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Major impacts and societal costs of seagrass loss on sediment carbon and nitrogen stocks

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Abstract. Seagrass meadows constitute important carbon sinks, and the ongoing global loss of seagrass habitats raises concerns about the release of carbon stored in their sediments. However, the actual consequences of seagrass loss for the release of carbon and nutrients remain unclear. Here, we take advantage of well-documented historic losses of eelgrass (*Zostera marina*) meadows along the Swedish NW coast to assess how the contents of organic carbon (C) and nitrogen (N) in the sediment change when a meadow is lost. We find unusually high contents of C and N (on average 3.7% and 0.39% DW, respectively) in Swedish eelgrass sediments down to >100 cm depth, suggesting that these habitats constitute global hot spots for C and N storage. However, the C and N stocks were strongly influenced by wave exposure and were almost twice as high in sheltered compared to exposed eelgrass meadows. The sediment composition and stable isotope values were distinctly different in areas that have lost eelgrass meadows, with on average >2.6 times lower contents of C and N. The results indicate an erosion of >35 cm sediment following the historical eelgrass loss, and that sheltered meadows have more vulnerable sediment stocks. The results suggest that eelgrass loss has resulted in a release of 60.2 Mg C and 6.63 Mg N per hectare, with an estimated economic cost to society of 7944 and 141,355 US$/ha, respectively. The value of N storage represents one of the highest monetary values presented for an ecosystem service provided by seagrasses and shows that Swedish eelgrass meadows are particularly important for mitigating eutrophication. Following a documented loss of approximately 10 km^2 of eelgrass in the study area, it is estimated that over 60,000 Mg of nitrogen was released to the coastal environment over a 20-yr period, which constitutes over three times the annual river load of nitrogen to the Swedish NW coast. The study exemplifies the significant role of seagrass sediments as sinks for both carbon and nutrients, and that the risk of nutrient release following vegetation loss should be taken into account in the spatial management of seagrass and other coastal habitats.

Key words: blue carbon; ecosystem services; eelgrass; eutrophication; marine spatial management; monetary valuation; nutrient release; sediment erosion; Swedish west coast; *Zostera marina*.

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Introduction

Seagrass meadows provide several key ecosystem functions, and one of the most important is their role in carbon (hereafter C) and nutrient cycling in coastal ecosystems. The high primary production in seagrass meadows and the high capacity of seagrasses to trap organic particles by reducing water flow, wave energy, and sediment resuspension result in very high accumulation of organic matter (hereafter OM) in seagrass meadows (e.g., Mateo et al. 1997, Duarte et al. 2005). Moreover, the anoxic conditions in seagrass sediments, and the generally high C:N:P ratios and proportion of refractory organic compounds in seagrass tissue, result in a very slow decomposition (Fourqurean et al. 2012). Together, these characteristics result in an unusually high accumulation and long-time storage of both autochthonous and allochthonous OM in seagrass sediments (Duarte et al. 2005, Fourqurean et al. 2012, Röhr et al. 2018). Seagrass meadows are therefore considered globally important blue carbon ecosystems.

The ability of seagrasses to capture and store carbon has received renewed interest in light of climate change, and many recent studies have demonstrated that per unit area, seagrass meadows are among the most effective C sinks on the Earth, where in particular the seagrass sediment constitutes globally important stocks of C, which can be buried for centuries or millennia (Mateo et al. 1997, Duarte et al. 2005, McLeod et al. 2011, Fourqurean et al. 2012, Pendleton et al. 2012, Röhr et al. 2018). However, anthropogenic impacts have caused extensive degradation and loss of seagrasses globally (Orth et al. 2006, Waycott et al. 2009, but see de los Santos et al. 2019), reducing their ability to capture and store C (McLeod et al. 2011, Pendleton et al. 2012). There is increasing concern that if seagrass ecosystems are disturbed or lost, they could shift from being a C sink to a C source by releasing vast amounts of stored C from the sediment back into the ocean–atmosphere system (Duarte et al. 2013, Macreadie et al. 2014, Marbà et al. 2015). However, although the sediment C stocks are often higher in pristine seagrass meadows compared to disturbed meadows or unvegetated areas (e.g., Ricart et al. 2015, Dahl et al. 2016, Samper-Villarreal et al. 2018), there are still major uncertainties regarding sediment erosion and subsequent release of C following the loss of seagrass meadows (McLeod et al. 2011, Macreadie et al. 2015, Marbà et al. 2015). In studies estimating the release of C resulting from seagrass loss, it has often been assumed that the top meter of the sediment is eroded as a result of the loss and that the C present there is remineralized and released as CO_2 to the ocean–atmosphere (Fourqurean et al. 2012, Pendleton et al. 2012). However, this assumption still largely lacks empirical support. One exception is the seagrass *Posidonia australis* in Australia, where two independent studies recently demonstrated that historic seagrass losses caused sediment erosion and loss of stored C (Macreadie et al. 2015, Marbà et al. 2015). Recent studies also show substantial variation in C stocks between sites and regions within the same seagrass species, driven by environmental variables such as hydrodynamic exposure (Dahl et al. 2016, Röhr et al. 2018). Thus, local environmental conditions may strongly influence sediment C and nutrient loss rates during seagrass declines.

In contrast to the increasing number of studies assessing blue carbon in seagrass meadows, much fewer studies have assessed sequestration rate and long-term storage of nutrients in seagrass meadows, even though nutrient cycling and uptake has long been recognized as an important ecosystem service provided by seagrasses (e.g., Costanza et al. 1997, Orth et al. 2006, Barbier et al. 2011). This lack of attention is surprising as nutrient pollution is considered a major environmental stressor to coastal ecosystems including seagrasses, and large resources are spent to decrease the impact of eutrophication in coastal areas (Orth et al. 2006, Rabalais et al. 2009). Measurements of nutrient burial in seagrass meadows are few and have mainly focused on *Posidonia* species, which show high burial rates and long-term nitrogen (hereafter N) burial (Mateo et al. 1997, see Aiko et al. 2019 for review). Recent studies also show that burial rates of N in restored eelgrass meadows (*Zostera marina* L.) can be 20 times higher than in unvegetated areas (McGlathery et al. 2012, Greiner et al. 2013, Aoki et al. 2019) and that eelgrass sediment N stocks can vary substantially between sites (Kindeberg et al. 2018, Dahl et al. 2020). A recent valuation of ecosystem services provided by Swedish eelgrass meadows found that the economic value of N uptake and storage was >50% larger than the value of C storage and sequestration (Cole and Moksnes 2016), indicating the societal importance of eelgrass N regulation. However, the limited knowledge about burial and long-term storage of N in seagrass sediments (Romero et al. 2006, Aoki et al. 2019), particularly regarding the fate of the sediment nutrients once the seagrass bed is lost, constitutes a major challenge to adequately assess the economic value of the ecosystem service (Cole and Moksnes 2016).

To bridge the knowledge gaps outlined above, we here take advantage of well-documented losses of eelgrass along the Swedish NW coast; an area considered a blue C hot spot for eelgrass (Röhr et al. 2018). We first compare the C and N contents in the sediment between existing and historic eelgrass meadow along a gradient in wave exposure to assess how the sediment stocks have been affected by eelgrass loss. We then estimate and discuss the economic cost to society resulting from the release of C and N from lost eelgrass meadows and the implication for coastal management.

Methods

Study system and historic losses of eelgrass

Eelgrass (*Zostera marina* L.) is the most abundant seagrass species in the northern hemisphere and plays a critical structural and functional role in many coastal ecosystems. Eelgrass is the dominant seagrass in Scandinavian waters, where it forms dense meadows from 1 to 5 m depth (Boström et al. 2014). In the early 1980s, eelgrass beds were mapped along the Swedish NW coast, showing abundant meadows in the archipelagoes and fjords with the largest meadows located in the Marstrand area in the southern part of the NW coast (Fig. 1). More than 1050 ha of eelgrass was mapped with continuous meadows covering >200 ha in the southern part. In 2000–2015, new inventories showed large losses of eelgrass along the Swedish NW coast (~60%), but with large variation between regions (Baden et al. 2003, Nyqvist et al. 2009). The largest losses were recorded in the Marstrand area, where close to 1000 ha had been lost (93% of the previously mapped areas) and the losses continue today (Moksnes et al. 2018). In comparison, <5% of the eelgrass had been lost in the Gullmarsfjord area (Fig. 1; Table 1).

Sampling of existing and lost eelgrass meadows

There is a lack of historical data on sediment composition from areas where eelgrass has been lost. We therefore used a site-for-time substitution design to assess changes in sediment composition when an eelgrass meadow is lost, similar to the approach used in earlier studies (Macreadie et al. 2015, Marbà et al. 2015). Four meadows with existing eelgrass and four areas that have lost large eelgrass meadows (39–214 ha) in the Marstrand area were sampled in the summers 2015 and 2016. Because many of the remaining meadows in the Marstrand areas are fragmented and reduced in size (Moksnes et al. 2018), we also sampled four reference eelgrass beds in the more pristine Gullmarsfjord, an area that has experienced only limited loss of eelgrass since the 1980s. This sampling design resulted in three area types: (1) Gullmarsfjord existing eelgrass, (2) Marstrand existing eelgrass, and (3) Marstrand historic eelgrass. Since wave exposure influences sediment granulometry and, subsequently, organic matter, nutrient, and C content in eelgrass sediments (e.g., Dahl et al. 2016, 2020, Röhr et al. 2016, 2018), we sampled four sites per area type that each represented one of four classes of wave exposure regimes (from sheltered to exposed). Since wave exposure accounts for one of the factors that may vary between the sites, this addition should make the site-for-time substitution design more reliable. The wave exposure regimes were calculated based on maximum fetch estimated from maps using all wind directions (Table 1). We reasoned that maximum fetch rather than fetch from dominant wind directions would be the best predictor of the sediment composition since the fetch correlates with wavelength and the shear stress on the bottom and because storms, also from unusual wind directions, would be the main cause of sediment erosion. Since some of the exposed areas that have lost eelgrass presently show compact glacial clay at the sediment surface (Moksnes et al. 2018), fetch was used to determine exposure in lieu of grain size and degree of sorting of the sediment. The chosen classes of wave exposure were to some degree determined by availability of meadows in the three areas, where the range of

