Seagrass meadows as a globally significant carbonate reservoir

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Abstract

There has been a growing interest in quantifying the capacity of seagrass ecosystems to act as carbon sinks as a natural way of offsetting anthropogenic carbon emissions to the atmosphere. However, most of the efforts have focused on the organic carbon (POC) stocks and accumulation rates and ignored the inorganic carbon (PIC) fraction, despite important carbonate pools associated with calcifying organisms inhabiting the meadows, such as epiphytes and benthic invertebrates, and despite the relevance that carbonate precipitation and dissolution processes have in the global carbon cycle. This study offers the first assessment of the global PIC stocks in seagrass sediments using a synthesis of published and unpublished data on sediment carbonate concentration from 403 vegetated and 34 adjacent un-vegetated sites. PIC stocks in the top 1 m sediments ranged between 3 and 1660 Mg PIC ha^{-1}, with an average of 654 ± 24 Mg PIC ha^{-1}, exceeding about 5 fold those of POC reported in previous studies. Sedimentary carbonate stocks varied across seagrass communities, with meadows dominated by *Halodule*, *Thalassia* or *Cymodocea* supporting the highest PIC stocks, and tended to decrease polewards at a rate of -8 ± 2 Mg PIC ha^{-1} per degree of latitude (GLM, $p<0.0003$). Using PIC concentration and estimates of sediment accretion in seagrass meadows, mean PIC accumulation rates in seagrass sediments is 126.3 ± 31.05 g PIC m^{-2} y^{-1}. Based on the global extent of seagrass meadows (177,000 to 600,000 km^{2}), these ecosystems globally store between 11 and 39 Pg of PIC in the top meter of sediment and accumulate between 22 and 75 Tg PIC y^{-1}, representing a significant contribution to the carbonate dynamics of coastal areas. Despite that these high rates of carbonate accumulation imply CO_2 emissions from precipitation, seagrass meadows are still strong CO_2 sinks as demonstrates the comparison of carbon (PIC and POC) stocks between vegetated and adjacent un-vegetated sediments.

1. Introduction

Calcium carbonate ($CaCO_3$) accounts for about a 25% of the surface marine sediments (Balch et al. 2005). Contemporary oceanic carbonate sediments are mainly composed by two main mineral forms of calcium carbonate, calcite (including Mg-calcite, magnesium-rich calcite) and aragonite, both primarily formed by biogenic precipitation (Smith, 2013). The coastal ocean accounts for around 33% of the global $CaCO_3$ production (Smith, 2013) but it is where the highest proportion of carbonate sediment accumulation takes place (nearly two-thirds of its production) whereas in open ocean sediments only one-third of the $CaCO_3$ produced is accumulated (Milliman and Droxler, 1996; Smith, 2013). A broad range of communities is involved in the production and subsequent accumulation of $CaCO_3$ in marine sediments, including benthic ecosystems dominated by coral reefs (Chave et al., 1972; Smith, 2013), calcareous algae (Milliman, 1993) and maerl beds (Bosence and Wilson, 2003); and planktonic communities including coccolithophores (Westbroek et al., 1989), foraminifera (Langer et al., 1997), and pteropods (Fabry, 1990). More recently the important contribution of echinoderms (Lebrato et al., 2010), molluscs (Chauvaud et al., 2003) and fish (Wilson et al., 2009) to $CaCO_3$ production has been revealed. Relative to other ecosystems, the production of $CaCO_3$ in seagrass meadows ecosystems and its accumulation in the sediments is poorly studied and not explicitly considered in any of the existing assessments of the global ocean carbonate budget (Milliman et al., 1993; Milliman and Droxler, 1996; Lebrato et al., 2010), despite the important load of carbonate often found in their sediments and leaves (Canals and Ballesteros, 1997; Gacia et al., 2003; Perry and Beavington-Penney, 2005; Serrano et al,. 2012, Enriquez and Schubert, 2014) and their role as a source of carbonate sand for beach formation and preservation (De Falco et al., 2003; Tigny et al., 2007). Indeed, a global estimate of the carbonate stock in seagrass sediments is not yet available and the potential contribution of these systems to the global ocean carbonate budget remains to be evaluated.

There is considerable interest in quantifying the capacity of the World's ecosystems to trap and store carbon, as this can offset anthropogenic carbon emissions to the atmosphere. To date, most work on the carbon pools in seagrass ecosystems has focused on the amount of particulate organic carbon (POC) stored (Fourqurean et al., 2012; Lavery et al., 2013) whereas, except for *Posidonia oceanica* in the Mediterranean Sea (Serrano et al., 2012), the inorganic component, particulate inorganic carbon (PIC), has not yet been considered in the assessment of carbon deposits in seagrass meadows. Seagrass ecosystems support diverse and active communities of calcifying organisms and through their photosynthetic activity their canopies provide pH environments that facilitate carbonate deposition (Hendriks et al., 2014). While

PIC, in the form of shells and other skeletal remains represent a substantial carbon stock, the production of PIC through calcification may act as a source of CO_2 to the atmosphere (Frankignoulle et al., 1994; Gattuso et al., 1998; Smith, 2013). Thus, understanding the amount of carbonate in seagrass ecosystems is crucial to determining their role in the global atmospheric carbon cycle. The evaluation of the carbonate accumulation rates and stocks in seagrass sediments is also relevant as they may significantly contribute to sediment accretion in coastal areas, a fundamental mechanism supporting the role of seagrass in coastal protection (Duarte et al., 2013).

Seagrass meadows accumulate PIC through calcium carbonate production by calcifying organisms inhabiting the meadows, such as epiphytes (Frankovich and Zieman, 1994; Perry and Beavington-Penny, 2005; James et al., 2009; Enríquez and Schubert, 2014) and benthic invertebrates (Jeudy de Grissac and Boudouresque, 1985) and the deposition of carbonate associated with sedimentation of particles (Gacia et al., 2003). In addition, a recent study demonstrates a direct implication of the seagrass *Thalassia testudinum* in the formation of aragonite needles that accumulate internally in the cell walls and as external deposits on the blades (Enríquez and Schubert, 2014). Other evidence for the existence of active carbonate processes in seagrass beds include calcification and carbonate dissolution in the canopy, associated with the daily cycles of photosynthesis and respiration (Frankovich and Zieman, 1994; Barrón et al., 2006; Yates and Halley, 2006), and the dissolution of calcium carbonate in the sediment as a result of below-ground release of CO_2 by respiratory processes (Hu and Burdige, 2007).

All the processes mentioned (precipitation, dissolution and sedimentation) partially depend on seagrass metabolic activity and plant structural features and thus, $CaCO_3$ stocks in seagrass sediments are likely to vary across meadows of different species (Duarte, 1991). In addition, $CaCO_3$ stocks in seagrass meadows will likely vary with latitude, as temperature regulates the seawater saturation state for carbonate minerals, that increases with increasing temperature (Zeebe and Ridgwell, 2011) thereby favouring biogenic carbonate precipitation in warmer waters (Mutti and Hallock, 2003).

