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First assessment of seagrass carbon accumulation rates in Sweden: A field study from a fjord system at the Skagerrak coast

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Abstract

Seagrass meadows are globally important blue carbon sinks. In northern cold-temperate regions, eelgrass (*Zostera marina*) is the dominant seagrass species, and although their sedimentary carbon stocks have been quantified across regions, information regarding the CO_2 withdrawal capacity as carbon sinks remains scarce. Here we assessed the carbon (C_{org}) accumulation rates (CARs) and stocks as well as the organic matter sources in five seagrass meadows in the Gullmar Fjord area on the Swedish Skagerrak coast. We found that the mean (±SD) CAR was 14 ± 3 g C_{org} m^{-2} yr^{-1} over the last ~120–140 years (corresponding to a yearly uptake of 52.4 ± 12.6 g CO2 m^{-2}). The carbon sink capacity is in line with other *Z. marina* areas but relatively low compared to other seagrass species and regions globally. About half of the sedimentary carbon accumulation (7.1 ± 3.3 g C_{org} m^{-2} yr^{-1}) originated from macroalgae biomass, which highlights the importance of non-seagrass derived material for the carbon sink function of seagrass meadows in the area. The C_{org} stocks were similar among sites when comparing at a standardized depth of 50 cm (4.6–5.9 kg C_{org} m^{-2}), but showed large variation when assessed for the total extent of the cores (ranging from 0.7 to 20.6 kg C_{org} m^{-2} for sediment depths of 11 to at least 149 cm). The low sediment accretion rates (1.18–1.86 mm yr^{-1}) and the relatively thick sediment deposits (with a maximum of >150 cm of sediment depth) suggests that the carbon stocks have likely been accumulated for an extended period of time, and that the documented loss of seagrass meadows in the Swedish Skagerrak region and associated erosion of the sediment could potentially have offset centuries of carbon sequestration.

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Introduction

Natural carbon sinks are vital for mitigating climate change [1] and seagrass meadows have the potential for accumulating large amounts of carbon in the sediment, and thereby constitute a globally important long-term sink for atmospheric CO_2 [2,3]. The accumulated sedimentary carbon is usually of both autochthonous and allochthonous origin as seagrass meadows trap and store organic matter produced within as well as outside the meadow, with most of the externally produced carbon derived from terrestrial and pelagic (seston) sources [4]. Recently, macroalgae have also been highlighted as an important external carbon donor to blue carbon ecosystems [5]. It is worth noting that macroalgae are an integral part of many seagrass ecosystems and can equally constitute an autochthonous carbon source, as they grow epiphytically on the seagrass leaves or attached to the sediment substrate, and contribute to the overall biomass production of seagrass meadows [6]. The high community production, low degradation of organic matter in the sediment and the allochthonous carbon contributions are the main reasons for seagrass meadows' ability to build up large organic carbon (C_{org}) sedimentary deposits [7]. These sediment deposits can extend several meters in thickness accumulated over centuries or millennia [8], but there is also a large variability in the seagrasses' capacity to sequester C_{org}, ranging from as low as 2 to more than 250 g C_{org} m^{-2} yr^{-1} (see for example [9–12]) This variability highlights the need to assess the seagrass carbon sink function in understudied geographical regions and species, to accurately estimate the capacity of seagrass meadows as natural carbon sinks for climate change mitigation.

Seagrass meadows are found in most coastal waters around the world and eelgrass (*Zostera marina*) is a dominant seagrass species in cold-temperate regions of the Northern Hemisphere [13]. The species show a great variability in carbon stocks and the *Z. marina* sediments on the Swedish Skagerrak coast has been found to be particularly rich in C_{org} compared to many other regions, with mean C_{org} stocks almost two times larger (~4900 g C_{org} m^{-2}, down to 25 cm sediment depth) than the *Z. marina* average (~2700 g C_{org} m^{-2}; [14]). However, seagrass meadows along the Swedish Skagerrak coast have suffered from severe decreases in areal distribution (about 60% loss) between the 1980s and early 2000s [15,16] due to coastal eutrophication and overexploitation of large predatory fish (leading to cascading effects), resulting in overgrowth of filamentous algae [17,18], and this has led to erosion of the sedimentary C_{org} stocks [19]. The C_{org} stocks of *Z. marina* have been studied across the Northern Hemisphere (e.g. [19–21]), but there are still only a few estimates on the species' C_{org} sequestration rates from any of its distribution range (but see [22–24]) and to our knowledge the carbon accumulation rates (CAR) has not yet been quantified in Swedish seagrass meadows. This information is useful for incorporating natural carbon sinks into national greenhouse gas inventories or in carbon credit schemes [25]. With focus on natural carbon sinks on the Swedish Skagerrak coast, we aimed to (1) estimate the carbon accumulation rates and stocks in *Z. marina* meadows within the area of a fjord environment, and (2) assess and determine the organic matter sources contributing to the sedimentary C_{org} pool of the seagrass meadows.

Methods

Study site

The sediment core sampling was conducted in the area of the Gullmar Fjord on the Swedish Skagerrak coast during August 2020. The Gullmar Fjord is a species-rich fjord, about 25 km in length, 1–3 km wide and with a deeper area in the central part (max. depth: 118.5 m). It is the only true fjord in Sweden and became the first marine conservation area (IUCN category V) in Sweden in 1983. The fjord is characterized by a mix of steep cliffs along the sloping fjord

