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Methane Emissions From Nordic Seagrass Meadow Sediments

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Shallow coastal soft bottoms are important carbon sinks. Submerged vegetation has been shown to sequester carbon, increase sedimentary organic carbon (C_{org}) and thus suppress greenhouse gas (GHG) emissions. The ongoing regression of seagrass cover in many areas of the world can therefore lead to accelerated emission of GHGs. In Nordic waters, seagrass meadows have a high capacity for carbon storage, with some areas being recognized as blue carbon hotspots. To what extent these carbon stocks lead to emission of methane (CH₄) is not yet known. We investigated benthic CH₄ emission (i.e., net release from the sediment) in relation to seagrass (i.e. Zostera marina) cover and sedimentary C_{org} content (%) during the warm summer period (when emissions are likely to be highest). Methane exchange was measured in situ with benthic chambers at nine sites distributed in three regions along a salinity gradient from ∼6 in the Baltic Sea (Finland) to ∼20 in Kattegat (Denmark) and ∼26 in Skagerrak (Sweden). The net release of CH₄ from seagrass sediments and adjacent unvegetated areas was generally low compared to other coastal habitats in the region (such as mussel banks and wetlands) and to other seagrass areas worldwide. The lowest net release was found in Finland. We found a positive relationship between CH₄ net release and sedimentary C_{org} content in both seagrass meadows and unvegetated areas, whereas no clear relationship between seagrass cover and CH₄ net release was observed. Overall, the data suggest that Nordic Zostera marina meadows release average levels of CH₄ ranging from 0.3 to 3.0 µg CH₄ m⁻² h⁻¹, which is at least 12–78 times lower (CO₂ equivalents) than their carbon accumulation rates previously estimated from seagrass meadows in the region, thereby not hampering their role as carbon sinks. Thus, the relatively weak CH₄ emissions from Nordic Z. marina meadows will not outweigh their importance as carbon sinks under present environmental conditions.

Keywords: seagrass, greenhouse gas, blue carbon, nordic, Zostera marina
INTRODUCTION

Methane (CH\textsubscript{4}) is a very potent greenhouse gas (GHG) with a global warming potential (GWP) of 28–34 times higher than carbon dioxide (CO\textsubscript{2}) per mole of CO\textsubscript{2} for a 100-year period (IPCC, 2001; Bridgham et al., 2016). Oceanic shelves, although marginal in area compared to deep oceans, contribute to about 75% of the CH\textsubscript{4} emission from aquatic sources, although there is high variability between regions and ecosystems (Saunois et al., 2020; Rosentreter et al., 2021). This is mainly due to the high CH\textsubscript{4} production in sediments during anaerobic degradation of organic matter in methanogenic archaea (Barker et al., 2014; Wilson et al., 2020). The produced CH\textsubscript{4} may be oxidized in the water column by diffusion, via plant–tissue or as gas bubbles (Reeburgh, 2007; Effrey et al., 2019). Generally, only a small portion of the produced CH\textsubscript{4} eventually reaches the atmosphere, since most CH\textsubscript{4} is oxidized by microorganisms in the sediment and water column (Reeburgh, 2007). The deep CH\textsubscript{4} bubbles released from sediments are usually not released to the atmosphere (Weber et al., 2019).

This explains why non-marine CH\textsubscript{4} emissions derive from the nearshore coastal environment, where there is less likelihood that the CH\textsubscript{4} is oxidized before reaching the atmosphere (Weber et al., 2019).

