Blue carbon stocks in Baltic Sea eelgrass (*Zostera marina*) meadows

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Abstract

Although seagrasses cover only a minor fraction of the ocean seafloor, their carbon sink capacity accounts for nearly one-fifth of the total oceanic carbon burial and thus play a critical structural and functional role in many coastal ecosystems. We sampled 10 eelgrass (*Zostera marina*) meadows in Finland and 10 in Denmark to explore seagrass carbon stocks (Corg stock) and carbon accumulation rates (Corg accumulation) in the Baltic Sea area. The study sites represent a gradient from sheltered to exposed locations in both regions to reflect expected minimum and maximum stocks and accumulation. The Corg stock integrated over the top 25 cm of the sediment averaged 627g C m^{-2} in Finland, while in Denmark the average Corg stock was over six times higher (4324 g C m^{-2}). A conservative estimate of the total organic carbon pool in the regions ranged between 6.98-44.9 t ha^{-1}. Our results suggest that the Finnish eelgrass meadows are minor carbon sinks compared to the Danish meadows, and that majority of the Corg produced in the Finnish meadows is exported. Similarly, the areal estimates for Corg accumulation in eelgrass meadows (30 km^2) in Finland (< 0.002- 0.033 t C y^{-1}) were over two orders of magnitude lower compared to Denmark (673 km^2; 0.376-3.636 Corg t y^{-1}). Our analysis further showed that > 40 % of the variation in the Corg stocks was explained by sediment characteristics i.e. density, porosity and silt content. In addition, the distance based linear model (DistLm) analysis showed, that the root: shoot- ratio of *Z. marina* explained > 12 % and contribution of *Z. marina* detritus to the sediment surface Corg pool >10 % of the variation in the Corg stocks, whereas annual eelgrass production explained additional 2.3 %. The mean monetary value for the present carbon storage and carbon sink capacity of eelgrass meadows in Finland and Denmark, were 281 and 1809 € ha^{-1}, respectively. For a more comprehensive picture of seagrass carbon storage capacity, we conclude that future Blue Carbon studies should in a more integrative way, investigate the role of sediment biogeochemistry, seascape structure, plant species architecture and hydrodynamic regime.

Keywords: Blue Carbon, eelgrass, seagrass, carbon stock, carbon accumulation, sequestration, carbon sink

Introduction

The atmospheric carbon dioxide (CO$_2$) enters the ocean via gas-exchange processes at the ocean-atmosphere interface. In the ocean dissolved inorganic carbon is fixed in photosynthesis by primary producers, and released again through respiration. A large percentage of this fixed carbon is stored and sequestered in the sediments of vegetated coastal ecosystems of which the three globally most significant are saltmarshes, mangrove forests and seagrass meadows (Herr et al. 2012). The carbon stored by these ecosystems is known as Blue Carbon (Duarte et al. 2005 Duarte et al. 2013a, Nellemann et al. 2009). Blue Carbon ecosystems function as carbon sinks, in which the rate of carbon sequestered by the ecosystem exceeds the rate of carbon lost through respiration and export.

Seagrass meadows play a critical structural and functional role in many coastal ecosystems (Orth et al. 2006). Although seagrass meadows only cover globally about 300 000 - 600 000 km^2 of the ocean sea floor, corresponding to 0.1 to 0.2 % of the total area, their carbon sink capacity (capacity of seagrasses to absorb and store carbon in living and dead biomass and in the sediments) may account for up to 18 % of the total oceanic carbon burial (Gattuso et al.1998, Duarte et al. 2005, Kennedy et al. 2010, Fourqurean et al. 2012). A large portion of the carbon sequestered (captured and stored) by seagrasses reach a conservative value of 10 Pg C in the top 1 meter of seagrass sediments (Fourqurean et al. 2012). Consequently, recent global estimates imply that seagrass sediments store almost 25 200-84 000 t C km^2 (Fourqurean et al. 2012). More importantly, carbon in submerged sediments is stored for timescales of millennia while terrestrial soils are usually less stable and only sequester carbon up to decades (Hendriks et al. 2008).

The coasts of Scandinavia and the Baltic Sea are key distribution area for eelgrass (*Zostera marina* L.) meadows (Boström et al. 2002, Boström et al. 2014). The meadows extend from the fully saline (>30) along the Norwegian coast to the brackish (5-6) archipelago areas of Finland. This region is estimated to support >6 000 individual meadows covering at least 1 500 – 2 000 km^2, which is four times more than the combined eelgrass area of the Western Europe (Spalding et al. 2003, Boström et al. 2014). Consequently, this region plays a key role in the coastal carbon dynamics, but we presently lack estimates of the role of eelgrass for carbon storage in temperate eelgrass sediments. Seagrasses are lost at accelerating rates and it has been estimated that 29 % of global seagrass area has disappeared since the initial recording of seagrasses in 1879 (Waycott et al. 2009). This decline could have severe consequences on the total capacity of marine ecosystems to store and sequester carbon in addition to the other ecosystem services seagrass meadows provide. Little is known about the magnitude of carbon emissions from degraded seagrasses ecosystems, not to mention its economic implications. Recent study points out, that despite the importance of these ecosystems to the global carbon budget, none of the three Blue Carbon ecosystems have been included the global carbon market protocols (Pendleton et al. 2012).

Seagrasses exhibit marked differences in shoot architecture and grow under variable environmental settings, making direct extrapolations between species and locations difficult. Consequently, there is a pressing need to better understand which factors are causing variability in carbon storage (carbon stored in living and dead seagrass biomass and sediments) and accumulation rates (Corg accumulation) in seagrass sediments. Indeed, recent studies show considerable influence of seagrass habitat setting, sediment characteristics and species-specific traits on the variability in carbon storage capacity in seagrass meadows (Duarte et al. 2013a, Lavery et al. 2013, Miyajima et al. 2015). Such differences contribute to uncertainty in local and global estimates of the carbon storage capacity and carbon dynamics in coastal seagrass areas.

In order to determine seagrass carbon stocks (Corg stocks) and the capacity of seagrass meadows to sequester carbon (Corg accumulation), knowledge on the sources of the carbon stored in the sediments is also crucial. The different Corg sources vary in their turnover compared to seagrasses (sources other than seagrasses being typically faster) and volumes of standing stock (typically less) and thus affect the dynamics of the Corg stocks and accumulation (Fry et al. 1977, Kennedy et al. 2004, Kennedy et al. 2010).Seagrasses are known to be enriched in δ^{13}C compared to other potentially sources of Corg in the seagrass sediments, such as plankton, macroalgae, allochtonous carbon material, seagrass epiphytes, and benthic microalgae (Kennedy et al. 2004, Kennedy et al. 2010, Fry and Sherr 1984, Moncreiff and Sullivan 2001, Bouillon et al. 2002, Bouillon and Boschker 2006, Macreadie et al. 2014). Thus, the stable isotope signals of seagrasses and other potential Corg sources can be relatively easily and reliably used as a proxy for identification of the origin of Corg in seagrass sediment carbon pool (Kennedy et al. 2010).Unfortunately, the current knowledge base on how these factors interact and influence carbon fluxes and storage is, at best, limited at both local and global scales.

In this study, we contrast storage, burial rates and sources of the accumulated carbon in eelgrass meadows in two regions differing in salinity, temperature and seagrass productivity, namely Finland and Denmark. Specifically we asked; (1) How large is the carbon storage capacity (Corg stocks) of Baltic Sea eelgrass meadows? (2) Which are the environmental factors determining the variability of carbon storage (Corg stocks) and accumulation (Corg accumulation) at local and regional scales? (3) How do the sediment characteristics influence the carbon storage (Corg stocks) of eelgrass meadows at local and regional scales? (4) How much carbon (Corg stocks) is presently stored in Finnish and Danish eelgrass meadows respectively and (5) what is the present and historical lost (Denmark) monetary carbon value?

Materials and methods

Study area

Plant and sediment samples were collected in June-September 2014 from 10 sites in Finland (The Archipelago Sea) and 10 sites in Denmark (Funen and Limfjorden) (Fig. 1). The Baltic Sea sediments are typically mineral sediments consisting of glaciofluvial deposits and only a small fraction of the sediment carbon content consists of carbonates (Kristensen and Andersen 1987). The inorganic carbon content in our samples was low (0.5 to 5 % inorganic carbon of total carbon content, n= 10 per region) and therefore carbonates were not removed from the sediment samples prior to the analysis to avoid analytical errors in low organic samples (Schlacher and Connolly 2014). The study sites in each region spanned a gradient from sheltered to exposed areas. The Archipelago Sea of southwestern Finland is a shallow (mean depth 23 m), brackish (salinity 5-6) coastal area characterized by a complex mosaic of some 30.000 islands and skerries (Boström et al. 2006, Downie et al. 2013). The region is heavily influenced by human pressures, especially eutrophication, and exhibits naturally steep environmental gradients, as well as, strong seasonality in temperature and productivity (Boström et al. 2014).

