

Esporles (Mallorca), 16th of July, 2015.

Dear Editor Gerhard Herndl,

First of all, we are very grateful for your consideration of our manuscript of interest enough to be published in Biogeoscience.

We are also grateful for the corrections and suggestions provided by the referees # 1 and #2 that helped us to improve the manuscript, especially concerning those issues that resulted less clear and needed to be further developed and discussed.

In the text below we provided a detailed description of all the actions taken to accommodate the comments from referee #1 and referee #2. During the revision process, few small little errors in the manuscript were found that have been corrected for this new version and are detailed bellow. All the changes made in the text according to referees #1 and #2 and authors' corrections with respect to the first version are highlighted in the new version of the manuscript.

We hope you would find the revised manuscript improved enough for publication in the journal.

Sincerely,

Ines Mazarrasa

On behalf of the authors

Actions taken to address the concerns of Anonymous Referee #1.

Mazarrasa et al. compiled a large data-set of particulate inorganic carbon (PIC) in seagrass meadows and discuss the potential significance of this reservoir globally. The figures are of high-quality, text is well written.

My major concern is to determine if seagrass meadows develop in areas with hydrodynamic conditions that are favorable for sediment deposition, and that these areas are naturally favorable for shell debris deposition. If this was correct, then these areas would anyway have sediments enriched in PIC even in the absence of seagrasses. In this case seagrasses would not be an additional and so far not accounted reservoir of PIC, and in fact this was already accounted in the

budgets of PIC for coastal/continental shelf sediments by Milliman et al. (1993) and others. Figure 6A strongly suggests that this is the case since there is no significant difference in the PIC content between the seagrass sediments and adjacent unvegetated sediments.

Response:

Seagrass meadows occur in a wide range of depositional environments (from estuarine to exposed coastal areas; Carruthers et al. 2007) and the dataset explored in this study compiles all or most habitat types (from highly depositional to erosional environments). It is true that in areas where carbonate precipitation is favoured, such as tropical areas of high temperature and salinity, CaCO₃ precipitation and accumulation occurs independent to the presence of seagrass meadows. However, much higher cycling in both CaCO₃ precipitation and dissolution has been described in seagrass patches compared to adjacent bare-sands (Barrón et al. 2006; Morse et al. 1987; Burdige and Zimmerman, 2002). In addition, seagrass meadows are likely to enhance CaCO₃ sediment accumulation rates by sustaining a large biodiversity including calcifying organisms (Jeudy de Grissac and Boudouresque, 1985), favouring the accumulation of carbonate epiphyte load (Frankovich and Zieman, 1994; Perry and Beavington-Penny, 2005), favouring particle trapping (Gacia et al. 2003) and/or preventing sediment resuspension (Gambi et al. 1990; Terrados and Duarte, 2000; Gacia et al. 1999). Canals and Ballesteros (1997) compared the production of carbonate particles within different benthic communities in the Mediterranean Sea, including seagrass meadows and sandy bottom communities and found that *Posidonia oceanica* meadows have more than 100-fold higher carbonate production rates than sandy bottoms (60-70 g m⁻² yr⁻¹ and 0.5 g m⁻² yr⁻¹ respectively). Unfortunately we don't have estimates on the sediment accumulation rates for the vegetated and adjacent un-vegetated patches included in this study. Therefore, figure 6a only shows PIC concentrations, and not accumulation rates, that would have probably been higher in the vegetated patches compared to the un-vegetated.

The message that we aimed to transmit with this figure (6a and 6b) is that, if considering the ratio POC:PIC in the sediment as a way of assessing the role that seagrass play as carbon sinks or sources, we find that seagrass patches, thanks to the POC accumulation, show higher POC:PIC ratios, compensating somehow the CO₂ emissions derived from the CaCO₃ precipitation and accumulation.

Action:

In the new version of the manuscript we clarify that figure 6a shows PIC concentrations and not accumulation rates, that would have probably been higher in the seagrass patches compared to the un-vegetated sites.

The text now reads (L385-L391):

Understanding the balance between CO₂ emissions from carbonate deposition and CO₂ 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).

Minor Comments.

Referee #1.

Please also compare the deposition fluxes per surface area (g PIC/m²/yr) in addition to the integrated fluxes.

Response: We agree.

Action: We include in the new version of the manuscript the deposition fluxes per surface area estimated for different habitats (pelagic system, coral reefs and *Halimeda bioherms*) based on the global accumulation rates and the surface area occupied by each system reported in the literature (Milliman and Droxler, 1996; Catubig et al. 1998).

The text will read (L330-L339)

“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 CaCO₃ accumulation and storage in the ocean. The global PIC accumulation rates 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) and larger than the global estimates for Halimeda bioherms (20 Tg PIC y⁻¹) but significantly lower when relative to their surface area (400 g PIC m⁻² y⁻¹) (Milliman and Droxler, 1996; Catubig et al., 1998; Table 3).”

In addition, we will modify Table 3 and include the estimated area occupied by each ecosystem and the correspondent PIC accumulation fluxes per surface are (g PIC m⁻² y⁻¹).

The new table 3 will read:

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
<i>Halimeda</i> 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)

The new Table 3 legend will read:

“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 seagrass in this study and a global estimation considering neritic, slopes, and pelagic areas along with organism-level data.”

L369-L373: The cited studies measured CO₂ fixation into organic carbon with chambers. However, these techniques under-estimate GPP because of photorespiration and also due to the discrete nature of measurements they miss “peak” production events (Champenois & Borges 2012). The biased GPP measurements by chambers could affect the estimates of the balance between organic and inorganic production.

Champenois W. & A.V. Borges (2012) Seasonal and inter-annual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow, *Limnology and Oceanography*, 57(1), 347–361

Response: We agree and are grateful for your comment. We considered the study by Barrón et al. (2006) to be especially relevant for the discussion as it is, to our best knowledge, the only study where both organic and inorganic metabolism were measured simultaneously during chamber incubations. By measuring changes in O₂, DIC and TALK, they estimate the net fluxes of CO₂ due to both organic metabolism and to CaCO₃ precipitation and dissolution. They found that despite CaCO₃ precipitation was determinant in the CO₂ community balance, the *P. oceanica* meadow was still acting as a CO₂ sink in a yearly scale. As explained by Champenois and Borges (2012) photorespiration may be favoured in confined incubation chambers during the day time, leading to a release of CO₂, a consumption of O₂ and as a consequence, to an underestimation of Net Community Production rates (NCP). Considering the possible bias in the NCP add force to the consideration of the ecosystem studied as net autotrophic.

Action:

We will introduce in the text the possible underestimation of the NCP due to the constraints derived by the use of incubation chambers in the study by Barrón et al. (2006) and explain the implications in the estimated carbon balance.

The text will read (L370-L377)

“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 CO₂ sinks systems at a yearly scale (Barrón et al., 2006), even despite the underestimating Net Community Production (NCP) rates that may derive from the use of confined incubation chambers related to photooxidation processes and subsequent CO₂ increase and O₂ decrease during daytime (Champenois and Borges, 2012).”

Actions taken to address the concerns of Anonymous Referee #2.

In this ms. authors have compiled literature and unpublished data on carbonate content of worldwide seagrass meadows. As underlined by Authors, such review is presently missing as recent “blue carbon” studies focus mainly on organic carbon stored (or not stored) in the seagrass meadow. Therefore, I think this study interesting for BG readers and deserving to be published. Nevertheless, I have some concerns and regrets that should be taken into account before acceptance.

