Estuaries and Coasts (2026) 49:29
https://doi.org/10.1007/s12237-025-01639-5

Brackish Water Rewetting of a Temperate Coastal Peatland: Effects on Biogeochemistry, Microorganisms and Greenhouse Gas Emissions

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Received: 13 December 2024 / Revised: 28 October 2025 / Accepted: 3 November 2025

Abstract

Around 4% of global greenhouse gas (GHG) emissions originate from drained peatlands. Unlike rewetting drained peatlands with freshwater, brackish water rewetting is expected to reduce CO_2 emissions, while keeping post-rewetting methane (CH_4) emissions low. Sulfate-containing brackish water should favor sulfate reduction and therefore limit CH_4 production and/or lead to increased CH_4 consumption. Here, we compared CO_2 and CH_4 fluxes, pore water geochemistry, and associated microbial communities of a coastal peatland along a transect one year before and after rewetting (Fig. 1) to evaluate the effect of brackish water rewetting. Brackish water rewetting increased the abundance of both CH_4 producing archaea (methanogens) as well as sulfate reducing bacteria (SRB) in most sub-sites along the transect. At the same time, the aerobic methanotroph community was overall less present after rewetting. Pore water CH_4 and CO_2 concentrations along with $\delta^{13}C$ records indicated that both methanogenesis and CH_4 oxidation increased post-rewetting. Although brackish water rewetting raised average net CH_4 emissions from 2 to 25 mg CH_4 m^{-2} d^{-1} at previously drained locations, these fluxes were lower than CH_4 emissions reported from most freshwater peatlands. Net CO_2 emissions remained high with levels around 4 g CO_2 m^{-2} d^{-1}, but ecosystem respiration strongly decreased from on average 19 to 6 g CO_2 m^{-2} d^{-1}. The remaining net CO_2 emissions were likely associated with a lower uptake of CO_2 compared to its release after extensive vegetation die-back. Hence, the re-establishment of site-specific vegetation is important to sustain the net CO_2 uptake besides low CH_4 emissions.

Keywords Greenhouse gas emissions · Methanogens · Methanotrophs · Sulfate reducing bacteria · GHG concentrations · Stable carbon isotopes

Communicated by Wen-Chen Chou.

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Published online: 12 December 2025

Introduction

Peatland drainage leads to large carbon dioxide (CO_2) emissions (Beetz et al., 2013; Hatala et al., 2012; Joosten, 2010). Therefore, conservation of intact and rewetting of degraded peatlands is necessary to mitigate greenhouse gas (GHG) emissions (Waddington & Price, 2000). Raising the water table to rewet drained peatlands reduces CO_2 emissions (Cui et al., 2017) and may even create a CO_2 sink (Tiemeyer et al., 2020). Freshwater rewetting, however, often induces high emissions of methane (CH_4) (Abdalla et al., 2016; Hahn et al., 2015; Joosten & Couwenberg, 2009; Wichtmann et al., 2010), potentially counteracting the reduction of CO_2 emissions on decadal timescales. While drainage reduces microbial CH_4 production (methanogenesis) and promotes microbial CH_4 consumption (oxidation) through aeration (Serrano-Silva et al., 2014), freshwater rewetting often leads to increased methanogenesis after the establishment of methanogenic microbial communities under anoxic conditions (e.g., Conrad, 2009; Nazaries et al., 2013; Wagner, 2017).

Rewetting can positively influence the structural diversity of peatland microorganisms, potentially supporting the recovery of near-natural functional and taxonomic diversity (Emsens et al., 2020; Kitson & Bell, 2020). However, a recent meta-analysis suggests that rewetted peatlands often diverge significantly from near-natural ones regarding plant community composition, biodiversity, geochemistry, and hydrology. On average, these differences are likely to persist for many years (Kreyling et al., 2021). The recovery of methane-cycling microorganisms following rewetting yet remains inconsistent across studies. Juottonen et al. (2012) observed lower CH_4 emissions, slightly reduced methanogenic community abundances, and greater heterogeneity in rewetted boreal peatlands compared to natural sites, even after 10–12 years. Methanotrophic communities in this study, however, showed no significant difference between restored and natural sites. In contrast, Wen et al. (2018) reported a rapid recovery of methanogens (CH_4 producing archaea), whose abundance exceeded aerobic methanotrophs (CH_4 oxidizing bacteria) by two orders of magnitude, suggesting that anoxic conditions from prolonged inundation may have disrupted methanotrophic niches.

Re-establishment of vegetation is another critical factor influencing microbial community development in rewetted peatlands. Bare peat tends to support only oligotrophic bacterial communities (Elliott et al., 2015), whereas pioneer plant colonization is essential for achieving higher microbial diversity (Yan et al., 2008). The composition of the archaeal community in the rhizosphere appears to be specific to the plant species and the substrate present (Andersen et al., 2013; Cadillo-Quiroz et al., 2010). Subsurface methanogenic archaeal diversity is strongly dependent on the peatland type, being greater in nutrient-rich fens than in nutrient-poor bogs (Andersen et al., 2013; Merilä et al., 2006; Yavitt et al., 2012). Plant diversity drives subsurface microbial communities, with plants supplying carbon substrates via root exudates that fuel microbial metabolic processes (Yarwood, 2018).

In natural nutrient-poor, acidic bogs, symbiotic relationships between peat mosses (Sphagnum species) and methanotrophic bacteria highlight the intricate interplay between vegetation and microbial communities. Methanotrophs utilize CH_4 from the anaerobic degradation of submerged mosses and, in turn, provide CO_2 for photosynthesis (Kip et al., 2010; Raghoebarsing et al., 2005). Given the strong influence of vegetation and soil chemistry on microbial communities, recovery after rewetting is not immediate. Kitson and Bell (2020) suggest a lag time of approximately three years before significant microbial community adjustments and potential recovery become apparent.

The presence of thermodynamically more favorable alternative electron acceptors such as nitrate, ferric iron (Fe^{3+}), manganese (Mn^{4+}) or sulfate (Froelich et al., 1979), as well as redox-active organic matter providing electron accepting capacities (Gao et al., 2019), can lower CH_4 emissions either due to the partial suppression of methanogenesis (Achtnich et al., 1995; Blodau, 2011; Dettling et al., 2006) and/or due to increased CH_4 oxidation (Segarra et al., 2013, 2015; Smemo & Yavitt, 2011). Only upon depletion of these terminal electron acceptors, CH_4 is formed (Achtnich et al., 1995; Blodau, 2011). For example, deposition of high sulfate loads was reported to lower CH_4 emissions from wet peatlands (Gauci et al., 2002; 2004), because methanogens were outcompeted by sulfate reducing bacteria (SRB) (e.g. Dean et al., 2018; van Dijk et al., 2019; Oremland, 1988). The interaction of methanogenesis and dissimilatory sulfate reduction has been described mainly in detail for brackish-marine ecosystems by, e.g., Barnes and Goldberg (1979), Boetius et al. (2000), Jørgensen and Kasten (2006) and Jørgensen (2021), but also for peatlands (e.g. Pester et al., 2012).

Coastal peatlands are positioned in the transition zone between land and sea and are still poorly understood considering their GHG production and emission potentials. Based on an overlay of the Global Peatland Database (UNEP, 2022) data with a 5 m above sea level elevation constraint within a buffer of 10 km distance to the coast, coastal peatlands cover an area of approx. 178.000 km^2 (Tegetmeyer, pers. comm.). This is well in line with Whittle and Gallego-Sala (2016), who estimated global coastal peatlands to cover an area of approximately 145.000 km^2. This considerable area will gain increasing relevance due to climate change induced sea-level rise and consequential increase

of salt-water influx into coastal peatlands (Jurasinski et al., 2018; Waller & Kirby, 2021). The demand and importance of climate protection measures will increase and rewetting of peatlands is a very promising nature-based solution to reduce GHG emissions in the short-term with the potential to create carbon sinks in the mid- to long-term (Tanneberger et al., 2021). The rewetting of low-lying coastal peatlands with sulfate-containing brackish water could mitigate CH_4 emissions that would otherwise be potentially high after rewetting of these systems with freshwater (Jurasinski et al., 2018; Pönisch & Breznikar et al., 2023; Yang et al.,2023; Whittle & Gallego-Sala, 2016). Therefore, understanding the microbial and biochemical drivers of GHG production and emissions is essential to exploit the potential of peatland rewetting as a climate mitigation measure. Studies combining microbiological analyses and GHG fluxes are to date mostly related to freshwater (rewetted) peatlands (Basiliko et al., 2013; Juottonen et al., 2012; Juottonen et al., 2021; Rey-Sanchez et al., 2019; Unger et al., 2021; Urbanová et al., 2011; Wen et al., 2018), but studies on coastal peatlands being rewetted or influenced by brackish water are still scarce (Gutekunst et al., 2022; Pönisch & Breznikar et al., 2023; Wang et al., 2020; Weil et al., 2020). In particular there is a lack of in-situ studies in peatlands that allow for a direct comparison of pre- and post-rewetting conditions.

Here, we studied the shift to a brackish water regime initiated by rewetting of a formerly drained temperate coastal peatland and its implication for the climate change mitigation potential of coastal peatland rewetting. To understand the underlying drivers of CH_4 and CO_2 fluxes, we analyzed the peat and pore water geochemistry, as well as the microbial community structure. We expected that brackish water rewetting increases both the abundances of SRB and of methanogenic microorganisms due to newly established anoxic conditions, while aerobic methanotrophs would likely decrease in the soil. However, a competition of methanogens with SRB could negatively impact the abundance of methanogens in the long run. We hypothesized that the potential for CH_4 production would remain low while the potential for not only aerobic but also anaerobic CH_4 oxidation would increase, resulting in lower total CH_4 emissions compared to freshwater rewetted peatlands. Further, we expected CO_2 emissions to decrease after rewetting due to the reduction of peat mineralization.

Materials and Methods

Study Area

The study area is a coastal fen (peatland mainly fed by minerotrophic water), representing large parts of the former polder Drammendorf, on the island of Rügen in the North-Eastern part of Germany (Fig. 2). The area was separated from the sea and drained in the late 1970 s and has since been used as grassland predominantly under freshwater impact. The peat thickness varies largely across the peatland and reaches up to 70 cm of strongly decomposed peat near our sampling site (Brisch, 2015). Although the peat is highly decomposed and intermitted mineral sediment deposits were observed, we call the peaty soil "peat" from here onwards. For a detailed description of the study site, see Pönisch and Breznikar et al. (2023). Prior to rewetting, the site was used extensively for livestock grazing and mowing for fodder production. Vegetation was dominated by common grassland species such as *Agrostis stolonifera*, *Lolium perenne*,

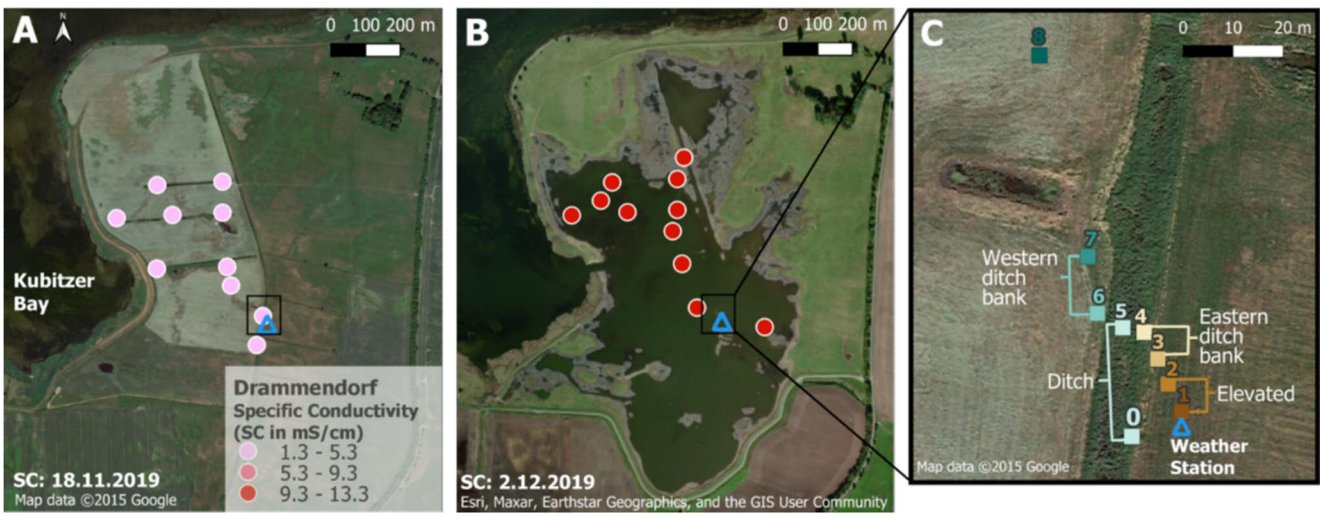


Fig. 2 Study site 'Drammendorf' with surface water specific conductivities (SC) (**A**) before (ditches) and (**B**) after brackish water rewetting. **C**) Study design with transect of 8 sampling stations. Please note that the beginning of the transect is depicted by the position of the weather station (blue triangle) in all map images. Station 8 belongs to the *Western ditch bank*, but was only measured before rewetting

Festuca rubra and *Phalaris arundinacea*, and *Phragmites australis* and *Elymus spec.* close to and within the ditches (Brisch, 2015).

Rewetting took place on 26th November 2019 through opening the dike that had separated the peatland from the adjacent bay "Kubitzer Bodden", which is part of a brackish lagoon system connected to the Baltic Sea. As a consequence, the area was nearly completely flooded and now resembles a shallow lagoon with highly fluctuating water levels, which adjust to the water level of Kubitzer Bodden (see Fig. S1, Supplementary information file and Pönisch & Breznikar et al., 2023). Since the southern Baltic Sea coast has very small tidal heights of less than 10 cm (Medvedev et al., 2016), the water levels at the study site are mainly driven by winds. The exchange with the bay is intense, especially when the water level changes frequently with high amplitude (for details, see Pönisch & Breznikar et al., 2023). As a consequence, the water retention time in the peatland is expected to be short. No significant differences in salinity and temperature were found between surface and bottom waters in the peatland over the course of the year, suggesting a pronounced vertical mixing (Pönisch & Breznikar et al., 2023). After rewetting with brackish water, most grassland and even ditch vegetation died, except at a few places at the banks of the now inundated former drainage ditches (Fig. S1).

Study Design and Field Installations

Measurements were taken along a water level gradient towards and across the main North-South oriented ditch, including four stations on the Eastern side of the ditch (1–4), two ditch stations (0, 5) and two stations (6, 7) on the Western side of the ditch. Station 8 was chosen as an additional station farther towards the adjacent bay on the Western side, but was only accessible before rewetting. For data analysis, sampling stations with comparable elevations and distances to the ditch were aggregated to form location groups (see also Sect. 3.3). In the following, stations 1 and 2, which frequently fall dry during low water levels, are referred to as the "*Elevated"* location. Stations 3 and 4 are combined to the "*Eastern ditch bank*", stations 0 and 5 are always wet and reflect the "*Ditch*", and stations 6, 7 and 8 are referred to as "*Western ditch bank*". Further, stations 1–4, 6 and 7, thus the *Elevated* location together with the *Eastern* and *Western ditch bank*, form the previously drained "former terrestrial locations" as opposed to station 0 and 5 (the *Ditch*).