Limfjorden is a brackish water area in the Jutland peninsula connected to both North Sea and Kattegat with salinity ranging from 17 to 35. The Fjord has a surface area of ~1500 km^2 and a mean depth of 4.7 m (Olesen and Sandjensen 1994, Wiles et al. 2006, Petersen et al. 2013). Funen is located between the Belt Seas in the transition zone where waters from Baltic Sea and Kattegat meet. The salinity of the area ranges between 10 and 25 and the annual mean water temperature ranges from 10-15° C (Rask et al. 1999). This study was conducted in shallow (< 10 m) fjords around Funen. Also the Danish areas are heavily influenced by human pressures, especially eutrophication from intense agricultural farming. (DMU; Danmarks Miljøundersøgelser, 2003).

Field sampling

All samples were collected from depths of 2.5-3 m by scuba diving. At all sites, three replicate sediment cores (corer: length: 50 cm, diameter: 50 mm) were taken randomly at a minimum distance of 5 m from each other. The corer was manually forced to a depth of 30-40 cm. The cores were capped in both ends under water, and kept in a vertical position during transport to the laboratory. Eelgrass production and biomass were measured at all sites from four randomly chosen locations within the eelgrass meadow. To insure statistical independence, each replicate core was separated by distance of at least 15 m within the meadow. In the vicinity of each sediment core, shoot density was counted using a 0.25 m^2 frame, and above- and belowground biomass samples were collected with a corer (diameter 19.7 cm) and bagged underwater. Sedimentation was measured at one exposed and one sheltered site in each region by deploying two sediment traps with five replicate collection tubes (length: 115 mm, diameter: 28 mm). Traps were positioned at a level corresponding to the upper canopy at a water depth of 2.5 m for

2 days. Additionally, when present, samples of plants and algae (drift algae, other angiosperms, phytoplankton and epiphytes) considered most likely to be carbon sources in the eelgrass meadows were collected from each site for identification and analysis of stable isotope composition. Approximately ~ 10 g wet material was collected for each species. Annual eelgrass production was determined from estimates of previous growth by applying the horizontal rhizome elongation technique (Short and Duarte 2001). From each site, five replicate rhizome samples with the longest possible intact rhizome carefully removed, were collected and transported to the laboratory for further analysis.

Seagrass variables

In the laboratory, the above- and belowground biomass was separated and eelgrass leaves and rhizomes were cleaned from epiphytes, detritus and fauna with freshwater and gently scrubbed with a scalpel. All plant material was dried to constant weight (48 h in 60° C). The belowground biomass was separated into living and dead rhizomes and dried separately. Only the living rhizomes were used for the belowground biomass measurements while samples of both living and dead rhizomes were used for analysis of POC and $\delta^{13}C$. The root: shoot-ratio was calculated as the ratio between below- and aboveground biomasses of *Z. marina* samples. A pooled sample of 2 youngest leaves from 10 randomly selected shoots were collected prior to drying from the aboveground biomass samples and dried separately for analysis of particulate organic carbon (POC) and stable isotopic composition of the organic carbon ($\delta^{13}C$). All samples were analyzed by Thermo Scientific, delta V advantage, isotope ratio mass spectrometer. The measured isotope ratios were represented using the δ- notation with Vienna Peedee belemnite as reference material.

Determination of annual eelgrass production was done by measuring length of each individual internode of the rhizomes to the nearest millimeters. To obtain an estimate of the mean annual production per site, internode length measurements of individual replicates (n= 5) were pooled. Due to lack of two annual production peaks in both regions the annual production was estimated based on the distance between shortest and longest measured internodes, assuming that they represent the time point when the water temperature was at its minimum and maximum average, respectively. The time points for the water temperatures were obtained from databases of the Finnish and Danish Meteorological Institutes, respectively.

Sediment variables and sedimentation

In the laboratory, sediment samples were sliced into sections of 2-5 cm, where the upper 10 cm layer was divided into 2 cm layers and the remaining part in 5 cm layers. From each subsample visible plant parts and fauna were removed before the sediment was homogenized. From the 0-2 cm section a subsample of 20 ml was taken for grain size analysis by a Malvern Mastersizer 3000 particle size analyzer. The sediment silt content was calculated as the fraction with particle size of 2-63 μm from the range of all particle sizes (Folk and Ward 1957). Sediment water content, dry bulk density and porosity were determined from a subsample of 5 ml that was taken using a cut-off 5 ml syringe and weighed before and after drying at 105°C for 6 h from all sediment layers. The dried sediment samples were homogenized in a mortar and divided into two subsamples from which one was used for analysis of sediment organic matter content (loss of ignition: 4 h in 520°C), and the other for analysis of sediment δ^{13} C and POC as described above for the plant materials. Inorganic carbon content was low in sediments from both regions (0.003-0.3 %DW) and considered insignificant compared to the organic fraction (1-2 order of magnitude higher).

The material collected in the sediment traps was filtered on pre-weighed and combusted 50 mm GF/C filters (Whatman) and dried at 60°C for 24 hours. Dried filters were weighed and each filter was divided into two subsamples, one for analysis of organic matter content (LOI, 520°C, 4

h) and the other for $\delta^{13}C$ and POC as described above. Sedimentation rates were calculated according to Gacia et al. (1999).

Corg stock and Corg accumulation calculations

To estimate sediment Corg stock and Corg accumulation of Finnish and Danish eelgrass area we used averages from 10 sites in each two regions in our calculations. The mean Corg stock (obtained by depth integration of the POC mg C cm^{-3} of 0-25 cm sediment layers) of the sampled region was multiplied with estimated seagrass area of the region based on the most recent areal estimates of seagrass distribution available in the literature (Boström et al. 2014) and given as g Corg m^{-2}. In Denmark, the extrapolations are based on the minimum and maximum estimates of the areal extent, respectively (673 and 1345 km^2, (Boström et al. 2014)). Results for carbon burial (applied by multiplying the Corg stock, regional seagrass area and sediment accumulation rate estimate from literature) in each area are given as Corg accumulation (t y $^{-1}$). Due to lack of long term monitoring of sediment accumulation in eelgrass meadows, , we used available minimum, average and maximum sediment accumulation rates in seagrass meadows obtained from literature (Duarte et al. 2013b, Serrano et al. 2014, and Miyajima et al. 2015).

To calculate the total Corg pool in Danish and Finnish eelgrass sediments, we summed the following three components: (1) the annual eelgrass carbon sequestration rate (Corg accumulation in t C ha^{-1}y^{-1}) storage), (2) the total POC (t ha^{-1}) in the average living aboveground and belowground *Z. marina* tissue, and (3) the mean Corg stocks (t ha^{-1}) in eelgrass sediments in Denmark and Finland, respectively. To calculate the present and lost economic value of eelgrass carbon stocks, we used a value (40.3 €) based on the social cost of carbon with 3 % discount rate reported in the United States Government Technical Support Document (2010) and multiplied this value with the Corg stocks (tonnes). To estimate the Danish eelgrass losses over the past 100 years in economic terms, we used the calculations above, but accounted for the annually lost sequestration value by multiplying the rate by 100. We used the most recent loss estimates for Denmark for the period 1900-2000, assuming that the present coverage constitutes 10% or 20% of the historical area, respectively (Boström et al. 2014).

Sediment carbon sources

The Isosource 1.3 isotope mixing model software (Phillips and Gregg 2003) was used to estimate the contribution of different carbon sources to the sediment surface Corg stock. We ran the Isosource model using the $\delta^{13}C$ values obtained from stable isotope analysis of *Z. marina* leaves, living and dead rhizomes and for samples (n=1-5) of other abundant Corg sources within the meadow (see above) with increments of 1 % and tolerance of 0.1. Numbers are given as percentage contribution to the sediment surface carbon pool.

