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Seasonal methane and nitrous oxide exchange in a sandy coastal eelgrass meadow

Gry Overvad Frederiksberg[1,2], Marianna Lanari[3], Anaïs Richard[4], Pere Masque[5], Erik Kristensen[1], Cintia Organo Quintana[1,2]

1. Department of Biology, University of Southern Denmark, Odense, 5230, Denmark
2. SDU Climate Cluster, University of Southern Denmark, Odense, 5230, Denmark
3. Institute of Oceanography, Federal University of Rio Grande, 96201-900, Rio Grande, Brazil
4. LIttoral ENvironnement et Sociétés (LIENSs), UMR 7266 CNRS, La Rochelle Université, 17000, La Rochelle, France
5. Centre for Marine Ecosystems Research, School Science, Edith Cowan University, Joondalup, WA, Australia

Correspondence to: Gry O. Frederiksberg (gfrederiksberg@biology.sdu.dk)

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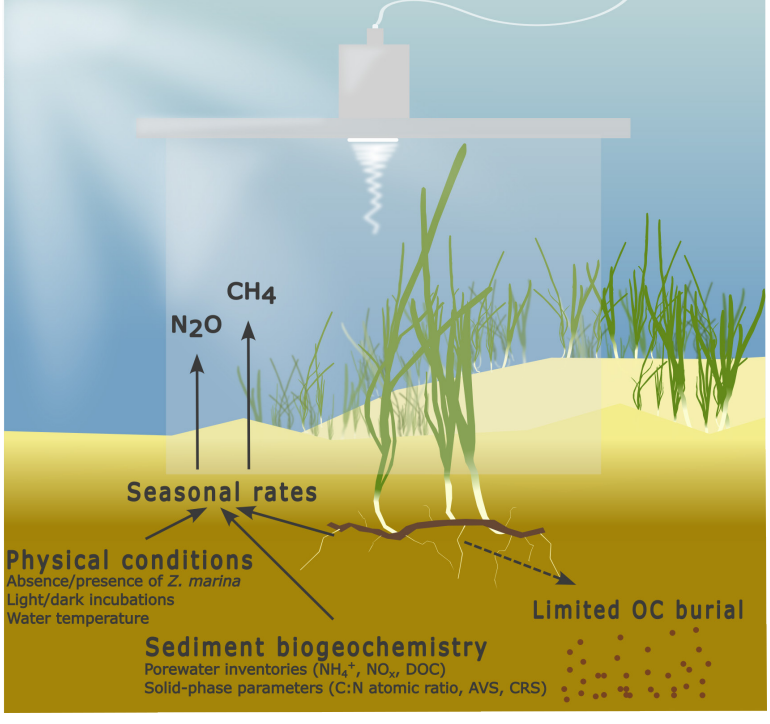
Abstract

Seagrass meadows are considered as potential blue carbon ecosystems through burial and long-term storage of organic carbon in their sediments. However, this climate benefit may be reduced or even negated by emissions of greenhouse gases (GHG) such as methane (CH_4) and nitrous oxide (N_2O). Here, we quantified seasonal CH_4 and N_2O fluxes and identified controlling biogeochemical factors in a shallow, sandy *Zostera marina* meadow (*Z. marina*) and an adjacent unvegetated site (Sand) in Denmark. We used in situ benthic chamber incubations under dark and light conditions, combined with measurements of plant biomass, porewater chemistry, solid-phase sediment variables, and ^{210}Pb concentration profiles. Fluxes of CH_4 were low overall, ranging from -0.8 to 15.5 µmol m^{-2} h^{-1}, with the largest emissions occurring in autumn. Across sites and seasons, CH_4 fluxes increased with *Z. marina* belowground biomass and decreased with the porewater NO_x (= NO_2^- + NO_3^-) inventories, indicating that root/rhizome-derived organic matter fueled methanogenesis, while more oxidizing conditions constrained net CH_4 release. In contrast, N_2O fluxes were small and variable (-0.44 to 0.32 µmol m^{-2} h^{-1}), without a clear seasonal pattern. The most important controllers of N_2O fluxes were light conditions and porewater NH_4^+, suggesting a role for coupled or light-driven NO_2^- reduction and nitrification-denitrification processes. Sediment OC concentrations were uniformly very low (< 0.4%), and excess ^{210}Pb was restricted to the upper few centimeters without a consistent downcore decline, reflecting sediment mixing and suggesting low sedimentation rates, although neither these nor the OC sequestration rates could be quantified. Together with the negligible fine-sediment content, these results point to very limited long-term OC burial at this site. We therefore conclude that, in shallow organic-poor sandy sediments of *Z. marina* such as those studied here, even modest CH_4 emissions are sufficient to offset any likely climate-mitigation benefit from sedimentary carbon sequestration.



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Short summary

The potential climate benefits of carbon capture and storage by seagrasses may be counteracted by emissions of strong greenhouse gases such a methane and nitrous oxide. We measured greenhouse gas rates from sediments of a sandy eelgrass meadow and an unvegetated area and compared them to carbon storage and burial. Greenhouse gas rates were controlled by porewater chemistry and vegetation parameters and even low rates, as observed here, offset the limited carbon burial within the site.

1 Introduction

Seagrasses are widely recognized for providing important ecosystem services such as habitat provision, water purification, shoreline stabilization and biodiversity support (Nordlund et al., 2016; Do Amaral Camara Lima et al., 2023). In recent years, the role of seagrasses for climate change mitigation has gained increased attention, inspiring efforts for conservation and restoration projects (Macreadie et al., 2021). Together with other vegetated coastal ecosystems (i.e. "blue carbon ecosystems"; Nellemann et al. (2009)), it has been suggested that seagrass meadows provide a climate benefit through sequestration and long-term storage of organic carbon (OC) derived from autochthonous and allochthonous sources (Mcleod et al., 2011; Fourqurean et al., 2012). OC sequestration rates of seagrass meadows display high variability (Eyre et al., 2023) with inherited OC storages varying across species and environments (Lavery et al., 2013; Leiva-Dueñas et al., 2023; Krause et al., 2025). For example, larger seagrass species such as *Posidonia* spp. tend to have larger sediment OC storages than smaller species (Lavery et al., 2013; Mazarrasa et al., 2018; Krause et al., 2025). High hydrodynamic exposure, as reflected in high grain size and low content of silt and clay in the sediment, is negatively correlated with OC stocks in seagrass meadows, suggesting that these settings that are common in many shallow coastal areas may not favor OC accumulation and sequestration (Mazarrasa et al., 2018; Röhr et al., 2018; Leiva-Dueñas et al., 2023)

The climate change mitigation potential of blue carbon ecosystems may also be partially offset by simultaneous emission of greenhouse gases (GHG) other than CO_2 (Johannessen, 2022; Williamson and Gattuso, 2022; Kristensen et al., 2025). The most relevant GHGs to consider in this context are methane (CH_4) and nitrous oxide (N_2O), with Global Warming Potentials (GWP) of 27 and 273 on a 100-year timeline, respectively (Forster et al., 2021), which are estimated to offset 7–35 % of the climate benefit from seagrasses globally (Eyre et al., 2023). Despite the strong capacity of these GHG to warm up the atmosphere, the factors controlling their dynamics in blue carbon ecosystems, and to which extend they offset carbon storage and sequestration potential, are poorly understood, particularly within seagrass meadows (Rosentreter et al., 2021). For instance, little is known about how sediment biogeochemistry and plant traits influence CH_4 and N_2O dynamics in seagrass meadows (Al-Haj and Fulweiler, 2020; Rosentreter et al., 2021). Therefore, a critical assessment of the climate benefits of seagrass meadows requires an understanding of the extent to which GHG emissions may offset carbon sequestration.