1. Methodology:

A. Bibliographical research: Bibliographical approach seem rather basic and, in absence of reference list in the supplementary material, it is not easy to check if it is exhaustive of existing literature. Grey literature (such PhD thesis) is not targeted by such approach. Moreover, a part of used data is unpublished (I have no problem with that) but we need to know who, when, how and where these data were obtained (to add in supplementary material).

Response:

We agree with your comment.

Action:

We have published online the database used for this study in the Spanish Research Council (CSIC) digital repository (<http://digital.csic.es/handle/10261/116550>) and cited it in the methods section as Supplementary Material. In the Supplementary Material the reference and the link to the database is specified.

The text in Supplementary Material now reads:

“Data used for analysis are archived on the Spanish Research Council database repository (CSIC digital) (<http://digital.csic.es/handle/10261/116550>) with the reference:

Mazarrasa, Inés; Marbà, Núria; Lovelock, Catherine E.; Serrano, Oscar; Lavery, Paul S.; Fourqurean, James W.; Kennedy, Hillary; Mateo, Miguel Ángel; Krause-Jensen, Dorte; Steven, Andy D. L.; Duarte, Carlos M. " Sediment inorganic carbon (PIC) deposits in

seagrass meadows and adjacent sand-patches", 2015, DIGITAL.CSIC.

B. Data processing: Using their compiled data, Authors make up-scaled calculation of carbonates accumulation in seagrass meadow. I think the way these calculations are done is too general or global and does not reflect the variability and the importance of these processes at worldwide scale. It produced very unconstrained estimations. For example, to obtain PIC accumulation rate in seagrass meadows they multiply an averaged PIC concentration by an averaged accretion rate (from Duarte et al. 2013). This value is multiplied by the global distribution area of seagrasses to obtain a (very) rough estimation of PIC deposition quantity in seagrass meadow. Because they demonstrate all these parameters are variable according to latitude and/or seagrass ecosystem type, I regret that Authors do not make their calculation at a lower scale (by geographical area and/or ecosystem type), using also Duarte et al. 's data at this "scale" then, using estimation of respective ecosystem area, sum the contribution of each seagrass type/ecosystem to provide a more realistic estimation (which would not be a mean of mean of mean). In any case, Authors do not take enough into account variability around the mean of these calculated values for their discussion or range presentation and should be more critic in face of their results.

Response:

We agree with your comment and acknowledge that the estimations of PIC at a more local scale, such as biogeographic region, based on local PIC stocks and seagrass extension is a much better and more accurate approach for estimating global accumulation rates. However, seagrass extension is not documented specifically for the regions considered in this study. To the extent of our knowledge, the most recent estimates of seagrass extension at a regional scale are summarized in Green and Short (2003). However the authors acknowledge that their estimates include a limited geographic area and a subset of known locations, which in fact, do not cover totally the biogeographic regions considered in our study.

In the absence of suitable estimates of seagrass area, a significant improvement is to estimate PIC accumulation rates separately for temperate and tropical seagrass meadows, assuming that the latter ones cover approximately 2/3 of the global seagrass area.

In response to this comment in the new version of this manuscript we now highlight the uncertainties in the estimates of global PIC accumulation rates derived from the variability found among biogeographic regions and/or ecosystems (i.e. dominant species) in terms of

PIC sediment stocks. In addition, we included PIC accumulation rates for temperate and tropical species, based on average PIC concentration in the top 10 cm of the sediment for each region (73.9 ± 2.8 mg PIC cm^{-3} for tropical meadows and 37.9 ± 4 mg PIC cm^{-3} for temperate meadows) and scaled to a global stock in the top 10 cm of 872-2955 Tg PIC and 223-758 Tg PIC respectively, assuming that tropical species occupy 2/3 of the global estimates of seagrass extension and depending on the global seagrass extension considered.

We also included in our estimates the propagated error derived from considering both the error in the top 10 cm PIC concentrations and the error in the sediment accretion rate reported in Duarte et al. (2013).

Action:

Section 4.1 has been moved to the second position 4.2 (*“Estimated PIC accumulation rates in seagrass meadows”*) and has been further developed to discuss the uncertainties of our estimates derived from the variability in the PIC stock among regions, sites and ecosystems (i.e. dominant species) now reported in the new section 4.1 (*“PIC global stocks and the effect of species and latitudinal distribution”*).

Estimates on global PIC accumulation rates now include the propagated error derived from the error in the top 10 cm PIC concentrations and the error in the sediment accretion rate reported in Duarte et al. (2013).

The text now reads (L320-L322):

“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} ”.

In this new section, we also include new estimates focusing on tropical and temperate regions separately (L322-L329).

The new text reads:

“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 PICy⁻¹), and temperate meadows (4.5 ± 1.5 and 15.3 ± 4.9 Tg PICy⁻¹, for the low and high global seagrass area estimate respectively), yielding a range for global PIC sequestration in seagrass meadows from 22 ± 6 to 75 ± 20 Tg PICy⁻¹, depending on the global seagrass extent considered”

2. Production vs. accumulation: In many places of this ms, Authors stated that seagrass are carbonate producers. Such as, this review does not allow such conclusion. Indeed, Authors focus on carbonate stocks and calculate an accumulation rate using Duarte et al.’s review (but see above). This does not allow to separate between in situ carbonate production (calcification by epiphytes or other organism inhabiting the meadows) and carbonate importation. They do not assess carbonate dissolution. The fact that carbonate content of unvegetated sediment are in the same range than in seagrass meadow indicate that, contrary to Authors conclusion, seagrass meadow are not particularly important (or unimportant) carbonate producers which is very contrasted compared to their organic carbon production. In fact, I think that this “carbonate producers” status is probably very variable depending of the seagrass ecosystem, local sediment nature, local hydrodynamism and seascape. For this last aspect, the role/presence of coral reef or carbonated sediment are probably of major importance to explain carbonate content in seagrass sediment, far more than in situ carbonate production. Here, I do not contest the fact that there is carbonate production in the seagrass meadow but its relative importance compare to carbonates import and its relative importance compared to other biota (such as coral reef or benthic soft habitats). Clearly for me, POC vs PIC producers status differ greatly and should be discussed more critically. Authors should at least be more rigorous in the terms they employ in some part of the discussion (production/accumulation/accretion). Importance of seascape (coral environment vs non coral for example) should be discussed.

Response:

We agree with the reviewer’s comment. We refer to “seagrass meadows” as the whole ecosystem, including the carbonate “producers”, which, as the reviewer indicates, are associated organisms (epiphytes or meadow inhabitants) (Frankovich and Zieman, 1994; Perry and Beavington-Penny, 2005) and seagrasses themselves (Enríquez and Schubert, 2014). However, we agree that the main contribution of seagrass meadows to the CaCO₃ cycle rests on their capacity to accumulate and store CaCO₃ produced *in situ* and imported from external sources. Whereas seagrass organic metabolism also controls the daily cycles of CaCO₃ precipitation and dissolution within the canopy (Hendriks et al. 2014) the import

of CaCO₃ produced elsewhere depends more on environmental conditions and/or the proximity of other ecosystems such as corals. The role of carbonate imports the reviewer suggested is consistent with the lack of differences in PIC content between vegetated and adjacent unvegetated sediments, although the rate of PIC accumulation is probably higher in seagrass meadows, which are depositional environments.

Action:

We have followed the reviewer's advice in the new version of this manuscript, where we now acknowledge that whereas seagrass meadows are important POC producers and sinks, their contribution to the PIC cycle is more dependent on their role as depositional sites accumulating and storing PIC. Specifically, we have now revised the use of the terms "production" and "accumulation" throughout the manuscript to change them or specify their meaning when this was not clear.