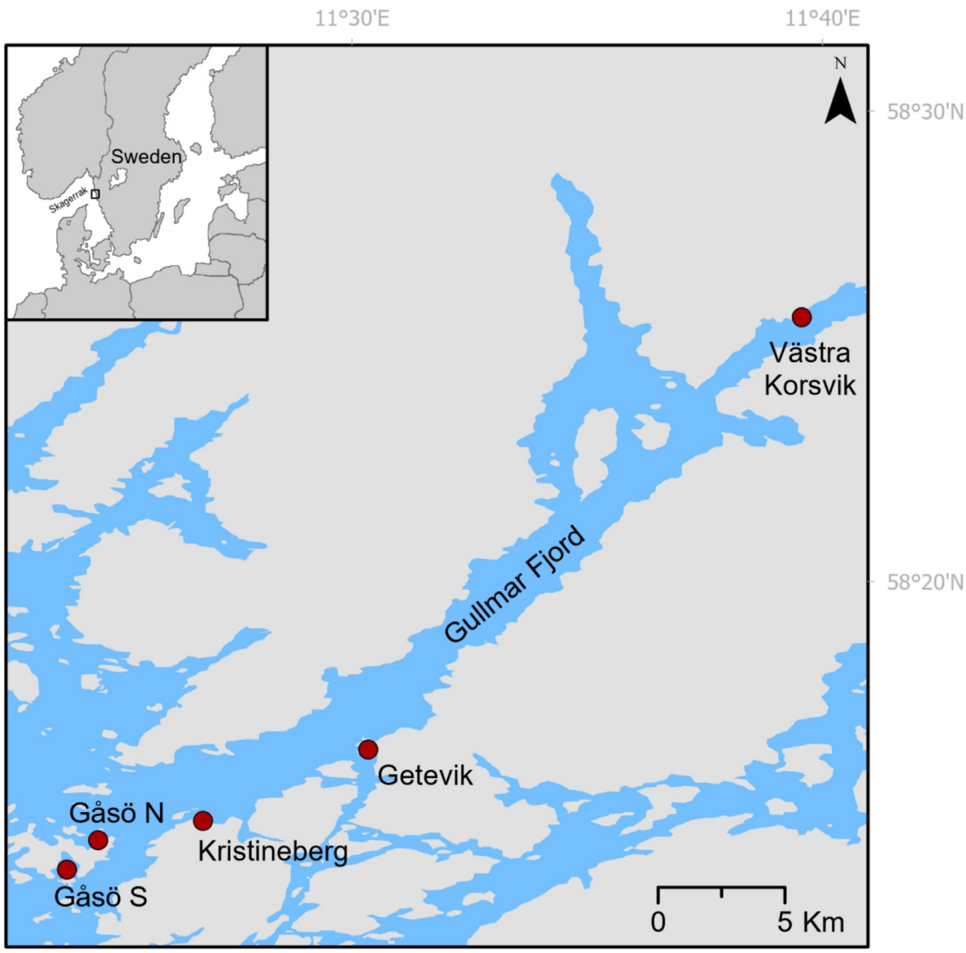

Fig 1. Map over the Gullmar Fjord area with sampling sites and mapped seagrass areas. The map has been generated in ArcGIS pro, version 2.5.0 (ESRI, 2020). The base map was provided by the EEA geospatial data catalogue and available from: https://sdi.eea.europa.eu/catalogue/srv/eng/catalog.search#/metadata/db4cfdd3-0687-4460-a2c7-fd10ca29c214.

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sides and fringing shallow-water areas composed of soft bottoms with numerous seagrass (*Z. marina*) meadows and other rooted macrophyte vegetation at water depths between 0.5 to 6 m. Generally, the fjord is located within a diverse coastal archipelago characterized by a mosaic of bays, inlets and small islands. The water body in the shallows comprises water from the Baltic current mixed with Kattegat and Skagerrak water, local runoff and supply of water from the Örekil river in the inner most part of the fjord [26]. The mean tidal amplitude is about 0.3 m, with oscillations up to 2 m due to variability in air pressure and wind conditions [27]. Five seagrass meadows in or near the fjord were selected, covering the most interior parts and areas towards the open ocean in the southwest, and represent typical environmental conditions for seagrasses in the area (Fig 1). The two meadows at Gåsö (located in sheltered bays in the north and south of the small island right outside of the fjord sill) have a similar hydrodynamic exposure and water depth distribution (ranging from ~0.5 to 4 m). The cores were collected at 1.8 m in Gåsö S and 3 m in Gåsö N. The Kristineberg site is more exposed to winds and waves [19] and the sediment ranges from a coarser sand-mud mixture in the shallower part of the meadow (about 10% mud content at 1–3 m water depth) to muddier in the deeper part (~35–50% mud content at 3–6 m water depth), where the cores were collected (at 4.3 to 4.5 m water depth) [28]. The Getevik site is situated in a highly sheltered embayment with low hydrodynamic exposure [29], and the seagrass meadow is found on 0.5 to 5 m water depth and the core was collected in the middle of the meadow at a depth of 2.5 m. The seagrass meadow at Västra Korsvik is situated next to the Örekil river mouth in the inner part of the fjord and due to high water discharge the water is turbid with low visibility. The water depth of the sampling site was 0.8 m, but the maximum water depth of the meadow is not known.

Sediment sampling and analysis

The sediment cores were collected using SCUBA and 2 m long PVC-cores (with an internal diameter of 7.5 cm). In each seagrass meadow site, one sediment core was sampled, except for in Kristineberg where two cores were taken approximately 50 m apart. Core compression was assessed by measuring the inner and outer parts of the core when pressed down into the sediment and based on the difference between these two values a linear compression factor was calculated. The core compression ranged from 7 to 69%, with the highest value found in Getevik (Table 2). The cores were sliced into 1 cm thick layers for the entire length of a core and dried at 60˚C until constant weight to obtain the dry weight of the sediment slices. For the determination of the sedimentation rates, an aliquot of the slices for the top 21 cm was analyzed for ^{210}Pb. The concentrations of ^{210}Pb were determined by measuring its decay product ^{210}Po in equilibrium using alpha spectrometry [30]. The concentrations of ^{226}Ra were also analyzed in three evenly distributed slices along the sediment profiles based on the decay products ^{214}Pb and ^{214}Bi using gamma spectrometry. The concentrations of excess ^{210}Pb were calculated from the difference between total ^{210}Pb and the average ^{226}Ra and used to obtain an age model for each profile. The mean sedimentation rates were calculated using the Constant Flux:Constant Sedimentation (CF:CS, [31,32] model for the sections of the sediment profiles where a clear decline in excess ^{210}Pb concentrations was present, usually below an upper mixed layer [31]. The Constant Rate of Supply (CRS, [33]) model was applied where possible (i.e. in the Gåsö cores where all sediment sections down to 21 cm were analyzed for ^{210}Pb). Only in the Gåsö cores, the age along the depth of the ^{210}Pb horizon was calculated as they showed constant decreasing ^{210}Pb trends from the surface down to the supported ^{210}Pb levels. Average sedimentation rates based on the concentration profiles of excess ^{210}Pb were calculated using the CF:CS model, frequently below the upper mixed layers, which implies that they need to be taken as upper limits.

