ROSTOCK UNIVERSITY

DOCTORAL THESIS

Nitrogen-related processes in coastal sediments of the Baltic Sea and a flooded peatland in NE-Germany

---

Author:
Tina LIESIROVA

Supervisor:
Prof. Dr. Maren Voss

A thesis submitted in fulfillment of the requirements
for the degree of Doctor rerum naturalium

Mathematics & Natural Sciences Department

Submission: 26.04.2023

Defense: 17.11.2023

https://doi.org/10.18453/rosdok_id00004616

Examiner:

Prof. Dr. Maren Voss - Leibniz Institute for Baltic Sea Research
Prof. Dr. Gerald Jurasinksi - University of Greifswald
Prof. Dr. Markus Weitere - Helmholtz Centre for
Environmental Research

Declaration of Authorship

I, Tina LIESIROVA, declare that this thesis titled, “Nitrogen-related processes in coastal sediments of the Baltic Sea and a flooded peatland in NE-Germany” and the work presented in it are my own. I confirm that:

- This work was done wholly or mainly while in candidature for a research degree at this University.
- Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.
- Where I have consulted the published work of others, this is always clearly attributed.
- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work.
- I have acknowledged all main sources of help.
- Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself.

Signed:

Date:

"I spent every night until four in the morning on my dissertation, until I came to the point when I could not write another word, not even the next letter. I went to bed. Eight o'clock the next morning I was up writing again. "

Abraham Pais

ROSTOCK UNIVERSITY

Abstract

Mathematics and Natural Sciences department of Rostock University

Doctor rerum naturalium

Nitrogen-related processes in coastal sediments of the Baltic Sea and a flooded peatland in NE-Germany

by Tina LIESIROVA

In the framework of "Baltic TRANSCOAST" funded by the German Research Society (DFG), this dissertation focuses on nitrogen-related processes in coastal sediments of the southern Baltic, as well as in an episodically flooded peatland of NE-Germany. Nitrogen (N) is crucial for organisms and through the nitrogen cycle, it is made bioavailable. However, the nitrogen cycle can be disturbed, which may affect the aqueous N-loading and stress entire ecosystems. Therefore, studies increasingly focus on nitrogen-related processes, especially in dynamic habitats where many biotic and abiotic variables interact with each other. This includes the marine-terrestrial transect between coastal sediments of the Baltic Sea and adjacent peatlands.

As first project, this thesis targeted sediment-associated N_2 fixation in coastal sediments of the Baltic. In times of climate change, the frequency of resuspension events (caused by storms) increases, thus, benthic N_2 fixation may occur in upper water layers during sediment resuspension. Resilient microbes like N_2-fixing sulfate reducing bacteria may be key players in this process. Sediments from five shallow locations along the north-eastern German coastline were sampled and - for comparison - from one deep muddy site in the Bay of Gdansk (Poland). The quantification of the N_2 fixation rates was carried out with the $^{15}N - N_2$ bubble method under dark conditions. The incubation occurred under simulated resuspension and usage of varying sediment depths reflected weak (0-5 cm) and strong (0-10 cm) resuspension events. In a parallel series, the contribution of sulfate reducing bacteria was assessed through the sodium molybdate technique. The N_2 fixation rates were related to sediment properties such as grain size distribution, dissolved nutrient concentrations, and organic matter content. Diazotrophy was found to be highest in the 0-5 cm section. Further, sulfate reducing bacteria were the dominant nitrogen fixers. The muddy sediments (Poland) reached the highest rates, while coarse-grained, shallow sediment deposits (Germany) displayed low rates due to organic carbon depletion. In summary, sediment-associated N_2

fixation was low, thus, increasing (storm and) resuspension events appeared not to lead to higher N_2 fixation in pelagic waters.

Storm events, however, also lead to flooding of low-lying coastal peatlands. Sudden seawater influx can disturb nitrogen cycling, which may cause aqueous nitrogen overload (eutrophication). Hence, the second aim of this thesis targeted nitrogen processes in a coastal peatland after a Baltic flooding event. With help of the ^{15}N-tracer method, dark ammonium assimilation and nitrification rates were determined in the surface water of the peatland over the course of one year. Nutrient concentrations (ammonium, nitrite, nitrate) and abiotic variables (salinity, dissolved oxygen, pH, temperature) were measured to monitor the ecological development of the peatland. Increased salinity was found to inhibit ammonium assimilation and nitrification. Despite low N-cycling rates, however, no inorganic nitrogen accumulation occurred. This shows, salt-stress dampened N-cycling, but did not cause immediate inorganic nitrogen overload.

Seawater intrusion, however, not only impacts surface waters, but also deeper soils, as cation exchange between seawater-sodium and soil-attached ammonium lead to ammonium leaching. Increased ammonium leaching pollutes ground- and coastal waters, thus, the third aim of this thesis quantified the ammonium loss from coastal peatland soils during seawater exposure. With help of a flow-through reactor, peat (0-10 cm) and mineral soils (30-40 cm) were flushed with artificial seawater ($<$ 1 ppt, 10 ppt, 35 ppt). The extracted ammonium concentrations were then related to the salinity of the respective solute treatment as well as the soil physical properties of the soils (soil organic matter, saturated hydraulic conductivity, bulk density, marco- and total porosity). Cation exchange between ammonium and sodium was not a dominant driver for N-loss. Instead, organic matter content associated with N-mineralization may induce ammonium-leaching, whilst other soil features (dual porosity) and processes (salinity-induced flocculation) may inhibit N-loss.

Acknowledgements

I want to thank my supervisor Prof. Dr. Maren Voß for her guidance throughout my doctorate studies. Special thanks goes also to my co-supervisors Prof. Dr. Gerald Jurasinski and Prof. Dr. Gregor Rehder, who supported me along the way. In addition I want to thank Iris Liskow and Christian Burmeister, and the lab staff at the University of Rostock including Evelyn Bolzmann and Dr. Stefan Köhler for lab assistance and general help. Further I want to thank Miaroun Wang (Rostock University), Cordula Gutekunst (Rostock University), Tobias Aarenstrup-Launbjerg (University of Copenhagen), Søren Hallstrøm (University of Copenhagen), Meriel J. Bittner (University of Copenhagen) and Lasse Riemann (University of Copenhagen) for our collaborative work. I also want to thank my working group at the IOW for their companionship in the past years. Lastly, I want to thank my family and especially my sister, since non of this would have been possible without their support.