A weather station (DALOS535-WA, F&C GmbH, Gülzow, Germany) was installed to permanently record continuous data on air temperature and relative humidity (sensor: HMP45, Vaisala, Helsinki, Finland), soil temperatures (5 cm below the ground, sensor: MCP9700A), photosynthetic photon flux density (PPFD, sensor: Type 5.3 and 6.3, Indium Sensor GmbH, Neuenhagen, Germany) next to the boardwalk in hourly intervals. The weather station was completely replaced in June 2020. The new station (HOBO 4-Channel analog-data logger, type UX120-006 M, Onset, Bourne, USA) recorded air temperature and relative humidity (sensor: U23-001/HOBO Pro v2 Temp/RH, Voltcraft; type: DET4R, Onset, Bourne, USA), water temperature 20 cm aboveground and soil temperatures in 5 cm depth (MCP9700A), as well as PPFD (quantum sensor: Type 5.3 and 6.3, Indium Sensor GmbH, Neuenhagen, Germany) in 15-minute intervals. Due to late installation/technical failure, some weather station data (air and soil temperature, PPFD) were not recorded continuously. The gaps cover approximately two weeks before and a total of six weeks (two weeks in June and four weeks in November/December 2020) after rewetting. To fit these periods, we used weather data from a close-by station operated by the German weather service (DWD, Putbus, WMO-ID 10093) and transferred data based on a linear regression model derived from the DWD station data and our data from the times when our station was running (dataset: $n = 8770$; R^2 fit for air temperature: 0.96; soil temperature: 0.84 and PPFD: 0.82). Additionally, we measured water levels continuously at five stations (1, 2, 3, 6 and 7), using water level loggers (Solinst, Barologger Gold and Levelogger Junior, Model 3001, Georgetown, Canada) in 2 m deep wells (DN050, 1 m DIN 4925, plus 1 m SW 0.2 mm, inner diameter: Ø 52 mm, PVC, Lotze Wassertechnik, Düdinghausen, Germany). Belowground logger depths (varied across stations from 97 to 160 cm) were determined by subtracting the height of the well heads above the surface from the wire lengths, where the loggers were attached. Water levels in the ditch and the dike opening were derived from 15-minute resolution pressure transducer loggers (Dipper-PTEC, SEBA Hydrometrie, Kaufbeuren, Germany) installed in observation wells with filter screens aboveground to capture changes in surface water levels.

Field Work

We conducted field work once a month on two consecutive days between June and November 2019 before rewetting and from June until December 2020 after rewetting. This field work included measurements of greenhouse gas (GHG) exchange, vegetation height and in-situ surface water variables as well as surface water sampling for lab analyses. In addition, we sampled peat soil for pore water CH_4 and CO_2 concentrations and stable carbon isotopes as well as microbial absolute abundance analysis in June/July as well as in November 2019 before rewetting and in August 2020 after rewetting. Sampling for soil characterization prior to

brackish water rewetting took place on August, 22th 2019. Additionally, we took cores for pre-rewetting pore water ion analysis in June/July. In order to assure the depiction of all stations including those that might have been too dry in summer (e.g., the *Elevated* location), we repeated pore water sampling in November pre-rewetting. For an overview of the various soil coring campaigns relevant for this study, see Table 1 below.

Surface Water Sampling

The set of variables measured in-situ included aboveground water level, pH, specific conductivity (mS cm^{-1}), temperature (°C) and oxygen (mg L^{-1}) concentrations. Before rewetting, these variables were measured using a ProDSS instrument (YSI, Ohio, USA) at stations 0 and 5 in the North-South running main ditch (Fig. 2). Surface water samples for concentration measurements of major ions, nutrients and dissolved carbon (DIC and DOC) were collected and filtered (pore size: 0.45 µm, polyethersulfone membrane material, Sarstedt, Nürmbrecht, Germany) in the field and stored at −20 °C upon arrival in the lab until further analysis. Before rewetting, this was done at the two stations (0, 5) within the *Ditch*. After brackish water rewetting, surface water variables could be obtained from the standing water column across all stations. However, water samples were only taken at both *Ditch* (0, 5) stations and one station on the *Eastern* (3) and one at the *Western ditch bank* (7), additionally, but at the same time intervals as the in-situ measurements. Additional specific conductivity (SC) measurements of surface water (~25 cm depth) across larger areas of the peatland (Fig. 2) were taken before (November 18th, 2019) and immediately after brackish water rewetting (December 2nd, 2019) using a handheld multiparameter probe (smarTROLL, In-Situ Inc, Fort Collins, Colorado, USA).

GHG Measurements

Fluxes of CH_4 and CO_2 were derived from manual closed chamber (Livingston & Hutchinson, 1995) measurements with portable laser-based analyzers (Picarro G4301, GasScouter, Santa Clara, USA; LI-820, LI-COR Biosciences, Lincoln, USA; Ultraportable Greenhouse Gas Analyzer (UGGA), Los Gatos Research Inc., Mountain View, USA) (see Pönisch and Breznikar et al. (2023) for details). In the drained stage, we measured GHG exchange at terrestrial locations (*Elevated*, *Eastern* and *Western ditch bank*) with standing transparent and opaque chambers (area = 3381 cm^2; height adjustable, approx. 100–150 cm) on a total of six measurement collars. For each measurement, a chamber was attached to a collar which was permanently installed and inserted into the ground at each station one month before measurements started. Since the net ecosystem exchange is highly dependent on solar radiation (Helfter et al., 2015), we conducted additional measurements with transparent chambers and shading cloths that reduced radiation (measured as PPFD) by 55% and 77%, respectively. Therefore, we measured up to four times per sampling day on the permanently installed measurement collars, which correspond to our above-mentioned stations. At *Ditch* stations, and under inundated conditions established after brackish water rewetting, GHG fluxes were repeatedly measured (three times per station and sampling day) with opaque floating chambers (area = 452.4 cm^2; height 22 cm). The *Elevated* location (stations 1 and 2) and partly the *Eastern ditch bank* (station 3) could still be measured with standing (transparent and opaque) chambers during low water level conditions. However, we thus could only conduct transparent chamber measurements on half of the transect after rewetting. Closure time of the standing chambers ranged between 3 and 5 min and 4–5 min for the floating chambers. Parallel to each flux measurement, we determined PPFD (sensor type 5.3 and 6.3, Indium Sensor GmbH, Neuenhagen, Germany), soil temperature in 5 cm soil depth (insertion thermometer; range: −20–250 °C; Typ: NTC; contact measurement), vegetation height, chamber air temperature and relative air humidity (digital thermometer with range: −40–70 °C, TFA Dostmann GmbH & Co, Wertheim, Germany). Vegetation height could only be measured occasionally after rewetting due to high water levels and intense plant die-back.

Table 1 Soil coring overview

Determined variables	Date	Coring device	Number of cores	Stations	Core depth
Physical and chemical site characterization	August 2019	Narrow (Ø 5 cm) PVC liners	Pre: 5	1, 2, 3, 6, 7	100 cm
Microbial abundances, GHG concentrations and stable isotopic composition	June/July/November 2019 and August 2020	Russian type peat corer	Pre: 15; Post: 14	Pre: 1, 2, 3, 4, 4, 4, 4, 5, 5, 6, 6, 7, 7, 8, 8 Post: 1, 1, 2, 2, 3, 3, 4, 4, 5, 5, 6, 6, 7, 7	50 cm
Solute chemistry of pore water	June/July/November 2019	Large (Ø 10 cm) and narrow (Ø 5 cm) PVC liners	Pre: 11	1, 2, 3, 4, 4, 5, 5, 6, 6, 7, 8	60–100 cm

Soil Coring

We took soil cores before and after rewetting. Before rewetting, five 1 m soil cores were taken once along the transect (stations 1, 2, 3, 6 and 7) for initial site characterization. The cores were taken in narrow plastic liners using a jackhammer system (BH 55, Wacker Neuson Produktion GmbH & Co. KG, Munich, Germany) and stored at −20 °C until further analysis.

Different soil cores for microbial, dissolved gas concentrations and isotopic analysis were taken using a Russian type peat corer (De Vleeschouwer et al., 2010) pre- and post-rewetting, respectively. We took two cores per sampling station, which resulted in four to six cores per location group. Each core was divided into three depth sections: 5–20, 20–40 and 40–50 cm. Subsamples for dissolved gas and stable carbon isotope analyses were taken with tip-cut syringes with a distinct volume of 3 ml (Omnifix, Braun, Bad Arolsen, Germany) and immediately placed into vials filled with saturated NaCl solution (20 ml, Agilent Technologies, 5182−0837, Santa Clara, USA) leaving no headspace and closed gas-tight using rubber stoppers and metal crimpers (both: diameter 20 mm, Glasgerätebau Ochs, Bovenden, Germany). Likewise, additional soil samples from each sampling station and core depth section were taken for analysis of water content and soil porosity using 1 ml tip-cut syringes (Omnifix, Braun, Bad Arolsen, Germany), which were covered with parafilm® (Bemis, Neenah, WI, USA) and stored at 4 °C. For microbial analysis, the subsamples from the core were completed by additional grab samples of the surface soil (0–5 cm). The soil was taken from the inner part of the core/shovel and collected into centrifugation tubes (15 ml, Falcon®, Corning Inc, Tewksbury, MA, USA) using sterile equipment, and was immediately cooled on ice. We stored these samples at −20 °C until further analyses.

Additional cores were taken to derive pore water samples for the analysis of pH, specific conductivity (SC), sulfate and chloride concentrations in June and July pre-rewetting. These cores were taken using large plastic liners (length: 60 cm; inner diameter: 10 cm), and pore water was extracted with Rhizon® suction samplers (0.12 µm pore size, Rhizosphere Research Products, Wageningen, The Netherlands; Seeberg-Elverfeldt et al., 2005), which were inserted into pre-drilled holes in the liner and attached to 10 ml syringes. A hand-held pH-meter (Handylab pH11, Schott Instruments GmbH, Mainz, Germany) and a refractometer (Master-S, Atago, Tokio, Japan) were used to measure pore water pH and SC.

Samples for dissolved total sulfide were preserved immediately after sampling with 5% Zn-acetate and were later measured according to the methylene blue method (Cline, 1969) using a spectrophotometer (SPECORD 40, Analytik Jena GmbH, Jena, Germany). We sampled at least one station per location group in summer 2019 before rewetting, except at the *Elevated* location, where it was too dry. Pore water measurements at all locations, including the *Ditch*, were repeated in November 2019 before rewetting, but coring was done in narrower PVC liners (length: 100 cm; inner diameter: 5 cm, Stitz GmbH, Gehrden, Germany), which were placed into a metal pipe and attached to a jackhammer (BH 55, Wacker Neuson Produktion GmbH & Co. KG, Munich, Germany).

Lab Work

Major Elements and Nutrients

Frozen soil samples from pre-rewetting site characterization cores were used to determine the concentrations of total carbon, nitrogen and sulfur (CNS) and for total element analysis (phosphorus (P), iron (Fe), calcium (Ca), aluminum (Al), and manganese (Mn)). Before thawing, each core was divided into 10 subsections of 10 cm length: 0–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90 and 90–100 cm. We dried the samples at 105 °C for at least 24 h, then ground them with a ball mill (Pulverisette 7, Fritsch, Idar-Oberstein, Germany) and measured CNS using a Vario Pyro cube (Elementar Analysensysteme GmbH, Langenselbold, Germany). Solute elemental analysis was done with an ICP-OES spectrometer (Optima 8300 DV, PerkinElmer LAS GmbH, Germany) after acid extraction using HCl-HNO_3 solution (Aqua Regia) in a microwave (Mars Xpress, CEM, Kamp-Lintford, Germany).

Furthermore, peat samples as well as collected surface water samples were analyzed for concentrations of inorganic N-species (nitrate, nitrite, ammonium), and ortho-phosphate (P) as well as dissolved organic (DOC) and inorganic carbon (DIC) in the lab. While filtered surface water samples were used directly, soil samples were extracted using 25 ml 1 M KCl solution. Both sample types were then measured with a continuous-flow analyzer (CFA, standards: 0.05 to 2.0 mg L^{-1}, minimum detectable concentration (MDC): 0.02 mg L^{-1}; AA3, Seal Analytical, Norderstedt, Germany) to investigate the availability of nutrients. For DOC/DIC analysis the samples were measured using a Dimatoc (Dimatec, Essen, Germany) and Multi N/C 2100 S (Analytic Jena, Germany, MDC: inorganic carbon (IC): 900 µg L^{-1}; total carbon (TC): 1.5 g L^{-1}). Both instruments were calibrated for DIC using standards between 1 and 500 mg L^{-1} C and for total carbon using 2.0 to 1000 mg L^{-1} C standards.

Surface and pore water samples (extracted directly using Rhizon® suction samplers from cores in plastic liners) were additionally measured for dissolved major and trace

elements, P, silicium (Si), and S (considered to essentially consist of sulfate (SO_4) by means of inductively coupled plasma optical emission spectrometry (ICP-OES) using an ICP-iCap 7400 Duo ICP Spectrometer (Thermofisher Scientific, Dreieich, Germany) following the protocol applied by Ehlert von Ahn et al. (2021; 2023). In this communication, only dissolved sulfate and sodium (Na) are reported. Chloride (Cl) concentrations were calculated from measured Na concentrations assuming seawater stoichiometry using PHREEQC (Parkhurst & Appelo, 2013). Other studies (see, e.g. Ehlert von Ahn et al., 2023) used a similar approach (back)-checking the calculated ion balances with anion and cation pairs such as [Na+K] versus [Cl], which were in accordance with the calculated concentrations.

Pore Water GHG Concentrations and Stable Isotopes

Pore water samples were analyzed for GHG mole fractions (CO_2, CH_4) using a gas chromatograph (GC; flame ionization detector (FID) for CH_4 and a thermal conductivity detector (TCD) for CO_2 mole fractions, Agilent Technologies 7890 A, Santa Clara, USA). Before sampling the NaCl-filled vials, a headspace was created (3 ml) using helium, and samples were left for equilibration for at least 24 h at room temperature (approx. 20 °C). For measurements of the gas mole fractions, we extracted 300 µl of the headspace volume and inserted 250 µl into the GC. Following the method described in Gutekunst et al. (2022), the measured mole fractions in ppm were converted into gas concentrations in µM, using Eq. 1:

$$c\left(CO_2/CH_4\right) = \left(\frac{G * H}{T * R * V * P}\right) * 1000 \quad (1)$$

with c the dissolved CO_2/H_2CO_3 (CO_2 from now on for simplification) and CH_4 concentrations (µM), G the headspace gas mole fraction (ppm), H the headspace volume (3 ml), T the absolute temperature (295.15 K), R the universal gas constant (0.0821 L*atm*K^{-1}*mol^{-1}), V the peat volume (3 ml), and P the peat porosity (ml cm^{-3}).

The isotopic analysis followed Gutekunst et al. (2022): After the diluted headspace samples were acidified with 2 M HCl to pH < 4.5, cavity ring-down spectroscopy (CRDS) and the small sample isotope module (SSIM; connected to a Picarro Instruments G 2201-i, Sunnyvale, USA) were used to measure $\delta^{13}C$ in CH_4 and in total inorganic carbon ($CO_2/H_2CO_3 + HCO_3^- + CO_3^{2-}$ = DIC). Hydrogen sulfide was fixed as solid ZnS by adding saturated Zn-acetate solution (1 ml, Zn-acetate dihydrate, >98%; Sigma Aldrich, Taufkirchen, Germany) to avoid spectral interference in CRDS. The required injection volume of 15–20 ml of gas, while only having a headspace maximum of 5 ml, made further dilution necessary and resulted in minimum detectable headspace CH_4 mole fraction of 10 ppm due to the necessary dilution. We calibrated $\delta^{13}C$ in CH_4 and CO_2 using a working standard of 1000 ppm CH_4 (−42.5‰), four certified standards of 2500 ppm CH_4 (−38.3, −54.5, −66.5, −69.0‰), 1000 ppm CO_2 (−31.1‰) and dilutions of pure CO_2 (ID="MN12">−27.1 and −4.6‰). We used certified standards from Air Gas (Air Liquide, Plumsteadville, PA, USA) or from Isometric Instruments (GASCo, Victoria, BC, Canada). Non-certified gas standards were calibrated against reference materials from the IAEA (RM8562) with an elemental analyzer (EA 3000, Eurovector, Redavalle, Italy) coupled to an isotope ratio gas mass spectrometer (Horizon, NU Instruments, Wrexham, UK). The stable isotope results were presented in the δ-notation.

