Duarte and Chiscano 1999). The meadows with the most productive seagrasses are multispecies meadows located in the Indo-Pacific region, those of *Phyllospadix* spp in the east Pacific region and those of *Posidonia oceanica* in the Mediterranean Sea (Duarte and Chiscano 1999). Despite the small global extension of seagrasse populations, their net primary production accounts for about 1 % of the global net marine primary production (Duarte and Cebrián 1996). The production of seagrass species accounts for most of the primary production of seagrass communities but not for all of it. The leaves and rhizomes of seagrasses are colonised by epiphytic autotrophic and heterotrophic organisms. Net primary production of seagrass autotrophic epiphytes, comprising microscopic and macroscopic algae, has been quantified for few seagrass communities (Hemminga and Duarte 2000). Net primary production of seagrass autotrophic epiphytes ranges from 0.038 g DW m^{-2} d^{-1} to 2.07 g DW m^{-2} d^{-1}, and it typically accounts for 20-60 % of total seagrass aboveground productivity (Hemminga and Duarte 2000). Therefore, photosynthesis of primary producers of seagrass communities produces a significant amount of total marine organic carbon.

Carbon accumulation in seagrass meadows

Whereas seagrass meadows comprise an important biomass, this represent a minor component of the carbon stocks in seagrass meadows, which are - by far - dominated by the sedimentary pool. Seagrass sediments are organic-rich, with an average organic concentration of 4.1 % (Kennedy et al. 2010). Seagrass meadows occupy coastal environments over millenary time scales and are able to form thick carbon deposits, raising the seafloor by about 1 mm per year (Kennedy et al. 2010). The thickest documented sedimentary deposit has been reported at 11 m thick for the *Posidonia oceanica* meadow at Port Lligat, Spain, corresponding to an accumulation of about 0.18 tons C m^{-2} over an estimated 6,000 years of seagrass growth at that size (Lo Iacono et al. 2008). Thick seagrass deposits, several meters in thickness, have been reported for other sites, including other sites in the Spanish Mediterranean, Shark Bay W. Australia) and Florida Bay (cf. Kennedy et al. 2010).

Hence, seagrass meadows do not only have a high metabolic capacity to act as carbon sinks, but they area also able to accumulate large pools of carbon in the sediments and retain these over millenary large. The long retention times of carbon in sedimentary deposits in seagrass meadows is quite unique and renders seagrass meadows some of the most carbon-rich ecosystems in the Biosphere. Understanding the reasons for the high capacity of seagrass to capture and store carbon is fundamental to manage these ecosystems in support of strategies to mitigate climate change.

Understanding the high seagrass capacity for carbon burial

Despite the high primary production of seagrass communities, they also support high rates of organic matter consumption through respiration (Duarte et al. 2010). In seagrass communities, the abundance and activity of heterotrophic organisms, such are animals and sediment bacteria, are highly enhanced, and they rise community respiration. Still, more than 80 % of seagrass production is not consumed by herbivores (Duarte and Cebrián 1996), and decomposition rates of seagrass detritus are slow, when compared with those of other organisms, because the low nutrient (nitrogen and phosphorous) concentrations in their tissues (Enríquez et al 1993). Hence, part of the organic carbon produced by seagrass communities is not consumed by heterotrophs, driving seagrass ecosystems to be autotrophic communities (Duarte and Cebrián 1996). This excess of organic carbon produced by seagrass ecosystems is buried (Duarte and Cebrián 1996). There is evidence, however, that in seagrass communities organic matter consumption (respiration) may exceed production (gross primary production) during some periods of the year (Hemminga and Duarte 2000). Yet, the vast majority of metabolic estimates of seagrass communities that are available at annual time scales reveal that they are autotrophic, and hence that they act as CO_2 sinks (Duarte et al. 2010).

Particle trapping: the role of seagrass meadows as filters.