Contents

List of Figures

List of Tables

List of Abbreviations

aeammox	**ae**robic **amm**onium **ox**idizers
aenitox	**ae**robic **nit**rate **ox**izers
AMO	**A**mmonia **M**ono**o**oxygenase
AOA	**A**mmonia **O**xidizing **A**rchaea
AOB	**A**mmonia **O**xidizing **B**acteria
AOB	**A**mmonia **O**xidizing **M**icrobes
AR	**A**mmonium assimilation **R**ate
ASV	**A**mplicon **S**equence **V**ariants
BD	**B**ulk **D**ensitiy
C	**C**arbon
DIC	**D**issolved **Inorganic** **C**arbon
DIN	**D**issolved **I**norganic **N**itrogen
DIP	**D**issolved **I**norganic **P**hosphate
DNRA	**D**issimilatory **N**itrate **R**eduction to **A**mmonium
DO	**D**issolved **O**xygen
DOM	**D**issolved **O**rganic **M**atter
FTR	**F**low -**T**hrough **R**eactor
HAO	**H**ydroxylamine **D**ehydr**o**genase
N	**N**itrogen
NCD	**N**on -**C**yanobacterial **D**iazotroph
nitros	anaerobic ammonium oxidizing archaea
NR	**N**itrification **R**ate
NOB	**N**itrite **O**xidizing **B**acteria

NXR	**N**itrite o**x**i**r**eductase
OC	**O**rganic **C**arbon
OM	**O**rganic **M**atter
OTU	**O**perational **T**axonomic **U**nit
P	**P**hosphate
PCR	**P**oly **C**hain **R**eaction
ppt	**p**arts **p**er **t**housands
SOM	**S**oil **O**rganic **M**atter
SRB	**S**ulfate **R**educing **B**acteria
T	**T**emperature
TDN	**T**otal **D**issolved **N**itrogen
TOC	**T**otal **O**rganic **C**arbon

Dedicated to my dad. You would have loved this.

Chapter 1

Introduction

This PhD-thesis was carried out in the framework of the Research Training Group Baltic TRANSCOAST, funded by the German Research society (DFG). Overall Baltic TRANSCOAST investigates as the first project the marine-terrestrial transect between coastal peatlands of NE-Germany and the Baltic Sea by researching the water and nutrient exchange across the coastal ecoline. The introduction of this dissertation provides essential information on the significance of nitrogen-related processes in coastal sediments and in seawater-flooded peatlands respectively. In the following, characteristics of coastal sediments and flooded peatlands of the southern Baltic are described. Moreover, nitrogen processes including heterotrophic nitrogen fixation, ammonium assimilation, nitrification, and ammonium leaching from soils are being elaborated.

1.1 The Baltic coastline

1.1.1 Sediments

The Baltic Sea is the one of the largest brackish water body globally. Through the Skagerrak in the west, the Baltic Sea is connected to the North Sea which supplies saline water to the Baltic which is otherwise predominantly fed by riverine freshwater. The Baltic Sea coastline was shaped during the last glacial transgression (Littorina Sea stage; 8,000 cal yr BP) and consists mainly out of post-glacial sediment deposits (Björck, 1995). Continuous coastal erosion, sea level fluctuations, as well as sediment transport and deposition have since lead to a cycle of land loss and -retrieval along the shorelines, which created unique ecosystems with strong interaction between marine and terrestrial site (section 1.3.3; Lampe et al., 2011). The sediment deposits along the northern German coastline cover a wide grain size spectrum. Around Bay of Lübeck there are predominately muds, however, with patches of fine and coarse sand around the island of Poel (Leipe et al., 2017). Eastwards along the shoreline passing Rostock and leading to Zingst, the sediments are alternating between fine and coarse sands. Around Greifswald, the sediments are composed out of coarse silts or muds, before turning into predominately fine sand deposits again (Leipe et al., 2017). The organic matter content in these sediments is closely related to the sediment type and is generally higher in the muddy and silty sediments and lower in the sandy deposits (Leipe et al. 2017). In the past, the land area adjacent to the southern Baltic Sea were largely used for agricultural purposes which created nutrient-rich runoff. These dissolved substances leached to the marine side and caused eutrophication and hypoxic conditions in estuarine sediments, as seen for instance in the Bay of Gdansk (Humborg et al., 2003). Previous studies suggested that the coastal zones of the Baltic have only limited exchange with the open Baltic Sea (Voss et al., 2005) and have therefore an internal elemental cycling system. Still, little is known about specific nitrogen cycling processes (e.g. N_2 fixation) in coastal sediments of the Baltic.