In the introduction section (L82-L83)

The sentence:

"Relative to other ecosystems, the production and accumulation of CaCO₃ in seagrass sediments is poorly studied and not explicitly considered in any of the existing assessments of the global ocean carbonate budget..."

has been changed to:

"Relative to other ecosystems, the production of CaCO₃ 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..."

In the methodology section (L156-L157)

"Lithogenic characteristics of the sites were not considered in this study, which, thereby, assumes that the seagrass meadows are the source of carbonate stocks in their sediments"

has been replace by:

“Lithogenic characteristics of the sites were not considered in this study, which, thereby, assumes that carbonate sediment stocks have a biogenic origin.”

L332:

“Production” has been replaced by “accumulation” and the text now reads, (including modifications following referee 1 comments):

“The rates of PIC accumulation estimated in this study, both globally (22 to 75 Tg PIC y⁻¹) and per surface area (126.3 ± 0.7 g PIC m⁻² y⁻¹), highlights the importance of seagrass meadows as major sites for CaCO₃ accumulation and storage in the ocean.”

In addition we introduce the relevance that the presence of CaCO₃ producer ecosystems (i.e. corals) close to seagrass meadows may have in the PIC stocks and accumulation rates.

The text now reads (L281-L287):

“The lack of a clear effect of the seagrass genera size could be partially due to factors that could not be considered in this study that control the precipitation and preservation of carbonate in the sediment at regional and local scales, such as geomorphology, salinity, water depth, nature of tidal and current regimes, CO₂ balance, nutrient or light availability, the nature and distribution of substrates (Lees, 1975) or the presence of other ecosystems nearby, such as corals in tropical regions, which may act as sources of carbonates to seagrass sediments.”

Finally, we further developed the section where POC and PIC content and POC:PIC ratio is compared between vegetated and unvegetated patches in the discussion section 4.3.

The text now reads (L388-L396)

“ 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 results indicate that, despite the significant carbonate sediment deposits identified and that seagrass 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 may derive on a significant fraction from external sources, such as adjacent carbonate producer systems (corals).”

Technical:

L185: Thalassodendron not Thalassodendrum.

Response:

We thank you for your comment.

Action:

In the new version of the manuscript this mistake has been correct.

Literature: no citation of Champenois & Borges (LO) for seagrass ecosystem metabolism

Response:

We thank you for your comment. In the final version of the manuscript the reference of Champenois and Borges (2012) has been included in the discussion on measurements of seagrass metabolism . The complete reference has been added to the reference list.

Action:

The text now reads (L370-L377).

“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 CO₂ sinks systems at a yearly scale (Barrón et al., 2006), even despite the underestimating Net Community Production (NCP) rates that may derive from the use of confined incubation chambers related to photooxidation processes and subsequent CO₂ increase and O₂ decrease during daytime (Champenois and Borges, 2012).”

No supplement with references used to make the data bank No supplement with mat met for unpublished data or list of unpublished studies (with Authors/place,etc.)

Response:

We have considered you comment and gathered all the data we have used for this manuscript in a single database, including all the reference for the papers found in the literature, along with the unpublished data provided by the authors with details on the authors, the sampling site, and/or the dominant species.

Action:

As mentioned before, the database has been published in the Spanish Research Council digital database repository with the reference:

Mazarrasa, Inés; Marbà, Núria; Lovelock, Catherine E.; Serrano, Oscar; Lavery, Paul S.; Fourqurean, James W.; Kennedy, Hillary; Mateo, Miguel Ángel; Krause-Jensen, Dorte; Steven, Andy D. L.; Duarte, Carlos M. " Sediment inorganic carbon (PIC) deposits in seagrass meadows and adjacent sand-patches", 2015, DIGITAL.CSIC and can be accessed through the link: <http://digital.csic.es/handle/10261/116550>.

Corrections made by the authors during the revision process:

1. During the revision process we found that the total amount of sites sampled included in the database (either cores or surface samples) was 403, instead of 402 as it was described in the first version of this manuscript. Considering this new number of total sites, in the new version of the manuscript we have updated the methods section and results (including figures, tables and supplementary materials) although the changes are minimal and have not affected in any case either the discussion or the main conclusions of the study. In the new version, all the numbers that have been changed are highlighted.

2. In addition there was an error in the abstract of the last version (L56).

The text now reads:

"...the comparison of carbon (PIC and POC) stocks between vegetated and adjacent un-vegetated sediments."

3. Finally we found a calculation error in the SE estimate of the PIC accumulation rates (L316).

In the previous version Avg. \pm SE = 126.3 \pm 0.7.

In the new version the Avg. \pm SE = 126.3 \pm 31.05.

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1 **Seagrass meadows as a globally significant carbonate reservoir**

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33 Abstract

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35 There has been a growing interest in quantifying the capacity of seagrass ecosystems to
36 act as carbon sinks as a natural way of offsetting anthropogenic carbon emissions to the
37 atmosphere. However, most of the efforts have focused on the organic carbon (POC) stocks and
38 accumulation rates and ignored the inorganic carbon (PIC) fraction, despite important
39 carbonate pools associated with calcifying organisms inhabiting the meadows, such as
40 epiphytes and benthic invertebrates, and despite the relevance that carbonate precipitation and
41 dissolution processes have in the global carbon cycle. This study offers the first assessment of
42 the global PIC stocks in seagrass sediments using a synthesis of published and unpublished
43 data on sediment carbonate concentration from 403 vegetated and 34 adjacent un-vegetated
44 sites. PIC stocks in the top 1 m sediments ranged between 3 and 1660 Mg PIC ha⁻¹, with an
45 average of 654 ± 24 Mg PIC ha⁻¹, exceeding about 5 fold those of POC reported in previous
46 studies. Sedimentary carbonate stocks varied across seagrass communities, with meadows
47 dominated by *Halodule*, *Thalassia* or *Cymodocea* supporting the highest PIC stocks, and
48 tended to decrease polewards at a rate of -8 ± 2 Mg PIC ha⁻¹ per degree of latitude (GLM,
49 p<0.0003). Using PIC concentration and estimates of sediment accretion in seagrass meadows,
50 mean PIC accumulation rates in seagrass sediments is 126.3 ± 31.05 g PIC m⁻² y⁻¹. Based on
51 the global extent of seagrass meadows (177,000 to 600,000 km²), these ecosystems globally
52 store between 11 and 39 Pg of PIC in the top meter of sediment and accumulate between 22
53 and 75 Tg PIC y⁻¹, representing a significant contribution to the carbonate dynamics of coastal
54 areas. Despite that these high rates of carbonate accumulation imply CO₂ emissions from
55 precipitation, seagrass meadows are still strong CO₂ sinks as demonstrates the comparison of
56 carbon (PIC and POC) stocks between vegetated and adjacent un-vegetated sediments.