Natural wetlands are vegetated ecosystems where the soil is water-saturated for most of the year and which store large amounts of carbon in their soils. Account for 20–40% of the global yearly CH\textsubscript{4} emissions and are thus the single largest non-anthropogenic source of CH\textsubscript{4} (IPCC, 2001; Bridgham et al., 2013; Helle et al., 2015). In the coastal zone, vegetated habitats (i.e., saltmarshes, mangroves, and seagrass meadows) are estimated to emit around 1.8 Tg CH\textsubscript{4} yr\textsuperscript{-1} (Al-Haj and Fulweiler, 2020). This emission level is much lower than the release from their sedimentary counterparts, although greater than the release from terrestrial soils (Z. marina) (Lyimo et al., 2018; Al-Haj and Fulweiler, 2020). In the Nordic region, seagrass meadows have high capacity for storing large amounts of carbon in their sediment, in particular, from the coastal southern Baltic Sea where CH\textsubscript{4} emissions are relatively high (Breier and Berger, 2000). Therefore, they are of particular interest for study of blue carbon habitats, such as seagrass meadows, that may store large amounts of organic carbon (C\textsubscript{org}) in their sediments to understand the fate of and store carbon as potential source for other GHG emissions. No previous reports have shown storage of 

Consequently, coastal vegetated ecosystems such as saltmarshes, mangroves, and seagrass meadows are efficient sinks of atmospheric CO\textsubscript{2} and referred to as blue carbon habitats (e.g., McLeod et al., 2011; Duarte et al., 2017; Howard et al., 2019). However, the same conditions that make these habitats ideal for carbon storage also provide the potential for CH\textsubscript{4} production (Al-Haj and Fulweiler, 2020). Conditions that favor methanogenesis could tip these coastal habitats from sinks to sources of CH\textsubscript{4} and CO\textsubscript{2} and thereby accelerate the greenhouse effect. Therefore, the importance of understanding the conditions governing the release of CH\textsubscript{4} and other GHGs from these habitats is evident. Studies from tidal saltmarshes show that CH\textsubscript{4} emission is strongly salinity-dependent, with significantly lower emissions at salinities over 10 (Poenburger et al., 2011). However, saltmarshes and seagrass reduce CH\textsubscript{4} emissions at salinities below 0 (Wang et al., 2017). Seagrass meadows at elevated salinities is low (Dowrick et al., 2006). However, in anoxic marine sediments, CH\textsubscript{4} production and CH\textsubscript{4} emission is not significantly impacted by salinity (Oremland et al., 2020). This is substantially lower than what has been observed in other marine habitats, for example saltmarshes and mudflats over 10,000 Tg CH\textsubscript{4} m\textsuperscript{-2} yr\textsuperscript{-1} (Whiting and Chanton, 1993). However, stressors such as high temperature and decomposition, salinity warming and nutrient enrichment increase CH\textsubscript{4} emissions in seagrass ecosystems (Lyimo and Holm-Hansen, 2018; Burkholder et al., 2020; Georgellis et al., 2020). Vegetation loss or alteration in macrophyte species composition may also stimulate methanogenesis in the sediment (Sutton-Grier and Megonigal, 2011; Moksnes et al., 2021). It is previously known that CH\textsubscript{4} emissions are positively correlated with the organic carbon content in sediments (Heyerdahl and Berger, 2000). Therefore, it is of particular interest to study blue carbon habitats, such as seagrass meadows, that may store large amounts of organic carbon (C\textsubscript{org}) in their sediments to understand the fate of and store carbon as potential source for other GHG emissions. No previous reports have shown storage of
MATERIALS AND METHODS

Study Area

Nordic coastal areas are of particular interest since they stretch from the Baltic Sea, which is a semi-enclosed waterbody and one of the largest brackish water areas in the world, to the marine environments of Skagerrak and Kattegat through the Danish straits (Storebælt, Lillebælt, and Øresund) of the region. Therefore, they are characterized by strong large-scale salinity gradients from freshwater conditions (0–2) in the Bothnian Bay to marine conditions (∼34) in the North Sea (Helcom 2017–2018). Coastal shallow habitats in northern areas are deemed by climate scenario models to be exposed to faster warming than the global average with an expected temperature increase ranging from 2°C in the southern part of the Baltic Sea to 4°C in the northern part by the end of this century (i.e., year 2100; Andersson et al., 2015). This may influence CH₄ emissions from coastal blue carbon habitats in the future. Further, the coastal waters of the Baltic Sea, the Kattegat, and Skagerrak are surrounded by nine countries and human activities in the area, adding pressure on the seagrass ecosystems (Boström et al., 2014). For example, severe seagrass losses of about 60% have been reported in the Swedish west coast between 1980 and 2000s (Baden et al., 2003; Nyqvist et al., 2009). From some of these areas in Sweden, where historical losses have occurred, it has been estimated that the resulting losses of carbon from the sediments could be up to 300 Mg C ha⁻¹ (Moksnes et al., 2021).

