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Sediment characteristics as an important factor for revealing carbon storage in *Zostera marina* meadows: a comparison of four European areas

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Abstract. The seagrass ecosystem is an important natural carbon sink but the efficiency varies greatly depending on species composition and environmental conditions. What causes this variation is not fully known and could have important implications for management and protection of the seagrass habitat to continue to act as a natural carbon sink. Here, we assessed sedimentary organic carbon in *Zostera marina* meadows (and adjacent unvegetated sediment) in four areas of Europe (Gullmar Fjord on the Swedish west coast, Askö in the Baltic Sea, Sozopol in Black Sea and Ria Formosa in southern Portugal) down to ~35 cm depth. We also tested how sedimentary organic carbon in *Z. marina* meadows relates to different sediment characteristics, a range of seagrass-associated variables and water depth. The carbon storage varied both among and within areas, where the Gullmar Fjord had a 15 times higher carbon storage compared to Askö and Sozopol. We found that high carbon content in *Z. marina* sediment is strongly related to a high proportion of fine grain size, high porosity and low density of the sediment. We suggest that sediment characteristics should be highlighted as an important factor when evaluating high priority areas in management of *Z. marina* generated carbon sinks.

Keywords: Carbon storage variability, *Zostera marina*, grain size, sediment characteristics, natural carbon sinks.

1. Introduction

Seagrass ecosystems are considered highly efficient natural carbon sinks (Mcleod et al., 2011) but there is a large variation in the capacity to store carbon, depending on species composition and habitat characteristics (Lavery et al., 2013; Rozaimi et al., 2013). While the carbon sequestration efficiency is quite well documented for many seagrass species (e.g. Kennedy *et al.*, 2010; Fourqurean *et al.*, 2012) the effects of different factors influencing intraspecific variation has only recently been investigated. To get a more accurate estimate of the global seagrass carbon sink capacity cause-effect relationships need to be better understood, and as seagrass loss is accelerating (Waycott *et al.*, 2009) information on habitat characteristics affecting carbon storage are of importance for an efficient protection and management strategy to increase carbon storage capacity (Duarte et al., 2011).

There are several environmental factors (e.g. water depth and hydrodynamic processes) and seagrass habitat variables (e.g. canopy height and shoot density) that influence the carbon storage in seagrass sediments (Samper-Villarreal et al., 2016). For example, seagrass meadows at shallower depths are known to have a high accumulation of sedimentary carbon, which could be associated with higher primary production and larger standing biomass stock (Serrano et al., 2014). Dense meadows have the ability to stabilize the sediment (and thereby preventing it from eroding) (Suykerbuyk et al., 2015) and seagrass habitats with a high canopy can trap a high amount of suspended particles and thus potentially increase the sedimentation of organic matter (Fonseca and Cahalan, 1992; Hendriks et al., 2008). Further, as the belowground biomass largely contributes to the carbon storage due to its high production, fast turnover and higher decay-resistant lignin content compared to the leaves (Duarte et al., 1998; Klap et al., 2000) a large root-rhizome system could render a higher carbon storage (Kenworthy and Thayer, 1984). In the coastal environment, sediment grain size is known to influence the aggregation of organic particles with finer grain sizes increasing the organic matter content of the sediment (Mayer, 1994b). By reducing water velocity and facilitating sedimentation processes a seagrass meadow could increase the amount of fine particles, which thus promote a high carbon storage. Grain size has, however, proven a poor overall predictor of sedimentary carbon content in seagrass habitats, except for in smaller species such

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as *Halodule uninervis*, *Zostera muelleri* and *Halophila* spp. (Serrano *et al.*, in review). Grain size is also strongly related to sediment porosity and density, which influence the oxygen conditions in the sediment. Oxygen levels together with the microbial community composition, biomass carbon and nutrient content are important factors for the degradation rate of organic matter in the sediment (Benner et al., 1984; Deming and Harass, 1993; Enriquez et al., 1993) and therefore influencing the carbon sequestration process.

Zostera marina L. is the most widely spread seagrass species in the northern hemisphere, with a distribution in Europe stretching from the southern Black Sea and the gulf of Cádiz (Southern Portugal) up to Iceland and the northern parts of Norway (Green and Short, 2003). The plant biomass is generally larger at higher latitudes (Short et al., 2007) because of more optimal growth temperatures (Moore and Short, 2003). Large seagrass populations can be found along the Swedish west coast and at the east coast of Denmark (Baden and Boström, 2001; Olesen and Sand-Jensen, 1994), where they form extensive meadows with shoots over 1 m in length. Due to its wide distribution *Z. marina* populations have adapted to a large range of environmental conditions, with potential differences in carbon storage capacity. The species can tolerate salinity ranging from 5 to 35 (Boström et al., 2003) and a depth distribution from the intertidal down to 30 m depending on water clarity (Phillips and Meñez, 1988). *Zostera marina* also grows in various substrates, from courser stone-sand bottoms to finer silt and clay sediment. In this study, we aim to assess and compare carbon storage in *Z. marina* meadows at four different areas in Europe as well as to examine relationships between sediment organic carbon content and several explanatory predictors including seagrass structural complexity, carbon and nitrogen content of the seagrass biomass and sediment characteristics (i.e. sediment porosity and density, and grain size) in order to determine factors influencing the storage capacity of *Z. marina* meadows in these areas.

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2. Methods

2.1 Study sites

This study was conducted in four different areas in Europe (the Swedish Skagerrak and Baltic coasts, Black Sea in Bulgaria and the southern coast of Portugal; Table 1 and Fig. 1) from June to October 2013 with one complimentary field sampling performed in October 2014. Our areas roughly correspond to the edge zones of the *Z. marina* distribution in Europe. In each area, two meadows and one unvegetated area (reference site) were sampled, except for Portugal with one additional unvegetated area and the Baltic Sea where one meadow and one unvegetated area were added (Table 1). The sampling on the Swedish west coast were carried out off the Sven Lovén Centre for Marine Sciences – Kristineberg in the Gullmar Fjord (58°20’N, 11°33’E; Table 1). The area is comprised of small islands and shallow bays making it highly productive and a suitable environment for seagrass growth with many sheltered soft bottoms covered by extended *Z. marina* beds. In the Baltic Sea, samples were collected in the area around the Askö Laboratory in Stockholm Archipelago (58°49’N, 17°39’E). The Baltic Sea is a brackish water system and the salinity is about 5-6 outside Askö, which is on the distribution limit for *Z. marina* (Boström et al., 2003). Low salinity is known to negatively affect production and growth of the plant (Salo et al., 2014). In the Baltic Sea, *Z. marina* grows at approximately 2-5 m depths (sometimes together with *Ruppia maritima*) and on more coarse sediment compared to the Skagerrak area (Baden and Boström, 2001). In the Black Sea, sampling was carried out in two sites around the Laboratory of Marine Ecology in Sozopol, Bulgaria (42°25’N, 27°41E). The salinity is around 17 and commonly *Z. marina* grows in mixed stands with *Z. noltii*. The Ropotamo (Rt) site is situated in the vicinity of the Ropotamo river mouth. Ria Formosa (Algarve Marine Sciences Centre – Faro) is located in southern Portugal (36°59’N, 7°52’W) and is a coastal lagoon with large intertidal areas and a tidal fluctuation of 2-3 m. This is the only area in the present study with pronounced tidal variation, and the water depth for the Portugal sites was standardized to mean low water (MLW) by calculating the difference between the measured water depth and the tide at the time of measurement. The tide values were obtained from Ria Formosa tidal station (Faro-Olhão) with the mean water level as reference depth. Ria Formosa is a lagoon

