



Rewetting effects on nitrogen cycling and nutrient export from coastal peatlands to the Baltic Sea

Anne Breznikar · Daniel L. Pönisch ·
Marvin Lorenz · Gerald Jurasinski ·
Gregor Rehder · Maren Voss

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Abstract Coastal nutrient loads from point sources such as rivers are mostly well-monitored. This is not the case for diffuse nutrient inputs from coastal catchments unconnected to rivers, despite the potential for high inputs due to intensive land use. The German Baltic Sea coastline consists of numerous peatlands that have been diked and drained. However, some of the dikes have been removed in order to re-establish the hydrological connection to the Baltic Sea, restore local biodiversity, and promote natural CO₂ uptake. Since these peatlands were used for agriculture, their rewetting may release accumulated nutrients, leading

to nutrient export into the Baltic Sea and intensified coastal eutrophication. Data on these potential nutrient exports are mostly lacking. Therefore, this study investigated nutrient exports from two former agricultural, coastal peatlands: Drammendorfer Wiesen, rewetted in 2019, and Karrendorfer Wiesen, rewetted in 1993. Nutrients (NO₃⁻, NO₂⁻, NH₄⁺, PO₄³⁻), nitrous oxide (N₂O), particulate organic matter (POM, comprising POC and PON; δ¹³C-POC), chlorophyll-*a*, and nitrification rates were analyzed in surface water and porewater sampled weekly to monthly in 2019 and 2020 to compare the effects of different time scales after rewetting on nutrient cycling and potential exports. NH₄⁺, NO₂⁻, and PO₄³⁻ concentrations were higher in the porewater than in the overlying water at both sites, while nutrient concentrations were generally higher at the recently rewetted

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A. Breznikar (✉) · M. Voss
Department of Biological Oceanography, Leibniz Institute for Baltic Sea Research Warnemünde (IOW), Seestraße 15, 18119 Rostock, Germany
e-mail: anne.breznikar@web.de

Present Address:
A. Breznikar
biota – Institut für ökologische Forschung und Planung GmbH, Nebelring 15, 18246 Bützow, Germany

D. L. Pönisch · G. Rehder
Department of Marine Chemistry, Leibniz Institute for Baltic Sea Research Warnemünde (IOW), Seestraße 15, 18119 Rostock, Germany

M. Lorenz
Department of Physical Oceanography and Instrumentation, Leibniz Institute for Baltic Sea Research Warnemünde (IOW), Seestraße 15, 18119 Rostock, Germany

G. Jurasinski
Institute of Botany and Landscape Ecology, University of Greifswald, Soldmannstraße 15, 17487 Greifswald, Germany

Drammendorfer Wiesen than at the Karrendorfer Wiesen. NO_3^- concentrations in porewater, however, were lower than in the overlying water, indicating NO_3^- retention within the peat, likely due to denitrification. Nitrification rates and N_2O concentrations were generally low, except for a high N_2O peak immediately after rewetting. These results suggest that denitrification was the dominant process of N_2O production at the study sites. Both peatlands exported nutrients to their adjacent bays of the Baltic Sea; however, N exports were 75% lower in the longer-rewetted peatland. Compared to major Baltic Sea rivers, both sites exported larger area-normalized nutrient loads. Our study highlights the need to monitor the impact of rewetting measures over time to obtain accurate estimates of nutrient exports, better assess negative effects on coastal waters, and to improve peatland management.

Keywords Peatland restoration · Nutrient release · Nitrous oxide · Coastal eutrophication · Nitrification · Nitrogen cycling

Introduction

Globally, 40% of the world's population lives near the coast (Martínez et al. 2007). This high population density accounts for high inputs of nutrients from land to coastal waters (Galloway et al. 2004; Lee et al. 2016). The negative impacts of these nutrient supplies to coastal zones include the development of harmful algal blooms and hypoxia (Diaz and Rosenberg 2008). Nutrient inputs from rivers are generally well-monitored whereas diffuse surface runoff from small catchments along the coast that do not drain through larger watercourses is more difficult to assess (HELCOM 2019; Malone and Newton 2020).

In the riparian states around the Baltic Sea, ~24% of the population (~20 million people) live in unmonitored coastal catchments that cover ~13% of the total catchment area (Hannerz and Destouni 2006). Along the German Baltic Sea coast, ~400 km² of low-lying areas are peatlands. In these ecosystems, due to the almost permanent water saturation and the resulting anoxic conditions, dead organic matter is accumulated and stored as a peat layer (Joosten and Clarke 2002). Pristine, undisturbed peatlands are characterized by nutrient levels lower than those of their

drained counterparts (e.g., Succow and Joosten 2001), as the anoxic conditions limit decomposition of the peat, such that nutrients are preserved in the form of biomass and not released into the pores or surrounding waters. However, decades of drainage for the purpose of alternative land use have disturbed the natural functions of pristine peatlands, including their retention of both nutrients (Fisher and Acreman 2004) and greenhouse gases (GHGs; e.g. Strack 2008), such as carbon dioxide (CO_2) and nitrous oxide (N_2O). The drainage and aerobic mineralization of peat result in an accumulation of nutrients within the peat (Cabezas et al. 2012; Van De Riet et al. 2013; Mettrop et al. 2014) that is further enhanced by decades of fertilizer application. Ultimately, the accumulated nutrients are transported into adjacent waters, e.g., via drainage ditches (Tiemeyer et al. 2007). Drainage of peatlands also result in the release of GHGs into the atmosphere (Kaat and Joosten 2009). One of these GHGs is N_2O , which is produced by microbial processes, including nitrification, denitrification, and nitrifier-denitrification (Kool et al. 2011; Liu et al. 2019), all of which are influenced by substrate availability and the soil moisture level, which in turn reflects the frequently changing water levels (e.g., Pihlatie et al. 2004). Nitrification can additionally provide substrates for denitrification, leading to the retention of reactive nitrogen (N) in the peat.

Over time, lowering of the water table has led to peat loss and land subsidence, often below sea level. The effect on coastal peatlands and their catchments has been an increased vulnerability to rising sea levels and to more frequent and powerful storm surges (Jurasinski et al. 2018). Artificial dike openings, conducted to restore former peatlands, have strengthened the hydrological connection between the low-lying land and the sea (e.g. Burmeister et al. 2021), exposing coastal waters to diffuse nutrient inputs from densely populated coastal regions and agriculture. However, data on nutrient inputs from land and potential nutrient retention capacities in these coastal areas are mostly lacking (HELCOM 2019).

In recent years, peatland restoration via rewetting measures has been promoted as a means to prevent CO_2 and N_2O emissions originating from peat mineralization and to re-establish the natural sink function of peatlands, both for GHGs and for nutrients (Günther et al. 2020). To reduce the risk of immediate nutrient leaching after rewetting, the

nutrient-rich topsoil is often removed, thereby preventing the export of high nutrient loads into adjacent waters (Harpenslager et al. 2015; Zak et al. 2017; Huth et al. 2022), but topsoil removal is cost-intensive and not always feasible. However, in the absence of topsoil removal, the re-established hydrological connection between the coast and the land allows the transport of these newly released nutrients from the peat into the overlying water column, facilitated by the lateral exchange that occurs due to water level fluctuations. The eventual transport of these nutrients into coastal waters leads to an intensified coastal eutrophication and thus to enhanced biomass production, the degradation of which consumes large amounts of oxygen, potentially inducing or intensifying hypoxia at the seafloor (e.g., Conley et al. 2011).

The time scales and actual effects of rewetting on nutrient leaching and biogeochemical cycling have so far been investigated mostly in laboratory studies (e.g., Van De Riet et al. 2013; Harpenslager et al. 2015) and in situ under freshwater conditions (e.g., Zerbe et al. 2013; Zak et al. 2017). A major focus in those studies was the impact of top-soil removal on nutrient release. However, rewetting with brackish waters, as occurs in the case of coastal peatlands, impacts microbial processes differently (Servais et al. 2021) and the effects have yet to be examined. In general, salinity supports NH_4^+ and P release (Rysgaard et al. 1999; Weissman et al. 2021; Wang et al. 2023), impacts nitrification (Damashek et al. (2016) and thus potential nutrient exports as well (Steinmuller and Chambers 2018).

In this study, the objective was to investigate the short- and long-term effects of rewetting on N and phosphorus (P) cycling/export in coastal peatlands by comparing two rewetted coastal fens in Mecklenburg-Vorpommern, Germany: one was rewetted in 2019 and immediately sampled thereafter; the other was rewetted in 1993 and sampled simultaneously with the first. Both sites had been diked and used for agriculture for decades, are located close to each other, were exposed to similar hydrological and meteorological forcing, and were rewetted with brackish water. As part of the rewetting process, permanent water exchange with the Baltic Sea was re-established by removing the dike and constructing new channels, such that the water levels in the fens are now directly connected to those of the adjacent coast.

To our knowledge, this is the first study to estimate the eutrophication potential of coastal peatlands rewetted with brackish waters and to calculate nutrient exports to the coast. Specifically, we hypothesized that (1) nutrients (N and P) are exported from the peatlands into coastal waters, with higher nutrient loads exported from the recently rewetted peatland than from the peatland that has been rewetted for decades and (2) biological processes (phytoplankton growth and nitrification) are enhanced in the freshly rewetted peatland, due to the higher substrate availability.

Material & methods

Study sites

The two study sites, Karrendorfer Wiesen (KW) and Drammendorfer Wiesen (DW), are located in Mecklenburg-Vorpommern (MV), in northeast Germany. They are separated by a distance of ~25 km (Fig. 1a, b).