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67 1. Introduction

68 Calcium carbonate (CaCO₃) accounts for about a 25% of the surface marine sediments
69 (Balch et al. 2005). Contemporary oceanic carbonate sediments are mainly composed by two
70 main mineral forms of calcium carbonate, calcite (including Mg-calcite, magnesium-rich
71 calcite) and aragonite, both primarily formed by biogenic precipitation (Smith, 2013). The
72 coastal ocean accounts for around 33% of the global CaCO₃ production (Smith, 2013) but it is
73 where the highest proportion of carbonate sediment accumulation takes place (nearly two-thirds
74 of its production) whereas in open ocean sediments only one-third of the CaCO₃ produced is
75 accumulated (Milliman and Droxler, 1996; Smith, 2013). A broad range of communities is
76 involved in the production and subsequent accumulation of CaCO₃ in marine sediments,
77 including benthic ecosystems dominated by coral reefs (Chave et al., 1972; Smith, 2013),
78 calcareous algae (Milliman, 1993) and maerl beds (Bosence and Wilson, 2003); and planktonic
79 communities including coccolithophores (Westbroek et al., 1989), foraminifera (Langer et al.,
80 1997), and pteropods (Fabry, 1990). More recently the important contribution of echinoderms
81 (Lebrato et al., 2010), molluscs (Chauvaud et al., 2003) and fish (Wilson et al., 2009) to CaCO₃
82 production has been revealed. Relative to other ecosystems, the production of CaCO₃ in
83 seagrass meadows ecosystems and its accumulation in the sediments is poorly studied and not
84 explicitly considered in any of the existing assessments of the global ocean carbonate budget
85 (Milliman et al., 1993; Milliman and Droxler, 1996; Lebrato et al., 2010), despite the important
86 load of carbonate often found in their sediments and leaves (Canals and Ballesteros, 1997;
87 Gacia et al., 2003; Perry and Beavington-Penney, 2005; Serrano et al., 2012, Enriquez and
88 Schubert, 2014) and their role as a source of carbonate sand for beach formation and
89 preservation (De Falco et al., 2003; Tigny et al., 2007). Indeed, a global estimate of the
90 carbonate stock in seagrass sediments is not yet available and the potential contribution of these
91 systems to the global ocean carbonate budget remains to be evaluated.

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

101 PIC, in the form of shells and other skeletal remains represent a substantial carbon stock, the
102 production of PIC through calcification may act as a source of CO₂ to the atmosphere
103 (Frankignoulle et al., 1994; Gattuso et al., 1998; Smith, 2013). Thus, understanding the amount
104 of carbonate in seagrass ecosystems is crucial to determining their role in the global
105 atmospheric carbon cycle. The evaluation of the carbonate accumulation rates and stocks in
106 seagrass sediments is also relevant as they may significantly contribute to sediment accretion in
107 coastal areas, a fundamental mechanism supporting the role of seagrass in coastal protection
108 (Duarte et al., 2013).

109 Seagrass meadows accumulate PIC through calcium carbonate production by calcifying
110 organisms inhabiting the meadows, such as epiphytes (Frankovich and Zieman, 1994; Perry
111 and Beavington-Penny, 2005; James et al., 2009; Enríquez and Schubert, 2014) and benthic
112 invertebrates (Jeudy de Grissac and Boudouresque, 1985) and the deposition of carbonate
113 associated with sedimentation of particles (Gacia et al., 2003). In addition, a recent study
114 demonstrates a direct implication of the seagrass *Thalassia testudinum* in the formation of
115 aragonite needles that accumulate internally in the cell walls and as external deposits on the
116 blades (Enríquez and Schubert, 2014). Other evidence for the existence of active carbonate
117 processes in seagrass beds include calcification and carbonate dissolution in the canopy,
118 associated with the daily cycles of photosynthesis and respiration (Frankovich and Zieman,
119 1994; Barrón et al., 2006; Yates and Halley, 2006), and the dissolution of calcium carbonate in
120 the sediment as a result of below-ground release of CO₂ by respiratory processes (Hu and
121 Burdige, 2007).

122 All the processes mentioned (precipitation, dissolution and sedimentation) partially
123 depend on seagrass metabolic activity and plant structural features and thus, CaCO₃ stocks in
124 seagrass sediments are likely to vary across meadows of different species (Duarte, 1991). In
125 addition, CaCO₃ stocks in seagrass meadows will likely vary with latitude, as temperature
126 regulates the seawater saturation state for carbonate minerals, that increases with increasing
127 temperature (Zeebe and Ridgwell, 2011) thereby favouring biogenic carbonate precipitation in
128 warmer waters (Mutti and Hallock, 2003).

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

135 and discuss its implications for current estimates of CO₂ sequestration in seagrass ecosystems.

136 2. Material and methods

137 We compiled the published data available on carbonate stocks in seagrass meadows and
138 adjacent un-vegetated sediments. We considered the total pool of CaCO₃ reported without
139 distinguish between the different possible biogenic carbonate mineral forms (calcite, Mg-
140 calcite and aragonite). Fourqurean et al. (2012) provided data for 201 sites, and a literature
141 search using both the Web of Knowledge (using the search terms “seagrass*” AND “inorganic
142 carbon*” AND [“calcific* OR sediment* OR CaCO₃ OR dissolut* OR diagenesis”]) and
143 Google Scholar (using the search terms “seagrass carbonate”) yielded data for an additional 82
144 sites. We amended the database with unpublished values for 154 additional sites sampled by
145 the authors. This yielded a total of 437 sites with data on sediment carbonate concentration in
146 coastal areas occupied by seagrasses, of which 34 corresponded to sand patches adjacent to
147 seagrass meadows (Supplementary Information). The final database comprised estimates for
148 403 seagrass vegetated sites, of which 219 consisted of values for sediment surface samples
149 (ca. 1-30 cm depth) and 184 consisted of values for sediment cores of variable length (149
150 cores < 100 cm-long, and 35 cores ≥ 100 cm-long).

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

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

162 When only one of the variables, CaCO₃ or PIC was reported, the other was estimated
163 assuming that PIC is 12% of the total molar mass of the CaCO₃. In most cases, particulate
164 inorganic carbon (PIC) was reported as a percentage of dry weight (%DW), where PIC, in mg
165 PIC cm⁻³, was calculated as the product of the fraction of sediment dry weight composed by
166 PIC and the dry bulk density (DBD) of a given core section (n = 340 sites). When DBD was
167 not reported (n = 113 sites), we used the average DBD (1.03 g cm⁻³) reported by Fourqurean et
168 al. (2012) for seagrass sediments in the calculations. The error introduced by this assumption

169 was small, as a paired t-test revealed an average deviation of 3.3% (t-ratio= 4.32; $p < 0.0001$)
170 when we tested the differences between estimating PIC concentration using the observed DBD
171 and the assumption of 1.03 for the sites where an observed DBD was reported.

172 Due to the variability in length of the sediment cores available for the study, mean PIC
173 concentration in seagrass sediments was estimated for the top 10 cm of sediment for a total of
174 385 sampled sites, for which at least one measure of PIC was reported for this depth zone. To
175 estimate the carbonate stock within the top meter of sediment for the total database available
176 we assumed a constant concentration of PIC in the top meter for those cores where shallower
177 profiles were reported, as almost half (46%) of the long cores (length >100 cm, n=35) showed
178 no significant change in PIC concentration with depth within the first top meter and the
179 remaining long cores showed only a slight increase of 0.011% DW cm⁻¹ on average.

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

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

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

201

202

203 3. Results

204 Particulate inorganic carbon concentration within the top 10 cm of seagrass sediments
205 ranged between 0.3 and 174 mg PIC cm⁻³, with an average of 62.5 ± 1.7 mg PIC cm⁻³ and a
206 median of 54 mg PIC cm⁻³ (n = 385). The PIC stock in the top meter of sediment in seagrass
207 meadows showed a wide variability, ranging between 3 and 1660 Mg PIC ha⁻¹, with an average
208 ± standard error and a median of 654 ± 24 and 643 Mg PIC ha⁻¹, respectively (n = 403; Fig. 2).
209 Estimated stocks (mean ± SE, 676 ± 26 Mg PIC ha⁻¹, Table S1) were significantly higher than
210 those derived from direct measurements (mean ± SE, 423 ± 52 Mg PIC ha⁻¹, Table S1, p >
211 0.05); however, estimated and measured paired values did not show a significant difference
212 (Fig. 2; paired t-test, p > 0.05).

