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Capturing of organic carbon and nitrogen in eelgrass sediments of southern Scandinavia

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Abstract

The ability of seagrass meadows to filter nutrients and capture and store CO₂ and nutrients in the form of organic carbon (OC) and nitrogen (N) in their sediments may help to mitigate local eutrophication as well as climate change via meadow restoration and protection. This study assesses OC and N sediment stocks (top 50 cm) and sequestration rates within Danish eelgrass meadows. At four locations, eelgrass-vegetated and nearby unvegetated plots were studied in protected and exposed areas. The average OC and N sediment 50 cm stocks were 2.6 ± 0.3 kg OC m⁻² and 0.23 ± 0.01 kg N m⁻², including vegetated and unvegetated plots. In general, OC and N stocks did not differ significantly between eelgrass meadows and unvegetated sediments. Lack of accumulation of excess ²¹⁰Pb suggested sediment erosion or low rates of sediment accumulation at most sites. OC accumulation rates ranged from 6 to 134 g m⁻² yr⁻¹ and N from 0.7 to 14 g m⁻² yr⁻¹. Generalized additive models showed that ≥ 80% of the variation in sediment OC and N stocks was explained by sediment grain size, organic matter source, and hydrodynamic exposure. Long cores, dated with ²¹⁰Pb, showed declining OC and N densities toward present time, suggesting long-term declines in eelgrass OC and N pools. Estimates of potential nation-wide OC and N accumulation in eelgrass sediments show that they could annually capture up to $0.7\% \pm 0.5\%$ of CO₂ emissions and $6.9\% \pm 5.2\%$ of the total terrestrial N load.

Extensive and productive marine meadows formed by seagrasses can be found along the coasts of most continents. These ecosystems are suffering rapid worldwide decline (Dunic et al. 2021), and with them we are also losing associated biodiversity and a wide range of critical ecosystem services. Food provisioning, enhanced water quality, carbon sequestration, nutrient filtration, sediment stabilization, and shoreline protection are

all services provided by seagrass meadows, making them crucial to human health and resilience (Gillanders 2006; Orth et al. 2006; Fourqurean et al. 2012; Cullen-Unsworth et al. 2014).

The dominant seagrass species in the North Atlantic region is *Zostera marina*, eelgrass, and Danish coastal waters are a hotspot for eelgrass distribution in Scandinavia and the Baltic Sea region. Eelgrass has, however, experienced the highest proportion of declines among seagrass species in Europe, and the Baltic Sea is the area with the largest percentage of losses of meadow area (67%) over the last 150 yr (de los Santos et al. 2019). The extent of *Z. marina* in Denmark around the year 1900 was estimated at 6726 km² (Petersen 1914) along the about 7300 km long coastline. Danish *Z. marina* meadows have not been fully mapped yet so the current actual extent remains uncertain, but a recent modeling study by Stæhr et al. (2019) comparing habitat requirements to current conditions estimated the current potential cover as three times lower than the historical area, 2200 km².

There has been increasing interest over the last decade in seagrasses due to their CO₂ sequestration potential in the form of organic carbon (OC) within their sediments over long periods of time. This OC in seagrass sediments, along with

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Additional Supporting Information may be found in the online version of this article.

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that stored and accumulated in other vegetated coastal ecosystems, such as mangroves and saltmarshes, is known as “blue carbon” (BC; Nellemann et al. 2009). BC sequestration may help to reach global climate mitigation goals if vegetated coastal ecosystems are managed and restored to enhance OC accumulation. Protection of these habitats against further losses is also essential to avoid further CO₂ emissions due to habitat loss and the degradation of the already buried OC (Moksnes et al. 2021).

Besides OC, seagrass can store nutrients, nutrients which are assimilated in the plant biomass, deposited as detritus as well as those from sestonic particles that are trapped and deposited in stabilized sediments thanks to the seagrass canopies and their belowground organs (Gacia et al. 2002). Moreover, eelgrass stimulates other biogeochemical processes of the nitrogen (N) cycling such as denitrification and N fixation (Eyre et al. 2016; Aoki et al. 2020) that play a role in N retention. Eutrophication affects the eelgrass N filter function and eelgrass sediment stocks can be either negatively impacted due to reductions in seagrass productivity or enhanced due to increased inputs of sestonic particles (see Kindeberg et al. 2018 and references there).

However, studies addressing the magnitude and variability of OC and N stocks in eelgrass meadows are scarce both globally and in Denmark (Röhr et al. 2016; Kindeberg et al. 2018; Röhr et al. 2018). Furthermore, Danish studies have focused solely on the top sediment layers (10–25 cm) and have not included direct quantification of accumulation rates. Limiting the research to the superficial sediment layers can bias regional BC estimates, because microbial remineralization is highest in those layers where OC pools are usually higher and cannot be considered to represent long-term buried OC (Johannessen and Macdonald 2016). Another key aspect, which has been overlooked so far for Danish sites, is the quantification of the sediment stocks in both vegetated and unvegetated areas to infer the additional (or net) impact of eelgrass on sediment storage. In addition, OC storage and sequestration can vary largely over local and regional scales, due to both biotic and abiotic factors (Mazarrasa et al. 2018; Mazarrasa et al. 2021). Understanding which factors enhance or limit OC sequestration and storage in eelgrass sediments is needed to upscale local measurements and to provide reliable national seagrass OC stock and sequestration estimates. Previous studies indicate that sediment characteristics (mainly grain size distribution), followed by the contribution of eelgrass detritus, the hydrodynamic exposure, and eutrophication are the main drivers of OC storage at Danish sites (Röhr et al. 2016; Kindeberg et al. 2018). Also, despite the long recognized role of seagrasses in nutrient cycling (Orth et al. 2006), very few studies have assessed their long-term burial and storage of N, even fewer in eelgrass meadows (Kindeberg et al. 2018; Aoki et al. 2020; Moksnes et al. 2021).

Here, we assess the OC and N storage in living biomass and sediments, as well as OC and N sediment accumulation rates (SAR) in *Z. marina* meadows along the Danish coast.

Specifically, we collected and synthesized data on OC and N stocks and sequestration rates from vegetated and adjacent unvegetated sediments in exposed and sheltered sites across four different coastal areas. We also attempted to identify the factors behind the spatial and temporal variability of OC and N storage. Last, we provide a first estimate of potential national-wide stocks and accumulation of sediment OC and N.

Material and methods

Study area and sample collection

Study sites were located in shallow (1.1–3.3 m) eelgrass meadows from four coastal areas: Nibe Bredning (“Nibe”), Horsens Fjord (“Horsens”), Roskilde Fjord (“Roskilde”), and the South Funen archipelago (“South Funen”) (Fig. 1). The fieldwork was conducted in May/June 2020. Samples were collected from eelgrass-vegetated and adjacent unvegetated plots to assess the relative effect of eelgrass presence. Samples from vegetated and unvegetated plots were collected from both sheltered and exposed meadows in each coastal area. Sediment cores were sampled in each meadow by SCUBA divers manually inserting 1-m-long plexiglass tubes (inner diameter of 5.2 cm) into the sediment using a sledgehammer. Unvegetated cores were taken at distances of ~ 50 m from each meadow and selected based on having similar substrate and exposure as the neighboring vegetated sites. Only in the sheltered site in South Funen, the bare plot was located further away from the vegetated plot, since a closer bare plot to the vegetated site could not be found. Four cores were collected at each vegetated sampling plot, while three cores were collected at unvegetated plots.

Sediment cores were compacted during retrieval of the cores in the field and during sediment extrusion in the lab. Compaction was measured at both stages and sediment depth was corrected to account for it (see Supporting information Data S1). The water depth, average sediment core length (decompacted) and % compaction for all sampling sites are shown in Table 1.

Triplicate 15-cm-diameter circular frames (0.0177 m²) were randomly placed in the vegetated plots and the diver collected all the aboveground and belowground biomass (located in ~ top 10 sediment cm) within the frame and transferred it to nets. A total of six biomass frames were harvested at each coastal area: three from the sheltered meadow and three from the exposed meadow.