For determining the C_{org} content (in % dry weight) and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes of the slices, a carbon and nitrogen elemental analyzer interfaced with an isotope ratio mass spectrometer was used. The delta isotope ratios are expressed in permille relative to the VPDB (Vienna PeeDee Belemnite) for $\delta^{13}C$ and to atmospheric nitrogen for $\delta^{15}N$, and by using acetanilid ($\delta^{13}C = -26.14 \pm 0.15‰$, $\delta^{15}N = 0.38 \pm 0.12‰$) as reference material. The C_{org} content and $\delta\ ^{13}C$ and $\delta\ ^{15}N$ stable isotope values of the topmost 50 cm layer were measured in each cm from 0 to 5 cm, followed by at 7 and 10 cm depths and at each 5 cm from 10 cm to the maximum extent of the sediment core. In Gåsö S, Gåsö N and Västra Korsvik, the total seagrass depth layers were found from 11 to 62 cm depth. Below this depth horizon, there were homogeneous clay layers, distinctly different from the organic sediment of the seagrass layer, which we interpreted as the sediment condition before establishing of the seagrass meadow. Prior to analysis, the samples were homogenized into a fine powder using a mixing mill, and treated with 1M HCl (direct addition using a pipet), following the protocol of Dahl *et al.* [34] in order to remove carbonates. The addition of HCl was continued until the reaction with the carbonate was complete.

Quantification of C_{org} sequestration rates and stocks

To calculate the CAR (g C_{org} m^{-2} yr^{-1}), the mass accumulation rate (MAR, g cm^{-2} yr^{-1}) was multiplied by the weighted %C_{org} concentration, as described in Arias-Ortiz *et al.* [31] for the section of the sediment profile where the CF:CS model was applied. As sediment mixing was present in some of the cores, we assumed that the MAR obtained from the underlying section (where sediment mixing was not present) was the same for the mixed layer. The average CAR for the most recent decades was then calculated for the length of the core where excess ^{210}Pb was present. The sediment dry bulk density (DBD, g cm^{-3}) was derived from the weight of each slice divided by the volume of the core slice. The C_{org} density (g C_{org} cm^{-3}) was calculated by multiplying the %C_{org} content with the sediment density of each slice. The C_{org} stocks were obtained by adding up the C_{org} density for each slice to the standardized depth of 50 cm for comparison between sites.

Estimate of contribution of potential C_{org} sources to the seagrass meadow C_{org} storage

The contribution of potential sources (i.e. terrestrial organic matter, macroalgae biomass and seagrass biomass) to the sedimentary C_{org} pool was analyzed using the Simmr package in R version 3.6.3 [35,36] with stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ as tracers down to 50 cm sediment depth, with the exception of Västra Korsvik, where the maximum seagrass sediment depth of 11 cm was used. The 50 cm sediment depth was used to align the C_{org} sources to the standardized sediment depth of the C_{org} stocks. As degradation of organic matter can alter the $\delta^{13}C$ over time [37], we also assessed the proportion of C_{org} sources in the surface sediment only (down to ~10 cm) but with no noticeable differences compared to the 0–50 cm depth (Table A in S1 Text). The three potential sources were selected based on previous findings from Gullmar Fjord [14], the high amount of macroalgae found in the meadows when sampling and the meadows relative proximity to land. For the terrestrial and macroalgae endmembers, we used literature values, while samples of seagrass biomass (average values of above- and belowground plant tissue) was collected (n = 3) at two sites (i.e. Getevik and Kristineberg) for this study. The isotopic values of the potential sources were distinct with stable isotopes for terrestrial organic matter of −28.9 ± 1.3‰ ($\delta^{13}C$) and 0.8 ± 2.5‰ ($\delta^{15}N$) [38,39], macroalgae biomass of –-19.8 ± 1.8‰ ($\delta^{13}C$) and 3.2 ± 0.7‰ ($\delta^{15}N$) [40] and seagrass plant biomass of −9.8 ± 1.8‰ ($\delta^{13}C$) and 1.0 ± 1.1‰ ($\delta^{15}N$) (this study). The macroalgae species used as potential sources were the brown algae *Saccharina latissima* and *Laminaria hyperborea*, which are commonly found on rocky shores in vicinity of the seagrass meadows on the Swedish Skagerrak coast. Other species of the macroalgae flora of the seagrass ecosystem in this coastal region are *Chorda filum* ($\delta^{13}C$ = −19.9), *Fucus serratus* ($\delta^{13}C$ = −17.6), *Pilayella* sp. ($\delta^{13}C$ = −15.57), *Ceramium rubrum* ($\delta^{13}C$ = −19.56) and *Ulva intestinalis* ($\delta^{13}C$ = – 20.3) [41], which all have similar $\delta^{13}C$ values.

Results

The concentrations of total ^{210}Pb in cores Gåsö N and Gåsö S decreased with depth to about 25 Bq kg^{-1} at around 10 cm and 18 cm depth, respectively, although the concentrations were relatively constant between 3 and 7 cm for core Gåsö S (Fig 2). A constant ^{210}Pb was interpreted as mixing or a sudden input of sediment [31]. For core Kristineberg 1, the concentrations of total ^{210}Pb were constant between 3 and 10 cm and decreased with depth thereafter, down to 32 Bq kg^{-1} at about 20 cm depth. For core Kristineberg 2, the concentrations of total ^{210}Pb decreased with depth to 24 Bq kg^{-1} at 20 cm, although the levels were relatively constant

