AGU100 ADVANCING EARTH AND SPACE SCIENCE

Global Biogeochemical Cycles

RESEARCH ARTICLE
10.1029/2018GB005941

Blue Carbon Storage Capacity of Temperate Eelgrass (*Zostera marina*) Meadows

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Key Points:

- The *Z. marina* C_{org} stocks varied widely within and across studied regions; majority of this variation was explained by five sediment and environmental variables
- The *Z. marina* C_{org} stocks were comparable to other seagrass species and other blue carbon habitats such as salt marshes and mangrove forests
- Carbon isotopic signatures indicated that at most sites, only less than half of the sediment carbon is derived from seagrass, though variation was significant

Supporting Information:

- Supporting Information S1

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Citation:
Röhr, M. E., Holmer, M., Baum, J. K., Björk, M., Boyer, K., Chin, D., et al. (2018). Blue carbon storage capacity of temperate eelgrass (*Zostera marina*) meadows. *Global Biogeochemical Cycles*, *32*, 1457–1475. https://doi.org/10.1029/2018GB005941

Received 2 APR 2018
Accepted 14 SEP 2018
Accepted article online 19 SEP 2018
Published online 8 OCT 2018
Corrected 21 JAN 2019

This article was corrected on 21 JAN 2019. See the end of the full text for details.

Abstract Despite the importance of coastal ecosystems for the global carbon budgets, knowledge of their carbon storage capacity and the factors driving variability in storage capacity is still limited. Here we provide an estimate on the magnitude and variability of carbon stocks within a widely distributed marine foundation species throughout its distribution area in temperate Northern Hemisphere. We sampled 54 eelgrass (*Zostera marina*) meadows, spread across eight ocean margins and 36° of latitude, to determine abiotic and biotic factors influencing organic carbon (C_{org}) stocks in *Zostera marina* sediments. The C_{org} stocks (integrated over 25-cm depth) showed a large variability and ranged from 318 to 26,523 g C/m^2 with an average of 2,721 g C/m^2. The projected C_{org} stocks obtained by extrapolating over the top 1 m of sediment ranged between 23.1 and 351.7 Mg C/ha, which is in line with estimates for other seagrasses and other blue carbon ecosystems. Most of the variation in C_{org} stocks was explained by five environmental variables (sediment mud content, dry density and degree of sorting, and salinity and water depth), while plant attributes such as biomass and shoot density were less important to C_{org} stocks. Carbon isotopic signatures indicated that at most sites $<50\%$ of the sediment carbon is derived from seagrass, which is lower than reported previously for seagrass meadows. The high spatial carbon storage variability urges caution in extrapolating carbon storage capacity between geographical areas as well as within and between seagrass species.

1. Introduction

The oceans contain the largest carbon pool on Earth and have absorbed about one third of anthropogenic CO_2 emissions through physical, chemical, and biological processes (Intergovernmental Panel on Climate Change, 2014; Sabine et al., 2004). Coastal vegetated ecosystems play a fundamental role in carbon storage, and the term *blue carbon* has been created to describe the carbon stored by marine ecosystems, seagrasses, salt marshes, and mangroves, in particular (Herr et al., 2012). Altogether, these ecosystems cover only 0.2% of the ocean floor but hold a sediment carbon storage equal to over half of the global green carbon storage (carbon stored in terrestrial ecosystems and their soils) and up to 33% of the total oceanic CO_2 uptake (Duarte, 2017; Duarte et al., 2005; Hemminga & Duarte, 2000; McLeod et al., 2011; Nellemann et al., 2009). Furthermore, some marine ecosystems can store carbon up to millennial time scales, while the carbon stored by terrestrial systems is usually sequestered up to decades (Mateo et al., 1997; Mazarrasa et al., 2017a; Samper-Villarreal et al., 2018). However, the longevity of carbon storage varies considerably among species and habitats within both marine and terrestrial systems, most likely due to species-specific traits such as length of the growing season, chemical composition of the plant tissues and plant growth rate, and environmental characteristics like temperature, disturbance, and sediment oxygenation (Mateo et al., 2006; Mazarrasa et al., 2018; Russel et al., 2013).

Within marine and estuarine ecosystems, seagrass sediment carbon storage is believed to average at 83,000 Mg/km^2, thus equivalent to a total global blue carbon storage of 19.9×10^9 Mg (Fourqurean et al., 2012; Macreadie et al., 2013). Despite the limited areal extent of seagrass meadows, their contribution to carbon accumulation per unit area is up to 3 orders of magnitude higher than that of terrestrial soils, primarily due to the high capacity of seagrasses to trap particles by reducing water flow, wave energy, and sediment resuspension (Agawin & Duarte, 2002; Bos et al., 2007; Fonseca & Cahalan, 1992; Gacia et al., 2002; Gacia & Duarte, 2001; Hendriks et al., 2008; Kennedy & Björk, 2009; Koch et al., 2006). High carbon accumulation rates are also promoted by slow decomposition of organic material in the often hypoxic seagrass sediments, high proportion of refractory organic compounds, and high C:N:P ratios. Together, these characteristics make seagrass material less labile and biodegradable and thus more easily stored than tissues of most other marine angiosperms and algae (Enriquez et al., 1993; Fourqurean & Schrlau, 2003; Holmer et al., 2009; Kennedy et al., 2010; Kristensen & Holmer, 2001; Pedersen et al., 2011; Vichkovitten & Holmer, 2004).

Seagrass habitats are highly productive ecosystems and most act as net sinks of carbon (Duarte & Cebrián, 1996; Duarte et al., 2010). Generally, seagrass species with high rates of production also support high sediment organic carbon stocks (the amount of carbon stored in the sediment down to a predefined depth, hereafter C_{org} stocks; Duarte et al., 2010; Hemminga & Duarte, 2000; Lavery et al., 2013; Rozaimi et al., 2016). In addition, larger seagrass species tend to have higher production rates, higher carbon burial rates, and higher sediment C_{org} stocks due to a taller plant canopy, which enhances particle trapping and growth of larger, more persistent belowground tissues (Duarte & Chiscano, 1999; Lavery et al., 2013). An extreme example of this is *Posidonia oceanica*, an endemic Mediterranean seagrass species capable of high levels of carbon sequestration in their extensive belowground rhizome mats, far exceeding the carbon sink capacity of other seagrasses, as well as other blue carbon sources (Duarte et al., 2005; Duarte, Kennedy, et al., 2013; Fourqurean et al., 2012; Kennedy & Björk, 2009; Lavery et al., 2013; Serrano et al., 2014, 2015). Furthermore, carbon stored in the mats formed by *P. oceanica* date back up to 12,500 years, while C_{org} stocks of other seagrass species, such as *Zostera marina* and *Cymodocea nodosa*, have typically formed within shorter time scales of up to several centuries of age (Alberto et al., 2001; Arnaud-Haond et al., 2012; Mateo et al., 1997; Reusch et al., 1999).

In addition to particulate organic carbon (hereafter POC) and seagrass biomass, the seagrass sediment C_{org} can be augmented by other carbon sources including phytoplankton, terrestrial plant detritus, macroalgae, epiphytes, and benthic microalgae (Bouillon & Boschker, 2006; Fry et al., 1977; Fry & Sherr, 1984; Holmer et al., 2004; Kennedy et al., 2010, 2004; Moncreiff & Sullivan, 2001; Ricart et al., 2017; Röhr et al., 2016). These additional sources vary considerably in input and decomposition rates over time, thus influencing the lability and magnitude of C_{org} stocks in seagrass sediments (Kennedy et al., 2010, 2004). In general, benthic microalgae, epiphytes, and phytoplankton are more labile sources of C_{org}, while the decay of macrophyte and terrestrial C_{org} is usually slower (Bouillon & Boschker, 2006; Mateo et al., 2006; Vichkovitten & Holmer, 2004). Recent studies have also emphasized how environmental conditions affect seagrass C_{org} stocks (Dahl et al., 2016; Dahl, 2017; Miyajima et al., 2015; Röhr et al., 2016; Serrano et al., 2016). For example, sediment density and grain size can influence the availability of oxygen in the sediment and therefore the rate of bacterial decomposition. Moreover, water temperature (Bouillon & Connolly, 2009; Clausen et al., 2014; Moore & Short, 2006), salinity (Watanabe & Kuwae, 2015), water depth (Serrano et al., 2014; Samper-Villarreal et al., 2016), dissolved inorganic carbon concentration (Beer et al., 2014), and light availability (Eriander, 2017; Serrano et al., 2014) all affect the balance of net community production and respiration, with high temperature and fraction of inorganic carbon content leading to elevated rates of carbon mineralization, while increased salinity and water depth usually lead to lower production rates, hence, influencing the formation of sediment C_{org} stocks.