Data analysis

All statistical analyses were performed using the PRIMER 6 PERMANOVA+ package (Anderson et al. 2008). A 2-factor mixed model was used, where sampling sites and region (FIN, DEN) were used as fixed factors for the biological response variable (sediment organic carbon stock, g C m^{-2}). Prior to analysis, the environmental predictor variables (degree of sorting, sediment dry density, sediment water content, sediment porosity, sediment silt content, sediment organic content, annual production, root: shoot-ratio, shoot density and percentage of *Z. marina* detritus contribution to Corg) were visually inspected for collinearity using Draftsman plots of residuals. Due to autocorrelation between sediment variables (water content, and dry density) sediment water content was removed from the environmental variables. To achieve normality in the retained environmental variables, data was log-transformed (log(X+1) and Euclidean distance was used to calculate the resemblance matrix. The biological response variable (Corg stock in g m^{-2}) was square-root transformed and Bray-Curtis similarity was used to calculate the abundance matrix. The relative importance of different environmental variables was determined by use of DistLm, a distance-based linear model procedure (Legendre and Anderson 1999). DistLm model was constructed using a step-wise procedure that allows addition and removal of terms after each step of the model construction. AICc (Akaike Information Criterion with a correction for finite sample sizes) was chosen as information criterion as it enables to fit the best explanatory environmental variables from of relatively small biological dataset compared to number of environmental variables (Burnham and Anderson 2002). An alpha level of significance of 95% ($p<0.05$) was used for all the analysis. All means are reported as mean ± SE (SEM).

Results

Seagrass meadow and sediment characteristics

In general, the Finnish meadows were found on exposed sandy bottoms while the environmental settings of the eelgrass meadows in Denmark were more variable (Fig. 2). Shoot density was nearly equal in both regions, averaging at 417± 75 (shoots m^{-2}) in Finland and 418±32 (shoots m^{-2}) in Denmark. In Finland variation between sites (112-773 shoots m^{-2}) was greater than in Denmark (300-652 shoots m^{-2}). In Denmark the highest shoot density was found at the most exposed site (Nyborg), while in Finland the highest shoot density was found at Sackholm, a fairly sheltered site. The lowest shoot densities in Finland and Denmark were found in Tvärminne and Løgstør, respectively. The mean aboveground biomasses were 101±3 and 145±5 (g DW m^{-2}) and the mean belowground biomasses 79±5 and 148±13 g (DW m^{-2}) at Finnish and Danish sites, respectively. In Denmark, the mean proportion of POC in above-ground and below-ground *Z. marina* tissue was 35% and 29%, respectively, while the corresponding numbers for Finland were 38% and 36%, respectively. Given an average total *Z. marina* biomass (above- and belowground) of 293 (Denmark) and 180 g DW m^{-2} (Finland), we estimate the Corg pool in bound in living seagrass biomass to 0.94 and 0.66 t ha^{-1} in Denmark and Finland, respectively. Root: shoot-ratio was slightly lower in Finland (0.87±0.05) than in Denmark (1.14±0.12), and varied between 0.29 to 3.29 and 0.15 to 6.45 in Finland and Denmark, respectively. The annual production of eelgrass for Finland (average 524±62 g DW m^{-2} y^{-1}) showed relatively low variation between sites (270-803 g DW m^{-2} y^{-1}) being lowest at Jänisholm and highest at Ryssholmen. In Denmark, the mean annual eelgrass production rate was almost twice as high (928±159 g DW m^{-2} y^{-1}) with large variation (470-2172 g DW m^{-2} y^{-1}). Production rates were lowest and highest at Dalby and Visby, respectively (Table 1).

The sediment characteristics varied significantly between Finland and Denmark. There was a significant difference ($F_{1, 9}$ = 14.7, $p<0.003$) between regions in terms of silt content, which was generally lower at Finnish (6.3±1%) sites than at Danish sites (20.2±3.9%), although in Denmark the variation between sites ranged from 0.8% at Nyborg to 31.6% at Thurøbund (Table 1, Fig. 2). In Finland, the variation between sites was lower and ranged from 1.6% (Kolaviken) to 15.5% (Sackholm). At the Finnish sites the mean sediment dry density was higher (1.30±0.04 g cm^{-3}) compared to the Danish sites (1.1±0.1 g cm^{-3}), and the Finnish sites exhibited lower within-region variability ranging from 1.1 g cm^{-3} at Lyddaren to 1.5 cm^{-3} at Långören, while the Danish sites varied from 0.3 g cm^{-3} at Thurøbund to 1.5 g cm^{-3} at Visby. The Finnish sites showed consistently lower pools of organic matter (LOI: 1.4±0.3% DW) compared to the average of Danish sites (LOI: 3.9±1.5 %DW). Consequently, the mean water content was similarly lower in Finland (20.9±0.4%: range 16-29 %) than in Denmark (37.4±1.8 %: range 17-76 %) ranging from 16.4 to 29.5 % in Finland to 17.2 to 76.0 % in Denmark (Table 1). Sediment porosity was similar in both regions, and ranged from 0.25 to 0.3 in Finland, and from 0.20 to 0.40 in Denmark. At the Finnish sites, the proxy that was used to estimate exposure (degree of sorting), varied from 0.8 to 1.5 (φ), with Kolaviken being the most exposed and Ängsö being the most sheltered site. In Denmark degree of sorting varied from 0.6 to 2.1 (φ,) with Nyborg and Visby being the most exposed and sheltered sites, respectively.

Organic carbon stocks

The profiles of Corg stocks (g C cm^{-3}) in the upper 25 cm of the sediment showed marked differences both between and within the sampled regions. At the Finnish sites, where eelgrass typically grows at exposed locations, the sediment Corg stocks were low (<0.001-22.1 mg C cm^{-3}) and declined with depth at most of the 10 study sites (Fig. 3). At the Danish sites, however, the Corg stocks were more variable (<0.001 to 176.7 mg C cm^{-3}) both within and between the sites (Fig. 3). Depth integrated Corg stocks (0-25 cm, g C m^{-2}, Fig. 4) were particularly high at one sheltered site in Funen, namely Thurøbund. This site is characterized by soft sediments with high organic content, high annual eelgrass production and high belowground biomass (Table 1). The lowest eelgrass Corg stocks in Denmark were found at two relatively exposed and sandy sites, namely Nyborg and Dalby (Fig. 4). The estimate of average total Corg stock in Finland was 19±1 t C taking the total area of eelgrass into account (30 km^2; Table 2). Using minimum and maximum estimates of the eelgrass area in Denmark the estimates for mean total sediment Corg stock in Denmark were 2164±5 or 5868±14 t C, respectively (673 and 1345 km^2; Table 2).

The estimated total Corg stocks in the upper 25 cm of the sediments was on average 6.27 and 43.6 t ha^{-1} in Finland and Denmark, respectively. Using an annual carbon sequestration value of 0.05 and 0.35 t ha^{-1} $y^{-1}$for Finland and Denmark, respectively, and assuming sediment accumulation of 2.02 mm y^{-1} on average (Table 2), the total pool of Corg in the *Z. marina* meadows (Corg bound in living biomass, sediment Corg stock and Corg sequestration) corresponds to 6.98 t ha^{-1} (698t km^{-2}) and 44.9 t ha^{-1} (4490 t km^{-2}) for Finland and Denmark, respectively. Using the social cost of carbon of 40.3 € t^{-1} (United States Government 2010), the present economic value of eelgrass carbon in Finnish and Danish eelgrass meadows is estimated at 281 and 1809 € ha^{-1}, respectively. Using an average of these values (1045 € ha^{-1}) and a conservative estimate of the eelgrass acreage in the Baltic Sea (2100 km^2: Boström et al. 2014), we estimate a total monetary value of the present sequestration by eelgrass meadows to be 219.4 million euro. Given the total eelgrass loss in Denmark for the time period 1900-2000 is between 5381 km^2 (present area 20% of historical distribution) and 6053 km^2 (present area 10% of historical distribution), this equals Corg loss of 0.042 and 0.048 Gt, respectively. Using the acerage value (1045 € ha^{-1}) these areal loss estimates corresponds to a lost economic value between 562 and 632 million euro, for the minimum and maximum areal loss estimates, respectively.