Soil porosity ϕ was estimated following DIN19683-14(2007) by determining the oven-dried weight, the bulk density (ρ_b = dry weight/volume) and the soil organic matter (SOM = carbon content (%) multiplied by 2), according to Eq. 2:

$$\phi = 1 - \frac{\rho_b * 100}{\rho_{s-org} * SOM + \rho_{s-min} * (100 - SOM)} \quad (2)$$

with the particle density of the organic material ρs-org = 1.40 g/cm³, and that of the mineral soil particles ρs-min = 2.65 g/cm³.

Microbial Abundances

We extracted DNA from the biological replicates using the GeneMATRIX Soil DNA Purification Kit (Roboklon, Berlin, Germany) and quantified DNA concentrations with a Qubit 2.0 Fluorometer (ThermoFisher Scientific, Darmstadt, Germany). We used up to 250 mg of just thawed soil material and followed the protocol provided by the manufacturers of the soil extraction kit as well as of the DNA High Sensitivity and Broad Range Assay Kit (dsDNA HS and BR Assay, ThermoFisher, Berlin, Germany). Quantitative PCR (qPCR, CFX Connect Real-Time PCR Detection System, Bio-Rad, München, Germany) was used to quantify the abundances of the target genes 16 S rRNA for bacteria (primer: Eub341-F/Eub534-R; Muyzer et al., 1993), methyl coenzyme M reductase α-subunit (*mcrA*) for methanogens (primer: mlas-F/mcrA-R; Steinberg & Regan, 2009), particulate methane monooxygenase (*pmoA*) for aerobic methanotrophs (primer: pmoA189-F/pmoA661-R; Kolb et al., 2003) and dissimilatory sulfate reductase β-subunit (*dsrB*) for sulfate reducing bacteria (primer: DsrB2060-F/DsrB4-R; Geets et al., 2006; Wagner et al., 1998). There are some limitations to this approach.

No further group specific methanotrophic primers e.g. for methanotrophs that oxidize atmospheric CH_4 and Verrucomicrobia were used, assuming that these groups are of minor relevance in the studied peatland. Moreover, targeting for the functional gene *pmoA* does not cover anaerobic methanotrophs. In turn, anaerobic methanotrophic archaea might be accounted for in the abundances of *mcrA* counts, because of their close relatedness. In addition, no archaea other than methanogens were targeted for this study, as 16 S rRNA only covers total bacteria. For the qPCR program, we mixed 10 µl of double-strand binding dye SYBR Green (KAPA universal), 0.08 µl of forward and backward primer (concentrations of 100 µM) with 4 µl template per reaction and added sterile water to get a total final volume of 20 µl. After initial denaturation at 95 °C for 3 min, 35 (16 S rRNA) to 40 qPCR cycles (*mcrA*, *pmoA* and *dsrB*) followed, including denaturation at 95 °C for 3 s, annealing for 20 s, elongation at 72 °C for 30 s and a plate read at 80 °C for 3 s to create the melting curve. Annealing temperature was 60 °C for 16 S rRNA gene, *mcrA*, and *pmoA* and 62 °C for *dsrB*. Absolute abundances of gene copy numbers were estimated using a dilution series of known standard gene copy numbers. We multiplied all absolute gene copy numbers (copies μl^{-1}) by the final DNA extraction elution volume (50, 60–100 µl), the dilution factor (mostly 10 or 100, rarely 1) and divided them by the initial fresh weight of the individual soil sample. In order to normalize the different soil water content values, a dry weight factor was determined (wet weight/dry weight) and multiplied by gene copy numbers to determine the gene copy numbers per g dry soil.

Data Analysis

Data Visualization

We used several functions and packages from the statistical software R (R Core Team, 2021) to analyze and visualize our results. To investigate the effect of brackish water rewetting on the surface water composition, we created boxplots comparing the situation before and after rewetting and used the Mann-Whitney-U-Test to determine significant differences. We created depth profiles showing the abundances of soil microbial groups and GHG concentrations in the pore water in different depths using the packages ggplot2 (Wickham, 2016) and ggpubr (Kassambara, 2020). In addition, we used the function *metaMDS()* of R package vegan (Oksanen et al., 2020) to construct a non-metric multi-dimensional scaling (NMDS) plot using the standard distance measure (Bray-Curtis) and default arguments in order to display the biogeochemical pre-rewetting state.

GHG Flux Estimation

We estimated GHG fluxes based on median-based regression as implemented in the *fluxx()* function of the R package *flux* (Jurasinski et al., 2014). The slopes between subsequent CH_4/CO_2 concentration values were calculated during the chamber closure time of 3–5 min (180–300 data points) and subsequently, the median of all slope values was used to estimate the flux (Siegel, 1982). Fluxes with non-linear slopes or fluxes that visually indicated ebullition-dominated linear slopes were excluded from further analysis. If possible, ebullition-based data points (e.g. in the beginning of the measurements) were excluded and when the general linear increase of concentrations started, the diffusive flux was estimated without these outlier data points. Before flux estimation all concentration values were transformed to masses *m* using Eq. 3:

$$m = \frac{Mpc}{RT} \tag{3}$$

where M is the molar mass of CO_2 (44 g mol^{-1}) or CH_4 (16 g mol^{-1}), p the total air pressure (101300 Pa), c the concentration of the respective gas species, R the universal gas constant (8.314 m^3 Pa K^{-1} mol^{-1}) and T the temperature (K) in the chamber headspace at the point in time when the concentrations were measured. Please note that air pressure inside the chamber was assumed not to differ from outside air pressure. GHG fluxes *f* (mg m^{-2} h^{-1}) were then derived using Eq. 4:

$$f = \frac{V}{A} \cdot \frac{\partial m}{\partial t} \tag{4}$$

where V is the chamber volume (m^3), A the surface area of the measurement collar (m^2) and $\partial m/\partial t$ the change of mass over time. Due to the relatively large effective height of our chambers, a saturation effect occurring during the chamber deployment time is not to be expected.

Modelling Greenhouse Gas Exchange

Although some correlations between CH_4 emissions and temperatures were found, they are highly season-dependent (Bartlett et al., 1987; Schrier-Uijl et al., 2008) and correlations between instantaneous CH_4 fluxes and the water level measurements are generally poor (Koch et al., 2014; Schrier-Uijl et al., 2008). Therefore, we did not use functional relationships to determine the CH_4 balances. Time periods under consideration ranged from June to November (pre-rewetting) and from June to December (post-rewetting) with 72 measurement dates covering the drainage phase and

111 measurement dates covering the period after rewetting (see Fig. S3 in Supplementary information for non-modeled CH_4 fluxes). Seasonally aggregated CH_4 emissions for each station were derived using linear interpolation implemented in the *auc.mc()* function of the *flux* package (Jurasinski et al., 2014): This function employs a jackknife approach to repeatedly integrate the fluxes linearly over the covered time period, each time excluding one measurement. From the resulting distribution of CH_4 flux estimates for the covered time periods for each sampling location, we calculated the mean (as the best estimate) and the standard deviation (as an error estimate accounting for temporal variation in sampling and the potential absence of extreme fluxes during regular sampling). These best estimates were averaged across the measurement stations per location to derive the reported seasonal efflux values. The associated standard errors were determined using the propagated standard deviations of the best estimates, following the law of error propagation. This procedure yields a more robust estimate of the seasonal CH_4 budgets, in particular under the occurrence of single emission peaks.

CO_2 fluxes are typically well correlated with environmental variables such as temperature and solar radiation (Davidson & Janssens, 2006; Helfter et al., 2015). Since transparent chamber measurements could not be conducted at approximately half the stations after rewetting (see Sect. 2.2.2 and Fig. S2), we modeled the missing net ecosystem CO_2 exchange (NEE) using a multiple linear regression model of NEE in dependence of the ecosystem respiration (R_{ECO}) and photosynthetically active radiation (PAR, expressed by the measured PPFD). The underlying idea is that $NEE = {}_{RECO} + GPP$ (gross primary production, i.e. photosynthesis) and that GPP is mainly determined by the received PAR in a specific ecosystem at a specific time of the year. We developed this approach following eddy covariance studies that have to use NEE to model RECO (e.g. Lasslop et al., 2010; Mitra et al., 2024). In that way changing shares of photosynthesis were considered and reached an R^2 of 0.7 for the multiple linear regression. We used this relationship to estimate NEE fluxes for all available R_{ECO} measurements in order to have a complete dataset of both R_{ECO} and NEE for each sampling day and station. The modeled post-rewetting NEE fluxes ($n = 220$) were then combined with the measured post-rewetting NEE fluxes ($n = 141$) and the measured post-rewetting R_{ECO} fluxes ($n = 232$). Together with a total of 412 pre-rewetting measured data points (NEE: $n = 236$, R_{ECO}: $n = 176$) this provided the base data for the model selection and later gap filling with continuous environmental variables.

Artificial neural networks (ANN, package *neuralnet* (Fritsch et al., 2019) were used to derive a continuous dataset of NEE and R_{ECO} fluxes for each sampling period (season) before and after rewetting, following in general the approach of Huth et al. (2021). Due to marked differences between terrestrial and ditch stations, and the pronounced shift caused by rewetting, we set up a model for the terrestrial pre- and inundated post-rewetting R_{ECO} and NEE, respectively. However, for the *Ditch*, only one R_{ECO} model was set up without differentiation between pre- and post-rewetting. This resulted in a total of five ANNs: "pre-rewetting NEE", "post-rewetting NEE", "pre-rewetting R_{ECO}", "post-rewetting R_{ECO}", and "Ditch R_{ECO}" (see Tab. S2 for details). The CO_2 flux data of each subgroup were used to build models with the influencing variables air and soil temperature, photosynthetic photon flux density (PPFD), vegetation height, water level aboveground and effective temperature index (ETI), which were measured parallel to each GHG measurement. Final models were constructed by a forward selection approach that subsequently added variables to the input layer. The maximum R^2 fit between measured and modeled data was used as a selection criterion of overall model fit and performance.

For the gap filling, each ANN was trained with a randomly selected subset comprising 80% of the data. The remaining 20% of the flux data were used to validate the performance of the model. Continuously measured variables (see Sect. 2.1.1 above) were used to fill the gaps between measurement times for each model and thus to predict hourly NEE and R_{ECO} for the CO_2 fluxes over the measured time period for each location group individually. Seasonal NEE and R_{ECO} balances were calculated based on the average of 100 runs with randomly varying training and test sets per location group and model (Huth et al., 2021). Sums of seasonal CH_4, NEE and R_{ECO} from all runs were depicted in boxplots. We normalized the values to daily averages for each location group to ensure better comparability, because the periods have slightly varying lengths. The given standard deviations for CH_4, NEE and R_{ECO} reflect the uncertainty ranges of the modelling in addition to the spatial and temporal variation of the flux data. Significant differences between pre- and post-rewetting GHG emissions were determined by the Mann-Whitney-U-Test to account for the non-normal distribution of the values.

Results

Aboveground Environmental Variables

The rewetting caused drastic changes in water levels, the presence and coverage of vascular plants, the availability of organic material, and in the nutrient and major ion concentrations in the *Ditch* (Figs. 3 and 4). The water level at all stations increased clearly and is shown according to both,

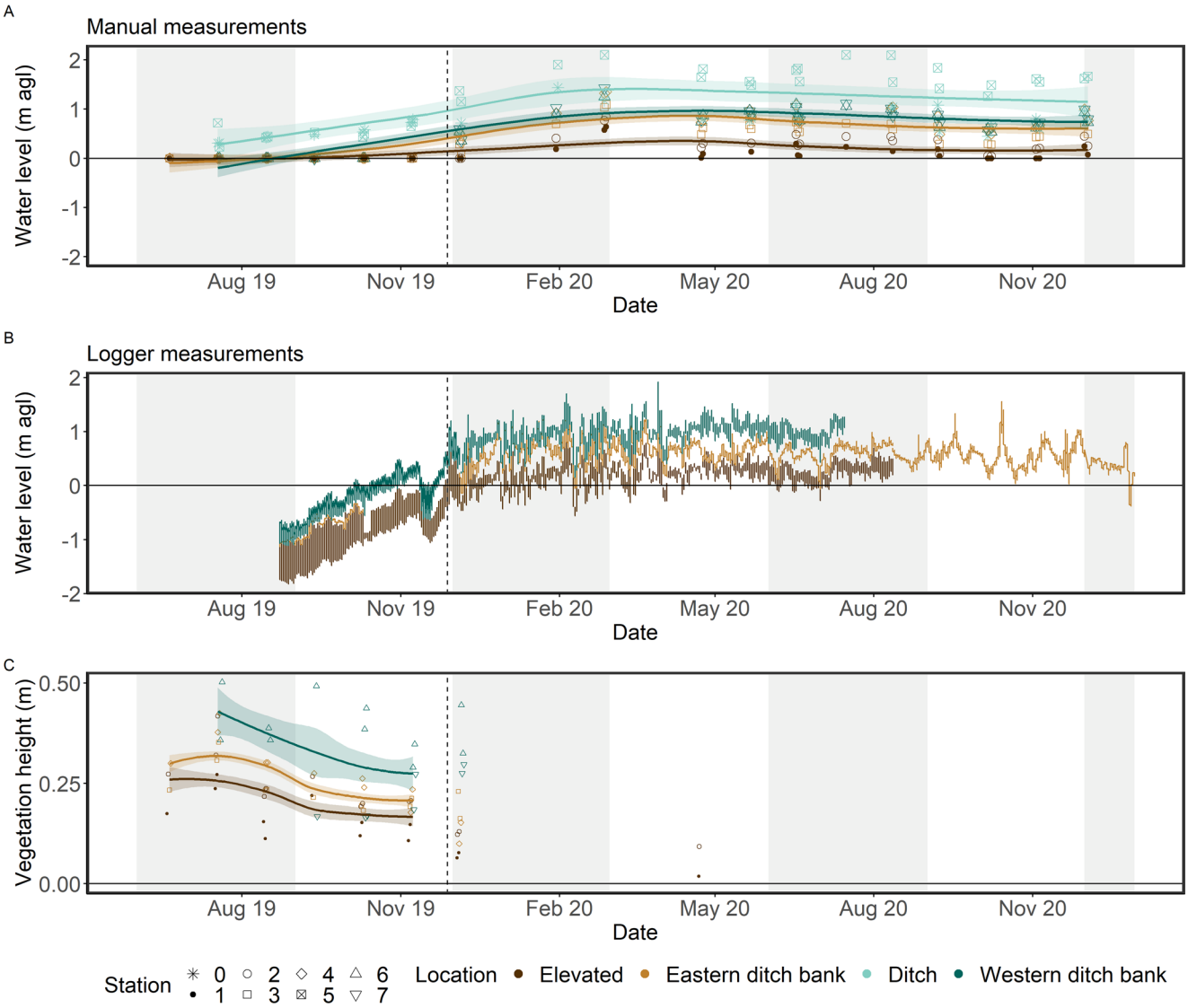


Fig. 3 Time series of surface water levels (meters aboveground level (m agl)) and vegetation height (meters (m)) during the investigation period. Manual water level measurements (**A**) were conducted at all stations along the transect including the deep *Ditch* stations (0–7) and were merged according to our study design: Stations 1 and 2 form location "*Elevated*" ($n=63$), stations 3 and 4 are "*Eastern ditch bank*" ($n=63$), stations 6 and 7 are "*Western ditch bank*" ($n=52$) and stations 0 and 5 are the "*Ditch*" ($n=61$). Automated water level measurements (**B**) are displayed per location. Note that these were only recorded at stations 1, 2, 3, 6 and 7. Please also note that water level was not measured continuously in the *Ditch*, which explains the depicted difference in water level ranges between manual and logger measurements. Vegetation height was measured manually mainly before rewetting at all former terrestrial stations (*Elevated*: $n=26$, *Eastern ditch bank*: $n=24$, *Western ditch bank*: $n=18$). The dashed line represents the rewetting event and the shaded areas indicate the four different seasons of the year (spring: 1 st March–31st May; summer: 1st June–31st August; autumn: 1 st September–30th November; winter: 1 st December–28th February)

water level loggers and manual measurements (Fig. 3A and B). In detail, average water levels measured by permanently installed loggers changed from −0.85 to 0.23 m (*Elevated*), −0.75 to 0.54 m (*Eastern ditch bank*) and from −0.24 to 0.96 m (*Western ditch bank*) during the vegetation period of the respective year. Note that negative values indicate water levels belowground, while positive values indicate water levels aboveground. After rewetting, water levels exhibited high temporal variability and closely followed the water levels at the dike opening and thus the adjacent bay (Fig. S4). The rapid increase in water levels after rewetting caused an extensive vegetation die-back (Fig. 3C and Fig. S1 in the Supplementary information, for visual impression). We did not observe new vegetation growth at our sampling locations in the first year post-rewetting. Before rewetting, the vegetation was tallest on the *Western ditch bank* and shortest at the *Elevated* location (Fig. 3C). Data from the *Ditch* stations allowed for a direct comparison between pre- and