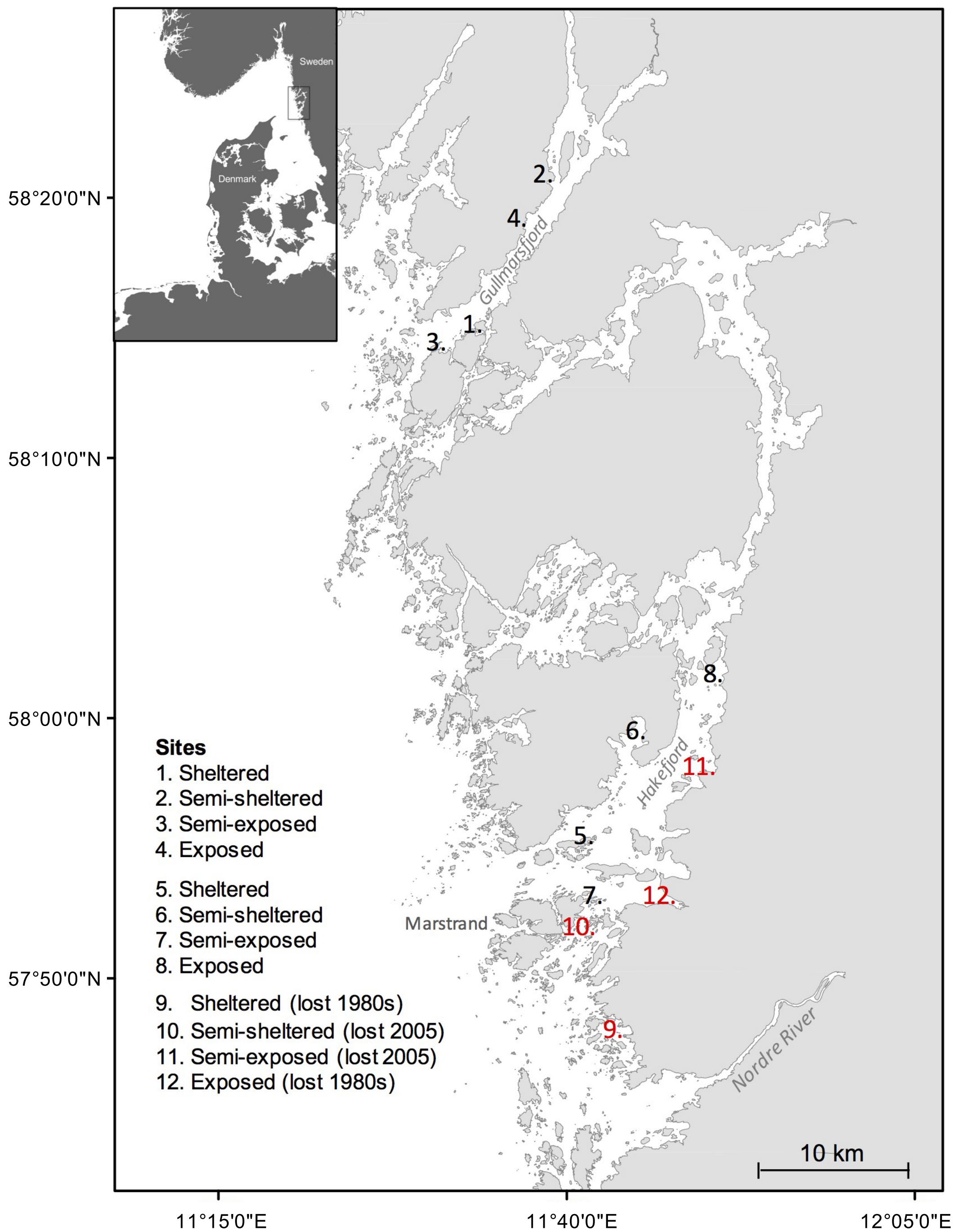

Fig. 1. Map of study sites in NW Sweden. Red number indicates areas where the eelgrass meadows have been lost (see Table 1 for details).

maximum fetch in our sheltered, semi-sheltered, semi-exposed, and exposed sites were 0.5–1.5, 1.9–2.4, 5.1–6.9, and 8.7–13.3 km, respectively (Table 1).

At each site, a total of three sediment cores (height, 50 cm; diameter, 80 mm) were taken down to a minimum of 35 cm. To include potential depth dependent variation in the data,

Table 1. Study sites.

Site by area type	Latitude	Longitude	Exposure type	Max fetch (km)	Eelgrass area (ha)
Gullmarsfjord (eelgrass)					
1. Lindholmen	58°15.803′ N	11°29.783′ E	Sheltered	0.54	1.8
2. Snäckebackebukten	58°21.702′ N	11°34.027′ E	Semi-sheltered	1.86	1.3
3. Bökevik	58°14.934′ N	11°27.158′ E	Semi-exposed	6.94	3.8
4. Torgestad	58°19.898′ N	11°32.477′ E	Exposed	8.65	0.2
Marstrand area (eelgrass)					
5. Lilla Dyrön	57°56.423′ N	11°39.932′ E	Sheltered	0.52	3.8
6. Wallhamn	58°0.451′ N	11°43.224′ E	Semi-sheltered	2.11	25.1
7. Storebrorn	57°53.859′ N	11°40.735′ E	Semi-exposed	5.10	2.4
8. Hakefjord	58°2.901′ N	11°48.532′ E	Exposed	13.17	17.7
Marstrand area (historic eelgrass)					
9. Ryskärsfjorden	57°49.240′ N	11°42.042′ E	Sheltered	1.45	1980s (214)
10. Lyngholmarna	57°52.901′ N	11°40.449′ E	Semi-sheltered	2.35	2004 (146)
11. Källnäs	57°59.427′ N	11°47.662′ E	Semi-exposed	6.63	2004 (94)
12. Lökebergskile	57°54.361′ N	11°46.077′ E	Exposed	13.28	1980s (39)

Notes: Three area types were selected: (1) Gullmarsfjord (eelgrass) control area where eelgrass is present and has shown little eelgrass declines over the last decades. (2) Marstrand area (eelgrass) where eelgrass is present but had some losses in cover area. (3) Marstrand area (historic eelgrass) where large eelgrass meadows have been lost. Within each area, four sites were selected according to four categories of wave exposure, based on maximum fetch. The areal extent of the present or lost eelgrass meadows (with the year of the last observation) is given in the last column (based on Baden et al. 2003, Nyqvist et al. 2009, Moksnes et al. 2018).

samples were collected from the upper (1.5 m water depth) to the lower (3.5 m) distribution range of the existing or lost meadow. The cores were sampled by SCUBA diving and were capped in both ends underwater and kept in a vertical position in coolers during transport to the laboratory. At sites with eelgrass, plant samples were collected in the vicinity of each sediment core, using a corer (height, 20 cm; diameter, 20 cm).

In the laboratory, the 35-cm sediment core was sliced into 5-cm subsections. The sediment sections were cleaned from visible parts of plants and fauna, homogenized, and dried at 105°C. From each subsection, seven sediment variables were determined: sediment dry density, water and OM contents (loss on ignition, LOI; 520°C, 5 h), particulate organic carbon (POC) and nitrogen (PON), and stable isotopes of C and N ($\delta^{13}C$ and $\delta^{15}N$; for details, see Röhr et al. 2016, 2018). Total C, total N, and stable isotopes were determined using a Thermo Scientific Delta V Advantage Isotope Ratio Mass Spectrometer (with Vienna PeeDee Belemnite as reference material) connected to a Carlo Erba CHN elemental analyzer EA 1108.

To assess possible bias from carbonate in estimations of the sediment C_{org} stocks, additional subsamples from the 0 to 5 cm sediment layers were acidified (pre-treated with 1 mol/L HCl; direct addition until the reaction of carbonate was complete) to remove inorganic C and then dried at 60°C for 24 h, prior to analysis for organic C content. In comparison with organic C, content of inorganic C is very low in eelgrass sediments in the study area (Dahl et. al. 2020) and in other Scandinavian sites (0.5–5%; Röhr et al. 2016). Inorganic C therefore likely plays a minor role for the C dynamic of the study system and was not further assessed in here. Total N was derived from untreated sediment samples due to possible alteration of the N values when treated with HCl and is reported as PON (Gee and Baudeer 1986).

Organic C and N density in each sediment layer (mg/cm^3) was calculated by multiplying the dry weight concentration of POC and PON with the sediment dry density (g/cm^3) of each corresponding sample. To decrease the risk of overestimating the POC content in sediment layers below 5 cm sediment depth (which were not acidified prior to analysis), the proportion of inorganic C found in the 0–5 cm sediment layer of the core (on average 15% of total C) was subtracted from TC values in each of the deeper sediment layers from the same core to achieve POC.

The stock of organic C and N (C_{org} and N_{org} density) down to the sampled sediment depth (0–35 cm) was calculated by depth integration of C and N density, following calculations described in detail in Lavery et al. (2013) and expressed per unit surface area (g C_{org} and N_{org}/m^2).

Eelgrass samples were cleaned and epiphytes removed, and the dry weight of leaves, rhizomes, and root tissue were measured after 24–48 h in 60°C until constant weight. Dry samples were analyzed for tissue POC and PON as described above.

Deep sediment cores in the Gullmarsfjord sheltered site

To assess the sediment composition at sediment depths >35 cm, a complementary study was carried out in August 2016 at the sheltered site in the Gullmarsfjord (site 1; Fig. 1). A 200-cm-long push corer (diameter, 110 mm) was used to obtain C and N samples from deeper sediment layers within and outside the eelgrass bed. The corer was pushed into the sediment by divers down to approximately 1.9 m depth and capped in both ends underwater. Three samples were collected within the meadow from 2.6 to 3.8 m depth and three samples from the adjacent, unvegetated bottom from 4.0 to 6.3 m depth. Since site 1 is very sheltered (Table 1), we expected the difference in depth between vegetated and unvegetated areas to have minor effect on the sediment characteristics. In the boat, the corer was placed horizontally, and subsamples of sediment were collected through holes (diameter, 40 mm) at 25-cm intervals along the corer using a cut-off, 20-mL syringe. Sediment samples were stored on ice and analyzed within 24 h. To collect large pieces of organic material for analysis, the remaining sediment was sliced at approximately 25-cm sections and sieved through a 1-mm sieve. The samples were sorted into dead rhizomes with roots, seeds, dead leaf material, and terrestrial material and dried at 60°C to constant weight to measure dry weight and analyze POC and PON. The same sediment variables were analyzed as described above. The proportion of inorganic C content (6%) measured at this site in the top 5 cm of the previously mentioned study was subtracted from the measured values at all depths, to avoid overestimating the POC.

Assessment of core compression

Sediment sampling often resulted in a sediment sample shorter than the core penetration depth, particularly in eelgrass sediment with high contents of OM and water. On average, the 50-cm and 200-cm corers showed 19% and 37% core shortening, respectively. To assess whether the shortening could be a result of core compression, that is, core shortening due to decrease of water content in the core (Blomqvist et al. 1991), we compared the water content with the two different corers used at site 1. The 50- and 200-cm corer showed very similar values (on average 84% and 80% vs. 84% and 82% water content) at 12.5 and 25 cm sediment depth, respectively. The similar water content suggests that loss of sediment is not caused by compression, but by increased friction and reduced sliding of sediment inside the tube at larger sampling depths (e.g., Cumming et al. 1993). This was also supported by very similar values of OM content in the upper 5 cm of the sediment in the present study using the 50 cm (25.7%) and in an earlier study at site 1, when only the top 5 cm was sampled and no core shortening occurred (25.2%; Jephson et al. 2008). Thus, there is no indication that the values of the sediment variables were affected by compression of the sediment.