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

222 The PIC stocks also differed among dominant species (ANOVA, F-ratio= 13.98; p <
223 0.0001). The highest PIC stocks were found underlying *Halodule*, *Thalassia* and *Cymodocea*
224 meadows while the lowest stocks were supported by *Zostera* and *Halophila* meadows (Fig. 3).
225 *Posidonia* meadows had intermediate PIC stocks.

226 Where both PIC and POC were measured concurrently (392 sites; n= 3076), mean PIC
227 concentrations tended to exceed mean POC concentrations (paired t-test: T-ratio= 64.77, p <
228 0.0001). The POC:PIC ratio ranged from nearly 0 to 108, with an average of 0.74 ± 0.05 and a
229 median of 0.20 (Table 2; Fig. 5). For the longest cores in the database (length ≥ 100 cm) which
230 had a minimum of three different observations reported over one meter depth (n= 26), the POC
231 concentration (mg POC cm⁻³) along the sediment profile of these cores tended to decrease with
232 depth whereas PIC (mg PIC cm⁻³) was more variable (Figure S1). The POC: PIC ratio declined
233 consistently with depth in the top meter of sediment in 69% of these cores at an average of
234 -0.00054% cm⁻¹.

235 There was a strong relationship between PIC content (%DW) in paired vegetated and
236 un-vegetated sediments (R² = 0.92, Fig. 6a), with a slope very close to 1 (0.99 ± 0.02) and an

237 intercept not different from 0 (0.17 ± 0.99), indicating that the PIC content in seagrass
238 sediments did not differ significantly from that in adjacent un-vegetated sediments (paired t-
239 test, T-ratio = 1.67, $p > 0.05$; $n = 195$) (Fig. 6a). However, no relationship was found between
240 the POC content (%DW) in seagrass sediments and adjacent bare sediments (Fig. 6b). POC
241 content was significantly higher in vegetated sediments (mean \pm SE, 0.66 ± 0.04) compared to
242 adjacent bare sediments (mean \pm SE, 0.35 ± 0.017 , paired t-test, T-ratio = -6.57, $p < 0.0001$; n
243 = 195).

244 4. Discussion:

245 4.1. PIC global stocks and the effect of species and latitudinal distribution.

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

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

264 Our results show that the PIC stocks of seagrass meadows vary depending on the
265 seagrass genera. Large genera, with larger leaf size and extended leaf life span (Duarte, 1991)
266 were expected to sustain a higher amount of calcareous epiphytes and favour a higher
267 accumulation of PIC. The age of the leaves affects the colonisation of seagrass leaves by
268 epiphytes (including calcareous organisms; Heijls, 1985; Borowitzka et al., 1990; Cebrián et al.,
269 1994) and the mineral load has been found to increase with increasing leaf age (Gacia et al.,
270 2003). The height of the canopy, which correlates with shoot size, has also been shown to

271 determine the epiphyte biomass and species biodiversity in meadows of *Amphibolis*
272 (Borowitzka et al., 1990). Sedimentation process and particle trapping in a meadow are also
273 linked to canopy height (Gacia et al., 2003) and leaf density (Fonseca and Cahalan, 1992) and
274 therefore PIC sedimentation and retention may be also favoured in seagrass meadows
275 dominated by larger species, where long leaves effectively slow water currents and increase
276 particle setting. In addition, larger seagrass species may favour carbonate precipitation through
277 their metabolic activity as the leaf area index has been seen to directly relate to maximum and
278 range Ω daily values in seagrass meadows (Hendricks et al. 2014). Hence, we expected to find
279 high storage of PIC in the sediment of large seagrass genera. However, some large genera, such
280 as *Posidonia*, did not support particularly large stocks, while some small genera, such as
281 *Halodule*, supported large stocks. The lack of a clear effect of the seagrass genera size could be
282 due to other controlling factors on the precipitation and preservation of carbonate in the
283 sediment at regional and local scales not covered by the current study. These may involve
284 differences in geomorphology, salinity, water depth, tidal and current regimes, nutrient and
285 light availability and CO₂ balance (Lees, 1975) as well as the presence of nearby ecosystems,
286 such as corals in tropical regions, which may act as sources of carbonates to seagrass
287 sediments.

288 Latitude also influenced the size of the PIC stocks in seagrass sediments, that tended to
289 decrease with increasing latitude, consistent with the higher epiphyte carbonate loads in
290 seagrass leaves in tropical compared to temperate regions (Gacia et al., 2003). This general
291 trend of decline with increasing latitude has been observed in other carbonate-intense
292 ecosystems, such as reef-building corals (Veron and Minchin, 1992; Veron, 1995) and
293 encrusting red algae communities, which are more heavily calcified in warm tropical than in
294 cold temperate waters (Lowenstam and Weiner, 1989). The latitudinal distribution of carbonate
295 stocks may be explained by temperature and salinity dependence of the saturation state of
296 carbonate minerals (Ω) (Zeebe and Wolf-Gladrow, 2001). The saturation of calcium carbonate
297 in seawater is mostly dependent on the availability of CO₃²⁻, as Ca²⁺ concentration is two orders
298 of magnitude higher than CO₃²⁻ concentrations (Gattuso et al., 1998). From a thermodynamic
299 perspective, cold and fresh water generally promotes lower Ω saturation states and prevents
300 CaCO₃ precipitation (Mucci et al., 1983). As both salinity and temperature tend to decrease
301 with increasing latitude the carbonate saturation state decreases polewards with respect to
302 tropical and temperate waters (Hoegh-Guldberg et al., 2007). Hence, the precipitation of
303 biogenic CaCO₃ is favoured in tropical and subtropical areas compared to temperate regions
304 (Mutti and Hallock, 2003). Discrepancies from the general trend, such as the low carbonate

305 stocks reported in the latitudinal bins -10 to 20° S are probably explained by local factors that
306 alter the Ω saturation states, such as inputs of fresh water and terrigenous sediments from river
307 discharges in the sites of study (Mellors et al., 2002; Fisher and Sheaves, 2003).

308

309 4.2. PIC estimated accumulation rates in seagrass meadows.