1.1.2 Peatlands

Peatlands are organic-rich wetlands, that have formed by the incomplete decomposition of plant residuals under anoxic conditions over millenia. At present, peatlands take up 3 % of global terrestrial space (Gorham, 1991; Hugelius et al., 2020), thereby, they store 30 % of land-based organic carbon (300-450 Pg C) and nitrogen (5.9 - 25.9 Gt N), and 10 % of all freshwater (Bragazza et al., 2013; Rezanezhad et al., 2016; Yin et al., 2022). For this reason, they are not only considered important carbon and nitrogen sinks on earth (Joosten and Clarke, 2002), but also important habitats for flora and fauna due to their intermediate state between aquatic and terrestrial ecosystems (Joosten and Clarke, 2002; Krüger et al., 2015). Peatlands are found in arctic, alpine, boreal, taiga, temperate and tropical settings (Joosten and Clarke, 2002; Rezanezhad et al., 2016). There are multiple types of peatlands, mainly categorized on grounds of their peat-formation capacity, vegetation, hydrology and water chemistry (Joosten and Clarke, 2002; Rezanezhad et al., 2016). Peatland types include mires, peat bogs, salt marshes, swamps, and fens, thereby, fens are one of the most common peatland-types in central Europe, especially at the German coastline (Höper, 2002; Zauft et al., 2010). Fens develop in terrestrial depressions (e.g. glacial kettle holes; Campbell et al., 1997) and are connected to a freshwater source. They receive their nutrient input both by atmospheric deposition (rain, snow) and from surrounding mineral terrain and are therefore also called minerotrophic peatlands (Joosten and Clarke, 2002). They have a neutral pH range (4.5 - 7.4) and grow mostly brown mosses and herbaceous plants (sedges; Joosten and Clarke, 2002). In Germany, agricultural land use and drainage has reduced prinstine, peat-forming fens by 99 % over the past two centuries, which resulted in aerobic decomposition of the peat soil (Giebels et al., 2010). The peat decay lead -amongst others- to increased gaseous carbon and nitrogen emissions (e.g. carbon dioxide, methane, nitrous oxide), soil subsidence, loss of habitats and eutrophication, which was further accelerated by rising soil temperatures (Schwieger et al., 2021). This effectively turned these peatlands into carbon and nitrogen sources with damaging impact on the climate (Giebels et al., 2010; Joosten, 2009; Leifeld et al., 2019). Due to their vulnerability, drained peatlands in Germany are nowadays being rewetted to re-establish waterlogged conditions, which should disable or moderate organic matter decomposition, and possibly stimulate peat formation again (Moore et al., 2007). Rewetting occurs by raising the water table in the peatland, for instance by build-up of ground sills to retain water (Miegel et al., 2016). At the German Baltic coastline, low-lying coastal fens are also rewetted by Baltic floodings, as protective dune dykes erode, and sea levels and the frequencies of storm events rise there (Dreier et al., 2012; Jurasinski et al., 2018). Despite the efforts of rewetting peatlands again, water saturation of the peat soil has proven to not solely restore the peatland to its pristine functioning again, since prior drainage permanently changed the peatland ecology (Lamers et al., 2015; Rezanezhad et al., 2016). Under times of climate change many studies focused therefore on the carbon emission and sequestration potential of rewetted peatlands (Bérubé and Rochefort, 2018; Tuittila et al., 1999), however, other biogeochemical processes equally important and related to the nitrogen cycle have been neglected.

1.2 Nitrogen-related processes along the Baltic coastline

Nitrogen is crucial for all living organisms to build up complex biomolecules such as DNA, proteins and organic biomass in general (Stankiewicz and van Bergen, 1998). Even though 78 % of the atmosphere consists of N_2, it is not available to most organisms due to its strong triple-bond, which makes N_2 almost inert (Karl and Michaels, 2001; Widdison and Burt, 2008). Nitrogen is made bioavailable by nitrogen fixing organisms, as N_2 is converted into ammonium. In a set of microbial processes, ammonium is transformed into further reactive N-compounds (nitrite, nitrate, dissolved and particulate organic nitrogen) before denitrification and anaerobic ammonium oxidation (anammox) release N_2 back to the atmosphere (Karl and Michaels, 2001). Three major processes investigated in this thesis are nitrogen fixation (section 1.2.1), which describes the conversion of N_2 into bioavailable NH_4^+, nitrification (section 1.2.2), which is the subsequent oxidation of ammonium to nitrite (NO_2^-) and nitrate (NO_3^-), and N-assimilation (section 1.2.2), by which inorganic nitrogen (e.g. NH_4^+) is used to build-up organic nitrogen (Karl and Michaels, 2001; Keiser et al., 2016; Widdison and Burt, 2008). The remaining major nitrogen pathways are dissimilatory nitrate reduction to ammonium (DNRA), and ammonification (decomposition of organic nitrogen), which both 'recycle' reactive nitrogen in ecosystems, as well as denitrification and anammox, which allow nitrogen to escape as N_2 (Karl and Michaels, 2001; Keiser et al., 2016; Widdison and Burt, 2008). The processes of the nitrogen cycle occur either aerobically or anaerobically, however, certain N-related microbes may also operate facultatively (Pajares and Bohannan, 2016). Through primary production, and the build-up and breakdown of organic matter, the nitrogen cycle is strongly linked to the water, carbon, and phosphorus cycle (Karl and Michaels, 2001). These complex cycles interact with each other often in a 'non-linear' manner (Ray et al., 2015), nevertheless, imbalances in the nitrogen pool (Gijzen, 2001) have immediate impacts on the other cycles and can affect entire ecosystems (Keiser et al., 2016; Malone and Newton, 2020). A prominent example of a large-scale nitrogen imbalance is the harmful nutrient-overload (eutrophication) in the coastal areas of the Baltic Sea during summer (Vigouroux et al., 2021). During eutrophication, N-availability exceeds N-removal (e.g. by increased nitrogen fixation or anthropogenic pollution) and growth of harmful algae and plants are accelerated. The high biomass loading in the water eventually decomposes due to aerobic degradation. Consequently, dissolved oxygen gets depleted and anoxia occurs (Malone and Newton, 2020; Nixon, 1995; Olofsson et al., 2020). As a result, organisms suffocate, aquatic biodiversity declines and critical habitats are lost (Murray et al., 2019).

Excess nitrogen loading may also occur through stress-induced inhibition of internal nitrogen-cycling e.g. by salinization. At the coast of Mecklenburg Western Pomerania (NE Germany) low-lying coastal peatlands are prone to be rewetted by Baltic floodings (Hoggart et al., 2014) which rises the salinity in the fen and thus, significantly changes the ecosystem chemistry (Wang et al., 2021). Salinization can stress *in situ* freshwater microorganisms and as a result, nitrogen-cycling (and ultimately removal) processes may be disturbed and the water quality is reduced. Soil exposure to saline water may also induce cation exchange between seawater salt (sodium) and ammonium, which is attached in the soil. This can lead to nitrogen loss through leaching and impact the nutrient pool of ground- and coastal waters (Gosch et al., 2019; Liu and Lennartz, 2019).