Statistical analyses

To assess how eelgrass loss affects the sediment composition, and how this may interact with wave exposure, we analyzed water content, OM (%), POC (%), PON (%), density (mg/cm^3) of organic C (C_{org}) and N (N_{org}), C:N ratio and stable C isotope δ^{13}C (0–5 cm), or C and N stock (g/m^2; in the 0–35 cm layer) as dependent variables in a series of two-factor ANOVA models including interactions. The analysis of stable isotopes was included to assess whether the sources of C in the sediment differed between existing and lost eelgrass meadows. Area type (three levels) and exposure types (four levels) were used as fixed, independent variables for the 0–5 cm sediment layer and the integrated 0–35 cm sediment layer in separate analyses. To assess potential vertical sediment composition changes down to 1.2 m sediment depth at site 1, the same variables were analyzed in a series of two-factor ANOVA models using sediment depth (five levels) and habitat type (two levels: eelgrass, unvegetated) as independent variables. Homogeneity of variances was tested using Cochran's C test (Sokal and Rohlf 2011), and heteroscedastic data were square root-transformed to meet assumptions of homogeneity. Multiple comparison post hoc tests were performed using the Student–Newman-Keuls (SNK) procedure.

Economic valuation of lost carbon and nitrogen stocks

To assess the economic value of long-term storage of C and N in relation to the documented loss of eelgrass in the Marstrand area, we used the valuation framework presented by Keeler et al. (2012) and developed for eelgrass ecosystems by Cole and Moksnes (2016). We focused on the economic cost to society and human well-being associated with the release of C and N from eelgrass tissue and sediments to the ocean–atmosphere that occur when an eelgrass bed is lost. Thus, we conservatively only assess the value of the one-time loss of C and N associated with this release and not the value of lost sequestration capacity of the eelgrass meadow.

To estimate the release of C and N from lost eelgrass meadows, we used sediment data at depth 0–35 cm from all 12 sites and data of C and N in eelgrass tissue from the eight existing eelgrass sites. We used two scenarios when estimating the release: (1) a very conservative approach where no sediment is assumed to have eroded and we only used the average difference of the depth-integrated (0–35 cm) C and N stocks between all sites with eelgrass and sites with historic eelgrass, and the average C and N in living eelgrass tissue, and (2) a less conservative (and perhaps more realistic) approach, which assumed that the top 35 cm of the sediment had eroded releasing all C and N in the sediment, in addition to the amount estimated in the first scenario. Here, we used the average C and N stocks in the top 35 cm in existing eelgrass meadows to estimate the release due to sediment erosion. We assumed that all C_{org} and N_{org} released from eelgrass and sediment were remineralized and returned to the ocean–atmosphere as CO_2 and dissolved inorganic N.

To estimate the economic value of C storage in eelgrass tissue and sediment, we used the social cost of carbon (SCC), that is, the long-term, global damage of carbon dioxide emissions in a given year, based on emission year 2015 and discount rate of 3% (132 \$/t C; EPA 2016). To estimate the economic value associated with N storage provided by eelgrass, we rely on the costs of N reduction measures undertaken by local authorities in the Marstrand area. This replacement cost valuation method is based on costs associated with reaching a N reduction target set by the EU Water Framework Directive (WFD) and implementing N-reducing measures, accounting for their annual effectiveness in the study area (see Cole and Moksnes 2016 for details). According to the WFD classification, the three water bodies within the Marstrand area have moderate ecological status due to elevated summer levels of N and chlorophyll-*a* (WISS 2018) and measures are therefore required to reduce levels of N. We use the average cost (193 SEK/kg N; 21.3 US\$/kg N in 2018) based on a number of measures used along the NW coast of Sweden, including construction of wastewater treatment plant, wetland creation, and catch crops (Cole and Moksnes 2016). These measures are also used in the affected Marstrand area (WISS 2018).

Results

Sediment composition in existing and historic eelgrass meadows

*Surface sediments (0–5 cm).—*The sediment composition at 0–5 cm depth was distinctly different for all assessed variables between existing and historic eelgrass beds, but also between sheltered and exposed sites. POC and PON were on average 3.5 times higher in areas with existing eelgrass compared to areas where eelgrass has been lost and 11.7 and 10.7 times higher in sheltered compared to exposed sites, respectively (Fig. 2). However, the difference between existing and historic eelgrass sediments decreased with increasing wave exposure. In eelgrass meadows, all variables decreased with exposure, whereas the effect of exposure was smaller in historic eelgrass areas, causing fewer differences between habitat area types in the more exposed sites. This resulted in significant interaction effects between area type and exposure for all variables, except C_{org} density (Table 2). The C_{org} density was significantly higher for all exposure types in the existing eelgrass meadows in Gullmarsfjord and

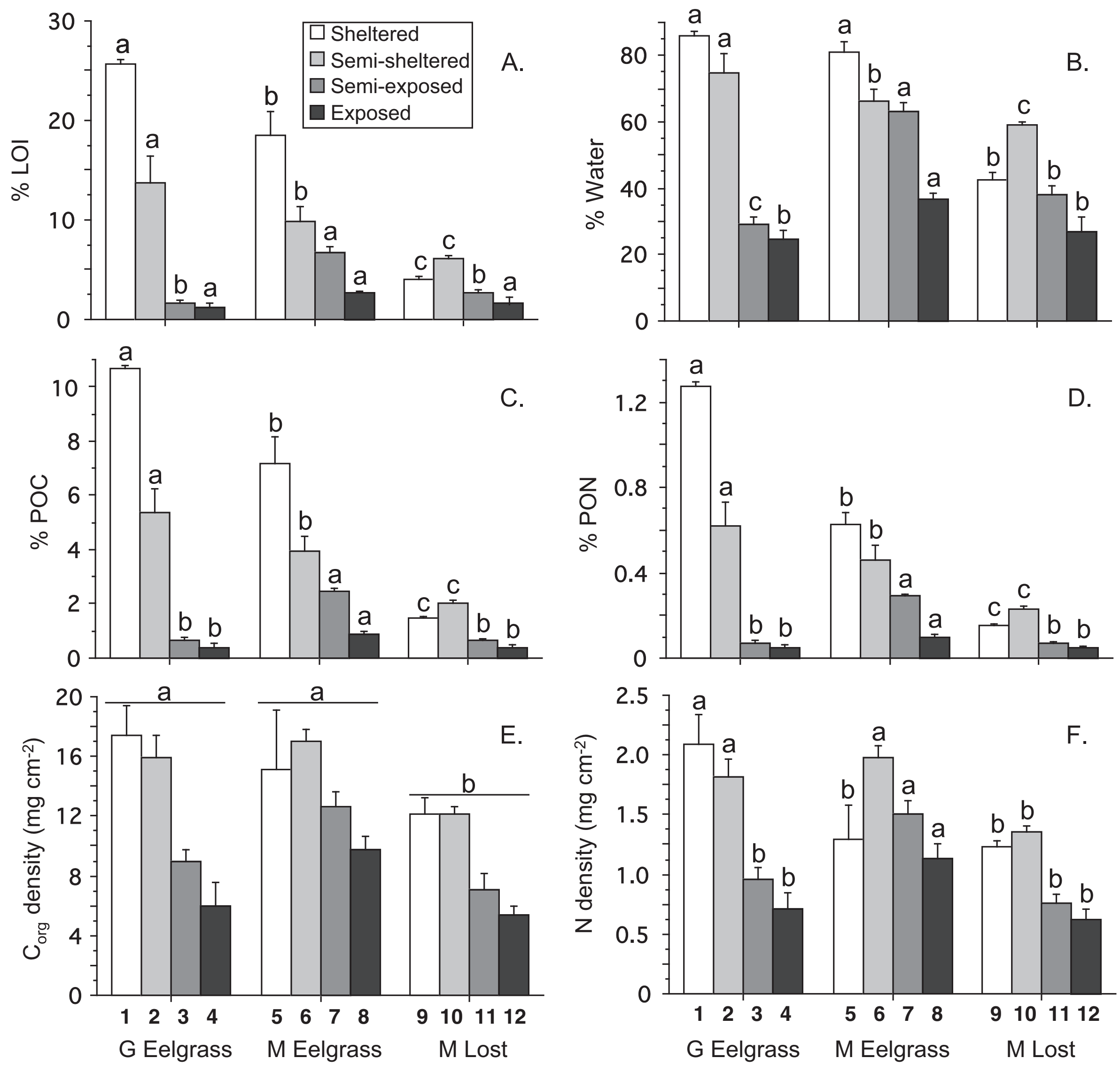

Fig. 2. Sediment 0–5 cm depth. Average concentration (+SE) of organic material (LOI), water, and particulate organic carbon and nitrogen as percent dry weight (%POC and %PON) and as weight per volume (mg/cm^3) in the surface sediment (0–5 cm sediment depth) collected at 12 different sites from three area types: four with eelgrass meadows in the Gullmarsfjord area (G Eelgrass), four with eelgrass meadows in the Marstrand area (M Eelgrass), and four from sites where the eelgrass has been lost in the Marstrand area (M Lost). Within each area, the sites were categorized into four levels of wave exposure types (sheltered, semi-sheltered, semi-exposed, and exposed). Letter above bars denotes significantly different values between area types within exposure types at $P < 0.05$ (SNK test).

Marstrand area (on average 12.1 and 13.6 mg/cm^3, respectively) compared to the historic sites (on average 9.2 mg/cm^3; Fig. 2E).

Among sheltered and semi-sheltered sites, water, OM, POC, and PON contents were significantly higher in eelgrass meadows in Gullmarsfjord and Marstrand area compared to historic eelgrass sites in the Marstrand area (Fig. 2A–D). A similar pattern was found for N_{org} density that was significantly higher in

Table 2. 0–5 cm sediment depth.