The climate in the study region is oceanic, with a mean annual air temperature of 9.1 °C and a mean annual precipitation of 599 mm near KW (German Weather Service, DWD, station “Greifswald”, ID 1757, 1991–2020) and 616 mm near DW (German Weather Service, DWD, station “Samtens”, ID 4376, 1991–2020). Both KW and DW can be classified as highly degraded coastal peatlands (von Post degradation status of the upper peat: H6–H8; Stanek and Silc 1977). The preserved peat layers have a thickness of up to 2 m (Seiberling 2003; Brisch 2015). Drainage was conducted several decades ago to convert the peatlands into arable land for pasture and grassland (Holz et al. 1996; Ostseestiftung, pers. comm. 2021). The historical use of the two sites is comparable, as described below, and topsoil was not removed from either one before rewetting. After rewetting, the water level eventually reached that of the adjacent brackish lagoon system, the so-called Bodden, where the salinity ranges between 7 and 10. Surface water nutrient data were obtained from two monitoring stations (KB90 and GB3), with mean water depths of 5 m and 7 m and mean salinities of 8.4 and 7.6, respectively.

The longer rewetted site KW (54.17° N, 13.40° E) is located south of the Greifswalder Bodden and covers an area of ~3.5 km² (Fig. 1c). It was diked around

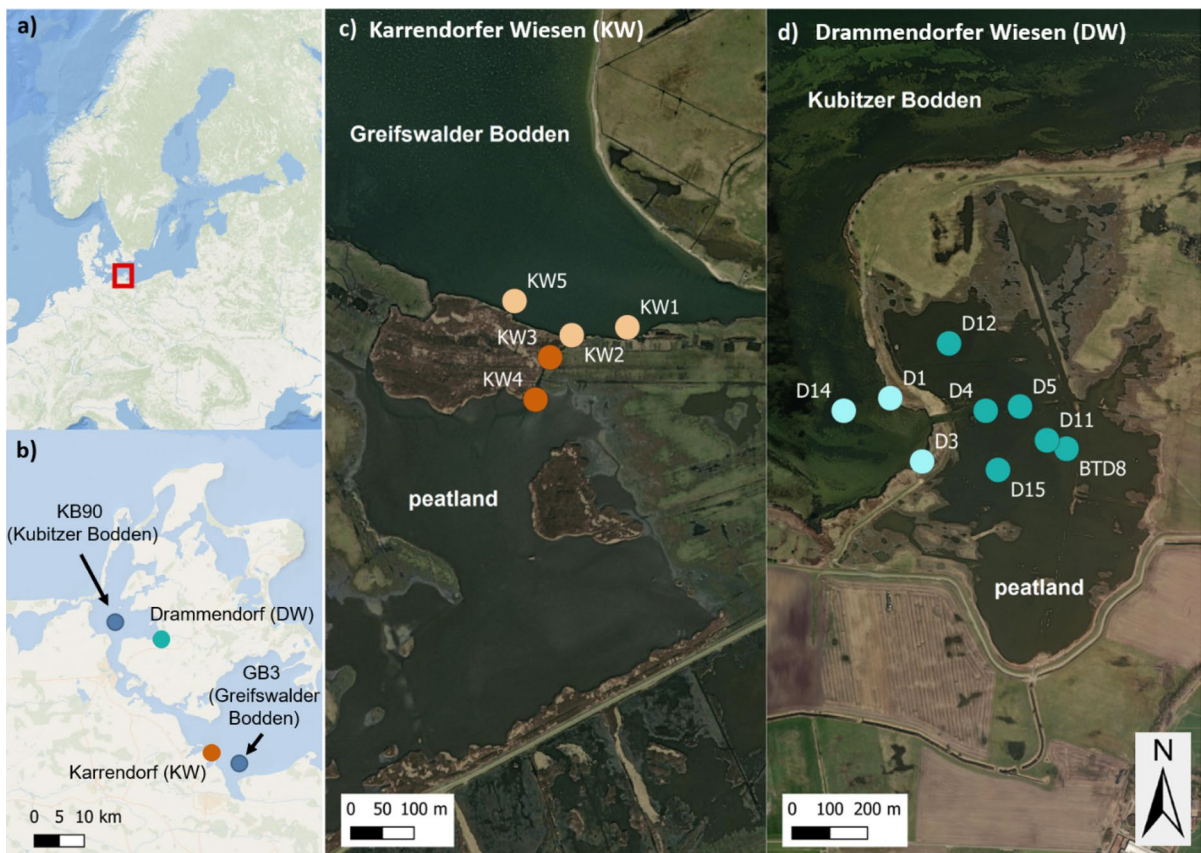


Fig. 1 (A) Overview of the study sites (Karrendorf, KW, and Drammendorf, DW), located in the southern Baltic Sea. **b** Location of both flooded peatland sites and the respective coastal monitoring stations (dark blue dots; used for nutrient data comparisons) at the northeastern German coast. **c** “Peat-

land” (dark colors) and “bay” (light colors) stations in the longer rewetted peatland (KW) and **d** in the recently rewetted peatland (DW). Data source: ESRI Satellite, ESRI Ocean, created with QGIS, vers. 3.16.0

1850 to allow its conversion to cropland and, in low-lying areas, to pasture for cattle grazing (Holz et al. 1996). Fertilizer use in the higher-elevation areas was documented between 1972 and 1989 and consisted of applications of N, P, and K (up to 80, 60, and 120 kg ha⁻¹ year⁻¹, respectively; Seiberling 2003). In 1993, the dike was partially removed, re-establishing the hydrological connection to the Greifswalder Bodden. Some areas of the KW are permanently inundated, resulting in water depths up to 50 cm, whereas others are irregularly flooded. After rewetting, land use shifted entirely to extensive cattle grazing, which is still conducted.

The freshly rewetted site DW (54.37°N, 13.24°E) comprises an area of 0.9 km² and borders the Kubitzer Bodden (Fig. 1d). The dike was erected around

1900 and the area was used as grassland and pasture thereafter (Ostseestiftung, pers. comm., 2021). From ~1980 until the rewetting, low-lying areas, permanently flooded today, were not fertilized and were used only for cattle grazing and mowing (three times per year). N fertilizer (~50–100 kg N ha⁻¹ year⁻¹) was applied once per year in higher-elevation areas that were not later affected by the rewetting (Dr. M. Möller and S. Klatt, pers. comm., 2023). Rewetting was performed in November 2019 by removing parts of the dike, thus re-establishing a connection with the Kubitzer Bodden (Pönisch and Breznikar et al., 2023). The mean water depth of the permanently inundated area is ~50 cm, comparable to that of the inundated areas of KW. Similar to the latter, DW is currently used for extensive cattle grazing. Overall,

the low-lying areas in both sites were used solely for cattle grazing, while areas of higher elevation were fertilized with comparable amounts of N.

Sampling

Data on environmental variables, nutrient concentrations, nutrient exports, and N_2O concentrations at DW were published in Pönisch and Breznikar et al. (2023). The focus of that study was on the early effects of a rewetting event on nutrient release and GHG emissions (CO_2 , CH_4 , and N_2O).

At both KW and DW, surface water (~0.2 m water depth) was sampled from a small boat. Subsamples were prepared for analyses of nutrient [nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+) and phosphate (PO_4^{3-})], chlorophyll-*a* (Chl-*a*), particulate organic matter (POM, including POC and PON) concentrations, and $\delta^{13}\text{C}$ -POC values as well as for determinations of the N_2O concentration and nitrification rate (detailed description below). Environmental variables (surface water temperature, salinity, oxygen, and pH) were measured in situ using a HACH HQ40D multimeter (HACH Lange GmbH, Germany) equipped with three outdoor electrodes (LDO10105, CDC40105, PHC10105). The precisions of the electrodes for temperature, O_2 saturation, salinity, and pH were $\pm 0.3^\circ\text{C}$, $\pm 0.8\%$, ± 0.1 , and ± 0.02 , respectively.

KW was sampled monthly from April 2019 to September 2020 (Supplementary Table S1). No sampling was conducted in September 2019 and March 2020 due to logistical issues. Surface water samples were collected with a beaker, while porewater samples were extracted from soil cores. Sampling at the peatland site of KW was conducted at two stations (KW3 in the channel, KW4 in the flooded area) and in the adjacent bay at three stations (KW1, KW2, and KW5; see Fig. 1c). Porewater samples for nutrient analyses were obtained at one peatland station (KW4) during each sampling.

DW was sampled from December 2019 to December 2020 at weekly to monthly intervals (for a detailed description, see Supplementary Table S1). The first sampling took place one week after rewetting. Surface water samples were collected using a 5-L Niskin bottle, which was horizontally introduced into the water. Nutrient concentrations were measured in samples collected at six stations in the peatland and at three stations in the bay (Fig. 1d). Samples for the

other variables (see above) were obtained at two stations in the peatland (D5, BTD8) and, until mid-July 2020, at three stations in the bay (D1, D3, D14). The values of some variables in samples from station D3 differed significantly from those measured at D1 and D14 and were deemed not representative of the Bodden. Sampling at D3 was therefore abandoned beginning in mid-July 2020. Porewater samples for nutrient analyses were collected at two to four stations in the peatland but only from July 2020 to December 2020. Before July 2020, porewater could not be obtained due to the dense peat soil surface.