1.2.1 Heterotrophic nitrogen fixation in coastal sediments

Even though dissolved dinitrogen in seawater is abundant (> 400 µmol L^{-1}; Voss et al., 2013), it is not accessible to most organisms. However, certain bacteria and archaea, called diazotrophs, are capable of N_2 fixation, which describes the conversion of inert N_2 into ammonium. Diazotrophs include anaerobes, facultative aerobes, aerobes, and phototrophs (Zehr, 2011), however N_2 fixation is an energetic-costly process, thus, only few species perform it. Diazotrophs carry the N_2-fixing enzyme complex called nitrogenase. The most common nitrogenase complex contains two distinct protein forms, an iron protein (dinitrogenase reductase) and a molybdenum-iron protein (dinitrogenase). The gene encoding of the complex can contain up to 20 *nif* (nitrogen-fixing) genes (e.g. *nifH, nifD, nifK*), but the *nifH* gene is generally used for molecular studies (Zehr, 2011). On a global scale, the calculated nitrogen fixation rates have an estimated range of 100 – 200 Tg N yr^{-1} (Capone et al., 2005; Deutsch et al., 2007), which provides significant amounts of bioavailable N to the marine N-pool. N_2 fixation occurs favorably in nutrient-poor aquatic environments and is important for primary production and the marine foodweb (Moore et al., 2013). Moreover, N_2 fixation is crucial for the build-up of organic matter in upper water layers and carbon export to deep sea regions, also known as the "biological pump" (Longhurst and Glen Harrison, 1989). Thus, N_2 fixation represents an important link between nitrogen and carbon cycle and enables carbon sequestration in oceans. Until recently, marine N_2 fixation was largely attributed to two types of cyanobacteria, namely free-living filamentous *Trichodesmium* and diatoms which live in symbiosis with *Richelia*. However, the identified diazotroph catalogue increased, and free-living unicellular cyanobacteria (*Crocosphaera*), and a group of novel unicellular cyanobacteria (UCYN-A) which occur in symbiosis with algae (Zehr and Capone, 2020) are representatives. To date, a few hundred cultivated species are known (Abadi et al., 2021).

N_2 fixation is controlled by many variables which can either promote or inhibit the process, including variables like temperature, dissolved oxygen, dissolved iron (Ibello et al., 2010) and phosphorous (Küpper et al., 2008), sometimes silica (Carpenter et al., 1999), and fixed nitrogen (Capone et al., 2005). The effect of these variables is species-specific, for instance some diazotrophs prefer warmer temperatures (Breitbarth et al., 2007), whilst others endure lower temperature ranges (Lehtimaki et al., 1997). The nitrogenase complex is highly oxygen sensitive and brief contact can deactivate it. Yet, certain diazotrophs have adapted and developed heterocysts (separate cell protecting nitrogenase) to enable N_2 fixation in presence of dissolved oxygen, or perform only in oxygen micro niches caused by intensive local O_2-consumption (Pedersen et al., 2018).

Other species adaptations include the use of alternative nutrient sources under limiting conditions, for instance phosphonate instead of phosphate (Sohm et al., 2011). Elevated amounts of fixed nitrogen (e.g. ammonium) were generally known to inhibit nitrogen fixation (Capone et al., 1990), as the breakup of inert N_2 is energetically more expensive than ammonium uptake. However, this understanding was recently challenged, since certain diazotroph strains displayed resilience against inorganic N, as they only experience some (Martín-Nieto et al., 1992; Andersson et al., 2014) or no inhibition (Sanz-Alferez and del Campo, 1994; Newell et al., 2016; Bertics et al., 2013). Possibly some of these diazotrophs profited from N_2 fixation by employing it as a viable electron sink (Joshi and Tabita, 1996; Tichi and Tabita, 2000). This helped them to control the redox balance inside the cell and making nitrogen availability negligible.

Amongst these nitrogen-resilient diazotrophs were heterotrophic diazotrophs (or non-cyanobacterial diazotrophs; NCD), which occupied light-deprived, nutrient-saturated sediments (Bertics et al., 2013; Pedersen et al., 2018). NCD activity was often considered negligible in comparison to cyanobacterial activity. Indeed, their importance was poorly understood due to high variability of benthic N_2 fixation (Steppe and Paerl, 2005; Severin and Stal, 2012) affected by seasonally fluctuating conditions (e.g. DO, DIN, organic matter; Burns et al., 2002, Fulweiler et al., 2013, Jabir et al., 2021). Nevertheless, NCD acitivity could be substantial enough to make up for the nitrogen losses through denitrification (Fulweiler et al., 2013; Fan et al., 2015). Prominent NCD are sulfate reducing bacteria (SRB; Gandy and Yoch, 1988; Zehr et al., 1995). SRB are already key players for the carbon and sulfur cycle (e.g. by organic matter mineralisation and sulfide production; le Gall and Postgate, 1973; Caffrey and Voordouw 2010; Stoeva et al., 2019; Niu et al., 2021). Also, SRB are strict anaerobs and are found worldwide in sediments. So far, studies on SRB focused on their environmental stress-responses and their detailed community composition in order to better understand their importance for benthic N_2 fixation (Bertics et al., 2013; Gier et al., 2016; Jabir et al., 2021). As expected, diazotrophic SRB were affected by dissolved oxygen (DO) fluctuations as it inhibits nitrogenase activity and stressed their strictly anaerobic metabolism (Bertics et al., 2010). Still, certain SRB also adapted to oxic conditions, thanks to the aforementioned oxidative stress protection systems securing nitrogenase activity (Lumppio et al., 2001; Jabir et al., 2021; Geisler et al., 2022).

Further studies reported that organic carbon stimulated N_2-fixing SRB (Spinette et al., 2019; Burns et al., 2002, Bertics et al., 2013) as they require external carbon sources (unlike phototrophs). Yet, interestingly single-factor experiments targeting N_2-fixing SRB under organic carbon supply remained inconclusive (Gandy and Yoch, 1988); other SRB satisfied their carbon needs by simply switching from carbon (as electron donor) to hydrogen (Lespinat et al., 1987) or engaged in symbiosis with microorganism like anaerobic methanotrophs (Pohlman et al., 2013; Dekas et al., 2014). Altogether, diazotrophic SRB seem to be able to inhabit a wide spectrum of environmental habitats with species-specific stress responses, and are thus, still poorly understood.