Source	df	SS	*F*	*P*
LOI (%)				
Area type (A)	2	8.0	40.5	0.0001
Exposure (B)	3	34.4	116.3	0.0001
A × B	6	12.3	20.9	**0.0001**
Residual	24	2.4		
Water (%)				
Area type (A)	2	2447	44.8	0.0001
Exposure (B)	3	10119	123.5	0.0001
A × B	6	3397	20.7	**0.0001**
Residual	24	656		
POC (%)				
Area type (A)	2	4.50	74.6	0.0001
Exposure (B)	3	15.75	174.2	0.0001
A × B	6	4.64	25.7	**0.0001**
Residual	24	0.72		
PON (%)				
Area type (A)	2	0.230	77.6	0.0001
Exposure (B)	3	0.797	179.2	0.0001
A × B	6	0.237	26.6	**0.0001**
Residual	24	0.036		
C density				
Area type (A)	2	0.202	8.72	**0.0014**
Exposure (B)	3	0.756	21.8	**0.0001**
A × B	6	0.101	1.46	0.23
Residual	24	0.278		
N density				
Area type (A)	2	1.62	12.8	0.0002
Exposure (B)	3	4.60	24.4	0.0001
A × B	6	1.73	4.59	**0.0031**
Residual	24	1.51		
C:N				
Area type (A)	2	22.8	2.80	0.081
Exposure (B)	3	1.38	0.113	0.95
A × B	6	20.8	0.851	0.54
Residual	24	97.9		
$\delta^{13}C$				
Area type (A)	2	134.9	170.2	0.0001
Exposure (B)	3	45.7	38.5	0.0001
A × B	6	27.2	11.4	**0.0001**
Residual	24	8.72		

Notes: Bold indicates statistically significant *P*-values.

ANOVA models testing the average concentration of organic material (LOI), water, POC and PON, the density of carbon and nitrogen, the C:N ratio, and the stable carbon isotope ($\delta^{13}C$) as a function of area type (live eelgrass Gullmarsfjord, live eelgrass Marstrand area, and historic eelgrass Marstrand area) and exposure type (four levels). Data of LOI, POC, and PON were sqrt-transformed, and data of carbon density were log-transformed prior to analysis to meet the assumption of homogenous variance.

eelgrass sediment compared to the historic sites (up to 2.1 and 1.4 mg/cm^3, respectively), except for the sheltered sites in the Marstrand area, that showed no significant difference (Fig. 2F). A less clear difference between existing and historic meadows was found for the semi-exposed sites. The highest values for water content, LOI, POC, PON, and N_{org} density were found in eelgrass beds in the Marstrand area, which were significantly higher than the semi-exposed sites without eelgrass, and the sites in Gullmarsfjord, which did not differ from each other (Fig. 2). The lowest values of all variables were consistently found in the exposed sites, which did not differ between eelgrass and lost eelgrass types for OM, but had significantly higher water, OM, POC, and PON contents and C_{org} density in the eelgrass site in Marstrand area compared to the other sites (Fig. 2).

The C:N ratio in the surface sediment was on average 9.6, 10.6, and 11.6 in the Gullmarsfjord and Marstrand area with and without eelgrass, respectively, but this difference was not significant due to high within-group variability (Table 2). The stable isotope values for C ($\delta^{13}C$) were significantly lower in areas with lost eelgrass in the Marstrand fjord (on average −20.7) compared to the two areas with eelgrass, that in turn did not differ from each other (on average −16.5 and −16.8, respectively; Fig. 3; Table 2). This clearly suggests that the C sources of the sediment differed between existing and historic eelgrass sites.

Sediment stocks (0–35 cm).—The depth-integrated sediment values (0–35 cm) showed a similar pattern compared to the surface sediment, with significantly higher values of water content, LOI, POC, and PON in areas with eelgrass than in areas with historic eelgrass among all exposure categories except the most exposed sites, resulting in significant interaction effect for all variables (Fig. 4A–D; Table 3). Because of a higher water content in the existing eelgrass sediment, the difference between existing and historic eelgrass sites was smaller for density-based measurement of C and N. However, the pattern was similar with a generally higher C_{org} and N_{org} stocks in eelgrass meadows compared to the historic sites at all exposure categories except the most exposed sites, causing significant interaction effects for both variables (Fig. 4E, F; Table 3). Overall, the average concentration of POC and PON was 156 and 167% higher, and the C_{org} and N_{org} stocks were 28 and 40% higher, in

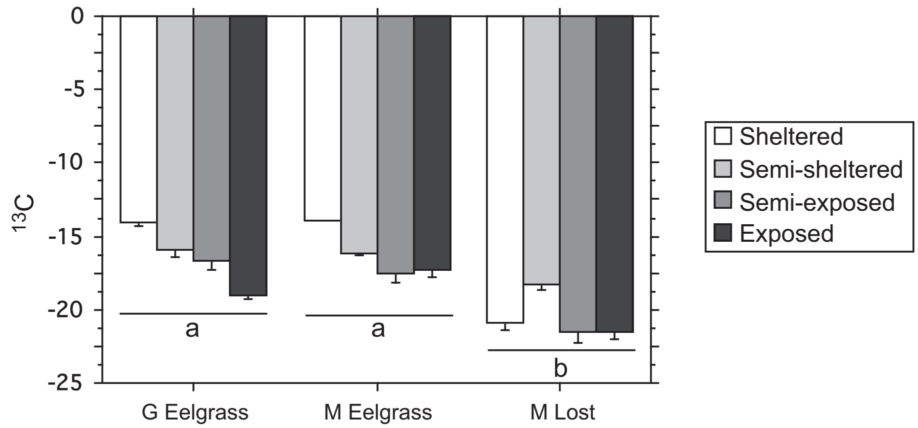

Fig. 3. Stable isotope composition of sediment 0–5 cm depth. Average stable isotope values (−SE) of carbon ($\delta^{13}C$) in the surface sediment (0–5 cm sediment depth) collected at 12 different sites from three area types: four with eelgrass meadows in the Gullmarsfjord area (G Eelgrass), four with eelgrass meadows in the Marstrand area (M Eelgrass), and four from sites where the eelgrass has been lost in the Marstrand area (M Lost). Within each area, the sites were categorized into four different levels of wave exposure. Letter above bars denotes significantly different values between area types at $P < 0.05$ (SNK test).

areas with eelgrass compared to areas with lost eelgrass, respectively (Fig. 5).

Sediment depth profiles 0–35 cm.—The sediment profiles (0–35 cm) of water, OM, POC, and PON showed similar patterns within sites, but varied strongly between sites. Although no consistent vertical profile in sediment characteristics within area type was found, some patterns still emerged. Within eelgrass sites, there was a decreasing profile in the top 15–25 cm, followed by a more stable profile (common in the Gullmarsfjord area, in particular at the sheltered site) or followed by an increasing trend deeper in the sediment (common in the Marstrand area; Fig. 6). A notable exception was the semi-exposed site in the Gullmarsfjord area, which showed an increasing profile at all depths (Fig. 6). In contrast, the dominant pattern at the historic sites in the Marstrand area was an increasing profile in the top 15–20 cm, followed by a more stable profile deeper in the sediment, a pattern particularly clear at the exposed site (Fig. 6). Although the values of the sediment variables at existing and historic eelgrass meadows became more similar with increasing sediment depth, the average contents of POC and PON at 20–35 cm depth at eelgrass sites (4.13% and 0.39%, respectively) were still 122% and 157% larger compared to historic sites (1.86% and 0.15%), respectively.

Deep sediment cores at the Gullmarsfjord sheltered site

Sediment depth profiles 0–120 cm.—At the sheltered site 1 in the Gullmarsfjord, the eelgrass sediment had very high water and OM contents down to at least 120 cm, that is, around 80% and 23%, respectively (Fig. 7). Based on how easily the core could be pushed into the sediment, this probably continued down to at least 2 m sediment depth. The contents of OM, POC, and PON were significantly higher within the eelgrass (on average 20.4%, 8.3%, and 0.81%, respectively) compared to the adjacent, unvegetated site (on average 12.6%, 5.0%, and 0.45%, respectively) at all assessed sediment depths (Table 4). Although the content of all variables decreased significantly with depth in both the eelgrass and the unvegetated sediment, the decline was much sharper in the unvegetated sediment (Table 4; Fig. 7). This pattern was even clearer for the water content, which was significantly higher in the eelgrass habitat only below 50 cm sediment depth, causing a significant interaction effect between habitat and depth (Table 4; Fig. 7). The C:N ratio was significantly lower in the eelgrass

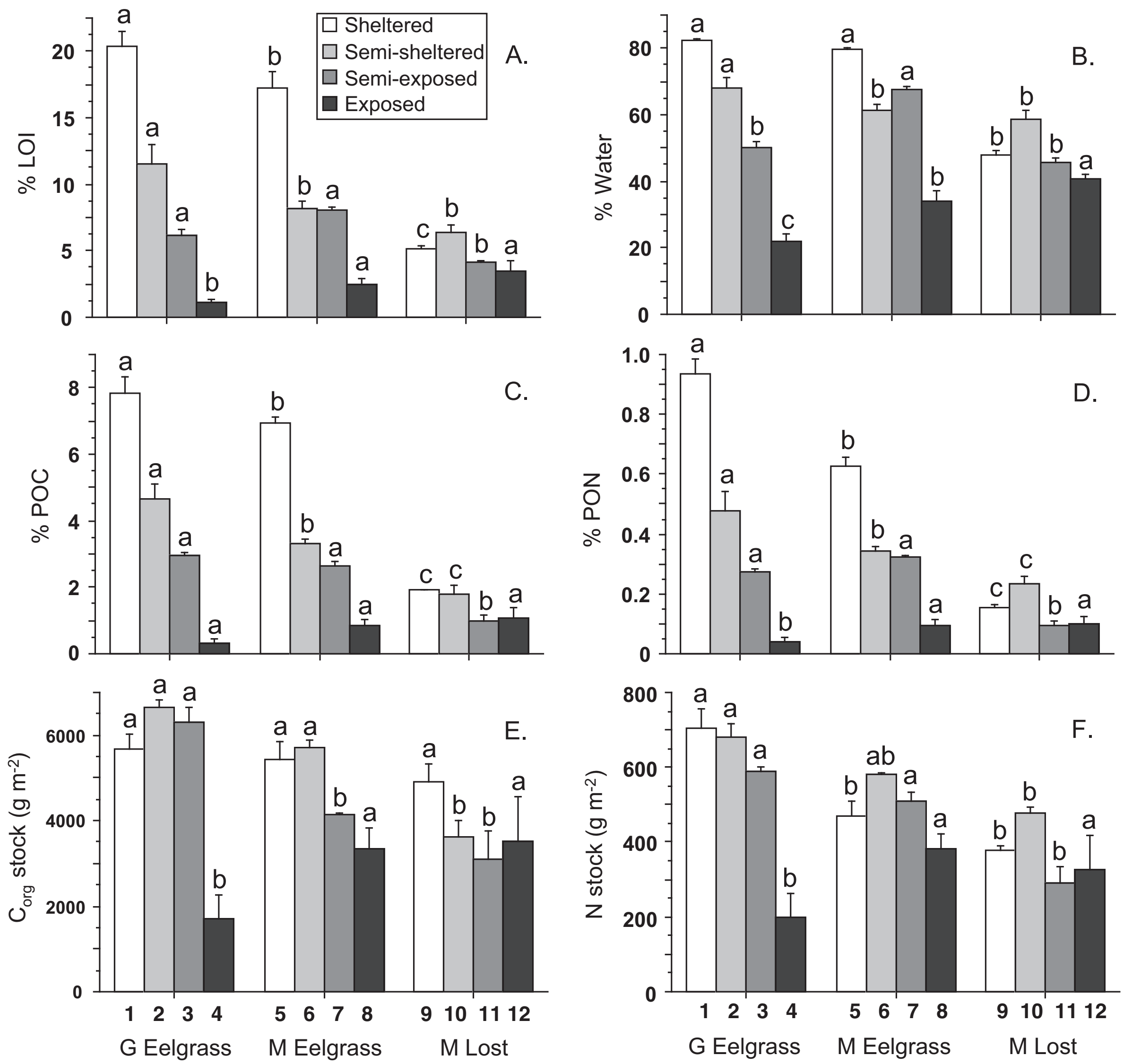

Fig. 4. Sediment 0–35 cm depth. Average concentration (+SE) of (A) organic material (LOI), (B) water, (C) particulate organic carbon and (D) nitrogen as percent dry weight (%POC and %PON), and (E) the total amount of carbon and (F) nitrogen per square meter (C_{org} stock and N stock), in the top 35 cm of the sediment, collected at 12 different sites from three area types: four with eelgrass meadows in the Gullmarsfjord area (G Eelgrass), four with eelgrass meadows in the Marstrand area (M Eelgrass), and four from sites where the eelgrass has been lost in the Marstrand area (M Lost). Within each area, the sites were categorized into four levels of wave exposure. Letter above bars denotes significantly different values between area types within exposure types at $P < 0.05$ (SNK test).