Corg accumulation

The estimates for annual Corg accumulation in the Finnish seagrass meadows (30 km^2) were low (0.002, 0.016, 0.033 Mt y^{-1}), when applying sediment accumulation rates of 0.32, 2.02 and 4.20 mm y^{-1}, respectively. Similarly, the sedimentation rates measured by use of sedimentation traps were 10–folds lower in Finland (3.6-7.7 gDW m^{-2} d^{-1}) compared to Denmark (37.6-63.4 gDW m^{-2} d^{-1}). The low Corg accumulation in Finnish meadows were a result of low mean Corg stocks and relatively small size of seagrass area in the region compared to Denmark (Table 2). The Corg accumulation for the Danish sites differed between the two sub-regions Limfjorden (18 km^2) and Funen (179 km^2). At the sampling sites around Funen, the Corg accumulation values were 0.139, 0.881 and 1.832 Mt y^{-1}, while in Limfjorden the Corg accumulation were lower (0.006, 0.038 and 0.079 Mt y^{-1}) and similar to Corg accumulation for Finland. Using upper and lower eelgrass areal estimates, total Corg accumulation based on 3 sediment accumulation rates (0.376, 2.373, 3.636 and 0.75, 4.741 and 9.859 Mt y^{-1}) in Denmark were more than four orders of magnitude higher than the estimated total Corg accumulation in Finnish eelgrass meadows.

Carbon sources

The $\delta^{13}C$ values of the surface sediment within regions where quite homogenous ranging from -22.8 to -18.9 ‰ and -17.6 to 13.5 ‰, in Finland and Denmark respectively. The $\delta^{13}C$ in *Z. marina* tissues ranged from-11.4 to -8.5 ‰ and from -12.5 to -8.2‰, in Finland and Denmark, respectively. There was no significant difference between living above- and belowground tissue and decomposed belowground tissue and samples were pooled in the isotope mixing model. Although *Z. marina* was the dominant seagrass species in Finland, the study sites included both monospecific and mixed seagrass meadows, where species like *Potamogeton pectinatus* and *Potamogeton perfoliatus* were growing in mixed stands with *Z. marina*. *P. pectinatus* ($\delta^{13}C$ -11.3 to -7.6 ‰) and *P. perfoliatus* ($\delta^{13}C$ -15.6 to -12.6 ‰) were both present at five of the Finnish study sites (Jänisholm, Sackholm, Hummelskär, Tvärminne and Fårö) and *P. pectinatus* was present at Kolaviken, Ryssholmen and Lyddaren. *Ruppia cirrhosa* (-11.5 to -8.8 ‰) was less abundant and found at three of the Finnish sites (Sackholm, Ängsö, Kolaviken) and at one study site in Denmark (Kertinge). The $\delta^{13}C$ for phytoplankton ranged from -24.6 to -22.6 ‰ and -18.6 to 16.4 ‰, in Finland and Denmark, respectively. Drift algae was present at all Danish study sites, except Thurøbund, and had $\delta^{13}C$ values from -17.9 to -13.5 ‰, but only at five Finnish sites (Ängsö, Ryssholmen, Fårö, Långören and Hummelskär) with $\delta^{13}C$ values ranging from -20.0 to -16.3‰.

The isotope mixing model showed that at all Finnish sites, phytoplankton and allochtonous material were the major contributors (43-86 %) to the sediment surface Corg pool. In Denmark *Z. marina* contributed with 13-81 % to the sediment surface Corg pool, contribution being lowest at the most exposed site Nyborg and highest in Visby. The corresponding numbers for Finland were 1.5-32 %, being lowest and highest in Tvärminne and Lyddaren, respectively (Fig. 5). The DistLm analysis showed that the *Z. marina* contribution to the sediment surface ^{13}C pool explained 10.9 % of the variation in the measured Corg stocks (Fig. 6, Table 3 and Table 4). Drift algae was a significant contributor (72%) to the sediment surface Corg pool at the Danish sites, while it appeared to play only a minor role (0-21%) in Finland. The carbon sources were generally more mixed at the Danish study sites compared to the Finnish sites where phytoplankton dominated (Fig. 5).

Discussion

Recent studies have shown considerable variation in the global estimates of carbon stocks (Corg stocks) and carbon accumulation rates (Corg accumulation) in seagrass meadows, indicating an incomplete understanding of factors influencing this variability (Fourqurean et al. 2012, Duarte et al. 2013a, Lavery et al. 2013, Miyayima et al. 2015). The Baltic Sea forms a key distribution area for eelgrass in Europe, but similarly to the global data sets, we have so far lacked estimates on seagrass carbon stocks and accumulation.

In our study, the Finnish eelgrass meadows showed consistently very low Corg stocks and Corg accumulation, and the meadows were minor carbon sinks compared to the Danish meadows. The Danish sites showed more variation in the sediment Corg stock and accumulation and Corg stock was particularly high at one site, Thurøbund (26138 ±385 g C m^{-2}), which is a relatively sheltered site with high organic sediments. Expectedly, due to both larger overall eelgrass acreage and larger Corg stocks in the Danish meadows, the total Corg accumulation (0.38- 9.86 t y^{-1}) was three to four orders of magnitude higher than in the Finnish meadows (0.002-0.033 t y^{-1}). As eelgrass in Finland generally grow in more exposed locations potentially due to increased interspecific competition with freshwater plants such as common reed (*Phragmites australis*) in sheltered locations (Boström et al. 2006), it is probable that most of the Corg produced in the Finnish meadows is exported, and thus incorporated in detrital food webs in deeper bottoms. This argument is supported when applying sediment accumulation rates from literature, as only 0.15 - 2% of the annual production accumulated in Finnish meadows, while the corresponding numbers for Denmark were 0.6 -7.8%. Duarte and Cebrian (1996) estimated that on average

25% of the global seagrass primary production is exported, and seagrass detritus may thus contribute significantly to Corg stocks in other locations, a fact that is often overlooked.

Extrinsic drivers of carbon sequestration in seagrass meadows

The DistLm analysis showed, that three sediment variables (dry density, silt content, porosity) and three plant variables (annual eelgrass production, the root: shoot-ratio and *Z. marina* contribution to the sediment ^{13}C pool) explained 67% of the variation in the sediment Corg stock (g C m^{-2}) (Table 3 and 4, Fig. 6). Specifically, sediment silt content alone explained > 36 % of the variation in Corg stocks (Table 3). In both regions, exposed sites characterized by sandy, low organic sediments and low silt content, had low Corg stocks. In contrast, at sheltered sites like Thurøbund in Denmark, we measured the highest sediment Corg stock along with highest silt and water content among all sites. Although sediment porosity and sediment dry density also contributed to the model, they were of minor importance (~2 % each). As proposed in previous work (Kennedy et al. 2010, Miyajima et al. 2015) accumulation of fine grained size fractions in seagrass sediments, relative to those accumulated in bare sediments, appears to be one of the major factors influencing the carbon sink capacity of seagrass meadows, and may thus be a useful proxy for the sink capacity.

In addition, it is well known, that seagrasses modify sediments by reducing water flow and consequently increasing particle trapping and sedimentation and reducing resuspension (Fonseca and Fisher 1986, Fonseca and Cahalan 1992, Gacia et al. 2002, Hendriks et al. 2008, Boström et al. 2010) and also increasing Corg (Kennedy et al. 2010). Our finding of low carbon sink capacity of Finnish seagrass meadows was supported by low sedimentation rates compared to the Danish sites . These rates are similar to sedimentation rates measured in previous studies (1.5 - 500 and 3.1- 20 gDW m^{-2} d^{-1}; Gacia and Duarte 2001, Holmer et al. 2004) from *Posidonia* *oceanica* meadows. Thus, at the Finnish sites, the input of organic particles and the potential for carbon accumulation of eelgrass detritus and external organic matter in the sediment is low.