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with scarce *Z. marina* distribution (which at times grows together with *Cymodocea nodosa*) and apart from one other area in Portugal (Óbidos Lagoon) the only one that still harbor *Z. marina*, which has decreased drastically during the past 20 years (Cunha et al., 2013).

2.2 Sediment sampling and biometrical measurements

At each site, six sediment cores were taken with a push corer (h=50 cm, ø =8 cm) at a distance of 10-30 m apart from each other. Each core was sliced into a maximum of six segments (0-2.5 cm, 2.5-5 cm, 5-12.5 cm, 12.5-25 cm, 25-37.5 cm, 37.5-45 cm) with the majority of samples lacking the deepest segment. Within a few meters from each core at the seagrass sites, shoot height (cm, n=20) was measured, percentage seagrass coverage (n=10) were estimated (in 0.5 x 0.5 m squares) and biomass samples (n=3) were collected (0.25 x 0.25 m). The biomass samples were used for estimating above- and belowground seagrass biomass (as dry weight) and for counting number of shoots. Before weighing the seagrass was cleaned and epiphytes removed, and the dry weight was measured after 24-48 h in 60°C until constant weight. One out of the three biomass samples collected around each core were analyzed for carbon and nitrogen content (n = 6 for each meadow). The sediment samples were cleaned from roots and rhizomes, larger shells and benthic organisms prior of drying and dried in the same way as the biomass. The sediment was divided into two subsamples, one for analysis of carbon and nitrogen content, and the other for grain size analysis. The carbon and nitrogen contents in biomass and sediment were analyzed using an organic elemental analyzer (Flash 2000, Thermo Fischer scientific). The sediment samples were pre-treated with 1 M HCl (direct addition) to remove inorganic carbon prior to analysis for C_{org} content. Total nitrogen (N_T) was measured due to possible alteration of the nitrogen values when treated with HCl (Harris et al., 2001). Sediment porosity was given as percentage (%) by calculating sediment wet weight minus dry weight divided by the sample volume, whereas sediment density (g DW mL^{-1}) was derived from dividing the dry weight of the sediment by the volume of the sample.

2.3 Grain size analysis

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Three sediment cores in each habitat were used for particle size analysis and each depth section was separately analyzed. Prior to analysis the total dry weight of sediment for each section was determined and 100 ml of 0.05 M $Na_4P_2O_7$ was added to break down aggregates of clay particles. Each depth section was dry-sieved for 10 min using a sieving tower (CISA electromagnetic sieve shaker, Spain) (including sieves of 0.074 mm, 0.125 mm, 0.25 mm, 0.5 mm, 1 mm and 2 mm) and the sediment of each sieve was weighed to determine the weight of the separate fractions. In depth sections with high organic carbon content (>0.5%), the organic matter was removed prior to dry sieving, through oxidation with 35% H_2O_2, as the organic matter content leads to aggregation of particles (Gee and Bauder, 1986). After the reaction with H_2O_2 had ceased the samples were centrifuged and washed in distilled water to remove the H_2O_2. Some of the samples from the Skagerrak and Ria Formosa regions had a high proportion of finer fractions (>15% was assessed as %<0.074 mm) and had to be analysed with hydrometer for an accurate estimate of total grain size. The samples were once more treated with 0.05 M $Na_4P_2O_7$ and placed in a 1L cylinder containing distilled water and kept in suspension. At fixed time intervals (1, 2, 4, 10, 20, 50, 100, 200, 400 and 1000 min) the hydrometer was inserted and the concentration of sediment (g L^{-1}) was noted. The mean grain size was presented in phi (ϕ) units.

2.4 Statistical analysis

All cores were standardized to a depth of 25 cm for the sediment characteristics (porosity, density, grain size and organic carbon content) prior to statistical analysis. Some of the cores at Askö (both seagrass- and unvegetated sites) lacked the 12.5-25 cm depth segment and in these cases logarithmic regressions were used to extrapolate the data down to 25 cm depth. All data were checked for normal distribution using the Shapiro-Wilk normality test and homogeneity of variances using Levene's test. When assumptions were not met the data was $\log_{10}$ or $\log_{10}(x+1)$ transformed. To test differences in sedimentary carbon storage among areas (with site nested in area), among sites (within each area separately) and among sediment depths (also within each area separately), one-way ANOVA was used. For the analysis across areas and among sites the carbon content was analyzed as a mean (% C) or amount of

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carbon per unit area (g C m^{-2}) for the top 25 cm of sediment. In those cases, where the ANOVA models were significant, Tukey's HSD post hoc test was used to determine significant differences between specific areas, sites and sediment depths, respectively. Partial Least Square (PLS) regression technique (by modeling of projections of latent structures; Wold et al., 2001) and Principal Component Analysis (PCA) were used to test the influence of sediment characteristics, water depth and seagrass-related variables on sediment carbon content (mean % C for the top 25 cm of sediment). The advantage of using PLS model is that it can handle collinear explanatory data as well as a large number of predictors.

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3. Results

3.1 Variation in sedimentary carbon storage

All areas, except Sozopol and Askö, were significantly different from each other in terms of % C_{org} ($P < 0.001$) and g C cm^{-2} ($P < 0.05$; Fig. 2). The highest amount of sedimentary carbon was seen in the Gullmar Fjord (on average ± SE, 2.79 ± 0.50 % C_{org} at 0-25 cm), followed by Ria Formosa (0.61 ± 0.09), Askö (0.18 ± 0.01) and Sozopol (0.17 ± 0.02). There was a within-area variation in carbon storage of the seagrass sites in Gullmar Fjord, Sozopol and Askö, while the sites at Ria Formosa did not differ from each other (Fig. 2; Table 2). There were clear within-area differences in both % C_{org} and g C cm^{-2} between seagrass sites in the Gullmar Fjord as well as between sites in Sozopol (Fig. 2, Table 2). At Askö the seagrass site Torö (T) differed from Storsand (S) and Långskär (L) in g C cm^{-2} but only to Storsand (S) in % C_{org}, while Storsand (S) and Långskär (L) were not significantly different from each other in any regards (Table 2). Both sites in the Gullmar Fjord and at Ria Formosa showed significantly higher carbon storage (% C_{org} and g C cm^{-2}) compared to their respective unvegetated areas ($P < 0.05$; Table 2). This was also seen in both sites at Sozopol in terms of % C_{org} but Gradina (G) did not differ in g C cm^{-2} compared to Bay of Sozopol (SB, unvegetated area; Table 2). All sites at Askö differed to one of the two unvegetated areas, Godahoppsudden (Gh), but not to Torö (Tr, unvegetated area), which was significantly higher in gC cm^{-2} compared to Långskär (L) and Storsand (S).