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Methanogenesis is the microbially mediated CH_4 production that occurs widely in anoxic coastal sediments. The influence of seagrasses on this process can be synergistic, antagonistic or negligible. Release of CH_4 from seagrass meadows is generally considered low compared to vegetated freshwater ecosystems, since methanogenesis is often outcompeted by sulfate reduction in marine sediments (Poffenbarger et al., 2011). Nevertheless, substantial emissions of CH_4 from seagrass meadows have been observed (Rosentreter et al., 2021; Eyre et al., 2023), suggesting that organic substrate availability or plant induced processes may control CH_4 production (Al-Haj and Fulweiler, 2020; Bijak et al., 2024). Traits of seagrasses, such as plant size, rhizome and root penetration, and metabolic activity may affect GHG dynamics in the surrounding sediment. For example, plant size seems to be a main factor explaining CH_4 production in seagrass sediments (Bijak et al., 2024). Radial oxygen loss from roots may inhibit methanogenesis and increase oxidation of CH_4 (Oremland, 1975; Oremland and Taylor, 1977; Yu et al., 2024) which may be further enhanced by the presence of other electron acceptors forms such as nitrite and nitrate (Bollag and Czlonkowski, 1973; Balderston and Payne, 1976; Welte et al., 2016). Exudation of labile dissolved OC (DOC) from roots or trapped OC in the meadow sediment may ease the competition with sulfate reducers and stimulate CH_4 production (Holmer and Kristensen, 1994; Holmer et al., 2001a; Schorn et al., 2022). Furthermore, temperature influences CH_4 productivity in coastal habitats, with low emissions observed below 10°C (Petersen et al., 2023). However, there is little evidence about the quantity and quality of OC and CH_4 production in seagrass meadows (Al-Haj and Fulweiler, 2020; Oreska et al., 2020; Asplund et al., 2022; Yau et al., 2023; Yu et al., 2024), as well as how CH_4 dynamics are expected to vary seasonally following vegetation activity, interactions with sediment biogeochemistry and temperature.

Even less is known about the N_2O dynamics within seagrass meadows (Eyre et al., 2023). N_2O transformations in coastal sediments are complex as this compound is a transient in several processes of the N cycle. Recent studies have reported both N_2O production and consumption in seagrass ecosystems (Rosentreter et al., 2021; Al-Haj et al., 2022; He et al., 2024), which are often attributed to nitrification, denitrification, nitrifier denitrification and dissimilatory nitrate reduction to ammonium (Baggs, 2008; Foster and Fulweiler, 2016; Maavara et al., 2019). N_2O production depends on the available N-substrates (e.g. NH_4^+ and NO_3^-) within the sediment for microbial processing (Murray et al., 2015). As these processes are either aerobic or anaerobic, the dominating pathway and subsequent flux of N_2O may be controlled by oxygen availability (Canfield et al., 2005a; Murray et al., 2015).

To our knowledge, a scarcity of studies has investigated CH_4 and N_2O emissions from sediments of *Zostera marina* meadows (Sansone et al., 1998; Asplund et al., 2022), with only few including multi-season variation (Oreska et al., 2020; Al-Haj et al., 2022), highlighting a knowledge gap concerning temporal GHG dynamics in *Z. marina* meadows. In this study, we investigate the seasonal fluxes of CH_4 and N_2O in a sandy, shallow water *Z. marina* meadow (referred to as "*Z. marina*") relative to an adjacent unvegetated sandy area (referred to as "Sand"). Corresponding measurements were performed of sediment OC content and sequestration rates combined with potential controlling factors including physical conditions (absence/presence of *Z. marina*, light/dark incubations and water temperature), plant traits (aboveground biomass, epiphytes, belowground roots and detritus and chlorophyll *a*), porewater chemistry (NH_4^+, NO_x (NO_2^- + NO_3^-), DOC) and sediment solid-phase biogeochemical parameters (C:N atomic ratio, acid volatile sulfide (AVS) and chromium reducible sulfide (CRS)). Our

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goal was to investigate the intricate dynamics and controls of the GHG balance in *Z. marina* meadows and evaluate the potential climate offset between CH_4 and N_2O emissions and OC sequestration. We hypothesize that **1**) *Z. marina* plant traits lead to higher release of CH_4 and N_2O compared with unvegetated sediments, **2**) CH_4 and N_2O dynamics are controlled by plant traits and porewater chemistry, and **3**) OC sequestration in *Z. marina* meadows in organic poor sandy sediment is relatively low and counteracted by GHG releases.

2 Materials and methods

2.1 Study area

The studied *Z. marina* meadow and adjacent unvegetated Sand site were located at Dalby Bay (55°31'34.3" N, 10°37'29.5" E) outside of Odense Fjord, in the Northern Belt Sea of Denmark. Dalby Bay has an area of 2.6 km^2 and an average water depth of 3.8 m. The *Z. marina* and Sand sites were located near the coast at about 1 m water depth in the microtidal (~0.4 m) bay. The average salinity was 19.8 during the study period. The median grain size of *Z. marina* and Sand sediments were 0.21 ± 0.004 and 0.23 ± 0.01 mm, with dominating fractions of fine and very fine (67.1 ± 1.6 and 64.6 ± 3.2 %), medium (28.2 ± 1.0 and 27.9 ± 1.7 %) and coarse sand (2.9 ± 0.7 and 5.4 ± 1.5 %) and negligble silt and clay contents (0.7 ± 0.2 and 0.6 ± 0.2 %), respectively.

2.2 Flux incubations

Seasonal in situ incubations to measure fluxes of CH_4 and N_2O across the sediment-water interface were performed from November 2022 to August 2023 in both *Z. marina* and Sand sites. The flux incubations were performed with three 30 cm tall acrylic chambers (diameter = 39 cm) for *Z. marina* to allow space for leaves, and three 18 cm tall chambers with the same diameter for Sand. The chambers were inserted 5–10 cm into the sediment with an open top ca. 1 hour prior to incubation. Five incubation campaigns were performed in November 2022, January 2023, April 2023, June 2023 and August 2023. During two consecutive days, incubations in dark and light conditions (~3–5 h) were performed with the *Z. marina* meadow on the first day and Sand on the following day. Chambers incubated in dark conditions (n = 2–3) were covered by hoods of black plastic surrounded by a metal frame, while chambers incubated in light conditions were exposed to ambient light conditions (n = 2–3; only one replicate in January and June 2023 due to chamber loss or leakage). Chambers were sealed tight with chamber lids equipped with a rotating magnetic stirrer (ca. 60 rpm) to ensure consistent water movement during incubations. Initial and final water samples from each chamber were collected using a 50 mL syringe at the beginning and end of each incubation. Water samples were separated into subsamples for CH_4 and N_2O in 12 mL exetainers (November 2022 and January 2023) and 17 mL Hungate tubes (April 2023, June 2023, August 2023) and fixed with saturated $ZnCl_2$ solution. In situ water column temperature and salinity were measured using YSI Model 30.