Incubation Chambers for Sampling CH₄ at Sediment–Water Interface

Incubation chambers, produced by transparent Plexiglas cores (inner diameter: 4.7 cm, height: 45 cm; Figure 2), containing an air-filled gas pocket with a gas-tight septum for extraction of
TABLE 1 | Sampling design showing number of replicates, water depth and water temperature in seagrass meadows and adjacent unvegetated habitats at the different sampling sites, and mean salinity for each of the three sampling regions.

| Sampling regions | Seagrass replicates (n) | Unveg. replicates (n) | Seagrass depth (m) | Unveg. depth (m) | Temp. (°C) | Salinity (mean) |
|------------------|-------------------------|-----------------------|--------------------|------------------|------------|----------------|
| Finland (Fin)    | 6                       | 6                     | 2                  | 2                | 20         | 6              |
| Fårö             | 6                       | 6                     | 2.1–2.2            | 2.3–2.4          | 20         | 20             |
| Hummelskär       | 6                       | 6                     | 2.2–2.3            | 2.1              | 20         | 20             |
| Ångsö            | 6                       | 6                     | 2.2–2.3            | 2.1              | 20         | 20             |
| Denmark (Den)    | 6                       | 6                     | 2                  | 2                | 21         | 26             |
| Holckenhavn Fjord | 5                      | 5                     | 2.5                | 2.5              | 23.5       |                |
| Nyborg           | 6                       | 6                     | 3.1                | 3.1              | 21         |                |
| Skallhavet       | 6                       | 6                     | 2.2                | 2                | 22.3       |                |
| Gåsö             | 6                       | 6                     | 2.5                | 2.7              | 23.5       |                |

FIGURE 2 | Deployed incubation chamber in a seagrass meadow (left) and collection of a gas sample (top right). Illustration (bottom right) of the sampling methodology using an incubation chamber inserted 15 cm into sediment with a 20 cm water column above the sediment. On the top, a 5 cm air-pocket is connected to a gas-tight septum from where a gas-sample (including methane) released from the sediment could be collected (using a syringe). Gas-samples were extracted periodically after insertion from the chamber and stored in gas-tight exetainers until analyzed with gas-chromatography (GC). Photos: K. Gagnon.
Analysis of Methane

The gas in the core collector was analyzed for CH₄ emissions using headspace analysis and gas chromatography (GC). Briefly, the headspace was injected into a gas chromatograph (GC8A, Shimadzu Corporation) equipped with a Retch 400 mixing mill for subsequent carbon analyses. The total carbon and nitrogen content (% C and % N) in each sediment depth section was analyzed against incubation time. The CH₄ emissions per surface area of the sediments were calculated based on the total amount of CH₄ accumulating over time within the gas-filled pocket of the incubation chamber and reported as µmol CH₄ cm⁻² h⁻¹. Since measurements were only conducted during daytime, values were not extrapolated to full diurnal estimates.

Collection of Sediment Cores

After incubation, sediment cores were collected adjacent to each incubation chamber using a corer with a diameter of 60 cm. The cores were sliced into three different depth sections: 0–1 cm representing the oxidized zone, 1–15 cm representing the rhizosphere and 15 cm representing the sediment without living seagrass. Sediment compression was accounted for in the depth section measuring the distance from the top of the core to the sediment surface inside and outside of the core after being inserted into the sediment (Glew et al., 2002).