compared to the unvegetated site (on average 10.3 and 11.3, respectively) and increased with depth in both habitats (Table 4). The estimated C_{org} stocks (0–125 cm depth) were on average 20.6 and 19.2 kg C_{org}/m^2 in the eelgrass bed and on unvegetated site, respectively, which did not differ significantly. For N, the estimated stock in eelgrass was significantly higher than on

Table 3. 0–35 cm sediment depth.

Source	df	SS	*F*	*P*
LOI (%)				
Area type (A)	2	173	52.3	0.0001
Exposure (B)	3	675	136.3	0.0001
A × B	6	287	29.0	**0.0001**
Residual	24	39.6		
Water (%)				
Area type (A)	2	926	43.3	0.0001
Exposure (B)	3	7219	255.6	0.0001
A × B	6	2718	42.5	**0.0001**
Residual	24	256		
POC (%)				
Area type (A)	2	41.8	103.2	0.0001
Exposure (B)	3	111.5	183.4	0.0001
A × B	6	38.8	31.9	**0.0001**
Residual	24	4.9		
PON (%)				
Area type (A)	2	0.340	74.4	0.0001
Exposure (B)	3	0.964	140.8	0.0001
A × B	6	0.386	28.2	**0.0001**
Residual	24	0.055		
C stock (g/m^2)				
Area type (A)	2	10.4 10^6	7.4	0.0031
Exposure (B)	3	37.3 10^6	17.8	0.0001
A × B	6	27.1 10^6	6.5	**0.0004**
Residual	24	16.8 10^6		
N stock (g/m^2)				
Area type (A)	2	19.4 10^4	17.1	0.0001
Exposure (B)	3	38.0 10^4	22.7	0.0001
A × B	6	23.5 10^4	7.0	**0.0002**
Residual	24	13.3 10^4		

Note: Bold indicates statistically significant *P*-values.

ANOVA models testing the average concentration of organic material (LOI), water, POC and PON, and the carbon and nitrogen stock (0–35 cm) as a function of area type (live eelgrass Gullmarsfjord, live eelgrass Marstrand area, and historic eelgrass Marstrand area) and exposure type (four levels).

unvegetated site (on average 2.00 and 1.71 kg N/m^2; Table 4).

Accumulation of eelgrass detritus in the sediment.—At site 1, large amounts of well-preserved eelgrass detritus (dead rhizomes, roots, leaves, seeds) were found at all investigated depths under the eelgrass meadow. The average biomass of eelgrass detritus in the sediment (0–120 cm) was 1737 g DW/m^2, containing on average 72.2 g C_{org}/m^2 and 2.4 g N/m^2. In comparison, the living above- and below-ground eelgrass biomass in the same meadow was on average 75.9 and 28 g DW/m^2, these compartments containing together on average 34.3 g C_{org}/m^2 and 1.2 g N/m^2. Thus, the biomass of eelgrass detritus underneath the eelgrass meadow was over 17 times higher than that of the living eelgrass tissue and contained more than twice the amount of C and N (Table 5). However, compared to the C and N stocks in the sediment itself, the stock in dead and living eelgrass tissue was <1% (Table 5). In the adjacent (20 m) unvegetated site, the amount of eelgrass detritus was relatively high (1161 g DW/m^2) in the sediment at 5.7 m depth, suggesting that eelgrass grew there historically. However, further away from the eelgrass meadow at 6.4 m depth, there was little evidence of eelgrass tissue in the sediment.

Economic valuation of eelgrass loss in the Marstrand area

The average biomass of above- and below-ground eelgrass tissue in the 8 sampled meadows was 138.3 and 60.5 g DW/m^2, respectively. These biomass compartments contained 36% and 30% C and 1.6% and 0.75% N, respectively. In total, the average C_{org} and N_{org} stocks in living eelgrass tissue in the study area were 68.2 and 2.6 g/m^2, respectively, or 682 and 26.2 kg/ha, respectively (Table 6). The average C_{org} and N_{org} stocks in the top 35 cm of the sediment in the same meadows were approximately 48.7 and 5.14 Mg per ha, respectively, constituting 98.6 and 99.5% of the total C_{org} and N stocks. In areas that have lost all eelgrass, there was no living eelgrass tissue, but the C_{org} and N_{org} stocks in the top 35 cm of the sediment were on average 37.9 and 3.68 Mg/ha, respectively (Table 6).

In the first, very conservative scenario that assumed no sediment erosion, we estimated a release of approximately 11.5 and 1.49 metric Mg of C and N/ha, respectively, from eelgrass tissue and sediment (Table 6). Using a social cost of carbon value of 132 US$/Mg C, equivalent to 1118 SEK/Mg C in 2020, the total value of the C lost with live eelgrass tissue and from the top 35 cm of the sediment is 13,638 SEK/ha (equivalent to 1515 US$/ha). Using an average cost of N-reducing measures in the study area of 992,000 SEK/Mg N, the total value of lost eelgrass in the same scenario is 285,312 SEK/ha (equivalent to 31,701 US$/ha; Table 6).

In the second, less conservative scenario that assumed that the top 35 cm of the organic-rich sediment had eroded after the eelgrass was lost,

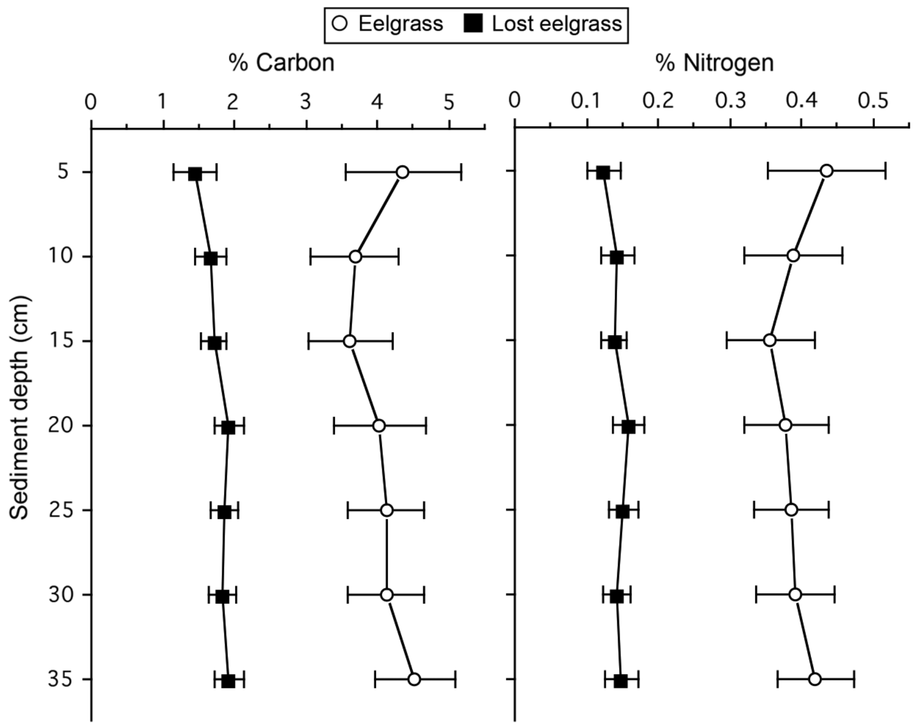

Fig. 5. Average sediment profiles. Average dry weight concentration (±SE) of particulate organic carbon and nitrogen from seven different sediment depths (0–35 cm) collected from eight eelgrass beds in the Gullmarsfjord and Marstrand area (Eelgrass) and from four sites in the Marstrand area that have lost eelgrass (Lost eelgrass).

we estimated the release C and N due to sediment erosion to 48.7 and 5.14 Mg/ha, respectively. These values were added to losses estimated in scenario 1, giving a total release of 60.2 Mg C_{org}/ha and 6.63 N_{org} Mg/ha (Table 6). Using the same price of C and N as above, the total value of the lost C and N is 71,494 and 1,272,192 SEK/ha, respectively (equivalent to 7944 and 141,355 US$/ha, respectively; Table 6).

Discussion

Seagrass sediments constitute important sinks of organic carbon (hereafter referred to as C), and there is increasing concern that the loss of seagrass ecosystems could release vast amounts of stored C from the sediment back into the ocean–atmosphere system (Duarte et al. 2013, Macreadie et al. 2014). However, there is limited understanding regarding the fate of the C stocks following the loss of seagrass meadows (McLeod et al. 2011, Macreadie et al. 2015, Marbà et al. 2015), particularly regarding the release of sediment-stored nutrients. Here, we used well-documented losses of eelgrass along the Swedish NW coast to compare the C and N stocks between existing and historic meadows that were lost 10–40 yr ago.

We found unusually high C and N stocks in the existing eelgrass meadows compared to other seagrass species and coastal habitats, in particular in sheltered areas, suggesting that these habitats constitute global hot spots for C and N storage. Moreover, the sediment composition and stable isotope values were distinctly different in areas that have lost eelgrass meadows, indicating an erosion of at least 35 cm sediment following the historical eelgrass loss. Finally, the difference between existing and historic meadows was much larger at sheltered compared to exposed sites, suggesting that the release of C and N has mainly occurred in more sheltered areas with unstable sediments.