Two ml of the samples for CH_4 and N_2O were replaced with Helium leaving a headspace in the exetainers. After equilibration, subsamples of the headspace were analyzed for CH_4 and N_2O using a Thermo Scientific TRACE 1300 Gas

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Chromatograph. The analysis for CH_4 was carried out with Nitrogen as carrier gas, Hydrogen + air as the make-up gas, TG-Bond Msieve 5A as the column and FID as the detector. The N_2O analyses used Helium as the carrier gas, 5% CH_4 + Argon as the make-up gas and ECD as the detector. Appropriate solubility constants were used to calculate the concentration of CH_4 (Wiesenburg and Guinasso Jr, 1979) and N_2O (Weiss and Price, 1980) in the water phase of the subsamples based on the respective concentrations in the headspace. Fluxes of both gases were calculated from the difference in concentration between the initial and final water samples (mM h^{-1}). Annual estimates of net CH_4 and N_2O exchanges were calculated conservatively by summing observed seasonal dark and light fluxes from the present study, while assuming constant exchange rates within each season, while correcting for the number of dark and light hours according to data from Årslev Meteorological Station (distance 27 km; Danish Meterological Institute (2025)).

2.3 Sediment parameters

Sediment cores (n = 3–5, diameter = 5.2 cm) for chlorophyll, porewater solutes and sediment solid-phase parameters were sampled in the *Z. marina* and Sand sites during incubation campaigns. *Z. marina* sediment cores were also used for assessing belowground plant biomass. The cores were sliced in intervals of 2 cm from surface to 10 cm depth and 5 cm to 15 cm depth. The belowground biomass from the *Z. marina* site was separated manually from the sediment matrix and grouped into living *Z. marina* biomass and detritus according to color, texture and size. Living biomass was identified by yellow color, rigid texture and intact structure while detritus had brown/black color, damaged and/or flaccid appearance. Both fractions were dried at 60°C until constant weight and weighed.

Subsamples of top sediments (0–2 cm depth) from both *Z. marina* and Sand sites were analyzed for chlorophyll after addition of 90% ethanol and reading the absorbance of the supernatants at 665 and 759 nm before and after acidification (Parsons et al., 1984). Subsamples for the sediment solid-phase inventories of AVS and CRS were separated from each slice and analyzed by two-step distillation according to Fossing and Jørgensen (1989). Porewater was extracted from the remaining sediment by centrifugation at 2000 rpm for 10 minutes using double centrifuge tubes and separated into subsamples for DOC, NH_4^+, and NO_x porewater inventory analysis. Subsamples for NH_4^+ and NO_x were analyzed using a SKALAR SANplus ANALYZER, while subsamples for DOC were analyzed using a SHIMADZU Total Organic Carbon Analyzer.

2.4 Aboveground *Z. marina* shoots and epiphytes

Z. marina shoot density and aboveground biomass were measured simultaneously with the flux incubations by sampling sediment cores (n = 3) within *Z. marina* meadows using a cylindrical steel corer (0.017 m^2, 30 cm long) allowing for larger area of sampling. The cores were sieved through a 1 mm mesh to isolate *Z. marina* shoots. Only shoots with attached roots were counted. In addition, 27-35 intact shoots from the *Z. marina* meadow were randomly handpicked to determine biomass of aboveground *Z. marina* shoots and epiphytes. Each shoot was carefully washed before the below- and aboveground parts were separated, and shoot height was measured. Epiphytes were collected from all leaves by scraping with a scalpel. Subsequently, all clean aboveground *Z. marina* shoots and epiphytes were dried at 60°C for determination of biomass.

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2.5 Elemental analysis

Sediment cores sampled at *Z. marina* (n = 5) and Sand (n = 4) in September 2022 were analyzed for OC. Cores were sliced in intervals of 2 cm to 10 cm depth, and 5 cm to 25 cm depth. The slices were dried at 60°C until constant weight, and samples (≈ 1 g) of each slice were acidified, ground, encapsulated and analyzed for OC using a Thermo Scientific FLASH 2000 Organic Elemental Analyzer. OC $stocks_{25cm}$ were calculated as the sum of OC (g C m^{-2}) to 25 cm depth. Additionally, seasonal concentrations of OC and total N (TN) in top sediments (0–2) of both *Z. marina* and Sand were obtained from the cores used for sediment parameters. Subsamples were ground, acidified and encapsulated for elemental analysis of OC and TN.

Dried samples of belowground living roots (n = 11), detritus (n = 4) and aboveground *Z. marina* shoots (n = 4) and epiphytes (n = 4) from August 2023 were analyzed for elemental OC as described above for sediment, except for acidification. Belowground OC stocks (g C m^{-2}) were calculated as the sum of living roots and detritus (g OC m^{-2}) down to 15 cm. Aboveground biomass and epiphyte stocks (g OC m^{-2}) were calculated as the shoots (g OC) multiplied by the shoot density (n m^{-2}).

2.6 ^{210}Pb profiling

Sediment cores from both *Z. marina* (n = 3) and Sand (n = 3) sites were collected in January 2023 for the determination of the ^{210}Pb concentration profiles to assess the sedimentation rates. Cores were sliced into 1 cm intervals to 20 cm depth and in 2 cm intervals to 30 cm depth. The slices were dried at 60°C and sieved through a 0.125 mm mesh to separate the fine particles, which were subsequently ground to powder. ^{210}Pb was determined through the analysis of ^{210}Po by alpha spectrometry after addition of ^{209}Po as an internal tracer, digestion in acid media using an analytical microwave and plating of Po isotopes onto silver discs. Some samples from each core were analyzed by gamma spectrometry to determine the concentrations of ^{226}Ra (supported ^{210}Pb). The concentrations of excess ^{210}Pb in each sediment core were calculated from the difference between total and supported ^{210}Pb.

2.7 Statistical analysis

To explore potential parameters influencing the dynamics of CH_4 and N_2O, Kendall-tau correlation matrices were computed to estimate the monotonically increasing or decreasing relationships between relevant variables. Kendall-tau' correlation coefficients were calculated for each interaction of variables across and within sites using R package "stats" (R Core Team, 2024). These coefficients indicate the strength of relationships between variables with ±1 representing a perfect monotonic negative or positive relationship and 0 showing no monotonic relationship (Reimann et al., 2008). A significance test computing p-values was applied to estimate the significance levels of the relationships between variables and visualizations of correlation matrices were performed using R package "corrplot" (Wei and Simko, 2024).