Seagrass meadows develop lush canopies that affect the water flow above them, thereby acting as ecosystem engineers modifying their abiotic environment (Jones et al. 1997). The presence of seagrass canopies at the benthic boundary layer alters the roughness of the bottom (Granata et al. 2001; Nepf and Vivoni 2000) and thereby the vertical flow profile from water column to bottom and turbulence (Ackerman and Okubo 1993; Fonseca et al. 1982; Gambi et al. 1990; Koch et al. 2006; Koch and Gust 1999), especially when canopy height represents more than 10 % of the height of the water column (Nepf and Vivoni 2000). Depending on shoot density and seagrass species, flow reduction resulting from current deflection by the canopy ranges from 2- to more than10 -fold compared to water flow outside the seagrass bed (Ackerman 1986; Gambi et al. 1990; Hendriks et al. 2008). Seagrass canopies also have a dampening effect on waves (Bouma et al. 2005; Fonseca and Cahalan 1992). When waves enter the near shore region, they encounter the friction (shear stress) of the seagrass canopy and become shallow water waves. This leads to wave-induced transport in a process referred to as Stokes drift, which may be of considerable impact in many coastal environments. Although wave attenuation is maximal when the meadow occupies a large portion of the water column (Fonseca and Cahalan 1992), reduction in wave energy and orbital velocity occurs even when beds are located at 5-15 m depth and the plants occupy a small portion of the water column (Granata et al.

2001). However, the capacity of seagrasses to trap sediment might be lost under wave-exposed, extreme flow conditions (Fonseca and Bell 1998; Koch and Gust 1999).

Apart from the direct effect of dampening of waves and currents by seagrass canopies leading to increased sediment deposition (Gacia and Duarte 2001; Gacia et al. 1999; Hendriks et al. 2008) and decreased resuspension (Lopez and Garcia 1998; Terrados and Duarte 2000), seagrass can also directly intercept suspended sediment particles with their canopies. Seagrass canopies increase the effective benthic surface by as much as twenty times thereby providing a large surface for sediment deposition and the probability of contact. The collision of suspended particles with seagrass leaves increases particle path length and causes momentum loss (Hendriks et al. 2008), which results in increased deposition. Field estimates indicate that the potential for particle contact with leaf surfaces sometimes approaches 100 % in *Zostera marina* canopies (Ackerman 2002). In addition, exopolymeric substances secreted by epiphytes can bind sediment particles to seagrass leaves (Agawin and Duarte 2002). Epiphytic layers on seagrass leaves may also contribute to the trapping of particles in seagrass beds by increasing the roughness of the canopy and increasing the velocity gradient layer on the leaf surface (Koch et al. 2006). The capacity of seagrass meadows to trap particles can be quite high, and, for instance, Barrón et al. (2004) calculated, using carbon budgets across seagrass patches of different age, that the input of allochthonous carbon, trapped into sediments of *Cymodocea nodosa* patches in a Mediterranean lagoon, must be about 157 mmol C m^{-2} day^{-1}.

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High carbon preservation in seagrass sediments

High metabolic carbon sink capacity and high carbon trapping capacity supports a large flow of carbon to seagrass sediments (Fig. 1). However, in order for seagrass meadows to be effective as carbon sinks this carbon must be effectively preserved in the sediments for centuries to milenia, as is indeed the case as discussed above. The mechanisms conducive to high carbon preservation rates in seagrass sediments include (1) low nitrogen and phosphorus content in seagrass tissues (Duarte 1990), which renders seagrass detritus a poor substrate to support microbial growth and results in low decomposition rates (Enriquez et al. 1993); (2) seagrass sediments are often anaerobic, which leads to inefficient microbial metabolism and enhances seagrass preservation; (3) a fraction of seagrass production (up to 50%), that of roots and rhizomes, is placed directly into the sediments, often at depths of tens of centimeters (Duarte et al. 1998), contributing to the preservation of the carbon in these tissues; (4) being underwater, seagrass sediments are free of fires, which are responsible for the emission as CO_2 of much of the organic carbon accumulated in forest soils on land, and (5) the dissipation of waves and turbulence by seagrass canopies prevents sediment resuspension and increases the retention of sediments, and the associated carbon (Fig. 1). The combination of these factors leads to high carbon preservation in seagrass sediments , which, together with high metabolic inputs and particle trapping rates, explain the role of seagrass meadows as intense carbon sinks in the biosphere (Fig. 1).

Assessing seagrass carbon burial.

Assessment of the net community metabolism of seagrass meadows.