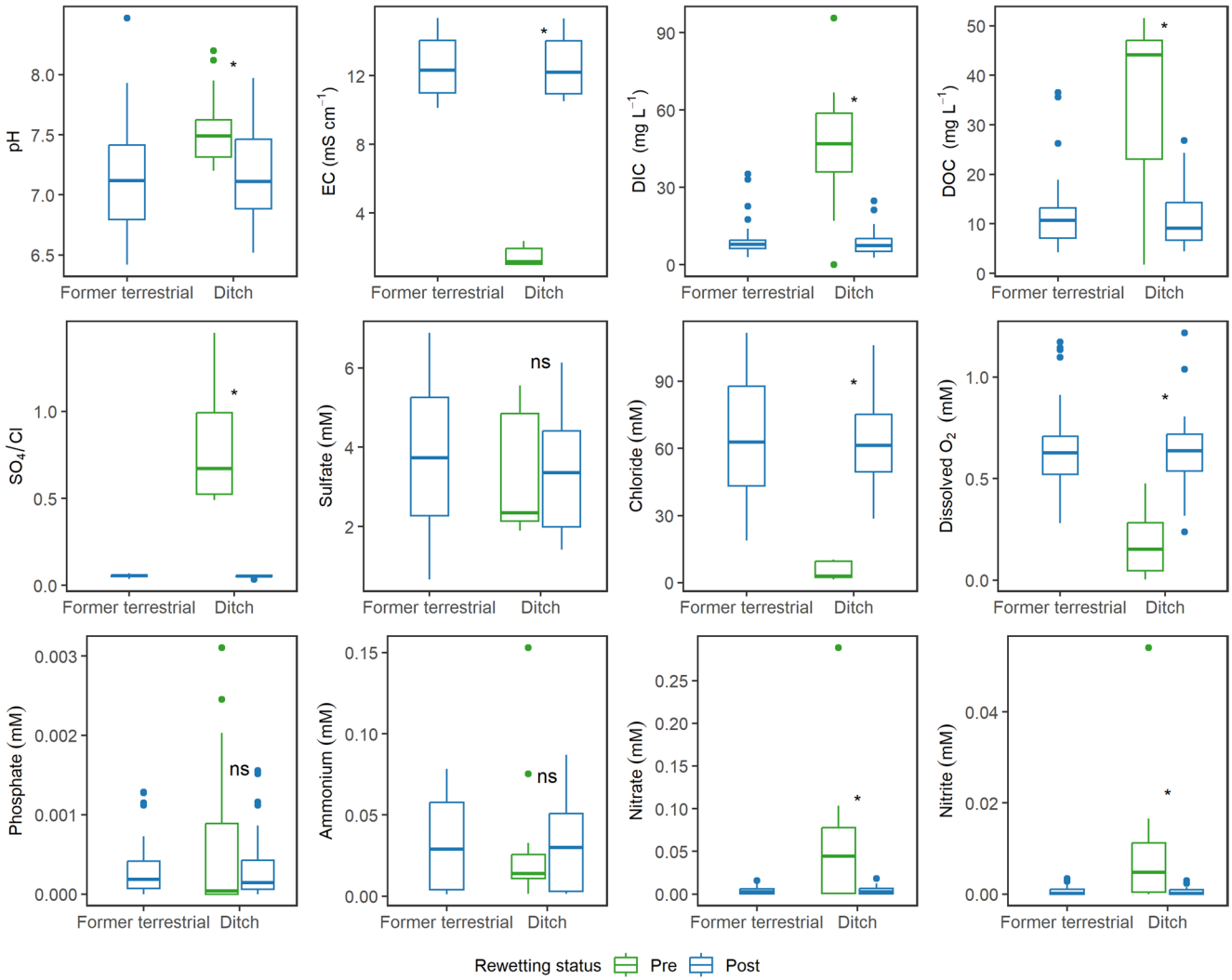


Fig. 4 Surface water solutes of formerly terrestrial (*Elevated*, *Eastern* and *Western ditch bank*) and *Ditch* locations after the rewetting with brackish water (blue, $n = 56–103$). Pre-rewetting data (green, $n = 16–20$) are derived from *Ditch* stations only. Significant differences ($p < 0.05$) between pre- and post-rewetting were determined using Mann-Whitney-U-Test and are indicated by asterisk '*', while no significant differences are shown by the abbreviation 'ns'

post-rewetting conditions (Fig. 4): Brackish water rewetting increased the *Ditch's* specific conductivity (SC) substantially from 1.4 ± 0.5 to 12.6 ± 1.6 mS cm^{-1} as well as chloride concentrations from 5.2 ± 3.8 to 64.8 ± 21.9 mM, but not sulfate concentrations (3.3 ± 1.5 and 3.5 ± 1.4 mM, pre- and post-rewetting, respectively).

In parallel, SO_4/Cl ratios decreased from 0.8 to 0.05, suggesting the shift from a sulfate-rich low-salinity composition to a stoichiometry common for brackish-water. After rewetting, most surface water solutes such as inorganic N- and P, dissolved organic matter, and sulfate and chloride concentrations did not vary substantially among the sampled locations, regardless of whether the stations were dry before rewetting or situated within the *Ditch* (Fig. 4). Thus, rewetting caused horizontal homogeneity along the transect through a strong lateral exchange in the water column.

Greenhouse Gases

Rewetting by inundation with brackish water led to a significant increase of CH_4 emissions at all former terrestrial locations, but no significant change in the *Ditch* (Fig. 5A). Further, while net CO_2 release (NEE) partly increased or remained high at locations that were dry before (Fig. 5B), R_{ECO} decreased at all locations (Fig. 5C). Before rewetting, the seasonally averaged CH_4 balance (Fig. 5A) was highest within the *Ditch* (40.2 ± 12.6 mg m^{-2} d^{-1}) whilst the *Elevated* location acted as a slight CH_4 sink (−0.19 ± 0.4 mg m^{-2} d^{-1}) and CH_4 emissions at the *Western ditch bank* were basically zero (0.04 ± 0.04 mg m^{-2} d^{-1}). The *Eastern ditch bank* showed pre-rewetting mean CH_4 emissions around 6.2 ± 9.5 mg m^{-2} d^{-1}. Brackish water rewetting elevated

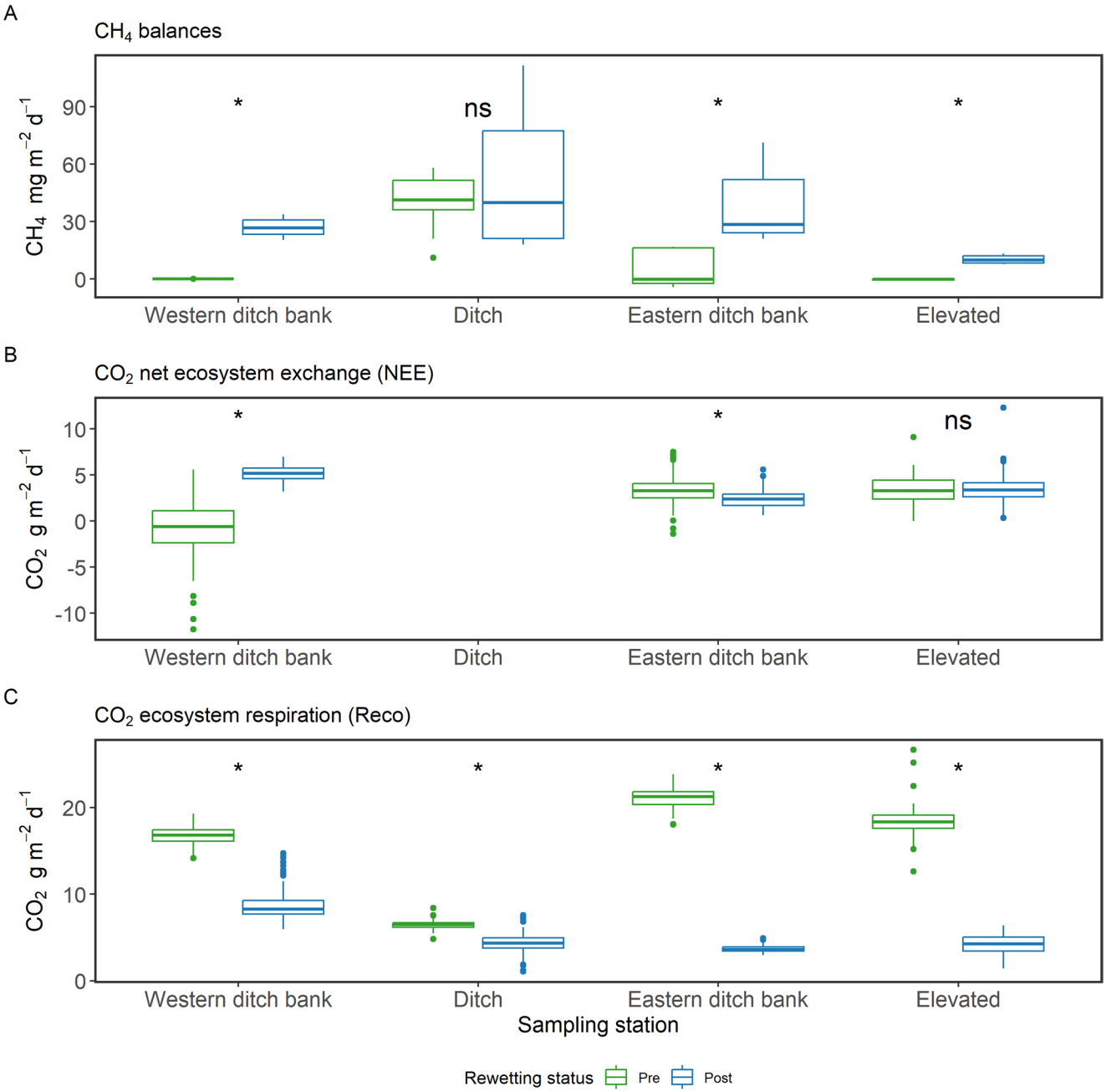


Fig. 5 Boxplots showing CH_4 (**A**) and CO_2 (NEE (**B**) and R_{ECO} (**C**)) balances normalized to daily values of the location groups from before (green) and after rewetting (blue). GHG balances were derived from flux measurements (see also Fig. S3 in Supplementary information) taken in summer and autumn of the respective year pre- and post-rewetting (CH_4: pre: 20th June–8th November 2019 (142 days), post: 18th June–3rd December 2020 (169 days); CO_2: pre: 19th June–26th November 2019 (161 days), post: 19th June–4th December 2020 (169 days)). CH_4 emissions were derived from summed interpolated measured CH_4 fluxes (pre: $n=72$; post: $n=111$). NEE ($n=300$, pre and post, respectively) and R_{ECO} ($n=400$) values are summed and gap-filled CO_2 fluxes over time using artificial neural networks (ANN). All GHG balances were modeled for the period covered and then normalized to daily values for better comparison. Significant differences ($p<0.05$) between pre- and post-rewetting GHG emissions were determined using Mann-Whitney-U-Test and are indicated by asterisk '*', while no significant differences are shown by the abbreviation 'ns'

CH_4 emissions across the area, whilst the relative differences along the elevation gradient were pertained. Accordingly, lowest CH_4 fluxes occurred at the *Elevated* location (10.3 ± 2.0 mg m^{-2} d^{-1}), moderate CH_4 flux levels at the *Western* (27.0 ± 4.1 mg m^{-2} d^{-1}) and *Eastern ditch bank* (38.1 ± 15.2 mg m^{-2} d^{-1}) and highest CH_4 emissions at the *Ditch* location (50.4 ± 30.3 mg m^{-2} d^{-1}). Although CH_4 emissions increased significantly

at former terrestrial locations, CH_4 emissions were still lower than *Ditch* CH_4 emissions pre- and post-rewetting. Brackish water rewetting did not increase the magnitude of *Ditch* CH_4 emissions, but caused an increased flux variability mainly due to strong differences post-rewetting between the two *Ditch* stations. Seasonal net CO_2 release (NEE, Fig. 5B) under drainage was overall higher at the *Elevated* location and the *Eastern ditch bank* (3.4 ± 1.6 and 3.3 ± 1.5 g m^{-2} d^{-1}, respectively) and lower at the *Western ditch bank* (-0.87 ± 3.3 g m^{-2} d^{-1}). After rewetting, NEE remained constant at the *Elevated* location, decreased down to a mean of 2.4 ± 1.0 g m^{-2} d^{-1} at the *Eastern ditch bank* and increased strongly at the *Western ditch bank* (5.2 ± 0.8 g m^{-2} d^{-1}) during the investigated period. Because we did not measure GHG fluxes in the *Ditch* with transparent chambers, we cannot determine *Ditch* NEE. Under drainage, R_{ECO} was highest at the *Eastern ditch bank* (21.1 ± 1.2 g m^{-2} d^{-1}), slightly lower at the *Elevated* location (18.5 ± 1.7 g m^{-2} d^{-1}) and the *Western ditch bank* (16.8 ± 1.0 g m^{-2} d^{-1}) and lowest at the *Ditch* location (6.5 ± 0.5 g m^{-2} d^{-1}). Brackish water rewetting decreased R_{ECO} throughout all former terrestrial locations with fluxes below 9 g m^{-2} d^{-1}. While R_{ECO} halved at the *Western ditch bank*, it decreased much more at the *Elevated* location and the *Eastern ditch bank* (4.2 ± 1.2 and 3.7 ± 0.4 g m^{-2} d^{-1}). In parallel, *Ditch* R_{ECO} decreased slightly to 4.3 ± 1.1 g m^{-2} d^{-1}.