Up to now, benthic N_2 fixation was mostly investigated in dark, deep sea environments (Bertics et al., 2013; Dekas et al., 2018). Consequently, physical factors irrelevant for deep sea environments, but possibly affecting diazotrophs were neglected such as sediment resuspension in near-coastal systems (Andersson et al., 2014). Especially the coastal environments of the Baltic Sea are increasingly subject to strong resuspension events due the higher frequency of storms (Dreier et al., 2021). Thereby, sediments and sediment-attached substances (inorganic nutrients, organic matter) are resuspended into pelagic layers, influencing benthic N_2-fixing communities and their activity. Andersson et al. (2014) reported on the inhibiting impact of resuspension on sediment-associated N_2 fixation along the Swedish coastline, whilst

Pedersen et al. (2018) observed that resuspended sediments of the Roskilde Fjord (Denmark) were microbial hotspots for NCD (and SRB) activity. It remains to be determined, if benthic N_2 fixation in shallow sediments of the Baltic Sea are a significant nitrogen source to pelagic layers under resuspension.

1.2.2 Ammonium assimilation and nitrification in flooded peatlands

Nitrogen (ammonium and nitrate) assimilation is crucial for the formation of organic molecules (e.g. amino acids), growth, and primary production (Forchhammer, 2007; Herrero et al., 2019) and acts as nitrogen sink (Masclaux-Daubresse et al., 2006; Mokhele et al., 2012). The assimilation of ammonium (NH_4^+) requires less energy than the assimilation of nitrate and is therefore advantageous under energy-limiting conditions (Ruan and Giordano, 2017). Key enzymes involved in NH_4^+ assimilation are glutamine synthetase (GS), glutamate synthetase (also known as glutamine oxoglutarate aminotransferase; GOGAT), and glutamate dehydrogenase. These enzymes turn ammonium into glutamine and glutamate and enable the intercellular nitrogen metabolism (Pengpeng and Tan, 2013; Wang et al., 2011). NH_4^+ assimilation is often bonded to photosynthesis and stimulated during summer months (LeCorre et al., 1996) and hence, a substantial source of organic N (Lea, 1985). Some cyanobacteria and plants can also assimilate under dark conditions at reduced rates (Kerby et al., 1987; Papen and Bothe, 1984; Rigano et al., 1996). There is also light-independent NH_4^+ assimilation by heterotrophs (Wheeler and Kirchman, 1986). Non-photosynthetic NH_4^+ assimilation has only recently gained attention (Laws et al., 1985), and it appears

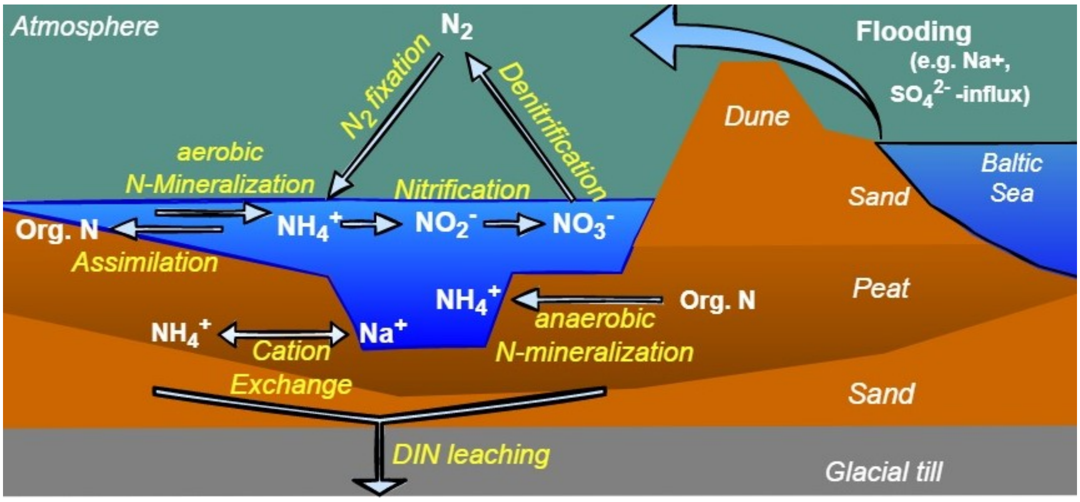


FIGURE 1.1: Topographic profile of the Hütelmoor (simplified). Yellow = nitrogen cycling- and nutrient related processes; white = dissolved and organic compounds.

to be a major organic N-source in dark waters (Caraco et al., 1998) and sediments (Sumi and Koike, 1990). Favoring conditions for dark NH_4^+ assimilation are DIN-rich environments (Suberkropp and Chauvet 1995) with increased carbon input (Caraco et al., 1998). Moreover, dark NH_4^+ assimilation occurs during all seasons (LeCorre et al., 1996). Lately, heterotrophic NH_4^+ assimilation has been detected in surface waters of wetlands (Ma et al., 2022), and was recognized as substantial NH_4^+-removal pathway in aquatic ecosystems (Sun et al., 2017). Whether dark NH_4^+ assimilation is also important in seawater-rewetted peatlands with increased salinity concentrations is uncertain. Interestingly though, cellular glutamate formation may protect the microbes from salt-stress, as glutamate can act as osmolyte and regulate the salt-concentrations within the cell (Csonka, 1989; Empadinhas and Viete-Vallejo, 2008) as seen in single-factor studies (Hudson et al., 1993; Smith et al., 1980). For this reason, enzymes linked to NH_4^+ assimilation may help freshwater microorganisms to counter seawater-induced osmotic stress in rewetted peatlands.