Recently, the available estimates of seagrass community metabolism, described by gross primary production, respiration and net community production, have been reviewed and synthesised in order to quantify the role of seagrass meadows as carbon sinks (Duarte et al 2010). Most seagrass metabolic estimates have been derived from changes in oxygen concentration in incubation chambers deployed in situ and diel oxygen concentration curves measured in the field (Duarte et al 2010). However, metabolic rates of seagrass communities have been also calculated from changes in CO_2, ^{14}C uptake and incubations of sediment cores, containing seagrass communities, in the laboratory. Since year 1956, seagrass community metabolism has been quantified for 155 sites. These estimates are geographically uneven distributed, most (67 %) of them assessing metabolism of tropical and subtropical seagrass meadows and more than one forth that of Mediterranean ones (Duarte et al 2010). There is a substantial gap of information on community metabolic rates for seagrass meadows along the coasts of the Southern Hemisphere and North and West Pacific regions (Duarte et al 2010).

This synthesis reveals that gross primary production (GPP) of seagrass communities averages 224.9 ± 11.1 mmol O_2 m^{-2} day^{-1}, and it tends to exceed respiration (R, average ± standard error = 187.6 ± 10.1 mmol O_2 m^{-2} day^{-1}, Duarte et al in press). This indicates that seagrass meadows tend to be autotrophic ecosystems, with an average net community production (NCP) of 27.2 ± 5.8 mmol O_2 m^{-2} day^{-1} (Duarte et al in press). The metabolic estimates of most (63%) seagrass meadows examined indicate that they are CO_2 sinks. Seagrass community metabolic rates vary across geographical regions and species, tropical seagrass meadows tending to have lower (although not significantly) NCP than temperate ones. Meadows of fast growing seagrass species have the highest GPP, and together with those of *Thalassia testudinum*, the highest R (Duarte et al 2010).

GPP and R are positively related, but seagrass meadows tend to be net autotrophic ecosystems (i.e GPP/R ≥ 1) when GPP exceeds 186 mmol O_2 m^{-2} day^{-1} (Duarte et al 2010). Since the mean ratio of GPP to aboveground seagrass biomass derived in this study is 4.45 ± 0.79 mmol O_2 g DW^{-1} day^{-1}, seagrass meadows act as CO_2 sinks when average aboveground biomass exceeds 41 g DW m^{-2} (Duarte et al 2010).

The average net metabolic capture of carbon by seagrass communities (9.9 ± 2.22 mol C m^{-2} yr^{-1}, Duarte et al 2010) is more than five times the C sink capacity of that of North American wetlands. And the net carbon captured by the10 % seagrass meadows with the largest carbon sink capacity is well above the rates of carbon sink in undisturbed Amazonian forests, assumed to be the largest terrestrial carbon sinks (Duarte et al 2010). Considering a global area of seagrass meadows ranging from 300,000 km^2 (Duarte et al 2005) and 600,000 km^2 (Carpy-Roubaud and Sournia 1990) and the average (± SE) NCP per unit of area, seagrass meadows would bury, only through their metabolic activity, between 20 and 50 Tg C $year^{-1}$ using the low estimate of global seagrass extension and between 41 and 101 Tg C $year^{-1}$ using the high estimate of seagrass cover. These estimates confirm that seagrass meadows rank amongst the strongest CO_2 sinks of the biosphere, and that despite their small global extension (less than 0.1 % of ocean surface) they bury about 20 % of the total carbon buried in the global ocean.

Assessment of carbon storage

The extent to which seagrass organic matter accumulates in the sediment can be determined in a number of ways (Table 1). In studies examining the fate of organic carbon, estimates of losses due to herbivory, decomposition and export can be compared with seagrass primary production to determine how much carbon is unaccounted for and hence is assumed to accumulate in the sediment. Duarte & Cebrian (1996) compiled the available data and estimated that, on average, 16% of seagrass primary production accumulates in the sediment. There are limitations to this technique as it generally provides only an indirect estimate of carbon accumulation. In addition, data compilations may have a mismatch between the amount of data available for primary production relative to that available for herbivory, decomposition and export. The data provided are also average values and do not therefore identify the relative importance of different seagrass species, which may be substantial. For example, Cebrian et al., (1997) followed the fate of carbon in four species of seagrass and found that *Posidonia oceanica* had about 23 times higher capacity to accumulate organic carbon stocks than *Zostera noltii.* This kind of carbon budgeting provides short-term (annual) estimates of carbon accumulation in seagrass meadows. A more direct approach to studying short-term carbon accumulation is provided by sediment trapping. Sediment traps are instruments that can be deployed in seagrass meadows to measure the quantity of sinking particles. The traps can be deployed on a weekly or monthly basis and the organic (and inorganic) content of collected particles determined. As yet, there is little data available that uses this technique (Table 1).