Analysis of Organic Carbon Content in the Sediment

Sediment core slices were weighed, homogenized, and dried. Subsamples were then dried at 60°C for ~48 h until constant weight, whereafter the dry bulk density (g DW cm⁻³) was calculated. The dry sediment samples were ground to a powder using a Retch 400 mixing mill for subsequent carbon analyses. The total carbon and nitrogen content (% C and % N) in each sediment depth section was analyzed using a carbon–nitrogen elemental analyzer (Flash 2000, thermo Fisher Scientific). Previous research in the studied regions has documented that inherent conditions of the three regions have no methane–nitrogen emission anomalies (Asplund et al., 2016; Dahl et al., 2020).

Data Analysis

Variations in CH₄ emission rates were compared between the different regions using the Wilcoxon rank sum test. For each region, linear regression analysis was performed on the data separately for environmental variables such as sedimentary C content and seagrass shoot density. The significance level was set at P < 0.05. The linear regression analysis was performed in IBM SPSS Statistics (version 27).

RESULTS

The CH₄ emissions were generally low but varied substantially both within and between sites. Results in the release of CH₄ to the air phase ranging from 0.36 to 8.1 µmol CH₄ g⁻¹ m⁻² h⁻¹ at the Finnish sites and 0.1–2.5 µmol CH₄ g⁻¹ m⁻² h⁻¹ at the Danish and Swedish sites (Figures 1, 2). Overall, there were no significant differences between the Swedish and Danish sites when compared to the Finnish sites, while there was a significant difference between the Swedish and Danish sites (Table 2). For the unvegetated areas, CH₄ emissions were significantly higher in the Swedish sites compared to the Finnish sites (Table 2). Overall, there was no significant difference in emissions between seagrass-covered and unvegetated sediments, even though differences between the seagrass types occurred in some sites within each region (Table 2 and Figure 3).

Methane emissions increased along the salinity gradient (Figures 4, 5). Although there was a significant difference in CH₄ emissions between seagrass meadows and adjacent unvegetated areas in Finland (FIN), Denmark (DEN), and Sweden (SWE). The solid lines within the boxes indicate median values, the boxes represent the 25th and 75th percentiles and the vertical whisker bars show the 5th and 95th percentiles of the data.
TABLE 2 | Summary of non-parametric Kruskal–Wallis tests of methane emissions among regions within (seagrass meadows and unvegetated areas) and between habitats.

| Pairwise comparison | Test statistic | Std. error | Std. test statistic | Adj p |
|---------------------|---------------|------------|---------------------|-------|
| Region-seagrass (total N = 51, df = 2, model p = 0.005) | | | | |
| Fin vs Den | 14.483 | 5.823 | 2.487 | 0.039 |
| Fin vs Swe | -14.479 | 4.798 | -3.018 | 0.008 |
| Den vs Swe | 0.004 | 5.413 | 0.001 | 1.000 |
| Region-unvegetated (total N = 47, df = 2, model p = 0.002) | | | | |
| Fin vs Den | 7.321 | 5.443 | 1.345 | 1.000 |
| Fin vs Swe | -16.010 | 4.635 | -3.454 | 0.003 |
| Den vs Swe | -8.688 | 5.103 | -1.703 | 0.532 |
| Habitat (total N = 98, df = 1, model p = 0.806) | | | | |

Significant values (p < 0.05) are shown in bold. Countries with bolded text indicate the higher values in the pairwise comparisons. Std. error: standard error; Adj p: Adjusted p-value.

FIGURE 4 | Box-and-whisker plot summarizing methane emissions from the sediment to the gas-filled pocket in the incubation chambers in seagrass meadows and adjacent unvegetated areas in relation to average salinities in the different regions. The solid lines within the boxes indicate median values, the boxes represent the 25th to the 75th percentiles and the vertical whisker bars show the 5th to the 95th percentiles of the data.