Furthermore, the DistLm analysis showed, that *Z. marina* contribution to the sediment surface carbon pool was an important driver (> 10.9%) of the variation in sediment Corg stock (Table 3 and 4, Fig. 6). We found increasing Corg stocks at the Danish sites, where *Z. marina* was the major source of organic carbon, contributing with 13 to 81% to the surface sediment Corg. In contrast, at the Finnish sites where only a minor fraction of carbon buried in sediments derive from eelgrass detritus (1.5 to 39.6%) the Corg stocks were low. Correspondingly, the average δ^{13}C value (-16.2‰) in the Danish sediment samples was similar to the global median value (−16.3‰±0.2‰) reported by Kennedy et al. (2010) in which on average 51 % of the carbon was derived from seagrass detritus . The importance of the *Z. marina* contribution to the Corg stocks may be explained by slow decomposition rates of seagrass tissue. Especially, the high proportion of refractory organic compounds in the seagrass belowground parts and high C:N:P-ratios of seagrass tissue in general make seagrasses less biodegradable than most marine plants and algae (Fourqurean and Schrlau 2003, Vichkovitten and Holmer 2004, Kennedy and Björk 2009, Holmer et al. 2011). The slow decomposition rates are also a result of reduced sediment conditions commonly encountered in Danish seagrass meadows (Kristensen and Holmer 2001, Holmer et al. 2009, Pedersen et al. 2011). Despite the extensive distribution (2-29 ha), high biomasses (300-800 g DW m^{-2}) and major impact of drifting algal mats on coastal ecosystem functioning (Norkko & Bonsdorff 1996, Salovius & Bonsdorff 2004,Rasmussen et al. 2013, Gustafsson & Boström 2014), the stable isotope composition of the sediments suggests that drift algae had a surprisingly minor influence on the sediment surface Corg pool in both regions. Thus, despite present on several sampling sites, drift algae is likely exported and mineralized in the water column and in deeper sedimentation basins. Furthermore, we found that at all study sites in both regions, there were several other potential sources influencing the sediment surface Corg pool. Bouillon et al. (2007) showed that in seagrass sediments adjacent to mangrove forests in Kenya, none of their sites had seagrass material as the sole source of Corg, instead mangrove-derived detritus contributed significantly to the tropical seagrass sediment Corg pool. Similarly, at majority of our study sites we observed several species of macroalgae and seagrasses that contributed to the sediment Corg pool, in particular at the Danish sites.

The root: shoot-ratio explained 12.7 % of the variation in the Corg stocks. The highest Corg stocks, below-ground biomass and root: shoot-ratio was found in Thurøbund (Denmark). The relatively high explanatory value of the root: shoot-ratio could be explained by lower decomposition rates of the *Z. marina* belowground tissue. In Finland, the highest root: shoot-ratio (2.07) was found at Kolaviken, with a relatively low Corg stock (397 gDW C m^{-2}). Due to higher degree of exposure at the site (degree of sorting 0.7 φ) compared to Thurøbund (1.4 φ) it is likely that large portion of the eelgrass production was exported away from the meadow and not stored in the sediment. The mean shoot densities were almost identical between regions, and shoot density did not contribute to the model explaining Corg.

The annual eelgrass production explained only 2.3 % of the variation in the Corg stocks. The annual production rates were almost twice as high at Danish sites compared to the Finnish sites. Regional differences in seagrass productivity may be caused by differences in e.g. the inorganic carbon concentration in water column and light availability between the regions (with higher values in Denmark), which both affect the photosynthetic capacity of the plant (Hellblom and Björk 1999, Holmer et al. 2009, Boström et al. 2014). Eelgrass production tend to be higher in physically exposed areas compared to more sheltered areas, which can be due to improved sediment oxygen conditions and hydrodynamical effects (Hemminga and Duarte 2000). This finding was not supported by our study, in which we found the highest annual eelgrass production rates at both the most sheltered and exposed sites, namely Visby and Nyborg (DK).

Carbon stocks and accumulation

Our estimated Corg stocks for the study sites were generally lower (627- 4324 t C km^{-2}) than estimates (25200-84000 t C km^{-2}) found in the literature (Duarte et al. 2005, Nellemann et al. 2009, Mcleod et al. 2011, Fourqurean et al. 2012). In Duarte et al. (2005) the data set used for the calculations was gathered from various studies conducted at different temporal scales and habitat types, as well as different methods for determination of Corg accumulation. Additionally, several of the studies were conducted in the Mediterranean *P. oceanica* meadows - a habitat with exceptionally high carbon sequestration and storage capacity (Duarte et al. 2005, Lavery et al. 2013). In addition, the average sizes of Corg stocks in Finnish and Danish eelgrass meadows were also considerably lower than the mean values reported by Alongi et al. (2014) for tropical seagrass meadows (14270 t C km^{-2}), mangroves (95600 t C km^{-2}) and salt marshes (59300 t C km^{-2}). In contrast, our estimate for the carbon stock in the top 25 cm for Danish and Finnish meadows (627-6005 g Corg m^{-2}) are comparable to Australian (262–4833 g Corg m^{-2}: Lavery et al. 2013) and Asian estimates (3800-12000 g Corg m^{-2}: Miyajima et al. 2015).

Consequences of seagrass loss for carbon pools

Despite the importance of seagrasses, their global distribution has decreased by 29% since 1879 primarily due to anthropogenic pressures (Waycott et al. 2009), thus weakening the carbon sink capacity of marine environments to sequester carbon (Duarte et al. 2005). Since the 1970s, the Baltic Sea has been subject to strong anthropogenic pressures (Conley et al. 2009) leading to eelgrass declines in several countries (Boström et al. 2014). In the 1930s, the Danish eelgrass meadows were significantly reduced by the wasting disease (Rasmussen 1977). These regime shifts in Denmark, have resulted in a 80-90 % decline corresponding to 6726 km^2 in the beginning of 1900`s to 673-1345 km^2 in 2005, using the minimum and maximum estimates for the current coverage area, respectively (Boström et al. 2014). Similarly, eelgrass meadows in

Sweden have declined by some 60 % since the mid-1980s resulting in a present coverage of 68 (minimum) to 138 (maximum) km^2. In Germany the eelgrass coverage area has decreased with 75 %, resulting in the present eelgrass area of 147 km^2 (Boström et al. 2014). In Finland there is a lack of long-term monitoring, but the meadows appear to be stable and cover at least 30 km^2. It is clear, that these large-scale seagrass declines have eroded the Corg stocks in the Baltic Sea significantly (Table 2). Using the mean Corg (17.45 mg C cm^{-3}) measured at the Danish sites, the lost Corg stock is estimated to 0.4-0.9, 23-27 and 1.9 Mt Corg in Sweden, Denmark and Germany, respectively.

For the Swedish west coast, Moksnes and Cole (2015) estimated an annual economic loss due to the lost seagrass carbon fixation capacity to be 248 € ha^{-1}y^{-1} (carbon price 117 € t). If also the carbon stored in the top 25 cm of sediment, as well as the loss of seagrass carbon sequestration capacity over 50 year period were taken into account, the value of the lost carbon storage and sequestration capacity was approximately 5321 € ha^{-1}. This value is higher than our estimates for the monetary value of the present carbon storage and sequestration capacity eelgrass meadows in Finland and Denmark (281 and 1809 € ha^{-1}). This difference is mainly due to the lower (40.3€) monetary value of carbon used in our calculations. Pendleton et al. (2014), calculated a global estimated economic cost of lost seagrass meadows (CO_2 price 41 $ t) to be 1.9-13.7 billion USD. This value was derived from the cost of lost carbon sink capacity, ignoring other lost ecosystem services including e.g. coastal protection, water quality management, food provision and the role of seagrasses as fisheries and key habitats for marine species (Barbier et al. 2011, Atwood et al. 2015). Thus, we estimate the present economic value of carbon storage and sequestration capacity of Baltic Sea and Norwegian eelgrass meadows to be between 1.7 and 12 % of the global seagrass blue carbon value.

While useful, our and previous work still remain snap shots of complex processes causing local and regional variability in estimates of seagrass Blue Carbon stocks and accumulation. Clearly, in order to produce more reliable estimates of global seagrass carbon sequestration rates and stocks, there is a need for more studies integrating and modeling the individual and joint role of e.g. sediment biogeochemistry, seascape structure, plant species architecture and hydrodynamic regime. Since seagrasses are lost at accelerating rates (Waycott et al. 2009), there is also an urgent need for a better understanding of the fate of lost seagrass carbon (Macreadie et al. 2014) and the development of the carbon sink capacity in restored seagrass ecosystems (Nellemann et al. 2009, Greiner et al. 2013, Marba et al. 2015). Nelleman et al. (2009) proposed the use of carbon trading programs using financial incentives for forest conservation, such as REDD+ (Reduced Emissions from Deforestation and Degradation) and NAMAs (Nationally Appropriate Mitigation Actions), to include the blue carbon ecosystems as part of their environmental protection protocol. Both of these carbon mitigation programs require ongoing monitoring of organic carbon storage and emission in the different Blue Carbon ecosystems. In order to manage seagrass meadows, mitigate climate change and produce information acquired for the carbon trading programs, it is fundamental to understand factors influencing the capacity of seagrass meadows to capture and store carbon. By solving these uncertainties, the conservation and restoration of seagrass meadows can be implemented in the most beneficial manner by e.g. giving priority to protection of the seagrass meadows and species with the highest carbon sink capacity and foundation of restoration projects in areas most suitable for seagrass growth (Duarte et al. 2013a).