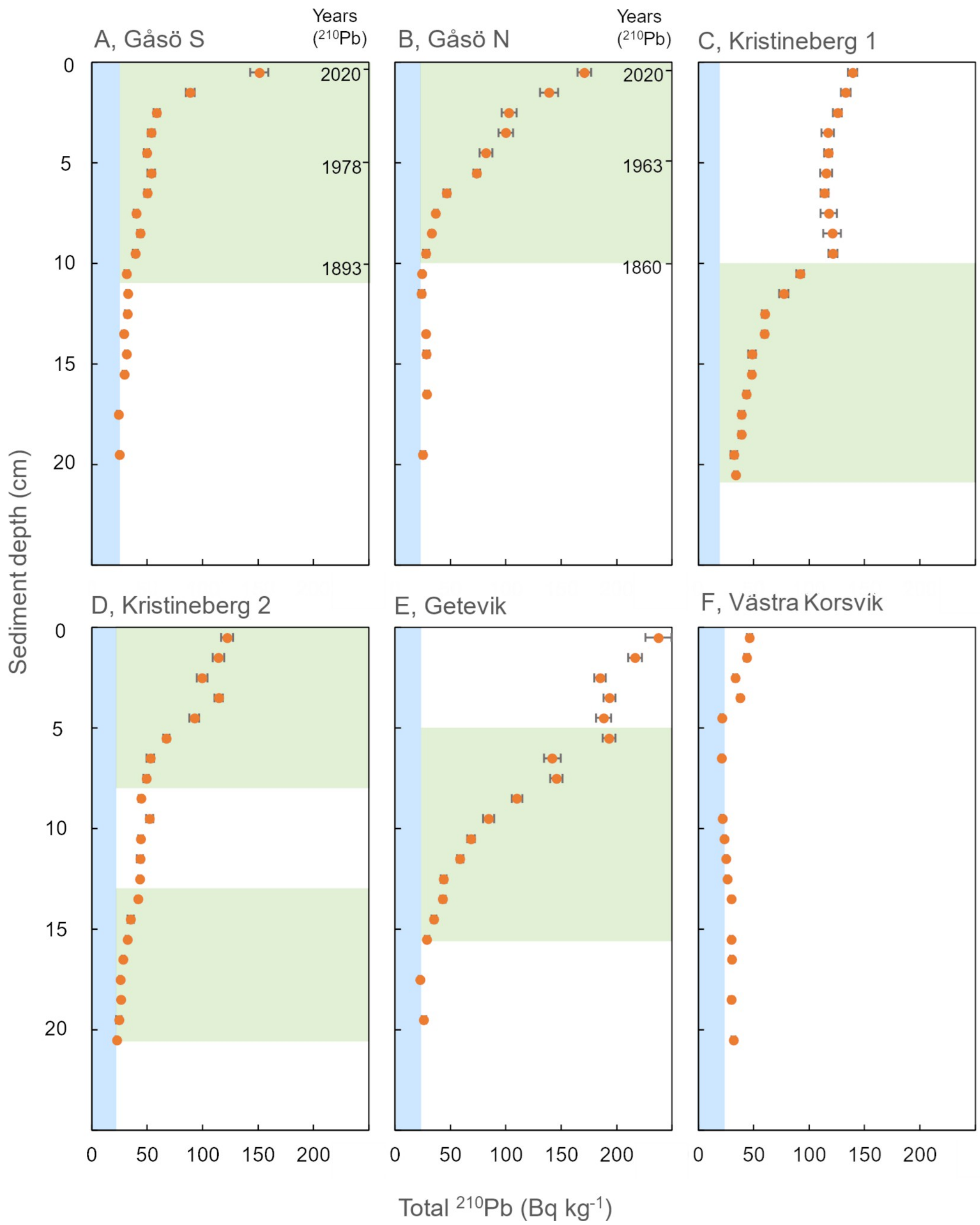

Fig 2. Concentration profiles of ^{210}Pb for the sediment cores. The blue fields represent the supported ^{210}Pb levels and the green fields show the sections for which sedimentation rates could be calculated.

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between 8 and 13 cm, coincidentally with somewhat lower values of DBD. The concentrations of total ^{210}Pb in core Getevik decreased with depth from 220 Bq kg^{-1} at the surface to about 25 Bq kg^{-1} at 16 cm depth, albeit with constant values between 2 and 6 cm. The concentrations of total ^{210}Pb in core Västra Korsvik decreased with depth to about 22 Bq kg^{-1} at 4 cm (Fig 2). For all cores, the concentrations of ^{226}Ra (^{210}Pb supported) ranged from 23 to 25 Bq kg^{-1}.

An average sedimentation rate of 0.0193 ± 0.0007 g cm^{-2} yr^{-1} (1.21 ± 0.05 mm yr^{-1}) was estimated for core Gåsö N (Table 1), but it could also be possible to interpret the ^{210}Pb concentration profile as evidencing a higher sedimentation rate from the 1960s (at around 5 cm; Fig 2),

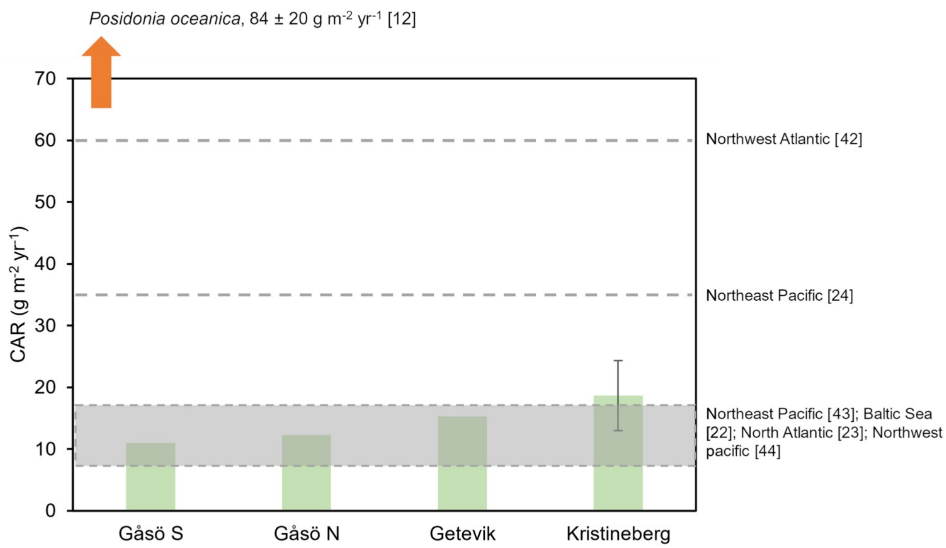

Fig 3. Carbon accumulation rate (CAR) for the different sites. Literature CAR values for *Z. marina* in other regions [22–24,42–44] are shown as dashed lines and shaded box (the width of the box covers the range of values for the referenced studies). The estimated mean value for *Posidonia oceanica*, which is considered the most efficient seagrass species for carbon sediment sequestration, is included as a reference for the seagrasses' potential as carbon sinks.