**DISCUSSION**

This study shows that CH\(_4\) emissions from cold-temperate Nordic seagrass meadows are relatively low when compared to other seagrass areas worldwide and when compared to other shallow-water habitats in the Nordic region. The amount of C\(_{org}\) stored in the sediments appeared to influence methane emissions, as there was a positive correlation between CH\(_4\) emissions and the sedimentary organic carbon content. The relatively low explanatory value suggested that besides CH\(_4\) emissions, C\(_{org}\) content, there might be other factors that are major contributors to methane release from these coastal sediments. Nevertheless, we found a significant influence of vegetation type (habitat) on CH\(_4\) emissions. The current study was conducted during the warm, high-productive season, when also the net release of methane is expected to peak. It represents the first survey of methane emissions from seagrass meadow sediments in Nordic coastal waters.

Methane release from Z. marina meadow sediments varied from 0.8 to 8.0 µg m\(^{-2}\) h\(^{-1}\). These values are an order of magnitude lower than what was reported from seagrass habitats globally, which reaches up to 780 g m\(^{-2}\) h\(^{-1}\) (see Table 3). It is further drastically lower than reported CH\(_4\) emissions from other shallow-water habitats in Nordic coastal waters (8.8, 583 g m\(^{-2}\) h\(^{-1}\)) or the grassland waterfowl Phragmites belts (15,200 g m\(^{-2}\) h\(^{-1}\)) (Table 3). The relatively low CH\(_4\) emission levels measured in our study agree well with those reported for coastal bare sediments (1.2–2.3 µg CH\(_4\) g\(^{-1}\) s\(^{-1}\)) in the Baltic proper (Bonaglia et al., 2017). Those sediments had similar particle content and collective Swedish shape of 5.5% in similar salinities and in the Finnish area (6.8). But the sampled depth (50 m) and the much lower temperature (8.0°C) compared to our study of range 20–23.5°C (Supplementary Table 1). The good agreement in rates may be explained by the fact that most of the CH\(_4\) generated deep inside the sediment is efficiently oxidized by the community of methane-oxidizing archaea and sulfate-reducing bacteria before it can reach the sediment-water interface (Orphan et al., 2001). Up to 90% of the CH\(_4\) produced in marine sediments are consumed already in the sediments (Lee & Keil, 1993).

Most studies where high emissions from seagrass habitats have been reported have come from warm-temperate to tropical waters (Table 3). However, the influence of temperature on CH\(_4\) production varies across regions. Nevertheless, an effect of water temperature on spatial and temporal scales could still influence the variation in emission rates, but this was not investigated here. We found no significant influence of vegetation type over CH\(_4\) emissions from the sediments in the seagrass meadows.
Seagrass meadows worldwide

| Region                      | Habitat type                  | Ranges (or average*) of emission rates, (µg CH₄ m⁻² h⁻¹) | References                                |
|-----------------------------|-------------------------------|--------------------------------------------------------|-------------------------------------------|
| Global estimation           | Seagrass in general           | 54*                                                    | Rosentretre et al., 2021                  |
| Portugal, Atlantic coast    | Zostera noltii (at night)     | 71                                                     | Bahlmann et al., 2014                     |
| Florida bay                 | Thalassia testudinum          | 14–185                                                 | Barber and Carlson, 1993                  |
| France, Atlantic coast      | Zostera spp                   | 66*                                                    | Deborde et al., 2010                     |
| Red Sea                     | Halophila stipulacea and     | 16–74                                                  | Garcia-Bonet and Duarte, 2017            |
|                             | Halodule univalvis            |                                                        |                                           |
|                             | Thalassodendron ciliatum      | 0.067–4.6                                              |                                           |
|                             | Thalassia hemprichii          | 0.20–11                                                |                                           |
|                             | Halophila decipiens           | 0.47–11                                                |                                           |
|                             | Enhalus acoroides             | −8.0 to 181                                            |                                           |
|                             | Cymodocea semutalata and     | 91–378                                                 |                                           |
|                             | Halodule univalvis            | 14–70                                                 |                                           |
| Western Indian Ocean        | Thalassia hemprichii          | 50* (controls), 224–291 (disturbed)                     | Lyimo et al., 2018                       |
| Florida Keys                | Syringodium sp.               | 2–5                                                   | Oremland, 1975                           |
|                             | Thalassia testudinum          | 29–30                                                 |                                           |
| Nordic waters               | Zostera marina                | 0.3–3.0                                                | Current study                            |
| Other shallow-water habitats in Nordic waters | | | |
| North-Eastern Germany       | Brackish fen, Phragmites australis | 538–15,200                      | Koch et al., 2014                        |
| Gulf of Bothnia             | Eutrustine wetlands          | 8,583*                                                 | Likanen et al., 2009                     |