Nutrient samples were filtered immediately onboard through $0.45\text{-}\mu\text{m}$ cellulose acetate syringe filters, stored frozen until the analysis. Water samples for measurements of POM, Chl-*a*, and nitrification rates were obtained using plastic canisters and kept cool and dark until further processing in the laboratory. Samples for N_2O analysis were taken using a gas-tight syringe (KW) or from the Niskin bottle (DW) and transferred to 250-ml glass crimp vials, which were then crimp-sealed with butyl rubber stoppers. In the laboratory, the samples were treated with 500 μl of saturated mercury(II) chloride solution and stored at 4°C in the dark until the analysis. For the POM analysis, each sample was filtered onto two pre-combusted (4 h at 450°C) Whatman glass-fiber (GF/F) filters (pore size $0.7\text{ }\mu\text{m}$) and stored frozen until the analysis. For Chl-*a* analysis, the samples were filtered through non-combusted GF/F filters. Water samples for the determination of nitrification rates were stored overnight in the dark at 4°C and processed the next day.

Porewater was retrieved from KW using acrylic liners with holes drilled at regular distances, allowing extraction of the porewater using rhizons (Rhizosphere Research Products B.V., The Netherlands; for details, see Seeberg-Elverfeldt et al. 2005). At DW, a porewater lance (M.H.E. Products, USA) was used. All porewater samples were obtained from the top-most ~5 cm, immediately filtered in the field using syringe filters, and stored frozen until the analysis.

Sample analysis

Nutrient analyses were carried out photometrically according to Grasshoff et al. (2009), using a continuous segmented flow analyzer (Seal Analytical QuAAtro, SEAL Analytical GmbH, Germany).

The detection limits were $0.05 \mu\text{mol L}^{-1}$ for NO_2^- , $0.1 \mu\text{mol L}^{-1}$ for PO_4^{3-} , $0.2 \mu\text{mol L}^{-1}$ for NO_3^- , and $0.5 \mu\text{mol L}^{-1}$ for NH_4^+ . For values below the respective detection limits, it is generally recommended to use the actual values of these measurements (e.g., Fiedler et al. 2022). However, since these data were not available, random values between 0 and the respective detection limit, with a uniform distribution, were generated to achieve a robust statistical analysis.

Chl-*a* was extracted from the GF/F filters by incubating them for 3 h with 96% ethanol (Wasmund et al. 2006) and then measured using a fluorometer (Turner 10-AU-005, Turner Designs, USA) at a wavelength of 670 nm.

POM filters were dried at 60°C for at least 12 h before the analysis, packed into tin capsules, and then pelletized. PON and POC concentrations were measured using an elemental analyzer (EA IsoLink, Thermo Fisher Scientific, USA). Acetanilide (CAS-no. 103–84-4, Merck KGaA, Germany), with C- and N-contents of 71.09% and 10.36%, respectively, was used for calibration, which was done before each sample run. $\delta^{13}\text{C}$ -POC was analyzed using the same filters. After combustion, the gas was injected via a split interface into an isotope ratio mass spectrometer (IRMS, Delta V Advantage, Thermo Fisher Scientific). IAEA-C3, -C6, and NBS 22 served as reference standards. The accuracy of the isotopic analysis was $\pm 0.2\text{‰}$.

Nitrification rates were determined using the ^{15}N - NH_4^+ tracer incubation method (Veuger et al. 2013). At each station, six 300-ml polycarbonate bottles were filled (bubble-free) and then closed with butyl septa before the injection of ^{15}N - NH_4^+ tracer. The injection volume of ^{15}N (as ^{15}N - NH_4Cl , 98 atom%, CAS-no. 39466–62-1, Sigma-Aldrich, Merck KGaA, Germany) was adjusted for every batch of samples to ensure an enrichment of $<10\%$ of the ambient NH_4^+ concentration. After injection, the contents of the three bottles were filtered immediately (t_0), while the other three bottles were incubated in the dark for 15–23 h at the in situ temperature (t_{final}). The incubation time used to determine nitrification rates is usually shorter; however, a previous study showed that $^{15}\text{NO}_3^-$ increases linearly during a 96-h incubation (Bartl et al. 2018), hence the decision to prolong

the incubation time for our measurements. After the incubation, the water in each of the three bottles (t_{final}) was filtered through precombusted (4 h at 450°C) GF/F filters. The filtrates were stored frozen (~ 3 months) until the analysis. The filtrates, containing ^{15}N of $\text{NO}_2^- + \text{NO}_3^-$, were analyzed using the denitrifier method of Sigman et al. (2001) and Casciotti et al. (2002), in which a denitrifying bacterium (*Pseudomonas chlororaphis*) lacking N_2O -reductase converts NO_3^- and NO_2^- to N_2O . The N_2O is extracted using an autosampler, purified, and then analyzed by continuous-flow IRMS (Delta V Advantage with a Finnigan Gasbench II, Thermo Fisher Scientific Inc., USA). IAEA-N3 and USGS-34 served as the reference standards. The precision of the isotope measurements was $\pm 0.1\text{‰}$. Negative rates were set to 0; rates from samples with a $\text{NO}_2^- + \text{NO}_3^-$ concentration $< 1 \mu\text{mol L}^{-1}$ were excluded.

For logistical reasons, the samples used to determine the N_2O concentrations were analyzed on two gas chromatographs (Shimadzu GC-2014, Shimadzu Corp., Japan; Agilent 7890B, Agilent Technologies, USA) using the purge-and-trap technique (for details, see Pönisch 2018 and Sabbaghzadeh et al. 2021). For quality control, a N_2O calibration standard (1533 ppb for the Shimadzu GC and 1982 ppb for the Agilent GC) was measured twice per day, before and after the measurements; the standard deviation was $< 1\%$.

N_2O saturations were calculated from the N_2O concentrations measured in the surface water and from the theoretical N_2O concentrations of brackish water at equilibrium with the atmosphere. The latter were calculated at standard atmospheric pressure (1 atm) with a dry mole fraction of 333.2 ppb- N_2O (World Meteorological Organization 2021), by calculating the saturated water vapor pressure (at 100% humidity) and using the solubility coefficients, as described by Weiss and Price (1980).

Comparison of nutrient data to monitoring stations

To identify a potential export of nutrients (NO_3^- and NH_4^+ , as the most abundant species) from the flooded peatlands into the adjacent bays, nutrient concentrations in the bays of both study sites were compared with monitoring data from the Landesamt für

Umwelt, Naturschutz und Geologie MV (LUNG MV). The latter consisted of data collected from 1986 to 2020 at two monitoring stations situated in the respective Bodden (KB90 in the Kubitzer Bodden for DW and GB3 in the Greifswalder Bodden for KW, Fig. 1b). As described for the nutrient samples of our two study sites (Sect. 2.3), nutrient concentrations of the monitoring stations being below the detection limit were included by using randomly generated values between 0 and the respective detection limit (NO_3^- : 0.1–0.8 $\mu\text{mol L}^{-1}$, NH_4^+ : 0.04–0.7 $\mu\text{mol L}^{-1}$) to ensure a robust statistical analysis.

Nutrient export calculation

A detailed description of the nutrient export calculation is provided in Pönisch and Breznikar et al. (2023). In brief, water-level data from two nearby monitoring stations (for KW: Stahlbrode, 54.23°N, 13.29°E; for DW: Barhöft, 54.43°N, 13.03°E; see Supplementary Figure S1) were used together with topographical data to calculate the water volumes at the two study sites. Mean water-volume changes (inflow vs. outflow) were determined and multiplied by the respective DIN-N and $\text{PO}_4\text{-P}$ concentrations of the peatland (outflow) and the bay sites (inflow) for each season. Finally, net nutrient transport (NNT) was calculated, with negative values indicating a net nutrient export from the peatland into the bay and positive values a net nutrient import into the peatland. For better comparability, the NNTs of both study sites were expressed in units of $\text{t km}^{-2} \text{ year}^{-1}$.

Calculation of nitrification rates

Nitrification rates (NR) were calculated using Eq. (1), according to Veuger et al. (2013):

$$NR = \frac{(15N - NO_x) \times x \frac{(NH_4^+)_{\text{tot}}}{(15N - NH_4^+)_{\text{add}}}}{\Delta t} \quad (1)$$

where $^{15}\text{N-NO}_x$ is the excess concentration of $^{15}\text{N-NO}_3^- + ^{15}\text{N-NO}_2^-$, $(\text{NH}_4^+)_{\text{tot}}$ the total NH_4^+ concentration (ambient + tracer), $(^{15}\text{N-NH}_4^+)_{\text{add}}$ the added tracer concentration, and Δt the incubation time. Nitrification rates are reported as the mean $\pm$ standard deviation based on triplicates for t_0 and t_{final} .

Data processing and statistical analysis

General trends at the two study sites were statistically analyzed by merging (a) the data from individual stations within the peatland and bay areas at each study site (see Fig. 1) and (b) the KW data from 2019 and 2020.

The use of means for each area (peatland and bay) within the study sites was validated in a two-way ANOVA. Non-normally distributed data were first log-transformed. The results showed that, within the study sites, the seasonal temporal variability (see below) was significantly higher than the spatial variability among the stations ($p < 0.05$).

To validate pooling of the data from 2019 and 2020 for KW, the similarities in the meteorology of the 2 years were confirmed by comparing the air temperature and precipitation height data obtained from two nearby monitoring stations (Samtens, ID 4376, and Greifswald, WMO-ID 10184; DWD). No significant differences between years were found (t-test and Mann–Whitney U-test). To ensure detailed visual insights into potential differences between the 2 years, monthly means ($\pm$ standard deviations) for 2019 and 2020 are displayed separately in figures comparing the study sites. For DW, values for December within time series labeled “DW 2020” consisted of measurements from December 2019 and December 2020.