Although the contribution of seagrasses to global oceanic carbon storage has been quantitatively acknowledged, most estimates come from just a few sites and seagrass species (Dahl et al., 2016; Greiner et al., 2013; Gullström et al., 2018; Macreadie et al., 2013; Miyajima et al., 2015; Serrano et al., 2014, 2015; Röhr et al., 2016). Importantly, the anomalously high belowground accumulation of carbon in *P. oceanica* meadows might lead to overestimation of the global seagrass C_{org} stock if values for this species are applied as broad proxies for other seagrass species. Furthermore, interactions between seagrass species identity and bed characteristics (e.g., shoot density, shoot size, and belowground structure) with local environmental drivers (e.g., sediment characteristics, allochthonous inputs, and temperature) may confound global extrapolation of the total magnitude of seagrass C_{org} stocks in the absence of standardized, broad-scale sampling, which incorporate these covariates.

The foundation species eelgrass (*Z. marina* L.) is a relatively fast-growing seagrass species forming dense meadows in both intertidal and subtidal areas across the temperate Northern Hemisphere (Moore & Short, 2006). *Z. marina* is among the most widespread seagrass species, covering a large geographic range (Boström et al., 2014; Moore & Short, 2006; Spalding et al., 2003), thus potentially contributing significantly to the global seagrass blue carbon stock. *Z. marina* is well known for its structural and functional role as a key species in many marine ecosystems (e.g., Boström et al., 2014; Spalding et al., 2003), but despite its large distribution area, information on local, regional, and global blue carbon stocks in *Z. marina* meadows is limited and generated from a handful of studies focusing on relatively small regional areas (Dahl et al., 2016; Greiner et al., 2013, 2016; Miyajima et al., 2015; Röhr et al., 2016).

Here we quantified the magnitude of *Z. marina* sediment carbon storage across its full geographic range. To do so, we coordinated a standardized sampling program spanning 36° of latitude and eight different ocean margins and seas. Specifically, we compared the organic carbon stored in the sediment among eelgrass meadows, identified the main carbon sources contributing to the sediment carbon stock, and explored the environmental variables driving the observed patterns. Finally, we compared the global carbon storage capacity of *Z. marina* to that of terrestrial and coastal ecosystems. Specifically, we addressed the following questions:

1. What is the magnitude and variation *of Z. marina* sediment C_{org} stocks?
2. What are the abiotic and biotic environmental factors explaining the variation in *Z. marina* C_{org} stocks among regions?
3. What are the main carbon sources in *Z. marina* sediments, and do they vary systematically across and within regions?
4. How do Northern Hemisphere *Z. marina* meadows rank globally in terms of magnitude of C_{org} stocks and carbon storage capacity compared to other coastal and terrestrial carbon sink ecosystems?

2. Materials and Methods

2.1. Study Area

Plant and sediment samples were collected from 54 sites located in 13 countries (Bulgaria, Canada, Denmark, Finland, France, Japan, Korea, Mexico, Norway, Portugal, Sweden, United Kingdom, and United States) across eight ocean margins and seas (Eastern and Western Atlantic, Eastern and Western Pacific, Baltic Sea, Black Sea, Mediterranean Sea, and Kattegat-Skagerrak) during summer (June to September) 2015 (Figure 1). Water depth at the sites ranged from 0.5 to 3 m covering subtidal, shallow subtidal, and intertidal zones, where the mean annual water temperature ranged from 7 to 20 °C and salinity ranged from 6.5 to 38.8. The light periods at the sampling time ranged from 12 to 24 hr (Table S1 in the supporting information). The samples were collected within the Zostera Experimental Network, ZEN (www.zenscience.org), a

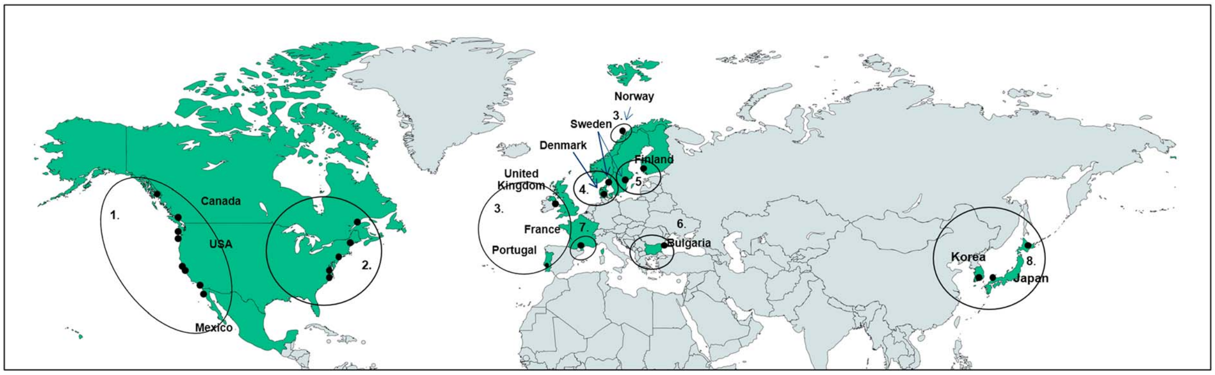

Figure 1. The study sites in the Northern Hemisphere (with sampled countries in green). Black dots indicate the sampling sites, except for in Bulgaria, Denmark, Finland, and Sweden, in which one dot indicates multiple (n = 2–10) sites. Ocean margins and seas are labeled by numbers: 1 = Eastern Pacific; 2 = Western Atlantic; 3 = Eastern Atlantic; 4 = Kattegat-Skagerrak; 5 = Baltic Sea; 6 = Black Sea; 7 = Mediterranean Sea; 8 = Western Pacific. For site names see Table S1.

collaboration between scientists addressing the structure and functioning of eelgrass ecosystems (see, e.g., Duffy et al., 2015).

2.2. Field Sampling

At each site, meadows in which *Z. marina* was the dominant seagrass species were chosen for sampling, when monospecific meadows were not abundant. Although *Z. marina* was the dominant seagrass species, 15 sites had mixed meadows that included other species such as *Ruppia* spp., *Potamogeton* spp., *Halodule* spp., *Zostera noltii*, and *Zostera japonica*, although only *Z. marina* was collected for sampling of the plant variables. *Z. marina* aboveground and belowground biomass samples were collected with a corer (length 20 cm and diameter 25 cm) from three randomly chosen plots separated by 15 m within the interior (5–10 m from the meadow edge) of the *Z. marina* bed. Shoot density was quantified within a 0.25-m^2 frame. Sediment carbon was sampled using a 50-cm-long acrylic corer (diameter 5 cm, n = 3). Three 25-cm sediment samples were randomly collected from a single meadow within the sampling site. The corer was manually forced to the depth of at least 25 cm, capped at both ends underwater and transported to the laboratory for further analysis. Due to limited resources, no samples were collected from adjacent bare (unvegetated) sediments. Finally, samples (approximately 10 g of wet material) of plants and algae (drift algae, other angiosperms, and epiphytes) considered to be the most likely alternative carbon sources were collected from each site for stable isotope analysis. The number of potential carbon sources within sites varied between 2 and 6.

2.3. Plant Variables

In a local laboratory at each site, aboveground and belowground parts of *Z. marina* were separated and rinsed with freshwater, then leaves and rhizomes were cleaned of epiphytes, detritus, and fauna using a scalpel. All plant material was dried for 48 hr at 60 °C. The belowground biomass was separated into living and dead rhizomes, and each fraction was dried separately. All samples were analyzed for stable isotopes of carbon and nitrogen (^{13}C and ^{15}N), organic carbon (OC), and particulate organic nitrogen (PON) content to determine their relative contribution to the sediment C_{org} stock. A pooled sample of two young leaves from 10 randomly selected shoots were used for the analysis of aboveground tissue, while samples of both living and dead rhizomes were used for analysis of belowground tissue. All samples, including additional carbon sources, were analyzed with Thermo Scientific, delta V advantage, isotope ratio mass spectrometer (with Vienna Peedee belemnite as reference material) connected to elemental analyzer. Site-specific values for measured plant variables are given in Table S2. Due to lack of in situ sampling of phytoplankton at the sites, δ^{13}C values from the literature were used in the stable isotope analysis (Conway-Cranos et al., 2015; Goering et al., 1990; Jorgensen et al., 2007; Kang et al., 2015; Kajihara et al., 2010; Miyajima et al., 2015; Pernet et al., 2012; Röhr et al., 2016; Tagliabue & Bopp, 2008; Tiselius & Fransson, 2015). The δ^{13}C values for plankton selected from the literature for each site and used in the analysis are given in Table S3.

2.4. Sediment and Environmental Variables

In the laboratory, sediment cores were sliced into five sections of 5 cm down to 25 cm. All visible plant material and fauna were removed, and the sediment was homogenized. A 20-ml subsample taken from the 0- to 5-cm section was used for grain size analysis, using a Malvern Mastersizer 3000 particle size analyzer to determine the sediment mud content (%). Sediment mud content was calculated as the size fraction (%) of clay and silt (0–63 μm) present. Degree of sorting, calculated from the different sediment grain size fractions, was used as a proxy for degree of exposure of the site (see Folk & Ward, 1957). A 5-ml subsample was then taken from each sediment section and weighed before and after drying at 105 °C for 6 hr for determination of basic sediment characteristics (sediment water content, dry bulk density, and porosity). These characteristics were then used in calculations of sediment C_{org} stocks. The dried subsamples from each layer were homogenized in a mortar and divided into two subsamples, from which one was used for analysis of sediment organic content (loss on ignition, 4 hr in 520 °C), and the other for analysis of δ^{13}C, δ ^{15}N, PON, and organic carbon (OC), as described above for the plant material. Prior to analysis, the 0- to 5-cm sediment layers were acidified to remove carbonate material that could cause possible bias in estimations of the sediment C_{org} stocks. The average sampling depth was calculated for each site, and values for mean annual water temperature and salinity were obtained from the ZEN database for the different study regions (Table S1).