Chemical analysis of radioactive components of sediments can provide longer term estimates of carbon accumulation. The two most common techniques use the naturally occurring radioactive isotopes of lead (^{210}Pb) and carbon (^{14}C). Both techniques rely on the radioactive decay of these isotopes, the rate of which is well known. The ^{210}Pb has a half-life of 22.3 years, which means that after 22.3 years, only half of the original amount is undecayed. If the sediment layers are undisturbed, then as the sediment ages it slowly loses its radioactivity. The age of a sediment layer can therefore be determined by how much ^{210}Pb it contains. For ^{14}C, its half-life of 5730 years and so the age of much older sediments can be dated. This radiocarbon dating can be used to estimate the age of carbon containing materials up to about 58,000 to 62,000 years. In sediments the ^{14}C of refractory seagrass organic matter such as roots and rhizomes is commonly measured (Table 1).

Estimates of the short-term carbon storage in sediments (years) averages about 53 g C m^{-2} yr^{-1} and compares well with direct estimates of longer term carbon burial, averaging 58 g C m^{-2} a^{-1} (Table 1). The data sets used in these calculations are, however, from a restricted geographical area and represent meadows of only a few of all seagrass species.

Isotopic fingerprinting and accountability of seagrass carbon burial

Organic matter sources that contribute and accumulate in the sediments of seagrass meadows have different, and identifiable, organic carbon stable isotope signatures that can be tracked and quantified. Besides the seagrass tissues themselves, other potential sources of organic carbon are plankton, (usually collected as suspended particulate organic matter), seagrass epiphytes, microphytobenthos, macroalgae and terrestrial organic matter, including mangroves. All these organic matter sources have isotopic signatures that are generally different from those of seagrass tissues (*Moncreiff and Sullivan*, 2001). So by measuring the organic carbon stable isotopic signature (™^{13}C) of seagrass sediments, the proportions of seagrass and other organic matter sources that have accumulated, can be estimated. *Kennedy et al.* (2010) compiled a data set containing 219 analyses the of the organic carbon stable isotopic signature of seagrass sediments which have been collected at 88 locations around the world and used the data to show that 50% of the organic matter that accumulates is derived from the seagrass tissues, with the other 50% of the organic matter that accumulates being derived from the trapping of phytoplankton and terrestrially derived particles of organic matter by the seagrass canopy.

Using the range of organic carbon accumulation rates reported for seagrass meadows as between 83 to 133 g C m^{-2} y^{-1} (*Duarte et al,.* 2005b), and combining this with the estimate that 50% of this organic matter is derived from seagrass tissues, it can be calculated that between 41 and 66 g C m^{-2} y^{-1} of the organic matter produced by seagrasses become buried in the sediment (Kennedy et al., 2010). The burial rate of seagrass derived organic matter can be now compared with the net amount of organic matter produced in seagrass meadows (net community production). A recent synthesis of net community production measurements from around the globe arrived at a value of around 120 g C m^{-2} y^{-1} (*Duarte et al.,* 2010). Comparing the net amount of organic matter produced in seagrass meadows with the amount buried it can be seen that 30-50% of the organic matter is unaccounted for. This unaccounted for organic matter could have been exported away from the seagrass meadows to be decomposed or stored elsewhere. Overall, the total organic carbon sink sustained by seagrass meadows is the sum of their net community production and the non seagrass derived carbon that has been trapped and accumulates in their sediments. The sum of these two terms gives a range of between 160 to 186 g C m^{-2} y^{-1} and further demonstrates the importance of seagrass meadows for carbon sequestration.