The percentage sedimentary carbon decreased with depth in Ria Formosa ($P < 0.001$) and Askö ($P < 0.05$) while not in the Gullmar Fjord and Sozopol (Fig. 3). For unvegetated areas the organic carbon decreased with sediment depth in Ria Formosa and Askö ($P < 0.001$), while it increased in the Gullmar Fjord ($P < 0.05$) and was unaffected in Sozopol.

3.2 Influence of sediment characteristics and seagrass-associated variables on carbon storage

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When the relationship between % C_{org} and explanatory variables (Tables 2, 3 and 4) was examined in a PLS (Partial least square) regression model the sediment characteristics explained most of the model (with a variance of importance value >1) where the proportion of sediment particles <0.074 mm (%) was the most important, followed by sediment porosity (%), sediment density (g DW mL^{-1}) and mean grain size (ϕ) (Fig. 4). These variables characterizing the sediment were all positively correlated to % C_{org} except sediment density that showed a negative relationship with % C_{org}. The cumulative fraction explaining the % C_{org} variation (R_y^2 cum) of the predictor variables combined was 0.81 and the models cross-validated variance (Q^2 statistics) showed high predictability with Q^2-value of 0.79, thus larger than the significant level of 0.05. The results of the model with g C cm^{-2} (not shown here) as response variable were highly similar to the results of % C_{org} (Q^2 = 0.77, R_y^2 cum = 0.78) with the same predictor variables (i.e. sediment characteristics) explaining most of the % C_{org} variation and correlated in the same way. All seagrass-associated variables showed a positive relationship with % C_{org} except for belowground (Bg) biomass N (%), which was the least influential variable in the model. In general, the seagrass-associated variables showed a lower contribution to the overall model compared to the sediment characteristics. Water depth (m) was also negatively correlated to % C_{org} but was, as with the seagrass-associated variables, of minor importance (Fig. 4).

Mean grain size (ϕ) and sediment particles < 0.074 mm (%) both showed strong positive linear relationship with % C_{org} in *Z. marina* meadows (mean phi (ϕ), $R^2 = 0.74$, $P < 0.001$; sediment particles < 0.074 mm (%), $R^2 = 0.91$, $P < 0.001$; Fig. 5a and b). For unvegetated areas, mean grain size (ϕ) did not show any relationship with % C_{org} but was positively related to sediment particles <0.074 mm (%) (linear regression, $R^2 = 0.42$, $P < 0.001$; Fig. 5c and d). The sediment density (g DW mL^{-1}) had a negative effect on % C_{org} in the seagrass sites (linear regression, $R^2 = 0.84$, $P < 0.001$) and sediment porosity (%) was positively related to % C_{org} (linear regression, $R^2 = 0.80$, $P < 0.001$; Fig. 6a and b). There was no significant relationship between % C_{org} and sediment density (g DW mL^{-1}) in unvegetated areas while sediment porosity (%) was significantly influencing % C_{org} but showed a low R_2-value (linear regression, $R^2 = 0.08$, $P < 0.001$; Fig. S2).

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The sedimentary organic carbon content relationship to the different predictor variables was not uniform among sites. In a PCA model, the Gullmar Fjord and Ria Formosa were grouped separately from other sites, while the Baltic- and Black Seas sites overlapped each other (Fig. 7). For the fine grain size seagrass sites of the Gullmar Fjord (Table 4), the sediment characteristics (i.e. sediment particles <0.074 mm (%), sediment porosity (%) and mean grain size (ϕ)) were important for the carbon content while the sedimentary carbon in Ria Formosa was more related to seagrass cover (%) and dry weight belowground biomass (m^2). The sedimentary organic carbon content in seagrass sites in Baltic- and Black Seas were also more related to the seagrass-associated variables, such as dry weight aboveground biomass (m^2) and shoot density (m^2), but also water depth (m) for one of the sites (Storsand, S).

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4. Discussion

In this assessment of four *Z. marina* areas in Europe, we found a large variation in organic carbon storage where the carbon-rich sediment of the Gullmar Fjord on the Swedish west coast where 15 times higher compared to levels in the Baltic- and Black Seas. The mean carbon content of the Gullmar Fjord was also higher than estimated global averages (Fourqurean et al., 2012; Kennedy et al., 2010), demonstrating the high carbon capacity of the area. Along with recent studies (Lavery et al., 2013; Samper-Villarreal et al., 2016), this study shows that the environmental conditions play an essential role in determining the carbon sink capacity. Here we demonstrate that sediment characteristics influence carbon storage in *Z. marina* meadows, where fine grain size, high sediment porosity and low sediment density correspond with high sedimentary organic carbon content. Seagrass meadows situated in areas characterized by these sediment properties are therefore suggested to have a high potential as natural carbon sinks.

Variation in sedimentary carbon content was also seen on a local scale where most of the sites differed from each other (except for Ria Formosa and two of the sites at Askö) demonstrating that the local variability in carbon storage is as high as the regional-based variation. Most of the sites, with the exception of the seagrass meadows with the lowest carbon storage, showed higher carbon content than nearby unvegetated areas, which illustrates just as previous studies have shown (e.g. Kennedy *et al.* 2010; Mcleod *et al.* 2011), that the seagrass ecosystem is a significant carbon sink. In general, carbon content in seagrass meadows decreases logarithmically with sediment depth (Fourqurean et al., 2012) due to degradation and remineralization of organic material with time (Burdige, 2007; Henrichs, 1992), a pattern seen in two of the study areas, Ria Formosa and Askö. The Gullmar Fjord and Sozopol did not show decreasing carbon content with sediment depth, which could be due to a slower degradation of organic matter in the sediment. Finer grain sizes in combination with high organic matter and nutrient content, as seen in the Gullmar Fjord sites, could cause a depletion of oxygen in the sediment because of increased oxygen consumption by detritus organisms and decreased permeability (Pollard and Moriarty, 1991; Wilson et al., 2008), which slows down the degradation process of organic matter. Sozopol, however, does not show such sediment characteristics but the stable carbon content with depth might be because the Ropotamo site was situated close to a river mouth with an input of terrestrial organic matter with a higher lignin content resulting in more decay-resistant carbon and a slower decomposition (Cowie and Hedges, 1984; Ertel and Hedges, 1985).