It is generally understood, that ammonium assimilation stands in direct competition with nitrification (Aldunate et al., 2020). Nitrification describes the two-step oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-) (Norton and Ouyang, 2019). Thereby, nitrification is mostly performed by slow-growing chemolithoautotrophs (Wang et al., 2012) which obtain energy by the aerobic oxidation from ammonium or nitrite whilst taking in dissolved inorganic carbon (DIC). Alternatively, some nitrifier can also use organic nitrogen (e.g. urea; Alonso-Sáez et al., 2012; Pommerening-Röser and Koops, 2005) or organic carbon (Qin et al., 2014) as respective N- and C-source. Each oxidation-step is carried out by a completely different group of prokaryotes, namely the ammonium-oxidizing archaea and bacteria (AOA, AOB) and the nitrite-oxidizing bacteria (NOB). AOA and AOB carry the ammonia-oxiziding genes ammonia monooxygenase (AMO) and hydroxylamine dehydrogenase (HAO), whilst NOB carry the nitrite-oxidizing gene nitrite oxidoreductase (NXR; Sun et al., 2020). Few microbial species carry both ammonia- and nitrite-oxidizing genes, and are therefore able to oxidize NH_4^+ directly to NO_3^-, (e.g. *Nitrospira*). This process is called "complete ammonia oxidation" (comammox) and was observed in drained, forested peat soils (Truu et al., 2020), tidal flat wetlands (Sun et al., 2020), and other soil types (Huang et al., 2021; Orellana et al., 2018). This shows, comammox is a widely-occurring process in terrestrial environments (Pjevac et al., 2017). However, comammox-organisms are understood to be distinctively ecophysiologically different from canonical nitrifiers (Koch et al., 2019; Lu et al., 2020), and will not be further discussed here.

Generally, the activity of canonical nitrifiers (AOA, AOB, NOB) is highly variable in terrestrial environments, as they are controlled by a complex interplay of biotic and abiotic factors, including substrate supply (NH_4^+, NO_2^-), temperature, pH, salinity, moisture and aeration (Norton and Ouyang, 2019). Substrate supply of NH_4^+ offers the means for ammonia oxidation, which is an important rate-limiting step for overall nitrification (Lehtovirta-Morley, 2018; Norton and Ouyang, 2019). The NH_4^+ availability in terrestrial environments is controlled by the use of N-fertilizers, animal excrements (urine and feces), atmospheric deposition, N_2 fixation and organic matter mineralization (Bouskill et al., 2012; Grant, 1994; Ouyang et al., 2018; Venterea et al., 2015). However, N-assimilation or competitive organisms (e.g. comammox bacteria; Lu et al., 2020; Norton and Ouyang, 2019; Verhagen et al., 1992), can limit NH_4^+ supply to nitrifiers, and reduce nitrification. Varying concentrations of ammonium can also influence the quantitative contribution of AOA and AOB to nitrification. For instance, under low NH_4^+ supply the contribution to gross nitrification by AOA is higher than by AOB (Hink et al., 2017a). In turn, with greater NH_4^+ availability gross nitrification by AOB is higher than by AOA (Rütting et al., 2021), even though total gene abundance of AOA in soils is generally higher (Di et al., 2009). Earlier, the NH_4^+-affinity of AOA and AOB were discussed being responsible for these variations, similar to marine environments (Horak et al., 2013; Martens-Habbena et al., 2009). Soil-studies revealed though, that AOA and AOB have equal NH_4^+-affinity (Hink et al., 2017b; Kits et al., 2017) and instead, the rate differences may be related to the 10-fold greater cell size of AOB compared to AOA (Prosser and Nicol, 2012), giving AOB an advantage in NH_4^+-rich environments (Jia and Conrad, 2009; Karlsson et al., 2012). This suggests that nitrifier abundance and community composition (AOA or AOB) directly affect nitrification (Aigle et al., 2020; Norton and Ouyang, 2019). Changes in the community composition can be derived by alternating environmental conditions, for instance by temperature and pH. The majority of nitrification-studies consider temperature and pH as single factors only (Aigle et al., 2020; Wallenstein and Hall, 2012; Kyveryga et al., 2004; Parton et al., 2001). However, the combined effect of temperature and pH on nitrifiers is rarely considered, even though both variables are strongly physio-chemically related to each other (Zaidi and Pal, 2015). Moreover, Lång et al. (1993) observed during incubation at low temperatures (4 °C), that the nitrification potential shifted its pH optima from pH 6 to 4, and suggested, that a microbial community change was responsible for the shift. Aigle et al. (2020) directly hints towards the possibility that neutrophilic nitrifiers - thriving at neutral pH - have a higher temperature optimum than acidophilic nitrifiers which prefer low pH. So far, studies are still scarce and correlations between temperature, pH, community composition and gross nitrification are weak (Aigle et al., 2020).

In seawater-flooded peatlands, the impact of salinity on nitrification is relevant. Studies showed, low saline conditions inhibit nitrification in natural soils (respectively 3.5 ppt or 4 mS cm^{-1}; Noe et al., 2013; Yao et al., 2022). Interestingly, NH_4^+- and NO_2^- oxidation rates appeared to be reduced disproportionally by sodium chloride (Moussa et al., 2006) and sulfide (Bejarano Ortiz et al., 2013), which indicates that AOM and NOB have varying tolerance to seawater-induced stress. Consequently the accumulation of dissolved inorganic nitrogen (Cortés-Lorenzo et al., 2015), or emission of nitrogen gases (e.g. nitrous oxide; Berendt et al., 2022) may occur. Nevertheless, soils that are naturally exposed to seawater at high frequency can establish halo-tolerant species (e.g. *Nitrosopumilus*) which are adapted to (episodically) saline conditions (Nacke et al., 2017). This underscores the importance of community versatility in dynamic ecosystems exposed to fluctuating environmental conditions such as seawater flooded soils. However, community composition and adaptive strategies cannot necessarily prevail against critical soil moisture concentrations and soil oxygen depletion. Soil moisture can be limiting for nitrifiers when the soil water-filled pore space is too low (< 40 %) as it causes cell dehydration (Parton et al., 2001). However, full water saturation (waterlogging) may deplete dissolved oxygen content and thus, limit oxidation of NH_4^+ and NO_2^- and respiration of nitrifiers (Norton and Ouyang, 2019). Interestingly though, nitrifiers have a microaerophilic lifestyle, which means they operate best at low oxic conditions as they are not obligate aerobes (Geets et al., 2006; Ward, 2008). With this, nitrification is not restricted to purely aerated locations, but can also occur at oxic-anoxic interfaces. This enables a close coupling to anoxic N-processes (e.g. denitrification, anammox) especially under fluctuating redox conditions (Nie et al., 2019). Still, seawater-rewetting of drained peatlands can change the metabolism and community composition of microorganisms (Groß-Schmölders et al., 2021) by reducing metabolic efficiency and enzyme activity (Rietz and Haynes, 2003). Therefore, these (potentially) vulnerable habitats require attention, as to gain a better understanding on internal N-cycling under salinization.