From the correlation matrix, we identified key explanatory parameters controlling the dynamics of CH_4 and N_2O using two linear models fitted with several explanatory parameter variables and the respective gases as response variables

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using "stats" package in R (R Core Team, 2024). Prior to model-fitting, response variables were explored for distribution of normality, homogeneity, outlier detection using QQ-plots and Cleveland plots (Zuur et al., 2007; Warton, 2022). Consequently, the fluxes of CH_4 were log-transformed using the natural logarithm plus 1. An initial screening of potential parameter variables to include in the linear models was performed based on the strength and significance of the relationships between these in the Kendall-tau correlation matrix. During this screening, parameter variables were discarded from the linear model computation if their relationship with response variables were weak and insignificant (CH_4 model: light/dark conditions, chlorophyll, sediment C:N, AVS; N_2O model: none excluded) or if they collineated with already selected strong and significant variables (CH_4 model: site, belowground detritus, aboveground *Z. marina*, epiphytes; N_2O model: epiphytes). Ultimately, the remaining parameter variables were included in further model selection. Identification and selection of the best fitted linear model of each gas was based on second-order Akaike Information Criterion and supported by the use of the functions "dredge" from the R package "MuMIn" (Bartón, 2025). Model assumptions were evaluated using the R packages "car" (Fox and Weisberg, 2019) and "performance" (Lüdecke et al., 2021) and residuals were explored using R packages "visreg" (Breheny and Burchett, 2017) and "effects" (Fox and Weisberg, 2018, 2019). All figures were plotted in R using "ggplot2" (Wockham, 2016).

3 Results

3.1 Seasonal dynamics and controls of CH_4 exchange

The exchange of CH_4 in both light and dark conditions was low at both sites throughout the study period and ranged from -0.2 to 15.5 and -0.8 to 10.4 µmol m^{-2} h^{-1} for *Z. marina* and Sand, respectively (Fig. 1a). Dark fluxes ranged from 0.2 to 11.2 µmol m^{-2} h^{-1} and -0.3 to 10.4 µmol m^{-2} h^{-1} and light fluxes ranged from -0.2 to 15.5 µmol m^{-2} h^{-1} and -0.8 to 9.0 µmol m^{-2} h^{-1} for *Z. marina* and Sand, respectively. There was no clear effect of light conditions on CH_4 exchanges at either site (Fig. 1a and 2). CH_4 fluxes displayed a temporal trend across sites with highest releases in November 2022 and August 2023 for *Z. marina*, while highest releases in Sand were observed in November 2022 and June 2023 (Fig. 1a). Rates were low and similar in the remaining months of January and April 2023 (Fig. 1a).

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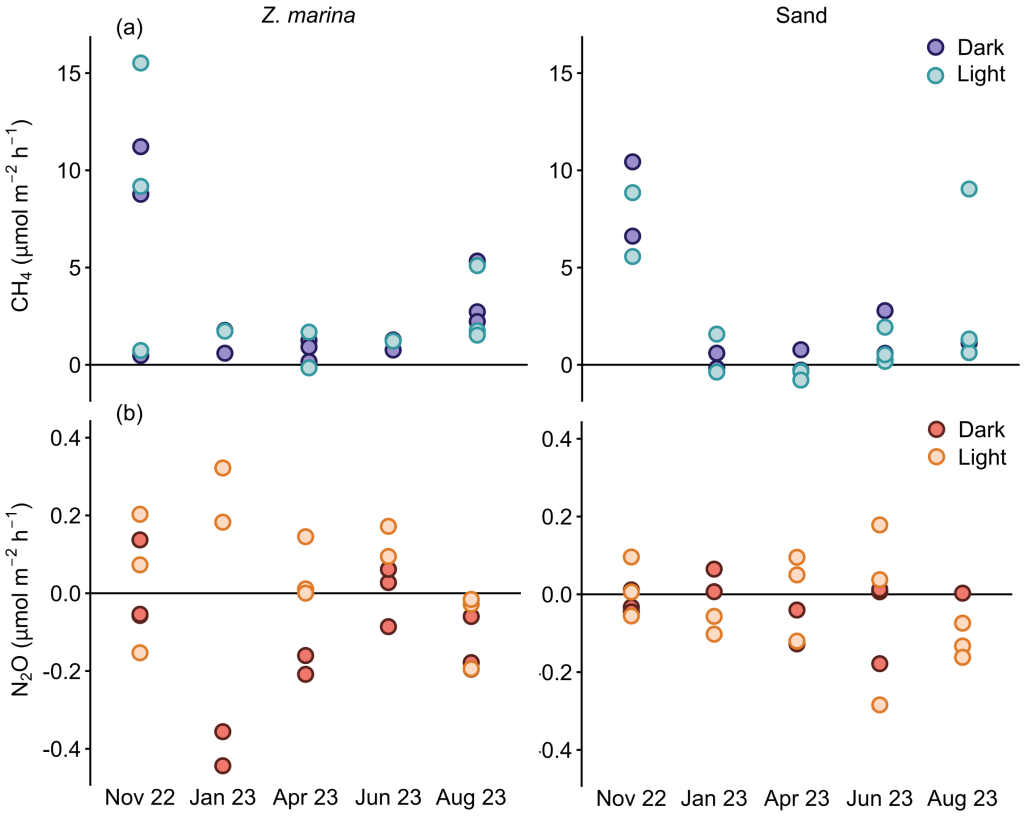

Figure 1: Seasonal GHG fluxes (n = 2–3) across the sediment-water interface during chamber incubations: (a) CH_4 exchange (µmol m^{-2} h^{-1}) at *Z. marina* site (left) and Sand site (right) in both dark and light conditions; and (b) N_2O exchange (µmol m^{-2} h^{-1}) at *Z. marina* site (left) and Sand site (right) in both dark and light conditions.

Most significant rank-based positive relationships between CH_4 fluxes and potential controlling factors were with belowground living biomass and detritus ($p < 0.05$), while also site, aboveground *Z. marina* biomass and epiphytes and temperature had a positive, although not significant, effect on CH_4 exchange (Fig. 2 and S1). Indeed, belowground living biomass also peaked with 16.5 ± 3.4 mol C m^{-2} in November 2022, while temperature had a similar seasonal pattern with peaks of 18.6–21.3 °C in June and August and lowest values in January and April 2023 (Table 1). Most significant rank-based negative relationships with CH_4 was NO_x ($p < 0.001$) and DOC inventory ($p < 0.05$; Fig. 2, S1 and S2).