A high carbon content in *Zostera marina* sediment seems to be related to the sediment characteristics of the area. A high proportion of finer grain size particles leads to preservation and accumulation of organic matter (Keil et al., 1994; Mayer, 1994a, 1994b), which also explains the strong correlation between finer grain size content and sedimentary carbon seen in our study. Sediment grain size has recently been described as a strong predictor for carbon storage in another blue carbon habitat, i.e. saltmarshes (Kelleway et al., 2016). For seagrass meadows, sediment grain size has shown to have little influence on sedimentary carbon content (Samper-Villarreal *et al.* 2016), except for sediment with a high proportion of finer particle sizes (Serrano *et al.* in review). Also in the present study the proportion of fine sediment particles was strongly coupled to a high carbon content. The grain size is directly linked to the sediment porosity and density where the organic carbon has a negative effect on sediment density (Avnimelech et al., 2001; Gullström et al. submitted). This was also seen in our study as higher sedimentary carbon values were found in areas with lower sediment density (and hence higher porosity). For these reasons, we suggest that sediment characteristics of the area where *Z. marina* meadows are situated is relevant for revealing the carbon storage potential. For example, the *Z. marina* meadows at Askö are usually found on coarser sand and in more exposed areas whereas the most sheltered bays with finer grain sizes are dominated by brackish water plants, such as *Potamogeton pectinatus* and *Zannichellia palustris* (Idestam-Almquist, 2000), which might explain the low carbon storage potential of the area. A high organic content in the sediment could, however, cause a depletion of oxygen (Holmer, 1999) and at too low oxygen levels seagrass can no longer maintain the aerobic conditions of the rhizosphere, eventually leading to seagrass mortality (Terrados et al., 1999) with consequences for the carbon storage capacity. The seagrasses could adapt to lower oxygen concentrations by reducing the shoot density (Folmer et al., 2012) and thereby lower the oxygen demand of the root-rhizome system, which may explain why the areas with high proportion of fine grain size particles in this study had the lowest shoot density. High canopy height, high shoot density and shallow depths are generally considered

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to increase sedimentation rates and thus promote accumulation of finer grain size particles (Bos et al., 2007; Fonseca and Cahalan, 1992; Peralta et al., 2008). This implies that aboveground seagrass structure and water depth should influence the sediment carbon storage, however, in our study these variables were of minor influence. The influence of seagrass meadow structure on sediment composition is complex and hard to predict, and may be highly influenced by environmental conditions (van Katwijk et al., 2010).

The carbon storage in *Z. marina* meadows in our study were clearly related to sediments with high proportion of fine grain size particles, high porosity and low density. In areas without these sediment properties other variables, i.e. above- and below-ground seagrass biomass, seagrass cover and shoot density, have an influence. For example, the influence of belowground biomass and seagrass cover on sedimentary carbon content in Ria Formosa could be due to the stabilizing properties of dense meadows (Suykerbuyk et al., 2015), the binding of sediment by the root-rhizome system (Christianen et al., 2013) and the high lignin content of the belowground biomass (Klap et al., 2000).

The continuous loss of seagrass areas (Waycott et al., 2009) leads to a decline in natural carbon sinks (Dahl et al., 2016; Marbà et al., 2015), and to ensure efficient management factors for high carbon storage capacity should be evaluated. Several environmental and seagrass-related factors have shown to be of importance, i.e. water depth (Serrano et al., 2014), meadow size (Ricart et al., 2015), hydrodynamics and seagrass canopy complexity (Samper-Villarreal et al., 2016). In our study, the main factors related to high carbon storage were the sediment density and porosity, and amount of fine grain size particles in the sediment, whereas the seagrass-associated variables had a minor influence. Therefore, we highlight that the sediment characteristics is an important factor for a high carbon storage potential in these types of *Z. marina* meadows, and should be taking into consideration when evaluating high priority areas for protection of efficient carbon storage *Z. marina* areas.

Data availability

All data is presented in the manuscript and supplementary figures. Figure S1, shows the variance of importance (VIP) for the response variables in the PLS model (see Fig. 4). Figure S2, semi-log plots showing the relationship between sediment porosity and density, and sedimentary organic carbon for unvegetated areas.

Author contribution

The design of this study was carried out by Martin Dahl, Martin Gullström, Mats Björk and Diana Deyanova. The collection of data was done by Martin Dahl, Diana Deyanova, Liberatus D. Lyimo, Martin Gullström, Maria E. Asplund and Ventzislav Karamfilov, and was analyzed by Martin Dahl, Martin Gullström, Mats Björk, Silvia Gütschow and Maria E. Asplund. Martin Dahl prepared the manuscript with contribution from Martin Gullström, Mats Björk, Maria E. Asplund, Diana Deyanova, Ventzislav Karamfilov, Silvia Gütschow and Rui Santos.

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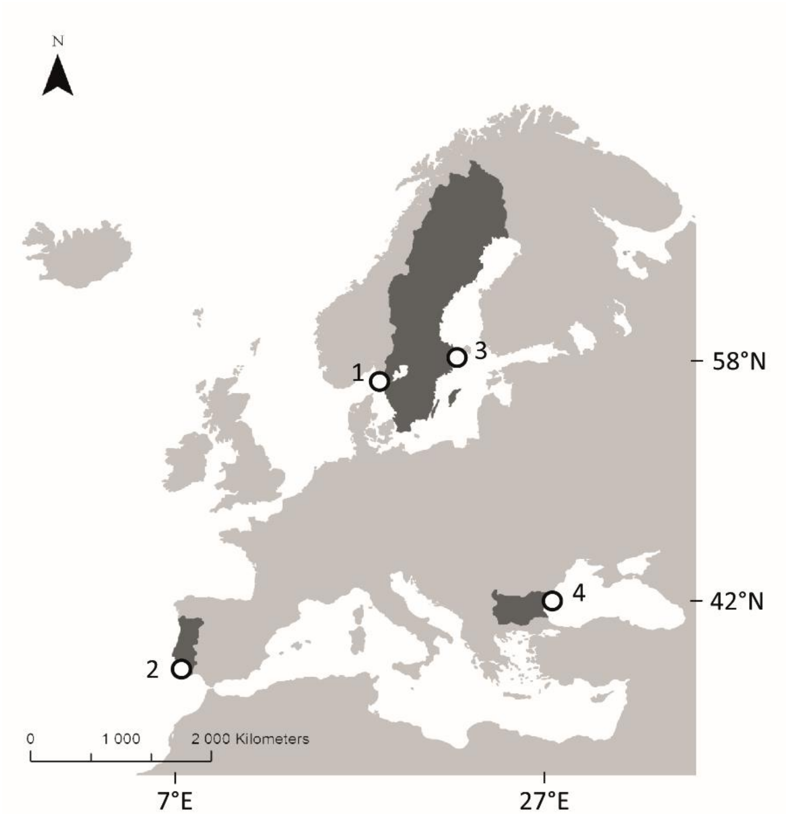

Figure 1. The four study regions, Gullmar Fjord (Skagerrak, Sweden) (1), Ria Formosa (gulf of Cádiz, Portugal) (2), Askö (Baltic Sea, Sweden) (3) and Sozopol (Black Sea, Bulgaria) (4).