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which would have increased from 0.009 to 0.026 g cm^{-2} yr^{-1} (or from 0.6 to 1.2 mm yr^{-1}). This interpretation is in good agreement with the results obtained when applying the CRS model. For core Gåsö S, an average sedimentation rate for the upper 11 cm was estimated of 0.0165 ± 0.0013 g cm^{-2} yr^{-1} (1.18 ± 0.09 mm yr^{-1}; Table 1). However, while this estimate is comparable to the results of the CRS model, it needs to be taken with caution because of the presence of the layer at 3–7 cm, likely evidencing some local mixing. For core Kristineberg 1, the average sedimentation rate was of 0.074 ± 0.006 g cm^{-2} yr^{-1} (1.86 ± 0.14 mm y^{-1}), but it could be possible that there had been a change of the sedimentation rate in the past (at around 13 cm), which would have decreased from 0.09 to 0.03 g cm^{-2} yr^{-1} (from 2.2 to 1.3 mm yr^{-1}). For core Kristineberg 2, the upper 8 cm had accumulated at an average rate of 0.079 ± 0.005 g cm^{-2} yr^{-1} (1.96 ± 0.13 mm yr^{-1}), while in the past it would have been of 0.063 ± 0.013 g cm^{-2} yr^{-1} (0.83 ± 0.17 mm yr^{-1}) below 13 cm (Table 1). The average accumulation in Kristineberg 2 was 0.069 ± 0.001 g cm^{-2} yr^{-1} and 1.39 ± 0.15 mm yr^{-1}. For the Getevik core, an average sedimentation rate of 0.0154 ± 0.0005 g cm^{-2} yr^{-1} (1.66 ± 0.05 mm yr^{-1}) can be calculated below the upper layers applying the CF:CS model. Finally, for core Västra Korsvik, the horizon of excess ^{210}Pb was reached at 4 cm, precluding the estimation of a sedimentation rate for this core, that, in any case, would be very low.

The lowest average (±SD) CAR values were found in Gåsö S and Gåsö N (10.9 ± 0.7 and 12.2 ± 0.4 g C_{org} m^{-2} yr^{-1}, respectively), followed by Getevik (15.3 ± 0.5 g C_{org} m^{-2} yr^{-1}) and Kristineberg, with a mean (±SD) for the two cores of 18.6 ± 8.0 g C_{org} m^{-2} yr^{-1} (Kristineberg 1: 24.5 ± 1.9 g C_{org} m^{-2} yr^{-1}, Kristineberg 2: 12.7 ± 1.4 g C_{org} m^{-2} yr^{-1}) (Fig 3). The difference in CAR seen at the Kristineberg site was due to a slightly higher accumulation rate and %C_{org} content in the topmost sediment of Kristineberg 1 (Table 1). The mean (±SD) CAR in the seagrass meadows averaged 14.3 ± 3.4 g C_{org} m^{-2} yr^{-1}, which corresponds to an uptake of 52.4 ± 12.6 g CO_2 yr^{-1}.

The cumulative C_{org} stocks corrected for core compression show a similar accumulation level across cores (Fig 4A) and for C_{org} stocks calculated to 50 cm sediment depth. The 0–50 cm C_{org} stocks were slightly lower in Gåsö S (4.61 kg C_{org} m^{-2}) and Getevik (4.67 kg C_{org} m^{-2})

Table 1. Summary of sediment and mass accumulation rates (SAR and MAR, respectively) and C_{org} content. For Kristineberg 1 and 2 and Getevik, SAR and MAR could not be established for the entire excess ^{210}Pb depth section (see Fig 2) due to sediment mixing and the values were therefore extrapolated towards the sediment surface. Bold values show the average sedimentation rates and were used for calculating the CARs in the cores. All values are presented as mean ± SD and SAR is corrected for core compression.

Core	Excess ^{210}Pb horizon (cm)	Mixing depth (cm)	SAR (mm yr^{-1})	MAR (g cm^{-2} yr^{-1})	C_{org} (%)
Gåsö S	**0–11**	-	**1.18 ± 0.09**	**0.017 ± 0.001**	**5.7 ± 1.7**
Gåsö N	**0–10**	-	**1.21 ± 0.05**	**0.019 ± 0.007**	**6.5 ± 2.2**
	0–5		1.64 ± 0.11	0.026 ± 0.002	
	5–10		0.59 ± 0.06	0.009 ± 0.001	
Kristineberg 1	**0–21**	**0–10**	**1.86 ± 0.14**	**0.074 ± 0.006**	**4.0 ± 1.4**
Kristineberg 2	**0–21**	**8–13**	**1.39 ± 0.15**	**0.069 ± 0.001**	**2.9 ± 1.7**
	0–8		1.96 ± 0.13	0.079 ± 0.005	
	13–21		0.83 ± 0.17	0.063 ± 0.013	
Getevik	**0–16**	**0–5**	**1.66 ± 0.05**	**0.015 ± 0.001**	**11.0 ± 1.9**
Västra Korsvik	0–4	-	N/A	N/A	0.4 ± 0.1

N/A = MAR and SAR could not be estimated due to a low sedimentation rate.

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compared to the other meadows, while the highest levels were found in Kristineberg (mean ± SD) and Gåsö N (5.11 ± 1.31 g m^{-2} and 5.88, respectively) (Fig 4B). For Västra Korsvik, no C_{org} stock value was calculated for the standardized depth as the seagrass sediment depth horizon was only 11 cm thick, while for the other sites the seagrass sediment ranged from 59 to at least 149 cm deep. The total C_{org} stocks in the entire core reflects the difference in sediment length of the core, with the highest value seen in the Kristineberg site (Kristineberg 1: 11.6 kg C_{org} m^{-2} at the depth of 111 cm, Kristineberg 2: 20.6 kg C_{org} m^{-2} at the depth of 149 cm) (Fig 4C).