Meteorological seasons were assigned as follows: winter (December to February), spring (March to May), summer (June to August), and autumn (September to November).

All data analyses and visualizations were performed in R (R Core Team 2020), using functions of the packages *tidyverse* (Wickham et al., 2019), *psych* (Revelle 2021), and *car* (Fox and Weisberg 2019). Potential relationships between variables were identified using linear regression analyses. Seasonal (factor “season”) and spatial (factor “area”) comparisons of the study sites were performed using two-way ANOVAs. If the data were non-normally distributed, a log transformation was applied. The significance level was set to $\alpha = 0.05$.

Porewater nutrient concentrations at KW and DW were compared based only on the time period from July to December, to ensure an overlap of the sampling. For KW, data from 2019 and 2020 were used.

Results

Physicochemical properties of the surface waters (temperature, salinity, O₂ saturation, pH)

Seasonal differences in the environmental conditions between the sites were minor (Fig. 2). However, water temperatures were significantly higher in spring and summer at KW than at DW (Supplementary Table S2). Salinity at both sites fluctuated around 8 and increased towards summer, with significantly higher salinities reached at DW (Supplementary Table S2). O₂ saturation at both sites was lowest (85–90%) in winter and autumn and highest in spring (up to ~120%). The pH fluctuated around 8 at both KW and DW but the seasonal changes were very distinct: At KW, the pH was highest (> 8.5) in late summer (August), while simultaneously reaching its minimum (~7.4) at DW, leading to significant differences between the two sites (Supplementary Table S2).

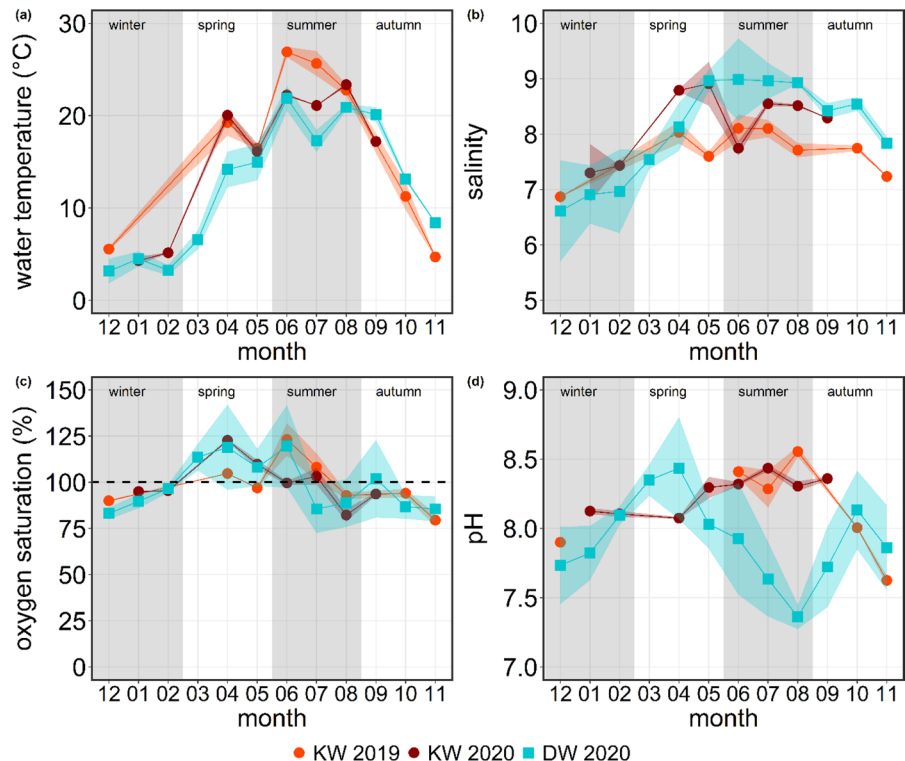
Nutrients

Surface water in the peatlands

Nutrient concentrations in the surface water differed between KW and DW (Fig. 3). DIN concentrations (NO₃⁻, NO₂⁻, and NH₄⁺) were generally higher at DW than at KW. However, only in winter, the first season after the rewetting of DW, DIN concentrations were significantly higher at DW, with maxima of ~212.0, ~3.0, and ~91.0 μmol L⁻¹ for NO₃⁻, NO₂⁻, and NH₄⁺, respectively (Supplementary Table S2). Overall, the typical seasonal pattern of DIN, with the lowest concentrations occurring in summer and increasing towards autumn, characterized both sites.

PO₄³⁻ concentrations fluctuated around ~0.5 μmol L⁻¹ at both sites but were frequently higher at KW, except in spring. A very high PO₄³⁻ concentration (~7 μmol L⁻¹) was measured only once at KW, during a high water level in winter. This outlier was omitted from the export calculations.

Fig. 2 Monthly mean (±SD, shaded area) **(a)** water temperature, **(b)** salinity, **(c)** oxygen saturation, and **(d)** pH at Drammendorf (DW, blue) and Karrendorf (KW, orange and dark red). The dashed line in **(c)** shows the O₂ equilibrium with the atmosphere (100% saturation)



Porewater in the peatlands

Between July and December, NO_2^- , NH_4^+ , and PO_4^{3-} concentrations in the porewater were significantly higher at DW than at KW (Fig. 4). NO_3^- concentrations did not differ significantly between the two sites. NH_4^+ and PO_4^{3-} concentrations in the porewater were one order of magnitude higher than in the surface water, while NO_2^- and NO_3^- concentrations were of the same order of magnitude.

However, when all sampling events were considered for each site, NO_2^- , NH_4^+ , and PO_4^{3-} concentrations were significantly higher in the porewater than in the surface water at both KW and DW. By contrast, NO_3^- concentrations in the porewater and the surface water did not differ significantly at either site.

Spatial gradients in nutrient concentrations at the study sites and comparisons with data from the monitoring stations

Spatial gradients of surface water nutrient concentrations (peatland vs. bay) differed between the study sites (Supplementary Figure S2, Supplementary

Figure S3). At KW, nutrient concentrations did not differ significantly between the peatland and the bay during any season. At DW, NO_2^- concentrations in winter and PO_4^{3-} concentrations in spring and summer were significantly higher in the peatland (Pönisch and Breznikar et al., 2023).

The mean monthly NO_3^- and NH_4^+ concentrations of the bays as determined in our study clearly differed from the long-term means measured at two nearby monitoring stations (GB3 for KW, KB90 for DW Fig. 5). At KW, differences in the NH_4^+ concentrations between the bay and GB3 were generally minor, while all NO_3^- concentrations were lower at KW than at GB3. At DW, NO_3^- concentrations in the bay were mostly within or below the 95% confidence level of those at KB90 (except in February), while NH_4^+ concentrations were much higher in the bay in winter and autumn.

Nutrient export

Calculations of net exports of DIN-N and PO_4 -P indicated that KW and DW were the likely sources of the nutrients in their adjacent bays (Supplementary

Fig. 3 Monthly mean ($\pm$ SD, shaded area) surface water nutrient concentrations of **a** NO_3^- , **b** NO_2^- , **c** NH_4^+ , and **d** PO_4^{3-} at Drammendorf (DW, blue) and Karrendorf (KW, orange and dark red)

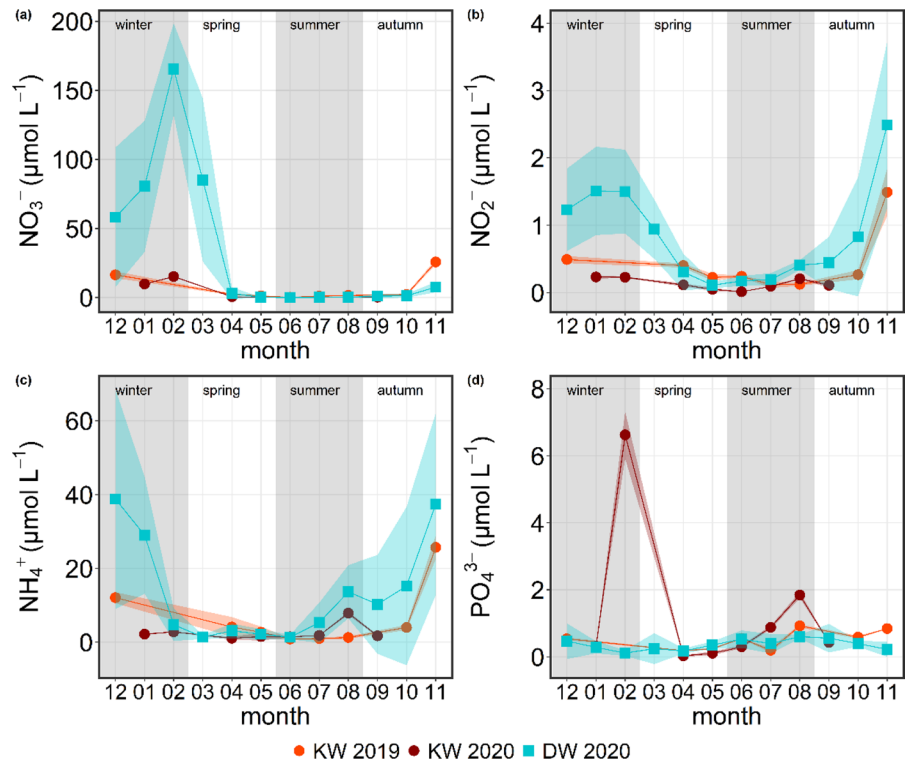


Fig. 4 Porewater nutrient concentrations of **a** NO_3^- , **b** NO_2^- , **c** NH_4^+ , and **d** PO_4^{3-} at the peatland of Drammendorf (DW, blue) and Karrendorf (KW, orange). Only concentrations of the overlapping sampling months were considered (July to December). Numbers at the bottom of each boxplot report the number of included values. Significance levels of the site comparisons are shown at the top (ns = not significant, ** $p < 0.01$, *** $p < 0.001$)