Sample processing and analyses

The sediment cores were brought to the laboratory and refrigerated at ~ 10°C until being subsampled a few days after sampling. One core per vegetated site was finely sliced (1-cm-thick slices down to 10- and 2-cm-thick slices down to the bottom) to be dated by ²¹⁰Pb, while the three remaining cores were subsampled at lower resolution (2-cm-thick slices down to 10- and 5-cm-thick slices down to the bottom) and used to

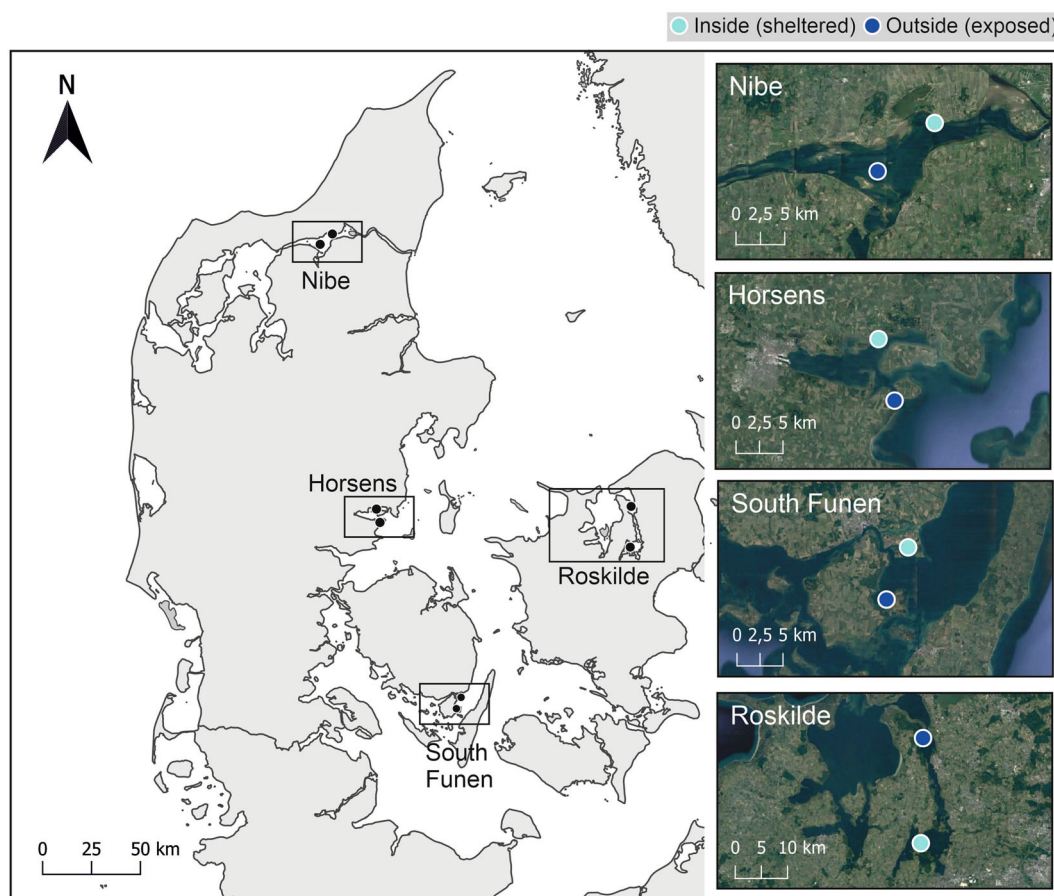


Fig. 1. Location of the study sites along the Danish coast. “Inside” stations are initially more sheltered than “outside” ones.

quantify the within-site variability of the sedimentary variables (details in Supporting Information Data S1). At unvegetated sites, no core was intended to be dated because the lack of eelgrass favors erosion and/or mixing of sediments, which usually disturbs the stratigraphy of the sediments (Arias-Ortiz et al. 2018). Therefore, all unvegetated cores were subsampled at lower resolution. Depth intervals were later corrected based on field and lab compaction (see above).

Grain size (volume) distribution was determined from a subsample of 3–5 g (sample size adjusted to achieve an obscuration level of 10–20%) of each of the pooled samples using a Malvern Mastersizer 3000 particle size analyzer (see Supporting information Data S1).

Dry bulk density (DBD, g cm^{-3}) was calculated for each slice by sampling a known volume of sediment, drying the sediment to a constant weight at 60°C for at least 48 h, and weighing the sediment. The volume and dry weight of the sample were measured after removing large shells, stones, and twigs (Howard et al. 2014). Sediment from each depth interval was homogenized (ground for 8 s and 1400 rpm, Retch RS) and a subsample was taken for chemical analyses.

Biomass samples were rinsed and sorted (see Supporting Information Data S1) and dried at 60°C for 48 h. Once dried,

the material was weighed and ground for OC and N elemental and stable isotopic analysis.

C and N analysis

Acidified sediment samples were analyzed for OC and N content and their stable isotopes on a C- and N-analyzer and isotope ratio mass spectrometer (Thermo Analytical Flash EA 2000 Elemental Analyzer coupled via a ConFlo IV interface to a Thermo Delta V Advantage Isotope Ratio Mass Spectrometer). Details of sediment acidification to remove carbonates are in Supporting Information Data S1.

Radioisotope analysis

Subsamples from the finely sliced cores, from each of the eight vegetated sites, were analyzed for ^{210}Pb and ^{137}Cs to assess the sediment OC accumulation rates (CAR) and N accumulation rates (NAR) during the last decades/century, where feasible. Lead-210 was determined through the analysis of its decay product ^{210}Po in equilibrium using alpha spectrometry (Sanchez-Cabeza et al. 1998). The concentrations of excess ^{210}Pb used to obtain the age models were determined as the difference between total ^{210}Pb and ^{226}Ra (supported ^{210}Pb , determined by gamma spectrometry). Sedimentation rates

Table 1. Summary of the cores collected from both vegetated and unvegetated sediments across Denmark. Values expressed as mean \pm standard error. Three cores were obtained in bare plots while four sediment cores were retrieved in vegetated plots.

Coastal area	Exposure	Sediment type	Decimal coordinates (°N, °E)		Water depth (m)	Relative exposure index	Average core length (cm) (decompacted)	Sediment compaction (%)
Nibe	Inside	Bare	57.018	9.590	1.3	2.1×10^6	62.5 ± 3.4	17.5 ± 1.0
		Vegetated					67.0 ± 1.5	15.8 ± 2.3
	Outside	Bare	57.062	9.686	1.1	2.2×10^6	60.1 ± 2.8	19.8 ± 2.9
		Vegetated					53.1 ± 1.7	19.7 ± 3.1
Horsens	Inside	Bare	55.874	10.03	1.35	1.3×10^6	46.3 ± 0.2	15.5 ± 6.1
		Vegetated					50.2 ± 9.0	6.6 ± 4.2
	Outside	Bare	55.815	10.057	1.25	1.6×10^6	27.3 ± 5.6	3.1 ± 0.5
		Vegetated					33.0 ± 4.5	6.8 ± 2.3
South Funen	Inside*	Bare	55.039	10.691	2.25	2.8×10^5	43.6 ± 7.1	17.2 ± 5.0
		Vegetated					77.7 ± 1.2	61.1 ± 0.5
	Outside†	Bare	54.997	10.669	1.1	1.2×10^6	45.8 ± 0.8	10.8 ± 1.8
		Vegetated					50.5 ± 3.5	9.2 ± 1.9
Roskilde	Inside‡	Bare	55.706	12.014	2.4	9.7×10^5	27.1 ± 2.8	24.7 ± 4.2
		Vegetated					29.7 ± 1.8	18.1 ± 3.7
	Outside§	Bare	55.886	12.021	3.3	9.9×10^5	67.4 ± 7.2	55.1 ± 2.5
		Vegetated					61.1 ± 4.1	42.6 ± 4.1

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†Lunkebugten.

‡Frederikssund.

§Bognaes.

were calculated using the constant rate of supply (Appleby and Oldfield 1978) dating model in the cores from Roskilde and using the constant flux constant sedimentation model (Krishnaswamy et al. 1971) in the core obtained in the sheltered site of South Funen due to the presence of a surface mixed layer at this site. Cores from other sites could not be reliably dated. Further details on radioisotope analyses are in Supporting Information Data S1.

Sediment and biomass stocks and sequestration rate calculations

OC and N densities (g cm^{-3}) were calculated as the product of the sample's OC or N content (%) and bulk density (g dw cm^{-3}). OC and N stocks were calculated as described by Howard et al. (2014), by summing the OC or N density expressed per unit surface area (g m^{-2}) from each subsection down to 50 cm depth. A depth of 50 cm was selected as most (two thirds) of our cores reached this depth or deeper. For the remaining, shorter (~ 17 – 47 cm) cores, we extrapolated to 50 cm by examining the depth trends in DBD, OC, and N (see Supporting Information Data S1). Stocks were also calculated down to 25 cm (stocks_{25cm}) to allow comparisons to OC stocks from previous studies in *Z. marina* meadows and to 1 m depth (stocks_{100cm}), used for national stock estimates so they can be compared to other BC ecosystems because 1 m is the standard

minimum sediment length suggested for BC studies (Howard et al. 2014).

The average CAR and NAR ($\text{g m}^{-2} \text{yr}^{-1}$) were calculated as the product of the average SAR (m yr^{-1}) and the average OC or N densities (g m^{-3}) from the sediment layers where excess ^{210}Pb is present. To scale up stocks and accumulation rates to the national ecosystem extent, average stocks and accumulation rates values were multiplied by the potential Danish eelgrass extent.

Data analysis

For shoot density, aboveground and belowground biomass and their associated OC and N stocks, and aboveground to belowground biomass ratio, differences among locations and exposure (sheltered vs. exposed) were evaluated using two-way ANOVAs. Statistical differences in sediment OC and N stocks were assessed using three-way ANOVA, where the fixed factors were location, exposure, and sediment type (vegetated vs. unvegetated). Differences among environmental conditions were assessed using post hoc Tukey's test when the result of ANOVA test showed a significant interaction between factors or a significant main effect with more than two levels.

A Bayesian mixing model (package *simmr*; Parnell 2021) was used to determine the relative contribution of primary producers to the composition of sediment organic matter (OM) over the top 50 cm of sediment. Three variables ($\delta^{13}\text{C}$,

$\delta^{15}\text{N}$, and C/N molar ratio) were used together and seven end members were initially considered as potential sources: saltmarsh plants, terrestrial plants, seston (or suspended particulate OM), marine macroalgae and microalgae, and roots, rhizomes, and shoots of eelgrass.