Pre-rewetting Characteristics of Soil and Pore Water

Soil characteristics pre-rewetting were relatively similar at the five sampled stations, showing overlapping parts (Fig. 6A). While the surface layers were most similar in their physio-chemical characteristics, the variation increased with increasing depths. In addition, nitrate concentrations were higher in upper peat layers of most stations, while phosphate, ammonium and total dissolved sulfur increased in deeper layers of station 2, 3, 6 and 7 (Fig. 6A). Pore water characteristics (Fig. 6B) clustered much more compared to soil variables (Fig. 6A), splitting the stations in almost distinct groups. Among higher sulfate values, there are overlaps between station 7 and 8, which are also geographically close to one another. Other overlaps occur around higher SC values among stations 1, 3 and 6. Station 2 seems to have high sulfate/chloride ratios and the *Ditch* station 5 seems to be very different regarding its ion concentrations, showing higher chloride concentrations.

Based on the geographical locations and supported by the results of the NMDS ordinations in Fig. 6 (especially B), the original measurement stations were aggregated to form four location groups (see also Sect. 2.1.1): *Elevated* (stations 1 and 2), *Eastern ditch bank* (stations 3 and 4), *Ditch* (station 5 and, where available, station 0) and *Western ditch bank* (stations 6, 7, and 8, where available). Pre-rewetting sulfate concentrations were highest at the *Western ditch bank* (mean across all depth layers: 10.9 mM, data not shown)

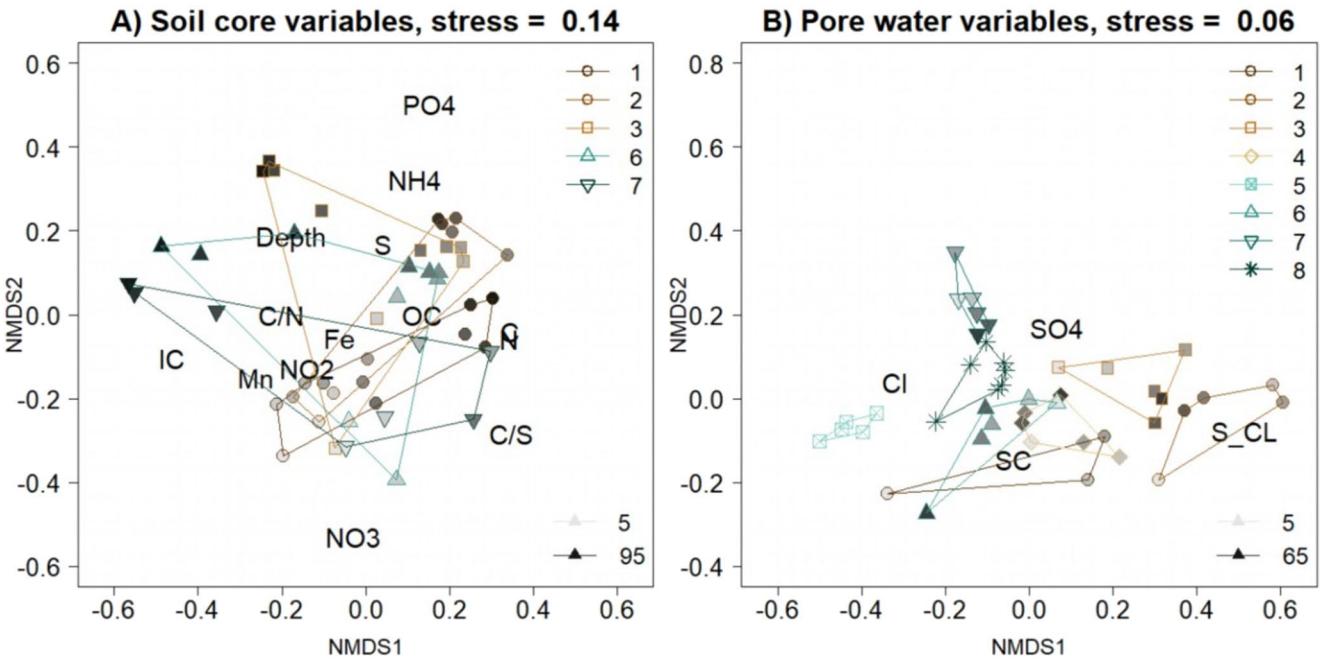


Fig. 6 NMDS ordination showing peat soil variables from the pre-rewetted state using two different sampling methods: (**A**) soil cores ($n=47$) and (**B**) pore water ($n=44$). Symbols and outline colors (see Fig. 2) represent the sampling stations, while symbol fills indicate the core depth (cm) by different shades

and lowest in the *Ditch* (2.55 mM). The *Elevated* location and *Eastern ditch bank* sulfate concentrations were 4.20 mM and 5.74 mM, respectively. In contrast, chloride concentrations were highest in the *Ditch* (9.40 mM) and lowest at the *Elevated* location (0.31 mM). Chloride concentrations at the *Eastern* and *Western ditch bank* were 1.67 mM and 4.58 mM, respectively. Accordingly, pore water SO_4/Cl ratios differed along the measured sampling locations and were highest at the *Elevated* location (20.62) and *Eastern ditch bank* (9.64), moderate at the *Western ditch bank* (2.55) and lowest in the *Ditch* (0.31).

Pore Water CH_4 and CO_2 Concentrations

The average pore water CH_4 concentrations before rewetting were highest in the *Ditch* (107.2 ± 98.2 µM, mean ± standard deviation) and lowest at the *Elevated* location (1.0 ± 1.9 µM). We observed similarly low CH_4 concentrations at the *Eastern* (16.5 ± 44.8 µM) and *Western ditch bank* (3.2 ± 9.8 µM). After rewetting, pore water CH_4 concentrations increased on average at all locations, but to a different degree across location groups: *Elevated*: 29.5 ± 22.4 µM, *Eastern ditch bank*: 82.4 ± 62.6 µM, *Ditch*: 337.1 ± 120.2 µM, and *Western ditch bank*: 96.2 ± 51.7 µM. CH_4 concentrations increased mainly in the upper 10 cm at the former terrestrial locations (*Elevated*, *Eastern* and *Western ditch bank*), whereas CH_4 concentrations in the *Ditch* increased at around 30 cm depth (Fig. 7A).

Pre-rewetting pore water CO_2 concentrations were highest at the *Western* (2.7 ± 1.8) and *Eastern ditch bank* (1.3 ± 0.8 mM) and lower within the *Ditch* (0.6 ± 0.1 mM) and the *Elevated* location (0.4 ± 0.1 mM). After rewetting, CO_2 concentrations increased at all former terrestrial locations and averaged between 3.4 ± 2.0 mM (*Elevated*) and 5.1 ± 2.1 mM (*Eastern ditch bank*). Note, that CO_2 concentrations (Fig. 7B) increased most strongly at the surface of the *Elevated* location and (only at station 2) around 45 cm post-rewetting, while at the *Eastern* and *Western ditch bank*, CO_2 concentrations increased mostly at around 30 cm and less strongly at the surface and at the bottom of the core. In contrast, CO_2 concentrations in the *Ditch* remained low as before the rewetting.

Pre-rewetting δ^{13}C-CH_4 usually showed values below −60‰, but at station 2, among the *Elevated* location, there was one sample with a maximum value of −29.7‰. Post-rewetting δ^{13}C-CH_4 values from the *Elevated* location were more depleted and averaged −79.7 ± 8.2‰. Mean δ^{13}C-CH_4 values also decreased at the *Eastern ditch bank* (from −68.6 ± 10.7‰ to −72.6 ± 7.0‰) but increased in the *Ditch* (from −65.7 ± 1.2‰ to −61.7 ± 1.1‰) as well as at the *Western ditch bank* (from −84.6 ± 19.0‰ to −73.2 ± 3.5‰) post-rewetting. The higher depletion of δ^{13}C-CH_4 post-rewetting at the *Eastern ditch bank* mainly occurred in peat layers below 20 cm depth, whereas δ^{13}C-CH_4 values increased in layers between 0 and 10 cm depth (Fig. 7C).

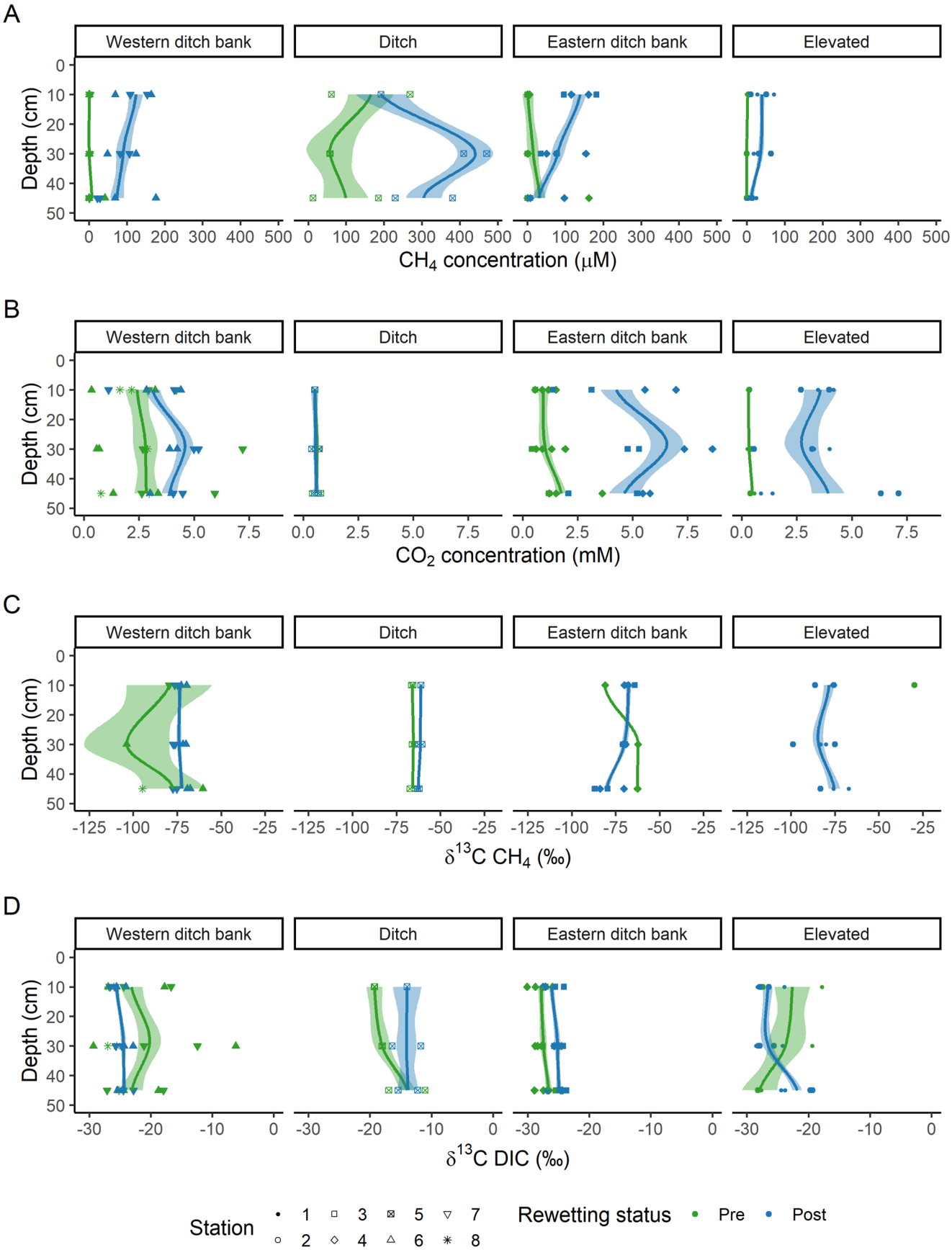
Fig. 7 Depth profiles of greenhouse gas (**A**: CH_4 and **B**: CO_2) concentrations and δ^{13}C-CH_4 (**C**) and δ^{13}C-DIC (**D**) before (pre: green, n = 14–45) and after (post: blue, n = 40–41) rewetting with brackish water. Data were derived from soil plugs taken from peat cores at stations along the sampled transect. Symbols show specific stations, which were aggregated into location groups (*Elevated*, *Eastern ditch bank*, *Ditch* and *Western ditch bank*). Trend lines were estimated using a LOESS curve (nonparametric weighted regression) with a span of 0.9 and serve visual guidance. Shaded areas show confidence intervals according to standard errors and were set to 50% in all plots

Pre-rewetting mean δ^{13}C-DIC values were highest at the *Ditch* location (−17.1 ± 3.1‰) and *Western ditch bank* (−22.1 ± 6.1‰), followed by the *Elevated* location (−24.8 ± 4.8‰) and the *Eastern ditch bank* (−27.3 ± 1.6‰). After rewetting, δ^{13}C-DIC increased at *Eastern ditch bank* (−25.4 ± 1.3‰) and in the *Ditch* (−14.0 ± 2.0‰), whereas δ^{13}C-DIC slightly decreased at the *Western ditch bank* (−24.8 ± 1.2‰). At the *Elevated* location, post-rewetting average δ^{13}C-DIC remained constant (−25.0 ± 3.1‰), but the depth profile showed a depletion of ^{13}C in DIC in the upper soil layers and an enrichment below 40 cm depth (Fig. 7D).

Microbial Abundances

Before rewetting, total bacterial abundances (16 S rRNA) were relatively uniform along depth sections and among sampling locations except for the *Ditch* (Fig. 8A). Here, total bacterial abundance decreased from the surface samples down to 30 cm depth and increased again from 30 to 50 cm depth. After rewetting, 16 S rRNA gene copy number had decreased slightly in the upper depth sections of both *ditch banks*, remained constant at the *Elevated* location, and decreased, on average, over one order of magnitude (from mean $6.1 \times 10^{10} \pm 7.03 \times 10^{10}$ to $5.8 \times 10^{9} \pm 6.1 \times 10^{9}$ copies g^{-1}soil) in the *Ditch* stations.

Pre-rewetting, *mcrA* gene abundance (methanogens) was on average two orders of magnitude higher ($7.9 \times 10^{7} \pm 1.1 \times 10^{7}$ copies g^{-1}) in the *Ditch* compared to the other location groups while it was lowest at the *Elevated* location (average: $1.1 \times 10^{5} \pm 1.4 \times 10^{5}$ copies g^{-1}). Methanogens increased after rewetting at the formerly terrestrial locations, but remained stable in the *Ditch* (Fig. 8B). At the *Elevated* location, *Eastern* and *Western ditch bank*, methanogens increased mostly in the surface peat layer, but the average of the whole depth profile showed an increase which was lower than one order of magnitude. At the *Elevated* location and at the *Eastern ditch bank* methanogenic abundance was lower than pre-rewetting abundance in deeper peat layers below 30–40 cm.