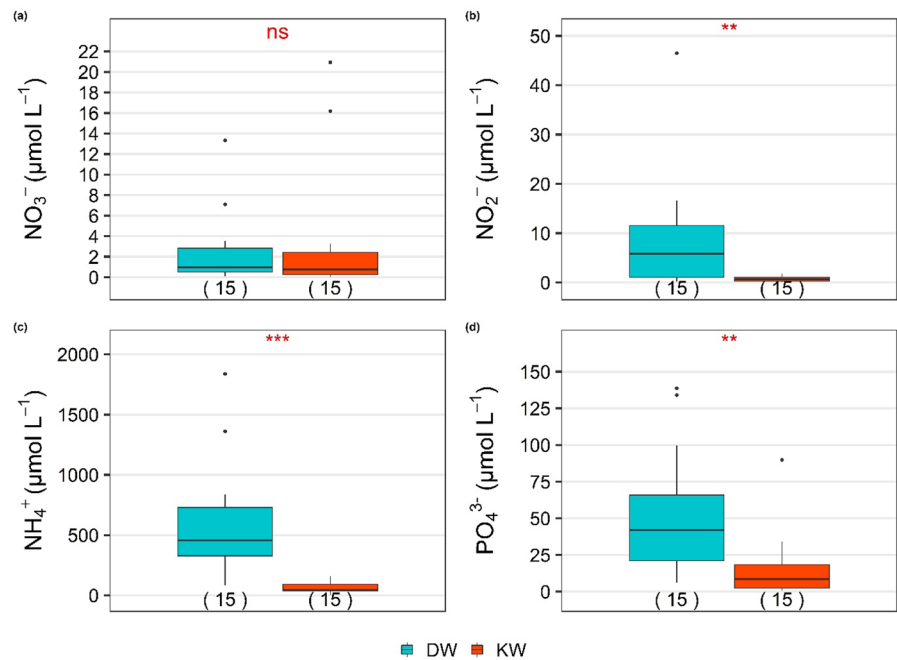


Table S3; high PO_4^{3-} values of February 2020 excluded). At KW, $6.1 \pm 20.3 \text{ t DIN-N km}^{-2} \text{ year}^{-1}$ and $0.04 \pm 1.8 \text{ t PO}_4\text{-P km}^{-2} \text{ year}^{-1}$ were released into coastal waters. DIN-N and $\text{PO}_4\text{-P}$ exports were highest in autumn and winter and lowest in summer. While DIN-N was exported during all seasons, $\text{PO}_4\text{-P}$ was imported only during winter and spring. At DW, $21.6 \pm 34.8 \text{ t DIN-N km}^{-2} \text{ year}^{-1}$ and $0.5 \pm 0.6 \text{ t PO}_4\text{-P km}^{-2} \text{ year}^{-1}$ were exported into the Baltic Sea, with the highest exports of DIN-N and $\text{PO}_4\text{-P}$ occurring in winter and the lowest exports in summer and spring, respectively. Overall, ~3 times more DIN-N was exported by DW than by KW (area-normalized values). $\text{PO}_4\text{-P}$ exports were one order of magnitude higher at DW than at KW.

Biological variables

Chlorophyll-*a* and particulate organic matter

Chl-*a* concentrations at KW and DW followed the expected seasonal pattern, only the magnitude differed between the two sites (Fig. 6a). Chl-*a* concentrations (up to $110 \mu\text{g L}^{-1}$) were highest in spring (KW) and summer (DW), coinciding with high POC and PON concentrations, and were significantly

higher at DW than at KW (Fig. 6b, c, Supplementary Table S2). The C:N ratios of particulate matter fluctuated between ~7 and ~10.5 and did not significantly differ between the sites during any season (Fig. 6d, Supplementary Table S2).

However, the two sites clearly differed with respect to their POC:Chl-*a* ratios (Fig. 7a), which serve as an indicator of fresh or degraded organic matter. At KW, the POC:Chl-*a* ratio was >200 during all seasons whereas at DW it was typically <200, except in winter.

The $\delta^{13}\text{C}$ -POC values at both study sites ranged between -34‰ and -22‰ , thus covering the entire range of values expected for terrestrial and marine environments (Fig. 7b). While $\delta^{13}\text{C}$ -POC values did not significantly differ between KW and DW during winter and spring, they were significantly lower at DW in summer and autumn (Supplementary Table S2). Overall, the opposite pattern characterized KW from spring onwards, with lower $\delta^{13}\text{C}$ -POC values in spring and higher values in summer and autumn.

Nitrification rates and N_2O saturations

Nitrification rates were generally higher at KW than at DW, evidenced by annual means of

Fig. 5 Monthly mean concentrations of **a** and **b** NO_3^- and **c** and **d** NH_4^+ at the respective bay sites off Karrendorf (KW, orange) and Drammendorf (DW, blue) compared to the mean concentrations determined at two nearby monitoring stations based on data from 1986 to 2020 (GB3 for KW, KB90 for DW, dark gray and light gray, with 95% confidence level, respectively)

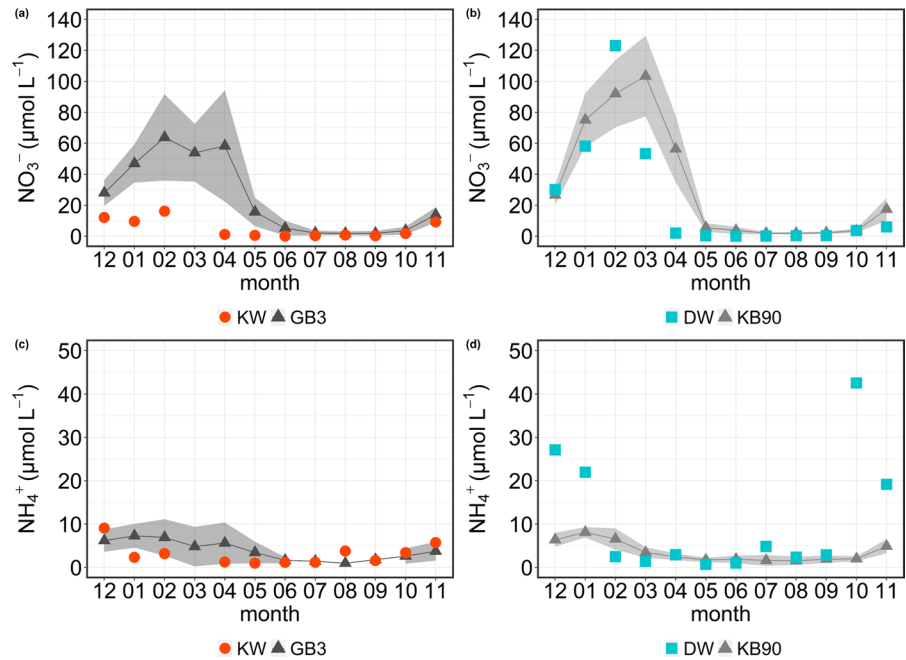


Fig. 6 Monthly mean ($\pm$ SD, shaded area) **a** chlorophyll-*a*, **b** particulate organic nitrogen (PON), **c** particulate organic carbon (POC) concentrations, and **d** C:N ratios of particulate matter at Drammendorf (DW, blue) and Karrendorf (KW, orange and dark red)