2.5. Sediment C_{org} Sources

The sediment surface δ^{13}C values were used in the analysis of contribution of different carbon sources to the sediment surface (0–5 cm) C_{org} pool. The sediment surface section was used for the analysis as this was the section in which other potential carbon sources were most likely to accumulate. To estimate the contribution of the potential carbon sources to the sediment surface C_{org} stock, the R function *mixSIR.unknownGroups* was used (Ward et al., 2011). This method is recommended when the number of sources exceeds the number of tracers +1, and the grouping of sources may be necessary to reduce bias in the posterior estimates. The function indicates the optimal number of groups and identifies groups by evaluating the likelihood of different source groupings, while simultaneously estimating the proportional contribution of each source group to the sediment surface C_{org} pool. The number of groups and source membership per site was based on the frequency of posterior cooccurrence, in order to identify the most parsimonious model formulation. However, for some sites other groupings with only slightly lower posterior probabilities were selected to prioritize biological or ecological similarities between sources. To characterize the δ^{13}C of *Z. marina* (n = 3), the δ^{13}C of *Z. marina* leaves, living, and dead rhizomes were averaged within each site prior to the analysis, since they were drawn from the same *Z. marina* shoots, and because all the *Z. marina* sources had statistically similar isotopic signatures. The number of samples of other abundant C_{org} sources within the meadow (e.g., epiphytes, phytoplankton, and drift algae) varied between 1 and 4. When n = 1, we assumed an standard deviation = 0.5 to reflect similar variability of the isotopic signatures as for the replicated sources of C_{org} in this study. Assuming isotopic variability for samples with no replicates is statistically desirable, since the posterior draws depend on the variance estimates and the extent to which the isotope mixing model precludes the contribution of sources included in the model. If the isotope signatures of source have no variances, very few of the random draws representing proportional contributions will be resampled, because most draws will have very low likelihoods (Ward et al., 2011). An advantage of Bayesian mixing models such as mixSIR.unknownGroups is that it explicitly deal with variability among mixture and source isotopic signatures, accounting for error propagation in their estimates of source contributions to a mixture (Phillips et al., 2014). By default mixSIR.unknownGroups incorporate a term for variation in consumer tracer values due to the sampling process (*process error*). We also included a *residual error* term, since sediment sourcing mixtures integrate large quantities of source particles, and it is realistic to assume that each mixture data point deviate from the mean of the population due to causes of mixture variability not accounted by process error. We ran 100,000 posterior draws for each model. Results are reported as percentage contribution from each source to the sediment surface carbon pool.

2.6. C_{org} Stock Calculations

Carbon density (mg C/cm^3) was calculated by multiplying OC (mg/g DW) measured at each sediment layer with the corresponding sediment dry density (g/cm^3). The C_{org} stock was calculated by depth integration of carbon density (0–25 cm) using calculations described in detail in Lavery et al. (2013) and given as C_{org}

stock (g C/m^2). The projected C_{org} stock for data from this study was estimated by multiplying the C_{org} stock by four to estimate the C_{org} stocks to 100-cm depth and given as projected C_{org} stock (t C/ha). It should be noted that the Mediterranean value was derived from a single site. The projected C_{org} stock in *Z. marina* sediments at the different ocean margins and seas was estimated by extrapolating to 100-cm depth to compare with previously reported C_{org} stocks of other seagrass species, other blue carbon habitats (e.g., saltmarshes and mangroves), and terrestrial ecosystems. The 25-cm depth has been previously shown to allow extrapolation to the top 100 cm (e.g., Fourqurean et al., 2012; Lavery et al., 2013), although it is unlikely that the sediment C_{org} stock would stay stable throughout the 100-cm sediment profile and often either decreases or increases with depth. While we recognize that these estimations represent extrapolation from a limited set of regions and require some untested assumptions (namely, uncertainty in the stability of the depth profiles of sediment C_{org} stocks), they are required to directly compare the carbon storage capacity of *Z. marina* with other known blue and green carbon stocks, as most of the values used for comparison in this study were measured from the top 1-m section.

2.7. Predictors of Among-Site Variation in Carbon Stocks

To explain the among-site variation in carbon stocks, we statistically assessed the relative importance of environmental variables (latitude, water depth, salinity, and water temperature), sediment variables (sediment density, sediment mud content, degree of sediment sorting, and ^{15}N content of sediment) and characteristics of seagrass meadows (^{15}N content of *Z. marina* eelgrass leaves, PON content of *Z. marina* leaves, *Z. marina* shoot density, aboveground *Z. marina* biomass, belowground *Z. marina* biomass, root: shoot ratio, and *Z. marina* contribution to the sediment surface C_{org} pool). We used partial least squares (PLS) regression in SIMCA 13.0.3 software (UMETRICS, Malmö, Sweden) to model projections to latent structures (Wold et al., 2001) on untransformed data. PLS is a developed generalization of multiple linear regression, where latent structures (i.e., variables with the best predictive power) are constructed based on linear associations between a set of predictor variables (x) and the response variable (y). PLS regression modeling was used since this technique can handle multicollinearity and large numbers of predictor variables (Carrascal et al., 2009). This regression technique is applicable in analyses of various types of ecological data (e.g., Asplund et al., 2011; Carrascal et al., 2009; Staveley et al., 2017) and has recently been used to address the influence of different types of predictors on carbon stocks (Dahl et al., 2016; Gullström et al., 2018). We also used principal component analysis (PCA) to visualize general relationships between ocean margins or seas and environmental predictors (i.e., the five predictors having a major contribution to the PLS model) and the C_{org} stock (g C/m^2). Prior to the PCA, data were transformed using Log(x + 1). A significance level of 95% ($p < 0.05$) was used in the analysis.

3. Results

3.1. Magnitude of Sediment Carbon Stocks

Carbon density (mg C/cm^3) in the upper 25 cm of the sediment showed marked differences between the ocean margins and seas with site-specific averages ranging from 1.7 ± 0.5 mg C/cm^3, in the Baltic Sea area to 37.9 ± 8.5 mg C/cm^3, in the Mediterranean Sea (Table 1). The average carbon density for all sites was 11.4 ± 4.3 mg C/cm^3 (Table 1). The average depth-integrated (0–25 cm) C_{org} stock for all sites was 2,721 ± 989 g C/m^2, but the range of variation between sites (318 ± 10 to 26,523 ± 667 g C/m^2) and regions (578 ± 43 to 8,793 ± 2,248 g C/m^2) was substantial (Table 1 and Figures 2a and 3). The average C_{org} stocks in the regions per unit area were lowest in the Baltic and Black Seas and highest in the Kattegat-Skagerrak and Mediterranean ocean margins, although sites within regions varied considerably (Table 1 and Figure 3). In addition, Kattegat-Skagerrak and Mediterranean Sea had twofold to eightfold higher average C_{org} stocks (4,862 ± 741 and 8,793 ± 2,248 g C/m^2, respectively) than the rest of the studied regions. The average C_{org} stocks for the Atlantic and Pacific Ocean margins were moderate compared to C_{org} stocks at the Kattegat-Skagerrak and Mediterranean regions and varied only modestly within each ocean margin (Table 1 and Figure 3). Furthermore, the average C_{org} stocks were almost equal in Eastern and Western Atlantic (1,384 ± 241 and 1,349 ± 194 g C/m^2, respectively), while average C_{org} stocks in Eastern and Western Pacific Ocean margins were slightly higher (1,736 ± 210 and 2,343 ± 122 g C/m^2, respectively). The average projected C_{org} stocks of the *Z. marina* sediments obtained by extrapolating to 100-cm depth ranged between

Table 1

Summary of Carbon Storage by Region

Ocean margin/sea	*n*	*Zostera marina* area (km^2)	C_{org} density (mg C/cm^3)	SedOC (% DW)	C_{org} stock (g C/m^2)	OC in biomass (g C/m^2)	Total C_{org} (Mt)	Projected C_{org} stock (Mg C/ha)
Baltic Sea	13	90	1.7 ± 0.5	0.3 ± 0.0	578 ± 43	79 ± 8	0.05	23.1
Black Sea	2	765	2.1 ± 1.1	3.5 ± 1.2	725 ± 159	63 ± 22	0.6	29.0
Eastern Atlantic	3	—	9.2 ± 5.4	0.7 ± 0.5	1384 ± 241	129 ± 35	—	55.4
Western Atlantic	5	374	4.5 ± 0.8	0.3 ± 0.0	1349 ± 194	100 ± 15	0.5	54.0
Eastern Pacific	8	1,500	5.6 ± 1.3	0.4 ± 0.1	1736 ± 210	107 ± 14	2.8	69.4
Western Pacific	3	—	11.2 ± 1.2	1.1 ± 0.1	2343 ± 122	86 ± 9	—	93.7
Kattegatt-Skagerrak	19	757	19.3 ± 3.9	2.5 ± 0.6	4862 ± 741	80 ± 7	3.7	194.5
Mediterranean Sea	1	—	37.9 ± 8.5	2.3 ± 0.0	8793 ± 2248	62 ± 8	—	351.7
Z. marina average	54	—	11.4 ± 4.3	1.4 ± 0.4	2721 ± 989	88 ± 5	—	108.9

Note. Ocean margin/sea, number of sites included (*n*), *Z. marina* distribution area (km^2), sediment organic carbon density (C_{org} density, mg C/cm^3), sediment organic carbon content (SedOC, % DW), average organic carbon stocks in the upper 25 cm of the sediment (C_{org} stock; g C/m^2), OC in living *Z. marina* biomass (g C/m^2), total organic carbon stocks in the region (total C_{org}; Mt), average projected organic carbon stocks extrapolated to 100-cm sediment depth (projected C_{org} stock; Mg C/ha) across the study regions. Mean ± SE (*n* = 1–19) is given. The areal estimates of the *Z. marina* coverage at the different regions were obtained from Green and Short (2003), Luisetti et al. (2013), and Boström et al. (2014). SE = standard error.