A
Western ditch bank
Ditch
Eastern ditch bank
Elevated
Depth (cm)
0
10
20
30
40
50
0 100 200 300 400 500
CH4 concentration (μM)
B
Western ditch bank
Ditch
Eastern ditch bank
Elevated
Depth (cm)
0.0 2.5 5.0 7.5
CO2 concentration (mM)
C
Western ditch bank
Ditch
Eastern ditch bank
Elevated
Depth (cm)
-125 -100 -75 -50 -25
δ13C CH4 (‰)
D
Western ditch bank
Ditch
Eastern ditch bank
Elevated
Depth (cm)
-30 -20 -10 0
δ13C DIC (‰)
Station
1 2 3 4 5 6 7 8
Rewetting status
Pre
Post

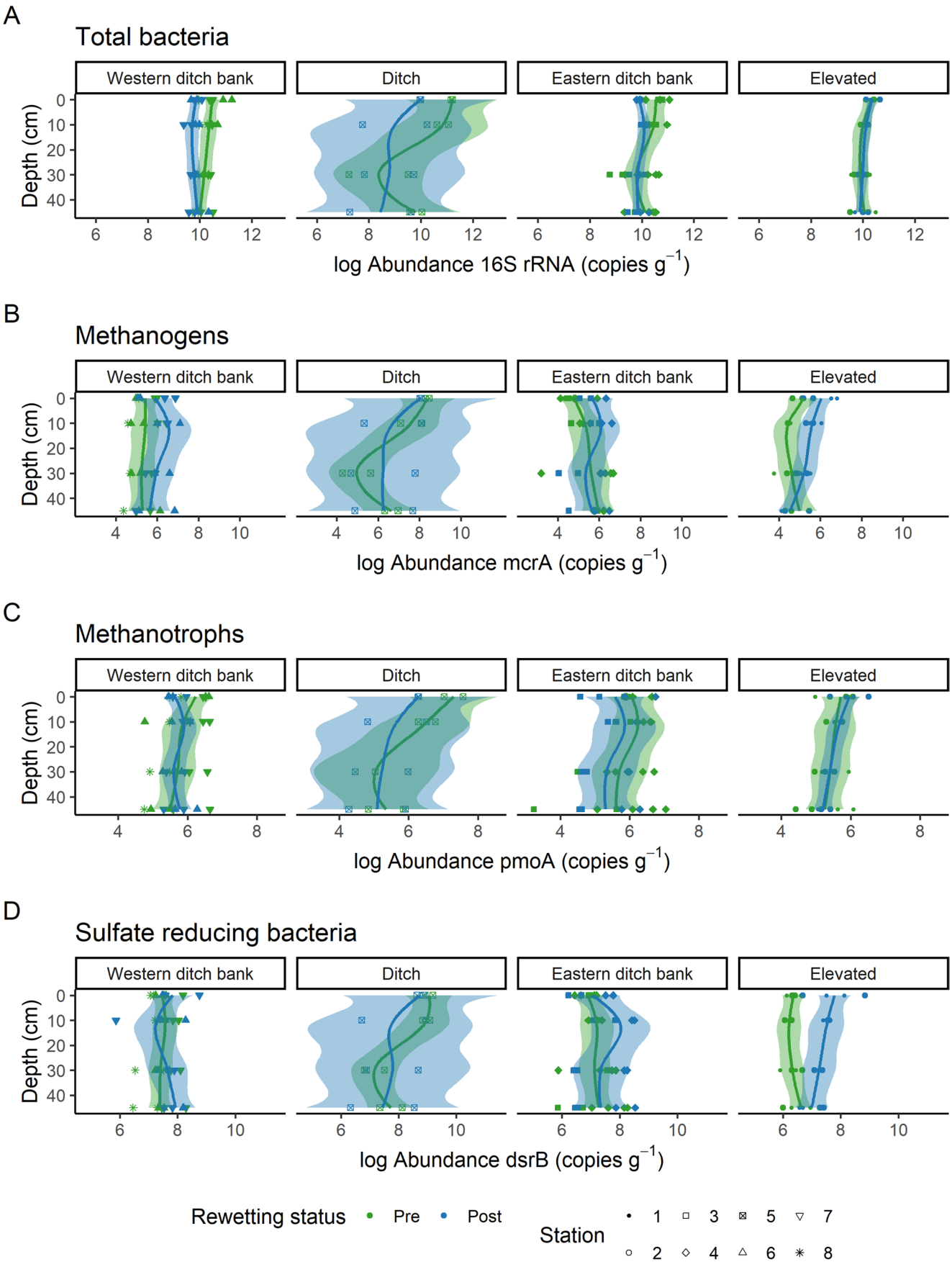

A
Total bacteria
Western ditch bank
Ditch
Eastern ditch bank
Elevated
Depth (cm)
log Abundance 16S rRNA (copies g^{-1})
B
Methanogens
log Abundance mcrA (copies g^{-1})
C
Methanotrophs
log Abundance pmoA (copies g^{-1})
D
Sulfate reducing bacteria
log Abundance dsrB (copies g^{-1})
Rewetting status
Pre
Post
Station
1
2
3
4
5
6
7
8

Fig. 8 Depth profiles of log10 abundances (copies g^{-1} dry soil) of microbial functional genes (**A**: 16 S rRNA, **B**: *mcrA*, **C**: *pmoA* and **D**: *dsrB*), pre- (green, $n=72$) and post-rewetting (blue, $n=56$) with brackish water. Data derived from qPCR analysis of stations along the sampled transect. Stations are marked by different symbol types and were aggregated into location groups (*Elevated*, *Eastern ditch bank*, *Ditch* and *Western ditch bank*). Each location's contribution differed depending on the number of samplings and according to the target gene: pre: 16 S rRNA: $n=8$–24, *mcrA*: $n=8$–20, *pmoA*: $n=7$–24, *dsrB*: $n=8$–24; post: 16 S rRNA: $n=8$–16, *mcrA*: $n=8$–16, *pmoA*: $n=8$–16, *dsrB*: $n=8$–16. Trend lines were estimated using LOESS with a span of 0.9 and serve visual guidance. Shaded areas show confidence intervals according to standard errors and were set to 95% in all plots

Aerobic methanotrophs, represented by the absolute counts of *pmoA* genes, were similar in number to *mcrA* gene abundances before rewetting and counts varied between $4.8\times10^5 \pm 3.9\times10^5$ copies g^{-1} (*Elevated*) and $8.1\times10^6 \pm 1.3\times10^6$ copies g^{-1} (*Ditch*). Unlike methanogens, aerobic methanotrophs decreased overall after rewetting except at the *Elevated* location (Fig. 8C), where gene copy number remained stable. Aerobic methanotroph gene copy numbers decreased throughout the whole soil profile at the *Eastern ditch bank*, while they decreased mostly at the surface in the *Ditch* and at the *Western ditch bank*.

Overall, sulfate reducing bacteria (SRB, identified based on the functional gene *dsrB*) increased after rewetting. Their abundance varied more strongly among the different locations before rewetting, ranging between $3.6\times10^6 \pm 4.5\times10^6$ copies g^{-1} (*Elevated*) and $5.6\times10^8 \pm 6.0\times10^8$ copies g^{-1} (*Ditch*). After rewetting, SRB abundances increased by more than one order of magnitude ($7.1\times10^7 \pm 1.7\times10^7$ copies g^{-1}) at the *Elevated* location, especially in the surface layer. The *Eastern* and *Western ditch bank* also showed an increase in SRB abundance, which remained below one order of magnitude. Interestingly, while SRB at the *Eastern ditch bank* increased most strongly in the peat layer between 5 and 20 cm, the *Western ditch bank* showed lower SRB abundance in that depth layer than before rewetting (Fig. 8D). SRB increased mostly at the very top and below 30 cm at the *Western ditch bank* after the rewetting. *Ditch* SRB abundance was already high before and remained similarly high after rewetting ($3.6\times10^8 \pm 3.4\times10^8$ copies g^{-1}).

Discussion

Rewetting Effects on GHG Fluxes

The increase in seasonal CH_4 release at former terrestrial locations of our study site was low (approx. 12-fold) in the first year after rewetting compared to freshwater rewetted coastal fens (e.g. 190-fold increase one year after rewetting; Hahn et al., 2015). Before rewetting, CH_4 emissions were zero or even negative at the *Elevated* locations, where water levels were lower than at other stations of the transect (see Sect. 3.1). CH_4 uptake prior to rewetting was most likely driven by methanotrophy in a thick, unsaturated, and thus air-filled pore space in the oxic soil zones, as has been shown by e.g. Roulet et al. (1993). The CH_4 emissions we recorded at the former terrestrial locations (average of *Elevated*, *Eastern*, and *Western ditch bank*: 25.1 mg CH_4 m^{-2} d^{-1}) after rewetting remained below the reported minimum of 140 kg CH_4 ha^{-1} a^{-1} annual emissions of rewetted organic soils (Tiemeyer et al., 2020), which corresponds to approximately 38.4 mg CH_4 m^{-2} d^{-1}, but was within the range of average CH_4 emissions of pristine northern peatlands (7.6–15.7 g C m^{-2} a^{-1} ≈ 15.6–32.3 mg CH_4 m^{-2} d^{-1}, Abdalla et al., 2016). The measured CH_4 emissions were also comparable with the strongly reduced CH_4 emissions after a brackish water inflow into a freshwater rewetted coastal fen (Gutekunst et al., 2022; Koebsch et al., 2020). This finding supports our hypothesis that brackish water has the potential to limit CH_4 emissions following rewetting compared with freshwater rewetted fens (e.g. Gauci et al., 2004). In the long-term, our study site might develop similarly to the brackish water rewetted coastal fen mentioned in Weil et al. (2020). Weil et al. (2020) suggested that competition for substrates between methanogens and sulfate reducing bacteria most likely led to low CH_4 exchange rates hovering around zero even approximately 25 years after rewetting.

CH_4 emissions at the *Ditch* stations remained relatively high post-rewetting (around 50 mg CH_4 m^{-2} d^{-1}) and were also still higher than post-rewetting CH_4 emissions at the formerly drained locations. However, even the *Ditch* CH_4 emissions ranged below the average CH_4 exchange rate of freshwater rewetted fens, which is 76.4 mg $m^{-2}d^{-1}$ (or 279 kg CH_4 ha^{-1} a^{-1}, Tiemeyer et al., 2020). Our *Ditch* CH_4 emissions were also much lower than the open water emissions in a eutrophic shallow lake on a drained fen (52.6 g CH_4 m^{-2} a^{-1} approximately corresponding to 144 mg $m^{-2}d^{-1}$) but fell into the broad range reported for the open water area in lakes (Franz et al., 2016). According to Tiemeyer et al. (2020), CH_4 emissions from ditches which existed already in the drained state of peatlands contributed approximately 55% to the total emissions, while making up only 1.3% of the area. In a rewetted state, ditch CH_4 emission hotspots can remain (Köhn et al., 2021), but the relative importance of the ditches decreases due to an overall increase in the total area emitting CH_4. Lowering *Ditch* CH_4 emissions in addition to areal CO_2 emissions through rewetting remains an important step towards improving the overall greenhouse gas balance of rewetted peatlands.

Seasonal net ecosystem exchange (NEE) of CO_2 in the first year after rewetting was similar among the formerly terrestrial locations, indicating net emissions ranging

between 2 and 5 g CO_2 m^{-2} d^{-1}. Compared to the literature, these NEE values were relatively high, since most rewetted peatlands turn into CO_2 sinks or only slight sources after rewetting (−2.4–1.3 t C ha^{-1} a^{-1}, Tiemeyer et al., 2020, which approximately corresponds to −2.4–1.3 g CO_2 m^{-2} d^{-1}). However, ecosystem respiration (R_{ECO}) was strongly reduced at all formerly terrestrial locations after brackish water rewetting (from average 18.8 to 5.6 g CO_2 m^{-2} d^{-1}). The decrease of R_{ECO} suggests a successful reduction of ongoing peat mineralization and indicates that the persisting net CO_2 emissions might have had a different source other than the peat or were the result of a lack of CO_2 uptake. Although the recorded R_{ECO} values ranged around or were higher than R_{ECO} from the open water section of a freshwater rewetted fen (1180 g CO_2 m^{-2} a^{-1}, Franz et al., 2016, which corresponds to approximately 3.23 g CO_2 m^{-2} d^{-1}), they were lower than R_{ECO} from a coastal brackish water fen (1420 mg CO_2 m^{-2} h^{-1}, Weil et al., 2020, which corresponds to approximately 34 g CO_2 m^{-2} d^{-1}). Franz et al. (2016) reported very high emissions arising from high R_{ECO} (2600 g CO_2 m^{-2} a^{-1}, approx. 7.13 g CO_2 m^{-2} d^{-1}) even nine years after freshwater rewetting and attributed them to large amounts of easily degradable substrate, following Hahn-Schöfl et al. (2011) and Hahn et al. (2015). However, abundant photosynthetic C uptake prevented this latter fen to become an even larger source for CO_2 emissions (Franz et al., 2016). The high NEE observed in the present study likely resulted from a lack of living, photosynthetically active vegetation in combination with ongoing high respiration in the peat via non-methanogenic anaerobic pathways (Corbett et al., 2013) such as sulfate reduction, though including CO_2 from methanogenesis (Moore & Dalva, 1993; Urbanová et al., 2011; Estop-Aragonés et al., 2013) and presumably also from CH_4 oxidation or heterotrophic respiration. Respiration of organic material in the water column could further have contributed (Solomon et al., 2013), although photosynthesis might also occur there. Pönisch & Breznikar et al. (2023) found chlorophyll α concentrations to be higher in the bay outside the study site after rewetting of the peatland (increase from 2.5 to 15.4 µg L^{-1}) compared to before rewetting, which suggests the presence of an active highly phototrophic community probably due to high nutrient availability. The chlorophyll α concentrations were even higher in the peatland compared to the bay shortly after rewetting in spring and summer (Pönisch & Breznikar et al., 2023), but this difference did not persist throughout the entire first post-rewetting year (Schultz et al., 2024). DIC concentrations in the drainage ditch in our study site decreased after rewetting (Fig. 4), possibly due higher oxygen availability (Fig. 4) and enhanced photosynthesis (chlorophyll α data are not available from the ditch pre-rewetting) in the water column, suggesting this compartment to be a buffer zone of CO_2 emissions. A recent study from the same research area (Pönisch et al., 2025) indicated that the high CO_2 and higher than before CH_4 emissions in the first year after rewetting are a transitional effect. In the mentioned study, GHG fluxes were derived from campaign-based concentration measurements in the water column in the first and second summer post-rewetting (i.e. comparable sampling, comparable time period). The comparison suggests that CO_2 and CH_4 fluxes in the second summer after flooding were 1.9 and 2.6 times lower than in the first summer (Pönisch et al., 2025), respectively.

Considering a conservative GHG balancing approach, total CO_2-eq. budgets (Table 2) suggest that all four location groups persisted to be a source of GHG emissions after the first year of rewetting with brackish water. N_2O was not actually measured for this study, because it seemed to be less important at the site after rewetting (Pönisch & Breznikar et al., 2023). We tried to include hypothetical N_2O emissions but found them to be negligible even prior to rewetting. According to our results the study site remained a GHG source in the first year after rewetting, mainly because the seasonal CO_2 emissions did not immediately decrease. This was also observed by Petrone et al. (2003) within the first two years post-restoration at a former harvested bog and mainly attributed to the availability of fresh straw mulch as labile organic material and lacking vegetation cover. In addition, this finding could partly be caused by measurement bias, since our CH_4, NEE and R_{ECO} balances were derived from summer and autumn fluxes, skipping lower emissions in winter, which might overestimate the resulting GHG balances even though we normalized them to daily values. Furthermore, GHG chamber measurements had to be adapted to the changed (high-water level) conditions. Post-rewetting CO_2 uptake by plants or microphytobenthos was likely underestimated (or not correctly modeled), because we did not cover photosynthesis fully with the opaque floating chamber measurements. This, in turn, suggests that we report the upper end of post-rewetting NEE even if the measurements with opaque floating chambers did not fully exclude uptake via photosynthesis since there was indirect light reaching into the water column with light penetration under the chamber increasing with water depth. Additionally, pre-rewetting CH_4 emissions in the *Ditch* via plant-mediated transport were not included in the measurements either. Thus, most likely CH_4 emissions in the *Ditch* before rewetting were even higher, because vegetation cover was more pronounced.