1.2.3 Salinity-induced ammonium loss from rewetted peatland soils

The functionality of pristine peat soils is characterized by its capacity of water retention, transport and release of dissolved compounds, the chemical composition of the water, and geophysical properties of the soil matrix (Hill and Siegel, 1991; Päivänen, 1973; Rezanezhad et al., 2016). Geophysical properties in peat soils include soil organic matter (SOM), bulk density, saturated hydraulic conductivity (K_S), and macro- and total porosity. Coinciding with a high total porosity of > 80 % , peat is also known for its complex dual-porosity structure (Boelter, 1968; Rezanezhad et al., 2012). Dual-porosity means there are active, open pores, where water can flow through (mobile soil water region; Kleimeier et al., 2014; Rezanezhad et al., 2016), but also partially closed or dead-end pores, where water movement is either negligible or limited to diffusion (immobile soil water region; Hoag and Price, 1997; van Genuchten and Wierenga, 1976). Hydraulic properties of peat are strongly dependent on its degree of decomposition, which alters with soil depth, age, type of plant residuals, and the drainage regime (Schoephorster, 1974; Swanson and Grigal, 1989) as described by the *von* Post humification scale (von Post, 1922).

So far, only few studies focused on solute transport within peat soil with these complex hydraulic properties (Hoag and Price, 1997; Reeve et al., 2001; Rezanezhad et al., 2016). However, recently nutrient solute release and transport gained attention in rewetted peatlands (Gosch et al., 2019; Liu and Lennartz, 2019), where former cultivation has altered the geophysical characteristics of the soil (e.g. by aeration, compaction; Jurasinski et al., 2020; Monteverde et al., 2022; Mustamo et al., 2016) and seawater rewetting changed the water (bio-) chemistry through salinization. For instance salinization can directly enable release of dissolved organic and inorganic carbon (DOC, DIC) and total dissolved nitrogen (TDN) from peat-soils (Liu and Lennartz, 2019). Regarding the latter (TDN), two prominent seawater compounds, namely sulfate (SO_4^{2-}) and sodium (Na^+) can induce dissolved nitrogen release by acting either as terminal electron acceptor for anaerobic N-mineralization (Gosch et al., 2019), or as cation exchange partner detaching ammonium from the peat (Liu and Lennartz, 2019). Excess NH_4^+ released from the peat during cation exchange may origin from former heavy N-fertilization and manure management, which enriched the top layers of the soil with nitrogen (Liu and Lennartz, 2019; Zak and Gelbrecht, 2007), however it remains ambiguous how this ammonium loss affects groundwater quality, the coastal seawater nutrient pool (e.g. due to submarine groundwater discharge; Racasa et al., 2021; see section 1.3.3) and if this is a temporary, long term, or an episodic effect.

1.3 Study site "Hütelmoor"

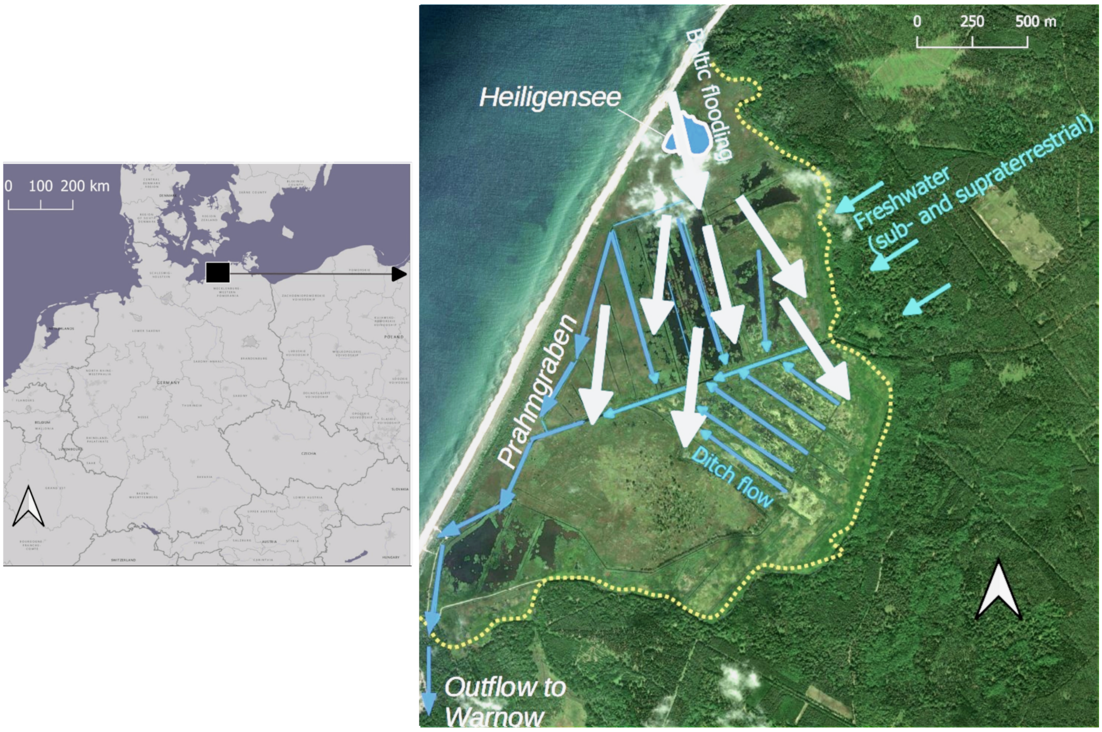


FIGURE 1.2: Hütelmoor area (framed with yellow dotted line) with Heiligensee in the north, ditches and channels leading to the outflow point in the south. Arrows display simplified hydrological flows. Blue: Flow direction of the ditches. White: Spreading of the Baltic seawater close to Heiligensee during flooding event in January, 2019. Light blue: Freshwater supply from higher terrains.