Here we provide the first global assessment of the particulate inorganic carbon (PIC) deposits in seagrass ecosystems. We do so through a synthesis of published and unpublished data on carbonate stocks in seagrass sediments. We examine the variability of PIC stocks with biogeographic region, latitude and taxonomic composition of the seagrass community. We also compare the PIC and POC stocks in seagrass ecosystems with those in adjacent un-vegetated sediments, provide a first global assessment of the PIC:POC ratio over sediment depth profiles and discuss its implications for current estimates of CO_2 sequestration in seagrass ecosystems.

2. Material and methods

We compiled the published data available on carbonate stocks in seagrass meadows and adjacent un-vegetated sediments. We considered the total pool of $CaCO_3$ reported without distinguish between the different possible biogenic carbonate mineral forms (calcite, Mg-calcite and aragonite). Fourqurean et al. (2012) provided data for 201 sites, and a literature search using both the Web of Knowledge (using the search terms "seagrass*" AND "inorganic carbon*" AND ["calcific* OR sediment* OR $CaCO_3$ OR dissolut* OR diagenesis"]) and Google Scholar (using the search terms "seagrass carbonate") yielded data for an additional 82 sites. We amended the database with unpublished values for 154 additional sites sampled by the authors. This yielded a total of 437 sites with data on sediment carbonate concentration in coastal areas occupied by seagrasses, of which 34 corresponded to sand patches adjacent to seagrass meadows (Supplementary Information). The final database comprised estimates for 403 seagrass vegetated sites, of which 219 consisted of values for sediment surface samples (ca. 1-30 cm depth) and 184 consisted of values for sediment cores of variable length (149 cores < 100 cm-long, and 35 cores ≥ 100 cm-long).

The greatest proportion of the sites (46%) was located in tropical and subtropical regions (20-40 degrees latitude) for both the southern and northern hemispheres whereas the data from higher latitude regions were scarce (Fig. 1). Data on surface sediment carbonate was broadly distributed, but most (80%) core data available was from subtropical and temperate seagrass meadows (Fig. 1).

Lithogenic characteristics of the sites were not considered in this study, which, thereby, assumes that carbonate sediment stocks have a biogenic origin. We cannot discard this leading to an overestimation of carbonate deposition rates in areas where lithogenic carbonate might be important. However, as the biogenic carbonate pool is considered to be the dominant in contemporary oceanic sediments (Smith et al., 2013), the local geological characteristics might not have a highly relevant impact in the results of this study.

When only one of the variables, $CaCO_3$ or PIC was reported, the other was estimated assuming that PIC is 12% of the total molar mass of the $CaCO_3$. In most cases, particulate inorganic carbon (PIC) was reported as a percentage of dry weight (%DW), where PIC, in mg PIC cm^{-3}, was calculated as the product of the fraction of sediment dry weight composed by PIC and the dry bulk density (DBD) of a given core section (n = 340 sites). When DBD was not reported (n = 113 sites), we used the average DBD (1.03 g cm^{-3}) reported by Fourqurean et al. (2012) for seagrass sediments in the calculations. The error introduced by this assumption was small, as a paired t-test revealed an average deviation of 3.3% (t-ratio= 4.32; $p < 0.0001$) when we tested the differences between estimating PIC concentration using the observed DBD and the assumption of 1.03 for the sites where an observed DBD was reported.

Due to the variability in length of the sediment cores available for the study, mean PIC concentration in seagrass sediments was estimated for the top 10 cm of sediment for a total of 385 sampled sites, for which at least one measure of PIC was reported for this depth zone. To estimate the carbonate stock within the top meter of sediment for the total database available we assumed a constant concentration of PIC in the top meter for those cores where shallower profiles were reported, as almost half (46%) of the long cores (length >100 cm, n=35) showed no significant change in PIC concentration with depth within the first top meter and the remaining long cores showed only a slight increase of 0.011% DW cm^{-1} on average.

The sites were classified based on (1) the seagrass biogeographic regions described by Hemminga and Duarte (2000) (North East Pacific, South East Pacific, Tropical Western Atlantic, North Atlantic, South Atlantic, Mediterranean, Indo-Pacific, Western Pacific and Southern Australia), (2) 10^o latitude bins and (3) the genus of the dominant seagrass species (*Amphibolis*, *Halophila*, *Halodule*, *Enhalus*, *Thalassia*, *Zostera*, *Posidonia*, *Syringodium*, *Thalassodendron* and *Cymodocea*).

PIC and POC concentrations were compared along the sediment depth profiles when both variables were reported in the same site (n = 392). The depth profile of POC, PIC and POC:PIC within the top meter was explored for the longest cores (length >100 cm) when at least three different data were reported within the top meter (n = 26). For those sites from where data for sediments from adjacent vegetated and un-vegetated patches were reported (n=34), POC and PIC concentrations were also compared.

We used a paired sample t-test to assess the difference between the frequency distribution and average of observed values and estimated values of top meter stocks and the difference between PIC and POC across the data set and between adjacent vegetated and un-vegetated patches. Analyses of Variance (ANOVA) and a post-hoc Tukey-test were applied to compare the PIC stocks among the biogeographic regions and among the dominant genera. We used general linear models (GLM) to test the effect of latitude on the PIC stocks, the depth-variability in the POC and PIC concentrations and their ratio POC:PIC and the variability in POC and PIC concentrations in vegetated and un-vegetated patches. All statistical analyses were conducted using the statistical software JMP 5.01a.

3. Results

Particulate inorganic carbon concentration within the top 10 cm of seagrass sediments ranged between 0.3 and 174 mg PIC cm^{-3}, with an average of 62.5 ± 1.7 mg PIC cm^{-3} and a median of 54 mg PIC cm^{-3} ($n = 385$). The PIC stock in the top meter of sediment in seagrass meadows showed a wide variability, ranging between 3 and 1660 Mg PIC ha^{-1}, with an average ± standard error and a median of 654 ± 24 and 643 Mg PIC ha^{-1}, respectively ($n = 403$; Fig. 2). Estimated stocks (mean ± SE, 676 ± 26 Mg PIC ha^{-1}, Table S1) were significantly higher than those derived from direct measurements (mean ± SE, 423 ± 52 Mg PIC ha^{-1}, Table S1, $p > 0.05$); however, estimated and measured paired values did not show a significant difference (Fig. 2; paired t-test, $p > 0.05$).