Our study reflects the transitional state after the first year of rewetting, with new vegetation not fully established, additional decomposition of plant material after die-back of the former vegetation, and incomplete development of methanotrophic potential. We assume that this will change

Table 2 Total net GHG balances without and including theoretical N_2O emissions

			Pre-rewetting | Post-rewetting			
			Western ditch bank	Ditch	Eastern ditch bank	Elevated
CH_4	CH_4	mg m^{-2} d^{-1}	0.04 | 27.03	40.19 | 50.39	6.23 | 38.10	-0.19 | 10.27
	CH_4 in CO_2-eq.	g m^{-2} d^{-1}	0.002 | 1.22	1.81 | 2.27	0.28 | 1.71	-0.04 | 0.46
CO_2	CO_2	g m^{-2} d^{-1}	-0.87 | 5.18	6.46 | 4.28	3.35 | 2.43	3.44 | 3.43
Net C-GHG balance	CH_4 + CO_2 (CO_2-eq.)	t ha a	-3.17 | 23.34	30.19 | 23.89	13.24 | 15.14	12.40 | 14.22
Transect average	CH_4 + CO_2 (CO_2-eq.)	t ha a		13.17 | 19.15		
N_2O	N_2O in CO_2-eq.	t ha a	1.24 | 0.03	1.24 | 0.03	1.24 | 0.03	1.24 | 0.03
Net GHG balance	CH_4 + CO_2 + N_2O (CO_2-eq.)	t ha a	-1.92 | 23.37	31.43 | 23.92	14.48 | 15.17	13.64 | 14.25
Transect average	CH_4 + CO_2 + N_2O (CO_2-eq.)	t ha a		14.41 | 19.18		

Budgets of total CO_2-eq were calculated using sustained-flux global warming potential (SGWP, emissions) of 45 and sustained-flux cooling potential (SGCP, uptake) of 203 for CH_4 over a 100-year time frame following Neubauer and Megonigal (2015). We calculated with N_2O emissions of 4.6 kg ha-1 a-1 before and 0.1 kg ha-1 a-1 after rewetting (Tiemeyer et al., 2020) assuming a sustained-flux global warming potential (SGWP) of 270 for N_2O. Please note that average columns represent the mean values of the sampled transect and not those of the entire peatland. Also note that units were adapted for easier readability and values were transformed accordingly.

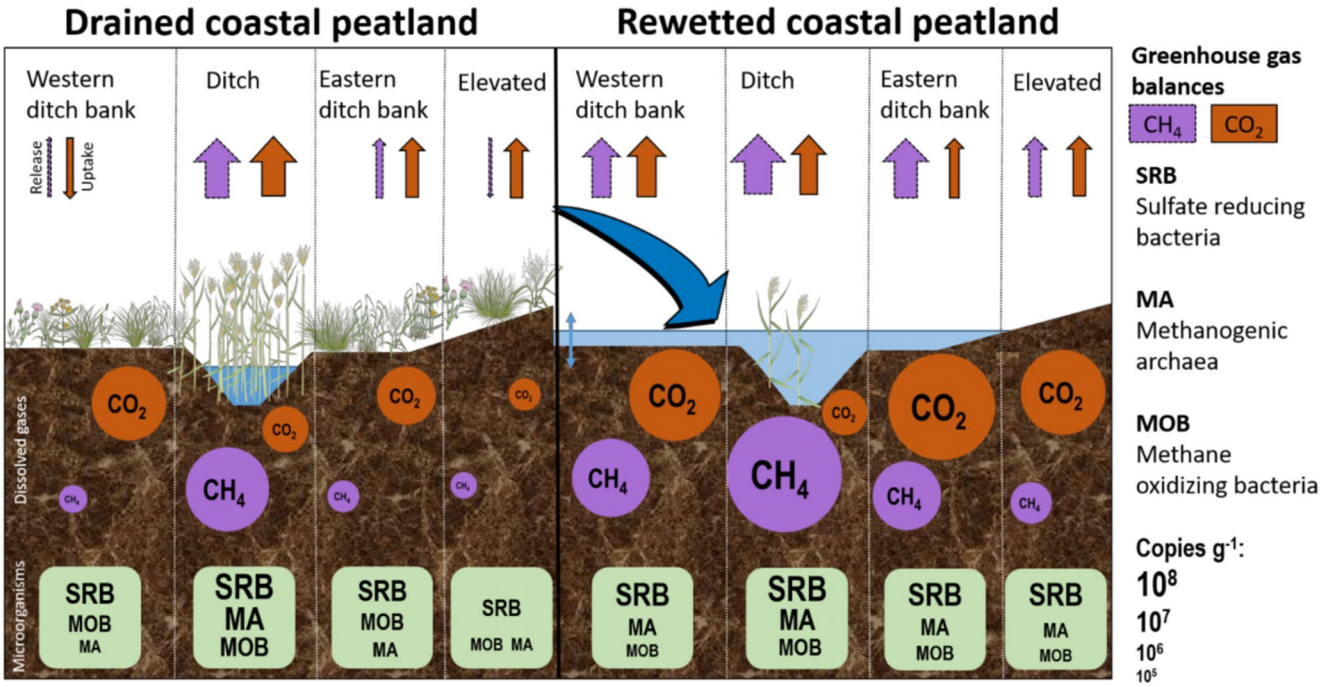


Fig. 1 Effects of brackish water rewetting on peatland biogeochemistry including pore water concentrations and greenhouse gas (GHG) balances (CH_4 and CO_2), and the absolute abundance of relevant specific methane- and sulfate-cycling microorganisms. While GHG emissions depict the summed net ecosystem exchange per day over summer and autumn (Jun–Nov) of the consecutive years 2019 and 2020, microbial and gas concentration data reflect one-time sampling pre- and post-rewetting, respectively. Microbial abundances and pore water GHG concentrations were averaged over all depth layers of the soil profile (0–50 cm). The font sizes, ranking order, and bubble sizes show the highest values of each location group. Please note that microbial absolute abundances are comparable across all location groups and taxa, while GHG concentrations and atmospheric GHG balances are only comparable across the location groups, but not across gas species. Further, the order of microorganisms only relates to their dominance in the whole peat profile, not in single depth horizons. The design of the plants was extracted from the media library of the Center for Environmental Science, University of Maryland (https://ian.umces.edu/media-library/symbols/#download, last access: 16 November 2021)

over time and the results of a recent short campaign-based study (Pönisch et al., 2025), comparing summer fluxes derived from GHG concentration measurements in the surface water, support this assumption. Overall, we already saw a clear effect of rewetting in (1) the decrease of CO_2 emissions that derived from ecosystem respiration (R_{ECO}) and (2) in the CH_4 emissions remaining at a low level, likely because of the sulfate-containing brackish water. Further monitoring of the GHG fluxes is needed to follow the effects of rewetting beyond the immediate ones.

Pore Water Dissolved Gases

At all locations along the transect, CH_4 concentrations in the pore water increased after rewetting (Fig. 7A). Similarly, pore water CO_2 concentrations increased at all formerly terrestrial locations, while they did not change in the soil underneath the *Ditch* (Fig. 7B). Due to high oxygen (Fig. 4) and other terminal electron acceptor (TEA) availability (Pönisch & Breznikar et al., 2023), methanogenesis was unlikely to occur in the surface water. Therefore, CH_4 production presumably increased in the soil or in a newly formed muddy layer on top of the former peat causing increased CH_4 emissions. However, due to the strong effect of water saturation and porosity on diffusivity, the increases in CO_2 and CH_4 concentrations may not serve as good proxies for increased CO_2 and CH_4 production and, thus, for the higher CH_4 and CO_2 emissions. Transport is strongly slowed down in water compared to air (Massman, 1998; Moradi et al., 2020; Wise & Houghton, 1966; Zarghami et al., 2017), so GHGs typically accumulate in the saturated peat soil, causing higher pore water concentrations, which do not necessarily correspond to higher gas production or emissions.

Nevertheless, assuming that peat physical properties did not change too much and considering the increase in CH_4 concentrations particular in the top layers, higher GHG concentrations may serve as a proxy for higher production rates at least under the mentioned limitations. Therefore, it seems plausible that CH_4 and CO_2 production increased after rewetting. CH_4 concentrations increased mainly close to the peat surface (−10 cm), where labile substrates were presumably available from die-back of plants and plant roots that were not adapted to the newly created anoxic conditions (Franz et al., 2016; Hahn et al., 2015; Hahn-Schöfl

et al., 2011) and the inundation with brackish water (Coops et al., 1994; Goodman et al., 2010). Fresh organic material fuels microbial activity especially in the upper 10–20 cm (Coles & Yavitt, 2004) and contributes to methanogenesis (Knorr et al., 2008; Popp et al., 1999; Whiting & Chanton, 1993). Moreover, Popp et al. (1999) found that removal of vegetation can stop CH_4 oxidation in the rhizosphere due to reduced oxygen supply.

At the *Elevated* location, methanogenesis and CH_4 oxidation were probably taking place in parallel in the same layers. The isotopic signatures showed more depleted δ^{13}C-DIC in the peat layers above 35 cm, indicating higher CO_2 production from anaerobic respiration or CH_4 oxidation, and DIC enriched in ^{13}C in the peat layers below 40 cm indicating a higher relative effect of methanogenesis on CO_2 isotopic composition. If excess substrates are available, methanogenesis can even occur in the presence of other electron acceptors such as sulfate, as the thermodynamic suppression of methanogenesis arises from a substrate limitation (Blodau & Moore, 2003; Yavitt et al., 1987). This was also indicated by higher abundances of methanogens in the surface layer of this location (Fig. 8B). At this specific location, the co-existence of processes (Achtnich et al., 1995; Chidthaisong & Conrad, 2000; Estop-Aragonés et al., 2013; Mountfort & Asher, 1981) most likely supports higher CO_2 production from organic matter oxidation at the cost of CH_4 production (Yao & Conrad, 2000). CO_2 concentrations increased stronger compared to CH_4 concentrations after rewetting, because CO_2 was likely produced during organic matter degradation via non-methanogenic CO_2 production, via methanogenesis, and possibly also via CH_4 oxidation. A parallel occurrence of CH_4 production further down in the peat soil and its consumption further up seems plausible at the *Elevated* location that occasionally falls dry during low water levels, and at which TEAs can be expected to be readily available for some time after rewetting. Simultaneously, the *Elevated* location remained high in methanotrophic abundance (Fig. 8C), which is a further indicator for the potential of aerobic CH_4 oxidation and thus mitigation of fluxes. The only available data point of δ^{13}C-CH_4 from before rewetting shows an unusually weak depletion of ^{13}C, which would support strong methanotrophy in the aerated upper peat layers as well.

The isotopic signatures of the *Eastern ditch bank* suggest a strong contribution of methanogenesis to anaerobic C mineralization after rewetting, because generally CH_4 became more depleted in ^{13}C, while DIC became enriched in ^{13}C (Fig. 7C and D). However, the upper surface layer showed CH_4 to be enriched in ^{13}C after the rewetting, which could be an indicator for a possible change towards the acetoclastic pathways of methanogenesis (δ^{13}C-CH_4 of −60 to −50‰, Whiticar et al., 1999). In layers with high abundance of labile substrates, such as the rhizosphere, often a high contribution of acetoclastic methanogenesis has been described (Chasar et al., 2000; Lee et al., 2015). Since the *Eastern ditch bank* was inundated most of the time, increased methanogenesis in the surface peat rather than methanotrophy has likely happened, and acetate as a substrate should have been available in higher amounts post-rewetting (Estop-Aragonés et al., 2013) due to the die-back of plants and roots, resulting in the associated possible input of highly labile organic matter.

In the soil underlying the *Ditch*, CH_4 concentrations increased at medium depths and remained unchanged in the surface peat. This could either indicate that methanogenesis was indeed stronger in the deeper peat, which is in line with the findings of the microbial abundance analysis showing that SRB dominated the surface layers (Fig. 8D). Or the intermediate layer accumulated CH_4, possibly due to slowed transportation, since plant-mediated transport (Chasar et al., 2000; Joabsson et al., 1999) must have decreased after rewetting due to plant die-back. CH_4 production in the upper soil layers likely increased, as suggested by a slight enrichment of ^{13}C in DIC, but the effect on the isotopic composition of CH_4 was minor, potentially because CH_4 was emitted via ebullition, a process with relatively small fractionation (Gu et al., 2004). It seems that methanogenesis has hardly been affected by the input of brackish water into the *Ditch* according to our data on CH_4 concentrations and δ^{13}C-CH_4 values (higher enrichment of ^{13}C in both CH_4 and DIC).

At the *Western ditch bank*, we saw indications for CH_4 oxidation, since CH_4 (Fig. 7C) was enriched and DIC (Fig. 7D) was depleted in ^{13}C (Whiticar, 1999), along with elevated CO_2 concentrations (Fig. 7B). In addition to methanogenesis and anaerobic mineralization, CH_4 oxidation might have contributed to the increase in NEE post-rewetting, while CO_2 emissions at the other formerly terrestrial locations on the Eastern side of the ditch increased less drastically after rewetting. The more pronounced increase in CO_2 release may also have resulted from the *Western ditch bank* being a slight CO_2 sink prior to rewetting. The die-back of very tall vegetation at this location (Fig. 3C) might explain the larger difference between pre- and post-rewetting CO_2 balances compared to the other locations.

Microbial Abundances

The abundance of methanogens increased at all formerly drained locations, according to our qPCR results (Fig. 8B), as could have been expected following water saturation and onset of anoxic conditions. Similarly, sulfate reducing bacteria (SRB) increased mostly at the *Elevated* location, but also at intermediate depths (5–20 cm) of the *Eastern ditch bank* (Fig. 8D). The abundance of aerobic methanotrophs

decreased at the *Eastern ditch bank* and in the surface peat of the *Ditch* and of the *Western ditch bank* (Fig. 8C). Since the abundance of methanogens increased in particular in the surface peat layers of formerly terrestrial locations, an effect of the abrupt increase in water level creating immediate anoxic conditions can be assumed (Urbanová et al., 2011). The predominant effect of methanogens in near-surface layers also supports our hypothesis that due to die-back of vegetation and roots, labile substrates have been highly abundant here. Unlike reported by Juottonen et al. (2012), our results suggest a quick response of methanogens to rewetting after anoxic conditions (re-) established. Interestingly, methanogenic abundance decreased at deeper peat layers (25–40 cm) of the *Elevated* location and the *Eastern ditch bank* that were already low in sulfate concentrations before rewetting (Fig. 6). Methanogens were found to be most abundant in deeper soil layers (below 30 (Wagner, 2017) and 45 cm (Emsens et al., 2020), but this can also be largely dependent on the water level and organic matter content and lability (Weil et al., 2020). In contrast, Weil et al. (2020) found that methanogens decreased with depth at three rewetted fens (percolation, alder and coastal peatland). Our post-rewetting methanogenic abundance in the surface peat (*Elevated* max: 6.5×10^6; *Eastern ditch bank* max: 4.0×10^6; *Ditch* max: 1.3×10^8; *Western ditch bank* max: 1.3×10^7) ranged among those reported in other studies after rewetting (Weil et al., 2020: 1.8×10^6; Gutekunst et al., 2022: around 10^8), again suggesting a stimulating effect of labile organic matter following vegetation and root die-back after rewetting.