Copyright statement

Field Code Changed

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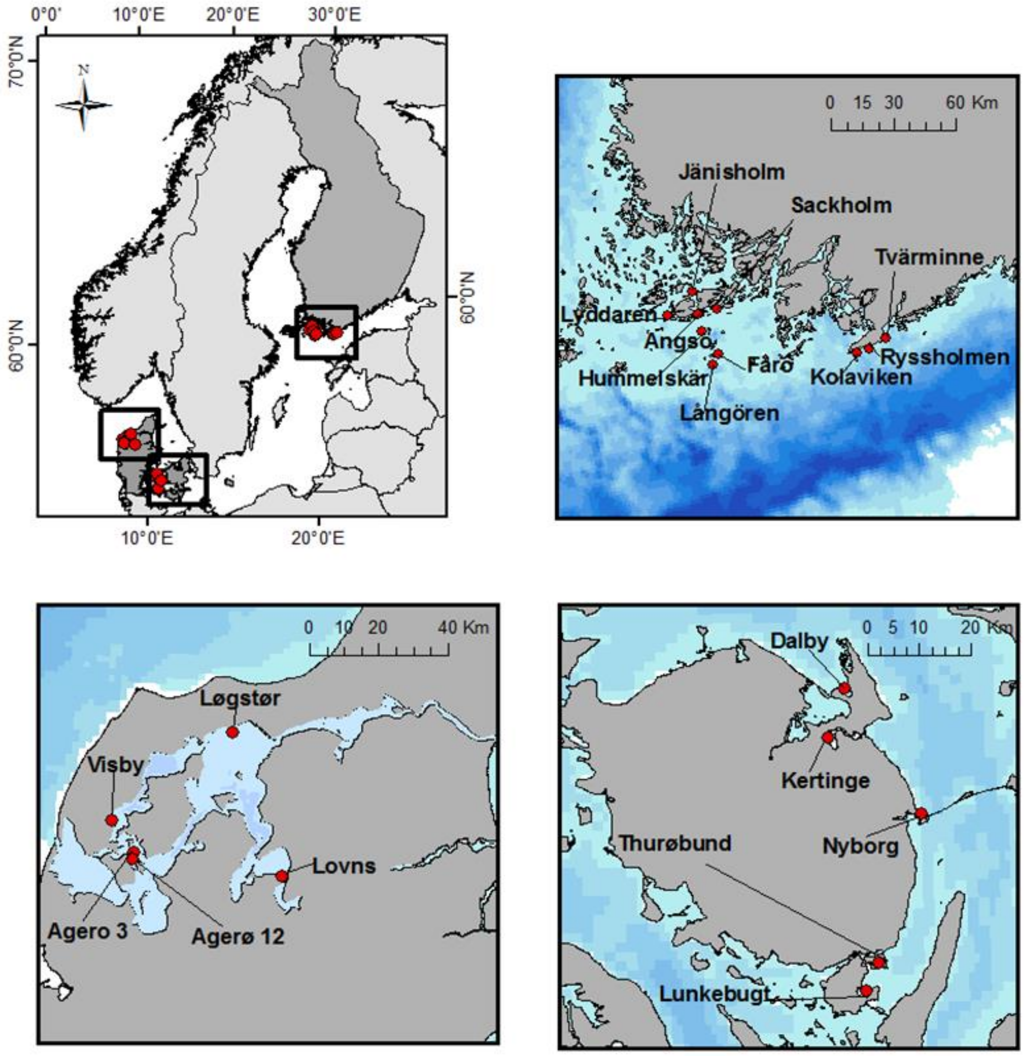

Fig.1. The study sites in Denmark and Finland.

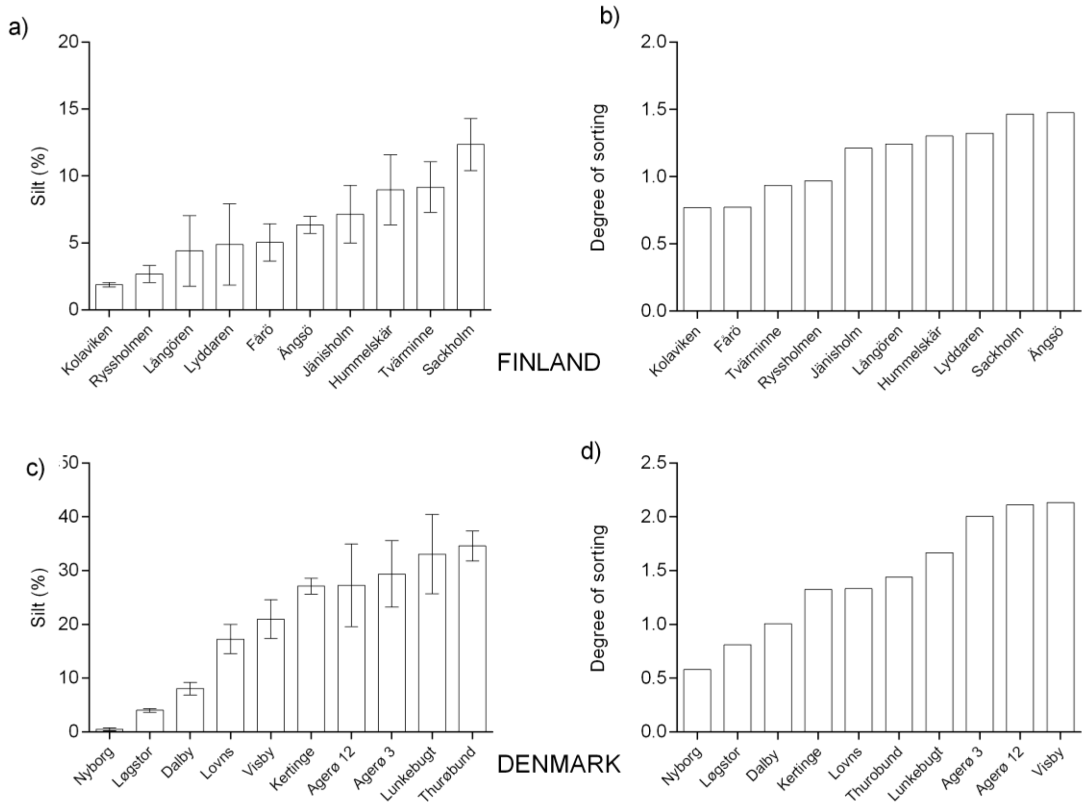

Fig. 2. A percentage silt (a, c) and degree of sediment sorting (b, d) at the study sites in Finland and Denmark, respectively. Lower values in degree of sorting indicate well-sorted sediment types.