In order to explain the variation in OC and N stocks, two generalized additive models were fitted for OC and N stocks as response variables. The explanatory variables included the three grain size variables (median grain size, sorting, and silt and clay content), sediment OM source tracers ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C/N ratio), the level of physical exposure by wind-driven waves of each study site, and the categorical variables of coastal area and sediment type (vegetated, bare). For the estimation of the physical exposure by wind-driven waves, a simplified approach as in Rasmussen et al. (2015) was used and the relative exposure index was reported as the average value for the year 2019 (Table 1). Since OC and N stocks are skewed and always positive, they were modeled using the gamma distribution with the log link function. The specific importance and effect of each predictor on the response were assessed by the significance (p -value) and the partial effect plot of each smoothed term. Besides the model assumptions of homogeneity and normality, we also checked concurvity, that is, nonlinear variable dependence, between smooth terms by obtaining matrices of pairwise concurvities, which show the degree to which one smooth term is non-linearly related to each of the other smooth terms. Generalized additive models were fitted using the “mgcv” package (Wood 2011). To supplement results from the generalized additive model with OC and N stocks as response variables, other generalized additive models were run using OC and N densities as response variables, which allowed using a larger dataset.

Data are provided as mean \pm standard error of the mean unless stated otherwise. All statistics were performed with R statistical software (R Core Team 2021). Further details of data analyses can be consulted in Supporting Information Data S1.

Results

OC and N stocks of eelgrass biomass

Averaged OC and N biomass stocks ranged 10–75 g OC m^{-2} and 0.4–2.6 g N m^{-2} for detritus, 22–186 g OC m^{-2} and 0.7–7.7 g N m^{-2} for aboveground eelgrass biomass, and 17–109 g OC m^{-2} and 0.7–11 g N m^{-2} for belowground eelgrass biomass across sites (Fig. 2A). The average OC stock of the aboveground eelgrass biomass was 73 ± 13 g OC m^{-2} , while the average belowground biomass OC stock (roots and rhizomes) was 44 ± 6 g OC m^{-2} . The average N stock of the aboveground living seagrass biomass was 2.8 ± 0.5 g N m^{-2} , while the average belowground biomass N stock (roots and rhizomes) was 1.15 ± 0.14 g N m^{-2} . The average N stock of the aboveground detritus biomass was 0.9 ± 0.2 g N m^{-2} .

The interaction between location and exposure on OC stocks affected all three biomass compartments: aboveground

biomass ($p = 0.034$), belowground biomass ($p = 0.029$), and detritus ($p = 0.001$) (Supporting Information Table S3). This same interaction also had an effect on N stocks of all biomass compartments: aboveground biomass ($p = 0.044$), belowground biomass ($p = 0.031$), and detritus ($p = 0.022$) (Supporting Information Table S3). For the aboveground biomass and the detritus, the interaction seemed to be driven by a large difference in stocks between exposures in Roskilde; while for belowground biomass, South Funen showed the greatest difference between exposures. Tukey's post hoc tests showed no significant differences in either of the biomass-associated stocks between exposed and sheltered sites. The only exceptions were the OC and N stocks associated with detritus in Roskilde fjord, which were significantly higher in the exposed site (Fig. 2B), as well as the N stocks associated with belowground biomass in South Funen, which was also higher in the exposed site.

Sediment OC and N stocks

The overall average OC stock in the top 50 cm (OC stock_{50cm}) of sediment was 2.6 ± 0.3 kg OC m^{-2} including both vegetated and unvegetated cores and ranged from 0.89 ± 0.08 to 9.9 ± 0.8 kg OC m^{-2} , both values from cores located at unvegetated areas of Horsens (Fig. 2B). The OC stock_{50cm} in eelgrass sediments averaged 2.2 ± 0.2 kg OC m^{-2} at vegetated plots while at nearby currently unvegetated plots, OC stock_{50cm} averaged 3.1 ± 0.6 kg OC m^{-2} . OC stock_{100cm} averaged 7.3 ± 0.8 kg OC m^{-2} and ranged from 1.4 ± 1.0 to 22.3 ± 0.1 kg OC m^{-2} . OC stock_{25cm} averaged 1.2 ± 0.2 kg OC m^{-2} and ranged from 0.47 ± 0.03 to 3.8 ± 1.1 kg OC m^{-2} (Fig. S1). As for the N stocks_{50cm}, the overall average was 0.23 ± 0.01 kg N m^{-2} . Vegetated sites averaged 0.22 ± 0.01 kg N m^{-2} , while unvegetated sites averaged 0.23 ± 0.02 kg N m^{-2} with no statistical difference between vegetated and unvegetated sites.

There was a significant interaction between location, exposure, and sediment type for OC stocks ($p < 0.001$) and for N stocks ($p < 0.001$) (Supporting Information Table S4) indicating complicated and site-specific patterns. Tukey's post hoc tests showed that, for OC stocks, there was a significant difference between vegetated and unvegetated plots in only one of the eight sites (Horsens exposed) which in fact had larger OC stocks in the unvegetated site (Fig. 2B). For N stocks, there were significant differences between vegetated and unvegetated plots in three sites, again including Horsens exposed, which, together with South Funen sheltered, showed larger N stocks in the unvegetated sites (Fig. 2B). For Nibe exposed the difference was the other way, with higher N stocks at the vegetated site. There was no consistent difference in OC and N stocks between sheltered and exposed sites (Fig. 2B).

Sedimentary CAR and NAR

The ^{210}Pb data showed either very small concentrations in the upper few layers or a complete lack of accumulation of

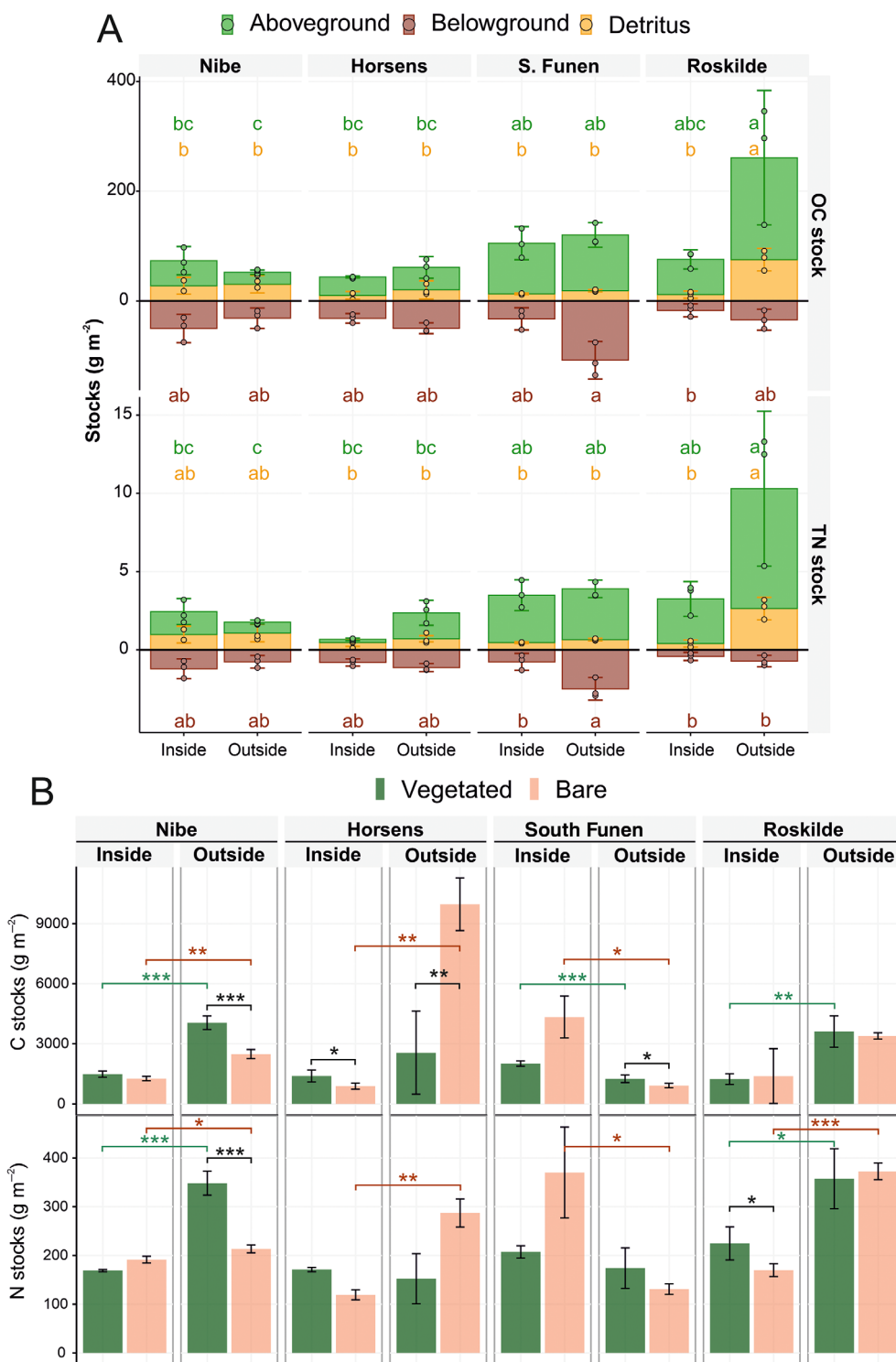


Fig. 2. (A) OC and N stocks associated with aboveground and belowground eelgrass biomass and detritus. Different lower-case letters over the barplots indicate statistically significant differences among conditions (Tukey's test comparisons, $p < 0.05$) for the eelgrass aboveground compartment (green letters), for the detritus stocks (yellow letters), and for the eelgrass belowground compartment (brown letters). (B) Mean cumulative amount of sediment OC and N stocks (g m^{-2}) on the top 50 cm depth (decompacted) sediment core. Different lower-case letters over the barplots indicate statistically significant differences among conditions (Tukey's test comparisons, $p < 0.01$) for the OC sediment stocks (top) and N sediment stocks (bottom). Error bars represent 95% confidence intervals. Note the different scales used in OC and N stocks.

excess ^{210}Pb in five out of the eight cores, pointing to minimal or negligible net sedimentation rates and indicating that these sites are either affected by erosion or are not depositional sites (Supporting Information Fig. S2). For example, at the sheltered site of Roskilde, the concentrations of excess ^{210}Pb reached the horizon at only 5 cm so we could not calculate a sedimentation rate with confidence, although it would likely be lower than 0.05 cm yr^{-1} .

Two cores that could be dated with confidence, one from the exposed site in Roskilde and one from the sheltered site in South Funen, yielded sediment accretion rates of 0.28 ± 0.05 , and $0.74 \pm 0.04\text{ cm yr}^{-1}$, respectively (Table 3). The estimate for South Funen should be considered an upper limit given the presence of an upper 17-cm-thick mixed layer. OC was accumulated at < 5 , 36 ± 20 and $134 \pm 26\text{ g OC m}^{-2}\text{ yr}^{-1}$ over the last decades at the exposed and sheltered Roskilde site and the sheltered Funen site, respectively. The corresponding NAR over the last decades were < 0.59 , 3.9 ± 0.2 and $14 \pm 1.9\text{ g m}^{-2}\text{ yr}^{-1}$.

At sites that did not show excess ^{210}Pb , CAR, and NAR were considered null based on negligible net accumulation of sediment. The overall CAR considering all cores averaged $22 \pm 17\text{ g OC m}^{-2}\text{ yr}^{-1}$. For NAR averaged $2.3 \pm 1.7\text{ g N m}^{-2}\text{ yr}^{-1}$ (Table 2).

Sediment OM sources

The Bayesian mixing model results indicated that algae-derived OM ($59\% \pm 18\%$, mean \pm SD) followed by seagrass ($33\% \pm 17\%$) were the main sources of OM across all sites. Seagrass was the most important source of OM in South Funen ($48\% \pm 14\%$) followed by Nibe ($43\% \pm 6\%$). In general, a higher proportion of OM was sourced from seagrass in vegetated plots compared to unvegetated plots, except for the sheltered sites of Nibe and Roskilde (Fig. 3). The OM in sediments from Roskilde was predominantly derived from algal OM ($84\% \pm 9\%$). There was no clear systematic difference between vegetated and unvegetated plots across coastal areas regarding the contribution of algal sources (Fig. 3). The contribution of terrestrial and saltmarsh plants to eelgrass sediments was

minimal but was slightly higher in unvegetated sediments. Terrestrial and saltmarsh plants contributed the most to OM in the exposed area of Horsens, particularly in the unvegetated sediments (Fig. 3).

Downcore profiles of sediment C/N, OC and N stable isotopes, and densities

Several (approximately one third) of the retrieved sediment cores reached deeper than 50 cm into the sediment. In these longer cores, depth profiles of OC and N density often showed two or even threefold increasing trends with depth below 40–50 cm (Fig. 4). In the longest cores, sediment profiles showed decreasing trends toward surface layers for $\delta^{13}\text{C}$ and C/N, ending with values in top sediments between -15% and -25% and 10–15, respectively, values which are comparable to those from algae and seston (Supporting Information Table S4). Similarly, there were increasing trends for $\delta^{15}\text{N}$ toward surface layers, reaching values between 5 and up to 15‰ in top sediments (Fig. 4). These trends toward the sediment surface seemed to start around or before the 1940s, according to the dates of the three cores that were successfully dated with ^{210}Pb (Fig. 4). Most depth profiles showed a reverse of the long-term trends of most variables over the top 10–20 cm, that is, increasing OC, N density, C/N ratio, and $\delta^{13}\text{C}$ from 10 cm depth toward the surface (Fig. 4) indicative of more recent deposits and ongoing diagenetic processes. It is remarkable that most of the depth profiles of the different sedimentary variables showed very similar trends and levels between bare and vegetated areas (Fig. 4).

Drivers of OC and N sediment stocks

The resulting generalized additive models used to assess potential mechanisms favoring OC and N stocks, had an adjusted R^2 of 84.2% and 94.3%, respectively (Supporting Information Table S5). Sorting, C/N ratio, and the relative exposure index correlated significantly with OC stocks while location (higher N stocks in Horsens and Roskilde compared to Nibe and South Funen), sorting, content of silt and clay,

Table 3. Summary of site-specific eelgrass variables and macroalgae biomass. Values expressed as mean \pm standard error ($n = 3$). Asterisks indicate sites where macroalgae biomass was only found in one out of the three sampled plots.

Coastal area	Exposure	Shoot density (shoots m^{-2})	Aboveground biomass (g m^{-2})	Belowground biomass (g m^{-2})	Aboveground to belowground biomass ratio	Macroalgae biomass (g m^{-2})
Horsens	Inside	1302 ± 114	96 ± 3	116 ± 17	0.86 ± 0.12	105 ± 9
Horsens	Outside	802 ± 198	118 ± 29	170 ± 19	0.67 ± 0.11	84^*
Nibe	Inside	415 ± 75	134 ± 38	167 ± 43	0.85 ± 0.23	4 ± 1
Nibe	Outside	340 ± 57	68 ± 8	106 ± 33	0.72 ± 0.14	34 ± 3
Roskilde	Inside	283 ± 65	194 ± 27	53 ± 20	4.4 ± 1.0	196 ± 57
Roskilde	Outside	453 ± 142	563 ± 190	103 ± 29	5.2 ± 0.8	0^*
South Funen	Inside	981 ± 147	272 ± 46	105 ± 38	3.5 ± 1.6	124 ± 18
South Funen	Outside	2339 ± 222	288 ± 32	335 ± 57	0.85 ± 0.14	89 ± 6

Table 2. Average \pm standard error (and range within parenthesis) for SAR, CAR, and NAR in eelgrass vegetated sediment cores. CAR and NAR values were calculated as the product of the average SAR and the average OC or N densities along the dated region. One vegetated core per site was attempted dated using ^{210}Pb . Five dated cores from Nibe, Horsens and South Funen (outside) showed lack of sediment deposition or intense sediment erosion preventing net sediment accumulation (see Supporting information Fig. S6).

Coastal area	Exposure	SAR (cm yr^{-1})	CAR ($\text{g OC m}^{-2} \text{yr}^{-1}$)	NAR ($\text{g N m}^{-2} \text{yr}^{-1}$)
South Funen	Inside	0.74 ± 0.04	134 ± 26	14.0 ± 1.9
Roskilde	Inside	0.28 ± 0.05	36 ± 20	3.9 ± 0.8
Roskilde	Outside	< 0.05	< 5	< 0.59

and the relative exposure index correlated significantly with N stocks (Fig. 5). The relative exposure index was the strongest predictor of OC stocks, considering the broader range of the partial effect (γ -axis values) affected by exposure (Fig. 5A-3). The sediment type (vegetated, bare) did not correlate significantly with either sediment OC or N stocks (Fig. 5A; Supporting Information Table S5).

The partial effect plots (Fig. 5) revealed that OC and N stocks decreased with increasing sorting degree, that is, the more poorly sorted the sediment, the lower the stock (Fig. 5A-1,B-1). OC stocks increased nonlinearly with higher values of sediment C/N ratio, with stabilization around 14 (Fig. 5A-5). OC and N stocks decreased with increasing exposure (partial plot for the relative exposure index, Fig. 5A-3,B-3). Silt and clay content showed positive linear relationships with OC and N stocks, although non-significant for OC stocks (Fig. 5A-2,B-2). It should be noted that there were high concurrency pair-wise values between relative exposure index and sorting, relative exposure index and silt and clay, as well as between sorting and $\delta^{13}\text{C}$ (Supporting

Information Table S6). The generalized additive models predicting OC and N densities showed a strong positive relationship between the content of silt and clay and both OC and N densities but showed no significant effect of sorting degree (Supporting Information Fig. S3; Table S5). Moreover, the interaction terms between OM tracers ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, CN) used in this second generalized additive models indicated more clearly that terrestrial ($\delta^{13}\text{C} < -22\text{‰}$ and $\text{CN} > 30$, see Supporting information Fig. S4) and eelgrass sources ($\delta^{13}\text{C} > -15\text{‰}$ and $\delta^{15}\text{N} < 10\text{‰}$, see Supporting information Fig. S4) were related with high OC and N densities, while sestonic sources ($\delta^{13}\text{C} < -22\text{‰}$ and $\delta^{15}\text{N} > 5\text{‰}$, see Supporting information Fig. S4) were associated with lower OC and N densities (Supporting Information Fig. S3).

Eelgrass variables and macroalgal biomass

Average shoot densities ranged from 283 ± 113 shoots m^{-2} in the sheltered site of Roskilde to 2339 ± 385 shoots m^{-2} in the exposed area of South Funen (Table 3). There was a significant

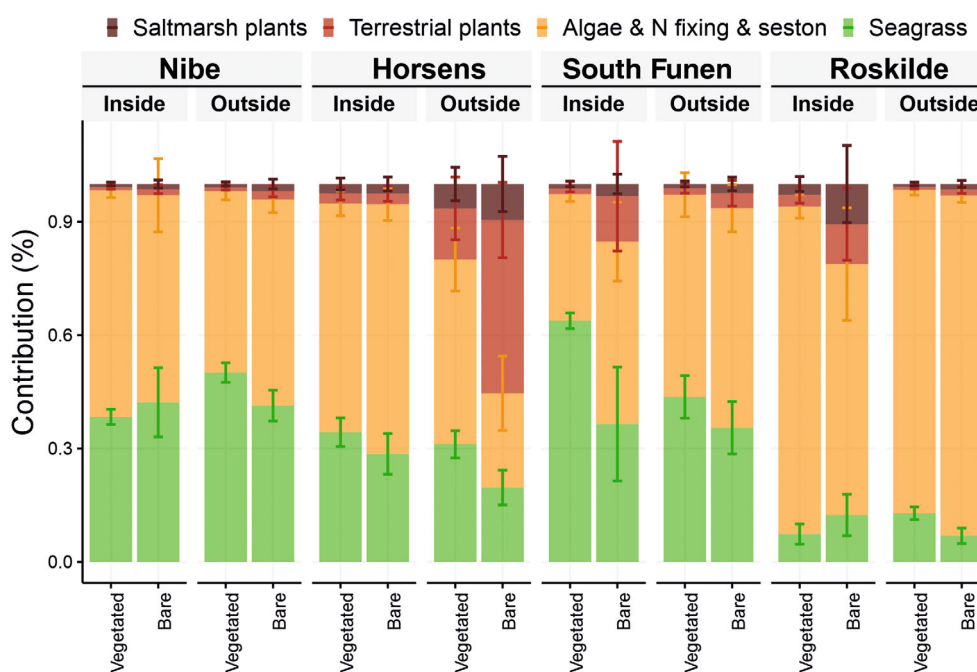


Fig. 3. Results obtained with the Bayesian isotopic mixing model displaying the average stacked proportional contributions by each source to the top 50 cm of vegetated and nonvegetated sediments. Rhizome, shoot, and rhizome were combined after running the model into a source called “Seagrass”; seston, and N-fixing algae and algae into another source called “Algae and N fixing and seston”. Error bars represent 95% confidence intervals.

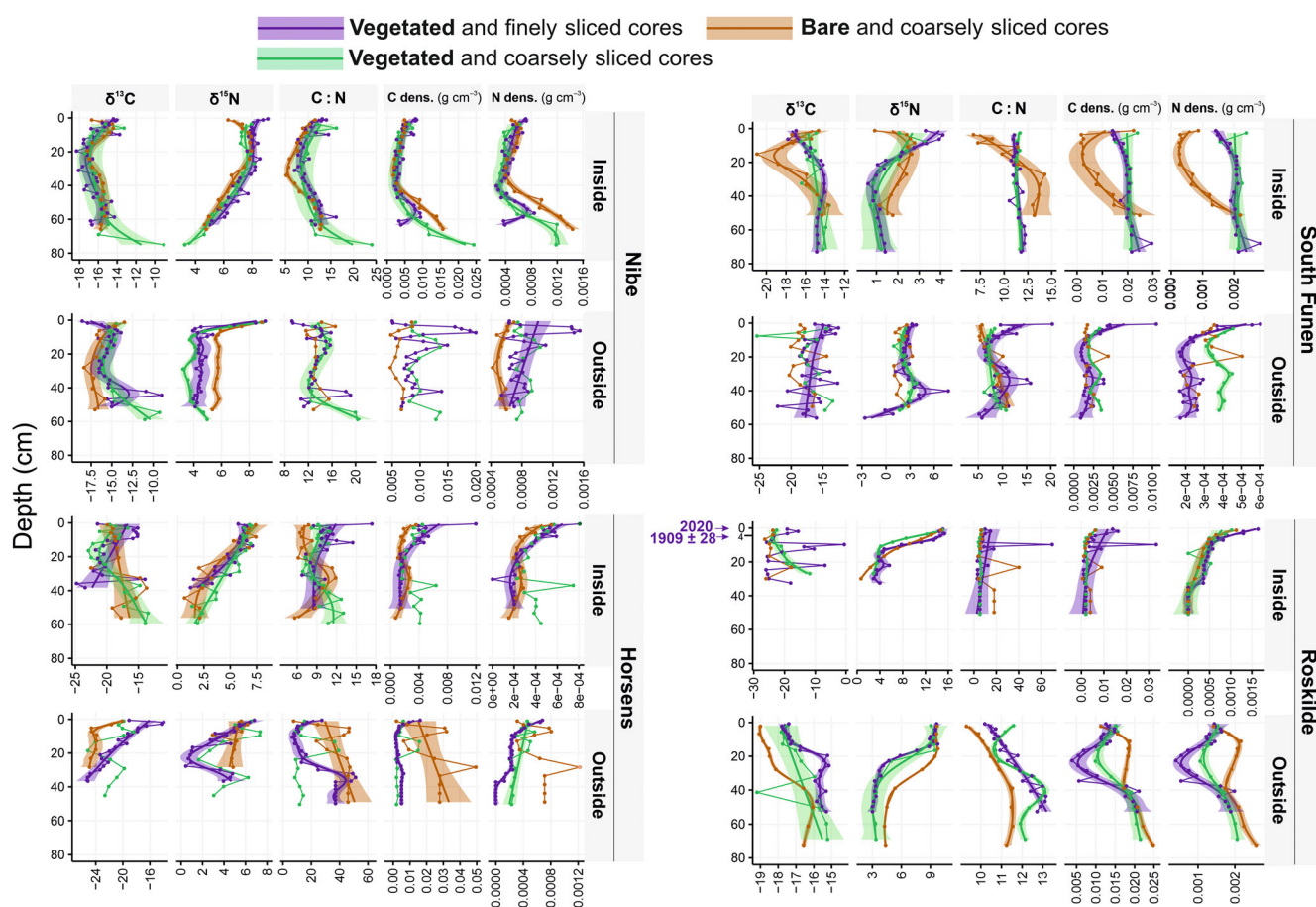


Fig. 4. Stable isotopes (‰), C : N ratios, and OC and N density (g cm^{-3}) depth profiles. Note the different scales used for every site. Colored solid lines indicate the fitted smooth functions of time (generalized additive models, formula = $y \sim s[x]$) and shaded regions are 95% point-wise confidence intervals. In the two cases where ^{210}Pb dating was possible (only the dark green profiles representing the finely sliced cores from each site were attempted dated), some dates are shown next to their corresponding depth. Only generalized additive models with significant ($p < 0.05$) trends are shown.

interaction between the effects of location and exposure ($p < 0.001$) on shoot density (Supporting Information Table S3). South Funen was the only location where the exposed site had a significantly different (higher) shoot density than the sheltered. The shoot density in the exposed site of South Funen was also the highest observed (Tukey's post hoc test: $p < 0.05$).

In terms of eelgrass biomass, aboveground biomass averaged $217 \pm 38 \text{ g DW m}^{-2}$ and belowground biomass averaged $147 \pm 21 \text{ g DW m}^{-2}$ across sites (Supporting Information Fig. S5A; Table 2). The ratio of aboveground to belowground biomass was 2.1 ± 0.4 across sites, with estimates per site ranging from 0.72 ± 0.14 in the exposed area of Horsens to 5.2 ± 0.8 in the exposed area of Roskilde (Supporting Information Fig. S5B; Table 3). There was a significant interaction between location and exposure on both, aboveground biomass ($p = 0.040$) and belowground biomass ($p = 0.031$) (Supporting Information Table S3). The significant interactions are likely driven by the greater difference in aboveground biomass between exposures in Roskilde and in belowground biomass in South Funen. There were no

significant differences neither in aboveground nor belowground biomass between the exposed and sheltered sites within coastal areas (Tukey's post hoc test: $p < 0.05$). There was a statistically significant effect only of location ($p < 0.001$) on aboveground to belowground ratio (Supporting Information Table S3). Roskilde had significantly higher aboveground to belowground ratio values compared to the rest of coastal areas (Tukey's post hoc test: $p < 0.05$; Supporting Information Fig. S5B).

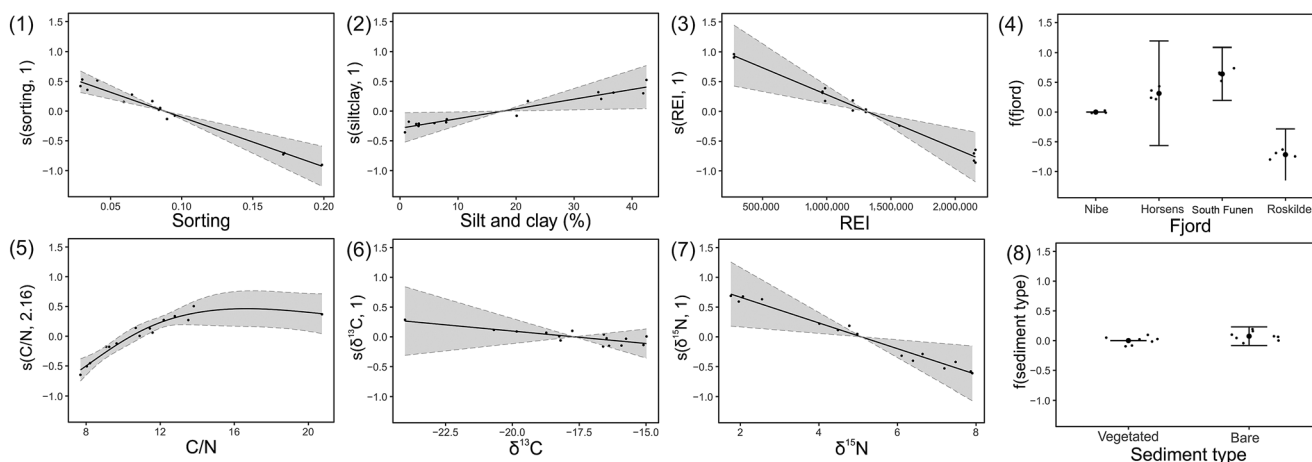
Average macroalgal biomass ranged from nearly 0 g m^{-2} in the exposed area of Roskilde to $197 \pm 57 \text{ g m}^{-2}$ at the inner area of the same coastal area. Except for Nibe, all coastal areas showed higher macroalgal biomass in inner, sheltered sites (Table 3).

Discussion

Factors controlling sediment OC and N density and stocks

Our results point to two key mechanisms that together influence OC and N densities and stocks in Danish eelgrass

A) GAM model with OC stocks as response variable



B) GAM model with N stocks as response variable

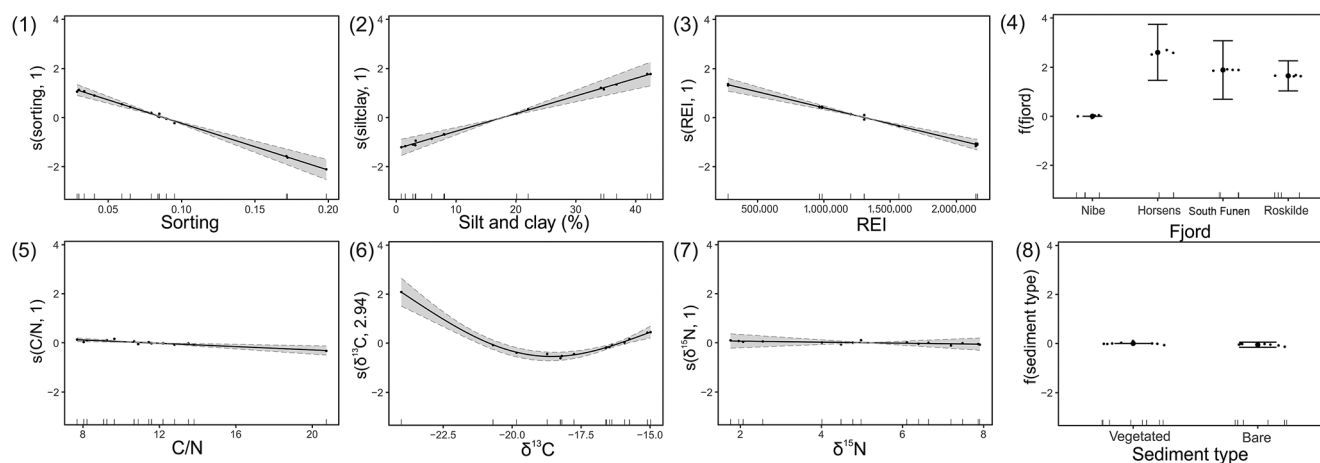


Fig. 5. Generalized additive model plots showing the partial effects (contribution of that term to the model prediction) of selected explanatory variables on (A) OC stocks and (B) N stocks. The y-axis represents the partial effect of each covariate to the fitted response, centered on 0. The y-axis label can indicate a smoothed variable, $s(x)$, with the degree of smoothing within parenthesis next to the variable name; or a categorical variable, $f(x)$. Positive values of the smoothed function (y-values) indicate a positive effect of the term on the x-axis on the response variable. The solid black lines represent the fitted curve of each independent variable, while the shaded areas indicate the 95% confidence intervals. The points represent the partial residuals.

meadows: the physical stabilization related to the sediment characteristics and the type and recalcitrance of the accumulated OM, both of which seem largely influenced by the site hydrodynamic exposure.

Regarding physical stabilization, higher content of silt and clay as well as better sorted sediments correlated with higher OC and N densities and stocks (Fig. 5). The association between sediment OM and smaller particles has been widely observed and attributed to the physical stabilization of the OM being adsorbed on the mineral surfaces, and hence protected from microbial activity, as well as to the consecutive biotic suppression as a result of the lower permeability and oxygen content in fine-grained sediments (Burdige 2007). This relationship is in line with the findings of former studies on

eelgrass meadows (Miyajima et al. 2015; Dahl et al. 2016; Ricart et al. 2017).

As for the type and recalcitrance of OM, the molecular composition of sediment OM is a widely recognized driving variable of OC storage in soils (Burdige 2007). This study showed that terrestrial OM, characterized by high content of lignocellulose and other refractory compounds, is linked with high sediment OC and N content. Eelgrass-derived material is also associated with higher OC and N densities, which indicate that the refractory lignin content of *Z. marina* tissues contributes to a slower degradation and an efficient OC and N preservation in the sediments (Klap and Hemminga 2000; Banta et al. 2004). In contrast, sediment OC and N densities were lower with higher algae and seston contribution,

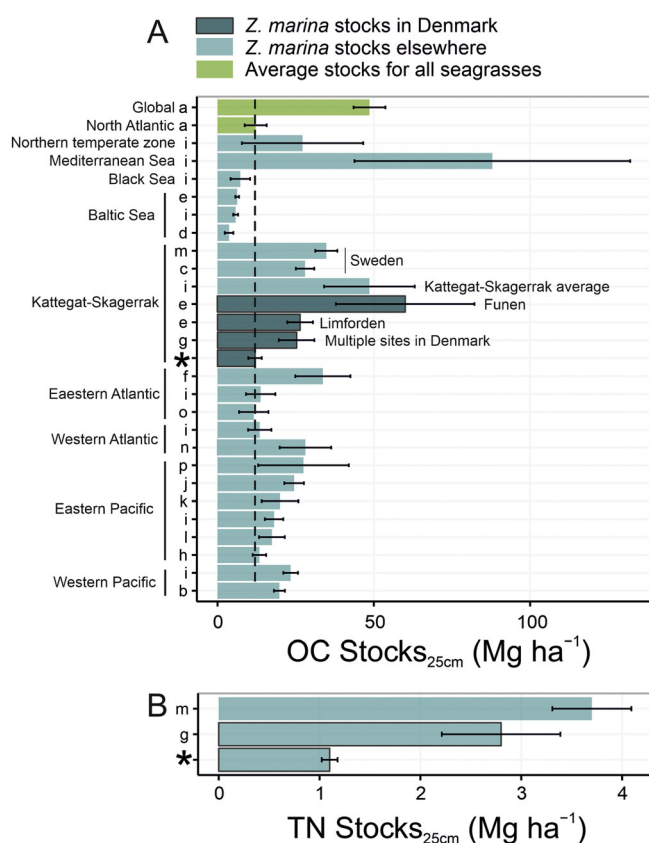


Fig. 6. Average cumulative amount of sediment OC stocks (**A**) and N stocks (**B**) in Mg ha^{-1} in the top 25 cm of sediment. Error bars represent 95% confidence intervals. Asterisks (*) indicate the results from the present study, which are compared with other data on *Zostera marina* in Denmark (bars with black outlines) and elsewhere along the species' distribution range. The dotted line shows the average OC stock for our study. The upper bar represents the average global OC stock for seagrasses while the second bar represents the average global OC stock for seagrasses located in the North Atlantic region. The letter a is Fourqurean et al. (2012); b is Miyajima et al. (2015); c is Dahl et al. (2016); d is Jankowska et al. (2016); e is Röhr et al. (2016); f is Green et al. (2018); g is Kindeberg et al. (2018); h is Postlethwaite et al. (2018); i is Röhr et al. (2018); j is Cuellar-Martínez et al. (2019); k is Kauffman et al. (2020); l is Prentice et al. (2020); m is Moksnes et al. (2021); n is Novak et al. (2020); o is Potouroglou et al. (2021); p is Ward et al. (2021).

probably because algae are often rich in compounds that are easily degraded (e.g., aliphatics and N-rich compounds; Laursen et al. 1996).

The degree of hydrodynamic exposure also strongly affected OC and N stocks in this study, with higher hydrodynamic energy linked to lower OC and N storage, which confirms previous observations in eelgrass meadows (Kindeberg et al. 2018; Röhr et al. 2018). Previous studies in tropical and subtropical meadows have also observed a large impact of the hydrodynamic setting on sediment OC storage (Howard et al. 2016; Samper-Villarreal et al. 2016; Barry et al. 2018). Hydrodynamic exposure can influence sediment OC and N

through different mechanisms: sites with high hydrodynamic energy do not favor the deposition of small sediment particles, have higher export rates of OM and erode more easily the already buried OC and N (Mazarrasa et al. 2018). Moreover, seagrasses do not thrive in highly exposed environments, and those meadows that can endure these environmental conditions are usually patchier, with lower efficiency at reducing water flow and trapping particles, and hence have lower OC and N storage (e.g., Ricart et al. 2017). The high concurrency between sediment particles, OM source, and hydrodynamics in the generalized additive models relate to the fact that the seagrass presence and the proportion of fine sediment particles would ultimately depend (conjunctly and independently) largely on the geomorphic and hydrological setting as explained.