Limitations in the assessment of seagrass carbon sink capacity

The initial calculations by Duarte et al. (2005a) that seagrass meadows act as intense carbon sinks and contribute a significant fraction of all carbon sequestered in marine sediments allowed the formulation of climate change mitigation strategies based on the conservation and recovery of seagrass meadows (Nellemann et al. 2009, Lafoley et al. 2009). Parallel research, improved our understanding of the processes conducive to the role of seagrass meadows as carbon sinks (e.g. Hendriks et al. 2008) and delivered improved estimates of the carbon pools stored in seagrass sediments (Lo Iacono et al. 2008). The adoption of climate change mitigation strategies based on the conservation and recovery of seagrass meadows requires that current uncertainties be dissipated. This need prompted recent synthesis assessing the metabolic capacity of seagrass meadows to act as carbon sinks (Duarte et al. 2010) and the identification of sources of carbon to seagrass sediments (Kennedy et al. 2010).

Despite these advances in our knowledge on the role of seagrass meadows as carbon sinks, a number of uncertainties remain that need be dissipated to provide the robust support required to implement climate change mitigation strategies based on the conservation and recovery of seagrass meadows. These include:

- Improved knowledge of global seagrass cover, currently limited by insufficient coverage of some regions and poorly constrained, by a factor of two, estimates of surface area covered by seagrasses. Improved estimates of regional and global estimates of seagrass carbon sink capacity are required to better incorporate seagrass meadows in regional and global carbon budgets. Major regions requiring investigation include Indonesia, Malaysia, Borneo, Bahamas and the Bahamas bank, Africa and South America.
- Improved models assessing suitable seagrass areas from environmental characteristics, improving current models based on light penetration (e.g. Gattusso et al. 2006) by incorporating bottom characteristics.
- A more extensive investigation of carbon stocks and burial rates over different time scales, including the thickness of sediments deposited under extant seagrass meadows. Particularly under-represented in current assessments are Africa and South America.

- Assessments of the impacts of seagrass loss on the fate of the carbon deposits stored by the seagrass meadow. The impacts of seagrass loss on carbon fluxes will be even more negative if these carbon stocks were eroded following the loss of the overlying seagrass meadows.
- Identification of the factors responsible for variability carbon sink capacity, allowing the development of predictive models as well as sound management strategies to maximise carbon sink capacity.
- Elucidation of the fate of the carbon exported from seagrass meadows, which could be buried elsewhere, as suggested by recent synthesis (Kennedy et al. 2010). This research would help resolve the size of the footprint of seagrass burial.

Future strategies

The questions listed above need be articulated into a research agenda conducive to a robust understanding of seagrass carbon burial underpinning climate change mitigation programs based on seagrass meadows. This programs also require the development of reliable protocols for the cost-effective measurement of carbon sequestration ensuring the accountability of carbon sequestered by seagrass meadows.

Whereas the benefits of conservation programs to preserve the carbon sink capacity of seagrass meadows can be readily evaluated, those of seagrass restoration programs involve greater uncertainties. Seagrass restoration programs are costly and have typically shown limited success at the time scales, typically two to four, years at which they have tested. However, the clonal nature of seagrasses leads to an expontential growth (Sintes et al. 2005, 2006), where planting units containing a few shoots may grow to millions of shoots extending over significant areas after a few decades. The explosive clonal growth of seagrasses offers a distinct difference from reforestation projects on land, where the larger initial planting costs may be offset by the explosive clonal growth coupled with the distinct intensity of seagrass meadows as carbon sinks. There is, therefore, a need to develop, and validate, models to predict the cumulative carbon sink associated with seagrass restoration project and evaluate their feasibility and cost efficiency.

Acknowledgements

This is a contribution to the MEDEICG project, funded by the Spanish Ministry of Science and Innovation (number CTM2009-07013). We thank G. Grimsditch for the encouragement to write this paper. I.H. was supported by a Juan de la Cierva fellowship from the Spanish Ministry of Research and Innovation.

References

Ackerman, J.D. 1986. Mechanistic implications for pollination in the marine angiosperm Zostera marina. Aquatic Botany 24:343-353.

Ackerman, J.D. 2002. Diffusivity in a marine macrophyte canopy: Implications for submarine pollination and dispersal. Aquatic Botany 89:1119-1127.

Ackerman, J.D., A. Okubo. 1993. Reduced Mixing in a Marine Macrophyte Canopy. Functional Ecology 7:305-309.