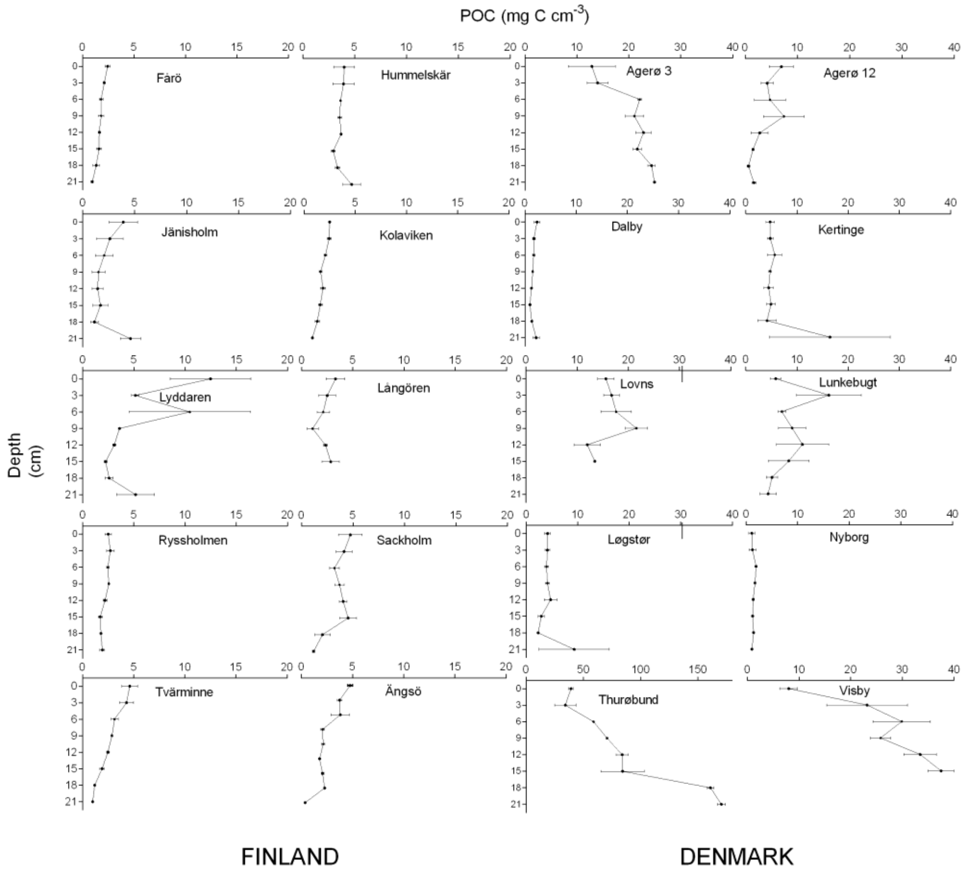

Fig.3. Sediment profiles of particulate organic carbon (POC) content (mg C cm^{-3}) in the top 25 cm of the Finnish and Danish eelgrass (*Zostera marina*) meadows. Note the difference in the scale of x-axis between the regions.

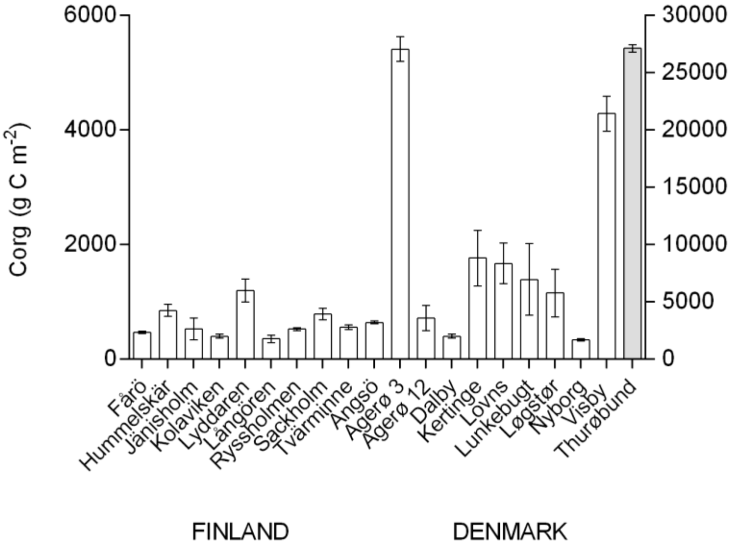

Fig.4. Organic carbon stocks (Corg, g C m^{-2}) in the top 25 cm of sediment in Finnish and Danish eelgrass (*Zostera marina*) meadows. Note that the value of Thurøbund (grey bar) corresponds to right y- axis.

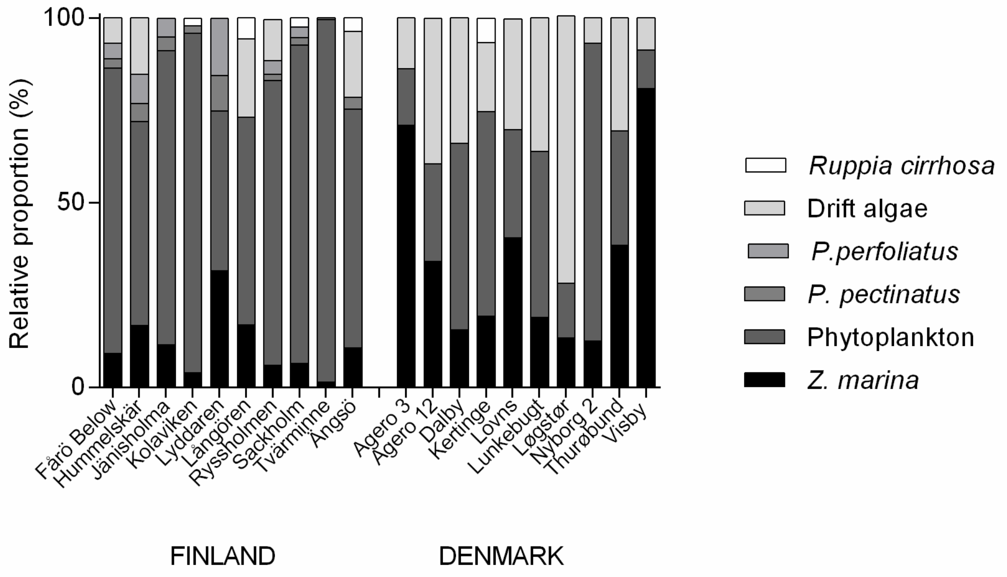

Fig.5. Relative contribution of organic matter sources (*Z. marina, P. perfoliatus, P. pectinatus*, *Ruppia cirrhosa,* phytoplankton and drift algae) to the ^{13}C signal of the sediment surface layer (0-2 cm) in Finnish and Danish eelgrass (*Z. marina*) meadows.

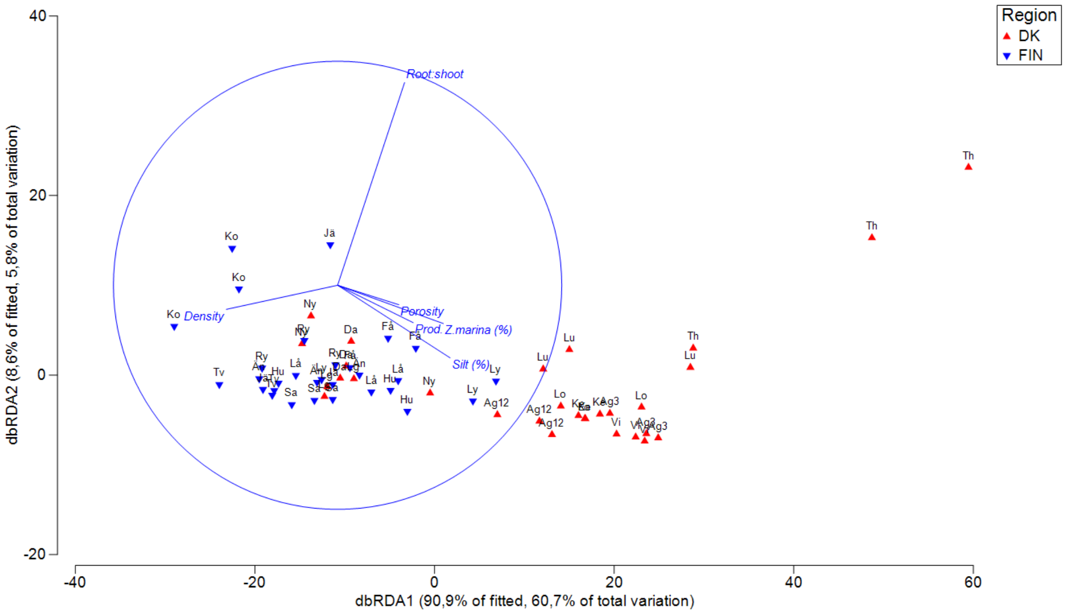

Fig.6. Distance-based redundancy analysis (DbRDA) plot showing the environmental parameters (percentage of *Z. marina* in sediment carbon pool, above: belowground- ratio, annual eelgrass production, sediment silt content, sediment dry density and sediment porosity) fitted to the variation in the Corg stock (g C m^{-2}) at the Finnish and Danish eelgrass (*Z. marina*) sites, respectively. Vectors indicate direction of the parameters effect. Site codes: Finland; Ko=Kolaviken, Ry=Ryssholmen, Tv=Tvärminne, Få=Fårö, Ly=Lyddaren, Lå=Långören, Hu=Hummelskär, Jä=Jänisholm. Site codes: Denmark; Ag12=Agerø 12, Ag3=Agerø 3, Vi=Visby, Lg=Løgstør, Lo=Lovns, Th=Thurøbund, Lu=Lunkebugt, Da=Dalby, Ke=Kertinge, Ny=Nyborg.