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Table 1. Description of study sites in the four areas of Europe.

Area	Site	Vegetation	Coordinates	Mean depth (m)
Gullmar Fjord (Skagerrak, Sweden)				
	Finnsbo (F)	*Z marina*	58°17'55N, 11°29'34E	2.8
	Kristineberg (K)	*Z. marina*	58°14'53N, 11°26'51E	3.0
	Rödberget (Rö) (r)	Unvegetated	58°15'06N, 11°27'54E	2.5
Ria Formosa (gulf of Cádiz, Portugal)[1]				
	Culatra channel (C)	*Z. marina/ C. nodosa*	37°00'14N 7°49'36W	1.9
	Ilha da Culatra (I)	*Z. marina*	36°59'50N, 7°49'41W	1.0
	Culatra channel (Cr) (r)	Unvegetated	37°00'15N, 7°49'33W	2.6
	Ilha da Culatra (Ir) (r)	Unvegetated	36°59'51N, 7°49'40W	1.8
Askö (Baltic Sea, Sweden)				
	Torö (T)	*Z. marina/R. maitima*	58°48'14N, 17°47'32E	3.2
	Långskär (L)	*Z. marina/R. maitima*	58°48'00N, 17°40'48E	2.2
	Storsand (S)	*Z. marina*	58°48'26N, 17°41'40E	3.8
	Torö (Tr) (r)	Unvegetated	58°48'21N, 17°47'31E	6
	Godahoppsudden (Gh) (r)	Unvegetated	58°48'09N, 17°42'24E	2.9
Sozopol (Black Sea, Bulgaria)				
	Ropotamo (Rt)	*Z. marina/ Z. noltii*	42°19'49N, 27°45'20E	2.7
	Gradina (G)	*Z. marina/ Z. noltii*	42°25'39N, 27°39'05E	4.2
	Bay of Sozopol (r)	Unvegetated	42°24'42N, 27°39'48E	5.7

r = reference site (unvegetated area)
[1]Depth values standardized to mean low water (MLW).

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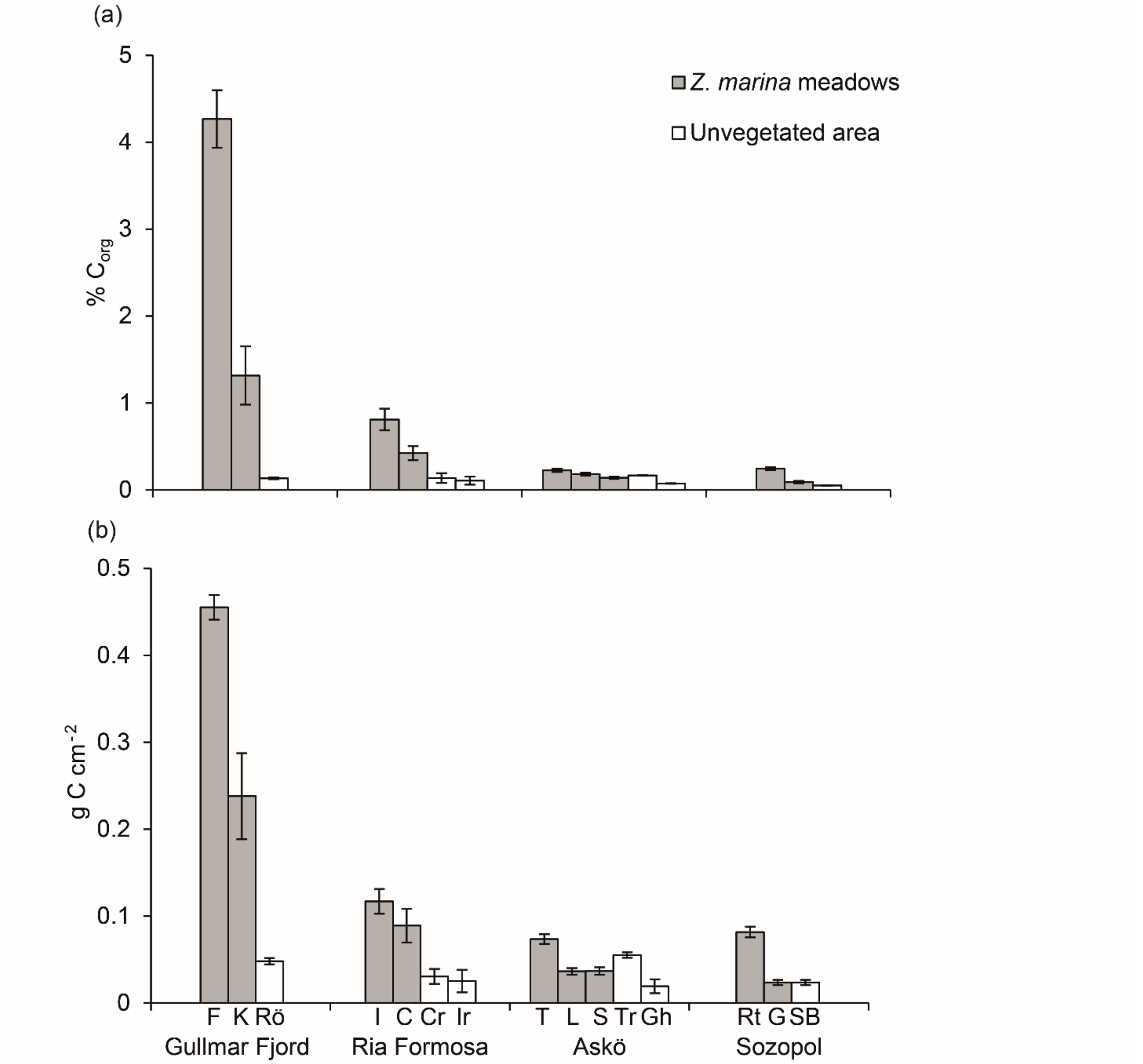

Figure 2. Mean (±SE) % C_{org} (a) and g C cm^{-2} (b) in sediment (for 0-25 cm sediment depth). The percent organic carbon (% C_{org}) is presented as a mean of the content of the top 25 cm sediment, while carbon per unit area (g C cm^{-2}) is the total (accumulated) amount of carbon in the top 25 cm of sediment. For full names of the sites see Table 1.