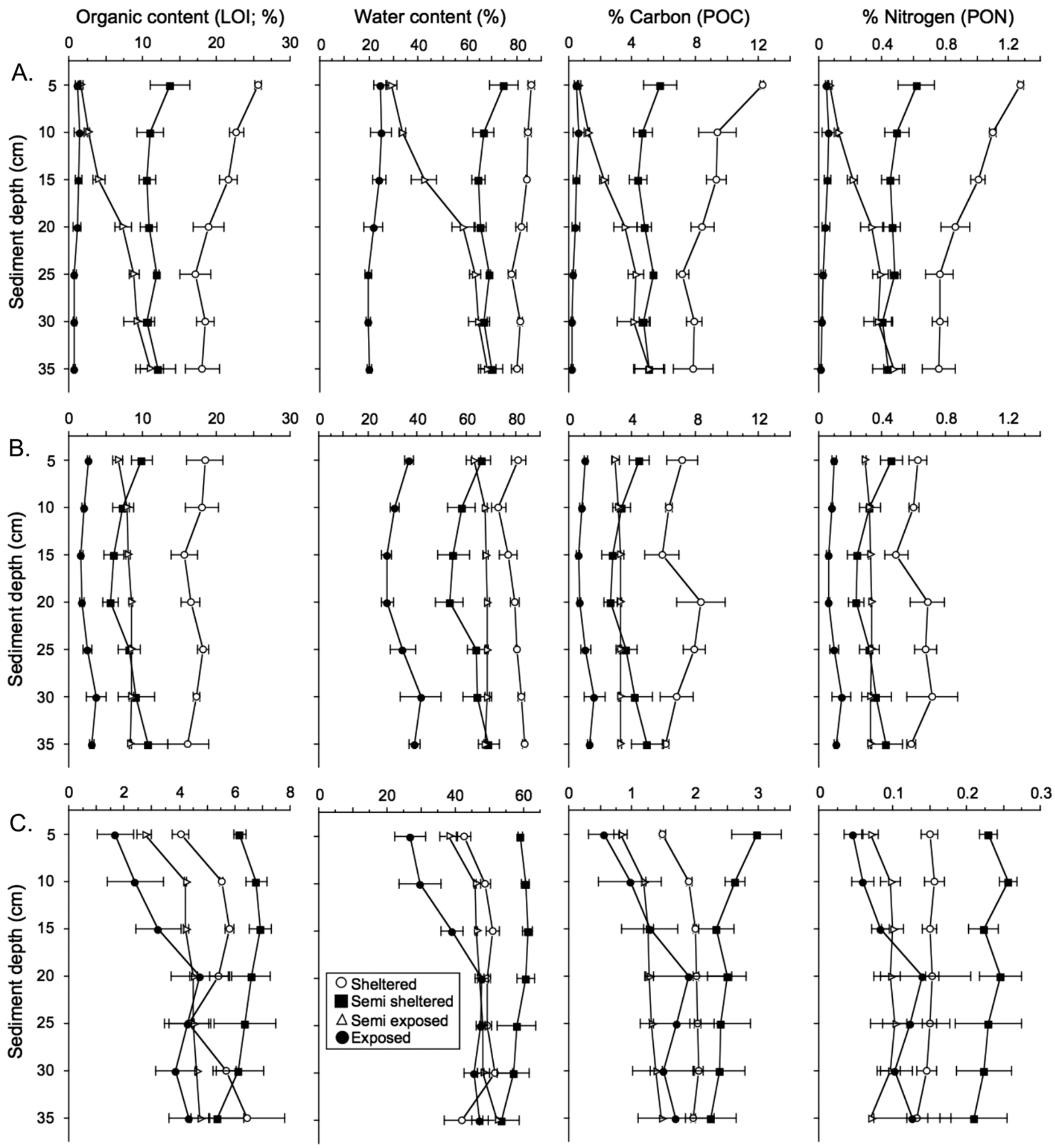

Fig. 6. Sediment depth profiles. Average concentration (±SE) of organic material (LOI), water, and particulate organic carbon (%POC) and nitrogen (%PON) from seven different sediment depths (0–35 cm), collected at 12 different sites from three area types: (A) eelgrass meadows in the Gullmarsfjord area, (B) eelgrass meadows in the Marstrand area, and (C) lost eelgrass meadows in the Marstrand area (please note the different scales between the eelgrass and the lost sites). Within each area, the sites were categorized into four levels of wave exposure.

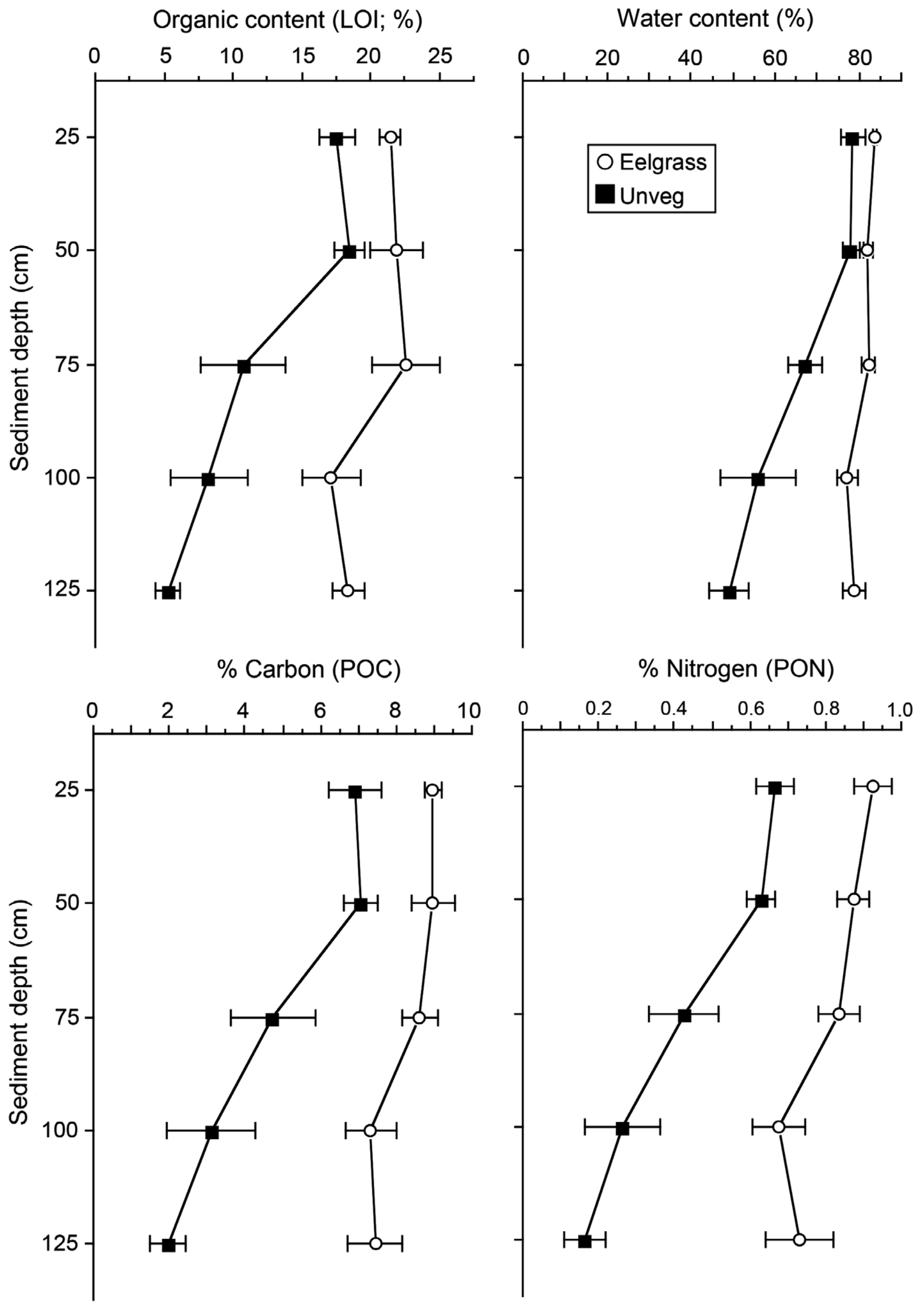

Fig. 7. Deep sediment profiles at sheltered site 1. Average concentration (±SE) of organic material (LOI), water, and particulate organic carbon (%POC_{org}) and nitrogen (%PON) from seven sediment depths (0–125 cm), collected at site 1, a sheltered bay in the Gullmarsfjord within an eelgrass meadows (eelgrass) at 2–3 m depth or just outside the eelgrass bed (unvegetated) at 3–4 m.

These results suggest that the historic losses of eelgrass in the study area released substantial amounts of C and N to the environment. In comparison with C, the estimated release of N constitutes approximately an 18 times larger economic cost to society. Thus, the Swedish eelgrass meadows appear to be particularly important for mitigating coastal eutrophication.

Table 4. Deep corer at site 1.

Source	df	SS	F	P
Organic material (%)				
Habitat (A)	1	460	38.7	**0.0001**
Sediment depth (B)	4	311	6.54	**0.002**
A × B	4	106	2.24	0.11
Residual	18	214		
Water (%)				
Habitat (A)	1	1548	36.9	0.0001
Sediment depth (B)	4	1274	7.59	0.0009
A × B	4	593	3.53	**0.027**
Residual	18	755		
POC (%)				
Habitat (A)	1	83.9	53.9	**0.0001**
Sediment depth (B)	4	48.8	7.85	**0.0008**
A × B	4	11.6	1.87	0.16
Residual	18	28.0		
PON (%)				
Habitat (A)	1	0.98	76.7	**0.0001**
Sediment depth (B)	4	0.54	10.7	**0.0001**
A × B	4	0.09	1.68	0.20
Residual	18	0.23		
C:N				
Habitat (A)	1	0.18	17.7	**0.0005**
Sediment depth (B)	4	0.15	3.6	**0.025**
A × B	4	0.04	1.01	0.43
Residual	18	0.19		
C stock (kg/m^3)				
Habitat (A)	1	577	1.45	0.24
Sediment depth (B)	4	795	0.50	0.73
A × B	4	3154	2.00	0.14
Residual	18	7103		
N stock (kg/m^3)				
Habitat (A)	1	24.0	6.96	**0.017**
Sediment depth (B)	4	13.9	1.01	0.43
A × B	4	32.9	2.38	0.090
Residual	18	62.1		

Notes: Bold indicates statistically significant *P*-values.
ANOVA models testing the average concentration of organic material (LOI), water, POC_{org} and PON, the C:N ratio, and the carbon and nitrogen stock (0–120 cm) as a function of habitat (eelgrass and unvegetated bottom) and sediment depth (five levels). Data of C:N ratio were square root-transformed prior to analysis to meet the assumption of homogenous variance.