The PIC stocks differed significantly among seagrass biogeographic regions (ANOVA, F-ratio=12.64, $p < 0.0001$). The largest stocks were found in the Tropical Western Atlantic similar to those from the Indo-Pacific and the Mediterranean regions. The North Atlantic PIC stocks were significantly lower (Table 1). The largest PIC stocks were found in equatorial and subtropical regions and tended to decrease polewards by -8 ± 2 Mg PIC ha^{-1} per degree of latitude (Fig. 4; GLM, ChiSquare=13.43, $p< 0.0002$). The low PIC values found between -10° and -20° in the southern hemisphere derive from Queensland (Australia), and the low values between 50-60º and 60-70º (Northern Hemisphere) correspond to meadows in Northern Denmark and south-west Greenland, respectively (Fig.4).

The PIC stocks also differed among dominant species (ANOVA, F-ratio= 13.98; $p< 0.0001$). The highest PIC stocks were found underlying *Halodule*, *Thalassia* and *Cymodocea* meadows while the lowest stocks were supported by *Zostera* and *Halophila* meadows (Fig. 3). *Posidonia* meadows had intermediate PIC stocks.

Where both PIC and POC were measured concurrently (392 sites; n= 3076), mean PIC concentrations tended to exceed mean POC concentrations (paired t-test: T-ratio= 64.77, $p < 0.0001$). The POC:PIC ratio ranged from nearly 0 to 108, with an average of 0.74 ± 0.05 and a median of 0.20 (Table 2; Fig. 5). For the longest cores in the database (length ≥ 100 cm) which had a minimum of three different observations reported over one meter depth (n= 26), the POC concentration (mg POC cm^{-3}) along the sediment profile of these cores tended to decrease with depth whereas PIC (mg PIC cm^{-3}) was more variable (Figure S1). The POC: PIC ratio declined consistently with depth in the top meter of sediment in 69% of these cores at an average of -0.00054% cm^{-1}.

There was a strong relationship between PIC content (%DW) in paired vegetated and un-vegetated sediments ($R^2 = 0.92$, Fig. 6a), with a slope very close to 1 (0.99 ± 0.02) and an intercept not different from 0 (0.17 ± 0.99), indicating that the PIC content in seagrass sediments did not differ significantly from that in adjacent un-vegetated sediments (paired t-test, T-ratio = 1.67, $p > 0.05$; n = 195) (Fig. 6a). However, no relationship was found between the POC content (%DW) in seagrass sediments and adjacent bare sediments (Fig. 6b). POC content was significantly higher in vegetated sediments (mean ± SE, 0.66 ± 0.04) compared to adjacent bare sediments (mean ± SE, 0.35 ± 0.017, paired t-test, T-ratio = -6.57, $p < 0.0001$; n = 195).

4. Discussion:

4.1. PIC global stocks and the effect of species and latitudinal distribution.

Available data on PIC stocks in seagrass meadows showed an important geographic bias. Whereas seagrass meadows are distributed along the coast of all continents except Antarctica (Hemminga and Duarte, 2000), data on PIC stocks in seagrass sediments are mostly restricted to tropical and temperate regions, with a particularly important contribution to the data set by meadows in Australia and the Mediterranean, especially for the profiles at least 1 m deep. Fourqurean et al. (2012), also found a similar bias on the distribution of data available for their review of particulate organic carbon (POC) stocks in seagrass meadows, although the data were more widely distributed. The geographic bias in data availability and the great variability in PIC stocks among the sites included in this study, add uncertainty in the assessment of the global estimates provided here. Even scarcer are data from un-vegetated sediments adjacent to seagrass meadows, with a comparative approach possible in only 34 over the total of 437 sites, limiting the certainty of comparisons of PIC and POC stocks in vegetated versus un-vegetated habitats.

The median PIC sediment top meter stocks of 643 Mg PIC ha^{-1} (n = 403), is nearly 5 times larger than the median stock of POC recently estimated by Fourqurean et al. (2012) at around 140 Mg POC ha^{-1} (n=89). Based on the available range of estimates of global seagrass area, between 177,000 and 600,000 km^2 (Mcleod et al., 2011), seagrass meadows store globally between 11 and 39 Pg of PIC in the top meter of sediment.

Our results show that the PIC stocks of seagrass meadows vary depending on the seagrass genera. Large genera, with larger leaf size and extended leaf life span (Duarte, 1991) were expected to sustain a higher amount of calcareous epiphytes and favour a higher accumulation of PIC. The age of the leaves affects the colonisation of seagrass leaves by epiphytes (including calcareous organisms; Heijs, 1985; Borowitzka et al., 1990; Cebrián et al., 1994) and the mineral load has been found to increase with increasing leaf age (Gacia et al., 2003). The height of the canopy, which correlates with shoot size, has also been shown to determine the epiphyte biomass and species biodiversity in meadows of *Amphibolis* (Borowitzka et al., 1990). Sedimentation process and particle trapping in a meadow are also linked to canopy height (Gacia et al., 2003) and leaf density (Fonseca and Cahalan, 1992) and therefore PIC sedimentation and retention may be also favoured in seagrass meadows dominated by larger species, where long leaves effectively slow water currents and increase particle setting. In addition, larger seagrass species may favour carbonate precipitation through their metabolic activity as the leaf area index has been seen to directly relate to maximum and range Ω daily values in seagrass meadows (Hendricks et al. 2014). Hence, we expected to find high storage of PIC in the sediment of large seagrass genera. However, some large genera, such as *Posidonia*, did not support particularly large stocks, while some small genera, such as *Halodule*, supported large stocks. The lack of a clear effect of the seagrass genera size could be due to other controlling factors on the precipitation and preservation of carbonate in the sediment at regional and local scales not covered by the current study. These may involve differences in geomorphology, salinity, water depth, tidal and current regimes, nutrient and light availability and CO_2 balance (Lees, 1975) as well as the presence of nearby ecosystems, such as corals in tropical regions, which may act as sources of carbonates to seagrass sediments.

Latitude also influenced the size of the PIC stocks in seagrass sediments, that tended to decrease with increasing latitude, consistent with the higher epiphyte carbonate loads in seagrass leaves in tropical compared to temperate regions (Gacia et al., 2003). This general trend of decline with increasing latitude has been observed in other carbonate-intense ecosystems, such as reef-building corals (Veron and Minchin, 1992; Veron, 1995) and encrusting red algae communities, which are more heavily calcified in warm tropical than in cold temperate waters (Lowenstam and Weiner, 1989). The latitudinal distribution of carbonate stocks may be explained by temperature and salinity dependence of the saturation state of carbonate minerals (Ω) (Zeebe and Wolf-Gladrow, 2001). The saturation of calcium carbonate in seawater is mostly dependent on the availability of CO_3^{2-}, as Ca^{2+} concentration is two orders of magnitude higher than CO_3^{2-} concentrations (Gattuso et al., 1998). From a thermodynamic perspective, cold and fresh water generally promotes lower Ω saturation states and prevents $CaCO_3$ precipitation (Mucci et al., 1983). As both salinity and temperature tend to decrease with increasing latitude the carbonate saturation state decreases polewards with respect to tropical and temperate waters (Hoegh-Guldberg et al., 2007). Hence, the precipitation of biogenic $CaCO_3$ is favoured in tropical and subtropical areas compared to temperate regions (Mutti and Hallock, 2003). Discrepancies from the general trend, such as the low carbonate stocks reported in the latitudinal bins -10 to 20º S are probably explained by local factors that alter the Ω saturation states, such as inputs of fresh water and terrigeneous sediments from river discharges in the sites of study (Mellors et al., 2002; Fisher and Sheaves, 2003).