Even though emissions measured from both vegetated and adjacent unvegetated sediments were low, CH₄ emissions partly counteract the seagrass meadows’ capacity as effective sinks for carbon in the only published data for carbon accumulation rates for seagrasses in the Nordic region (Röthlein et al., 2006) shows annual mean values of 0.05–0.15 t C ha⁻¹ yr⁻¹ for Finland, 0.15–1.0 t C ha⁻¹ yr⁻¹ for Denmark, while a comparable data set for Sweden has been published for only the north of the country and calculated as CO₂ (George et al., 2015). If the CH₄ emissions from this study are added (from 0.007 to 0.040 t C ha⁻¹ yr⁻¹ in Finland, from 0.004 to 0.005 t C ha⁻¹ yr⁻¹ in Denmark, and from 0.009 to 0.006 t C ha⁻¹ yr⁻¹ in Sweden), the CH₄ carbon accumulation rate in Finland was between 2 and 7 times higher, and in Denmark between 65 and 877 times higher than the estimated emissions from CH₄ from the Nordic region. Seagrass meadows will not outweigh their importance as carbon sinks under present environmental conditions.

Climate simulations for the Baltic Sea ecosystems indicate a 2–4°C warming and a significant increase in precipitation by the year 2100, which may increase the run-off of allochthonous organic matter and decrease salinity (Andersson et al., 2015). This might have multifaceted effects on the seagrass systems. While healthy seagrass meadows contribute to mitigate the effects of run-off and capture part of the increased input of nutrients and organic matter, an increased organic content in the sediments might result in increased respiration and lower oxidation rates, thus the sediment will not oxidize itself. Instead, oxidation will influence the anaerobic respiration and might thus lead to increased production and emissions from CH₄ and other GHGs. As temperatures are predicted to increase more drastically in the Nordic region than on a global scale (Andersson et al., 2015), this may accelerate the CH₄ emissions from blue carbon habitats such as seagrass meadows (Vyon-Durocher et al., 2011).

It has been previously shown in tropical seagrass sediments that CH₄ emissions more than doubled during high temperature stress (George et al., 2020) for the Nordic seagrass systems. Today’s functioning in effective links of atmospheric CO₂ might thus be hampered by climate change effects. Seagrasses are important carbon sinks in the ocean, but their emission of CHGs increased. This may eventually turn Nordic seagrass meadows from sinks of CO₂ to sources of CO₂.

In conclusion, the relative low CH₄ release from Nordic seagrass meadows presented in this study may reinforce...
their capacity to naturally lower carbon sinks to fully understand the extent of methane emission and other GHGs from Nordic coastal habitats, multiple spatial (from microhabitat to seascape level) and temporal (diurnal and seasonal) aspects should be considered in future studies.

DATA AVAILABILITY STATEMENT

The original data presented in this study are included in the article (Supplementary Material). Further inquiries about access and any modifications required to the data should be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MA, MB, JB, and MG conceived and designed the study. MA, MB, DB, CB, and KG carried out the fieldwork. MA, MB, and MG carried out the lab work and analysis. MA, MB, and MDB wrote the first draft of the manuscript with aid from MB and MG. All authors contributed to the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

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