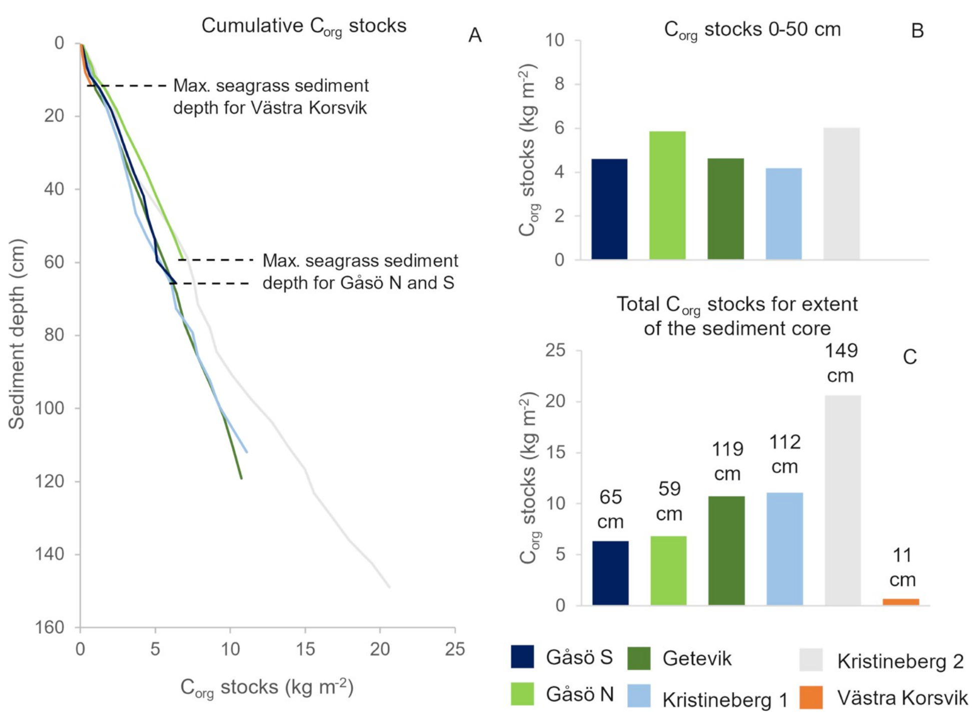

Fig 4. C_{org} stocks (kg C m^{-2}) shown as (A) cumulative accumulation of the sediment depths, (B) standardized stocks down to 50 cm sediment depth and (C) the total accumulation for the entire sediment core depths.

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Table 2. Seagrass sediment depth, sediment compression, and mean (± SD) of C_{org} content and stable isotopic signatures for 0–50 cm depth layer.

			0–50 cm depth layer			
Core	Depth of seagrass sediment layer (cm)	Core compression (%)	C_{org} (%)	C_{org} density (mg cm^{-3})	$\delta^{13}C$	$\delta^{15}N$
Gåsö S	59	18	5.3 ± 2.3	7.8 ± 2.5	-15.71 ± 0.74	3.76 ± 0.86
Gåsö N	62	17	6.6 ± 2.1	11.8 ± 3.4	-15.98 ± 0.46	4.58 ± 0.89
Kristineberg 1	>112	31	3.3 ± 1.7	7.7 ± 1.5	-17.45 ± 0.92	4.85 ± 0.74
Kristineberg 2	>149	27	3.0 ± 1.8	11.6 ± 3.8	-17.35 ± 1.14	5.05 ± 0.58
Getevik	>119	69	10.6 ± 2.0	8.1 ± 1.4	-15.79 ± 0.64	4.86 ± 0.57
Västra Korsvik	11*	7	0.6 ± 0.3	4.6 ± 2.4	-21.91 ± 0.51	3.89 ± 0.88

*The values are calculated for 0–11 cm sediment depth.

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The $\delta^{13}C$ values were lowest in Västra Korsvik, followed by Kristineberg, while Gåsö S, Gåsö N and Getevik showed similarly higher values (Table 2). The $\delta^{13}C$ values showed only minor variation along the upper 50 cm in all sites (Table 2; Fig A in S1 Text). In all cores, there was a high proportion of macroalgae biomass contribution (ranging from 41 to 64%) to the sedimentary C_{org} pool. The terrestrial source input was generally low (7–11%), except for Västra Korsvik, where terrestrial organic material contributed with 36% of the C_{org} and the seagrass plant biomass isotopic signal was low (9%). For the other sites, seagrass input varied from 29% in Kristineberg to a maximum of 49% in Getevik (Fig 5). Given the C_{org} accumulation rates of the seagrass meadows (Table 1), an estimate of 5.2–7.4 g C_{org} m^{-2} autochthonous seagrass biomass, 4.8–11.9 g C_{org} m^{-2} macroalgae material and 0.9–1.6 g C_{org} m^{-2} of terrestrial organic matter is being stored annually.

Discussion

This first estimate of seagrass carbon sink capacity in Sweden, which was performed in the Gullmar Fjord area on the Skagerrak coast showed an average (±SD) CAR of 14 ± 3 g C_{org} m^{-2} yr^{-1} during the last century. In a Swedish perspective, this rate of seagrass C_{org} accumulation is comparable to more well-documented carbon sink habitats, such as forest soils (18 g C m^{-2} yr^{-}