4.2. PIC estimated accumulation rates in seagrass meadows.

Our review of the literature indicated that PIC accumulation in seagrass sediments is high and comparable to other carbonate producing ecosystems. Based on our identified mean PIC concentration of 62.5 ± 1.7 mg PIC cm^{-3} in the top 10 cm of seagrass sediments (sites = 385, n= 802) and a mean rate of sediment accretion in seagrass meadows of 0.2 ± 0.04 cm y^{-1} (Duarte et al., 2013) we estimate that the PIC accumulation rates in seagrass sediments would average 126.3 ± 31.05 g PIC m^{-2} y^{-1}. This rate is somewhat below the range of PIC sedimentation rates reported by Gacia et al. (2003) in seagrass meadows of SE Asia, based on direct measures of daily sediment deposition at 8 different sites (145 – 9443 g PIC m^{-2} y^{-1}) but higher than the average PIC accumulation rate in sediments of *Posidonia oceanica* meadows (54.3 ± 1.9 g PIC m^{-2} y^{-1}) estimated from sediment stock assessment and sediment dating (Serrano et al., 2012). Extrapolation, assuming an estimated range of global area of seagrass meadows between 177,000 and 600,000 (Mcleod et al., 2011), suggests a total accumulation of PIC in seagrass sediments ranging between 22 ± 5 and 76 ± 19 Tg PIC y^{-1}. These estimates are subject to uncertainties derived from the high variability in PIC stocks among regions and species, and the absence of estimates on seagrass extent for each region/system considered in this study. Assuming that tropical seagrass represent 2/3 of the total seagrass, PIC accumulation rates can be calculated separately for tropical (17.6 ± 4.5 and 59.7 ± 15.2 Tg PIC y^{-1}), and temperate meadows (4.5 ± 1.5 and 15.3 ± 4.9 Tg PIC y^{-1}, for the low and high global seagrass area estimates respectively), yielding a range for global PIC sequestration in seagrass meadows from 22 ± 6 to 75 ± 20 Tg PIC y^{-1}, depending on the global seagrass extent considered.

The rates of PIC accumulation estimated in this study, both globally (22-75 Tg PIC y^{-1}) and per surface area (126.3 ± 31.05 g PIC m^{-2} y^{-1}), highlight the importance of seagrass meadows as major sites for $CaCO_3$ accumulation and storage in the ocean. The global PIC accumulation rates of seagrasses are substantially lower than in deep oceans by pelagic communities (100–132 Tg PIC y^{-1}) but significantly higher when considering their contribution per surface area (0.34-0.45 g PIC m^{-2} y^{-1}). Seagrass PIC accumulation rates were comparable to those of coral reefs both globally (84 Tg PIC y^{-1}) and per surface area (140 g PIC m^{-2} y^{-1}). Relative to *Halimeda* bioherms (20 Tg PIC y^{-1}) seagrass PIC accumulation showed higher global rates but significantly lower rates per surface area (400 g PIC m^{-2} y^{-1}) (Milliman and Droxler, 1996; Catubig et al., 1998; Table 3).

4.3. Implications in the assessment of the CO_2 sink capacity of seagrass meadows.

While PIC represents a substantial carbon stock, carbonate precipitation results in a rise of the partial pressure of CO_2 (pCO_2), which, can result in CO_2 supersaturation and release of CO_2 to the atmosphere (Ware et al., 1992). The net release of CO_2 with carbonate deposition is defined by the molar ratio of CO_2 flux:$CaCO_3$ precipitation (Ψ), which decreases with decreasing temperature while increasing with pCO_2 (Frankignoulle et al., 1994). Ψ varies from 0.63 in surface waters in low to mid-latitudes, where carbonate precipitation takes place, to 0.85 below 500 m depth throughout the ocean, where most dissolution takes place (Smith, 2013). Due to the vertical variation in Ψ, Smith (2013) identified the pelagic carbonate system as a net sink of CO_2, as most of the surface production (Ψ =0.63) dissolves as it reaches deep waters (Ψ =0.85) compensating for the CO_2 emitted by $CaCO_3$ precipitation in surface waters. In contrast, carbonate deposition in shallow ecosystems, such as seagrass meadows, would act as a CO_2 source as approximate two-thirds of the $CaCO_3$ produced in shallow benthic ecosystems accumulates in the sediment, and Ψ has the same value for $CaCO_3$ precipitation and dissolution (Milliman and Droxler, 1996; Smith, 2013). Given that seagrass meadows are sites of strong net primary production, any pCO_2 increase due to calcification may be more than compensated for, by organic production. Hence, Ψ has been interpreted to imply a POC:PIC production ratio threshold, with a value of 0.63 equivalent to no net change in pCO_2 and values greater or smaller than this value implying a net sink or source respectively.

The median POC:PIC ratio of seagrass sediments found in this study was 0.2, independent of depth (median of surface sediments 0.17), well below the POC:PIC ratio threshold of 0.63, with only 18% of seagrass sediments showing POC:PIC ratios > 0.6. Following the rationale above and assuming that organic carbon and calcium carbonate accumulate in the sediment in proportion to their production, these results could be interpreted to imply that CO_2 emissions derived from carbonate deposition may offset the CO_2 sink capacity associated with organic carbon burial in seagrass sediments globally, as discussed before for *Posidonia oceanica* in the Mediterranean (Mateo and Serrano, 2012; Serrano et al., 2012). However, such interpretation would be premature. In general terms, the organic and inorganic carbon cycles in the ocean run at very different rates and although organic matter is produced at much faster rates than $CaCO_3$, it is also decomposed more rapidly (Smith, 2013). However, the carbonate precipitation in seagrass meadows is intimately regulated by the organic metabolic rates of the ecosystem (Smith and Atkinson, 1983; Barrón et al., 2006; Yates and Halley, 2006; Hendriks et al., 2014) and when both organic and inorganic carbon metabolic pathways have been measured in situ simultaneously, seagrass meadows have been found to be mainly net CO_2 sinks systems at a yearly scale (Barrón et al., 2006), even despite the underestimated Net Community Production (NCP) rates that may derive from the use of confined incubation chambers related to photoxidation processes and subsequent CO_2 increase and O_2 decrease during daytime (Champenois and Borges, 2012). In addition to carbon burial, a significant fraction of the net community production of seagrass, supporting a CO_2 sink, is also exported as DOC and POC (Cebrián et al., 1997, Barrón and Duarte, 2009). Hence, the comparison of sediment standing stocks would reflect only a fraction of the sink capacity of the seagrass ecosystems but not the net effect of the organic and inorganic carbon metabolic pathways on the net CO_2 flux. Therefore, more research, which takes into account both the organic and inorganic carbon cycles associated with these systems, is needed to better assess the role of seagrass ecosystems as carbon sinks or sources.