Table 1. Location, silt content (% silt), sediment organic matter content (%DW), δ^{13} C sediment surface, Δ13 C *Z. marina* leaves , Δ13 C *Z. marina* rhizomes, seagrass shoot density (shoots m^{-2}), seagrass above and below-ground biomass (gDW m^{-2}), root:shoot-ratio, and above-ground production (gDW m^{-2} y^{-1}) at the sampling sites. SE (n= 3–4) is given. Annual seagrass production is calculated from pooled values of replicates per site and therefore no SE is shown.

Location	Silt content (% silt)	Organic matter content (% DW)	δ^{13} C sediment surface	δ^{13} C *Z. marina* leaves	δ^{13} C *Z. marina* rhizomes	Shoot density (shoots m^{-2})	Above-ground biomass (gDW m^{-2})	Below-ground biomass (gDW m^{-2})	Root: shoot-ratio	Above-ground production (gDW m^{-2}y^{-1})
Finland										
Fårö	5.0±1.4	0.66±0.07	-20.58±0.27	-9.66±0.35	-9,01±0.20	304±32	138±20	167±28	1.27±0.13	773
Hummelskär	9.0±2.6	1.06±0.20	-19.36±1.22	-9.31±0.28	-9,83±0.25	364±31	70±11	28±2	0.45±0.06	446
Jänisholm	7.1±2.1	0.93±0.20	-22.05±0.37	-10.84±0.39	-11,01±0.28	128±17	65±16	46±2	1.44±0.53	270
Kolaviken	1.9±0.2	0.75±0.02	-19.48±0.23	-10.32±0.28	-11,36±0.34	476±96	74±6	149±16	2.07±0.27	324
Lyddaren	4.9±2.5	1.75±0.70	-13.53±3.52	-8.75±0.35	-9,58±0.29	228±42	86±7	57±12	0.64±0.09	505
Långören	4.4±2.1	2.70±2.10	-18.88±0.35	-8.51±0.14	-8,87±0.15	436±53	121±46	68±25	0.58±0.06	788
Ryssholmen	2.7±0.6	0.89±0.20	-20.70±0.34	-11.45±0.13	-11,49±0.29	756±57	160±3	136±16	0.86±0.11	803
Sackholm	12.4±1.9	0.95±0.20	-21.07±0.78	-10.34±0.68	-9,90±0.34	774±234	110±18	37±9	0.31±0.04	377
Tvärminne	9.2±1.9	0.88±0.20	-22.73±0.59	-11.61±0.09	-11,50±0.25	112±11	99±16	38±7	0.37±0.01	436
Ängsö	6.3±0.5	0.84±0.02	-20.05±0.28	-10.28±0.08	-10,27±0.28	604±98	91±6	63±9	0.67±0.05	521
Finland average	**6.3±1**	**1.4±0.3**	**-19.85±0.32**	**-10,11±0.33**	**10,28±0.32**	**417±75**	**101±3**	**79±5**	**0.87±0.06**	**524**

Denmark									
Agero 3	29.4±6.2	1.94±0.60	-12.95±1.67	-9,24±0.47	-11,14±0.22	448±89	181±33	84±8	0.52±0.07	1075
Agero 12	27.3±7.7	1.65±0.80	-17.35±0.84	-10,68±0.25	-11,94±0.21	404±90	110±2	46±9	0.40±0.08	576
Dalby	8.1±1.2	0.67±0.03	-17.29±0.69	-9,68±0.27	-10,50±0.56	400±48	76±7	83±10	1.09±0.11	470
Kertinge	27.1±1.5	12.59±1.60	-16.64±0.20	-9,18±0.10	-9,75±0.08	328±64	90±17	64±14	0.68±0.02	527
Lovns	17.3±2.7	2.90±0.50	-16.25±2.44	-11,51±0.35	-12,16±0.37	360±27	141±4	100±11	0.70±0.06	848
Lunkebugt	33.0±7.4	4.72±2.40	-16.93±0.25	-8,86±0.87	-10,60±0.38	347±81	210±10	382±24	1.82±0.08	1056
Løgstør	4.0±0.4	0.75±0.03	-17.68±0.35	-9,67±0.40	-10,39±0.51	300±14	149±11	63±13	0.42±0.07	755
Nyborg	0.5±0.3	0.42±0.02	-17.57±1.09	-9,33±0.17	-10,62±0.34	652±30	203±24	214±50	1.00±0.14	1179
Thurøbund	34.6±2.8	14.48±0.80	-15.54±0.42	-8,17±0.14	-9,03±0.22	420±98	101±16	398±15	4.54±0.70	619
Visby	21.0±3.6	1.17±0.06	-13.79±1.17	-11,97±0.56	-12,41±0.70	520±21	193±13	49±4	0.25±0.01	2172
Denmark average	**20.2±3.9**	**3.9±1.5**	**-16.20±0.22**	**-9.82±0.37**	**-10.85±0.33**	**418±32**	**145±5**	**148±14**	**1.14±0.13**	**928**

Table 2. Estimated average carbon stocks (g C m^{-2} and Mt), annual areal carbon accumulation (Corg seq t C ha^{-1}y^{-1}) and annual carbon accumulation (Annual Corg (Mt y^{-1}) in Finnish and Danish eelgrass (*Z. marina*) meadows. Denmark$_{lost}$ = eelgrass area of the region lost since the beginning 1900`s. Limfjorden$_{lost}$= eelgrass area of the region lost since the 1900`s. See text for calculations. *) mean Corg (mg C cm^{-3}) calculated for Denmark is used. n.d= no data. For calculations of annual carbon accumulation three different sediment accumulation rates were applied (0.32 mm y^{-1}; Miyayima et al. 2015, 2.02 mm y^{-1}; Duarte et al. 2013b and 4.2 mm y^{-1}; Serrano et al. 2014), for Corg seq the sediment accumulation rate of 2.02 mm y^{-1} was used.

Region	Seagrass area (km^2)	Corg stock (mg C cm^{-3})	Corg stock (g C m^{-2})	Corg stock (Mt)	Corg seq. (t C ha^{-1}y^{-1})	Annual Corg accumulation (Mt y^{-1})		
						0.32 mm y^{-1}	2.02 mm y^{-1}	4.20 mm y^{-1}
land	30	2.60±0.09	627±25	0.019±< 0.001	0.052	0.002	0.016	0.0328
njorden	18	10.57±1.66	2644±207	0.047± 0.007	0.213	0.006	0.038	0.079
nen	179	24.32±9.15	6005±1127	1.090±0.410	0.491	0.139	0.881	1.832
nmark$_{min}$	673	17.45±9.42*	4324±1188*	2.164±0.005	0.352	0.376	2.373	3.636
nmark$_{max}$	1345	17.45±9.42*	4324±1188*	5.868±0.014	0.352	0.75	4.741	9.859
nmark$_{lost}$	5381-6230	17.45±9.42*	17.45±9.42*	23.478-27.183	n.d	n.d	n.d	n.d

Table 3. Table from DistLm analysis showing variables in the marginal tests and the results for statistical analysis.

MARGINAL TESTS

Variable	Sum of Squares	Pseudo-F	P-value	Proportion
1. Root: shoot- ratio	5309	10.64	0.002	0.155
2. Sediment dry density	10704	26.37	0.001	0.313
3. Annual eelgrass production	4959	9.82	0.002	0.145
4. Shoot density	48	0.08	0.911	0.001
5. Porosity	3507	6.61	0.01	0.102
6. % silt	12653	33.99	0.001	0.369
7. C:N-ratio of plant material	464	0.79	0.397	0.014
8. Z. marina %	12179	32.02	0.001	0.356
9. Degree of sorting	9725	23.01	0.001	0.284

Table 4. Table from DistLm analysis showing results from the sequential tests and solution given by the analysis.

Variable	AICc	Sum of squares	Pseudo-F	P- value	Proportion	Cumulative proportion	Degrees of freedom
6. % silt	357.4	12653	33.9	0.001	0.369	0.369	58
1. Root :shoot-ratio	346.0	4375	14.5	0.001	0.127	0.497	57
8. *Z. marina* %	333.6	3745	15.6	0.001	0.109	0.606	56
3. Production	332.2	805	3.5	0.037	0.023	0.630	55
2. Density	331.3	700	3.2	0.049	0.020	0.650	54
5. Porosity	330.8	602	2.8	0.056	0.017	0.668	53
BEST SOLUTION	AICc	R^2	RSS	Variables	Selections		
	330.8	0.668	11363	6	1-3;5;6;8		