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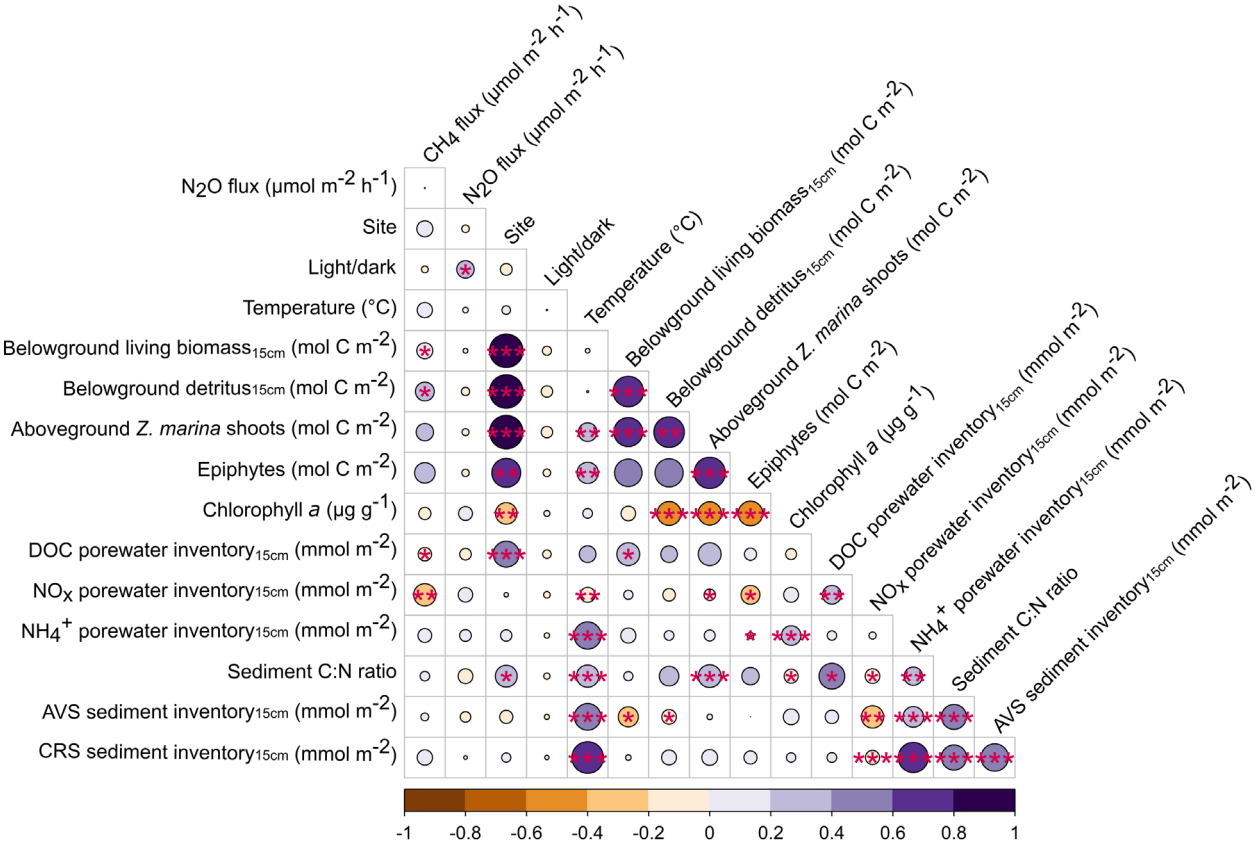

Figure 2: Kendall-tau correlation matrix showing a rank-based association from -1 (negative) to 1 (positive) between variables across both *Z. marina* and Sand sites indicated by size and colour of circles. Levels of significance from significance test of association are indicated as p < 0.001*, p < 0.01**, p < 0.05*, while insignificant associations (p > 0.05) are not indicated.**

NO_x and DOC inventories followed an inverse pattern with peaks of 0.73 ± 0.13 mmol NO_x m^{-2} and 109.4 ± 32.7 mmol DOC m^{-2} in *Z. marina* in April 2023 and 0.82 ± 0.24 mmol NO_x m^{-2} and 44.9 ± 3.8 mmol DOC m^{-2} in Sand in April and June 2023 respectively (Table 1).

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Table 1: Seasonal averages ± SE of key environmental variables at *Z. marina* and Sand included as explanatory parameters in the linear models of CH_4 and N_2O exchange. ZM = *Z. marina*, BGL biomass = belowground living biomass.

Month	Site	Temp. (°C)	BGL biomass (mol C $m^{-2}_{15\ cm}$)	NH_4^+ inventory (mmol $m^{-2}_{15\ cm}$)	NO_x inventory (mmol $m^{-2}_{15\ cm}$)	DOC inventory (mmol $m^{-2}_{15\ cm}$)	AVS inventory (mmol $m^{-2}_{15\ cm}$)
Nov	ZM	10.5	16.5 ± 3.4	4.1 ± 0.9	0.17 ± 0.02	36.8 ± 3.6	10.4 ± 0.7
2022	Sand	9.5	N/A	2.5 ± 0.4	0.09 ± 0.02	15.7 ± 0.8	20.1 ± 9.2
Jan	ZM	4.8	6.4 ± 0.4	2.4 ± 0.1	0.11 ± 0.06	59.7 ± 1.9	37.8 ± 12.4
2023	Sand	3.0	N/A	1.6 ± 0.2	0.15 ± 0.03	28.4 ± 3.3	27.8 ± 6.8
Apr	ZM	7.8	8.1 ± 2.8	3.3 ± 0.8	0.73 ± 0.13	109.4 ± 32.7	19.9 ± 9.8
2023	Sand	6.8	N/A	1.5 ± 0.3	0.82 ± 0.24	39.5 ± 3.9	1.2 ± 0.6
Jun	ZM	19.5	6.8 ± 1.8	5.1 ± 0.6	0.27 ± 0.08	86.9 ± 11.3	95.3 ± 17.4
2023	Sand	21.3	N/A	6.7 ± 1.9	0.21 ± 0.01	44.9 ± 3.8	131.2 ± 25.8
Aug	ZM	18.8	7.3 ± 1.9	1.9 ± 0.7	0.04 ± 0.01	64.7 ± 8.7	61.9 ± 9.1
2023	Sand	18.6	N/A	3.9 ± 1.2	0.02 ± 0.01	39.1 ± 0.4	86.2 ± 20.9

Consistent with the correlation trends, belowground living biomass, temperature, DOC and NO_x inventories were the most important variables to explain the dynamics of CH_4 in a linear model. Together, these variables explained 37 % of the variation in CH_4 exchanges (Table 2) with a statistically significant association between these and CH_4 exchanges ($p < 0.001$). The most significant positive controlling factors were belowground living biomass ($p < 0.01$; 32.8 % of explained variance), while NO_x inventory was the most important negative control ($p < 0.05$; 46.9 % of explained variance). The annual net CH_4 release in CO_2 eq. using a GWP of 27 for *Z. marina* and Sand were 108 ± 33 and 96 ± 16 kg CO_2 eq. ha^{-1}, respectively.

Table 2: Estimates ± SE, significance levels (p-values), T-values and proportion of explained variance of total variance of linear correlations between log-transformed CH_4 fluxes and key environmental parameters at both *Z. marina* and Sand sites (sample size = 48). d.f = degrees of freedom.