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Table 2. Summary of Tukey's post hoc tests from significant one-way ANOVA models for comparison of sedimentary carbon between sites within each area separately. The percent organic carbon (% C_{org}) is presented as a mean of the content of the top 25 cm sediment, while carbon per unit area (g C cm^{-2}) is the total (accumulated) amount of carbon in the top 25 cm of sediment. The full names of the sites are included in Table 1.

Area	Sites	% C_{org} *P*	g C cm^{-2} *P*
Gullmar Fjord			
	F vs. K	**<0.001**	**0.009**
	F vs. Rö (r)	**<0.001**	**<0.001**
	K vs. Rö (r)	**<0.001**	**<0.001**
Ria Formosa			
	I vs. C	ns	ns
	I vs Cr (r)	**<0.001**	**0.005**
	I vs. Ir (r)	**<0.001**	**<0.001**
	C vs. Cr (r)	**0.009**	**0.035**
	C vs. Ir (r)	**0.002**	**0.002**
Askö			
	T vs L	ns	**<0.001**
	T vs. S	**0.002**	**<0.001**
	T vs. Tr (r)	ns	ns
	T vs. Gh (r)	**<0.001**	**<0.001**
	L vs. S	ns	ns
	L vs. Tr (r)	ns	**0.021**
	L vs. Gh (r)	**<0.001**	**<0.001**
	S vs. Tr (r)	ns	**0.026**
	S vs. Gh (r)	**<0.001**	**<0.001**
Sozopol			
	R vs. G	**<0.001**	**<0.001**
	R vs. SB (r)	**<0.001**	**<0.001**
	G vs. SB (r)	**<0.001**	ns

r = reference site (unvegetated areas).

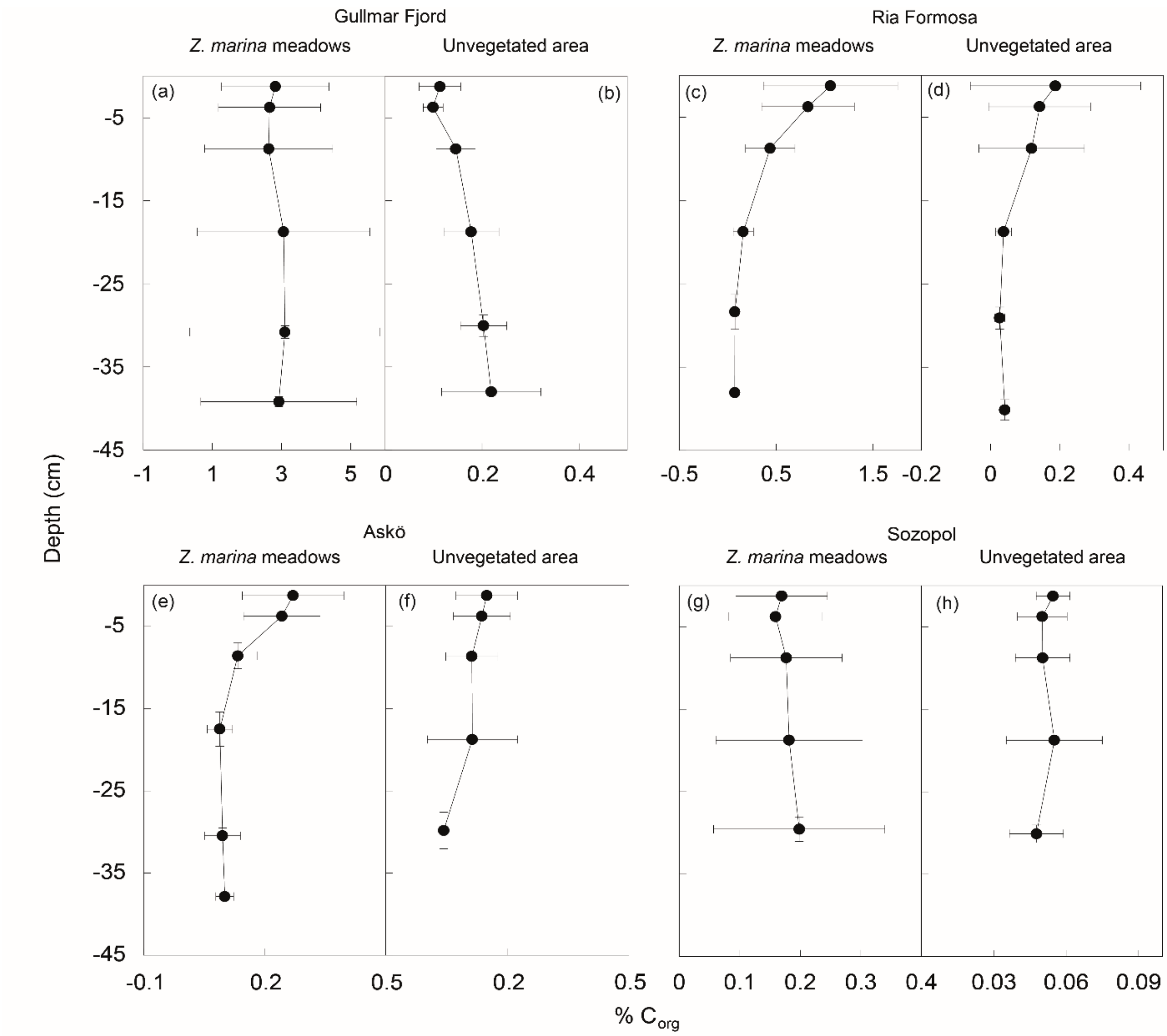

Figure 3. Mean sedimentary carbon (% C_{org} ± SD) depth profiles grouped for the different regions showed as mean slice depth. Note that the scale on the x-axes differs among the different depth profiles.

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Table 3. Seagrass meadow variables (mean ± SD) for the different regions.