310 Our review of the literature indicated that PIC accumulation in seagrass sediments is
311 high and comparable to other carbonate producing ecosystems. Based on our identified mean
312 PIC concentration of 62.5 ± 1.7 mg PIC cm^{-3} in the top 10 cm of seagrass sediments (sites =
313 385, n= 802) and a mean rate of sediment accretion in seagrass meadows of 0.2 ± 0.04 cm y^{-1}
314 (Duarte et al., 2013) we estimate that the PIC accumulation rates in seagrass sediments would
315 average 126.3 ± 31.05 g PIC $\text{m}^{-2} \text{y}^{-1}$. This rate is somewhat below the range of PIC
316 sedimentation rates reported by Gacia et al. (2003) in seagrass meadows of SE Asia, based on
317 direct measures of daily sediment deposition at 8 different sites ($145 - 9443$ g PIC $\text{m}^{-2} \text{y}^{-1}$) but
318 higher than the average PIC accumulation rate in sediments of *Posidonia oceanica* meadows
319 (54.3 ± 1.9 g PIC $\text{m}^{-2} \text{y}^{-1}$) estimated from sediment stock assessment and sediment dating
320 (Serrano et al., 2012). Extrapolation, assuming an estimated range of global area of seagrass
321 meadows between 177,000 and 600,000 (McLeod et al., 2011), suggests a total accumulation of
322 PIC in seagrass sediments ranging between 22 ± 5 and 76 ± 19 Tg PIC y^{-1} . These estimates are
323 subject to uncertainties derived from the high variability in PIC stocks among regions and
324 species, and the absence of estimates on seagrass extent for each region/system considered in
325 this study. Assuming that tropical seagrass represent 2/3 of the total seagrass, PIC accumulation
326 rates can be calculated separately for tropical (17.6 ± 4.5 and 59.7 ± 15.2 Tg PIC y^{-1}), and
327 temperate meadows (4.5 ± 1.5 and 15.3 ± 4.9 Tg PIC y^{-1} , for the low and high global seagrass
328 area estimates respectively), yielding a range for global PIC sequestration in seagrass meadows
329 from 22 ± 6 to 75 ± 20 Tg PIC y^{-1} , depending on the global seagrass extent considered.
330 The rates of PIC accumulation estimated in this study, both globally ($22-75$ Tg PIC y^{-1}) and per
331 surface area (126.3 ± 31.05 g PIC $\text{m}^{-2} \text{y}^{-1}$), highlight the importance of seagrass meadows as
332 major sites for CaCO_3 accumulation and storage in the ocean. The global PIC accumulation
333 rates of seagrasses are substantially lower than in deep oceans by pelagic communities ($100-132$
334 Tg PIC y^{-1}) but significantly higher when considering their contribution per surface area
335 ($0.34-0.45$ g PIC $\text{m}^{-2} \text{y}^{-1}$). Seagrass PIC accumulation rates were comparable to those of coral
336 reefs both globally (84 Tg PIC y^{-1}) and per surface area (140 g PIC $\text{m}^{-2} \text{y}^{-1}$). Relative to
337 *Halimeda* bioherms (20 Tg PIC y^{-1}) seagrass PIC accumulation showed higher global rates but

338 significantly lower rates per surface area ($400 \text{ g PIC m}^{-2} \text{ y}^{-1}$) (Milliman and Droxler, 1996;
339 Catubig et al., 1998; Table 3).

340 4.3. Implications in the assessment of the CO_2 sink capacity of seagrass meadows.

341 While PIC represents a substantial carbon stock, carbonate precipitation results in a rise
342 of the partial pressure of CO_2 (pCO_2), which, can result in CO_2 supersaturation and release of
343 CO_2 to the atmosphere (Ware et al., 1992). The net release of CO_2 with carbonate deposition is
344 defined by the molar ratio of CO_2 flux: CaCO_3 precipitation (Ψ), which decreases with
345 decreasing temperature while increasing with pCO_2 (Frankignoulle et al., 1994). Ψ varies from
346 0.63 in surface waters in low to mid-latitudes, where carbonate precipitation takes place, to
347 0.85 below 500 m depth throughout the ocean, where most dissolution takes place (Smith,
348 2013). Due to the vertical variation in Ψ , Smith (2013) identified the pelagic carbonate system
349 as a net sink of CO_2 , as most of the surface production ($\Psi = 0.63$) dissolves as it reaches deep
350 waters ($\Psi = 0.85$) compensating for the CO_2 emitted by CaCO_3 precipitation in surface waters.
351 In contrast, carbonate deposition in shallow ecosystems, such as seagrass meadows, would act
352 as a CO_2 source as approximate two-thirds of the CaCO_3 produced in shallow benthic
353 ecosystems accumulates in the sediment, and Ψ has the same value for CaCO_3 precipitation and
354 dissolution (Milliman and Droxler, 1996; Smith, 2013). Given that seagrass meadows are sites
355 of strong net primary production, any pCO_2 increase due to calcification may be more than
356 compensated for, by organic production. Hence, Ψ has been interpreted to imply a POC:PIC
357 production ratio threshold, with a value of 0.63 equivalent to no net change in pCO_2 and values
358 greater or smaller than this value implying a net sink or source respectively.

359 The median POC:PIC ratio of seagrass sediments found in this study was 0.2,
360 independent of depth (median of surface sediments 0.17), well below the POC:PIC ratio
361 threshold of 0.63, with only 18% of seagrass sediments showing POC:PIC ratios > 0.6 .
362 Following the rationale above and assuming that organic carbon and calcium carbonate
363 accumulate in the sediment in proportion to their production, these results could be interpreted
364 to imply that CO_2 emissions derived from carbonate deposition may offset the CO_2 sink
365 capacity associated with organic carbon burial in seagrass sediments globally, as discussed
366 before for *Posidonia oceanica* in the Mediterranean (Mateo and Serrano, 2012; Serrano et al.,
367 2012). However, such interpretation would be premature. In general terms, the organic and
368 inorganic carbon cycles in the ocean run at very different rates and although organic matter is
369 produced at much faster rates than CaCO_3 , it is also decomposed more rapidly (Smith, 2013).
370 However, the carbonate precipitation in seagrass meadows is intimately regulated by the
371 organic metabolic rates of the ecosystem (Smith and Atkinson, 1983; Barrón et al., 2006; Yates

372 and Halley, 2006; Hendriks et al., 2014) and when both organic and inorganic carbon metabolic
373 pathways have been measured in situ simultaneously, seagrass meadows have been found to be
374 mainly net CO₂ sinks systems at a yearly scale (Barrón et al., 2006), even despite the
375 underestimated Net Community Production (NCP) rates that may derive from the use of
376 confined incubation chambers related to photooxidation processes and subsequent CO₂ increase
377 and O₂ decrease during daytime (Champenois and Borges, 2012). In addition to carbon burial, a
378 significant fraction of the net community production of seagrass, supporting a CO₂ sink, is also
379 exported as DOC and POC (Cebrián et al., 1997, Barrón and Duarte, 2009). Hence, the
380 comparison of sediment standing stocks would reflect only a fraction of the sink capacity of the
381 seagrass ecosystems but not the net effect of the organic and inorganic carbon metabolic
382 pathways on the net CO₂ flux. Therefore, more research, which takes into account both the
383 organic and inorganic carbon cycles associated with these systems, is needed to better assess
384 the role of seagrass ecosystems as carbon sinks or sources.

385 Understanding the balance between CO₂ emissions from carbonate deposition and CO₂
386 sequestration from organic carbon storage in seagrass sediments should not only focus on the
387 POC:PIC ratio, but also on resolving how seagrass affect the POC:PIC ratio compared to
388 adjacent un-vegetated sediments. When comparing the carbon content (%DW) between
389 vegetated and adjacent un-vegetated patches, there was no difference in PIC whereas the POC
390 content was about two-fold larger in vegetated sediments compared to adjacent un-vegetated
391 sediments as previously observed (Duarte et al., 2010, Kennedy et al., 2010). This result
392 indicates that, despite the significant carbonate sediment deposits identified and that seagrasses
393 favour carbonate precipitation and accumulation by epiphytes and other organisms inhabiting
394 the meadow, sediment PIC largely depends on local environmental conditions that control
395 carbonate precipitation and a significant fraction may derive from external sources, such as
396 adjacent carbonate producer systems (corals). As a consequence, the POC: PIC ratio of
397 seagrass sediments (mean ± SE, 0.28 ± 0.06) exceeded that of adjacent un-vegetated sediments
398 (mean ± SE, 0.19 ± 0.040) in 73% of the meadows examined. Hence, the organic carbon stock
399 present in seagrass sediments would be expected to be reduced to half if seagrass cover was lost
400 while the inorganic stock will be comparable, thereby confirming the role of seagrass meadows
401 as intense CO₂ sinks. It is important to point out that the rationale above relates to the content
402 (%DW) of both PIC and POC and not to the rate of accumulation, which may be significantly
403 higher in seagrass compared to adjacent sand patches due to autotrophic production and
404 sediment trapping.