Understanding the balance between CO_2 emissions from carbonate deposition and CO_2 sequestration from organic carbon storage in seagrass sediments should not only focus on the POC:PIC ratio, but also on resolving how seagrass affect the POC:PIC ratio compared to adjacent un-vegetated sediments. When comparing the carbon content (%DW) between vegetated and adjacent un-vegetated patches, there was no difference in PIC whereas the POC content was about two-fold larger in vegetated sediments compared to adjacent un-vegetated sediments as previously observed (Duarte et al., 2010, Kennedy et al., 2010). This result indicates that, despite the significant carbonate sediment deposits identified and that seagrasses favour carbonate precipitation and accumulation by epiphytes and other organisms inhabiting the meadow, sediment PIC largely depends on local environmental conditions that control carbonate precipitation and a significant fraction may derive from external sources, such as adjacent carbonate producer systems (corals). As a consequence, the POC: PIC ratio of seagrass sediments (mean ± SE, 0.28 ± 0.06) exceeded that of adjacent un-vegetated sediments (mean ± SE, 0.19 ± 0.040) in 73% of the meadows examined. Hence, the organic carbon stock present in seagrass sediments would be expected to be reduced to half if seagrass cover was lost while the inorganic stock will be comparable, thereby confirming the role of seagrass meadows as intense CO_2 sinks. It is important to point out that the rational above relates to the content (%DW) of both PIC and POC and not to the rate of accumulation, which may be significantly higher in seagrass compared to adjacent sand patches due to autotrophic production and sediment trapping.

In addition there are possible interactions between carbonate and organic carbon deposition that might enhance carbon sequestration in seagrass meadows. One possibility may be that high carbonate deposition rates may promote organic carbon sequestration and storage by enhancing sediment accretion and by rapidly removing organic carbon from surface sediments and away from the oxic zone, thereby enhancing preservation of organic carbon. The accumulation of carbonates in seagrass sediments may also influence below-ground biomass through the stimulation of vertical growth in the sediments, or through alteration of sediment composition and nutrient availability (Short, 1987, Ferdie and Fourqurean, 2004). In fact, Erftemeijer (1994) found higher below-ground biomass in seagrass meadows growing in carbonate sediments, compared to meadows from the same species that develop in terrigenous sediment. Thus, the potentially higher below-ground production in carbonate-rich meadows may enhance organic carbon burial.

4.4. Implications in the role of seagrass meadows as coastal protection.

Carbonate stocks represented an average of 51 ± 1% of the dry weight in the top 10 cm (range 0.2 to 100%) of the seagrass sediments examined, therefore contributing significantly to the sediment accretion rate and coastal protection from increased sea level rise and storminess with climate change (Duarte et al., 2013). The capacity of seagrass meadows to raise the seafloor at speeds that could match or exceed current sea level rise allows them to remain effective in protecting coastal areas (Duarte et al., 2013). A recent review of coastal ecosystems sediment accretion rates found an average accretion rate of 2 ±0.4 mm y^{-1} for seagrass communities (Duarte et al., 2013; Mazarrasa et al., 2013), highlighting the important role these ecosystems may play in climate adaptation in coastal areas. Carbonate production and accumulation supports about half of this accretion rate.

This study offers the first global compilation of carbonate deposits in seagrass sediments. Despite some limitations in the geographic distribution of the data available, the scarcity of data from adjacent sand patches and the lack of local sediment accretion rates, we identified a significant role of seagrass ecosystems in the carbonate dynamics of coastal areas, with carbonate stocks and rates relevant at the global scale. Carbonate stocks, markedly higher in tropical and subtropical meadows, play a significant role in supporting the accretion rate of seagrass meadows, and while high carbonate deposition lead to CO_2 emissions, comparison of vegetated vs. adjacent un-vegetated sediments still identify seagrass meadows as strong CO_2 sinks. In order to enhance knowledge of the effect of carbonate accumulation in seagrass meadows on the function they play as CO_2 sinks, further investigation is required, especially on the coupling of the organic and inorganic metabolic processes that take place within the meadows.

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TABLES:

Table 1: Number of observations, mean ± standard error, median and range of values for the PIC stocks in each biogeographic region (Tropical Western Atlantic, Indo-Pacific, Mediterranean, Southern Australia and Northern Atlantic). The results of the comparison among different regions (Tukey-Kramer HSD test) are shown in the last column where different letters represent a significant difference ($p<0.05$).

Biogeographic region	n	Mean (Mg PIC ha^{-1})	SE (Mg PIC ha^{-1})	Median (Mg PIC ha^{-1})	Range (Mg PIC ha^{-1})	Tukey-Kramer HSD test
T.W. Atlantic	60	869.5	54.6	891.4	16 - 1660	A
Indo-pacific	145	713.9	47.0	795.2	3 - 1611	AB
Mediterranean	42	654.4	71.3	658.2	87 - 1542	AB
S. Australia	121	603.9	34.2	566.5	8 - 1475	B
N. Atlantic	35	204.9	35.4	68.2	8 - 555	C

Table 2: Mean ± Standard Error (SE), median, minimum and maximum values of particulate inorganic carbon (PIC), particulate organic carbon (POC) and the estimated POC: PIC ratio for the data set where both POC and PIC were reported (392 sites; n= 3076).

	PIC (mg cm^{-3})	POC (mg cm^{-3})	POC:PIC
Mean ± SE	72.5 ± 0.8	51.6 ± 0.6	0.74 ± 0.05
Median	68.3	49.4	0.20
Max	325.1	321.0	107.6
Min	0.2	0.4	0.00038

Table 3: Estimated area, and PIC accumulation rates globally (Tg PIC y^{-1}) and per surface area (g PIC m^{-2} y^{-1}) for different carbonate producing ecosystems including the results found for seagrasses in this study and a global estimation considering neritic, slopes, and pelagic areas along with organism-level data.

Ecosystem	Area (10^{12} m^2)	Global (Tg PIC y^{-1})	Per surface area (g PIC m^{-2} y^{-1})	Reference
Planktonic communities	290	100-132	0.34-0.45	Catubig et al. (1998), Milliman and Droxler (1996)
Coral reefs	0.6	84	140	Milliman and Droxler, 1996
Halimeda bioherms	0.05	20	400	Milliman and Droxler, 1996
Bank/Bays	0.8	24	30	Milliman and Droxler, 1996
Seagrass meadows	0.6-0.177	22-75	126.3	Mcleod et al.2011; This study
Global		1,500		Lebrato et al. (2010)

FIGURES.