23.1 (Baltic Sea) and 351.7 Mg C/ha (Mediterranean Sea; Table 1). The average projected C_{org} stock for all the studied regions was 108.9 Mg C/ha (Table 1).

3.2. Environmental Factors Driving Among-Site and Regional Variation in Sediment C_{org} Stocks

Overall, we found that the sediment organic content was considerably higher in the Kattegat-Skagerrak and Mediterranean Sea than in the other study regions (Table 2 and Figure 4a). In contrast, sediment mud content varied widely across and within the ocean margins and was nearly 1 order of magnitude lower in the Baltic Sea and in the Black Sea than the other regions (Table 2 and Figures 2b and 4b). Both sediment organic and mud content were positively related to the sediment C_{org} stocks (g C/m^2) ($p < 0.0001$, $R^2 = 0.58$, $R^2 = 0.53$, respectively), indicating the importance of sediment grain size distribution for the size of sediment C_{org} stocks. Sediment mud content was also negatively related with the percent contribution of *Z. marina* to the sediment surface C_{org} pool ($p = 0.0287$, $R^2 = 0.09$). Degree of sorting at the individual sites indicated that our study areas encompassed both sheltered and exposed sites, with no consistent pattern in exposure across the geographical range (Table 2).

The cross-validated variance (Q2 statistics; estimates of the level of predictability of the model) of the PLS model was 51%, which is clearly higher than the 5% significance level. The cumulative fraction of the 15 environmental predictor variables combined (R^2y cumulative) displayed a high degree of determination and explained 62.5% of the variation in the sediment C_{org} stocks (g C/m^2) across the study sites. Specifically, five predictors, sediment mud content, sediment density, salinity, degree of sediment sorting, and water depth, had variable influence on the projection values above 1, thereby being the major drivers (contributing more than average on the model performance) of the variation in the sedimentary C_{org} stocks (Figure 5). Sediment mud content, salinity, and degree of sediment sorting were all positively related to sedimentary C_{org} stocks, while sediment density and water depth had negative relationships, respectively (Figure 5). The remaining predictors had less than average influence on the model performance (Figure 5).

The PCA indicated a similar pattern across the different ocean margins, supporting the PLS results of five key environmental indicators, except for Baltic Sea, which showed clear within-regional site similarity (Figure 6). The PCA model explained a large part of the variation (eigenvalues of PC1 and PC2 were 78.2% and 10.7%, respectively). PC1 and PC2 were both associated with the total variation of six variables, that is, sediment dry density, mud content (%), water depth, salinity, degree of sorting, and C_{org} stock. For PC2, the variation was explained in a ranking order by C_{org} stock, mud content (%), salinity, water depth, sediment dry density, and degree of sorting.

3.3. Relative Contribution of Different Sources to Sediment Organic Carbon in *Z. marina* Beds

Z. marina was the main carbon source (contribution ranging between 60% and 94%) to the sediment surface C_{org} pool at eight sites, whereas it contributed only 3%–47% at the remaining 46 sites (Figure 2c). The average

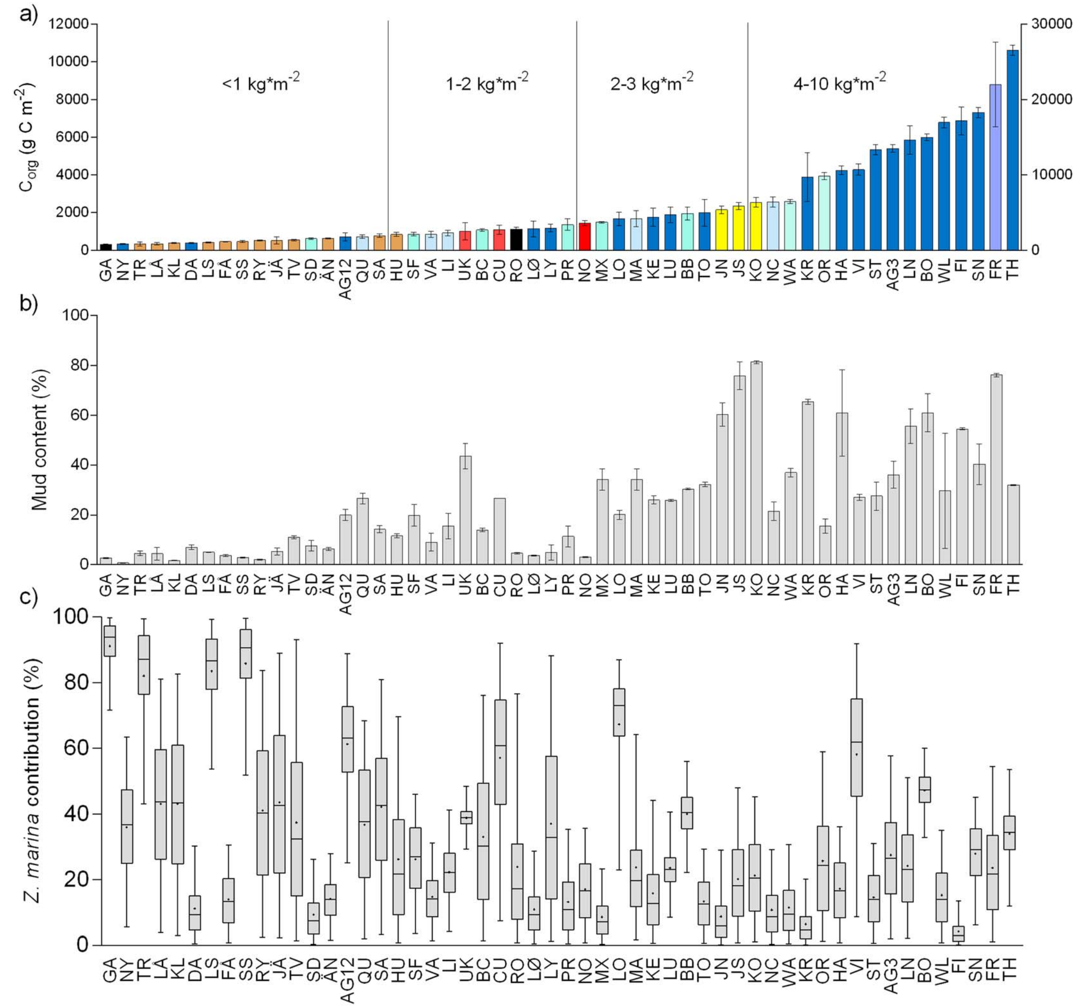

Figure 2. (a) C_{org} stocks (g C/m^2 ± SE) in the top 25 cm of sediment at all sites. Note that value at site TH corresponds to right *y* axis. (b) Sediment mud content (% ± SE) and (c) the relative contribution of *Z. marina* tissues to the δ^{13}C of the sediment surface layer (0–5 cm) at the sites. Box plots represents first and third quartiles and are shown with medians (horizontal line), means (+). The whiskers represent the 2.5–97.5th percentiles. *Z. marina* contribution was calculated from a pooled δ^{13}C value of aboveground and belowground tissue. Sites are ordered according to the magnitude of C_{org} stocks (from lowest to highest). In Figure 2a, the sites are colored according to the study region: Black = Black Sea; brown = Baltic Sea; dark blue = Kattegat-Skagerrak; turquoise = Eastern Pacific; light blue = Western Atlantic; red = eastern Atlantic; yellow = Western Pacific; purple = Mediterranean Sea. For site names, see Table S1.