Bouma, T.J., et al. 2005. Trade-offs related to ecosystem engineering: a case study on stifness of emerging macrophytes. Ecology 86:2187-2199.

Denny, M.W., 1988. Biology and the Mechanics of the Wave-Swept Environment. Princeton University Press, Princeton, New Jersey.

Duarte, C.M. 1990. Seagrass nutrient content. Mar. Ecol. Progr. Ser. 67: 201-207.

Duarte, C.M., M. Merino, N.S.R. Agawin, J. Uri, M.D. Fortes, M.E. Gallegos, N. Marbá y M. Hemminga. 1998. Root production and belowground seagrass biomass. Marine Ecology Progress Series 171: 97-108.

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

Enríquez, S., C. M. Duarte, and K. Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia 94: 457-471.

Fonseca, M.S., S.S. Bell. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Marine Ecology Progress Series 171:109-121. 10.3354/meps171109

Fonseca, M.S., J.A. Cahalan. 1992. Preliminary evaluation of wave attenuation by four species of seagrass. Estuarine, Coastal and Shelf Science 35:565-576.

Fonseca, M.S., J.S. Fisher, J.C. Ziemann, G.W. Thayer. 1982. Influence of the seagrass, *Zostera marina*, L. on current flow. Estuarine, Coastal and Shelf Science 15:367-380.

Gacia, E., C.M. Duarte. 2001. Sediment Retention by a Mediterranean *Posidonia oceanica* Meadow: The Balance between Deposition and Resuspension. Estuarine, Coastal and Shelf Science 52:505-514.

Gacia, E., T.C. Granata, C.M. Duarte. 1999. An approach to measurement of particle flux and sediment retention within seagrass (*Posidonia oceanica*) meadows. Aquatic Botany 65:255-268.

Kennedy H, Beggins J, Duarte CM, Fourqurean JW, Holmer M, Marbà N, and Middelburg JJ. 2010. Seagrass sediments as a global carbon sink: Isotopic constraints. Global Biogeochemical Cycles 24, doi:10.1029/2010GB003848.

Gambi, M.C., A.R.M. Nowell, P.A. Jumars. 1990. Flume Observations on Flow Dynamics in *Zostera marina* (Eelgrass) Beds. Marine Ecology Progress Series 61:159-169.

Laffoley, D.d'A. and Grimsditch, G. (eds). 2009. The management of natural coastal carbon sinks. IUCN, Gland, Switzerland. 53 pp.

Lo Iacono C, Mateo MA, Gracia E, Gasch L, Carbnell R., Serrano L et al. 2008. Very high-resolution seismo-acoustic imaging of seagrass meadows (Mediterranean Sea): Implications for carbon sink estimates. Geophysical Research Letters, 35, L18601, doi:10.1029/2008GL034773

Nellemann, C., Corcoran, E., Duarte, C. M., Valdés, L., De Young, C., Fonseca, L., Grimsditch, G. (eds). 2009. Blue Carbon. A Rapid Response Assessment. United Nations Environment Programme, GRID-Arendal.

Granata, T.C., et al. 2001. Flow and particle distributions in a nearshore seagrass meadow before and after a storm. Marine Ecology Progress Series 218:95-106.

Hendriks, I.E., T. Sintes, T.J. Bouma, C.M. Duarte. 2008. Experimental assessment and modeling evaluation of the effects of seagrass (Posidonia oceanica) on flow and particle trapping. Marine Ecology Progress Series 356:163-173.

Jones, C.G., J.H. Lawton, M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946-1957.

Koch, E.W., J.D. Ackerman, J. Verduin, M. van Keulen, 2006. Fluid dynamics in seagrass ecology - from molecules to ecosystems. In: Larkum, A.W.D., R.J. Orth, C.M. Duarte (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, The Netherlands, pp. 193-225.

Koch, E.W., G. Gust. 1999. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. Marine Ecology Progress Series 184:63-72.

Lopez, F., M. Garcia. 1998. Open-channel flow trhough simulated vegetation: Suspended sediemnt transport modeling. Water Resources Research 34:2341-2352.

Nepf, H.M., E.R. Vivoni. 2000. Flow structure in depth-limited, vegetated flow. Journal of Geophysical Research 105:28547-28557.