Parameter	Estimate (± SE)	T-value	Variance explained (%)
BG living biomass (mol C m^{-2})	0.064 ± 0.020**	3.16	32.8
NO_x inventory (mmol $m^{-2}_{15\ cm}$)	-1.176 ± 0.495*	-2.38	46.9
DOC inventory (mmol $m^{-2}_{15\ cm}$)	-0.007 ± 0.005	-1.49	14.8
Temperature (°C)	0.009 ± 0.019	0.52	5.4
Model overview			
Residual standard error	0.69 on 43 d.f.		
Adjusted R^2	0.37		
p-value	0.00***		

$p < 0.001$***, $p < 0.01$**, $p < 0.05$*, $p < 0.1^{\dagger}$

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3.2 Seasonal dynamics and controls of N_2O exchange

N_2O fluxes were generally low and variable, ranging from -0.44 to 0.32 µmol m^{-2} h^{-1} and -0.28 to 0.18 µmol m^{-2} h^{-1} at *Z. marina* and Sand sites, respectively (Fig. 1b), with no distinct seasonal or site-dependent pattern. Highest rates were observed in January 2023 for *Z. marina* and in June 2023 for Sand, with a trend for N_2O influxes during dark conditions and releases during light conditions (Fig. 1b). Indeed, light conditions were the only significant rank-based association related to N_2O exchanges, although chlorophyll *a*, porewater inventories (DOC, NO_x and NH_4^+) and sediment solids (C:N ratio and AVS) displayed stronger, albeit still low and insignificant, relationships compared with the remaining variables (Fig. 2) and NH_4^+ displayed a significant positive relationship with N_2O exchange in the *Z. marina* meadow alone (Fig. S1). The NH_4^+ inventory peaked in June 2023 with 5.2 ± 0.6 mmol m^{-2} at *Z. marina* and 6.7 ± 1.2 mmol m^{-2} at Sand (Table 1). The AVS inventory in *Z. marina* ranged from 10.4 ± 0.7 mmol m^{-2} in November 2022 to 95.3 ± 17.4 mmol m^{-2} in June 2023, while the range in Sand was from 1.2 ± 0.6 mmol in April 2023 to 131.2 ± 25.8 mmol m^{-2} in June 2023 (Table 1). Indeed, light conditions, NH_4^+ inventory and AVS combined were revealed as most fitted controls to explain the dynamics of N_2O exchanges across sites in a linear model. In accordance with the rank-based correlations, light conditions were the most significant control ($p < 0.05$; 61.14 % of explained variance) associating higher N_2O emissions with light during incubations, followed by NH_4^+ inventory as a slightly significant positive control ($p < 0.1$; 23.27 % of explained variance) and AVS as a non-significant negative control ($p > 0.1$; 15.59 % of explained variance; Table 3).

Table 3: Estimates ± SE, significance levels (p-values), T-values and proportion of explained variance of total variance linear correlations between log-transformed N_2O fluxes and key environmental parameters at both *Z. marina* and Sand sites (sample size = 52). d.f = degrees of freedom.

Parameter	Estimate (± SE)	T-value	Variance explained (%)
Light/dark	0.088 ± 0.037*	2.36	61.1
NH_4^+ inventory (mmol $m^{-2}_{15\ cm}$)	0.032 ± 0.017†	1.84	23.3
AVS inventory (mmol $m^{-2}_{15\ cm}$)	-0.0011 ± 0.0007	-1.63	15.6
Model overview			
Residual standard error	0.14 on 48 d.f.		
Adjusted R^2	0.10		
p-value	0.04*		

$p < 0.001$***, $p < 0.01$**, $p < 0.05$*, $p < 0.1$†

Together these variables show a significant association with N_2O fluxes ($p < 0.05$) although explaining only 10 % of the variance. The annual estimated N_2O release in CO_2 eq. using a GWP of 273 for *Z. marina* and Sand showed a net uptake of N_2O of -29 ± 8 and -8 ± 7 kg CO_2 eq. ha^{-1}, respectively.

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3.3 Sediment OC and ^{210}Pb profiles

The sediment OC concentrations at both sites were small throughout the examined sediment depth (Fig. 3a). In *Z. marina* the OC concentrations were slightly more elevated (approx. 0.3 %) in the upper 10 cm of sediment, whereafter they decreased to levels of 0.1–0.2 %, comparable to those observed throughout in Sand. The sediment $OC_{25\ cm}$ stocks in *Z. marina* sediments averaged 0.86 ± 0.08 kg OC m^{-2} and were higher, but not significantly (Welch's t-test: t = 2.052, d.f = 4.723, p = 0.099), than in the Sand site, with an average of 0.68 ± 0.05 kg OC m^{-2}. The presence of excess ^{210}Pb was limited to the upper few cm in all cores, with concentrations ranging from 7.6 to 43.3 Bq kg^{-1}, and showed no decreasing trend with depth (Fig. 3b). This suggests mixing of the upper approximately 5 cm and limited accumulation of silt and clay sediment and organic matter at these sites. Therefore, it was not possible to estimate reliable sedimentation rates and consequently quantify OC sequestration rates, although these would be very low given the low concentrations of OC.

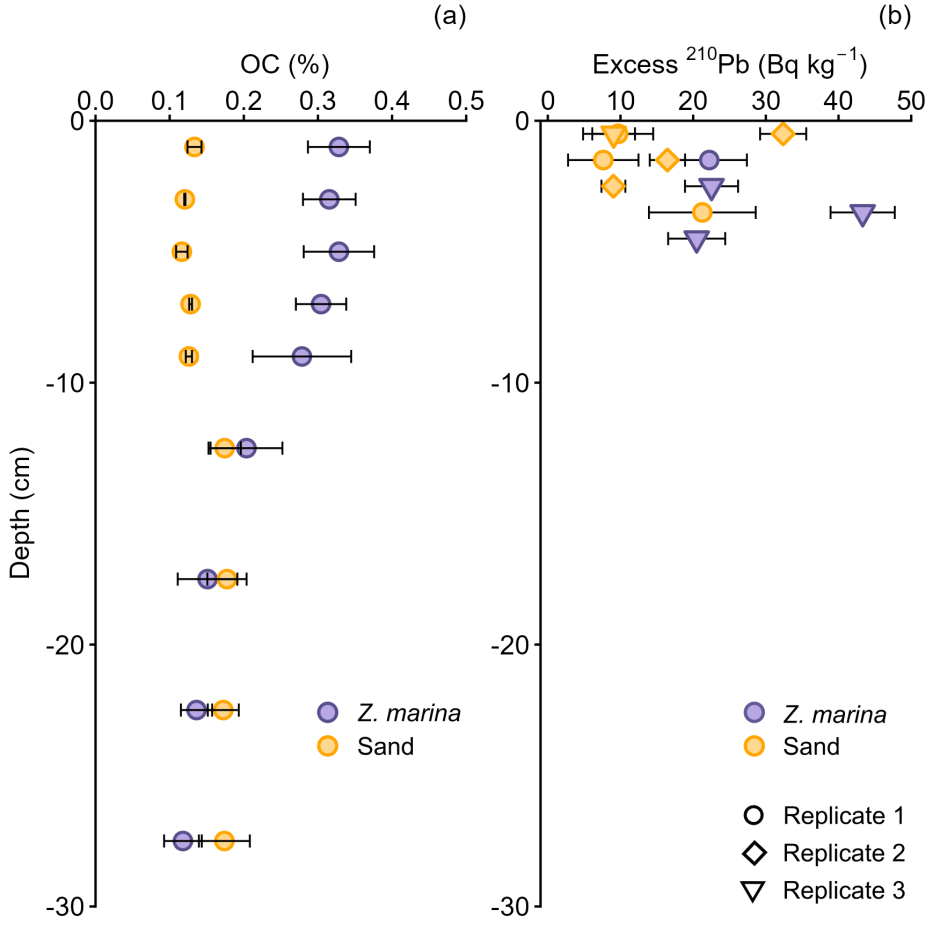

Figure 3: Sediment depth profiles of OC and ^{210}Pb in *Z. marina* and Sand respectively, (a) Sediment depth profiles of mean OC in *Z. marina* and Sand including ± SE and (b) Sediment depth profiles of excess ^{210}Pb for three replicates of *Z. marina* and Sand including ± SD.

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4 Discussion

By combining GHG emissions and concentration profiles of OC and ^{210}Pb, the present study adds to the comprehension of the climate benefits promoted by seagrasses meadows. This study documents how the presence of *Z. marina* influences the dynamics of CH_4 and N_2O in sandy sediments along shallow temperate coasts. Previous reported CH_4 fluxes from seagrass meadows range from 1.25–401.50 µmol m^{-2} d^{-1}, which aligns well with the fluxes observed here (Al-Haj and Fulweiler, 2020). We present the first *Z. marina* community exchange fluxes of N_2O within the Baltic Sea. Our observed N_2O fluxes are also similar to the N_2O flux range from -7.2 to 3.7 µmol m^{-2} d^{-1} reported from other seagrass communities (Eyre et al., 2023). *Z. marina* meadows act as net sources of CH_4, and our results suggest that production of CH_4 is associated directly or indirectly with roots and rhizomes and thus the presence of *Z. marina*. Previous works have shown that high redox driven by NO_x or O_2 availability within the sediment can hamper the production or stimulate the oxidation of CH_4 leading to low CH_4 effluxes, which also seems a controlling mechanism in this study (Bollag and Czlonkowski, 1973; Balderston and Payne, 1976; Welte et al., 2016; Mao et al., 2022). In our work, *Z. marina* plant traits and porewater chemistry i.e. NO_x were the most important controllers of CH_4 dynamics. In contrast to CH_4, there is no clear effect of *Z. marina* plant traits on N_2O fluxes, which instead seems influenced by light and porewater NH_4^+ availability for nitrification-denitrification processes.

Both sites only display relatively small exchanges of CH_4 and N_2O, consistent with other sandy, coastal settings (Murray et al., 2015; Oreska et al., 2020; Al-Haj et al., 2022). Indeed, sediments from both sites have low organic content, with only slightly more elevated OC concentrations in the root-zone of *Z. marina* (upper 10 cm) likely derived from OC of *Z. marina* root and detritus origin (Holmer et al., 2001a; Schorn et al., 2022). The concentration profiles of ^{210}Pb reveal mixing and likely negligible net sedimentation in either site (Arias-Ortiz et al., 2018; Johannessen, 2023). Our combined results of OC sequestration and GHG emissions thus show that seagrasses meadows in temperate sandy sediments may yield limited climate benefits.

4.1 CH_4 flux dynamics in *Z. marina* and sandy sediment

CH_4 exchange is the net outcome of methanogenesis and methanotrophy within the sediment and in this study is dominated by net methanogenesis. Our results suggest a positive effect of *Z. marina* belowground biomass on CH_4 release. As methanogenesis is the last step of C degradation, the substrate utilized are simple organic compounds (Canfield et al., 2005b). Belowground biomass i.e. living roots and detritus may act as labile OC substrate for CH_4 production inducing emissions of CH_4 (Middelboe et al., 1998; Ziegler and Benner, 1999; Holmer et al., 2001b; Hall et al., 2025). Besides the positive relationship between belowground biomass and CH_4 exchanges, we also observed higher porewater DOC inventories and sediment OC concentrations in the upper sediment of *Z. marina* compared to Sand. As our study was carried out across seasons, it includes conditions with increased belowground biomass or DOC inventories expected to promote CH_4 production, but with simultaneously low net CH_4 release from the sediment as for example in April and June 2023. This indicates highly dynamic processes of CH_4 production-oxidation influenced by other chemical, oxidizing solutes within the sediment, e.g. NO_x (see

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below), reflected as an inverse relationship between DOC and CH_4 production as seen in the best fitted linear model for CH_4 exchange. The root and rhizome structures of *Z. marina* may also drive CH_4 emissions by translocating CH_4 from deep sediments to the surrounding water column via root aerenchyma which allows for internal gas transport as described in other wetland plants (Kristensen et al., 2022; Ge et al., 2024; Maatta et al., 2024). The positive effect of *Z. marina* i.e. belowground biomass, on CH_4 emissions is a trend observed before, however the dynamics of CH_4 in the vicinity of *Z. marina* are variable and should be further examined. For example, Asplund et al. (2022) found no difference in CH_4 release between *Z. marina* meadows and unvegetated sandy Baltic sediments. However, they did not include seasonal measurements as in the present study, potentially neglecting periods with significant differences. More like our findings, other studies have found the presence of *Z. marina* (Oreska et al., 2020) as well as inter-species traits like plant size to increase CH_4 production (Bijak et al., 2024).

The inverse relationship between CH_4 exchange and NO_x porewater inventories aligns with previous findings indicating that high redox inhibits CH_4 formation and release, due to inhibition of methanogenesis and oxidation by NO_x and other oxidizing agents (Bollag and Czlonkowski, 1973; Balderston and Payne, 1976; Welte et al., 2016; Mao et al., 2022). However, the negative relationship between NO_x and water temperature indicates that the dynamics between CH_4 emission and NO_x may be caused by an overall seasonal control on both variables. A reason for NO_x accumulation in spring is likely high availability of O_2 for nitrification when the overall sediment metabolism is low and limits coupled denitrification in the cold environment (Canfield et al., 2005a). Similar net generation of NO_3^- in the sediment during early spring have been observed previously in Danish estuaries (Jørgensen and Sørensen, 1985). Indeed, temperature positively influences methanogenesis (Yvon-Durocher et al., 2014), as also observed in the best fitted model with temperature as a non-significant control, indicating that temperature may drive CH_4 exchanges, while other controllers are more important during periods of high temperatures.

4.2 N_2O flux dynamics in *Z. marina* and sandy sediment

The N_2O uptake by *Z. marina* observed in this study is within the range of reported values (Al-Haj et al., 2022). The non-significant effect of *Z. marina* plant traits on N_2O exchange is opposite to previously observed increases of N_2O release in the presence of *Z. marina* (Oreska et al., 2020) and emphasizes the variable dynamics and controls of N_2O exchange and pathways. N_2O is an intermediate and transient compound that is produced and consumed by several processes of the N cycle. Many of these processes are affected differently by environmental factors i.e. temperature, substrate availability and O_2 levels (Canfield et al., 2005a), complicating the identification of key drivers of N_2O exchange in estuarine communities. This complexity is also reflected in this study where only few variables showed a significant relationship with N_2O exchange.