Region	Shoot density (m^{-2})	Shoot height (cm)	Seagrass cover (%)	Aboveground biomass %C	Aboveground biomass %N	Aboveground biomass C:N	Aboveground biomass g DW m^{-2}	Belowground biomass %C	Belowground biomass %N	Belowground biomass C:N	Belowground biomass g DW m^{-2}
Gullmar Fjord	157.9 ± 43.8	81.4 ± 18.2	36.9 ± 14.0	38.8 ± 0.7	2.1 ± 0.3	18.4 ± 2.0	39.4 ± 31.1	34.2 ± 1.4	1.1 ± 0.1	30.2 ± 2.8	253.0 ± 86.0
Ria Formosa	264.9 ± 107.8	32.5 ± 4.4	79.1 ± 10.6	34.4 ± 1.2	1.4 ± 0.1	25.2 ± 1.2	108.3 ± 58.5	30.8 ± 3.2	1.1 ± 0.1	37.8 ± 4.5	494.2 ± 230.2
Askö	338.1 ± 160.3	51.7 ± 12.4	47.6 ± 18.1	37.2 ± 2.0	1.8 ± 0.3	20.9 ± 2.9	255.7 ± 193.4	32.8 ± 2.9	1.1 ± 0.1	31.5 ± 3.2	205.9 ± 88.7
Sozopol	419.6 ± 315.3	63.5 ± 11.2	63.5 ± 11.1	36.0 ± 1.3	1.9 ± 0.3	19.6 ± 3.2	122.0 ± 110.8	30.3 ± 3.0	0.8 ± 0.2	28.6 ± 5.7	86.4 ± 80.6

473 Table 4. Seagrass sediment data as mean (± SD) for the depth profile (0-25 cm) in the different regions. Mean grain size is
474 presented with phi (ϕ) units.

Region	Sediment porosity (%)	Sediment density (g DW mL^{-1})	% N	C:N	Mean grain size (ϕ)	Sediment particles <0.074 mm (%)
Gullmar Fjord	67.0 ± 14.1	0.71 ± 0.33	0.28 ± 0.16	9.39 ± 1.26	4.89 ± 0.93	62.8 ± 25.6
Ria Formosa	43.0 ± 5.4	1.13 ± 0.14	0.08 ± 0.01	7.15 ± 0.83	2.34 ± 0.56	17.9 ± 5.8
Askö	31.9 ± 2.4	1.4 ± 0.15	0.03 ± 0.01	5.60 ± 1.27	1.19 ± 0.79	3.7 ± 0.6
Sozopol	41.8 ± 5.2	1.25 ± 0.04	0.05 ± 0.04	3.22 ± 1.25	2.08 ± 0.27	2.6 ± 1.9

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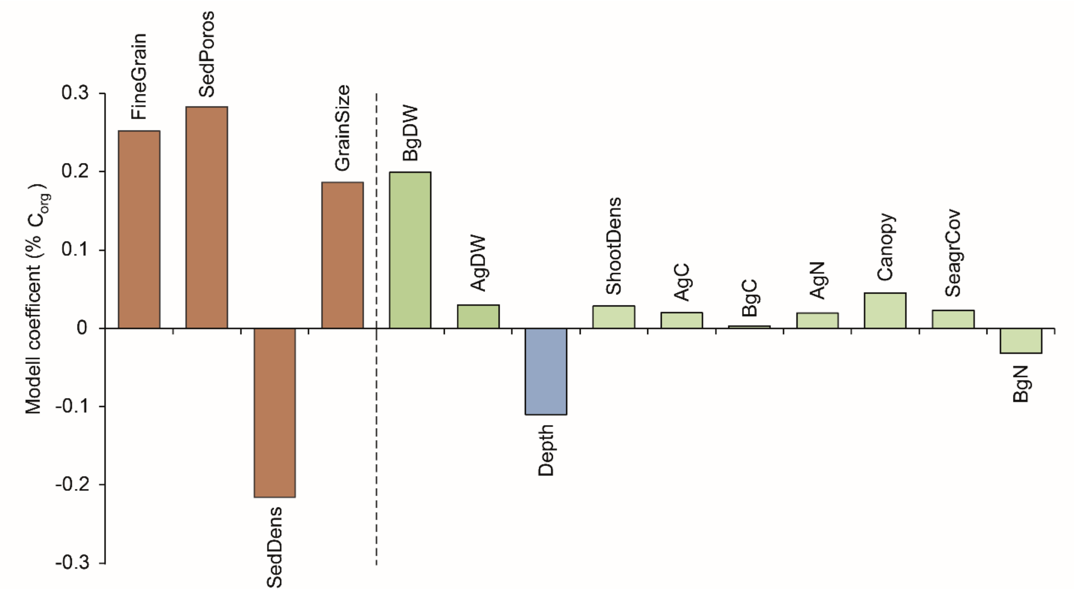

Figure 4. PLS (Partial Least Square) regression model coefficient plot for % C_{org} in sediment (using a mean of the carbon content for the top 25 cm sediment). The predictor variables are ranked in level of importance (left to right) where the four variables left of the striped bar having a VIP-value >1 (i.e. FineGrain, SedPoros, SedDens and GrainSize) and hence significantly influencing % C_{org}. Brown = sediment characteristics, green = seagrass-associated variables and blue = water depth; Variables included in the model were FineGrain (sediment particles <0.074 mm, %), SedPoros (sediment porosity, %), SedDens (sediment density, g DW mL^{-1}), GrainSize (mean grain size, ϕ), Bg and Ag DW (belowground biomass dry weight, m^2), Depth (water depth, m), ShootDens (shoot density, m^2), Ag and Bg biomass C and N (biomass carbon and nitrogen content, %), Canopy (shoot height, cm) and SeagrCov (seagrass cover, %).

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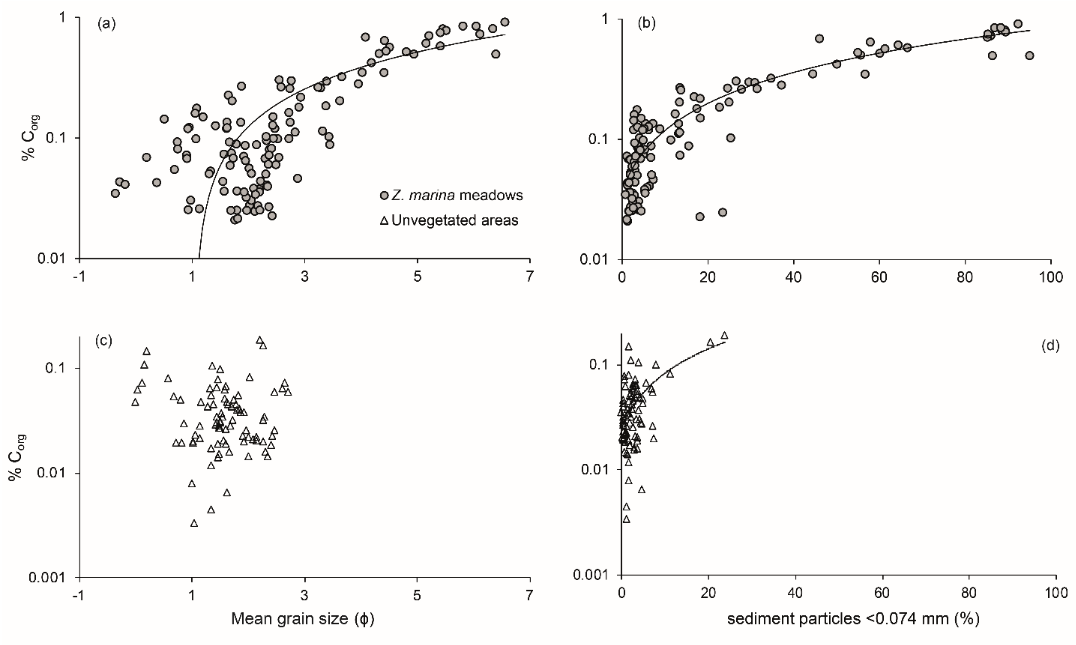