Terrados, J., C.M. Duarte. 2000. Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L.) meadow. Journal of

Experimental Marine Biology and Ecology 243:45-53. Hemminga MA, CM. Duarte. 2000. Seagrass Ecology. Cambridge University Press. 298 pp.

Duarte CM, CL Chiscano. 1999. Seagrass biomass and production: a reassessment. Aquatic Botany, 65: 159-174

Duarte CM, J Cebrián. 1996. The fate of marine autotrophic production. Limnology and Oceanography, 41: 1758-1766

Duarte C. M, JJ Middelburg, N Caraco. 2005b. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences, 2: 1-8.

Duarte, C.M. 2002. The future of seagrass meadows. Environmental Conservation 29: 192-206

Duarte, C. M., Borum, J., Short, F. T., and Walker, D. I. 2005a. Seagrass Ecosystems: Their Global Status and Prospects. In: Polunin NVC (ed) Aquatic Ecosystems: Trends and Global Prospects, Cambridge Univ. Press.

Enríquez S, CM Duarte, K Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia, 94: 457-471.

Duarte CM, N Marbà, E Gacia, JW Fourqurean, J Beggins, C Barrón, ET. Apostolaki. Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. Global Biogeochemical Cycles, doi:10.1029/2010GB003793.

Charpy-Roubaud C, A Sournia. 1990. The comparative estimation of phytoplanktonic and microphytobenthic production in the oceans. Mar. Microb. Food Webs, 4: 31–57.

Hemminga, M.A., y C.M. Duarte. 2000. Seagrass Ecology. Cambridge Univ. Press, Cambridge.

Gattuso, J.-P., B. Gentili, C. M. Duarte, J. A. Kleypas, J. J. Middelburg, and D. Antoine. 2006. Light Availability in the Coastal Ocean: Impact on the Distribution of Benthic Photosynthetic Organisms and their Contribution to Primary Production. Biogeosciences 3: 489–513.

Green, E. P. and Short, F. T. 2003. World Atlas of Seagrasses, California University Press, 310 pp.

Barron, C. N. Barron, C., Marba, N., Terrados, J., Kennedy, H. & Duarte, C.M. (2004) Community metabolism and carbon budget along a gradient of seagrass (Cymodocea nodosa) colonization. Limnology & Oceanography, 49, 1642–1651.

Belperio AP, J.R Hails V.A Gostin and H.A Polach 1984 The stratigraphy of coastal carbonate banks and Holocene sea levels of northern Spencer Gulf, South Australia. Marine Geology , 61, 297-313.

Cebrian J., Duarte CM, Marba N, Enriquez S (1997) Magnitude and fate of the production of four co-occurring western Mediterranean seagrass species. Marine Ecology Progress Series, 159, 308-308.

Duarte, C. M. and J. Cebrián (1996), The fate of marine autotrophic production, Limnology andl Oceanography., 41 (8), 1758- 1766.

Duarte, C. M., J.J.Middelburg and N. Caraco (2005a), Major role of marine vegetation on the oceanic carbon cycle, Biogeosciences, 2 (1), 1-8.

Duarte C.M., N. Marba, E. Gacia, J.W. Fourqurean, J. Beggins, C. Barron and E.T. Apostolaki (2010), Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. In press Global Biogeochem Cycles.

Gacia, E; Duarte, CM; Middelburg, JJ. (2002), Carbon and nutrient deposition in a Mediterranean seagrass (Posidonia oceanica) meadow. Limnology &. Oceanography, 47 (1), 23-32.

Kennedy Hilary, Jeff Beggins, Carlos M. Duarte, James W. Fourqurean, Marianne Holmer, Núria Marbà, and Jack J. Middelburg 2010 Seagrass sediments as a global carbon sink: Isotopic constraints. Global biogeochemical cycles doi:10.1029/2010GB003848. In press.

Lo Iacono, C., M.A. Mateo, E. Gracia, L. Guasch, R. Carbonell, L. Serrano, O. Serrano and J. Danobeitia (2008), Very high-resolution seismo-acoustic imaging of seagrass meadows (Mediterranean Sea): Implications for carbon sink estimates. Journal of Geophysical Research. 35, L18601, doi:10,1029/2008GL034773.