Z. marina contribution to the sediment surface C_{org} pool was highest in the Black Sea (56%) and lowest (15%) in the Western Pacific region. The average *Z. marina* contribution to the sediment surface C_{org} pool at the other regions ranged between 20% and 46% (Figure 4c). Other macrophyte species (*Ruppia* spp., *Potamogeton* spp., *Halodule* spp., and *Z. japonica*) contributed 12–40% at the 15 sites in which they were abundant. Phytoplankton contribution ranged between 6% and 97% and was the major (57–97%) source at 12 sites (Figure S1). Contribution of macroalgae (12 sites) (*Laminaria* spp., *Fucus* spp., *Chara* spp., and *Dictyota* spp.) was 12–49% and 10–59% for drifting algae (26 sites), respectively. Epiphyte carbon contributed 12–20% at the four sites in which it was abundant. Terrestrial sources contributed 14–32% to the C_{org} pool at five sites. The δ^{13}C of the surface sediment at the sites showed no consistent patterns across the ocean margins (Table 2 and Figure 4d). The average δ^{13}C of *Z. marina* leaves and rhizomes in the ocean margins showed higher variation than sediment surface samples, being heavily depleted in ^{13}C the Black Sea, while the δ^{13}C at the other regions were more homogenous (Table 2 and Figure 4e). The average δ^{15}N of *Z. marina* leaves was quite homogenous for the different ocean margins and seas being highest in Black Sea, Eastern and Western Pacific and lowest at Baltic Sea, Kattegat-Skagerrak, Eastern and Western Atlantic, and the Mediterranean Sea (Table 2).

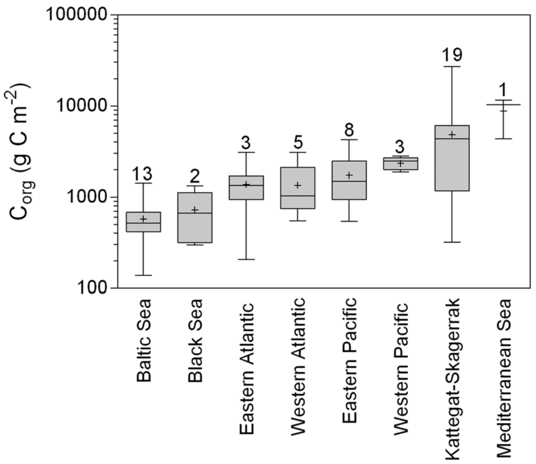

Figure 3. Seagrass (*Z. marina*) sediment organic carbon stocks (C_{org} g C/m^2) across the ocean margins and seas in the top 25 cm of the sediment. Box plots represents first and third quartiles and are shown with medians (horizontal line), means (+). Whiskers represent the 2.5–97.5th percentiles. Number of sites per ocean margin/sea is given above the whiskers.

4. Discussion

4.1. Geographic and Species-Specific Comparisons of Carbon Stocks

Our geographically widespread sampling of 54 sites in eight ocean margins and seas spanning three continents and 36° of latitude shows that the C_{org} stock at the temperate *Z. marina* beds is notable and appears to be on the same order of magnitude as beds dominated by many other species whose role in carbon dynamics are broadly appreciated (Figure 7). *Z. marina* meadows in the temperate Northern Hemisphere exhibit substantial regional and local variation in carbon storage (e.g., over eightfold differences between the C_{org} stocks in the Mediterranean Sea and Kattegat-Skagerrak compared to the Baltic Sea). These differences are at large explained by sediment characteristics, salinity, and depth. In the brackish waters of the Northern parts of the Baltic Sea, *Z. marina* grows in relatively exposed locations (Boström et al., 2014). The exposed habitats do not promote extensive carbon sequestration due to hydrodynamic effects that export the organic matter produced in the meadows to further adjacent locations. In addition, water depth is likely to have larger indirect effects on carbon storage affecting other variables such as hydrodynamics, sediment resuspension, and erosion, which was not accounted for in this study. In contrast, the meadows in, for example, the Kattegat-Skagerrak region usually grow in sheltered depositional environments with relatively high production rates and accumulation of autochthonous organic and inorganic particles. This variation in *Z. marina* C_{org} stocks among sites and regions makes it clear that previous global scale extrapolations of carbon storage in seagrass beds based on limited sampling must be regarded as tentative and are likely in need of refining.

4.2. Comparing Magnitude of Carbon Stocks in *Z. marina* Versus Other Seagrasses

The average total *Z. marina* C_{org} stock in the upper 25 cm of the sediment ranged from 5.8 to 87.9 Mg C/ha (average 27.2 Mg C/ha) and was lowest in the Baltic Sea and highest in Kattegat-Skagerrak region and at one site in the Mediterranean. In addition, the highest carbon storage among all sites (265.2 ± 0.67 Mg C/ha) in this study was found at a single site TH (Thurøbund) in the Kattegat-Skagerrak, indicating a potential *carbon hot spot* in the area. In addition, 9 out of 10 of sites exhibiting the highest C_{org} stocks were found in the Kattegat-Skagerrak region, further supporting the role of this region as potential carbon hot spot, largely explained by the high organic matter content sediments found in the highly productive and sheltered seagrass meadows in the region. Comparing the amount of carbon in living *Z. marina* tissue with that in the upper 25 cm of the sediment, the aboveground and belowground *Z. marina* biomass contributed only 3.1% of the total carbon stock, on average. Thus, the sediment carbon content is much more important that the standing biomass of *Z. marina* for the carbon stock and pool. This means that even though the areal extent of *Z. marina* meadows along Eastern Pacific Ocean margin is twice that in Kattegat-Skagerrak (1,500 versus 757 km^2, respectively), the meadows in Kattegat-Skagerrak contains 35% more carbon in total (2.76 and 3.74×10^9Mg, respectively). This finding is supported by earlier studies in which seagrass carbon has been shown to be a minor contributor to the seagrass C_{org} pool compared to the sediment C_{org} stock (e.g., Fourqurean et al., 2012; Macreadie et al., 2013).

We projected the greatest average carbon storage in a region by extrapolating to 100-cm depth (351 Mg C/ha), at the Mediterranean region, although this value was derived from a single site (FR), while the mean projected carbon storage across the study sites was 108.9 Mg C/ha (Figure 7). The average projected *Z. marina* C_{org} stock from this study was over twofold higher than that reported for Australian seagrass sediments (50.5 Mg C/ha; Lavery et al., 2013; Figure 7). Moreover, the average projected *Z. marina* C_{org} stock for all the studied regions was higher than the average for East and Southeast Asian seagrasses (72.4 Mg C/ha; Miyajima et al., 2015) and even higher than the global average estimated (70 Mg C/ha) by Kennedy and Björk (2009). In contrast, the average projected C_{org} stock from this study was ~23% lower than that

Table 2
Summary of Potential Environmental Drivers for Carbon Storage by Region

Ocean margin/ sea	*n*	Shoot density (shoots m^{-2})	AB (gDW m^{-2})	BB (gDW m^{-2})	R:S	δ^{13}C *Z. marina* leaves	δ^{13}C *Z. marina* rhizomes	δ^{13}C sediment surface	^{15}N *Z. marina* leaves	SedOM (% DW)	Mud content (%)	Dry dens. (g/cm^3)	DS (φ)
BS	13	397 ± 63	118 ± 17	102 ± 19	1.3 ± 0.5	−11.8 ± 0.9	−11.4 ± 0.7	−18.9 ± 0.8	6.7 ± 0.4	1.1 ± 0.1	5.9 ± 0.8	1.3 ± 0.1	1.3 ± 0.1
BLS	2	736 ± 459	120 ± 56	72 ± 32	0.5 ± 0.1	−17.8 ± 0.7	−15.5 ± 0.7	−16.6 ± 5.6	10.0 ± 1.1	0.7 ± 0.1	3.6 ± 0.6	1.3 ± 0.1	1.6 ± 0.3
EA	3	774 ± 275	78 ± 10	264 ± 134	1.6 ± 0.4	−10.2 ± 1.5	−9.9 ± 1.2	−19.1 ± 0.5	6.7 ± 0.7	2.3 ± 0.4	24.0 ± 9.2	1.2 ± 0.2	1.3 ± 0.4
WA	5	381 ± 202	183 ± 46	180 ± 41	1.1 ± 0.1	−9.2 ± 0.8	−10.1 ± 0.6	−18.1 ± 0.6	7.2 ± 0.8	1.2 ± 0.2	21.4 ± 3.2	1.5 ± 0.1	1.7 ± 0.2
EP	8	549 ± 316	232 ± 61	111 ± 47	0.6 ± 0.2	−10.5 ± 0.4	−10.6 ± 0.4	−20.2 ± 0.9	9.9 ± 1.1	3.8 ± 1.9	21.3 ± 2.8	1.4 ± 0.1	1.4 ± 0.2
WP	3	287 ± 80	194 ± 53	56 ± 16	0.4 ± 0.2	−9.9 ± 0.7	−10.4 ± 0.6	−18.9 ± 0.7	9.2 ± 1.5	4.1 ± 1.1	72.5 ± 4.4	1.0 ± 0.0	2.1 ± 0.1
K-S	19	319 ± 35	129 ± 15	125 ± 26	1.2 ± 0.3	−9.4 ± 0.5	−10.4 ± 0.5	−17.6 ± 0.9	6.1 ± 0.7	7.2 ± 1.2	32.9 ± 3.3	0.9 ± 0.1	1.6 ± 0.1
MED	1	223 ± 55	73 ± 14	144 ± 40	2.4 ± 1.0	−5.1 ± 0.4	−7.4 ± 0.9	17.5 ± 0.8	5.1 ± 0.4	7.0 ± 2.2	76.3 ± 0.7	1.3 ± 0.2	2.1 ± 0.0
Z. marina average	54	419 ± 57	146 ± 13	127 ± 17	1.8 ± 0.6	−10.5 ± 3.5	−10.8 ± 0.3	−18.3 ± 0.4	7.1 ± 0.4	3.00 ± 0.6	24.9 ± 3.0	1.00 ± 0.1	1.5 ± 0.1

Note. The ocean margin/sea, number of sites included (*n*), shoot density (shoots m^{-2}), seagrass aboveground and belowground biomass (AB and BB, g DW/m^2), root: shoot ratio (R:S), δ^{13}C of *Z. marina* leaves, δ^{13}C of *Z. marina* rhizomes, δ^{13}C of sediment surface, ^{15}N content of *Z. marina* leaves, sediment organic matter content (SedOM, % DW), sediment mud content (%), sediment dry density (dry dens., g/cm^3), and degree of sorting (DS, φ) at the ocean margins and seas. ±SE (*n* = 1–19) is given. EA = Eastern Atlantic; WA = Western Atlantic; EP = Eastern Pacific; WP = Western Pacific; BS = Baltic Sea; K-S = Kattegat-Skagerrak; BLS = Black Sea; MED = Mediterranean Sea.

estimated for tropical seagrass meadows (142.2 Mg C/ha; Alongi, 2014). In addition, the global median value widely cited in literature (139.7 Mg C/ha; Fourqurean et al., 2012) was nearly threefold higher than the median projected C_{org} stock from this study (48.6 Mg C/ha; Figure 7). Fourqurean et al. (2012) accounted for regional variation in seagrass C_{org} stocks, but we suggest that global estimates of seagrass carbon storage will also require understanding the species composition of the meadows, in addition to acknowledging the species-specific variation and the environmental factors affecting this variation. Indeed, results from this study suggest that a combination of specific environmental variables can greatly increase the carbon storage potential of *Z. marina* meadows. This can be applied to conservation and restoration efforts, which focus on sites with the greatest potential contribution to offset carbon. Similar carbon hot spots exist for beds dominated by other species, such as *P. oceanica*, where average C_{org} stocks were over sixteenfold higher at 2-m depth than at the 32-m depth (470 and 7,550 Mg C/ha, respectively; Serrano et al., 2014).

4.1. Environmental and Biological Factors Driving the *Z. marina* Carbon Stocks

Given the considerable variation among sites, and the influence of this variation on global estimates outlined above, better estimations for seagrass C_{org} stocks require an understanding of the causes of this variation. PLS analysis revealed that five environmental variables explained over 62% of the variation in the *Z. marina* sediment carbon stocks across study sites (Figure 5). Three of these were sediment variables (mud content, sediment density, and degree of sediment sorting), and two were environmental variables (water depth and salinity; Figure 5; but see Figure S2 for region-specific PLS). These findings are in line with results from earlier studies (Dahl et al., 2016; Macreadie et al., 2013; Miyajima et al., 2015; Röhr et al., 2016; Serrano et al., 2016), which have indicated that sediment characteristics, specifically the sediment grain size distribution and sediment density, appear to be the most important predictors for the carbon sink capacity of seagrass meadows. Thus, these variables could be used as relatively reliable proxies for estimating *Z. marina* sediment carbon stocks, especially in regions where funding for research is limited (Röhr et al., 2016; Serrano et al., 2016).

The differences in sediment density and mud content are mainly driven by the exposure of the sampled meadow. Consequently, local and regional differences in exposure also influence the dynamics of accumulation of inorganic and organic particles into the meadows (Hendriks et al., 2008). In this study, we used degree of sorting as a proxy for exposure (physical exposure through movement of water masses), which was derived from the results of sediment grain size analysis (Folk & Ward, 1957; Mazarrasa et al., 2017b). According to PLS analysis, degree of sorting was approximately of the same relative importance as salinity and was mainly driven by exposed *Z. marina* meadows of the Baltic Sea (Figure S2). Consequently, high exposure leads to the export of carbon to other adjacent locations and ecosystems. The importance of carbon export and connectivity among ecosystems has been partly overlooked in blue carbon studies, but recent evidence suggests that carbon exported away from blue carbon ecosystems may contribute significantly to organic carbon stocks in other locations and ecosystems, thereby potentially biasing estimates of global carbon budgets (Barron et al., 2014; Barron & Duarte, 2015; Duarte &

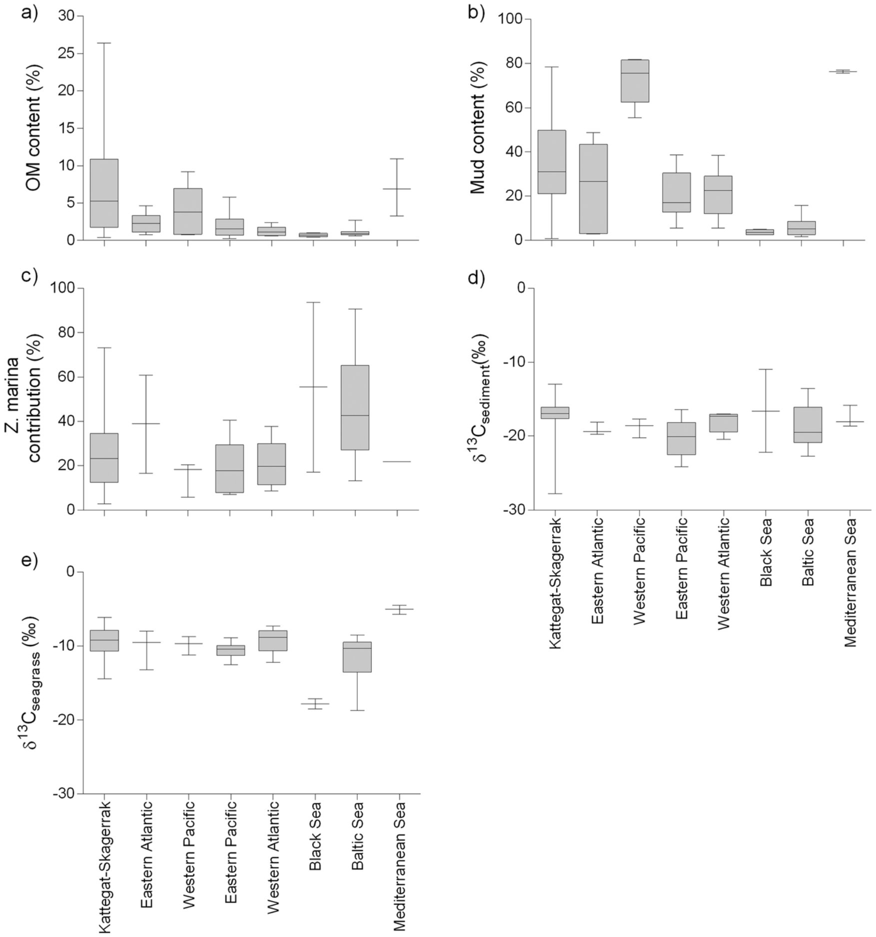

Figure 4. The (a) organic content (organic matter, OM %), (b) mud content (%), (c) *Z. marina* contribution to the upper 5 cm of the sediment surface C_{org} pool (%), (d) $\delta^{13}C$ of sediment surface samples, and (e) $\delta^{13}C$ of *Z. marina* leaves across the ocean margins and sea box plots represents first and third quartiles and are shown with medians (horizontal line), means (+). Whiskers represent the 2.5th to 97.5th percentiles. Boxes are not shown for sites in which $n \leq 3$.

Krause-Jensen, 2017; Hyndes et al., 2014). Earlier studies support this hypothesis; for example, Duarte and Cebrián (1996) showed that ~25% of the net primary production in seagrass meadows is being exported. Similarly, they estimated that ~30% and 19% of net primary production is being exported from mangroves and salt marsh ecosystems. Moreover, recent studies have highlighted that macroalgae, which have not previously been recognized as contributing to carbon storage, might make significant contributions to blue carbon stocks as a carbon donors to adjacent blue carbon habitats (Hill et al., 2015; Krause-Jensen & Duarte, 2016; Trevathan-Tackett et al., 2015). This exchange of organic matter across ecosystem boundaries has inevitable consequences for the availability of the organic matter and burial, mineralization, and consumption of organic carbon by microbial communities and higher trophic levels (Barron et al., 2014; Barron & Duarte, 2015; Duarte & Krause-Jensen, 2017; Hyndes et al., 2014). Carbon export is also highly important for the implementation of blue carbon offset credits due to the risk of duplicating carbon sequestration estimates, both at source and sink ecosystems (Hejnowicz et al., 2015).