405 In addition there are possible interactions between carbonate and organic carbon

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

417 4.4. Implications in the role of seagrass meadows as coastal protection.

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

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

439

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629 TABLES:

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

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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

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

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	PIC (mg cm ⁻³)	POC (mg cm ⁻³)	POC:PIC
Mean \pm SE	72.5 \pm 0.8	51.6 \pm 0.6	0.74 \pm 0.05
Median	68.3	49.4	0.20
Max	325.1	321.0	107.6
Min	0.2	0.4	0.00038

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

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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
<i>Halimeda</i> 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)

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707 FIGURES.

708 Figure legends.

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

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

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

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

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

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

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Figure 1.

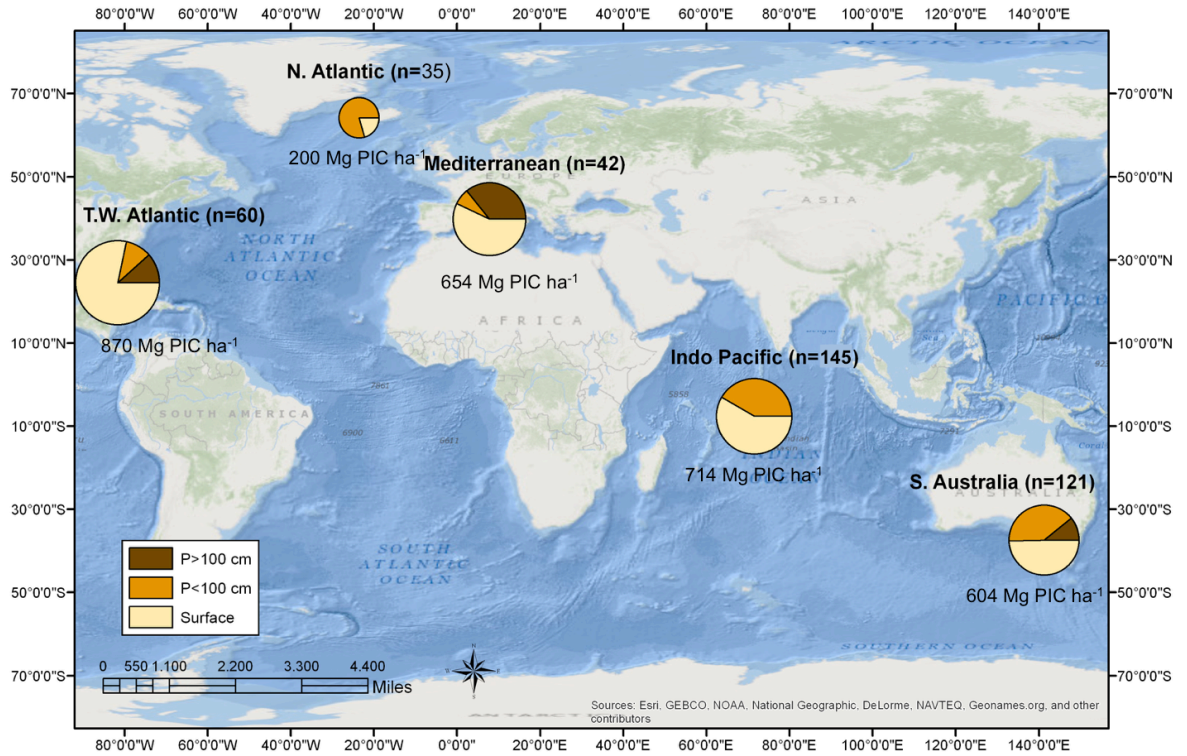


Figure 2:

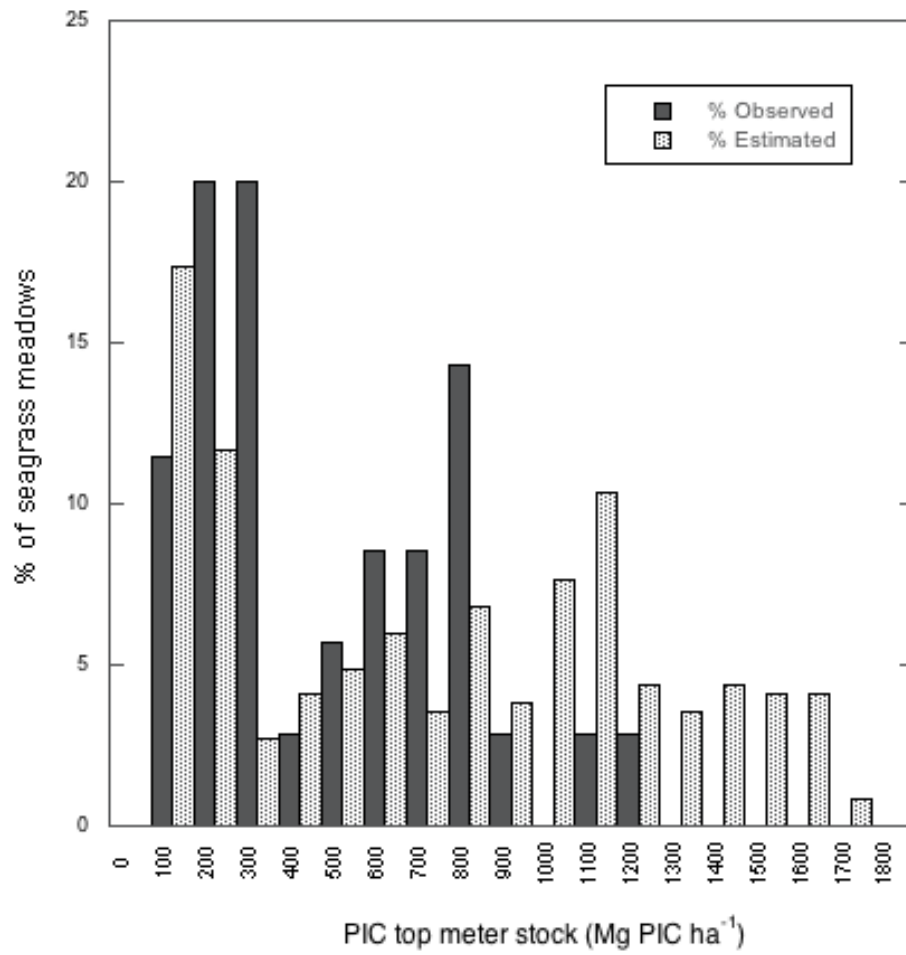


Figure 3:

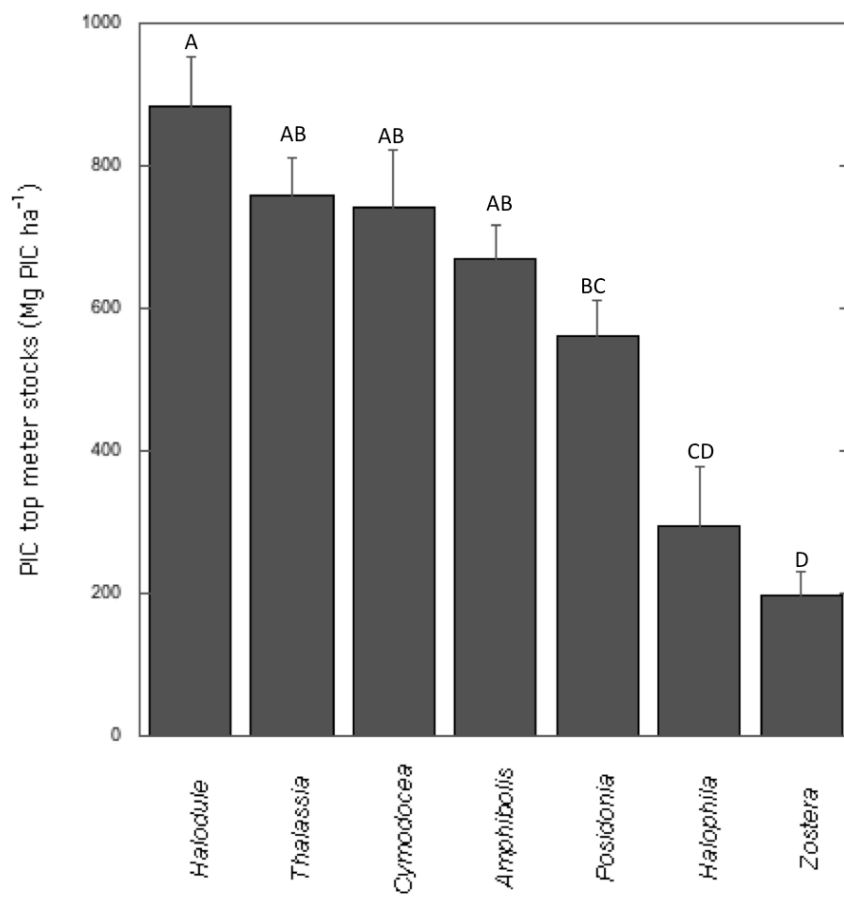


Figure 4:

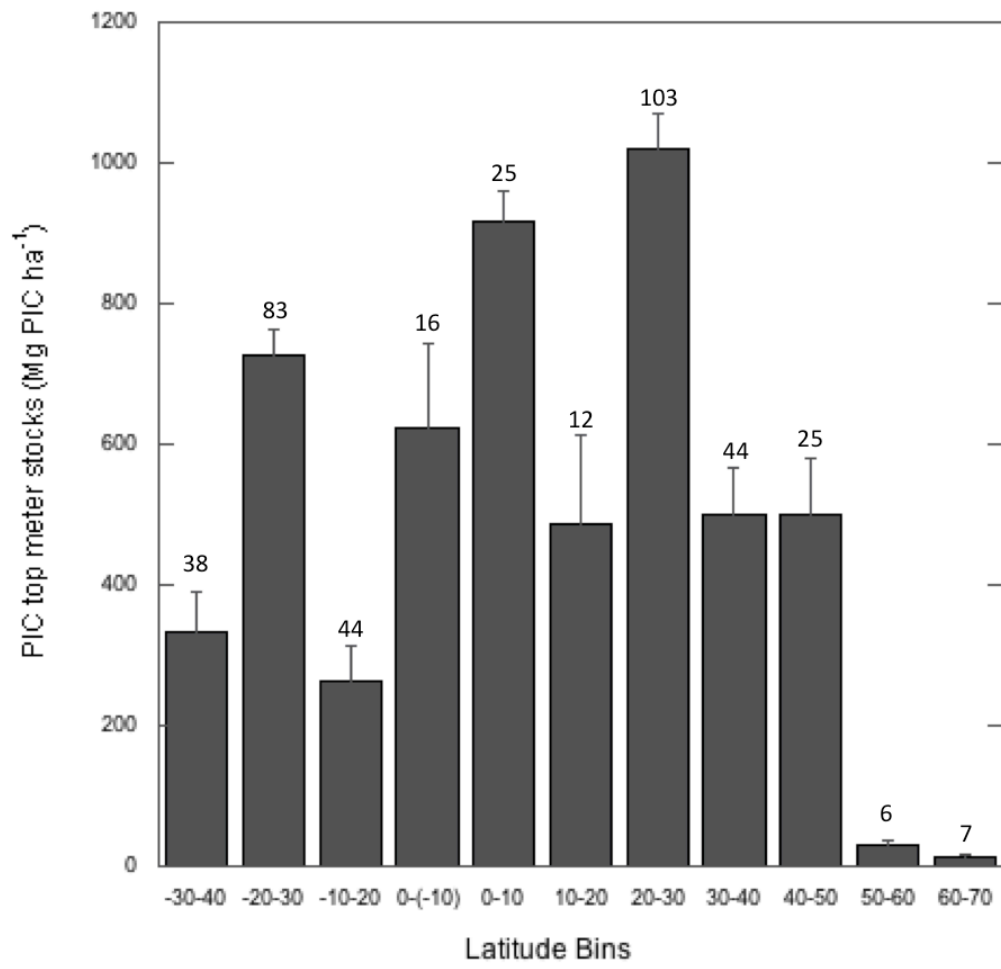


Figure 5:

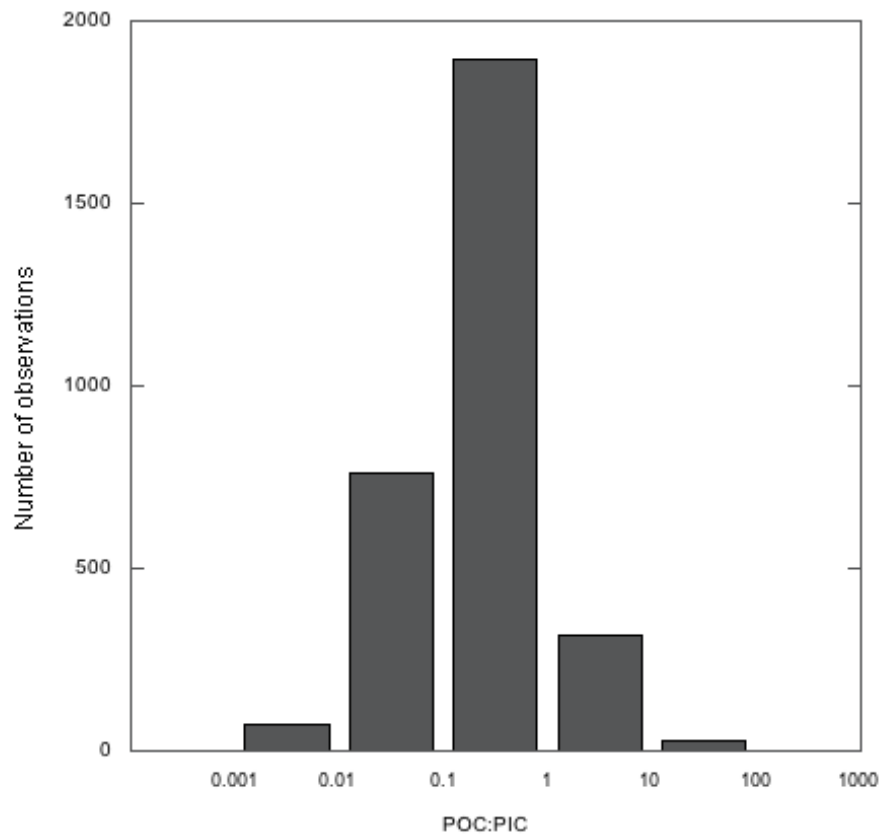


Figure 6:

