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Substantial seagrass blue carbon pools in the southwestern Baltic Sea include relics of terrestrial peatlands

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Seagrass meadows have a disproportionally high organic carbon (C_{org}) storage potential within their sediments and thus can play a role in climate change mitigation via their conservation and restoration. However, high spatial heterogeneity is observed in C_{org}, with wide differences seen globally, regionally, and even locally (within a seagrass meadow). Consequently, it is difficult to determine their contributions to the national remaining carbon dioxide (CO_2) budget without introducing a large degree of uncertainty. To address this spatial heterogeneity, we sampled 20 locations across the German Baltic Sea to quantify C_{org} stocks and sources in *Zostera marina* seagrass-vegetated and adjacent unvegetated sediments. To predict and integrate the C_{org} inventory in space, we measured the physical (seawater depth, sediment grain size, current velocity at the seafloor, anthropogenic inputs) and biological (seagrass complexity) environment to determine regional and local drivers of C_{org} variation. Here we show that seagrass meadows in Germany constitute a significant C_{org} stock, storing on average 1,920 g C/m^2, three times greater than meadows from other parts of the Baltic Sea, and three-fold richer than adjacent unvegetated sediments. Stocks were highly heterogenous; they differed widely between (by 22-fold) and even within (by 1.5 to 31-fold) sites. Regionally, C_{org} was controlled by seagrass complexity, fine sediment fraction, and seawater depth. Autochthonous material contributed to 12% of the total C_{org} in seagrass-vegetated sediments and the remaining 88% originated from allochthonous sources (phytoplankton and macroalgae). However, relics of terrestrial peatland material, deposited approximately 6,000 years BP during the last deglaciation, was an unexpected and significant source of C_{org}. Collectively, German seagrasses in the Baltic Sea are preventing 2.01 Mt of future CO_2 emissions. Because C_{org} is dependent on high seagrass complexity, the richness of this pool may be contingent on seagrass habitat health. Disturbance of this C_{org} stock could act as a source of CO_2 emissions. However, the high spatial heterogeneity warrant site-specific investigations to obtain accurate estimates of blue carbon, and a need to consider millennial timescale deposits of C_{org} beneath seagrass meadows in Germany and potentially other parts of the southwestern Baltic Sea.

KEYWORDS

climate change, Germany, nature-based solution, radiocarbon dating, submarine peatland, underwater archaeology, Zostera marina, carbon dioxide removal

Introduction

The oceans have absorbed approximately one-third of anthropogenic carbon dioxide (CO_2) emissions to date (Mcleod et al., 2011), making the marine biome one of the largest carbon stores on Earth and thus an integral part of the climate change mitigation strategy. Despite having a relatively small global extent (0.5% of total ocean seafloor; Macreadie et al., 2021), coastal vegetated ecosystems, like seagrass meadows, mangrove forests, and tidal salt marshes, account for almost half of the total organic carbon (C_{org}) buried in marine sediments (Duarte et al., 2005; Mcleod et al., 2011; Krause-Jensen and Duarte, 2016), collectively estimated to mitigate approx. 3% of global CO_2 emissions (Macreadie et al., 2021). Seagrass meadows alone have been estimated to contribute to 10% of the total buried C_{org} in ocean sediments (Duarte et al., 2005). Extraordinary rates of C_{org} accumulation and long-term storage in seagrass meadows have been attributed to high primary productivity (Hendriks et al., 2008; Duarte et al., 2013; Macreadie et al., 2014), efficient ability to capture particles from outside meadow boundaries (Kennedy et al., 2010; Miyajima et al., 2015; Oreska et al., 2018), a heavy network of roots and rhizomes that stabilize sediments and the carbon accumulated within them (Duarte et al., 2013), and formation of muddy anoxic sediments that prevent decomposition of the C_{org}, which can thus be stored for centuries to millenia (Fourqurean et al., 2012; Duarte et al., 2013; Greiner et al., 2016).

Seagrass meadows are found in tropical and temperate bioregions, on the coasts of all continents (except Antarctica) and thus occur within the exclusive economic zones (EEZ) of many coastal nations, including Germany (Hemminga and Duarte, 2000; Short et al., 2007). Through careful management of seagrass habitats, such nations can use this natural carbon sink as a way to sequester part of their CO_2 emissions. However, high spatial heterogeneity is observed in soil C_{org} storage potential, with wide differences seen globally (i.e. tropical vs. temperate environments), regionally, and even locally (within a seagrass meadow) (e.g. Kennedy et al., 2010; Röhr et al., 2018; Prentice et al., 2020; Mazarrasa et al., 2021). Consequently, it is difficult to apply ecological economic approaches to provide accurate economic valuations and determine seagrass habitat contributions to the national remaining CO_2 budget without introducing a large degree of uncertainty.

Regional estimates are contingent on site-specific evaluations because the mechanism involved in C_{org} storage is largely based on local environmental factors, such as (1) local hydrodynamic regimes (e.g. seawater depth, Lavery et al., 2013; Serrano et al., 2014; Mazarrasa et al., 2017a; decreased water motion, Prentice et al., 2019; lower wave height and exposure, Samper-Villarreal et al., 2016), (2) anthropogenic inputs (Macreadie et al., 2012; Mazarrasa et al., 2017a; Mazarrasa et al., 2017b; Ricart et al., 2020), (3) seagrass properties (e.g. species composition, Serrano et al., 2014; Serrano et al., 2019; increased seagrass complexity, Jankowska et al., 2016; Samper-Villarreal et al., 2016; Mazarrasa et al., 2018; Mazarrasa et al., 2021), and (4) sediment characteristics (e.g. Dahl et al., 2016; Röhr et al., 2016; Miyajima et al., 2017; Gullström et al., 2018).

The Baltic Sea coast of Germany is home to lush *Zostera marina* seagrass meadows, where seagrasses span a total area of approximately 285 km^2 between 1-8 m seawater depth (Schubert and Steinhardt, 2014; Schubert et al., 2015; Schubert and Schygulla, 2016). Provided that the ambitious nutrient abatement targets of the Baltic Sea Action Plan are met, there is the potential that seagrass meadows could expand by at least 57 km^2 by the year 2066 (Bobsien et al., 2021) and restoration activities could increase the existing area, leaving a large potential to gain negative emissions via restoration or improved growing conditions of these habitats.

The objectives of the present study were to (i) provide a detailed assessment of the regional (between sites) heterogeneity of blue carbon stocks along 350 km of German Baltic Sea coastline; (ii) compare C_{org} content between seagrass-vegetated and adjacent unvegetated sediments to understand local (within site) C_{org} variation; (iii) determine the source of C_{org} contributing to these stocks (autochthonous vs allochthonous); (iv) combine biophysical parameters such as seawater depth, sediment grain size, current velocity at the seafloor, and seagrass complexity with C_{org} content into a predictive model to understand regional drivers of C_{org} variation; (v) scale up measurements and convert to CO_2 equivalent units to determine the role of seagrass conservation in the total CO_2 budget of Germany.

Materials and methods

Study area

Sampling took place in 20 seagrass meadows in the western part of the Baltic Sea, along the coasts of Schleswig-Holstein (n = 17) and Mecklenburg-Vorpommern (n = 3) in northern Germany (Figure 1). The German Baltic Sea coast consists of shallow bays and fjords that experience weak water currents and low wave heights (Petterson et al., 2018). Like the whole Baltic Sea region, German coastal waters were geologically shaped by the last glacial periods (Schmölcke et al., 2006; Andrén, 2012). As a consequence of the last deglaciation, a conglomerate of differently sized stones, sand, and clay settled in the southwestern part of the Baltic Sea basin. The seabed consists of shallow sandy and muddy layers with consolidated marl underneath. A maximum water depth of 40 m is reached in the western part of the Baltic Sea. However, seagrasses here are rarely observed deeper than 8 m seawater depth (Schubert et al., 2015). The Baltic Sea is the largest brackish water basin in the world and because of the narrow Danish Straits connecting the Baltic Sea to the North Sea, low rates of water exchange are observed (residence time of 35-40 years) resulting in high eutrophication from nutrient discharge by the nine Baltic Sea nations that enclose it (HELCOM, 2018). However, eutrophication, which negatively impacts seagrass health and bathymetric range, is most pronounced in Germany, Russia and Poland (Thorsøe et al., 2022).

Sites in the study area represent the greatest environmental gradient, ranging from wave exposed (e.g. Heidkate, Falshoeft lighthouse, Teichhof, Goehren; Figure 1 star shape) to sheltered (e.g. Orth, Maasholm; Figure 1 square shape), relatively pristine (nature reserve e.g. Gelting Bay and Graswarder; Aschau is

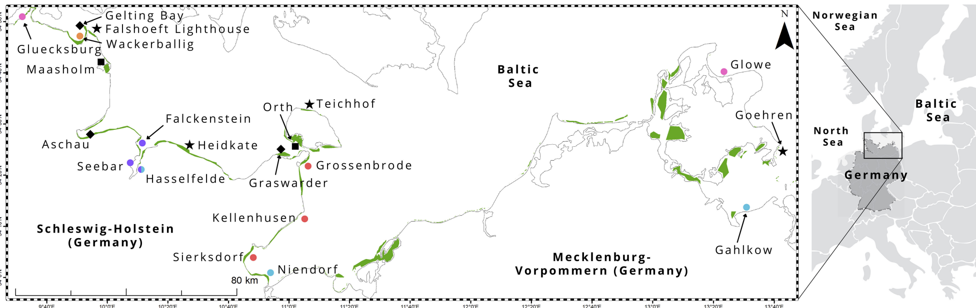

FIGURE 1
Study area, including 20 sampling locations, in the Baltic Sea coast of northern Germany. Seagrass area (green) was extracted from Schubert and Steinhardt (2014); Schubert et al. (2015); Schubert and Schygulla (2016). Shapes: stars - wave exposed, squares – sheltered, diamond - relatively pristine (nature reserve or some degree of protection from human impact), circle - anthropogenic inputs (pink = adjacent to a marina, purple = heavy ship traffic or near urban area, orange = agricultural land, red = tourist area, blue = proximity to river influx).

protected from human impact due to military controlled access to the area; Figure 1 diamond shape) to varying degrees of anthropogenic inputs (Figure 1 circle shape), such as adjacent to a marina (e.g. Gluecksburg, Glowe; Figure 1 pink circles); heavy ship traffic and near urban areas (e.g. Kiel Fjord, including Falckenstein, Seebar, Hasselfelde; Figure 1 purple circles); agricultural land (e.g. Wackerballig; Figure 1 orange circles); tourist areas (e.g. Grossenbrode, Kellenhusen, Sierksdorf; Figure 1 red circles), and proximity to river influx (e.g. Gahlkow, Hasselfelde, Niendorf; Figure 1 blue circles).

Sample collection and core subsampling

A total of 169 sediment cores (30 cm length; 5.5 cm inner diameter) were sampled in seagrass meadows (n = 110 cores) and nearby unvegetated sediments (n = 59 cores). Nine cores (with some exceptions) were collected at each site, from three sublocations: (1) in the high-density part of the meadow ('dense seagrass' hereafter), (2) low density or fringe of the meadow ('sparse seagrass' hereafter), and (3) adjacent unvegetated sediments at least 5 m from seagrass ('unvegetated'). Dense and sparse seagrass sublocations are collectively referred to as 'seagrass-vegetated' sediments or sublocations. Sediment cores taken within the seagrass meadow were sampled at least 10 m apart from each other. Seawater depth was measured from a diver computer. Seagrass shoot density was counted using a 0.04 m^2 frame, and the leaf lengths of five randomly selected plants were measured next to the location where the core was extracted. Seagrass density and leaf length vary between sites and at meadow stage of maturity. The measure of "seagrass complexity" was defined as the product of seagrass canopy height and shoot density, to obtain the sum of leaf heights within a unit of area (in m/m^2) (Prentice et al., 2019). Seagrass canopy height and shoot density exhibit seasonal variations, and so it must be noted that all sampling took place between July 15th and September 1st of 2019 or 2020, at the peak of the seagrass growing season for *Z. marina* in Germany, except for the samples in Gelting Bay and Falshoeft lighthouse which were collected in late November (23rd and 24th of 2020) due to permitting and accessibility issues.

Cores were collected between 1-5 m seawater depth manually via SCUBA divers (self-contained underwater breathing apparatus) pounding impact resistant PVC tubes into the sediment with a rubber mallet. Cores were capped at both ends by the divers and stored upright for transport to shore, and in a cooler thereafter for transport to the lab. Cores were stored at 0°C until further processing.

Sediments are known to shift during the coring process, so the degree of compression was measured by divers once the core was fully inserted. Compaction was calculated as the distance (in cm) from the top of the core to the sediment surface outside of the core, divided by the sample depth (cm of compression/cm core depth). A compression correction factor was calculated by dividing the length of the sample recovered by the length of core penetration (Howard et al., 2014). Cores were subsectioned into 5 cm depth intervals, and depth intervals were adjusted based on compaction.

Sediments from each depth interval were homogenized, measured for dry-bulk density and subsampled for chemical analyses (total C_{org}, $\delta^{13}C$, $\delta^{15}N$, ^{14}C, each described in detail in subsections below). A total of 394 sections underwent total C_{org} analyses: all top (0-5 cm) layers of all cores were processed for total C_{org}, but the selection of subsequent core depth intervals depended on color changes throughout the core (color changes indicate potential changes in C_{org} content) (Nederbragt et al., 2006, and e.g. Klingler et al., 2020). If no color change was apparent, the mid (10-15 cm) and bottom sections of the core were processed (typically 20-25 cm, except where cores were shorter due to marl or difficult sediments, such as large rocks or bolder field beneath the surface of the sediment). If a color change occurred, the respective section was instead examined. It must be noted that the total C_{org} was measured in 0-5 cm, 10-15 cm and 15-20 cm sections of all sites, but not all cores as described above. The 5-10 cm depth interval of all cores was used for grain size analysis (described below, under 'grain size analysis'). Visible plant material (seagrass roots and rhizomes) and infauna (lug worm *Arenicola marina*, and, in some cases, soft tissue of clams and mussels) were removed from the sediment prior to chemical analyses (hereafter referred to as 'visible organic'), but all other materials (e.g. such as wood) were left in the sediment (referred to as 'sediment organic carbon' or 'SOC').

Shells, were also left in the sediment after the organic tissue was removed.

Maximum orbital velocity

These values were represented as maximum wave-generated orbital velocity (MOV) at the seafloor, modelled for the year 2021. Due to the limited availability of simulated wave data, MOVs were calculated only for cores taken at the outer coast sites of Schleswig-Holstein, not for the Schlei fjord site (Maasholm) and also not for any of the sites in Mecklenburg-Vorpommern (Gahlkow, Glowe, Goehren). MOV was calculated as a function of wave height, mean wave period, mean wave length (all simulated values), and seawater depth for each site according to linear wave theory as per the procedure described in Bobsien et al. (2021). MOV averages ('avg. MOV') and maximum MOV ('max MOV') were based on MOV calculations for simulated hourly seastate values within the year 2021 (n = 365 days x 24 hours). Average maximum MOV ('avg. max MOV') at each site was obtained by averaging the highest MOV observed at the depth and location of each core.

Grain size distribution

The 5-10 cm depth interval of each core was processed for grain size distribution. Visible organics were first removed, then the sediments were oven dried at 60°C for a minimum of 48 hrs. Dry sieving was conducted with stainless steel Test Sieve ISO 3310-1 and sieve shaker (Fritsch Analysette 3 Spartan Pulverisette 0) set to amplitude 2 mm for 15 min. The fractions of sediment in 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, 63 µm, and <63 µm (herein referred to as 'fine sediment' fraction) size classes were determined to the nearest 0.01 g, and the percent amount of each size class was calculated using the total sample mass obtained from the sum of each fraction.

C_{org} stock quantification

Sediment total C_{org} was determined using an Elemental Analyzer (EURO EA Elemental Analyzer). Sediments were first dried at 60°C for 48 h and then ground to a homogeneous fine powder using a mechanical agate ball mill (Fritsch Pulveisette 5) set at rotational speed 240-300 rpm for 15-20 minutes. A subsample of this homogenized sediment was acidified to remove inorganic carbon by adding 1 M HCl drop-by-drop until gas evolution ceased. Samples were observed under a dissecting microscope to ensure CO_2 had fully evolved. These acidified samples were re-dried at 60°C for 48 h, ground again (with mortar and pestle), and encapsulated into silver capsules. Total organic carbon concentrations were calculated based on a linear regression. Acetanilide and sediments were used as standards to measure data accuracy and analytical uncertainty. For sections that were not measured by EA, the section carbon content was taken from the quantify produced in the layer above (with similar coloration, see core subsampling method above for further details).

Stable isotope analyses

To decipher the source material of the remaining (non-visible) organic fraction in the sediments (referred to as SOC), four sites (Falckenstein, Graswarder, Grossenbrode, Wackerballig) underwent further examination using biotracers of $\delta^{13}C$ and $\delta^{15}N$. Samples were pre-treated as outlined above (see 'C_{org} stock quantification'), and then combusted in an elemental analyzer system (NA 1110, Thermo) coupled to a temperature-controlled gas chromatography oven (SRI 9300, SRI Instruments), connected to an isotope ratio mass spectrometer (DeltaPlus Advantage, Thermo Fisher Scientific) as described by Hansen et al. (2009). $\delta^{15}N$, $\delta^{13}C$ ratios were reported in delta notation relative to the international Air-N_2 and VPDB scale following the equation:

$$\delta^{15}N, \delta^{13}C(‰) = ([Rsample/Rstandard] - 1) \times 10^3$$

where R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$. N_2 and CO_2 gases were used as reference gases and calibrated against International Atomic Energy Agency (IAEA) reference standards (N1-,N2-, NO3-) and National Institute of Standards and Technology (NBS-22 and NBS-600) compounds. To measure analytical uncertainty, acetanilide and caffeine were used as internal standards after every sixth sample to test if the analytical setup was working properly. Precision for Caffein was ± 0.13 ‰ for $\delta^{15}N$ and ± 0.09 ‰ for $\delta^{13}C$; and ± 0.20 ‰ for $\delta^{15}N$ and ± 0.27 ‰ for $\delta^{13}C$ for Acetanilide.

A two biotracer ($\delta^{13}C$ and $\delta^{15}N$), five-source Bayesian mixing model using R package (R Core Team, 2022) MixSIAR (Stock and Semmens, 2016) was used to determine the contribution of C_{org} to seagrass-vegetated and unvegetated sediments in Falckenstein, Grossenbrode, Graswarder, and Wackerballig. Signatures of five potential sources were compiled from previous studies in Kiel Fjord, Germany and Gulf of Gdansk, Poland, and consisted of: (1) *Pilayella littoralis*, a filamentous brown algae known to form thick drifting mats accumulating in seagrass meadows in Germany (Kruk-Dowgiallo, 1991; Kiirikki and Lehvo, 1997), (2) other macroalgae (e.g. *Ulva intestinalis* and *Cladophora fracta*) extracted from Table 2 in Maksymowska et al., 2000; and (3) phytoplankton (collected by seston), (4) epiphytes attached to seagrass leaves, (5) seagrass leaves (there is little difference between above- and below-ground biomass signatures, see Röhr et al., 2016) extracted from Table 1 in Mittermayr et al. (2014). Sampling location (four locations) and vegetation state (two states: seagrass-vegetated vs unvegetated) were included as random effects in the stable isotope mixing model. Vegetation state was nested within sampling location for the random structure. We specified an uninformative, generalist prior and discrimination factor of 0 as no further fractionation is expected in stored C_{org} (Greiner et al., 2016; Miyajima et al., 2017). Note that visible seagrass roots and rhizomes were omitted from this analysis, which may lead to a lower contribution of autochthonous organic carbon sources.

Radiocarbon dating

Large amounts of exceptionally well-preserved wood pieces were discovered in sediment cores extracted from the seagrass meadow in Sierksdorf, Luebeck Bay (Figure 2). Of those, eleven pieces from a depth of 5 to 24 cm in four sediment cores were radiocarbon dated. The samples were visually inspected under a microscope and an appropriate amount of wood material was selected for dating. A standard decontamination procedure was subsequently applied to remove carbonates and soil humic contaminants, consisting of 1% HCl, 1% NaOH at 60°C and again 1% HCl. All radiocarbon measurements were conducted at the Leibniz-Labor, using the type *HVE 3MV Tandetron 4130* accelerator mass spectrometer (AMS). Following standard procedures, the $^{14}C/^{12}C$ and $^{13}C/^{12}C$ isotope ratios were simultaneously measured by AMS, compared to the CO_2 measurement standards (oxalic acid II), and corrected for effects of exposure to foreign carbon during the sample pretreatment. The resulting ^{14}C-content was corrected for isotope fractionation, related to the hypothetical atmospheric value of 1950, and reported in pMC (percent Modern Carbon). This value was used to calculate the radiocarbon age according to Stuiver and Polach (1977). The reported uncertainty of the ^{14}C result takes into account the uncertainty of the measured $^{14}C/^{12}C$ ratios of sample and measurement standard, as well as the uncertainty of the fractionation correction and the uncertainty of the applied blank correction. The radiocarbon ages were translated to calendar ages using the software package OxCal4 (Ramsey and Lee, 2013) and the Intcal20 dataset (Reimer et al., 2020). Note that this is not an observation unique to Sierksdorf as our diver and drop camera surveys showcase old wood material that has become visible on the fringes of seagrass meadows where erosion has occurred: in other parts of Sierksdorf that were not cored in this study, Neustadt, Fehmarnsund, Kellenhusen, Heidkate, wendtorf, Dollerupholz (Table 1).

Statistical analyses

Statistical analyses were performed in R version 4.1.3 (R Core Team, 2022) for Mac OS X, and all mixed models were implemented with package "lme4" (Bates et al., 2015). For all tests, significance was determined at $p < 0.05$. Visual inspection of standard model validation graphs was used to verify model assumptions: residuals versus fitted values were used to verify homogeneity; a histogram or Quantile–Quantile (q–q) plot of the residuals for normality; and residuals versus each explanatory variable to check independence.

Generalized linear mixed models (GLMM) with a Gamma distribution and log link function were used to test: (1) core position effect on C_{org} between sublocations (dense seagrass, sparse seagrass, unvegetated) within each site (locally), with a

FIGURE 2
Sediment cores from *Zostera marina* seagrass-vegetated **(A)** and adjacent unvegetated **(B)** sublocations in Sierksdorf, Luebeck Bay, where unexpected large amounts of exceptionally well-preserved wood pieces were discovered.

random intercept of sublocation nested in sampling location (site), and (2) biophysical factors influencing regional differences in stocks within seagrass-vegetated sediments, with sampling location as a random intercept. In the local model (1), a posthoc test using Tukey contrasts was performed with package “multcomp” to examine multiple comparisons between sublocations of each site. A multi-model inference approach based on AICc was used to determine the strongest predictors of regional C_{org} (2). Selection criteria AICc was used (instead of AIC) due to a small sample size (n/k < 40; n = total number of observations; k = total number of parameters in the most saturated model, including both fixed and random effects). The saturated model included four factors: seagrass complexity, average MOV, seawater depth, percent fine sediments, and their interactions. However, it is important to consider multicollinearity when interpreting model outputs as coefficient estimates (i.e. beta coefficients) and p-values become very sensitive to any small changes in the model. Multicollinearity of parameters in the dataset and among saturated model terms were examined using the Pearson correlation coefficient (ρ) and variance inflation factor (VIF). Correlation coefficients < 0.6 and VIFs approx. < 5 indicate an acceptable level of collinearity, VIFs > 10 warrant further investigation (Montgomery and Peck, 1992). Low collinearity was observed in the data itself (ρ = -0.43 to 0. 35), but structural multicollinearity (between some model terms) was observed in the saturated model (VIF 1.876 to 14.051), so all terms with VIF >10 were removed from the global model. Hence, the final, global model included four factors: seagrass complexity, average MOV, seawater depth, percent fine sediments and two-way interactions between all variables except average MOV and fine sediment fraction, and all three- and four-way interactions were excluded (excluded VIFs: 10.055 to 14.051). After model selection, statistically indistinguishable (ΔAICc <2) candidate models were averaged using package ‘MuMIn’ (Bartoń, 2022). To estimate the importance of each variable, the RVI (relative variable importance) value was computed by summing Akaike weights across all averaged models where a particular variable appeared. Model-averaged coefficients and p-values were obtained from the ‘full average’ (rather than the ‘conditional average’).

TABLE 1 Locations where old wood co-occur with seagrass meadows.

Location name	WGS_Lat	WGS_Lon
Neustadt	54,079385132100001	10,804154774700001
Sierksdorf	54,058742358700002	10,768929873899999
Fehmarnsund	54,386747962299999	11,138406546200001
Kellenhusen 1	54,170028967299999	11,043240012100000
Kellenhusen 2	54,178261040999999	11,059126494099999
Heidkate	54,438457532100003	10,338865629400001
Wendtorf	54,437861865099997	10,307044620099999
Dollerupholz	54,812584788700001	9,705288137309999
Sierksdorf (HICAM)	54,071436	10,786538
Gelting	54,76617	9,88119

WGS, World Geodetic System.

Results

C_{org} stocks

Averaged across all sediment cores in seagrass-vegetated sublocations, including dense and sparse seagrass sublocations (n = 110 cores total) and integrated to 25 cm core length, C_{org} stocks averaged at 1,920 ± 402 g C/m^2, and varied 22-fold between sites, ranging from 475 ± 61 and 10,577 ± 6,178 g C/m^2 (Figure 3). For seagrass-vegetated sediments, the highest average C_{org} stocks were found in Maasholm (Schlei Fjord) and Sierksdorf (Luebeck Bay), while the lowest values were observed in Heidkate (Kiel Fjord) and Grossenbrode (Luebeck Bay).

An examination of the local (within site) variation in C_{org} content across all sites showed significantly greater (by three-fold) stocks in seagrass-vegetated sediments (both dense and sparse seagrass) compared to nearby unvegetated sediments (dense seagrass: average 1,523 ± 244 g C/m^2; sparse seagrass: 2,316 ± 795 g C/m^2; unvegetated: 611 ± 93 g C/m^2) (Table 2; Figure 3). However, considering sites individually, within site comparisons ranged widely: in all but four cases (Gluecksburg, Gohren, Hasselfelde, Seebar), seagrass-vegetated sediments had 1.5 to 31 times more C_{org} than nearby unvegetated sediments, with Sierksdorf and Maasholm showing the greatest discrepancies (10 and 31 times that of unvegetated sediments). Gluecksburg and Hasselfelde had the same; Gohren, and Seebar less C_{org} than nearby unvegetated sediments. Seebar had the highest average C_{org} stocks, twice as much as in nearby seagrass-vegetated areas. C_{org} content did not differ significantly between sparse and dense seagrass sublocations.

Sources of sediment C_{org} ($\delta^{13}C$, $\delta^{15}N$, ^{14}C)

Overall, the stable isotope signatures of the SOC fraction of seagrass-vegetated sediments (including dense and sparse seagrass sublocations along the entire core depth) were near identical to those of unvegetated sediments ($\delta^{15}N$ 5.2 ± 0.3‰, $\delta^{13}C$ -21.9 ± 0.2‰ vs $\delta^{15}N$ 5.3 ± 0.2‰, $\delta^{13}C$ -21.6 ± 0.2‰). In seagrass-vegetated sediments, signatures ranged between $\delta^{15}N$ 4.1 ± 0.2 (Grossenbrode) to 7.3 ± 0.3 (Falckenstein), and $\delta^{13}C$ -23.1 ± 0.4 (Falckenstein) to -19.4 ± 0.5 (Wackerballig) (Figure 4B). $\delta^{13}C$ and $\delta^{15}N$ signatures were also homogenous across core depth; top sediments (0 to 5 cm) averaged across all seagrass cores were ^{15}N depleted by 0.48‰ and ^{13}C enriched by 0.68‰ compared to the 10 to 15 cm and 15 to 20 cm sections.

Averaged across all sites, visible organic material such as invertebrates and seagrass root, shoot, rhizome material on average contributed to 12% of the average total C_{org} in seagrass-vegetated sediments and 9% in unvegetated sediments. Visible organics were responsible for 65% of the C_{org} in unvegetated sediments in Hasselfelde. Results from the five-source two-biotracer ($\delta^{13}C$, $\delta^{15}N$) mixed model of the remaining organic fraction (the non-visible fraction, called SOC) in the sediments of Falckenstein (SOC fraction = 94%), Wackerballig (SOC = 56%), Grossenbrode (SOC = 78%), Graswarder (SOC = 55%), showed that

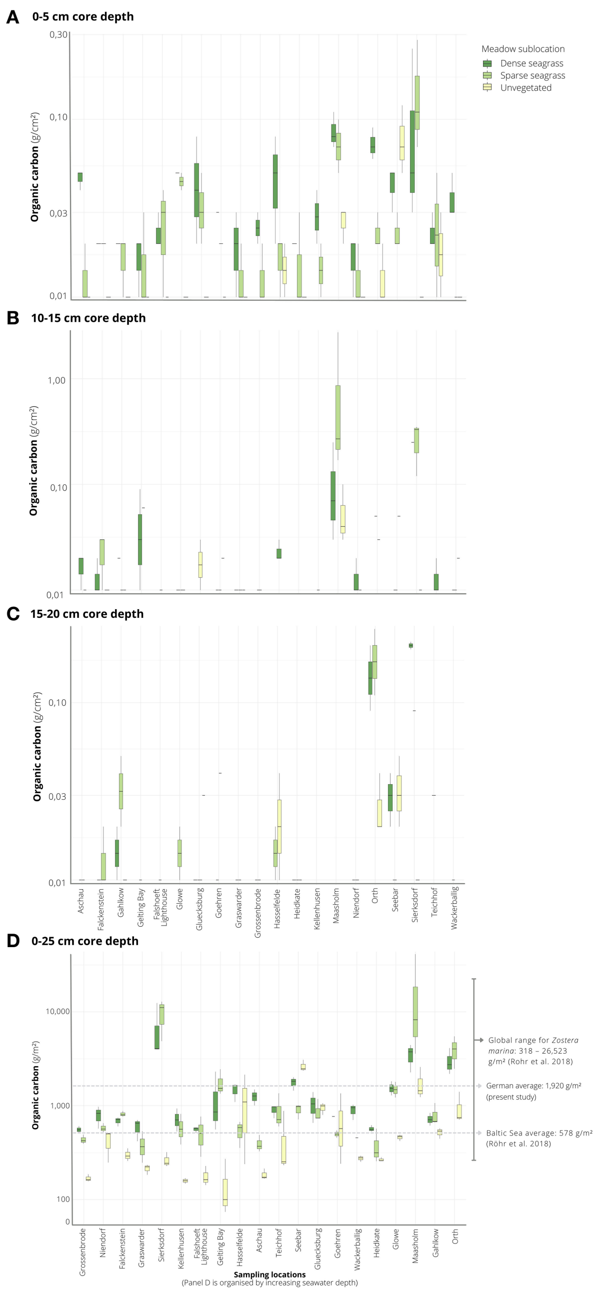

FIGURE 3
Overview of the organic carbon (C_{org}) stocks for core sections 0-5 cm **(A)**, 10-15 cm **(B)**, 15-20 cm **(C)** measured by elemental analyzer, and integrated to 25 cm sediment depth **(D)** across 20 sampling locations situated in the Baltic Sea coast of northern Germany. Box and whiskers show the median as a line, first and third quartiles as hinges, and the highest and lowest values within 1.5 times the inter-quartile range as whiskers.

phytoplankton (24%), *P. littoralis* (18%) and other macroalgae (22%), made the largest contribution to C_{org} overall, not seagrass biomass or its epiphytes, and a combination of two of these three dominant carbon sources could be seen at each site (Figure 4A). Sampling location accounted for most of the variation in the mixing model (50th percentile σ = 6.311), while vegetation coverage (seagrass-vegetated vs unvegetated) had a negligible effect (50th percentile σ = 0.105).

Radiocarbon dating of wood pieces found in Sierksdorf cores revealed no age-depth correlation within a single core, but all dates fell in two well separated time intervals, averaging at 5,806 years BP and 5,095 years BP (before present), i.e. a hiatus of approx. 700 years between these time intervals (Table 3).

Biophysical predictors of C_{org}

The percent fine sediment fraction of seagrass-vegetated sediments varied greatly between sites, from 0.09 ± 0.04% (Gahlkow) to 7 ± 3% (Goehren). All unvegetated sediments and 17 of 20 seagrass-vegetated sites had a low fine sediment fraction (<3%) (Table 4). The unvegetated sediments of Orth and Seebar had the highest fine sediment fraction (2.5 and 3%), and of the seagrass-vegetated sites Glowe, Goehren, Niendorf, Orth, Sierksdorf had 2.7 to 7% fine sediments. Seagrass-vegetated sediments contained similar or more (by 1-31 times) fine-grained sediments than adjacent unvegetated sublocations, except in Graswarder, Gluecksburg, Seebar, where unvegetated sublocations contained 2-10 times more fine-grained sediments than their vegetated counterparts. For seagrass complexity, Maasholm exhibited the lowest (92 ± 21 m/m^2) and Wackerballig the highest (539 ± 132 m/m^2) average seagrass complexity of all sites (including sparse and dense seagrass sublocations) (Table 4). Dense seagrass sublocations were one to five times more complex than sparse seagrass sublocations, with the greatest difference observed in Teichhof and Aschau, and smallest difference seen in Sierksdorf and Grossenbrode. Average MOV varied six-fold, ranging from 0.155 ± 0.007 m/s (Niendorf) and 0.91 ± 0.03 m/s (Teichhof) between sties, but some (Falshoeft lighthouse, Heidkate, Kellenhusen, Teichhof, Wackerballig) experienced strong peak MOVs (> 3 m/s) (Table 4).

Six alternative candidate models were deemed statistically indistinguishable (ΔAICc < 2) from each other (summarized in Table 5A). Meaning, there was no strong support for one particular model. In the averaged model, seawater depth, seagrass complexity, and fine sediment fraction were similarly important in predicting C_{org} within seagrass-vegetated sediments (RVI 1.00 for each, Table 5B), and they had a significant negative (seawater depth) or positive (fine sediment fraction, seagrass complexity) effect on C_{org} stocks (see 'Estimate' in Table 5B). Avg. MOV had a weaker (by approx. 2.5 times) and insignificant effect in predicting C_{org}. There were no significant interactive effects between variables, except for that of seawater depth and seagrass complexity, but it had a weak (by approx. 5 times) predictive effect on C_{org} stocks.

Discussion

Spatial heterogeneity of blue carbon stocks in Germany

C_{org} stocks in the top 25 cm of seagrass-vegetated sediments in the German Baltic Sea were high (average 1,920 ± 402 g C/m^2), and richer than adjacent unvegetated sediments, but differed widely

TABLE 2 Results of the Generalized Linear Mixed Model (Gamma, log link function), testing for the effect of sublocation on local (within site) sediment organic carbon (C_{org}) content of seagrass meadows in the German Baltic Sea.

Source of error	Estimate	Std. Error	t-value	*p*-value
Intercept	6.9814	0.2273	30.713	**<0.0001**
Sparse seagrass	-0.1813	0.3213	-0.64	0.6
Unvegetated	-0.9744	0.3240	-3.008	**0.003**
Posthoc test				
Sparse vs dense seagrass	-0.1813	0.3213	-0.564	0.8
Unvegetated vs dense seagrass	-0.9744	0.3240	-3.008	**0.007**
Unvegetated vs sparse seagrass	-0.7931	0.3238	-2.449	**0.04**

Statistically significant effects in bold; α = 0.05.

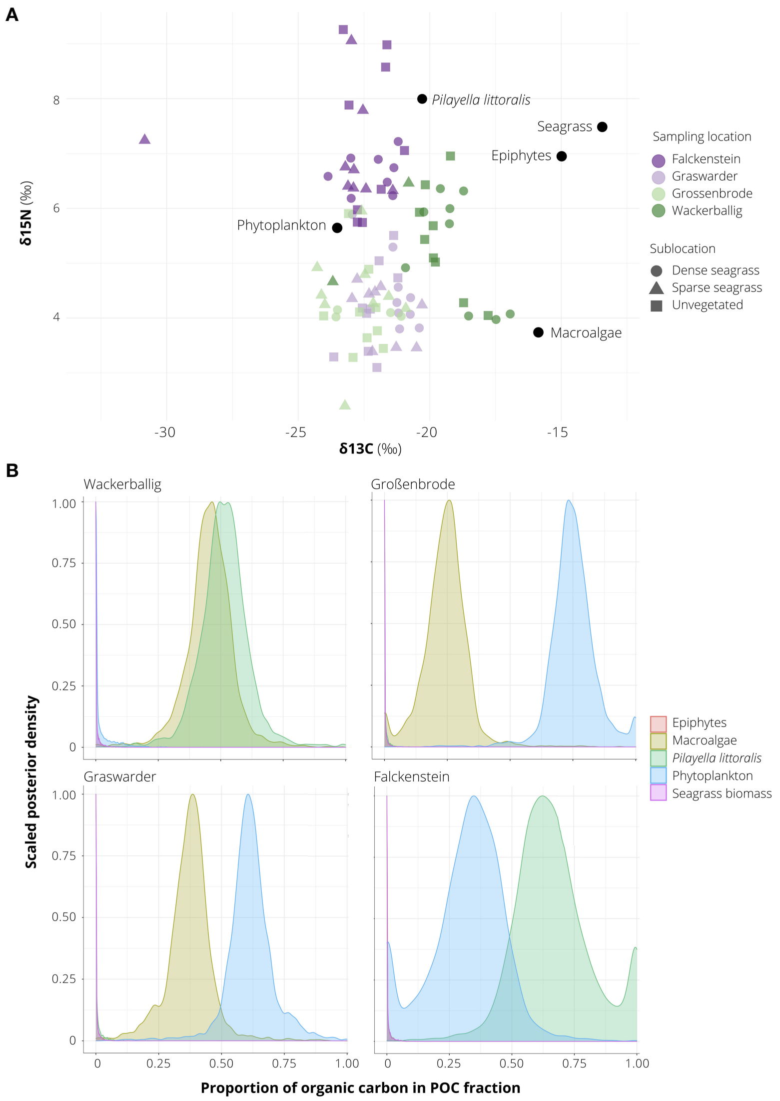

FIGURE 4
$\delta^{13}C$, $\delta^{15}N$ stable isotope signatures **(A)** and posterior estimates of the proportion of organic carbon (C_{org}) sources **(B)** of sediments sampled in seagrass-vegetated and unvegetated sublocations off the coasts of Falckenstein (FS), Wackerballig (WB), Grossenbrode (GB), Graswarder (GW), in northern Germany. Sources (black circles) were obtained from Table 1 in Mittermayr et al. (2014) and Table 2 in Maksymowska et al. (2000).

TABLE 3 Radiocarbon ages (in years before present, BP) of wood material collected from *Zostera marina* seagrass-vegetated sediment cores in Sierksdorf, Luebeck Bay, in northern Germany.

Core ID	Core depth interval (cm)	^{14}C age (Year BP ± SD)
C2	5-10	5,755 ± 30
	15-20	5,795 ± 30
	15-20	**5,131 ± 29**
C4	5-10	5,850 ± 30
	15-20	5,920 ± 30
	20-24	5,775 ± 29
	20-24	5,745 ± 35
C7	5-10	**5,116 ± 28**
	5-10	**5,044 ± 28**
	10-15	**5,090 ± 28**
C12	5-10	5,805 ± 35

In some instances, two different wood pieces were dated from the same core section. Note: the material originated from two distinct time intervals (avg. 5,806 and 5,095 BP; younger time interval in bold), with a hiatus of approx. 700 years. BP is related to the hypothetical atmospheric value of 1950; SD – standard deviation.

between and even within sites. Regional heterogeneity observed here was comparable to previous regional evaluations of blue carbon in *Z. marina* meadows (e.g. Röhr et al., 2016; Prentice et al., 2019), but local heterogeneity was much greater, with previous measurements reporting <10 times more C_{org} content in seagrass-vegetated vs unvegetated sediments (Table 6), or similar carbon content between these sublocations (Prentice et al., 2019; Prentice et al., 2020; Mazarrasa et al., 2021; Krause et al., 2022). Overall, average C_{org} stocks in the German Baltic Sea fit within the global range reported for those of *Z. marina* (318 ± 10 to 26,523 ± 667 g C/m^2), but more closely resembled *Z. marina* C_{org} stocks in the Mediterranean Sea (8,793 + 2,248 g C/m^2), Funen area of Denmark, and Skagerrak coast of Sweden, than C_{org} stocks in other parts of the Baltic Sea (Table 6). In fact, German blue carbon stocks were on average richer (by three times) than the Baltic Sea average (578 ± 43 g C/m^2, excluding Germany, Röhr et al., 2018). A similar geographical trend was also reported for sites along the coast of Sweden, where percent C_{org} in top sediments were 10 to 25 times higher along the west (in Skagerrak) vs south and east coasts (in the Baltic Sea) of Sweden (Jephson et al., 2008). Consistent with the present study, wide regional variation in C_{org} stocks were observed in eastern Jutland of Denmark, which included "carbon hot spots" (stocks as high as 26,523 ± 667 g C/m^2 in Thurøbund) that were comparable to those observed in Germany (10,577 ± 6,178 g C/m^2). Two biophysical parameters were thought to be responsible for the C_{org} hotspot found in Thurøbund: low wave exposure and high seagrass productivity (420 ± 98 shoots/m^2) – seagrass densities and exposures that were similar in magnitude to those measured in the sheltered bay of Orth (467 ± 98 shoots/m^2) where the third highest C_{org} was found in Germany. It is worthwhile contemplating explanations for the higher C_{org} stocks reported in Skagerrak-Kattegat and southwestern Baltic Sea relative to other parts of this basin (Table 6). The rich geological history that shaped the Baltic Sea, including northward retreat of the Scandinavian ice sheet that caused land uplift in the south and changed coastal landscapes as a consequence of sea-level rise during the Littorina Transgression, but also shaped the geology that enhanced its ability to sequester C_{org}. For instance, hard-bottom and rocky shores dominate in the northern coasts, whereas till material and sandy/muddy beaches are common in the south (Schiewer, 2008).

Sources of C_{org}

Our results suggest that the C_{org} accumulating in seagrass meadows in the German Baltic Sea is primarily (88%) originating from allochthonous sources, material originating from outside the seagrass meadow, thus, most of the C_{org} making up stocks here are imported from outside the boundaries of the meadow. Of the five C_{org} sources tested, this material was predominantly derived from a combination of phytoplankton, drift algae *P. littoralis*, and other macroalgae. It must be noted that the determination of the source materials in the SOC fraction was derived from stable isotope analyses of materials from sites in Schleswig-Holstein only, and so the source material for Mecklenburg-Vorpommern may differ from these. Nonetheless, these findings are consistent with those of neighboring Baltic Sea nations, like Finland, where phytoplankton material was the primary source of C_{org} (43 – 86%), while seagrass made a relatively small contribution to the overall sediment C_{org} pool (1.5 – 32%) (Röhr et al., 2016), and along the northwest Pacific coast, *Z. marina* meadows primarily sequestered allochthonous C_{org}, originating from plankton, terrestrial, and kelp sources rather than seagrass material (Prentice et al., 2019; Krause et al., 2022). The latter contributed less than 25.3% to the C_{org} pool. However, in Denmark and Poland, seagrass biomass was found to be the biggest contributor to sediment C_{org} pools (13 – 81%, Röhr et al., 2016; 40 – 45%, Jankowska et al., 2016). A country-wide analysis of blue carbon stocks in Australia revealed that coastal meadows in temperate regions were dominated by autochthonous C_{org} sources (72% was derived from seagrass), whereas allochthonous material prevailed in tropical meadows (64%) (Mazarrasa et al., 2021). In a global analysis (across 88 locations and multiple seagrass species) of seagrass blue carbon stocks, seagrass biomass accounted for approximately 50% of the C_{org} stocks, while the remainder originated from allochthonous sources (Kennedy et al., 2010).

In the mixing model, sampling location (not vegetation coverage) was the main driver of the variation in C_{org} sources (for the non-visible fraction of C_{org}; SOC). Coastal landscape and differences in inputs to marine foodwebs, including currents, upwelling, as well as point (e.g. sewage outfall, rivers) and diffuse (e.g. atmospheric, rainwater runoff) sources of nutrients may help explain some of the dissimilarity observed between locations. For example, phytoplankton contribution was abundant in the seagrass meadow in Graswarder, but absent in Wackerballig. The former is situated near a point source contamination of sewage outflow (Schubert et al., 2013), and the latter is adjacent to a large marine national park. Phytoplankton composition and abundance are often

TABLE 4 Summary of average (± SE) of each biophysical variable calculated (seagrass complexity), modelled (average and maximum Maximum Orbital Velocity; MOV), or measured (seawater depth, % fine sediments) in seagrass-vegetated sediments of 20 seagrass meadows along the Baltic Sea coast of Germany.

Sampling location	Average seagrass complexity (m/m^2)	Average MOV (m/s)	Average max. MOV (m/s)	Average seawater depth (m)	Fine sediments in seagrass-vegetated and unvegetated (in brackets) sublocations (<63 µm;%)
Aschau	186 ± 57	0.5 ± 0.2	1.7 ± 0.1	2.7 ± 0.3	1.9 ± 0.6 (0.22 ± 0.05)
Falckenstein	154 ± 29	0.184 ± 0.001	0.989 ± 0.005	3.7 ± 0.0	1.9 ± 0.6 (0.06 ± 0.01)
Gahlkow	188 ± 45	na	na	1.12 ± 0.05	0.09 ± 0.04 (0.09 ± 0.04)
Gelting bay	139 ± 60	0.360 ± 0.005	2.05 ± 0.02	3.0 ± 0.0	1.5 ± 0.5 (0.11 ± 0.00)
Falshoeft lighthouse	224 ± 39	0.49 ± 0.06	3.5 ± 0.3	3.1 ± 0.4	0.4 ± 0.1 (0.09 ± 0.02)
Glowe	293 ± 64	na	na	1.35 ± 0.09	4 ± 1 (1.6 ± 0.1)
Gluecksburg	108 ± 17	0.32 ± 0.02	1.67 ± 0.08	2.1 ± 0.2	0.6 ± 0.1 (1.6 ± 0.1)
Goehren	163 ± 69	na	na	2.03 ± 0.03	7 ± 3 (1.7 ± 0.9)
Graswarder	241 ± 47	0.446 ± 0.003	2.071 ± 0.008	3.4 ± 0.0	0.16 ± 0.06 (1.6 ± 0.2)
Grossenbrode	210 ± 30	0.331 ± 0.002	1.959 ± 0.008	4.3 ± 0.0	0.4 ± 0.1 (0.18 ± 0.01)
Hasselfelde	155 ± 34	0.3 ± 0.1	0.9 ± 0.1	2.7 ± 0.5	0.9 ± 0.2 (0.19 ± 0.05)
Heidkate	268 ± 60	0.66 ± 0.02	3.32 ± 0.07	1.4 ± 0.0	0.24 ± 0.07 (0.12 ± 0.05)
Kellenhusen	211 ± 29	0.45 ± 0.04	3.0 ± 0.2	3.1 ± 0.3	1.06 ± 0.06 (0.4 ± 0.1)
Maasholm	92 ± 21	na	na	1.23 ± 0.02	1.2 ± 0.2 (1.2 ± 0.3)
Niendorf	175 ± 31	0.155 ± 0.007	1.34 ± 0.04	4.2 ± 0.2	3.2 ± 0.2 (1.9 ± 0.1)
Orth	239 ± 66	0.58 ± 0.01	1.36 ± 0.03	1.0 ± 0.0	2.7 ± 0.7 (2.5 ± 0.3)
Seebar	100 ± 22	0.244 ± 0.007	1.00 ± 0.03	2.2 ± 0.1	0.8 ± 0.2 (3 ± 1)
Sierksdorf	194 ± 47	0.265 ± 0.003	1.89 ± 0.02	3.3 ± 0.0	2.8 ± 0.9 (0.13 ± 0.05)
Teichhof	246 ± 73	0.91 ± 0.03	4.3 ± 0.1	2.2 ± 0.1	1.3 ± 0.5 (0.09 ± 0.02)
Wackerballig	539 ± 132	0.6 ± 0.1	3.3 ± 0.5	1.5 ± 0.6	2 ± 1 (0.06 ± 0.00)

'Average max. MOV', 'Average MOV' – average maximum MOV and average MOV values observed for each core location. 'Fine sediments' – percent fraction of the sediment with grain size <63 µm. Averages presented are for seagrass-vegetated sublocations only, except the fine sediment fraction where values are available for unvegetated sediments also (in brackets).
na, not applicable.

used as bioindicators of enhanced nutrient concentrations (2000/60/EC, EU, 2000). For the drift algae *P. littoralis*, large mats can become entrapped in narrow fjords (Falckenstein) and bays (Wackerballig), whereas they may be carried away from sites along open coasts (Grasswarder, Grossenbrode), which fits with the pattern seen in the sediment sources of the present study.

While C_{org} content was consistently higher in seagrass-vegetated vs unvegetated sediments, two cases had similar (Gluecksburg and Hasselfelde) or more (Gohren and Seebar) C_{org} in their unvegetated sediments. A similar phenomenon was previously reported for *Z. marina* meadows and other temperate seagrass species (see Mazarrasa et al., 2017a; Mazarrasa et al., 2017b; Prentice et al., 2019; Prentice et al., 2020; Mazarrasa et al., 2021; Krause et al., 2022). Some of this discrepancy was attributed to the export of organic material originating from seagrass habitats to adjacent unvegetated sediments (Duarte and Krause-Jensen, 2017). A similar spillover effect of C_{org} from adjacent seagrass meadows may be contributing to the high C_{org} accumulating in nearby unvegetated sediments in Hasselfelde, where visible C_{org} (not SOC, but also not seagrass biomass) were the main source of C_{org} in unvegetated sublocations. Also, there is a dense community (several cm thick) of bivalve *Cerastoderma edule* populated unvegetated sediments at this site (but not in seagrass-vegetated sediments) and their soft tissue would have contributed to C_{org} sinks (or CO_2 sinks) measured in these sediments. Autochthonous export is not a valid justification for Gohren, Seebar and Gluecksburg as bare sediments were dominated by non-visible C_{org} (100% SOC) and the latter two had a sludge-like consistency

TABLE 5 Summary of alternative candidate Generalized Linear Mixed Models (Gamma, log link function) with ΔAICc < 2 (A) and their model-averaged coefficients (B) for biophysical predictors of regional sediment organic carbon (C_{org}) content of seagrass-vegetated sublocations along the Baltic Sea coast of Germany.

A. Summary of statistically indistinguishable candidate models					
Candidate model	df	Log L	AICc	ΔAICc	Weight
Avg. MOV + fine sed. + SG complexity + depth + depth x SG complexity	8	-754.85	1527.78	0.00	0.24
Avg. MOV + fine sed. + SG complexity + depth + fine sed. x depth	8	-754.94	1527.97	0.20	0.22
Avg. MOV + fine sed. + SG complexity + depth + fine sed. x depth + avg. MOV x SG complexity	9	-753.91	1528.47	0.69	0.17
fine sed. + SG complexity + depth	6	-757.70	1528.59	0.81	0.16
Avg. MOV + fine sed. + SG complexity + depth + avg. MOV x SG complexity	8	-755.52	1529.12	1.34	0.12
Avg. MOV + fine sed. + SG complexity + depth + avg. MOV x depth	8	-755.81	1529.70	1.92	0.09

B. Model-averaged coefficients (full average)							
Source of error	RVI	VIF	Estimate	Std. Error	Adj. SE	z value	*p*-value
Intercept	na	na	8.78745	0.13957	0.14190	61.926	**<0.0001**
Avg. MOV	0.84	1.623	0.11958	0.12247	0.12397	0.965	0.2
Seawater depth	1.00	1.386	-0.29598	0.13372	0.13602	2.176	**0.03**
Seagrass complexity	1.00	2.008	0.27167	0.12119	0.12278	2.213	**0.03**
Fine sediments	1.00	1.138	0.27037	0.11570	0.11768	2.297	**0.02**
Depth x SG complexity	0.24	3.688	0.04699	0.09493	0.09530	0.493	**0.03**
Depth x fine sed.	0.39	1.423	-0.08818	0.13270	0.13340	0.661	0.06
Avg. MOV x SG complexity	0.29	3.220	-0.05116	0.10025	0.10089	0.507	0.1
Avg. MOV x depth	0.09	1.372	0.01989	0.07520	0.07561	0.263	0.1

In all models, location (site) was included as a random effect. Avg. MOV – average Maximum Orbital Velocity; SG – seagrass. Statistically significant effects of model-averaged coefficients (B) are in bold; $\alpha = 0.05$. '+' designates a main effect and 'x' an interaction.
na, not applicable.

TABLE 6 Spatial heterogeneity (average, min, max) of C_{org} (g C_{org}/m^2) in the upper 25 cm sediments of *Zostera marina*-vegetated and unvegetated sublocations of the Baltic Sea.

Country (number of sites)	Geographical division within Baltic Sea	C_{org} in *Z. marina*-vegetated sediments (g C_{org}/m^2)		C_{org} in unvegetated sediments (g C_{org}/m^2)	Source
		Mean	Range		
Germany (20)	Danish Straits & Baltic Proper (SW Baltic Sea)	1,920 ± 402	475 ± 61 to 10,577 ± 1,445	1,840 ± 666	Present study
Denmark (Funen region, 5)	Danish Straits (SW Baltic Sea)	6,005 ± 1,127	400 (estimate) to 22,518 ± 3,753	NA	Röhr et al., 2016
Gullmar Fjord, Sweden	Skagerrak Strait	3,500 ± 410	NA	500 (estimated from Figure 2)	Dahl et al., 2016
Finland (10)	Bothnian Sea (N Baltic Sea)	627 ± 25	400 to 1,300 (estimated from Figure 4)	NA	Röhr et al., 2016
Askö, Sweden	Bothnian Sea & Baltic Proper (N Baltic Sea)	500 ± 50	NA	200 to 600 (estimated from Figure 2)	Dahl et al., 2016
Poland (3)	Baltic Proper (S Baltic Sea)	370 ± 15	125 ± 6 to 570 ± 29	134 ± 4	Averaged from Jankowska et al., 2016

Geographical positioning within Baltic Sea based on seven subbasins defined by HELCOM (2022).
NA, not applicable.

with the top (Seebar) and sixth (Gluecksburg) highest fine (muddy) particle fraction of all sites and sublocations in the study. Heavy anthropogenic pressure at these sites may be contributing to the excess nutrient inputs that would elevate baseline C_{org} in the sediments (Nixon, 1995; Short and Burdick, 1996; Bowen and Valiela, 2001; Nedwell et al., 2002). Also, Seebar was not populated by seagrass only 8 years prior to the study, which could have contributed to these findings as well (pers. obs. P. Schubert). It must be noted that visible seagrass roots and rhizomes were omitted from this analysis, which may lead to a lower contribution of autochthonous organic carbon sources, as observed in the present study.

Unexpected large amounts of well-preserved wood pieces were found in one location: Sierksdorf, Luebeck Bay. Radiocarbon dating of this wood suggests that it was deposited here during two distinct time intervals, averaging at 5,806 BP and 5,095 BP, that coincide well with the second phase of the Littorina Transgression (dated approx. 6,000 to 3,800 BP) following the last deglaciation (Schmölcke et al., 2006; Kostecki et al., 2021). In this period, rapid changes occurred especially in the southwestern part of the Baltic Sea, where fast sea level rise combined with a flat landscape led to the widespread die off of forests situated along the coast. These events caused the demise of coastal alder woodlands that subsequently produced peat containing abundant alder-wood remains (Schmölcke et al., 2006). Indeed, the lack of age (^{14}C) correlation across core depth is typical of natural wood pieces (rather than man-made artefacts) because younger wood can be found in deeper parts of the core due to the roots of the living tree. The two distinct time intervals occurring 700 years apart may suggest a recolonization event took place at this site. Interestingly, the two-time intervals are situated on either side of a brief cooling period (the Subboreal period), which started 5,650 BP and caused widespread natural environmental changes in the southwestern part of the Baltic Sea (Schmölcke et al., 2006). Note that while only one site was radiocarbon dated, we report old wood co-occurring with seagrass meadows in other parts of Schleswig-Holestein, Germany (see Table 1).

The oldest known submarine peatlands globally are dated 5,616 ± 46 years BP and correspond to the thick *matte* formed by *Posidonia oceanica*, a long-lived Mediterranean seagrass, which constitute deep and significant C_{org} stocks (Lo Iacono et al., 2008). *Z. marina* does not form similarly thick and old sedimentary deposits, but our investigation confirms that it too can store millennia of carbon by protecting former (and now submerged) forested peatlands, acting as a protective covering for these rich carbon deposits (Krause-Jensen et al., 2019). Even well-preserved prehistoric settlements have been previously discovered beneath *Z. marina* meadows in Denmark (Fischer, 2011; Andersen, 2013; Pedersen et al., 2017) and Germany (Goldhammer and Hartz, 2017). Submerged wood artefacts are also present in the Baltic Sea coast of Germany, including a site in Neustadt near Sierksdorf (Klooß, 2014), and they too overlap with seagrass habitats. Recognition that some seagrass meadows in Germany are sitting atop ancient terrestrial carbon deposits that are potentially several meters thick has important consequences for avoiding the re-emission of CO_2 (via C_{org}) stored on a millennial timescale. However, our understanding of submerged coastlines is incomplete, so it is likely that many more submarine peatlands, like that found in Sierksdorf, await discovery near the German Baltic Sea coast.

Predicting blue carbon stocks across Germany

A fourth objective of the study was to use the identified relationships between seagrass meadow attributes and environmental parameters on C_{org} to extrapolate stocks for the entire German Baltic Sea region. This regional variation in C_{org} was best explained by seawater depth, seagrass complexity, and the fraction of fine particles in the sediment, not average MOV or interactions between parameters. The latter two had a positive effect on the C_{org} content in the sediment, whereas stocks decreased with seawater depth, suggesting that the highest stocks were found in shallow locations with high seagrass complexity and the ability to accumulate fine-grained particles, regardless of MOV at the seafloor. However, these parameters do not demonstrate a clear ability to predict the regional distribution of C_{org} (Figure 5). A combination of these three parameters, along with water motion, is consistently found to be the main biotic and abiotic driver of C_{org} in the literature, but its influence varies widely across regions and seems principally coupled to local hydrodynamic regimes. Because sediment erosion and detritus export rates are typically heavily influenced by water motion (e.g. lower wave height and exposure, fetch, and currents), sediment C_{org} content is typically lower in dynamic systems compared to more static ones (e.g. Samper-Villarreal et al., 2016; Mazarrasa et al., 2017a; Prentice et al., 2019; Novak et al., 2020; Mazarrasa et al., 2021). But in the absence of strong water movement, like in the German Baltic Sea where tides are negligible, water currents are weak, and wave heights are low, other aspects of the systems can shape C_{org} stocks. The lack of a trend observed in our data in spite of sampling extremes in hydrodynamics of our system, is a testament to this hypothesis, whereby the sites that experienced weakest (Orth, Maasholm, Sierksdorf) maximum current speeds at the seafloor both had the highest C_{org} pools of all sites examined in this study. However, sites with the strongest (Teichhof, Wackerballig) currents did not have low C_{org} pools, in fact they had the 10th and 11th highest C_{org} of all sites. Reduced hydrodynamics may also mean enhanced particle trapping from the water column, which may help explain the mainly allochthonous provenance of the C_{org} and overall high stocks in our study.

The positive relationship observed between the amount of fine particles in the sediment and C_{org} in seagrass-vegetated sublocations is not surprising as it is well known that more C_{org} is associated with finer mineral particles in soils and sediments (Calvert et al., 1995; Lin et al., 2002). These fine particles nurture anoxic conditions in the uppermost layer of the soil that protect organic particles from remineralization (Schrameyer et al., 2018; Brodersen et al., 2019). Our findings are consistent with previous findings for *Z. marina* meadows in other than the German parts of

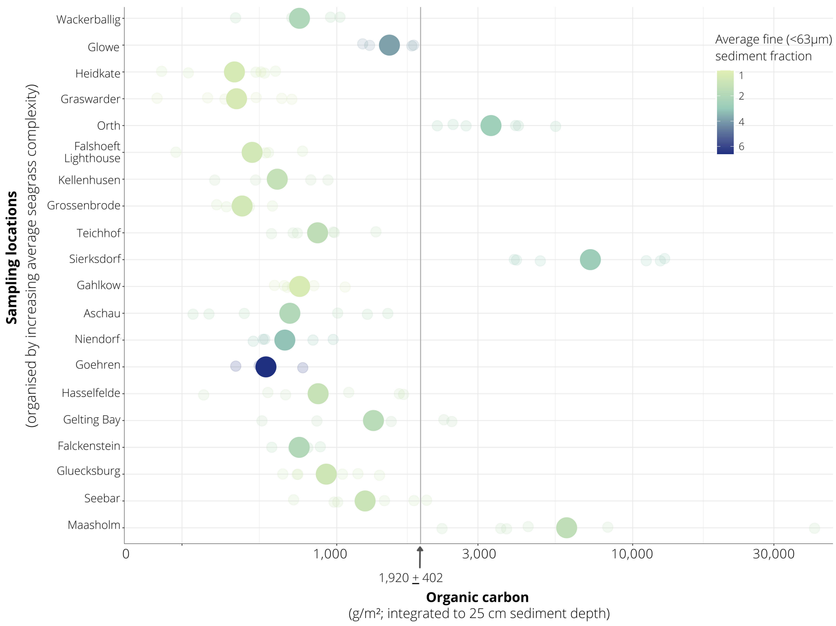

FIGURE 5
Interplay between seagrass complexity and fine grain (<63 µm) sediment predictors of organic carbon (C_{org}) content in seagrass-vegetated sediments along the Baltic Sea coast of Germany.

the Baltic Sea (e.g. Sweden, Dahl et al., 2016; Denmark and Finland, Röhr et al., 2016) and elsewhere (*Z. marina* outside Baltic Sea: Miyajima et al., 2015; Miyajima et al., 2017; Prentice et al., 2019; Krause et al., 2022; multiple species, including *Z. marina*: Kennedy et al., 2010; *P. oceanica*: Gacia et al., 2002; Hendriks et al., 2008). For example, in Denmark and Finland, more than 40% of the variation in C_{org} between sites could be explained by sediment characteristics, including the fine sediment content.

The thick canopy of seagrass leaves is known to effectively intercept particles in the water column, as well as decrease sediment erosion and seagrass detritus export (Ward et al., 1984; Fonseca and Cahalan, 1992; Madsen et al., 2001; Christianen et al., 2013). While seagrass complexity is a strong positive predictor of the regional differences in C_{org} in our study, and that of others (Jankowska et al., 2016; Samper-Villarreal et al., 2016; Serrano et al., 2016), this was not the case for *Z. marina* meadows off the coast of British Columbia, in Canada, where no clear relationship (negative or positive) was observed between the two parameters (Prentice et al., 2019). Here, water motion was the strongest predictor of C_{org}.

The dampening effect of seawater depth on surface water motion is correlated to the trend of increasing C_{org} content with deeper depths (Lavery et al., 2013; Mazarrasa et al., 2017a). While we also observed a dampened effect of water currents (but at the seafloor, rather than surface waters) by increasing seawater depth (ρ = -0.43), an opposite relationship was seen between C_{org} content and depth. A fourfold decrease in C_{org} was also observed with increasing seawater depth (from 2–4 m to 6–8 m) in *P. oceanica* seagrass, in the Mediterranean Sea (Serrano et al., 2014). Regarding the Baltic Sea, seagrass was historically present at deeper depths (e.g. observed beyond 8 m in the past ten years), but today it is rarely observed beyond 5 m seawater depth in Germany. The realization of the Helsinki Commission's Baltic Sea Action Plan (BSAP) goals, which implicate a considerable nutrient abatement, would result in seagrass expansion into deeper waters, as was shown by Bobsien et al., 2021 for the German part of the Baltic Sea. This expansion would lead to an enhancement of the CO_2 storage potential by these habitats, but it is important to consider that this potential is diminished at deeper depths (relative shallow depths) – an important consideration for carbon accounting when including seagrass blue carbon contributions to the German national CO_2 budget.

Scaling up for CO_2 accounting and further considerations

Our measurements confirm that seagrass meadows in the Baltic Sea coast of Germany store a large C_{org} pool. The high spatial heterogeneity seen across the region warrant site-specific investigations to obtain accurate estimates of blue carbon. However, localities with high seagrass complexity, high fine sediment fraction, and low seawater depth could help select localities with more favorable C_{org} accumulation potential. An unexpected and significant relic terrestrial C_{org} pool was found beneath the seagrass meadow in Sierksdorf (Luebeck Bay), and also confirmed in other locations (see Table 1). It is likely that many more submarine peatlands await discovery along the southwestern Baltic Sea region, and that they hold millennial timescale C_{org} deposits similar to those found in Germany.

Based on a conservative scaling up of measurements (integrated to 25 cm sediment depth), collectively (total of approx. 285 km^2, Schubert et al., 2015) seagrass meadows in the German Baltic Sea are preventing 2.01 Mt of future CO_2 emissions from being released into the atmosphere. However, it must be noted that in some locations (Gelting Bay, Teichhof) the sediment has been eroded to the marl layer, which seagrass roots cannot penetrate, while in other locations the sediment is known to extend to 7 m sediment thickness below the seafloor, e.g. within the inner areas of Mecklenburg Bay (Lemke, 1998), such as Sierksdorf, Niendorf, Kellenhusen, Grossenbrode in the present study.

Because C_{org} is dependent on high seagrass complexity, accumulation of blue carbon in Germany may be contingent on healthy seagrass habitats. Furthermore, loss of these habitats will have negative consequences for the German remaining CO_2 budget because the C_{org} stored beneath meadows may be rereleased into the water column and later to the atmosphere. Their loss would also impact their many co-benefits (see Heckwolf et al., 2021). Given the pressing need to offset and prevent future CO_2 emissions, more stringent and concerted efforts are urgently needed to enhance the C_{org} storage potential (via habitat restoration and improving growing conditions) and prevent further degradation (via conservation) of seagrass habitats along the Baltic Sea coast of Germany. Our study provides urgently needed knowledge and constitutes a further incentive to enhance efforts in protecting existing seagrass meadows in Germany, and restore them where natural recolonization is likely slow, such as in enclosed embayments or areas that have seen a loss in seagrass habitat, especially where the distance to the next seagrass-vegetated site is high.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://doi.pangaea.de/10.1594/PANGAEA.947704.

Author contributions

AS: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. TÓC: Investigation, Methodology, Writing – review & editing. WH: Data curation, Formal analysis, Methodology, Software, Writing – review & editing. PS: Conceptualization, Funding acquisition, Methodology, Resources, Writing – review & editing. TR: Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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