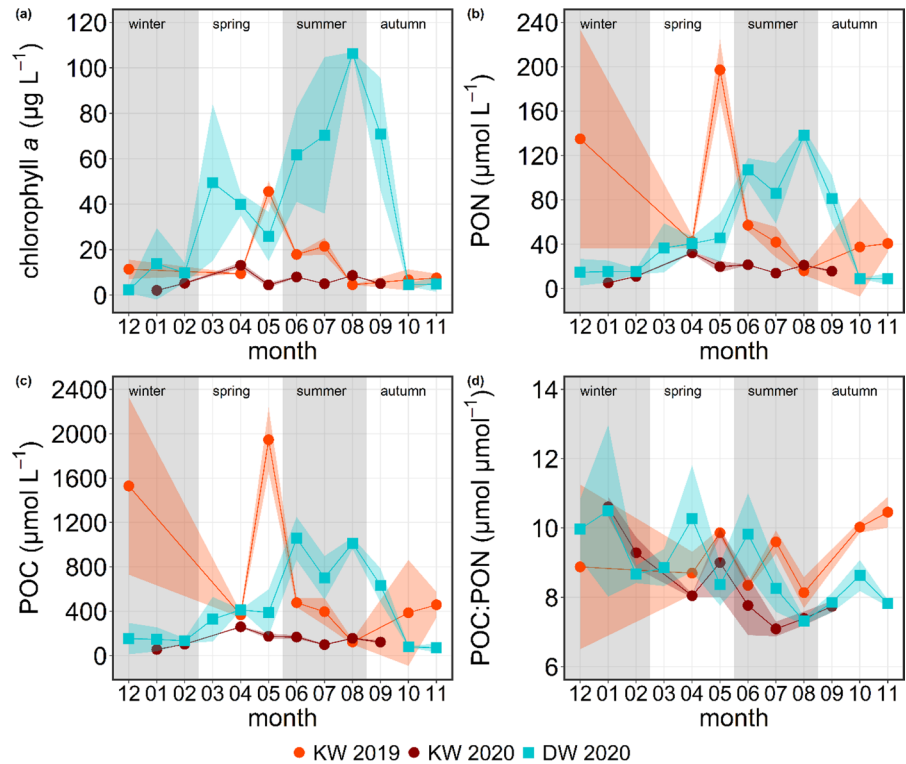
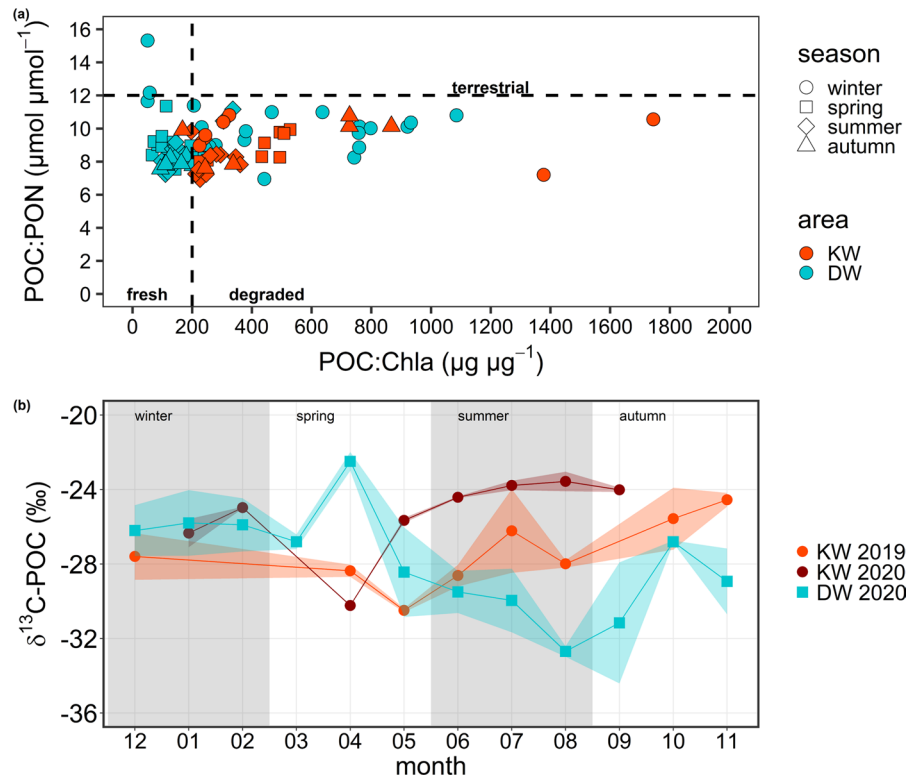


Fig. 7 **a** C:N ratios of particulate matter plotted against the POC:Chl-*a* ratio in the surface water at Drammendorf (DW, blue) and Karrendorf (KW, orange) during all seasons. See the Discussion section for the definitions of “fresh”, “degraded” and “terrestrial”. **b** Monthly mean ($\pm$ SD, shaded area) $\delta^{13}\text{C}$ -POC ratios at Drammendorf (DW, blue) and Karrendorf (KW, orange and dark red)



$77.9 \pm 161.3 \text{ nmol L}^{-1} \text{ d}^{-1}$, and $5.6 \pm 9.1 \text{ nmol L}^{-1} \text{ d}^{-1}$, respectively (Fig. 8a). However, nitrification rates at KW were significantly higher only in winter (Supplementary Table S2), due to a single sampling event characterized by a very strong resuspension that led to high PON and POC concentrations.

Pooling the data from all seasons resulted in a significantly positive correlation between the nitrification rate and the NH_4^+ concentration at KW and DW (KW: $r_s = 0.63$, $n = 17$, $p < 0.01$; DW: $r_s = 0.39$, $n = 31$, $p < 0.05$) as well as the NO_3^- concentration at KW ($r_s = 0.83$, $n = 17$, $p < 0.001$).

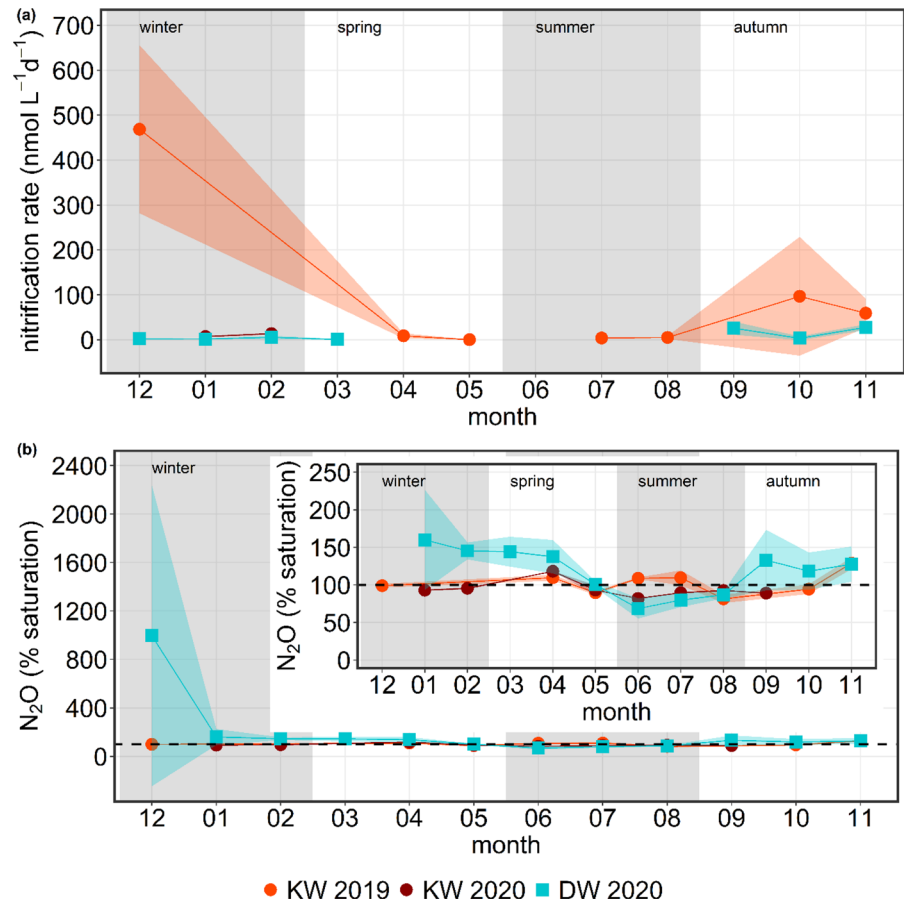
Both the magnitude and the temporal variability of the N_2O saturations differed between KW and DW (Fig. 8b). At DW, rewetting led to N_2O saturations of up to 4000%, measured in winter (mean: $486 \pm 874\%$), whereas N_2O saturations at KW were significantly lower (mean: $96 \pm 3\%$; Supplementary Table S2). Beginning in spring and continuing thereafter, N_2O saturations at DW decreased strongly. During summer, a higher undersaturation was determined at DW than at KW. Overall, the N_2O saturation range at DW was ~ 30 –4000% and therefore much larger than the ~ 80 –140% at KW.

N_2O concentrations (nmol L^{-1}) correlated positively with the nitrification rate at DW in autumn ($r_s = 0.94$, $n = 6$, $p < 0.05$), but not with any of the seasonal rates at KW (Supplementary Figure S4). At both sites, the correlations between annual N_2O and DIN concentrations were significantly positive (KW: $r_s = 0.63$, $n = 31$, $p < 0.001$; DW: $r_s = 0.83$, $n = 147$, $p < 0.001$) as were those between N_2O and O_2 (in mg L^{-1} ; KW: $r_s = 0.84$, $n = 31$, $p < 0.001$; DW: $r_s = 0.50$, $n = 148$, $p < 0.001$).

Discussion

In this study, two coastal rewetted peatlands with a similar decades-long history of drainage and agricultural use but differing in the amount of time since their rewetting (30 years vs. freshly rewetted at the time of sampling) were compared. Our aim was to determine how the duration of rewetting impacts N and P reservoirs, internal nutrient cycling, nitrification rates, and organic matter cycling. Potential nutrient (N and P) exports to adjacent coastal waters were also calculated.