Figure legends.

Figure 1. Distribution of the data of PIC stocks in seagrass meadows (average top meter; Mg PIC ha^{-1}) compiled in this study by the biogeographic regions described by Hemminga and Duarte (2000). The size of the pie charts is proportional to the top-meter PIC stocks in each region. The fraction of PIC stocks estimated from surface sediments (yellow) and short sediment cores (P<100 cm, orange) and longer cores than 100 cm (P>100 cm, brown) is indicated.

Figure 2. Frequency distribution of observed (i.e. sites reporting data to at least one meter depth, n = 35) and estimated (i.e. sites where shallower depths were reported, n = 368) PIC stocks (Mg PIC ha^{-1}) in the top meter of seagrass sediments.

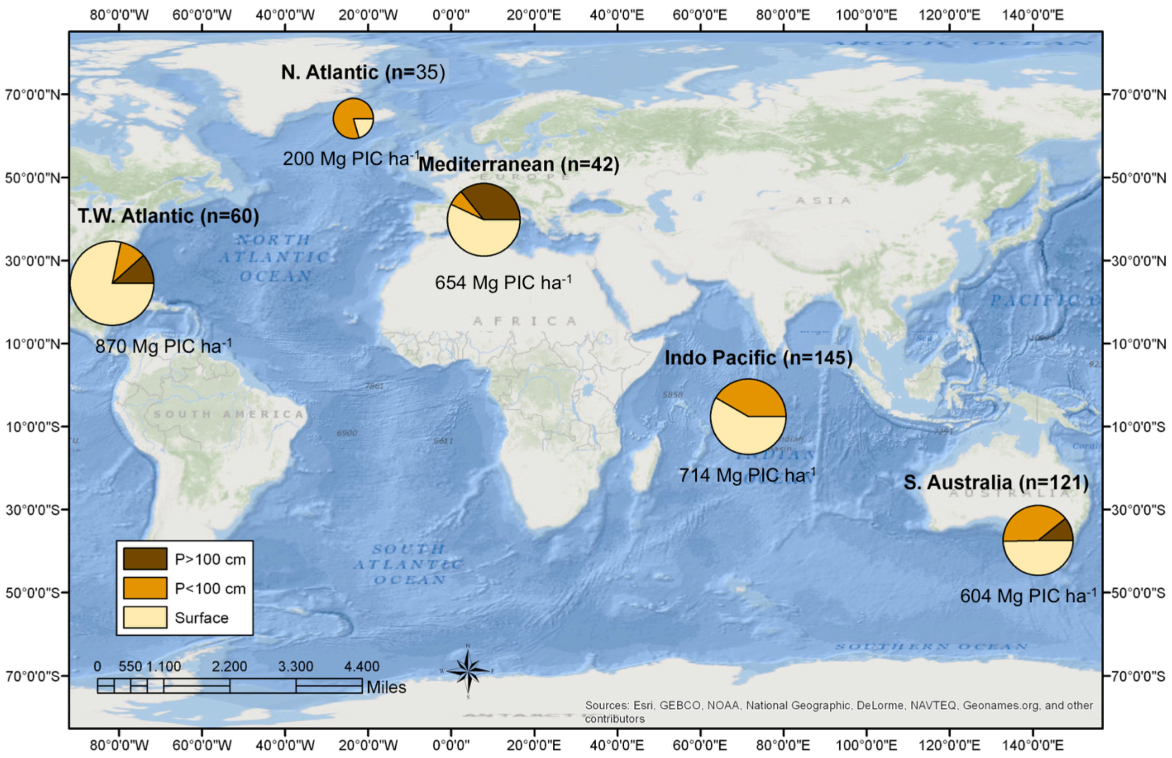
Figure 3. Average PIC stocks (Mg PIC ha^{-1}) ± SE across the dominant seagrass genera forming the meadows. Only genera with more than 10 observations have been represented. Identical letters indicate no significant differences between dominant species forming the meadows (ANOVA and Post-hoc Tuckey-test).

Figure 4. Average PIC stocks (Mg PIC ha^{-1}) ± SE by 10º latitude bins. The number above each bar indicates the number of observations reported for each latitude bin.

Figure 5. Frequency distribution of the POC:PIC ratio in the seagrass sediments examined (392 sites; n = 3076).

Figure 6. Relationship between a) PIC content (%DW) in seagrass sediments (x-axis) and adjacent un-vegetated sediments (y-axis) and b) POC content (%DW) in seagrass sediments (x-axis) and adjacent un-vegetated sediments (y-axis). Dash line shows the 1:1 relationship whereas the continuous line in panel a) represents the linear regression model between PIC content (%DW) in vegetated patches vs. adjacent un-vegetated patches.

Figure 1.



Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, NAVTEQ, Geonames.org, and other contributors

Figure 2:

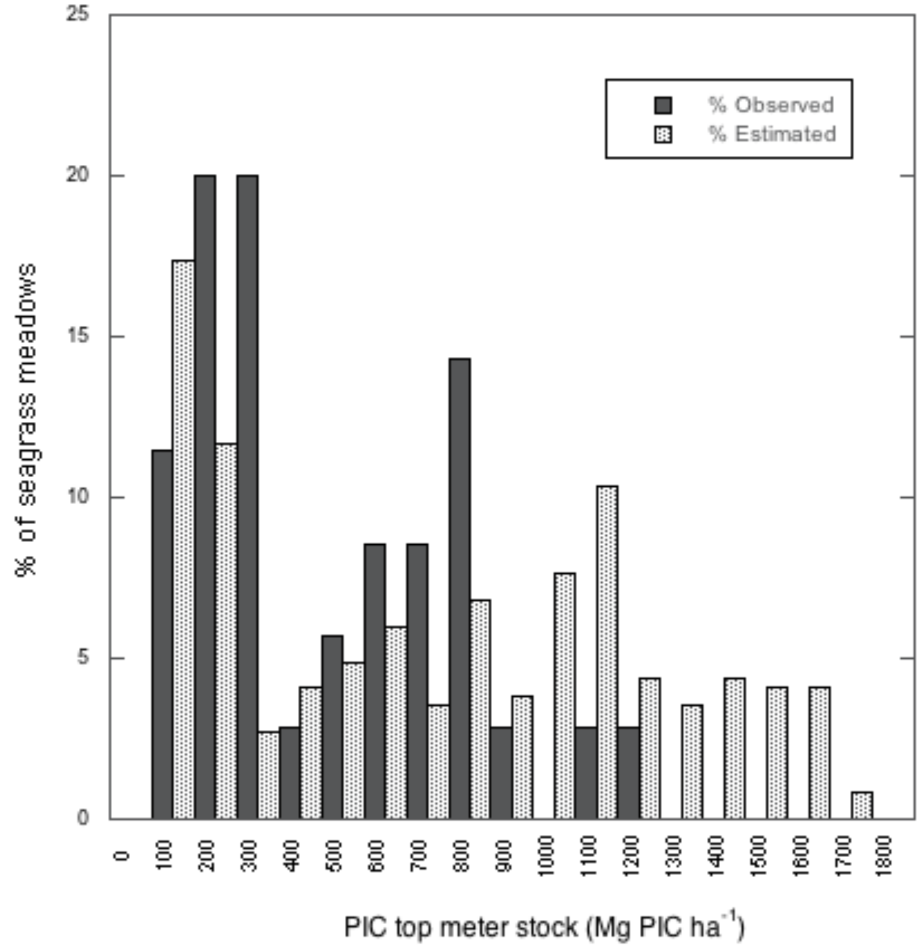
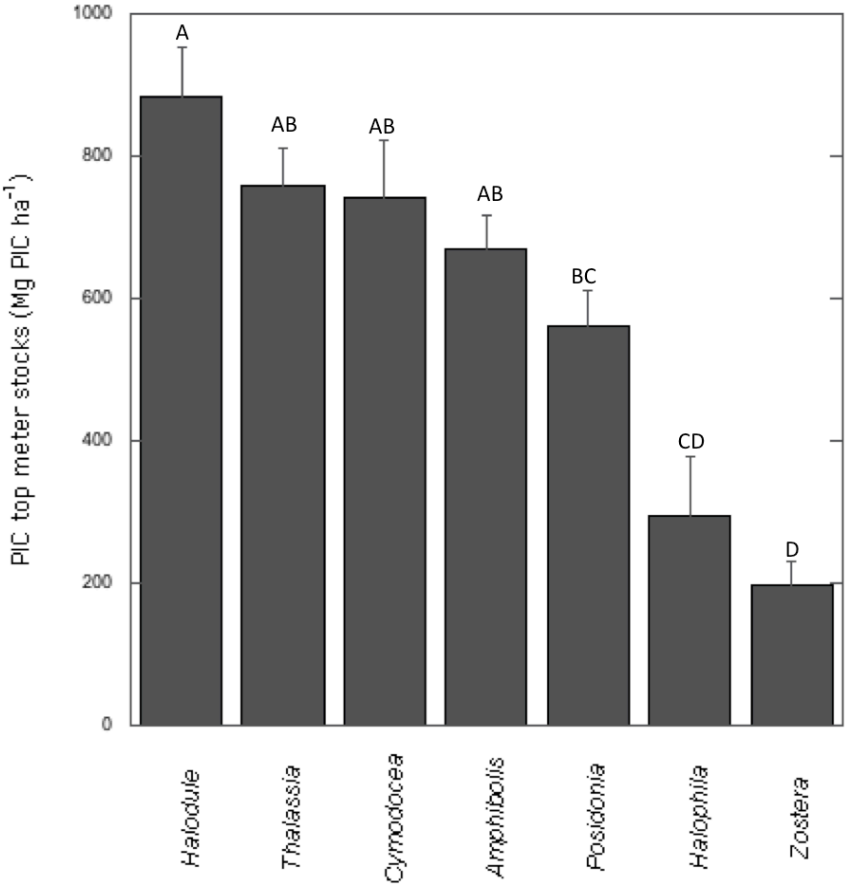
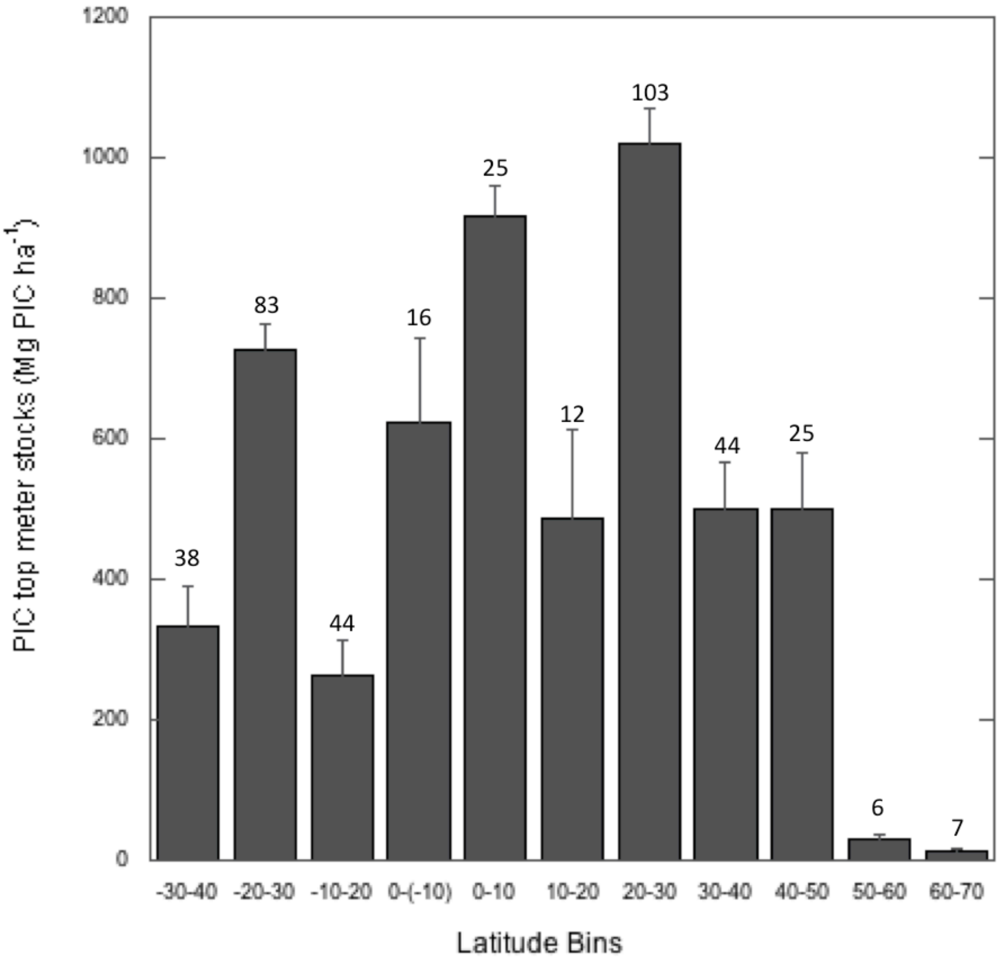

% Observed
% Estimated
25
20
15
10
5
0
% of seagrass meadows
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
PIC top meter stock (Mg PIC ha^{-1})

Figure 3:



PIC top meter stocks (Mg PIC ha^{-1})
1000
800
600
400
200
0
A
AB
AB
AB
BC
CD
D
Halodule
Thalassia
Cymodocea
Amphibolis
Posidonia
Halophila
Zostera

Figure 4:



PIC top meter stocks (Mg PIC ha^{-1})
1200
1000
800
600
400
200
0
38
83
44
16
25
12
103
44
25
6
7
-30-40
-20-30
-10-20
0-(-10)
0-10
10-20
20-30
30-40
40-50
50-60
60-70
Latitude Bins

Figure 5:

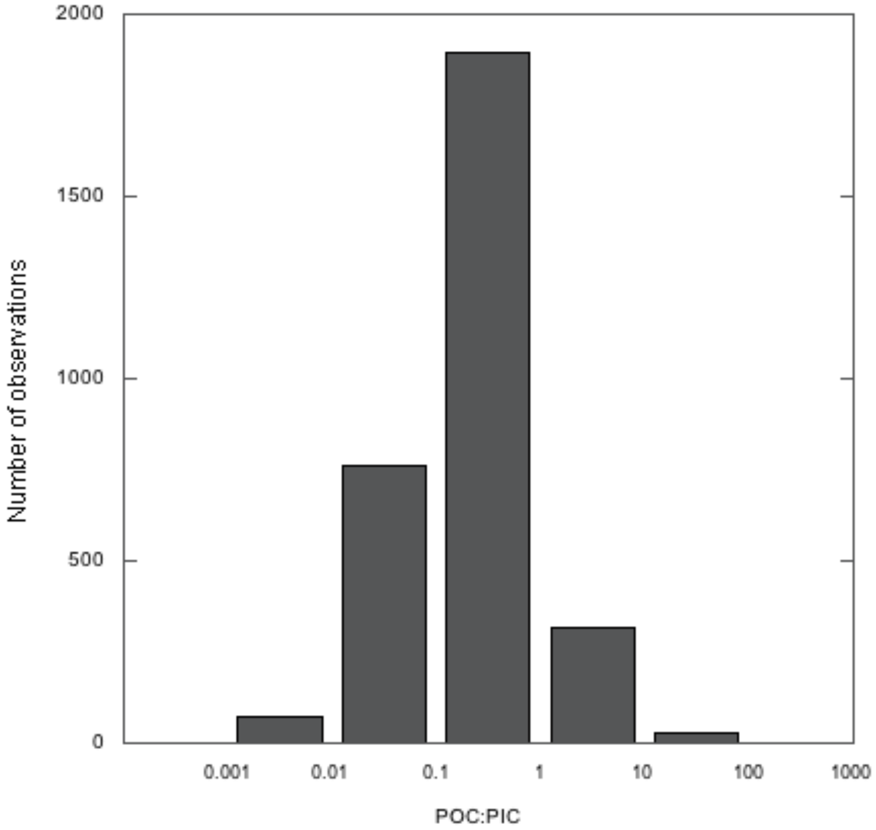
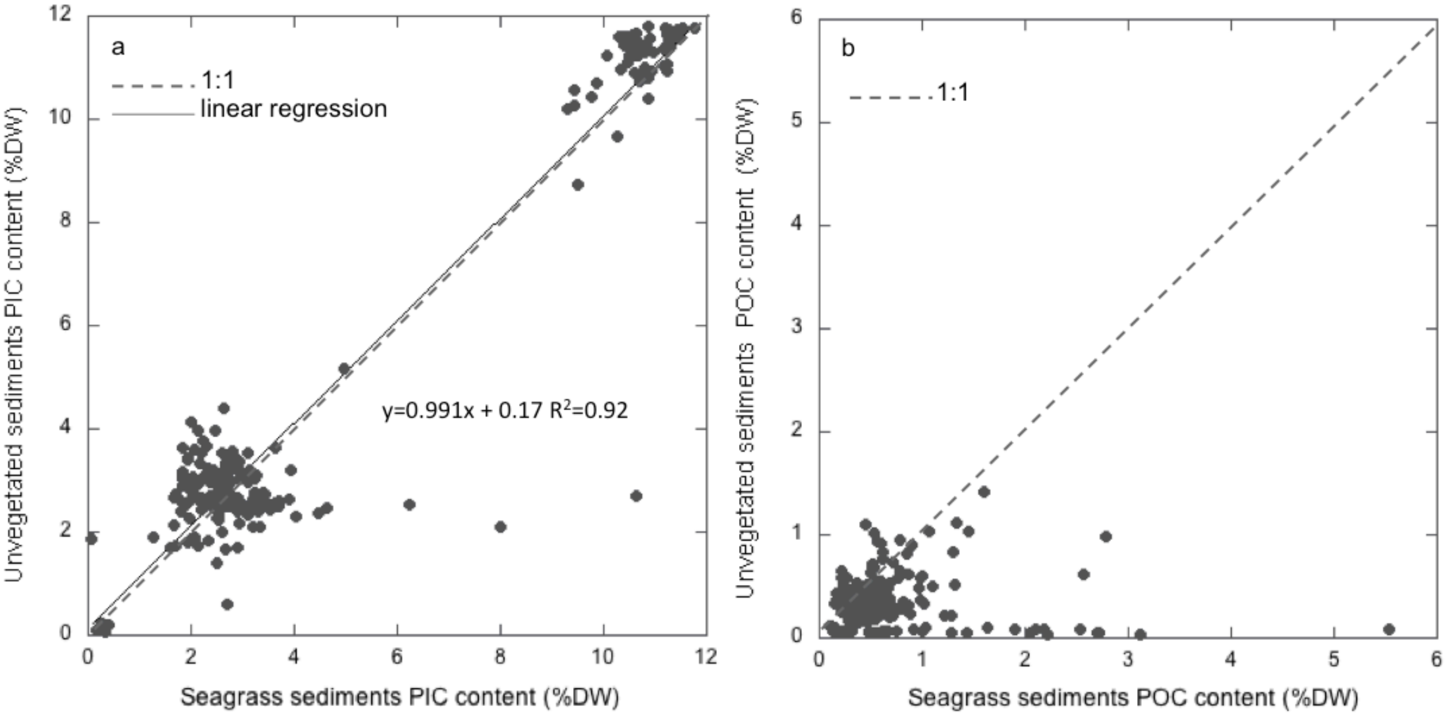

2000
1500
1000
500
0
Number of observations
0.001
0.01
0.1
1
10
100
1000
POC:PIC

Figure 6:


a
1:1
linear regression
y=0.991x + 0.17 R²=0.92
Unvegetated sediments PIC content (%DW)
Seagrass sediments PIC content (%DW)
0
2
4
6
8
10
12
b
1:1
Unvegetated sediments POC content (%DW)
Seagrass sediments POC content (%DW)
0
1
2
3
4
5
6