Figure 5. Semi-log plots ($\log_{10}[x+1]$) showing the relationship between % C_{org} and grain size. The % C_{org} is presented with a log scale as it gave the best fit of the models. Grain size is shown as mean grain size (ϕ) and sediment particles <0.074 mm (%) for *Z. marina* meadows (a and b) and unvegetated areas (c and d). The % C_{org} was positively linked to both sediment particles <0.074 mm (%) ($R^2 = 0.91$, $P < 0.001$) and mean grain size (ϕ) ($R^2 = 0.74$, $P < 0.001$) for *Z. marina* meadows but for unvegetated area only sediment particles < 0.074 mm (%) showed this relationship with % C_{org} ($R^2 = 0.42$, $P < 0.001$).

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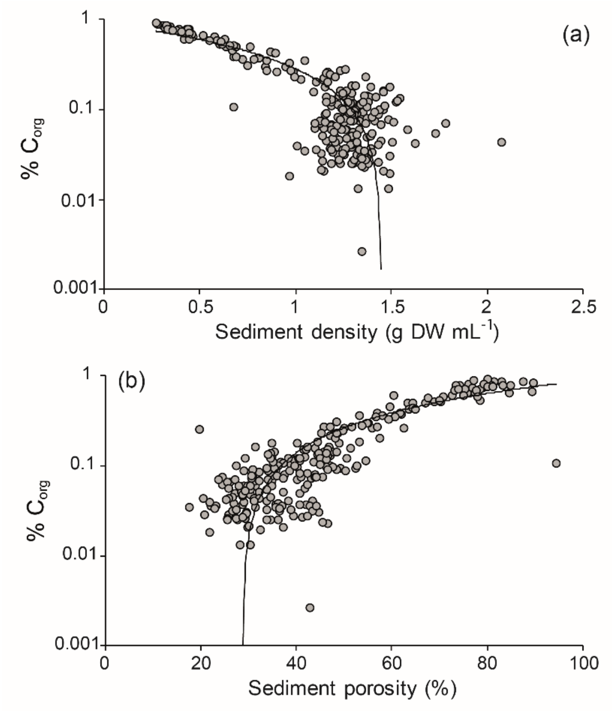

Figure 6. Semi-log plots ($\log_{10}[x+1]$) for sediment density (a) and sediment porosity (b) in relation to % C_{org} for the *Z. marina* sites. The sediment density (g DW mL^{-1}) was negatively influencing the amount of organic carbon ($R^2 = 0.84$, $P < 0.001$), while there was a positive relation between sediment porosity (%) and % C_{org} ($R^2 = 0.80$, $P < 0.001$).

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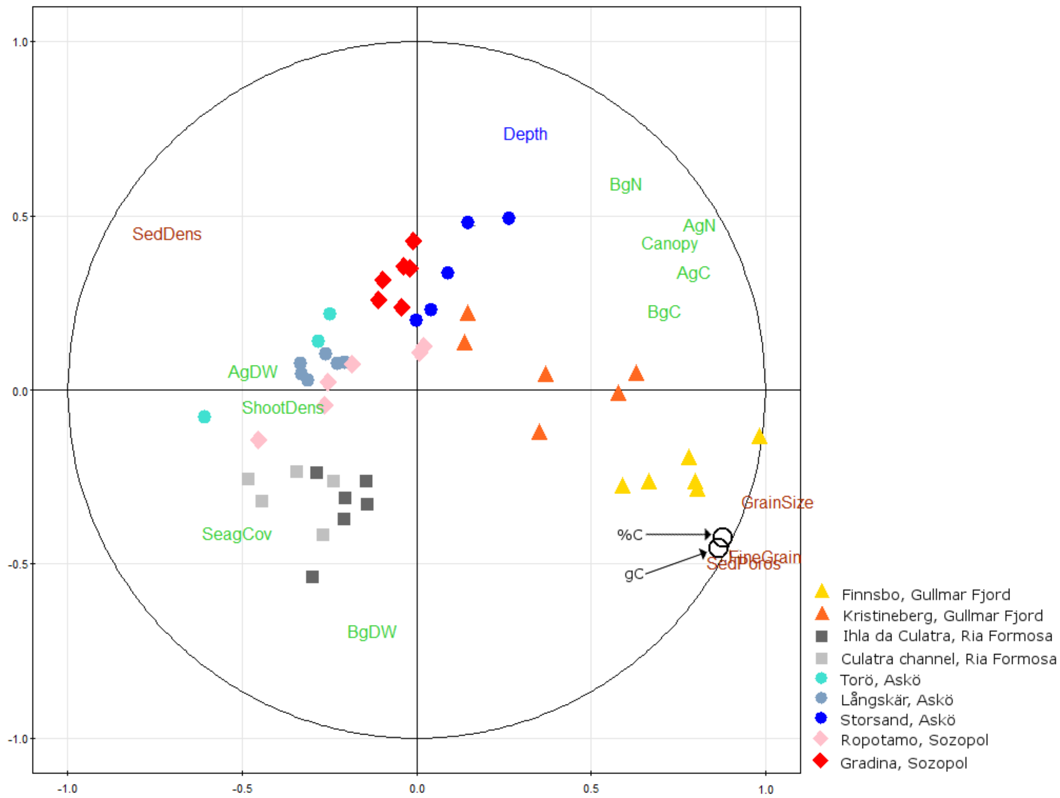

Figure 7. PCA (Principal Component Analysis) showing the nine seagrass sites, the two response variables (sedimentary % C_{org} and g C cm^{-2}) and predictor variables (14 in total). The percent organic carbon (% C_{org}) is presented as a mean of the content of the top 25 cm sediment, while carbon per unit area (g C cm^{-2}) is the total (accumulated) amount of carbon in the top 25 cm of sediment. The colors of the letters represent different groups of predictor variables; brown = sediment characteristics, green = seagrass-associated variables, blue = water depth. Black circles are the response variables, i.e. organic carbon (%C = % C_{org} and gC = g C cm^{-2}). For explanations to the abbreviations of predictor variables see Fig. 4.