Fig. 8 Monthly mean ($\pm$ SD, shaded area): **a** nitrification rates (in $\text{nmol L}^{-1} \text{d}^{-1}$) and **b** N_2O saturation (in %) at Drammendorf (DW, blue) and Karrendorf (KW, orange and dark red). Nitrification rates with $\text{NO}_3^- + \text{NO}_2^-$ values $< 1 \mu\text{mol L}^{-1}$ were excluded, leading to a discontinuous timeline in spring and summer. In (b), the dashed horizontal lines indicate the atmospheric equilibrium (100% saturation)



Factors regulating nutrient cycling and export from rewetted peatlands to coastal waters

Nutrient and N_2O cycling in the surface water and porewater

Environmental variables such as salinity and O_2 saturation in the surface water were often comparable at the two study sites, suggesting similar impacts of rewetting on nutrient biogeochemistry (Fig. 2). Only the water temperatures differed, as they were slightly higher at KW in spring and summer, reaching 25°C , which is not uncommon for shallow coastal bays (e.g., Broman et al. 2021). O_2 saturation did not differ between KW and DW during any season and thus was likely not responsible for the differences in the microbial processes taking place near the water surface. However, since our O_2 measurements were conducted only near the water surface, a gradient of decreasing O_2 saturations towards the bottom water, with anoxic

conditions within the peat soil favoring anaerobic microbial processes, would have been missed. The overall impact of these physicochemical drivers on biogeochemical processes was evidenced by the similar seasonal patterns at the two study sites, with the highest O_2 saturations, lowest N-nutrient concentrations, and highest Chl-*a* concentrations occurring during spring and summer, indicating high productivity and high rates of nutrient consumption. By contrast, the opposite pattern, i.e., lowest O_2 saturations, highest N-nutrient concentrations, and lowest Chl-*a* concentrations during autumn and winter, supported the dominance of remineralization processes requiring oxygen and producing inorganic nutrients.

Rewetting leads to nutrient release and thus to high nutrient concentrations in the overlying water (Goldberg et al. 2010; Jørgensen and Elberling 2012; Van De Riet et al. 2013; Harpenslager et al. 2015), as also observed in incubation studies (Zak and Gelbrecht 2007; Cabezas et al. 2012). Our finding that nutrient

concentrations (NO_2^- , NH_4^+ , and PO_4^{3-}) at both study sites were significantly higher in the porewater than in the surface water identifies the peat itself as the main source of nutrients for the overlying water, even 30 years after rewetting. This suggests that previously farmed, highly degraded peat soils contain large amounts of nutrients that are prone to leaching after rewetting with brackish water, a conclusion in line with the high surface water DIN concentrations determined at DW immediately after rewetting. Nutrient leaching following rewetting is in strong contrast to pristine peatlands, which tend to retain and remove nutrients from the surface water instead of releasing them into the surface water (e.g., Fisher and Acreman 2004). Consequently, N and P concentrations in the peat, and thus the potential for significant nutrient leaching, are much lower (e.g., Succow and Joosten 2001). This was demonstrated in the mesocosm experiments conducted by Laine et al. (2013), who compared pristine and drained peat from a Finnish bog and showed that porewater nutrient concentrations were generally higher in the latter.

The high nutrient reservoirs in rewetted peatlands and the release of nutrients after the intrusion of brackish water can lead to enhanced microbial activity and thus also to the production of N_2O by nitrification and denitrification. Typically, during nitrification, N_2O is produced as a side-product and is therefore more likely to be released into the environment than during denitrification, where N_2O is an intermediate that is further reduced to N_2 (e.g., Stein and Yung 2003).

A previous study showed that the state of peat degradation influences N_2O emissions after rewetting, with a higher degree of degradation, as in our study sites, and therefore a lower C:N ratio resulting in higher emissions (Liu et al. 2019). Lower C:N ratios originate either from drainage and the preferential mineralization of C or from fertilization, both ultimately leading to an enrichment of N in the peat (Berglund et al. 2010; Krüger et al. 2015). These high N-loads can strongly increase the production of N_2O (e.g., Chmura et al. 2016; Roughan et al. 2018), as also shown by our results. Thus, the high N_2O saturation (up to 4000%) at DW one week after rewetting indicated high microbial activity, likely fueled by the release of nutrients after the intrusion of brackish water (Fig. 8). In contrast to DW, N_2O saturation at KW did not reach a corresponding peak; instead,

much lower deviations around the N_2O equilibrium with the atmosphere were determined that indicated a more balanced system that has mostly equilibrated with the atmosphere 30 years after rewetting. Other studies from rewetted peatlands also reported low N_2O emissions, in some cases even lower than those from pristine peatlands (e.g., Minkinen et al. 2020).

Surprisingly, nitrification rates in the surface water, especially at DW, remained low, even in response to a higher substrate availability, and were thus comparable to rates determined e.g. in the coastal waters of the Bay of Gdansk (Bartl et al. 2018). However, high rates are possible following a strong resuspension (e.g., Happel et al. 2018). This was the case at KW, where nitrification rates reached $\sim 600 \text{ nmol L}^{-1} \text{ d}^{-1}$ during a single event in which sediments were resuspended. However, a high nitrification potential may be restricted by the availability of particulate matter, due to the preferential association of nitrifiers with particles (e.g., Brion et al. 2000; Kache et al. 2021).

Other studies have identified denitrification rather than nitrification as the dominant N_2O production process in a fully water-saturated peat soil (Pihlatie et al. 2004; Masta et al. 2022), as was also present in our study sites due to their permanent inundation. Pihlatie et al. (2004) showed (1) that N_2O production was four orders of magnitude higher in fully water-saturated peat (100% water-filled pore space, WFPS) than in less water-saturated peat (40% WFPS) and (2) that the contribution of nitrification decreased with increasing water saturation. Thus, it is likely that denitrification was the dominant N_2O production process at KW and DW, indicating that the conditions and nutrient concentrations within the peat were among the most important drivers of N_2O cycling.

Besides being sources, KW and DW were occasionally also sinks, both for N_2O and for NO_3^- , as shown by N_2O saturations $< 100\%$ (especially in summer) and lower NO_3^- concentrations in the porewater than in the surface water. When peat is constantly water-saturated, the O_2 saturation decreases such that the soil very likely becomes hypoxic or anoxic. However, as we did not measure O_2 levels in the soil, we can only speculate that O_2 was quickly depleted within the first few centimeters or even millimeters, as is known for wet peatlands (e.g., Joosten and Clarke 2002). The occasional undersaturation of N_2O in the surface water of DW in spring and summer can be explained by a switch from oxic to hypoxic/

anoxic conditions within the peat, which would favor microbial processes that consume NO_3^- and N_2O , such as denitrification or dissimilatory NO_3^- reduction to NH_4^+ (DNRA). The higher undersaturation of N_2O in summer at DW than at KW therefore reflected higher organic matter mineralization, stronger oxygen demand, and in turn the intensified use of N_2O as electron acceptor at DW (Fig. 8b). For rewetted peatlands, including KW and DW, these processes ultimately lead to the termination of N_2O emissions (e.g., Regina et al. 1999; Strack 2008), in some cases allowing the peat to become a sink for N_2O (Minkinen et al. 2020), which is in agreement with our results.

Particulate organic matter cycling

Sources of POM can be characterized by using the C:N and POC:Chl-*a* ratios to distinguish between marine vs. terrestrial and fresh vs. degraded POM. A C:N ratio > 12 reflects terrestrial POM, and a C:N ratio < 12 phytoplankton-derived POM (Savoye et al. 2003). Since the majority of the C:N ratios determined for KW and DW were < 12 (Savoye et al. 2003) and the Chl-*a* concentrations during spring and summer were high, most of the POM at the two sites probably originated from phytoplankton growth or fresh plant material. According to Cifuentes et al. (1988), a POC:Chl-*a* ratio < 200 indicates fresh phytoplankton and a ratio > 200 degraded phytoplankton. At DW, the majority of the POC:Chl-*a* ratios were < 200, consistent with the presence of fresh plankton, whereas the ratios at KW during all seasons were mostly > 200, indicative of the availability of more degraded phytoplankton (Cifuentes et al. 1988). The Chl-*a* and POM concentrations in summer were significantly higher at DW than at KW (Fig. 6), likely due to a higher nutrient availability (e.g., Nixon 1995). This finding supported our second hypothesis, that biological processes (phytoplankton growth and nitrification) in freshly rewetted peatlands are enhanced by the higher substrate availability.

Even during the period of highest phytoplankton growth, POM and other sources of organic material were probably actively degraded at DW, as suggested by a pH of 7.4, the lowest measured, during summer, attributable to the dominance of organic matter (OM) remineralization over production and the production

of CO_2 (Fig. 2, e.g., Zhou et al. 2021). This low pH in connection with the buildup of a large pool of isotopically light POC (Figs. 6c, 7b) implies a high rate of primary production and an even higher rate of fresh organic matter mineralization. The low $\delta^{13}\text{C}$ -POC values suggest that the organic material was of terrestrial origin (Fig. 7b), possibly the peat itself ($\sim -29.2\text{‰}$), and/or dead macrophytes such as *Phragmites australis* ($\sim -30\text{‰}$), or grassland vegetation that died after the rewetting (Müller and Voss 1999).

This supports the findings by Pönisch and Breznikar et al. (2023), who reported large net emissions of CO_2 from DW in the first year after rewetting, with the amounts comparable to those of the annual net CO_2 release before rewetting. The authors hypothesized that the CO_2 release from DW would eventually cease, due to a decrease in the supply of fresh degradable material and the establishment of a carbon-fixing ecosystem over the productive period. The latter is strongly supported by the data from KW, where 30 years after rewetting the annual maximum pH of 8.5, measured in summer (Fig. 2), clearly pointed to the dominance of primary production over mineralization.

The occasionally higher $\delta^{13}\text{C}$ -POC values at both study sites, exceeding -25‰ , revealed that the POM pool was at times dominated by OM from marine sources. Possible differences due to varying precipitation heights can be excluded due to the proximity of the study sites (Supplementary Figure S5). Previously reported $\delta^{13}\text{C}$ -POC values for marine phytoplankton in nearby areas include -23.8‰ in the Arkona Basin (Voss and Struck 1997) and -25.1‰ in the Greifswalder Bodden (Müller and Voss 1999). Therefore, the high $\delta^{13}\text{C}$ -POC values together with the relatively low Chl-*a* concentrations at KW during summer suggest an additional import of degraded phytoplankton from the Greifswalder Bodden.