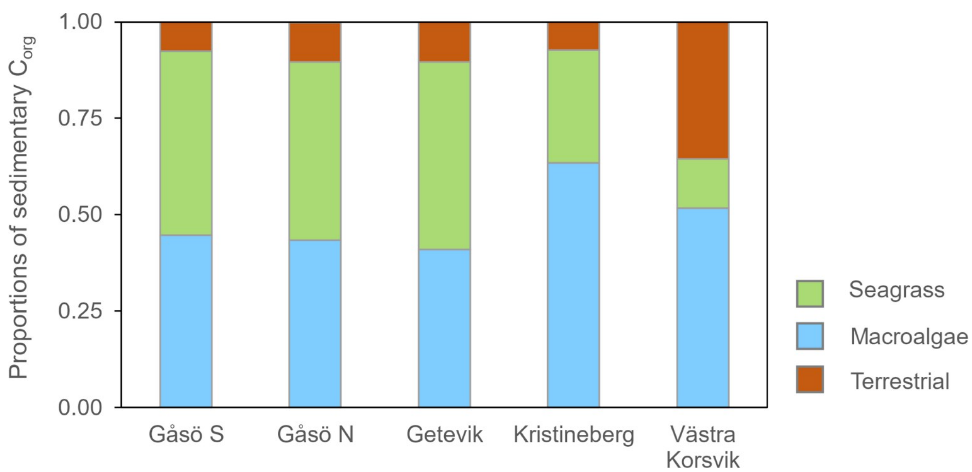

Fig 5. The proportion of seagrass, macroalgae and terrestrial organic matter contributing to the sedimentary C_{org} pool for the sediment depth of 0–50 cm, except for Västra Korsvik, for which the seagrass sediment depth was 0–11 cm.

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[1]) [45] and peatlands in Sweden (around 12–16 g C m^{-2} yr^{-1}) ([46], and references within). The *Z. marina* carbon sink function in the Gullmar Fjord area was highly dependent on the accumulation of macroalgae biomass (ranging from 41 to 64% of the total C_{org} pool), being equal or even higher than the seagrass plant contribution (that ranged from 9 to 49%). The findings from this study highlight that the *Z. marina* meadows in the area of the Gullmar Fjord is a sink of atmospheric CO_2 (of both autochthonous and allochthonous organic matter), with a yearly CO_2 uptake of 52 ± 13 g yr^{-1}. Given the extensive loss of seagrass meadows on the Swedish Skagerrak coast [15], it is crucial to protect the seagrass meadows to avoid C_{org} erosion and for continuous atmospheric CO_2 uptake.

The C_{org} accumulation in the seagrass meadows varied from 11 to 25 g C_{org} m^{-2} yr^{-1}, with the highest CAR found in Kristineberg and due to mixing of the topmost sediment in some of the cores, the CAR values should be seen as upper estimates. The Kristineberg site is relatively exposed to hydrodynamic forces (with a mean wave height of 0.25 m) in relation to the other sites (for instance 0.10 m in Getevik) [29], which in this area has been shown to positively influence the carbon storage in these low sediment density and silty seagrass beds [28,47] and with a high input of allochthonous sources transported by waves and currents could promote the C_{org} accumulation of the meadow [14]. The Gåsö and Getevik sites had similar CAR (11–15 g C_{org} m^{-2} yr^{-1}) and with equivalent autochthonous–allochthonous source ratios of the sedimentary C_{org} pool. Gåsö and Getevik are both located in sheltered embayments of the fjord area with comparable hydrodynamic conditions, and this could explain the similarity in C_{org} accumulation and organic matter sources, as hydrodynamic exposure is highly affecting the sediment deposition and allochthonous C_{org} input [48], in smaller and fast-growing seagrass species, including *Z. marina* [12,49–51]. The cores at Gåsö also displayed an increase in sedimentation rates during the 1960s but this needs further investigation as the island is located in a relatively remote area with no major coastal development or human activities, such as dredging, which could alter the sedimentation processes [52]. This study only presents one core from each site (except for Kristineberg) and in order to account for seagrass meadow heterogeneity, several cores should ideally be collected [53] as C_{org} accumulation can vary within a meadow due to e.g. edge effects [54] and water depth [55]. Indeed, the difference in CAR for the two Kristineberg cores (13–25 g m^{-2} yr^{-1}) indicates within-meadow variability, which in this case may have been influenced by differences in sediment properties, such as mud content, between the two sampling sites [56]. Though, this was not assessed in this study and needs to be evaluated in more detail. As Västra Korsvik is located on shallow water depth and close to the Örekil river mouth in the interior of the fjord, the water discharge of the river could cause high turbidity (the high turbidity was also visually noticed during core sampling) and sediment resuspension preventing organic matter deposition and seagrass sediment stabilization. This might explain the shallow seagrass sediment accumulation (down to 11 cm) in the core. The influence of the river in Västra Korsvik is further seen by the relatively large proportion of terrestrial organic matter sources in the sediment (36%), likely derived from the outflow of the river [57] compared to the other sites in this study, although this site was generally low in C_{org} content.

The cumulative accumulation of C_{org} stocks showed a relatively small variation between cores with similar C_{org} stocks at 50 cm, ranging from about 4.6 to 5.9 kg C_{org} m^{-2}, which are comparable to previous assessments in the Skagerrak-Kattegat region [14,19,29,58]. The main difference in C_{org} stocks between the cores was due to the variation in seagrass sediment depth thickness resulting in a storage from 0.7 kg C_{org} m^{-2} at Västra Korsvik (with a seagrass sediment depth of 11 cm) up to 20.6 kg C_{org} m^{-2} in the Kristineberg 2 core (accumulated in 149 cm thick seagrass sediment). The high C_{org} storage in Kristineberg 2 is in line with what has been reported in a deep seagrass sediment core (20.6 kg C_{org} m^{-2} in 120 cm thick sediment deposit) in the area [19]. This highlights the importance of information on total sediment thickness for evaluating areas of high C_{org} stocks as standardized depths, such as 0.5 or 1 m, which might lead to erroneous conclusions on the extent of the C_{org} stock. Furthermore, due to variation in CAR for the different sites in the Gullmar Fjord, the sedimentary C_{org} deposits have been accumulated over different time periods. Although Gåsö N had a relatively high C_{org} stock, the CAR was approximately 40% higher in Kristineberg in comparison. While both measurements are relevant to quantify, this shows that the stocks per unit area and the CAR will provide with different information crucial for blue carbon management (standing stock or rate of efficiency) and highlights the need to assess the rate of accumulation over time in order to estimate and compare the C_{org} sequestration capacity of *Z. marina* meadows.