Mateo MA, Romero J, Pérez, Littler MM, Littler DS. 1997 Dynamics of Millenary Organic Deposits Resulting from the Growth of the Mediterranean Seagrass Posidonia oceanica. Estuarine, Coastal and Shelf Science 44: 103-110.

Mateo MA Cebrian J Dunton K Mutchler T 2006 Carbon flux in seagrass ecosystems. In W.D. Larkum, R.J. Orth, C.M. Duarte (Eds). Seagrasses: Biology, Ecology and Conservation. Springer 567-593.

Moncreiff, C.A., and M.J. Sullivan (2001), Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. Marine Ecology Progress Series, 215, 93-106.

Waycott, M., C.M. Duarte, T. J.B. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck, Jr., A.R. Hughes, G.A. Kendrick, W.J. Kenworthy, F.T. Short and S.L. Williams. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the USA (PNAS) 106: 12377-12381

Sintes T., Marbà N., Duarte C.M., Kendrick, G. 2005. Non-linear processes in Seagrass Colonisation Explained by Simple Clonal Growth Rules. Oikos 108: 165 –175.

Sintes, T., Marbà, N. and C.M. Duarte. 2006. Modeling non-linear seagrass clonal growth: Assessing the efficiency of space occupation across the seagrass flora. Estuaries and Coasts 29: 72–80.

Orth, R.J., T.J.B. Carruthers, W.C. Dennison, C.M. Duarte, J.W. Fourqurean, K.L. Heck, Jr., A. R. Hughes, G.A. Kendrick, W. J. Kenworthy, S. Olyarnik, F. T. Short, M. Waycott, and S.L. Williams. 2006. A Global Crisis for Seagrass Ecosystems. Bioscience 56: 987-996.

Table 1.

Location	Dating technique	Sediment accumulation rate (mm m^{-2} y^{-1})	Carbon burial (gC m^{-2} y^{-1})	Seagrass	Reference
Fanals point, NW Mediterranean	direct measure of sedimentation rate		198	*P. oceanica*	1
Ischia, NW Mediterranean	Radiocarbon,^{14}C Annual carbon budget	1.65	30 19.5	*P. oceanica*	2 6
Culip, NW Mediterranean	Radiocarbon,^{14}C	0.61	9	*P. oceanica*	2
Port Lligat, NW Mediterranean	Radiocarbon,^{14}C	4.14	75	*P. oceanica*	2
Campello, NW Mediterranean	Radiocarbon,^{14}C	2.03	112	*P. oceanica*	2
Tabarca 1, NW Mediterranean	Radiocarbon,^{14}C	1.14	62	*P. oceanica*	2
Tabarca 2, NW Mediterranean	Radiocarbon,^{14}C	1.88	104	*P. oceanica*	2
Medas, NW Mediterranean	Radiocarbon,^{14}C Annual carbon budget	0.79	12.6 72.5	*P. oceanica*	2 6
Bay of Calvi, Corsica	Annual carbon budget		16.6	*P. oceanica*	6
Spencer Gulf, S. Australia	^{210}Pb	2 – 2.7		*P. australis*	3
Spencer Gulf, S. Australia	^{14}C	0.2 – 1.4		*P. australis*	3
Port Lligat, NW Mediterranean	^{14}C	1.1		*P. oceanica*	4
Ebro delta, NW Mediterranean	Carbon content of different aged sand waves.		43.8	*C. nodosa*	5
Cala Jonquet, NW Mediterranean	Annual carbon budget.		52.4	Zostera marina	7

Cala Jonquet, NW Mediterranean	Annual carbon budget.		4.4	Cymodocea nodosa	7
Cala Jonquet, NW Mediterranean	Annual carbon budget.		2.9	Zostera noltii	7
Cala Jonquet, NW Mediterranean	Annual carbon budget.		66.4	Posidonia oceanica	7

1] Gacia et al., 2002; 2] Mateo et al., 1997. 3] Belperio et al., 1984; 4]Iacano C.L. et al., 2008; 5] Barron et al., 6] Mateo et al., 2006; 7] Cebrian et al., 1997

Figure Headings

Figure 1. Conceptual diagram summarising the processes conducive to the high carbon sink capacity of seagrass meadows.

Ethical Statement

The authors declare no conflict of interest and that the present submission complies with the highest Ethical Standards.