Impact of eutrophication over time

The dated cores revealed temporal trends going back to the mid-20th century. Changes observed over the top 10 cm cannot be clearly linked to historical ecosystem changes since the top sediment layers are often affected by diverse physical and biogeochemical processes which modify the sediment characteristics (Marbà et al. 2006; Moksnes et al. 2021). However, below the active sediment layers, the observed temporal profiles of stable isotopes and C/N ratios in dated cores indicate a decreased contribution of eelgrass-derived material and an increased contribution of seston-algal OM toward surface layers and, hence, present time.

The decreasing levels of sediment OC and N densities toward present in dated cores reflect a long-term reduction and loss of eelgrass ecosystem services related to OC and N retention, likely in response to the overall increasing eutrophication in Denmark since 1900 (Conley et al. 2007). Observed increasing trends in sediment $\delta^{15}\text{N}$ over the last century could be attributed to these overall increased loadings of land-derived anthropogenic N (characterized by high positive values of $\delta^{15}\text{N}$, 10–30‰; Peipoch et al. 2012). The depth profiles of $\delta^{15}\text{N}$, with lower values in deeper layers, were opposite to the trends driven by postdepositional diagenetic changes since the majority of studies suggest that bacterial degradation usually leads to an increase in $\delta^{15}\text{N}$ with depth (Robinson et al. 2012). Moreover, the orders of change with depth in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are much wider ($\sim 4\text{--}8\text{‰}$ for $\delta^{13}\text{C}$ and $\sim 3\text{--}12\text{‰}$ for $\delta^{15}\text{N}$) than the orders of change attributed to kinetic fractionation during the decay of sediment OM (1–3‰ for $\delta^{13}\text{C}$ and $\leq 5\text{‰}$ for $\delta^{15}\text{N}$; Boström et al. 2007; Sigman and Fripiat 2019). The changes of the sediment stable isotopes with depth can be, hence, attributed primarily to changes in OM sources, rather than only to postdepositional degradation. The same depth trends of $\delta^{15}\text{N}$ reported here have already been described in sediments under eelgrass meadows in Denmark and Sweden (Kindeberg et al. 2019). Increasing nutrient concentrations likely changed the composition of coastal primary producers with less eelgrass and more (opportunistic) algae dominating (Krause-Jensen et al. 2012; Boström

et al. 2014). A reduced eelgrass distribution means less refractory eelgrass material inputs into sediments as well as lower retention of fine particles (as confirmed by the temporal and depth trends of silt and clay; Supporting Information Fig. S6), both leading to lower OM preservation. Increased contribution of labile algal material would further favor the decay as opposed to the preservation of the sedimentary OM (Laursen et al. 1996; Klapp and Hemminga 2000).

Comparison between vegetated and bare sites

OC and N stocks showed surprisingly no significant differences between currently vegetated and bare sediments in most study sites. Furthermore, only one out of the eight study sites (Horsens exposed site) had significantly different OC and N stocks between vegetated and bare plots, with in fact higher stocks in the bare plot. The stable isotope values in the bare plot of the exposed site in Horsens pointed to a content of more than 50% of terrestrial OM, suggesting that this bare site may not be comparable to its corresponding vegetated site. Considering previous studies nearby our exposed study site in Horsens, this terrestrial organic material could be gyttja deposits, OC-rich and fine sediments deposited before the sea level rise during the late Pleistocene in low-energy environments, formed from the partial decay of vegetation remains, and usually protected by eelgrass meadows above them (Skriver et al. 2018). The proportion of eelgrass-derived OM was higher in most vegetated plots as expected. Differences in OC, N, and OM between vegetated and adjacent bare sites have been reported in many other studies (Miyajima et al. 2015; Jankowska et al. 2016; Prentice et al. 2020). However, there are also cases of nonsignificant differences in OC storage in seagrass meadows compared to unvegetated adjacent areas (Novak et al. 2020; Potouroglou et al. 2021; Ward et al. 2021).

The absence of a consistent difference in stocks between vegetated and nonvegetated sites could be attributed to the contrasting environmental conditions among our sites. We identified a positive linear relationship between the hydrodynamic exposure and the ratio of OC stocks_{50cm} between vegetated and bare adjacent areas (adj. $R^2 = 0.60$, $F[1, 5] = 10.12$, p -value = 0.025; Supporting Information Fig. S7). This could indicate that eelgrass meadows do have a higher net OC storage compared to bare areas in locations with high hydrodynamics, where eelgrass can more effectively reduce water flow compared to unvegetated spots. In contrast, it is possible that in sheltered areas, eelgrass meadows do not have such net impact because these depositional environments would already favor allochthonous OC accumulation and storage. In fact, our results show that the allochthonous sources have the highest relative contribution to the organic stocks (59%), followed by eelgrass (33%) across all sites. These results align with previous findings, which reported that while seagrasses could contribute, on average, 50% of OC in sediments (Kennedy et al. 2010), that percentage was down to $\sim 30\%$, in

Z. marina meadows (Röhr et al. 2018), which highlights the relevant contribution of allochthonous sources to eelgrass sediment stocks. On top of this, the spatial dynamics of eelgrass meadows should be taken into consideration, *Z. marina* meadows can substantially change its area cover for short periods (Frederiksen et al. 2004). Hence, although currently unvegetated, the bare sites we studied could have been formerly vegetated and sediment pools could still represent past belowground eelgrass stocks. The fact that most depth profiles of stable isotopes and OC and N densities at currently unvegetated sites have very similar values and trends as their corresponding vegetated plots (Fig. 4) reinforces the hypothesis that these plots have been vegetated until recently and highlights the difficulty in finding adequate unvegetated reference sites. To fully comprehend the eelgrass net enhancement effect also on OC and N accumulation, it would have been relevant to get SAR from nearby bare areas. However, bare sites previously vegetated usually show low, negligible modern net accumulation of sediments (Arias-Ortiz et al. 2018).

Difficulties to assess the additional OC storage by eelgrass and the negligible SARs due to erosion in most of our study sites in Denmark complicate proving additionality (showing net gains in OC stocks or sequestration from a project compared to a baseline scenario) in future BC projects based on our current understanding. Additionality is an essential requirement of C verification schemes (Needelman et al. 2018).

OC and N storage and accumulation: A comparison

The average OC stock associated with living *Z. marina* biomass (above and belowground) is 117.4 ± 15.3 g OC m⁻², which is within the range estimated for *Z. marina* in temperate regions (63 ± 22 to 129 ± 35 g OC m⁻²; Röhr et al. 2018). On average, the OC stock in living *Z. marina* biomass contributes to $\sim 5\%$ of the total OC stock_{100cm}, which confirms the larger contribution of sediment OM to OC stocks compared to living tissues (Fourqurean et al. 2012; Röhr et al. 2018).

The average OC and N stocks_{25cm} of this study are lower than earlier estimates for the Kattegat-Skagerrak region (Fig. 6; Supporting Information Table S7). The difference is especially remarkable for OC stocks previously reported for Thurøbund, the sheltered South Funen site, where Röhr et al. (2018) reported the highest OC storage so far for temperate eelgrass meadows (265.2 ± 0.67 Mg OC ha⁻¹), while we estimated an order of magnitude lower (12.2 ± 1.1 Mg OC ha⁻¹). This large difference is striking considering that the study area is the same. Such a difference between our study and previous studies in Denmark could be due to, first, the inherent spatial variability of eelgrass meadows, which can be quite high (Frederiksen et al. 2004), and second, a methodological difference. We corrected for sediment compaction that occurs both in the field and during sediment extraction from the plexiglass core, but previous studies in Denmark do not report any such correction. Our cores from the inner vegetated South Funen

site suffered the highest compaction ($61\% \pm 0.1\%$; Supporting Information Table S8). If compaction is not corrected for, stocks are overestimated (up to 22% according to Smeaton et al. 2020) because the calculation does not take into account the reduced thickness of the soil profile during compaction, and therefore, the sediment layers over which the OC is added up is thicker than it should really be.

Our average OC stocks_{25cm} are within the range of averages reported for eelgrass meadows located in the Atlantic and the Pacific, as well as for eelgrass meadows across all temperate latitudes reported by Röhr et al. (2018) (Fig. 6; Supporting Information Table S7). By contrast, the global mean value for world seagrass ($48.6 \text{ Mg OC ha}^{-1}$; Fourqurean et al. 2012) is fourfold higher than the average OC stock_{25cm} from this study ($12 \pm 1.1 \text{ Mg OC ha}^{-1}$), this high difference is mainly due to the fact that the global mean value is biased toward data from larger seagrasses with higher capacity to capture and store OC (Miyajima et al. 2015). However, the average OC stock_{25cm} for all seagrass in the North Atlantic region (12.2 ± 1.8 , Fourqurean et al. 2012), is similar to the OC_{25cm} stock reported in the present study (Fig. 6; Supporting Information Table S7).