Interestingly, we found a significant positive correlation of N_2O fluxes with light conditions. Light conditions sustain a higher availability of photosynthetically produced O_2 e.g. from radial O_2 loss of *Z. marina* roots (Jovanovic et al., 2015) which will increase nitrification and thus the generation of N_2O as an intermediate (Canfield et al., 2005a). In support of this, He et al. (2024) confirmed that nitrification is important for N_2O production in seagrass sediments. In addition, N_2O formation by photochemodenitrification has been identified, where sunlight induces NO_2^- reduction and N_2O production

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(Leon-Palmero et al., 2025). Leon-Palmero et al. (2025) observed that N_2O produced by this process exceeds N_2O produced by microbial nitrification. Furthermore, the positive relationship between the NH_4^+ inventory and N_2O exchange may point to the importance of NH_4^+ availability as a substrate for nitrification (Canfield et al., 2005a).

The negative relationship between the AVS inventory and N_2O exchange may indicate that reduced conditions within the sediment change the net N_2O metabolism from a net release to a net uptake i.e. by allowing substantial denitrification or dissimilatory nitrate reduction to ammonium which include a N_2O consuming step (Chapuis-Lardy et al., 2007; Foster and Fulweiler, 2016). Elevated AVS inventories also indicate high sulfate reduction (King et al., 1985) which inhibit other processes such as nitrification (Joye and Hollibaugh, 1995).

4.3 The role of *Z. marina* for climate mitigation

The distribution of excess ^{210}Pb, with relatively low concentrations, only present in the upper 5 cm of the sediment and with no decreasing trend with depth, together with the sandy nature of the sediment, indicates intense mixing of the sediment and precludes the quantification of the sedimentation rates, which would be very low in any case (Arias-Ortiz et al., 2018; Johannessen, 2023). Dalby Bay is shallow and exposed to wave energy and erosion, as reflected by the negligible contents of silt and clay. Furthermore, a low *Z. marina* aboveground:belowground biomass ratio of 0.3 in the growth season indicates that plant structures in exposed hydrodynamic environments need good anchoring and efficient nutrient uptake in the low organic sediments (Hemminga, 1998; Peralta et al., 2006). Sediment depth profiles of low OC support that neither the *Z. marina* nor Sand site are significantly accumulating OC, and a sediment C:N ratio around 8, compared to a *Z. marina* biomass C:N ratio of 44, indicate that the OC present is not autochthonous (Canfield et al., 2005a). Instead, the profiles of OC in *Z. marina* sediment illustrate a pattern of depletion with depth in the root zone, reaching the background concentrations beneath. Accordingly, sediment OC_{25cm} stocks from both sites were small with no significant effect of *Z. marina* presence. Leiva-Dueñas et al. (2023) estimated an average OC_{25cm} sediment stock in several Danish *Z. marina* meadows of 1.2 ± 0.2 kg OC m^{-2}, which is comparable to our estimates. The majority of their studied *Z. marina* meadows also had limited excess ^{210}Pb pointing, in accordance with our findings, to the limited OC sequestration potential of *Z. marina* meadows. Such limited OC accumulation has the implication that even low CH_4 and N_2O releases may significantly counteract any climate mitigation by *Z. marina* meadows. The estimated annual emissions of GHGs from *Z. marina* sediments in Dalby Bay of 79 ± 34 kg CO_2 eq. ha^{-1} accounts for 2–36 % of the short-term OC accumulation rates observed in other Danish *Z. marina* meadows (220-4.900 kg CO_2 eq. ha^{-1} y^{-1}; Leiva-Dueñas et al. (2023)).

The seasonal pattern of CH_4 exchanges and generally variable exchanges of N_2O in *Z. marina* meadows supports a strong temporal dynamic of GHGs. Seasonal changes in *Z. marina* biomass i.e. belowground living biomass due to natural diebacks and regrowth also complicate any GHG and OC sink assessments. Thus, climate mitigation assessments must acknowledge and include seasonal changes. Furthermore, limited data and bias towards environments with high OC burial rates inflate earlier global averages of OC burial in seagrasses with up to 75%, thus highlighting the site dependency of climate benefits from seagrass meadows (Arias-Ortiz et al., 2026). In contrast to the widely reported role of seagrass as an important

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blue carbon ecosystem in the literature, *Z. marina* meadows in Dalby Bay apparently have opposite effects with limited sediment OC storage and net emissions of GHGs. The role of *Z. marina* ecosystems for climate mitigation may indeed be complicated. On one side, *Z. marina* plant traits have positive impact on CH_4 emissions, while on the other side, we document a small overall N_2O uptake with no effect of *Z. marina* and plant traits. Anyway, there is no clear climate benefit of *Z. marina* in Dalby Bay, questioning the role of seagrass meadows as an important blue carbon ecosystem in organic-poor, sandy sediments.

5 Conclusions

GHG exchange was generally low at both *Z. marina* and Sand throughout the study period. There was an overall net emission of CH_4 and both uptake and release of N_2O. Sedimentation rates in the *Z. marina* meadow are low as indicated by limited excess ^{210}Pb and low contents of silt, clay and OC. As hypothesized, exchanges of CH_4 were positively associated with *Z. marina* belowground biomass indicating that plant structures provide substrate for CH_4 formation. Another factor affecting CH_4 fluxes is the oxidizing effect of porewater NO_x illustrating the importance of redox conditions for CH_4 dynamics. Thus, our hypothesis that *Z. marina* plant traits and porewater chemistry to a large extent control CH_4 dynamics appears to be valid. In contrast to our hypothesis, there was no net release of N_2O in the *Z. marina* meadow and porewater chemistry only explains a small fraction of the variance in N_2O exchange. Nonetheless, N_2O fluxes from *Z. marina* ecosystems in the Baltic Sea are linked to several N pathways not documented before. As hypothesized, *Z. marina* meadows in shallow, sandy sediments are not sites of OC accumulation or sequestration and even modest GHG emissions are sufficient to offset any climate mitigation.

Code and data availability

Research data and code used in this article will be made available upon request.

Supplement link

Supplement material is provided.

Author contributions

GF contributed with conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, original draft preparation, writing, reviewing and editing. ML contributed with conceptualization, formal analysis, investigation, methodology, validation, visualization, original draft preparation, writing, reviewing and editing. AR contributed with formal analysis, methodology, validation, visualization, writing, reviewing and editing. PM contributed with formal analysis, methodology, validation, visualization, writing, reviewing and editing. EK contributed with conceptualization, formal

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analysis, investigation, methodology, validation, visualization, original draft preparation, writing, reviewing and editing. CQ contributed with conceptualization, funding acquisition, data curation, formal analysis, investigation, methodology, supervision, validation, visualization, original draft preparation, writing, reviewing and editing.

Competing interest

The authors declare that they have no conflict of interest.

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