Carbon and nitrogen storage capacity in Swedish eelgrass sediments

The sediment composition varied strongly between sites, but had on average very high contents of C and N (on average 3.7% and 0.39%), representing average C and N stocks at 0–35 cm sediment depth of 4872 g C/m^2 and 514 g N/m^2, respectively. The C content is almost threefold larger than the global average C content in eelgrass sediment (1.4%; Röhr et al. 2018), consistent with recent suggestions that the Swedish and Danish coast in Kattegat and Skagerrak constitutes a global hot spot for sediment C storage (Dahl et al. 2016, Röhr et al. 2018). Also, the average N content reported here is several times higher than found in eelgrass meadows in countries in Europe and the United States (Greiner et al. 2013, Dahl et al. 2016, Kindeberg et al. 2018), suggesting that eelgrass meadows along Swedish Skagerrak coast may also be a hot spot for N storage. This notion is supported by results from the deep core sampling (120 cm) in the Gullmarsfjord, which showed C and N stocks of 20.7 kg C/m^2 and 2.01 kg N/m^2, respectively. Since the sampling indicated that the organic-rich sediment continued at least 200 cm into the sediment, the stocks may in fact be much larger. The very high C and N contents deep in the sediment suggest that decomposition of OM is very slow in these anoxic sediments. This was supported by high amounts of intact eelgrass rhizomes, leaves, and seeds found at all investigated sediment depths (0–120 cm). The biomass of eelgrass detritus in the sediment (0–120 cm) was 17 times larger than the biomass of living eelgrass in the meadow and contained twice as much C and N. This result suggests that eelgrass detritus should be included in C and N stock assessments for more accurate estimates.

The deep core samples show that eelgrass sediments in sheltered areas along the Skagerrak coast have a capacity of C and N storage that rivals most other seagrass species, salt marshes, and mangroves (on average 13.8, 16.2, and 25,5 kg C/m^2, respectively, in top 1 m of the sediment; Duarte et al. 2013), as well as other coastal hot spots for C sequestration such as deltas and fjords (average C content of 0.7–4% DW; Bornhold 1978, Smith et al. 2015). The reason for the unusually high C and N stocks along the Swedish NW coast is not clear, but may be related to (1) the predominantly sheltered locations with low particle transport and high deposition rates, and (2) the glaciofluvial fine sediment deposits with unusually high content of silt and clay (30–77%; Dahl et al. 2016, Moksnes et al. 2018). Accumulation of OM is higher in fine-grained sediments due to a higher particle surface area (Mayer 1994), and finer grained particles decrease permeability resulting in more oxygen-

Table 5. Comparison of C and N stock sources at site 1.

Material	Biomass (DW g/m^2)	C_{org} stock (g/m^2)	N stock (g/m^2)	C_{org} stock (Mg/ha)	N stock (Mg/ha)	C_{org} stock (%)	N stock (%)
Eelgrass meadow							
Live eelgrass tissue	104	34.3	1.2	0.34	0.012	0.17	0.06
Dead eelgrass tissue	1737	72.2	2.4	0.72	0.024	0.35	0.12
Sediment	n.a.	20,661	2009	207	20.1	99.5	99.8
Total	1841	20,768	2013	208	20	100	100
Unvegetated bottom							
Dead plant material	712	35.4	1.1	0.35	0.011	0.18	0.06
Sediment	n.a.	19,206	1713	192	17.1	99.8	99.9
Total	712	19,242	1714	192	17	100	100

Note: Average values of live eelgrass tissue, dead eelgrass tissue, and other plant material in the sediment (0–120 cm), and carbon and nitrogen stocks in eelgrass tissue and the sediment (0–120 cm) in an eelgrass meadow and on unvegetated bottom at site 1 in the Gullmarsfjord. n.a.; not applicable.

depleted sediments (Wilson et al. 2008). Together with low winter temperatures at this high-altitude area, which also reduce decomposition rates, these conditions may result in a very slow mineralization of organic matter in the sediment (Dahl et al. 2016).

The sediment composition within the assessed eelgrass meadows was strongly affected by wave exposure; for example, the contents of C and N were on average seven times higher at sheltered than exposed sites. This result is consistent with earlier studies showing that hydrodynamic exposure influences organic C and N contents in eelgrass sediment (Dahl et al. 2016, 2020, Röhr et al. 2018) as well as other seagrass species (Samper-Villarreal et al. 2016, Mazarrasa et al. 2017). The present study also found the highest C and N sediment stocks in the sheltered eelgrass meadows (on average 90 and 70% higher stocks at 0–35 cm compared to exposed meadows, respectively) suggesting that sheltered meadows with muddy sediments are particularly valuable as sinks for C and N. This result is not consistent with a recent study of eelgrass sediment along the Swedish NW coast that found no correlation or even a positive correlation between modeled exposure and C and N stocks in the sediment (0–35 cm) of seven investigated meadows (Dahl et al. 2020). These contrasting results may be partly due to the use of different approaches addressing core shortening in the two studies, which warrants further methodological studies. However, when assessing stock size, it is important to account for the entire thickness of the organic-rich sediment, which is expected to be larger in sheltered areas (Dahl et al. 2020). The present study demonstrated that this layer can be >2 m thick in sheltered areas, suggesting that C and N stocks are particularly high in sheltered eelgrass meadows along the Swedish NW coast.

Effects of eelgrass loss on sediment storage

The sediment composition at the historic eelgrass sites was distinctly different from existing eelgrass sites and showed significantly lower contents of all assessed variables at all investigated sediment depths, including on average 156% and 167% lower contents of C and N, respectively, at 0–35 cm sediment depth (Fig. 5). These results suggest a substantial loss of organic-rich sediment from the historical sites following the eelgrass loss. However, the effect of eelgrass loss on sediment composition was strongly influenced by wave exposure, and the marked difference between existing and historic eelgrass sites was much smaller at the exposed sites, suggesting that sheltered areas have more vulnerable sediment stocks.

The contents of water OM, C, and N at sheltered to semi-exposed historic eelgrass sites in the Marstrand area were on average 1.3–3.1 times lower compared to sheltered to semi-exposed existing eelgrass sites. These historic eelgrass meadows were much larger (94–214 ha) compared to the assessed existing eelgrass meadows (1.3–25.1 ha; Table 1). Since large, continuous meadows show higher accumulation of OM than smaller or fragmented meadows (Oreska et al. 2017, Ricart et al. 2017, Samper-Villarreal et al. 2018), these historic eelgrass meadows

Table 6. Estimates of loss and costs.

Source	Living eelgrass (Mg/ha)	Lost eelgrass (Mg/ha)	Released (Mg/ha)	Cost release (SEK/ha)	Loss eelgrass (ha)	Total released (Mg)	Cost total loss (M SEK)
Scenario 1							
Carbon							
C_{org} in eelgrass tissue	0.68	0	0.68	808			
C_{org} in sediment	48.7	37.9	10.8	12,830			
Total	49.4	37.9	11.5	13,638	998	11,457	13.6
Nitrogen							
N_{org} in eelgrass tissue	0.026	0	0.026	4992			
N_{org} in sediment	5.14	3.68	1.46	280,320			
Total	5.17	3.68	1.49	285,312	998	1483	284.7
Scenario 2							
Carbon							
C_{org} in eelgrass tissue	0.68	0	0.68	808			
C_{org} in sediment	97.4	37.9	59.5	70,686			
Total	98.1	37.9	60.2	71,494	998	60,060	71.4
Nitrogen							
N_{org} in eelgrass tissue	0.026	0	0.026	4992			
N_{org} in sediment	10.28	3.68	6.6	1,267,200			
Total	10.3	3.7	6.63	1,272,192	998	6613	1270

Notes: Estimated average stock of carbon and nitrogen in live eelgrass tissue and sediment (0–35 cm) based on eight sampled eelgrass meadows in the Marstrand and the Gullmarsfjord, and estimated average stocks in areas that has lost all eelgrass in the Marstrandfjord. The price for carbon is based on the social cost of carbon (equivalent of 1118 SEK/Mg; EPA 2016) and for nitrogen on average cost of nitrogen-reducing measures in the study area (192,000 SEK/Mg; Cole and Moksnes 2016). The total release of carbon and nitrogen resulting from the documented loss of eelgrass in the Marstrand area (998 ha) and their cost to society are estimated for two different scenarios: (1) assuming that no sediment has eroded and using the difference in average stocks between area with and without eelgrass, and (2) assuming that the 35 cm of the sediment has eroded in areas that has lost eelgrass in addition to the amount estimated in scenario 1. In both scenarios, all released carbon and nitrogen have returned to the ocean/atmosphere.

should have supported C and N stocks comparable to or larger than the existing eelgrass meadows. The significantly lower content at the historic eelgrass sites indicates that a large proportion of the fine, organic-rich sediments have eroded, most likely down to at least 35 cm depth.

The smaller differences found between the exposed eelgrass and historic sites may be partly explained by the small areal extent of the exposed eelgrass meadow in Gullmarsfjord (0.2 ha), and the deteriorated state of the exposed meadow in the Marstrand area. The latter meadow is located just north of an area where large-scale losses of eelgrass are presently occurring, and the meadow is fragmented and consists of a small (10–100 m^2) patches with low shoot density (Moksnes et al. 2018). Since accumulation of OM decreases with meadow size and fragmentation (see references above), our site selection may have caused an underestimation of the loss of C and N from exposed sites. Thus, it is most likely that a significant amount of sediment has eroded and the OM has been lost also from exposed historic eelgrass sites.

The loss of surface sediment (0–5 cm) by erosion at all historic sites was supported by the stable isotope analyses, which showed significantly higher $\delta^{13}C$ values in the existing eelgrass meadows compared to the historic sites (on average −16.6 and −20.7, respectively) across all exposure regimes. The $\delta^{13}C$ in the existing meadows is similar to a global average for eelgrass sediment (−18.3; Röhr et al. 2018). In contrast, the average sediment $\delta^{13}C$ at historic sites resembles values from phytoplankton and drift algae (−20.1 and −21.0, respectively; Tagliabue and Bopp 2008), demonstrating that the OM in the surface layers at these sites was dominated by other C sources than eelgrass. In addition, signs of sediment erosion were evident in the shallower parts (<1.5 m) of the more exposed historic sites in the Marstrand area. Here, compact layers of glacial clay were exposed on the sediment surface in areas where eelgrass grew 10–30 yr earlier (Moksnes et al. 2018), suggesting that the organic-rich surface sediment has eroded following eelgrass loss. This was also supported by the increasing POC and PON profiles at 0–20 cm sediment depths that dominated at the historic eelgrass sites, in contrast to the decreasing POC and PON profiles that dominated at eelgrass sites (Fig. 6). High levels of OM below 20 cm sediment were particularly evident at the exposed historic site in the Marstrand area (Fig. 6). This may be remains of the historic meadow, indicating that the top 20 cm of the remaining sediment is affected by mixing.