A recent study, encompassing both intertidal and subtidal and tropical and temperate seagrass ecosystems showed that presence of seagrass resulted in an average difference in surface elevation rate of 31 mm/year, compared to adjacent unvegetated sediments (Potouroglou et al., 2017). Furthermore, although not measured in this study, the structure of seagrass meadows can also be a potentially important predictor for the magnitude and source of seagrass C_{org} stocks. Gullström et al. (2018) showed that in tropical East Africa, landscape configuration, along with sediment characteristics and seagrass biomass, was the most important predictor variables for seagrass sediment C_{org} stocks. Similarly, Ricart et al. (2017) showed that continuous *P.*

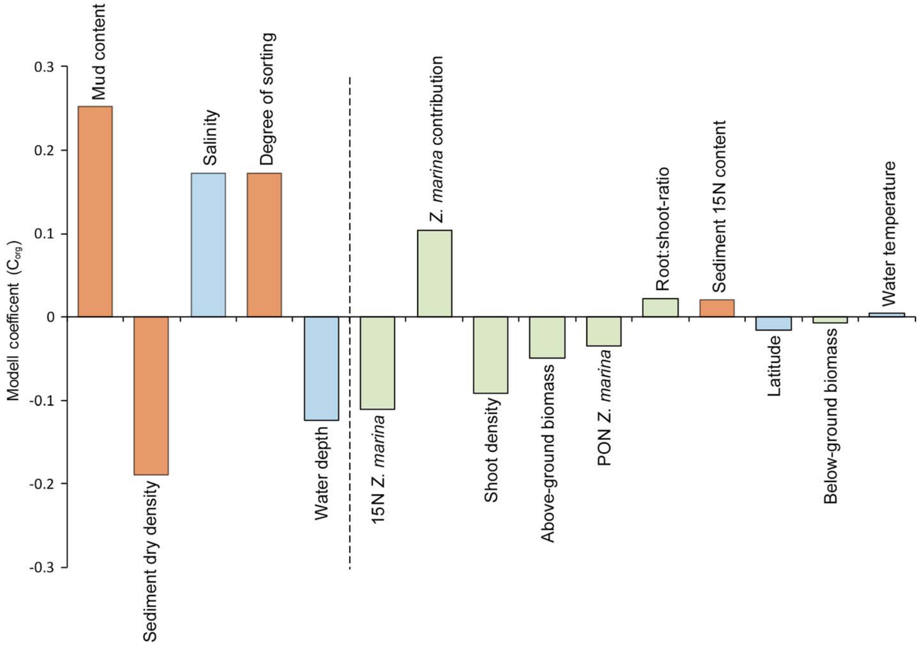

Figure 5. Partial least square regression model coefficient plot showing the relative importance of different predictor variables. Predictor variables are ranked in order of importance (from the left to the right), in which the five variables left of the dashed line have variable influence on the projection values above 1 (and hence an above average influence on C_{org} stocks). Brown bars represent sediment characteristics, green bars represent seagrass-associated variables, and blue bars are environmental variables. PON = particulate organic nitrogen.

oceanica meadows may store up to three times more C_{org}, per area, than seagrasses growing in small patches, and it is likely that similar trends can be found also in other seagrass species. This variation was explained by elevated rates of remineralization and resuspension, caused by reduced plant canopy in small, patchy meadows. In addition, in patchy meadows, seston, and other allochthonous inputs were the major sources of accumulating C_{org}, while in continuous meadows with higher C_{org} stocks, the major C_{org} source was of autochthonous origin. Various studies have reported higher C_{org} accumulation rates for

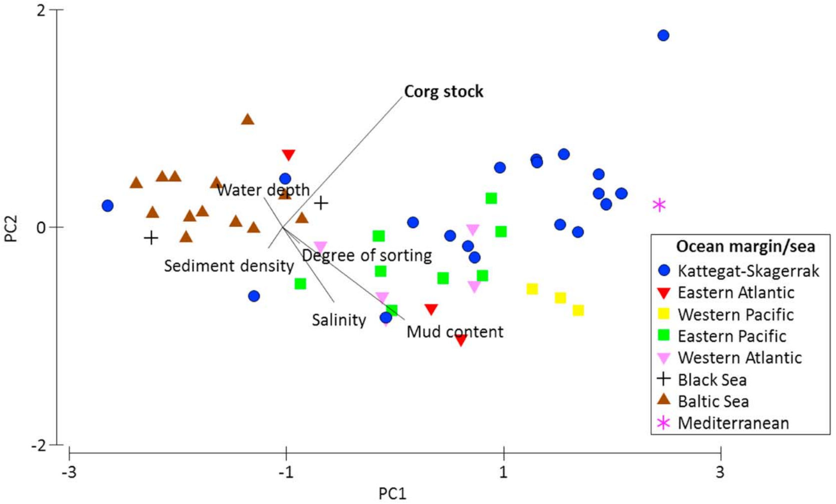

Figure 6. Principal component analysis showing how the eight regions are related to the most influential predictor variables (see Figure 5) and in terms of C_{org} stock data (i.e., the response variable). The horizontal axis (PC1) accounts for 78.2% of the total variance, while the vertical axis (PC2) accounts for 10.7% of the total variance.

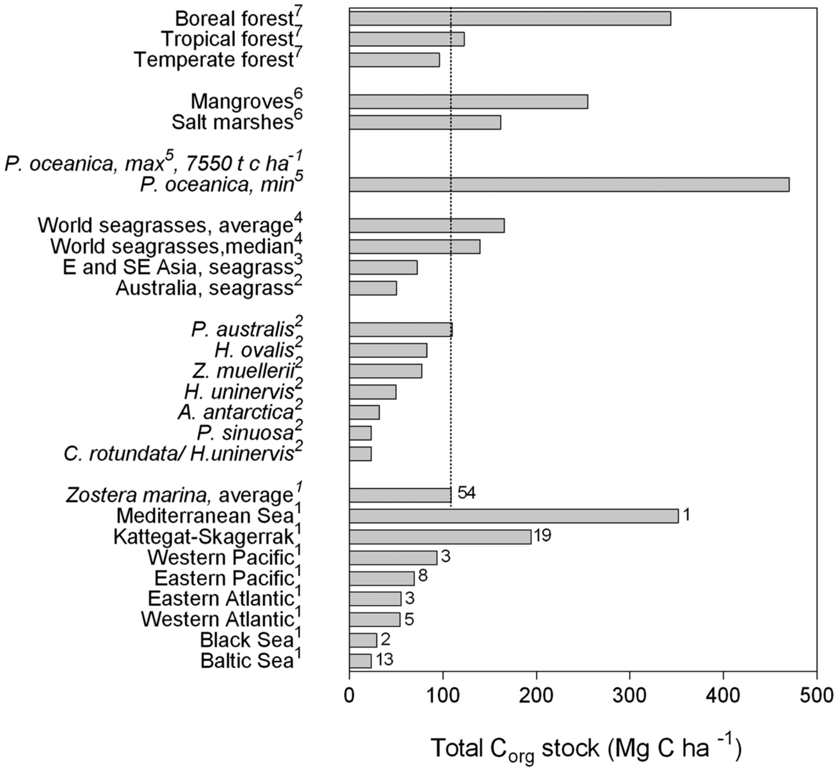

Figure 7. The total C_{org} stock (Mg C/ha) in top 100 cm of soil in terrestrial and blue carbon ecosystems (boreal forest, mangroves, salt marshes, tropical forest, and temperate forest), other seagrass species (*Posidonia sinuosa*, *Posidonia australis, Halophila ovalis, Zostera mullerii, Halodule uninervis, Amphibolis antarctica, Cymodocea rotundata/Halodule uninervis, Posidonia oceanica,* Australian seagrass meadows; average, East and Southeast Asia; average, world seagrasses; median) and C_{org} projected for *Z. marina* at the different ocean margins and seas in the study area (Baltic Sea, Black Sea, Eastern and Western Atlantic, Eastern and Western Pacific, Kattegat-Skagerrak, and Mediterranean Sea). Number of sites per ocean margin/sea is given next to the bars. 1 = this study; 2 = Lavery et al. (2013); 3 = Miyajima et al. (2015); 4 = Fourqurean et al. (2012); 5 = Serrano et al. (2014); 6 = Duarte, Losada, et al. (2013; derived from Siikamäki et al., 2012; Pendleton et al., 2012); 7 = Kennedy and Björk (2009; derived from Duarte & Cebrián, 1996; Duarte & Chiscano, 1999; Janzen, 2004; Duarte et al., 2005).

seagrass sediments than predicted from plant production alone, indicating that allochthonous sources must be important contributors to the seagrass sediment C_{org} stocks (Bouillon & Boschker, 2006; Kennedy et al., 2010). Kennedy et al. (2010) compiled data from 123 seagrass meadows and showed that on average, ~50% of C_{org} in seagrass sediments was of autochthonous origin. In our study, *Z. marina* derived detritus was the major contributor (60–94%) to the sediment surface C_{org} pool at only 8 out of 54 sites contributing on average 30.5 ± 3.1% to the sediment surface C_{org} pool across the study regions. Although results from the PLS analysis revealed that *Z. marina* contribution to the sediment surface C_{org} pool explained only relatively small fraction of the variation in C_{org} stocks, we note that a sizable fraction of the C_{org} at many sites was derived from seagrass, although the proportion of this fraction varied considerably among sites (Figure 2c). Furthermore, even though *Z. marina* contribution was not among the most important predictors, the presence of *Z. marina* meadows still enhances the production of epiphytes, microalgae, and macroalgae, traps allochthonous organic particles, and reduces sediment resuspension and water flow, thus resulting in high sequestration contributing to the formation of sediment C_{org} stocks (see Figure S14 for phytoplankton contribution to the sediment surface C_{org} pool). In addition, due to limited resources, we could not date our sediment cores and interpret the results from stable isotope mixing model in context of the information given by dating the core. The analysis of source contribution to the sediment C_{org} pool was run only for the surface layer, which gives us a proxy of the potential contribution of different carbon sources in the most recent times, but does not really hold information about the past. The $\delta^{13}C$ value typically gets closer to $\delta^{13}C$ of seagrass in the deeper layers especially in the high C_{org} stock sites (Fourqurean & Schrlau, 2003), but in the absence of information on the age and stability of the sediment studied and analysis of the full sediment $\delta\ ^{13}C$ profile, we cannot make solid conclusions about the contributions of the different carbon sources to the meadow in long term.