The lack of excess of ^{210}Pb in most of the cores we dated, which suggests a very low accumulation of sediments or even erosion over the last decades, seems to be related to higher hydrodynamic conditions at these sites, and hence erosion. This is seen in part with the exponential relationship observed between CAR, NAR, and the relative exposure index, the proxy of hydrodynamic exposure (Supporting Information Fig. S8). The temporal and depth trends pointing to less fine sediments and reduced seagrass contribution toward present times indicated a tendency for lower accumulation and/or increased resuspension of sediments toward present. The CAR and NAR estimated from the three cores that could be dated did align, however, with rates reported from other *Zostera* sp. meadows (Table 4). The very high CAR found in the inner site of South Funen ($134 \pm 26 \text{ g OC m}^{-2} \text{ yr}^{-1}$, Thurøbund) is remarkable and certainly points to this eelgrass meadow as a hotspot for OC drawdown.

Significance of OC and N stocks and burial rates for Denmark

To put our results in a larger context and to provide a rough national estimate for the current OC and N stock over the top 1 m and CAR and NAR over the last decades, we considered the data obtained in this study and the potential distribution area of Danish eelgrass meadows under current environmental conditions of 2200 km^2 (Staehr et al. 2019). The estimated OC stock in the upper 100 cm of eelgrass sediments based on this study is $16 \pm 2 \text{ Tg}$, which corresponds to more than 2 yr (225%) of Danish annual emissions emitted in 2020 (26.2 million metric tons of $\text{CO}_2\text{-eq}$, Friedlingstein et al. 2021; Supporting Information Table S9). The estimated annual OC burial rate over the last decades for Danish eelgrass meadows was $0.05 \pm 0.04 \text{ Tg yr}^{-1}$,

which means that eelgrass meadows could potentially capture $0.7\% \pm 0.5\%$ of total national CO_2 emissions by Denmark in 2020 (Supporting Information Table S9). As this estimate relates to the current potential eelgrass area in Denmark, it represents potential maximum baseline for latent OC storage and sequestration by eelgrass in Denmark. For eelgrass to contribute appreciably to climate change mitigation would require an expansion of the current areas via restoration of lost meadows (Oreska et al. 2020). The national scope for restoration has not been estimated, but only partial restoration is realistic as major stressors are still in play in Danish coastal habitats (Krause-Jensen et al. 2021).

Regarding N, Danish eelgrass meadows could store $1.5 \pm 0.2 \text{ Tg}$ over the top 100 cm of sediment, 20 times the terrestrial N load by Denmark in 2019 (74,000 tons, Thodsen et al. 2021; Supporting Information Table S9), and annually sequester $0.005 \pm 0.004 \text{ Tg}$ of N, which corresponds to $6.9\% \pm 5.2\%$ of the total terrestrial N load by Denmark in 2019 (Supporting Information Table S9). This confirms recent studies from Sweden that also found that the N-sink capacity of seagrass is greater than their OC-sink potential (Cole and Moksnes 2016; Moksnes et al. 2021).

The stocks and rates used for the above calculations were not exclusively attributed to the seagrass presence, as such an estimate would have required subtracting background values from those found in eelgrass sediments. However, the low reliability in the chosen unvegetated plots as adequate background areas prevented such an estimate. Therefore, these national estimates are likely overestimating the eelgrass meadow's enhancement of OC and N sequestration and storage.

Further investigation into fluxes of other major greenhouse gases, such as methane and nitrous oxide, and their drivers is needed in eelgrass meadows to determine their present and future role in mitigating climate change and, hence, to be able to fully implement BC estimates, inventories, or projects (Macreadie et al. 2019). Asplund et al. (2022) investigated CH_4 emissions in two *Z. marina* meadows in Denmark and found low rates equivalent to $0.017\text{--}0.02 \text{ t eCO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$. Our CAR in eelgrass meadows with net sediment accumulation ($6\text{--}134 \text{ g OC m}^{-2} \text{ yr}^{-1}$, Table 3, equivalent to $0.22\text{--}4.9 \text{ t eCO}_2 \text{ ha}^{-1} \text{ yr}^{-1}$) are between 10 and 298 times higher than the eCO_2 emissions from CH_4 . Hence, these three sites would still be net BC sinks after accounting for greenhouse gas emissions. If eelgrass ecosystems provide current and future net greenhouse gas sequestration, BC credits could be used in carbon markets to stimulate restoration. However, BC strategies will only contribute modestly to tackle such urgent problems as climate change. Hoegh-Guldberg et al. (2019) and Macreadie et al. (2021) estimate that BC strategies fully executed for global seagrass, saltmarsh, and mangrove ecosystems could, at most, represent 2–3% of global greenhouse gas emissions. The eelgrass in Denmark, if fully restored to its past extent (estimated to be three times higher than current extent) may be able to offset up to $2\% \pm 1.5\%$ of Denmark's annual

Table 4. Summary of previously reported CAR and NAR in seagrass meadows (mostly including data from eelgrass meadows) over the last decades or century. Values are reported as mean \pm standard error or as ranges.

Study	Species	Location	OC acc. Rate (g C m ⁻² yr ⁻¹) (mean \pm SE)
This study	<i>Zostera marina</i>	Denmark	22 \pm 17 (0–134)
Cuellar-Martínez et al. (2019)		San Quintín Bay (Mexico)	58.2 \pm 0.3
Jankowska et al. (2016)		Puck Bay (Baltic Sea, Poland)	12.1 \pm 9.7
Greiner et al. (2013)		South Bay (Virginia, USA)	36.7 \pm 2.8
Miyajima et al. (2015)		Seto Inland Sea (Japan)	6.8 \pm 2.0
Postlethwaite et al. (2018)		Southern Clayoquot Sound (Canada)	10.8 \pm 1.7
Prentice et al. (2020)		Pacific Northwest coast (Canada and USA)	24.8 \pm 4.5
Novak et al. (2020)		New England (USA)	60.1 \pm 30.3
Martins et al. (2021)	<i>Zostera nolteii</i>	Ria Formosa lagoon (South Portugal)	49.9 \pm 24.6
Mcleod et al. (2011)	World seagrasses, global estimate		138 \pm 38.0

Study	Specie	Location	N acc. rate (g N m ⁻² yr ⁻¹) (mean \pm SE)
This study	<i>Zostera marina</i>	Denmark	2.3 \pm 1.7 (0–14)
Aoki et al. (2020)	<i>Z. marina</i>	Virginia coastal bays (USA)	3.52 \pm 0.6
Martins et al. (2021)	<i>Zostera nolteii</i>	Ria Formosa lagoon (South Portugal)	6.02 \pm 2.9
Eyre et al. (2016)	<i>Zostera</i> sp.	SE Australia	2.7–3.9
	<i>Halophila</i> sp.	SE Australia	1.3–8
	<i>Ruppia</i> sp.	SE Australia	1.8–8.2
	<i>Posidonia</i> sp.	SE Australia	5.8
Saderne et al. (2020)	<i>Halophila uninervis</i>	Arabian gulf coast (Saudi Arabia)	21.8 \pm 18.3
Gacia et al. (2002)	<i>Posidonia oceanica</i>	NW Mediterranean	13.4
Pedersen et al. (1997)	<i>Cymodocea nodosa</i>	NW Mediterranean	3.57

Bold indicates results for the present study.

emissions. Carbon removal through nature-based solutions cannot be considered a stand-alone alternative to decarbonizing our economies, but a parallel and complementary action to reducing emissions at source. Reducing emissions at source means abandoning the paradigm of continued economic growth as the empirical evidence so far do not show that continued economic growth could be completely decoupled from resource use, carbon emissions, and biodiversity loss, and even if theoretically feasible, this decoupling is unlikely to be achieved fast enough to meet the Paris Agreement's 1.5°C warming limit (Parrique et al. 2019; Hickel and Kallis 2020).

Conclusion

This is the first study in Scandinavia and the Baltic Sea region to quantify SAR using ²¹⁰Pb dating in eelgrass meadows, determine OC and N stocks down to 50 cm, and analyze the temporal evolution of the Danish eelgrass meadows over the last century. OC stocks were in line with previous estimates for *Z. marina* in the North Atlantic area and our results highlighted how both spatial and temporal variability play a key role in eelgrass OC storage. Higher OC and N stocks were found in meadows with smaller sediment grain sizes, higher contribution of terrestrial or eelgrass material and lower hydrodynamic exposure. Sediment profiles

showed lower OC and N densities parallel to increases in labile algae-derived OM and reductions in seagrass-derived OM toward present, which suggested seagrass loss related to eutrophication in recent decades. The fact that most eelgrass meadows we studied did not accumulate excess ²¹⁰Pb, leading to null CAR and NAR, was related with higher levels of hydrodynamic exposure. Sites where OC and N did accumulate showed values in keeping with estimates for other eelgrass meadows. A first estimate shows that the current eelgrass meadows could capture at most 0.7% \pm 0.5% of annual CO₂ emissions by Denmark. Difficulties to assess the additional OC storage by eelgrass and the negligible sedimentation rates due to erosion in most of our study sites would complicate implementation of C verification schemes based on our current understanding in a Danish context. The role of eelgrass in buffering coastal eutrophication seems more impactful, potentially sequestering up to 7% of the current annual N load. This underlines that eelgrass meadows provide essential ecosystem services beyond OC sequestration, which should be considered holistically to protect and restore these ecosystems.

Data availability statement

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.21681329.v1>.

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Conflict of Interest

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