The higher availability of nutrients and OM offer an explanation for the up to 10 times higher phytoplankton growth at DW than at KW. As noted above, the POM at DW derived mostly from freshly produced phytoplankton; however, there were also clear signs of the remineralization of terrestrial POM during summer, likely due to the die-back of inundated vegetation. At KW, the majority of the POM derived from degraded marine phytoplankton, but signs of phytoplankton growth were also found. The fluctuating mixture of terrestrial and marine sources at both

sites well demonstrates the intensive water exchange between the peatlands and their adjacent bays (Supplementary Figure S1).

Nutrient exports, consequences for coastal areas, and comparisons with rivers

The higher NH_4^+ concentrations in the bay off DW than at monitoring station KB90 support our first hypothesis of an elevated nutrient export from the freshly flooded peatland into coastal waters (Fig. 5). Our data strongly suggest that the higher NH_4^+ concentrations and, on one occasion, the higher NO_3^- concentration in the bay off DW were caused by the rewetting and the subsequent outflow of nutrient-enriched waters.

A comparison of the annual DIN-N and $\text{PO}_4\text{-P}$ exports from KW and DW clearly demonstrates that rewetted peatlands can be sources of nutrients in coastal regions. The area-normalized DIN-N export from KW was $6.1 \pm 20.3 \text{ t km}^{-2} \text{ year}^{-1}$ whereas from DW it was threefold higher, $21.6 \pm 34.8 \text{ t km}^{-2} \text{ year}^{-1}$ (Supplementary Table S3). The high uncertainty range derives mostly from the seasonal, but also the spatial differences within the peatland areas. Due to the lack of comparable studies on nutrient exports from similar rewetted sites, we compared our data with mean river loads, which showed that nutrient exports from KW and DW were higher than the area-normalized riverine exports (Table 1). Specifically, among the five largest rivers entering the Baltic Sea, area-normalized DIN-N loads from 1995 to 2019 were highest in the Oder and Vistula rivers, with a mean of $0.3 \pm 0.1 \text{ t DIN-N km}^{-2} \text{ year}^{-1}$ for each river (HELCOM 2021). The Warnow River, near Rostock, drains $\sim 3000 \text{ km}^2$ of mostly agricultural land and

exports $0.4 \text{ t DIN-N km}^{-2} \text{ year}^{-1}$ (HELCOM 2021). When converted to absolute loads, $\sim 41,000 \text{ t DIN-N year}^{-1}$ are delivered by the Oder River (HELCOM 2021), compared to 10.8 and 21.5 t year^{-1} by DW and KW, respectively.

Area-normalized $\text{PO}_4\text{-P}$ exports from DW and KW were 0.5 ± 0.6 and $0.04 \pm 1.8 \text{ t km}^{-2} \text{ year}^{-1}$, respectively, whereas among the largest rivers around the Baltic Sea, the highest mean area-normalized $\text{PO}_4\text{-P}$ loads between 1995 and 2019 were those of the Vistula and Daugava rivers: 0.01 and $0.008 \text{ t km}^{-2} \text{ year}^{-1}$, respectively (HELCOM 2021). Absolute $\text{PO}_4\text{-P}$ exports from the Vistula River and Daugava River were $\sim 2800 \text{ t year}^{-1}$ and $\sim 700 \text{ t year}^{-1}$ (HELCOM 2021), whereas for DW and KW they were 0.2 t year^{-1} , respectively.

The much lower area-normalized loads of the rivers are the result of N and P reduction processes along the water flow, from surface soils to groundwater and to the coast, which reduce loads by $> 80\%$ (e.g., Seitzinger et al. 2006; Asmala et al. 2017; Xenopoulos et al. 2017). When coastal areas such as our study sites drain directly at the coast, the residence time of the water is much shorter, leaving nutrient loads mostly unprocessed. The finding that area-normalized DIN-N and $\text{PO}_4\text{-P}$ exports calculated for KW and DW were much higher than the exports of some major rivers of the Baltic Sea points to these rewetted peatlands as significant sources of local nutrient inputs into coastal waters.

To evaluate the potential magnitude of nutrient inputs from coastal peatlands in MV, the area-normalized exports determined in this study were extrapolated to the total area of the coastal diked and undiked (possibly wet) peatlands used for agricultural purposes, which according to Schiefelbein

Table 1 Comparison of nutrient exports from coastal peatlands (this study) and from major rivers of the Baltic Sea

Site	Area (km^2)	DIN-N export		$\text{PO}_4\text{-P}$ export		References
		Absolute (t year^{-1})	Area-normalized ($\text{t km}^{-2} \text{ year}^{-1}$)	Absolute (t year^{-1})	Area-normalized ($\text{t km}^{-2} \text{ year}^{-1}$)	
Karrendorf (KW)	~ 3.5	21.5 ± 71.0	6.1 ± 20.3	0.2 ± 6.3	0.04 ± 1.8	This study
Drammendorf (DW)	~ 0.9	10.8 ± 17.4	21.6 ± 34.8	0.2 ± 0.3	0.5 ± 0.6	This study
Oder	$\sim 119,000$	$\sim 41,000 \pm 15,000$	0.3 ± 0.1	$\sim 855 \pm 530$	0.007 ± 0.004	HELCOM (2021)
Vistula	$\sim 194,000$	$\sim 59,000 \pm 19,000$	0.3 ± 0.1	$\sim 2800 \pm 1500$	0.014 ± 0.008	HELCOM (2021)
Daugava	$\sim 88,000$	$\sim 18,000 \pm 4700$	0.2 ± 0.1	$\sim 690 \pm 250$	0.008 ± 0.003	HELCOM (2021)
Warnow	~ 3000	$\sim 1200 \pm 500$	0.4 ± 0.2	$\sim 20 \pm 7.6$	0.007 ± 0.003	HELCOM (2021)

(2018) is $\sim 225 \text{ km}^2$. The estimated area-normalized exports derived from the annual exports at our study sites are $13.9 \text{ t DIN-N km}^{-2} \text{ year}^{-1}$ and $0.3 \text{ t PO}_4\text{-P km}^{-2} \text{ year}^{-1}$. When related to the total area of coastal, farmed peatlands, potential nutrient exports are $\sim 3100 \text{ t DIN-N km}^{-2} \text{ year}^{-1}$ and $\sim 60 \text{ t PO}_4\text{-P km}^{-2} \text{ year}^{-1}$, which are significant loads compared to those of rivers. However, this extrapolation is a maximum estimate of potential exports; the nutrient reservoirs of other coastal peatlands may well be different from those of KW and DW. Nonetheless, the potentially significant contributions of small coastal catchments directly connected to coastal waters to nutrient inputs into the Baltic Sea highlight the need for better monitoring strategies following rewetting measures.

Conclusion

Two rewetted coastal peatlands, both formerly used for agriculture but clearly differing in their current nutrient reservoirs and nutrient cycling, were investigated in this study. DW was characterized by a high seasonal dynamic in the first year after rewetting. In contrast to the relatively large reservoir of nutrients within the peat of recently rewetted DW and considering that DW and KW were subjected to comparable fertilization regimens, the nutrient reservoir at KW had clearly declined since the rewetting in 1993. Our results suggest high microbial activity (nitrification and denitrification) within the peat. At KW, the retention of nutrients, i.e., NH_4^+ via nitrification and NO_3^- via denitrification, and the apparently tight link between these microbial processes ensure a well-balanced N-cycle, evidenced by surface water nutrient concentrations similar to those of the Bodden and lower rates of phytoplankton growth. At DW, however, nutrients have leached out of the soil rather than being retained, thus supporting a high rate of phytoplankton production in the surface water in spring and summer. The $\delta^{13}\text{C}$ -POC values of both peatlands indicated that they contain a mixture of marine and terrestrial POM, implying intense water exchange with the adjacent Bodden. Site-specific differences in the seasonality of the pH and $\delta^{13}\text{C}$ -POC values suggest that at DW, the remineralization of young dead organic material and peat was the dominant source of C uptake. By contrast, the high summer pH at KW is indicative of substantial C fixation.

The hydrological exchange with the adjacent Bodden resulted in a net nutrient export out of both peatlands. However, at KW, rewetted for 30 years, the area-normalized DIN export was $6.1 \pm 20.3 \text{ t km}^{-2} \text{ year}^{-1}$, which was only $\sim 25\%$ of the export at DW ($21.6 \pm 34.8 \text{ t km}^{-2} \text{ year}^{-1}$); $\text{PO}_4\text{-P}$ exports from the two sites were lower ($0.04\text{--}0.5 \text{ t km}^{-2} \text{ year}^{-1}$). Compared to riverine exports, the absolute exports from our study sites were low; however, the high area-normalized exports suggest the potential for intensified coastal eutrophication on a local scale. Our study shows that, despite being rewetted for decades, a peatland can still export nutrients into its adjacent waters, although the export rates will be highest immediately after rewetting and decrease over time. The potentially high, currently unmonitored nutrient exports to the Baltic Sea should be monitored regularly to enable accurate estimations of nutrient inputs from former agricultural (peat) soils.

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Data availability Environmental, nutrient, and N₂O data of DW were first analyzed in Pönisch and Breznikar et al. (2023) and are available at <https://doi.org/10.12754/data-2022-0003>. Data of KW and DW together are available at <https://doi.org/10.12754/data-2023-0008>.

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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