The contribution of seagrass plant material to the sedimentary C_{org} pool is estimated to about 50% in general [4] although there is large variation among species. In *Z. marina* sediments and other smaller species, the seagrass plant contribution to the carbon stocks is usually lower in comparison to e.g. *P. oceanica* [59], which build up thick carbon- rich seagrass root-rhizome "mattes" [8] that constitute a large proportion of the sedimentary C_{org} pool. In line with other studies in *Z. marina* [24,44], we found that substantial part of the accumulated C_{org} stocks (up to 64%) was of macroalgae origin. This shows that the seagrass meadows are not only relevant sinks for autochthonous seagrass-derived plant material but also for other macrophytes, such as macroalgae, and support the hypothesis that macroalgae are important C_{org} doners to blue carbon habitats [5]. The high proportion of macroalgae in the sediment could be a direct response to the increase in filamentous algae in the Gullmar Fjord [60]. This has been related to eutrophication, which a major environmental problem of the Swedish Skagerrak coast [61,62] and have caused (together with food web cascades) substantial decline in seagrass meadows [15,17,18]. Although eutrophication is of concern for the marine environment and the seagrass ecosystem health, this indicates that high macroalgae growth could increase the C_{org} accumulation rate in the seagrass meadows. However, there is clearly an upper limit for the seagrass meadows' capacity to sequester macroalgae biomass as a high production of macroalgae can result in seagrass smothering and overgrowth with adverse effects on the seagrass ecosystem and C_{org} storage potential [63]. The yearly mean (± SD) uptake of 7.1 ± 3.3 g C_{org} m^{-2} (ranging from 4.8 to 11.9 g C_{org} m^{-2}) of macroalgae material shows the seagrass meadows' capability as filters of the coastal zone by tapping and storing organic matter of allochthonous origin [4]. Given the extensive distribution of both perennial and annual filamentous macroalgae in seagrass meadows of the Swedish Skagerrak coast and the fact that the carbon and nitrogen stable isotopes cannot distinguish between algae species, part of the macroalgae contribution to the sedimentary C_{org} pool is likely from species growing within the meadows, including *Ectocarpus* sp., *Ceramium* sp. and *Ulva* sp. [18], although the amount of algae drifting from elsewhere, such as *F. serratus* and *Furcellaria lumbricalis* could also be substantial.

The Swedish Skagerrak coast has experienced a large reduction of seagrass area, with an average loss of 60% since the 1980s [15,16]. However, the loss rate for the Swedish Skagerrak regions has been widely different, with the Lysekil municipality area (where the Gullmar Fjord is situated) experiencing only a slight decrease in seagrass coverage (2%) between the 1980s and early 2000s. In contrast, other areas have suffered major seagrass regressions; for example Kungälv (located about 40 km south of the Gullmar Fjord) has experienced a catastrophic total decline of 82% (648 ha) [15] during this period, and with further decline being reported during the 2000s [64]. This could indicate that the loss of seagrass areas (estimated to 1069 ha) has reduced the meadows' capacity to sequester carbon by 150 Mg C_{org} yr^{-1} for the whole Swedish Skagerrak coast, and the region of Kungälv alone with 92 Mg C_{org} yr^{-1}. Furthermore, as seagrass meadows disappear, this does not only impair the carbon sequestration function but also risk sedimentary C_{org} stock erosion [65–67]. Given the sedimentation rates in the Gullmar Fjord area is slow (less than 2 mm yr^{-1}, which is below the average seagrass SAR [68]), and the thickness of the sediment deposits (from about 60 to at least 150 cm), carbon stocks in this region have been accrued over a long period of time and therefore a loss of seagrass areas would cause erosion of ancient C_{org} and potentially have counteracted centuries of carbon sequestration. However, the eroded C_{org} could avoid remineralization (and therefore not emitted as CO_2) if deposited in other areas where its preserved, e.g. the deeper part of the fjord [69].

The seagrass CAR in this study is similar to those reported for other *Z. marina* sites [22,23,43,44], although higher values (up to 60 g C_{org} m^{-2} yr^{-1}) have also been reported [24,42]. The CAR in this study, and for *Z. marina* meadows in general, is however considerably lower compared to other species and regions (see e.g. [3,10–12,70]). For instance, the Mediterranean seagrass *Posidonia oceanica*, which has shown to have the highest CAR for seagrasses worldwide can have an accumulation rate of up to 249 g C_{org} m^{-2} yr^{-1} [10], but *Z. marina* meadows are still relevant carbon sinks for climate change mitigation, especially considering the low greenhouse gas (i.e. methane) emission from these ecosystems [71]. The low sedimentation and CAR found in cold-temperate *Z. marina* meadows could be related to the strong seasonality in these regions, which influences seagrass biomass growth and production [72,73] and carbon storage [29]. During the winter season (December to March), the seagrass shoot biomass is reduced (in some cases the aboveground is completely detached) [74] leading to a lower primary production [75] and presumably less seston filtering and trapping within the canopy [76]. Furthermore, storms tend to increase during autumn (September to November) and with a low shoot biomass to protect the sediment from the sudden increased hydrodynamic forces, this could lead to resuspension and erosion of surface sediments [77].

This study adds to the growing literature of seagrass C_{org} sink capacity, and we found that the cold-temperate *Z. marina* carbon sinks of the Gullmar Fjord area store large C_{org} stocks that have been slowly accumulated. The high accumulation of macroalgae biomass in the sedimentary C_{org} pool shows that organic matter sources besides the seagrass plants are important for blue carbon storage of these ecosystems. We also highlight the importance of assessing the total sediment deposits when quantifying C_{org} storage as the main difference in C_{org} stocks was related to the large difference in seagrass sediment thickness.

Supporting information

S1 Text. Fig A. Sediment depth profiles down to ~50 cm showing sediment density, Corg density, δ13C isotopic values and percent Corg in the different sites. Table A. The proportion of Corg sources (mean ± SD) to the surface layer of the seagrass sedimentary pool. The estimated proportions are based on stable isotopes (δ13C and δ15N) analyzed with the Simmr package in R.
(DOCX)

S1 Data. Data.
(XLSX)

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