The presence of high sulfate concentrations is known to inhibit the establishment of acetoclastic methanogens as SRB outcompete them for substrate (Kristjansson & Schönheit, 1983; Lovley & Klug, 1983). However, we observed higher abundance of methanogens pre-rewetting at the *Western ditch bank* and the *Ditch* compared to the Eastern side of the *Ditch* (*Elevated* location and *Eastern ditch bank*). Most likely, SRB and methanogens co-existed (Dar et al., 2008) at the *Western ditch bank* before and especially under anoxic conditions after rewetting, presumably due to an excess in labile substrates, easing the above described suppressive effect of sulfate on methanogenesis (Egger et al., 2016; Ozuolmez et al., 2015; Sela-Adler et al., 2017). In addition, spatial separation along the peat layers could also help to avoid competition among methanogens and SRB, as seen at the *Western ditch bank*: Below the surface, methanogens increased in the same depth layer that showed slightly decreased SRB abundance (Fig. 8B and D). Similar spatial separations were shown by Jurasinski et al. (2018) for another coastal fen peatland. Egger et al. (2016) observed that in case of high input of organic matter in saline coastal sediments, CH_4 passes the sulfate reduction zone without being effectively removed due to the slow growth rate of methanotrophs. Furthermore, competition between methanogens and SRB might also be avoided if methylotrophic methanogenesis (e.g. Penger et al., 2012; Söllinger & Urich, 2019) as an alternative pathway is occurring, which has been documented for different wetland types before (Conrad, 2020; Yuan et al., 2019).

The *Ditch* showed constant, but highly depth-dependent patterns with high pre-rewetting microbial abundances in upper peat layers and lower microbial abundances in deeper layers. The average decrease of 16 S rRNA counts by one order of magnitude after rewetting might be an effect of the overall increase in salinity, mostly driven by increased chloride concentrations, which provides osmotic stress to microorganisms (Baldwin et al., 2006). Post-rewetting, the microbial abundances were more homogenous along the depth-profile and less depth-dependent. As reported in Gutekunst et al. (2022), this might have been due to the infiltration of brackish water from the top enabling an intermixing of soil components in the fluffy and less compacted peat (sediment) layers in the *Ditch* due to decreased variation in ionic composition with depth in the pore water. However, the *Ditch* profile also showed a large spatial heterogeneity as represented by the differences of functional target gene abundances between the two sampled cores post-rewetting (Fig. 8, *Ditch* A-D).

Abundance of aerobic methanotrophic bacteria, which are adapted to anoxic-oxic interfaces (Conrad, 2009), was negatively affected by the increasing water levels at locations with permanently ponding water above the peat surface (Fig. 8C). Only the *Elevated* location, which experienced the highest wet-dry oscillations showed very little change in methanotrophic abundance (Fig. 8C). In general, aerobic methanotrophs are responsive towards drainage of peatlands (Roulet et al., 1993) and seem to be mostly limited by CH_4 availability (Basiliko et al., 2007). Ma et al. (2013) found that aerobic methanotrophs were two to three magnitudes lower in copy numbers in the anoxic bulk soil compared to oxic niches in the surface and rhizosphere soil. The establishment of a permanent water column fostering anoxic conditions on the bulk scale most likely caused aerobic methanotrophs to decrease (Ma et al., 2013) at locations other than the *Elevated* one. At the *Eastern ditch bank*, aerobic methanotroph abundance decreased, potentially because CH_4 availability was limited by competition with anaerobic methanotrophs (Guerrero-Cruz et al., 2021). Unfortunately, it is not possible to measure the abundances of anaerobic methanotrophs by universally targeting the functional genes *pmoA* and *mcrA* with qPCR as we did. Anaerobic methanotrophs are archaea that share the functional gene *mcrA* with methanogenic archaea (Boetius et al., 2000; Hallam et al., 2003) and are not included in the *pmoA* cluster like aerobic

methanotrophic bacteria. Increased presence of SRB might enable the formation of consortia with anaerobic methanotrophs and might lead to increased anaerobic CH_4 oxidation (Boetius et al., 2000; Holler et al., 2011; Knittel et al., 2018; Ruff et al., 2016; Wrede et al., 2012). Interestingly, aerobic methanotrophs seem to remain abundant at the *Western ditch bank* and the *Ditch*, where they only decreased in the surface layers. Here, they might even be partly responsible for the occurring CH_4 oxidation at the *Western ditch bank*, possibly thriving in oxic niches.

Synthesis and Future Implications

Our microbial abundance data showed that SRB established especially at the surface soil of the *Elevated* location and the *Eastern ditch bank* following the rewetting with brackish water, while the *Western ditch bank* showed only slightly increased SRB abundances (Fig. 8D). Unfortunately, we lack post-rewetting sulfate concentration data from the pore water to support our hypothesis, but we argue that shortly after rewetting pore water sulfate concentrations increased at the *Elevated* location and *Eastern ditch bank*, refilling a depleted sulfate reservoir to serve as an electron acceptor, as reported in another coastal fen study (Koebsch et al., 2019). In contrast, the Western side (*Western ditch bank*) had already twice as high pore water sulfate concentrations pre-rewetting compared to the other side of the *Ditch*. This suggests that the Western location was hardly depleted in sulfate, which might have originated from earlier brackish water inflows or from former coastal peatland conditions as reported in Koebsch et al. (2019). High pore water chloride concentrations and low SO_4/Cl ratios at the *Western ditch bank* and especially at the *Ditch* also indicated a higher influence of brackish water compared to low chloride values and high SO_4/Cl ratios at the Eastern side of the *Ditch*. Compared to the SO_4/Cl stoichiometries of the Baltic Sea (0.07, Rheinheimer, 2013), the *Ditch* still showed a slight sulfate accumulation prior to rewetting in the pore water (0.3) and especially in the surface water (0.8). After rewetting, *Ditch* surface water SO_4/Cl ratios (0.05) approached those of the Baltic sea, clearly showing the exchange with the adjacent bay. In addition, groundwater flow paths from the mentioned coastal fen in the work of Koebsch et al. (2019) have been diverted by ditches surrounding and crossing the peatland (Toro et al., 2022). Possibly, the North-South running *Ditch* represented a barrier for incoming seawater in the drained state of the peatland as well as for fresh groundwater coming from the East, enabling sulfate accumulation at the *Western ditch bank* and even in the *Ditch*, but not on the Eastern side. As such, less input of freshwater would be expected for the *Western ditch bank* since most freshwater would potentially come from atmospheric inputs. This is supported by groundwater facies classifications in additional monitoring wells established along a transect perpendicular to the *Ditch* (Racasa, pers. comm.). Wells on the Eastern side of the *Ditch* (135 m east of the weather station) exhibited a $CaCl_2$ (freshwater influence) and mixed type of water before and after rewetting, respectively. In contrast, before rewetting, the groundwater sample from the well on the Western side of the *Ditch* (65 m west) was classified as a NaCl type of water (seawater influence).

Differently distributed sulfate concentrations before rewetting might have led to spatially different processes occurring simultaneously. It seems like our sampling locations represented a gradient of brackish water influence from high influence on *Western ditch bank* and *Ditch* to lower influence towards the *Eastern ditch bank* and *Elevated* locations. From GHG concentrations and $\delta^{13}C$ measurements, we interpreted that methanogenesis seems to have dominated the *Elevated* location, the *Eastern ditch bank* and the *Ditch*, while CH_4 oxidation clearly occurred at the *Western ditch bank*. The hypothesis of increasing methanogenesis after rewetting is supported by the increasing methanogenic abundance, while the occurrence of CH_4 oxidation was harder to show with our microbial abundances data since we lack data on the abundance of anaerobic methanotrophs. However, CH_4 oxidation is also possible through aerobic methanotrophs in oxic microhabitats. The abundance of aerobic methanotrophs remained stable at the *Elevated* location but decreased at the *Eastern ditch bank*.

Further, GHG concentration and isotope data indicated CH_4 oxidation at the *Elevated* location and the *Eastern ditch bank* as well. Therefore, methanogenesis, CH_4 oxidation, and CO_2 emissions from anaerobic decomposition processes such as sulfate reduction might have occurred in parallel (Wieder et al., 1990) due to the excess availability of labile organic substrates (Böttcher et al., 1997; Rusch et al., 1998) and of TEAs. The produced CH_4 may thus have been emitted to a lesser extent to the atmosphere compared to freshwater rewetted peatlands and could at least partly have been consumed in the benthic-bottom water realm.

Another important finding of our study are the relatively high net CO_2 emissions after rewetting. We assume that the net ecosystem CO_2 exchange remained quite stable or even increased, because the reduction of peat mineralization through rewetting was far outweighed by the reduced photosynthetic CO_2 uptake of vegetation that suffered severe die-back from brackish water input. The rewetting clearly led to reduced ecosystem respiration and therefore we see great potential for CO_2 emission reduction by increased CO_2 uptake in the future once brackish water adapted plants (e.g., marine meso- and macrophytes or terrestrial emergent macrophytes like *Phragmites australis* and *Schoenoplectus tabernaemontanii*) have established. However, a high

fluctuation of the water column and occasionally strong waves will probably delay successful establishment and plant growth. A slow increase of the water level (e.g. using two-way pumping system) would likely help the vegetation to keep pace with the biogeochemical changes and enable the shift from grassland to salt-grass meadow. This is well in line with what van Diggelen et al. (2020) discussed on management of coastal peatland rewetting based on a review of coastal restoration projects and with Darusman et al. (2023) who stressed that vegetation cover and development matter for the reduction of GHG emissions based on a meta-analysis of 28 studies. Pönisch and Breznikar et al. (2023) further recommended to consider seasonal effects and initiate rewetting of coastal peatlands rather in spring or summer than in winter to prevent release of nutrients to the adjacent waters. This hints at the important variables that should be monitored in any coastal peatland rewetting project: Water level (automated and online to capture temporal variation), vegetation (community composition), and nutrient loads in surface and pore water.

Limitations

In our study, we focused on the direct comparison of gas fluxes and the soil biogeochemical and microbiological drivers in particular of CH_4 production and emission between the vegetation period just before rewetting and the same period within the first year after rewetting. In this setting with a very limited time frame to conduct the pre-rewetting measurements and the demand to have a comparable post-rewetting sampling campaign under other challenging conditions, we used CH_4 and CO_2 concentrations and $\delta^{13}C$ analyses in CH_4 and CO_2 as proxies for CH_4 and CO_2 production and consumption estimates. Including the microbial abundance data, the core sampling data refer to the situation at a certain point in time. However, we expect these data to be less variable in time compared to the atmospheric gas fluxes. We chose core sampling campaigns in summer of the respective year (pre- and post-rewetting) in order to align the data with the gas flux measurements covering the entire vegetation period.

To our knowledge, this is the first study to directly compare in-situ field measurements pre- and post-rewetting in a coastal peatland that was rewetted with brackish water by dike removal. This approach might lack some details such as direct rate measurements as well as information on microbial activity rather than abundances as done here (i.e. mRNA extraction) or a complete coverage of net ecosystem exchange of CO_2. From our perspective, studying the respective variables under full environmental influence is important regarding the meaning of such studies on applied rewetting management. This is particularly important in the light of the large number of planned coastal peatland rewetting projects along the Baltic Sea coast. Despite the limitations, this study presents a so far unique dataset and it allows insights into the effects of rewetting coastal peatlands with brackish water.

Conclusions

Coastal peatland rewetting re-established a brackish and anoxic regime and caused substantial shifts in biogeochemical and microbiological conditions. Above all, rewetting with sulfate-containing brackish water increased the CH_4 emissions only slightly, but not to the extent of initial CH_4 peaks as reported from freshwater rewetted peatlands. Further, ecosystem respiration was effectively lowered after rewetting, although net CO_2 emissions were not immediately reduced. The abundance of methanogens and sulfate reducing bacteria increased after rewetting, while the number of aerobic methanotrophs decreased. In accordance with the microbial investigations, we also saw indicators for increased methanogenesis (higher CH_4 concentrations and lower $\delta^{13}C$-CH_4), especially at stations with higher CH_4 emissions under water-saturated conditions. CH_4 production most likely originated from the anoxic conditions and the availability of labile substrate, which formed after the die-back of vegetation in particular in surface near layers. Further, indicators for CH_4 oxidation were found in particular at locations with a high pre-rewetting sulfate reservoir. Thus, the surprisingly high CO_2 emissions (NEE) likely did not result from ongoing peat mineralization, but from the lack of sustained CO_2 uptake via photosynthesis and—albeit to a smaller extent—from the oxidation of CH_4. It is quite likely that net CO_2 release will decrease in the near future after excess substrates are depleted and/or adapted vegetation is successfully established, highlighting the importance of a fast establishment of new vegetation after rewetting. Production and emission of CH_4 might decrease as well, when competitive suppression of methanogens by SRB increases as a result of substrate scarcity and when anaerobic methanotrophs are established to foster CH_4 oxidation. Our study unravels indicators for biogeochemical processes and the resulting GHG flux dynamics that occur in the very initial phase of brackish water rewetting. This immediate phase of rewetting is characterized by a system under disequilibrium and it remains to be seen how long it will take until a new equilibrium state is reached. This study provides the foundation for long-term monitoring to evaluate whether peat mineralization is successfully stopped by rewetting and whether CH_4 emissions can remain low in coastal peatlands.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-025-01639-5.

Acknowledgements We received great support from various people, without whom this work would hardly be possible. First of all, we would like to thank our editors Wen-Chen Chou and Paul A. Montagna and the anonymous reviewers. Further, we would like to thank Chyntia Yuliawati, who conducted the microbial abundance analysis, Simone Kühnreich, Mona Dalkowski, Lina Francke and Pascal Becker for the soil core preparation and analysis, Marcel Ackermann for the according element analysis, Diana Werner for the CNS analysis and Daniel Brüggemann for measuring ^{13}C in CO_2 and CH_4 from the pore water. Special thanks also go to Stefan Köhler for further soil core analysis (CFA and dissolved carbon) and student supervision and to Anke Saborowski, Oliver Burckhardt und Jan Axel Kitte for their assistance and advice during microbial abundance analysis and GHG pore water concentration measurements. Further, we thank, Anne Köhler and Iris Schmiedinger for measuring surface and pore water ions, and Anke Günther, Vytas Huth, and Caroline Daun for their help with gas flux estimation and modelling. We thank Joachim Hoffmann and Claudia Tonn for setting up the weather station and their further technical assistance in the field. Finally, we thank all the volunteers and student helpers assisting during field set-up and especially during the monthly field work: Marius Baudis, Heiner Meißner, Finja Albrecht, Mona Dalkowski, Lina Francke, Pascal Becker, Salome Hassar, Bjarne Schneider, Chyntia Yuliawati, Jan-Philipp Krabel, Anna-Lena Obermann, Raijana Schiemann, Dominik Locker, Lukas Böhm, Leonie Kandler, Werna Werna, Sate Ahmad, Anne Breznikar, Natascha Ouillion and Kristin Steinfurth.

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Funding Open Access funding enabled and organized by Projekt DEAL. This study was conducted within the framework of the Research Training Group 'Baltic TRANSCOAST' funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) - GRK 2000 (www.baltic-transcoast.uni-rostock.de). Finalization was made possible by funding of the Joachim Hertz Foundation within the scope of the project 'Klima- und Moorbodenschutz durch Kombination von Photovoltaik und Moorwiedervernässung' (Moor-PV, founder: Joachim Herz Stiftung, project number: 950000).

Declarations

Ethics approval This is an observational study, so no ethical approval is required.

Data Transparency The data used in this manuscript were uploaded to the PANGAEA database and are available using the following link: https://doi.pangaea.de/https://doi.org/10.1594/PANGAEA.972115.

Conflict of interest The authors declare that they have no conflicts of interests.

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