4.2. Consequences of Seagrass Loss for Global Blue Carbon Stocks

To date, vast areas of blue carbon ecosystems have been lost due to changes in land use and human-induced eutrophication. Mcleod et al. (2011) reported that 0.7–7% of the blue carbon ecosystems are lost annually. In the past 130 years, ~29% of the global seagrass area has been lost, and in many regions, these rates are accelerating (Bertelli et al., 2017; Furman et al., 2015; Marba et al., 2015; Orth et al., 2006; Waycott et al., 2009). In contrast, salt marsh loss rates have remained relatively stable and loss rates for mangrove forests have slowed from 1.04%/year in the 1980s to 0.66%/year in 2000 (Waycott et al., 2009). The consequences of loss of blue carbon ecosystems to the oceanic carbon flux are still in need to be quantified, as there is likely to be substantial variation between different regions and habitats. Furthermore, the fate and magnitude of inorganic carbon stocks stored in seagrass sediments have largely been overlooked by previous studies, although its contribution to sediment carbon pool in some regions have been shown to exceed that of organic carbon stocks by several factors (Mazarrasa et al., 2015). Using the annual loss rates for seagrass ecosystems, Pendleton et al. (2012) calculated a conservative estimate of 50- to 330 × 10^9-Mg CO_2 emissions from seagrass habitats annually, equivalent to approximately 33% of the total blue carbon emissions and economic damages. Furthermore, Macreadie et al. (2013) showed that disturbed *P. australis* meadows had up to 72% lower sediment C_{org} stocks compared to the sediments in adjacent undisturbed seagrass meadows. Similarly, Marba et al. (2015) showed that in sites experiencing a permanent seagrass vegetation loss, also 90 years' worth of carbon accumulation was lost through erosion of the sediments. The extensive loss of sediment C_{org} stock in the disturbed seagrass meadows was most likely being caused by microbial priming, an activation of previously dormant bacteria under the altered environmental conditions causing a release of ancient carbon stored in the sediments (e.g., Trevathan-Tackett et al., 2018).

Our results reveal that the magnitude of *Z. marina* C_{org} stocks is comparable not only to other seagrass species but also to other blue carbon habitats such as salt marshes and mangrove forests. The circumpolar distribution of *Z. marina* meadows suggests that the overall value of the total carbon stored in the world's *Z. marina* ecosystems is high. This finding is corroborated by the fact that the global areal extent of *Z. marina* could potentially be much more extensive than currently mapped (Gattuso et al., 2006). *Z. marina* meadows of the Northern Hemisphere have suffered from similar losses as seagrass meadows at other regions, for example, as a consequence of wasting disease caused by pathogenic strain of *Labyrinthula* (Short et al., 1987). The Danish *Z. marina* meadows in our suggested carbon hot spot, Kattegat-Skagerrak, were reduced by 80–90% in the beginning of 1930s (Rasmussen, 1977). *Z. marina* had recolonized many coastal areas by the 1970s, but new losses have occurred in the area since the 1980s, mainly due to eutrophication, and the *Z. marina* distribution in Denmark today is only around 20–25% of the historic distribution (Frederiksen et al., 2004). Similar losses have occurred along the Swedish Skagerrak coast, where over 60% of the *Z. marina* has vanished since the 1980s (equivalent to 125 km^2) and the losses continue today (Baden et al., 2003). Despite improvements in the nutrient status and water quality in these regions, the restoration success of seagrasses has until now remained poor. Moksnes et al. (2018) has suggested that local regime shifts result in increased sediment resuspension and accumulation of drifting algae, and by these negative feedback mechanisms preventing the successful recovery and restoration of the meadows in the region. Similar trend has been observed in other parts of the world where a recent study by van Katwijk et al. (2015) shows a success rate of only 37% for seagrass restoration projects globally.

Although the loss rates are accelerating, neither seagrasses nor any of the other blue carbon ecosystems were until recently included in carbon trading programs such as REDD (Reduced emissions from deforestation and degradation) and REDD+ (Mcleod et al., 2011; Pendleton et al., 2012). However, some promising initiative to involve Blue Carbon ecosystems in the carbon trading programs have been made, such as the Andalusian Law of Climate Change and Verified Carbon Standard, which now include an option for Wetlands Restoration and Conservation. In addition, economic incentives such as PES (Payment for Ecosystem services) could serve as financial initiations for protection of coastal carbon (Hejnowicz et al., 2015; Locatelli et al., 2014; Murray et al., 2011). However, the cost of these losses in terms of carbon storage cannot be accurately assessed without knowing the C_{org} stock of the same areas in the absence of seagrass. Although seagrass presence can increase the C_{org} in sediments (Dahl et al., 2016; Marba et al., 2015; Miyajima et al., 2015; Ricart et al., 2015; Rozaimi et al., 2016; Samper-Villarreal et al., 2018), in some systems vegetated and unvegetated sediments have similar organic matter content (Richardson et al., 2008). The comparison can be difficult to accurately assess, however, because simply sampling bare patches outside of seagrass beds may not provide adequate reference sites due to environmental or sedimentary characteristics that differ from those in the beds, and the proximity of seagrasses may also alter other adjacent ecosystems. While we recognize this deficiency and note that we cannot calculate exactly how much carbon the presence of seagrasses adds to the system, these data suggest that the proportion is likely to be substantial, although varying considerably among sites and regions.

Unfortunately, the current lack of acknowledgement and protection of seagrass meadows and the ecosystems services they provide, both in terms of carbon sequestration and other services, such as nursery habitat, nutrient accumulation, and sediment stabilization (e.g., Cole & Moksnes, 2016; Hejnowicz et al., 2015; Luisetti et al., 2013; Maxwell et al., 2016; Nordlund et al., 2016; Unsworth & Cullen-Unsworth, 2013), suggest that the global decline of seagrass meadows will most likely continue. The poor restoration success of seagrass meadows globally urges to protect the meadows, which still persist. We emphasize that there is an urgent need to reverse the current trend of losses of blue carbon ecosystems by conserving and involving blue carbon habitats as part of climate change mitigation programs and global carbon budgeting. Both in a global and regional contexts, there are still many unknowns in blue carbon research that must be defined. The most important gaps include determination of the total areal extent of global blue carbon storage zones, examination of the fate of both inorganic and organic carbon exported from existing and disturbed blue carbon ecosystems, seascape connectivity between blue carbon ecosystems, and finally identification of the possible thresholds limiting ecosystem shifts (Maxwell et al., 2016; Van der Heide et al., 2011). By answering these questions, we could potentially create incentives to contribute to more relevant policy making and legislation and identify areas in which restoration and conservation could benefit both the management of atmospheric CO_2 emissions and the protection of biodiversity and other ecosystem services that these valuable ecosystems sustain.

Acknowledgments
This work is part of the coordinated experimental network, *Zostera Experimental Network* (ZEN, www.zenscience.org) a collaborative network of scientists studying the structure and functioning eelgrass ecosystem, that provided an unique opportunity to explore globally the C_{org} stocks in eelgrass meadows with homogenic sampling methodology and protocol. This work is also part of a double degree program between Åbo Akademi University (ÅAU) and the University of Southern Denmark (SDU). The study was funded by the Maj and Tor Nessling Foundation (project 201600125: Baltic Sea blue carbon: environmental gradients influencing the carbon sink capacity of seagrass meadows), the Åbo Akademi University Foundation Sr, the University of Southern Denmark, and U. S. National Science Foundation grants OCE-1336206, OCE-1336741, and OCE-1336905. We acknowledge Archipelago Centre Korpoström and the University of Southern Denmark for excellent working facilities. We also acknowledge all the field and laboratory assistants enabling gathering of this global data set. Data is provided at Zenodo repository under doi:10.5281/zenodo.1412380.

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Erratum

In the originally published version of this article, Katharyn Boyer was omitted from the list of authors. Additionally, the number cited in Figure 7 for world seagrass average was incorrect, and a table in the Supporting Information was duplicated. These errors have been corrected, and this may be considered the authoritative version of record.