Erosion of surface sediment (0–100 cm) following seagrass loss has been assumed in studies estimating the release of C resulting from seagrass loss (Fourqurean et al. 2012, Pendleton et al. 2012). Although there are several small-scale studies demonstrating that sediment resuspension and erosion increase as seagrass density decreases (e.g.Hansen and Reidenbach 2012, Gurbisz et al. 2017, Potouroglou et al. 2017), there has, until recently, been little empirical support of sediment erosion following large-scale loss of seagrass. However, two studies of the seagrass *Posidonia australis* in western and southeastern Australia used profiles of ^{210}Pb concentration and radiocarbon dating of the sediment, respectively, to demonstrate that historic losses of seagrass had resulted in significant erosion of sediment and loss of stored C (Macreadie et al. 2015, Marbà et al. 2015). As far as we know, the present study is the first to provide support that significant erosion of sediment may result also from loss of eelgrass meadows, resulting in a large release of C and N stocks. Importantly, the results also suggest that the loss of sediment stocks has mainly occurred from the more sheltered meadows following the loss of eelgrass. Compared to the exposed sites, the eelgrass sediment in sheltered areas had much higher contents of water and OM, consistent with earlier studies (e.g., Dahl et al. 2016, 2020, Röhr et al. 2016, 2018). Since the high contents of water and OM negatively affect the stability of the sediment by lowering the erosion threshold (Bale et al. 2007), the sediment is more easily resuspended, and eelgrass shoots more easily dislodged in organic-rich sediments (Lillebø et al. 2011, Dahl et al. 2018). Thus, the unstable sediments of sheltered meadows appear to make the sediment stocks more vulnerable to erosion, despite lower wave exposure, resulting in a high release of C and N following eelgrass loss.

Societal costs of carbon and nitrogen release

The estimated economic cost to society from the release of C from lost eelgrass meadows in the scenario assuming 35 cm of sediment erosion was 71,495 SEK/ha (equivalent to 7944 US$/ha). This value is high in comparisons to earlier valuation studies of climate mitigation by seagrass; a result of including the release of C stored in the sediment, and the unusual high C stock in eelgrass sediment in the study area. Most studies assessing the monetary value of C uptake have focused on the annual sequestration rate by seagrasses and not on the value of C stored in the sediment (but see Pendleton et al. 2012, Luisetti et al. 2013), producing estimates of C sequestration (total discounted values) in the range of 2000–4000 US$/ha (e.g., Mangi et al. 2011, Cole and Moksnes 2016). Here, the value of C and N sequestration lost after the loss of the meadows was not included in the valuation, since the sequestration rates of Swedish eelgrass meadows have not been assessed. The high monetary value of the C released from the sediment in the present study demonstrates the importance of including C sediment stocks in the valuation.

In the same scenario, the estimated economic cost to society from the release of N was very high (1,272,192 SEK/ha; equivalent to 141,355 US $/ha). In fact, it represents one of the highest monetary values presented for an ecosystem service provided by seagrasses. Although nutrient cycling and uptake has long been recognized as an important ecosystem service provided by seagrasses (e.g., Orth et al. 2006, Barbier et al. 2011), surprisingly few studies have assessed the sequestration and storage capacity or its monetary value. To the best of our knowledge, the only other similar studies are global estimates of nutrient cycling by seagrass/algal meadows of approximately 26,200 US$/ha (Costanza et al. 2014) and an earlier assessment of eelgrass N sequestration and storage along the Swedish NW coast (approximately 9500 US$/ha; Cole and Moksnes 2016). In both these studies, a replacement coast approach was used to estimate the value as in the present study. The substantially higher value in the present study, compared to the earlier Swedish attempt, was due to the use of the new empirical data of N concentrations from eelgrass sediments in the study area. This was not available for the earlier study, which instead used 15× times lower values derived from studies along the east coast of the United States (Cole and Moksnes 2016). Considering that loss of N sequestration and decreased denitrification after the eelgrass loss was not included in the calculation, the economic cost to society regarding N from the loss of eelgrass is in fact higher than the numbers presented here. Recent studies show that rates of denitrification and N burial are 2.9 and 20 times higher in eelgrass meadows compared to unvegetated areas, respectively (Aoki et al. 2019).

These results suggest that the economic value of N is approximately 18 times higher than the value of C storage in the same area. Although it is difficult to compare the value of ecosystem services that has been assessed with different valuation methods, it is clear that substantial amounts of N are released when an eelgrass meadow is lost and that it is very costly to compensate for this release using the management measures available in Sweden today.

Understanding the extent of sediment erosion following the loss of a seagrass meadow is critical for accurate estimates of the amount of C and nutrient released to the ocean–atmosphere. This is because erosion will increase the volume of sediment that is exposed to oxygen and subsequently the amount of C and N that is remineralized (e.g., Fourqurean et al. 2012, Pendleton et al. 2012). In the present study, the estimated release of C and N was 5.2 and 4.5 times larger in a scenario assuming that 35 cm of the sediment had eroded compared to a scenario with no erosion. One limitation with the erosion-based estimate is that we assumed that all organic C and N in the eroded sediment had been remineralized and returned to the ocean–atmosphere. However, this proportion is still unknown (Fourqurean et al. 2012, Pendleton et al. 2012, Macreadie et al. 2014), which warrants some caution. Still, we believe that our estimates are conservative since it is likely that more than 35 cm of the sediment has eroded. The scenario assuming no erosion is therefore less realistic and represents a minimum estimate of the release of C and N.

Implications for management

The presented study is, to the best of our knowledge, the first quantitative assessment of carbon and nitrogen release from the sediment following the loss of seagrass meadows, and the results have several important implications for management of coastal habitats. Along the Swedish NW coast, an estimated 12,500 ha eelgrass has vanished since the 1980s (Baden et al. 2003, Moksnes et al. 2016). These losses have largely been attributed to the effects of coastal eutrophication and overfishing of large predatory fish, causing an increase in ephemeral macroalgae that cover and smother the eelgrass meadows (Moksnes et al. 2008, Baden et al. 2010, 2012). The best documented and largest loss has occurred in the Marstrand area, where approximately 998 ha of eelgrass has been lost (Moksnes et al. 2018). Assuming that on average 35 cm of the sediment has eroded from these historic meadows, the loss in Marstrand is equivalent to a release of 60,060 Mg C and 6613 Mg N, representing a total cost to society of approximately 1.27 billion SEK (equivalent to approximately 141 million US$; Table 6). Most of the C and N release likely occurred shortly after the eelgrass was lost, as the sediment eroded after, for example, a winter storm. However, it is not well documented when the loss of eelgrass in this area occurred. Surveys in 2000–2004 showed that ~700 ha had been lost since the last inventory in the 1980s (Baden et al. 2003, Nyqvist et al. 2009). New surveys showed that an additional 300 ha had been lost by 2015 (Moksnes et al 2018). Assuming that the total losses occurred over a 20-yr period, the average loss rate of eelgrass has been ca 50 ha/yr, resulting in a release of ca 3000 Mg C and 330 Mg N/yr.

To put these numbers in perspective, the estimated total release of C is 0.11% of the total CO_2 equivalent emissions in Sweden 2016 (52.9 million Mg). Although this is a small proportion, it is still equivalent to over 44% of the total emission from Swedish domestic air transportation in 2016 (SEPA 2017). The estimated total release of N in the Marstrand area is approximately 5.7% of the estimated total anthropogenic load of N to all Swedish sea areas in one year (SwAM 2017). The estimated annual release of N over a 20-yr period in the Marstrand area is in the same range as, for example, the total annual N released from all fish farms in Sweden (481 Mg/yr; SwAM 2017).

Thus, the loss of eelgrass in the Marstrand area has not only resulted in a significant emission of C, but perhaps more importantly resulted in a substantial increase in the nutrient load to the local ecosystem, which likely have exacerbated eutrophication in this area. Nitrogen pollution and eutrophication are still considered major environmental problems along the Swedish NW coast, where mats of filamentous algae increase and eelgrass meadows decrease in distribution, despite reduced N loads to the coast (SwAM 2012, 2017, Moksnes et al. 2018).

Taken together, these results highlight the significant role of eelgrass meadows in sequestering C and nutrients in their sediments over long time periods and the importance of protecting these large stocks from being released into the environment. The local importance of the sediment stocks and the risk of nutrient release should therefore be taken into account when selecting areas for spatial protection and during environmental impact assessments of coastal activities that threatens eelgrass ecosystems. Coastal exploitation for recreational docks and marinas is presently causing continuing losses of eelgrass meadows along Swedish coasts (Eriander et al. 2017, Moksnes et al. 2019). Our study shows it is important to raise awareness about the fact that these and other activities, by negatively impacting eelgrass meadows, contribute to climate change and eutrophication, in addition to deteriorating important habitats for biodiversity and fish production (e.g., Cole and Moksnes 2016). For example, estimated release of nitrogen from a hectare of eelgrass following the loss of vegetation is on the same scale as the average annual release of nitrogen from a fish farm in Sweden (8 Mg N/yr; Ejhed et al. 2016). Environmental impact assessments of activities that negatively affect eelgrass meadows should therefore also assess the predicted release of N following the loss of eelgrass, to ensure, for example, that it does not negatively affect the water quality and the Ecological status of the water body according to EU Water Framework Directive.

The results also suggest that protection of the eelgrass meadows constitutes an important and cost-efficient measure to mitigate coastal eutrophication. The study suggests that sheltered meadows with muddy sediments are particularly valuable as sinks for C and N and, importantly, that they are especially vulnerable to sediment erosion following eelgrass loss. These meadows should therefore be targeted for spatial protection, in particular since their unstable sediment makes them sensitive to hydrodynamic disturbances (Lillebø et al. 2011, Dahl et al. 2018). In shallow, sheltered environments, wake from commercial and recreational boat traffic can constitute the main source of wave energy with strong negative effects on benthic communities (e.g., Mosisch and Arthington 1998, Klein 2007). In Sweden, estimates suggest that close to 20% of soft bottom vegetation in shallow, sheltered coastal areas are negatively affected by recreational boat activities (Hansen et al. 2019, Moksnes et al. 2019). Mitigation of anthropogenic derived wave energy is therefore critical in these sensitive areas. Finally, identifying the most valuable and vulnerable eelgrass meadows may be particularly important in the future climate change scenario where the frequency of storms is predicted to increase (e.g., Vose et al. 2014). The present results suggest that simple indicators of wave exposure, such as maximum fetch, could be used for initial identification of these meadows for further studies and protection.

Recent studies have identified the most valuable and vulnerable eelgrass meadows along the Swedish west coast based on connectivity and genetic diversity (Jahnke et al. 2018, 2020). The present study may provide complementary information to the seascape management of eelgrass by identifying meadows that provide important ecosystem services by mitigating climate changes and eutrophication. Together, such information would be valuable for an effective marine spatial planning, in particular design of networks of marine protected areas and seagrass restoration efforts.

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