1.3.1 Background and history

The nature reserve “Heiligensee und Hütelmoor” is a low-lying peatland (fen) situated close to Rostock (54°12′36.66" N, 12°10′34.28" E) at the Baltic Sea coast of northern Germany (Figure 1.2). Until the 1970s, the fen was used for agricultural purposes and drained with help of ditches and channels, which lowered the water tables < 1.6 m below surface (Glatzel et al., 2011). In addition, a coastal protection dune was built in 1903 and rebuilt in 1963 to strengthen the sand dune along the beach which protected the area from the Baltic (Jurasinksi et al., 2018). In the 1990s the nature reserve was subsequently rewetted by freshwater to restore the peatland ecology.

Also, the coastal protection dune was eventually not serviced anymore enabling coastal erosion with retreat rates of 120 - 210 cm yr^{-1} (Generalplan Küsten und Hochwasserschutz, Mecklenburg- Vorpommern). Until today, the ditches and channels still exist (Koch et al., 2014; Hahn et al., 2015; Unger et al., 2021; Figure 1.2), are (partly) active and lead southwestwards to the dredged and widened shipping channel that includes the Warnow and enters the Baltic Sea (Toro et al., 2022). The water tables returned to 0.3 m below ground after abandonment of active drainage in the 1990s (Glatzel et al., 2011). To effectively retain water in the peatland, a ground sill (of app. 0.5 m HN) was built in 2009/ 2010 at the outflow point of the peatland (Figure 1.2), and subsequently, water levels mostly ranged above surface in large parts of the areas (Miegel et al., 2016). The annual mean outflow rate from the peatland is about 44 L s^{-1}. During summer the outflow stops when the water level declines below the ground sill and is increased during strong precipitation events especially during autumn and winter (Miegel et al., 2016). In 1995 the Hütelmoor was flooded with brackish water from the Warnow river via the Sohlschwelle in the west of the peatland by reversed inflow through the ditches and channels, as well as through a dyke breach (Bohne and Bohne, 2008). This led to salinization of the fen, reaching also deeper soil layers through leaching (ca. 2 - 7 ppt; Koebsch et al., 2013; Jurasinksi et al., 2018). The dyke was rebuilt after the breach, but maintenance stopped in 2000. In Januar 2019, a major storm event occurred, which caused again a dyke breach close to the Heiligensee, a beach lake in the north of the study area. Baltic seawater (22 mS cm^{-1} or ca. 13 ppt; Gutekunst et al., 2022) infiltrated the peatland directly from the seaside for the first time in more than two decades. The seawater spread out via Heiligensee and further across the peatland and increased the previously low peatwater salinities (2 mS cm^{-1} or ca. 1 ppt; Koebsch et al., 2019; Gutekunst et al., 2022; Figure 1.2).

1.3.2 Topography

The fen spans an area of 540 ha of which 315 ha are peatland. The area is confined by a forest which stands on slightly higher terrain (0.5 - 2 m amsl; Figure 1.2; (Miegel et al., 2016)). The elevation of the peatland itself is between -0.1 m to $+0.7$ m amsl (Jurasinski et al., 2018; Miegel et al., 2016), thereby the areas below 0 m HN are mostly in the southwest of the area (Miegel et al., 2016), which aligns with the horizontal water flow direction in the ditches and channels.

The average air temperature accounts for 9.6 °C, annual precipitation is approximately 635 mm (measured between 1991 and 2020; freely available data by German Weather Service), and evaporation 641 mm (Bohne and Bohne 2008). Both the forest in the north and the dyke along the Baltic coast offer wind protection to the peatland, which has suggested to lead to a microclimate similar to the "oasis effect" and high humidity (Bohne and Bohne 2008). The upper soil profile consists of peat, which overlies a mineral (sand) and a glacial till layer. The thickness of the different layers varies across the peatland, thereby the peat is mostly 1 - 3 m thick and increases with proximity to the coastline (Miegel et al., 2016). Parts of the peat horizon continue underneath the soil surface and reemerge at the beach, representing a minor, vertical connection between fen and Baltic Sea (Jurasinski et al., 2018). Due to drainage and cultivation the topsoil of the peat experienced aeration, which enabled increased organic matter mineralization and led to a high degree of peat degradation. Lower peat sections remain moderately to strongly decomposed (Jurasinski et al., 2018).

1.3.3 Marine-terrestrial transect

The 3 km coastline adjacent to the Hütelmoor represents a shallow offshore continuation (0 - 10 m depth) of the peatland and is crossed by layers of peat (Kreuzburg et al., 2018). The resurfacing peat layers developed due to coastal erosion which lead to peatland loss towards eastern direction. Marine currents transported sediments alongshore in northeastern direction (Lampe et al., 2011) which subsequently covered and abraded the peat layers at the beach (Kreuzburg er at., 2018). The peat deposits reach upto 90 m from the coastline with an areal extent of 0.16 - 0.2 km^2 (Kreuzburg et al., 2018). The resurfacing peat deposits in the northern coastal area are most likely connected with the land side through submarine groundwater discharge (SGD; Jurasinski et al., 2018). SGD are common along the Baltic Sea coastline connecting the terrestrial groundwater with coastal waters by enabling outflow of (nutrient-rich) groundwater from land to sea (Racasa et al., 2021).

1.4 Analytical approaches and calculations

1.4.1 ^{15}N- tracer method

Nitrogen has two stable isotopes, namely ^{14}N and ^{15}N. Both N-isotopes share the same number of protons (here: 7), but different numbers of neutrons (here: 7 or 8). The less abundant isotope is the heavier isotope, ^{15}N, which only takes in 0.365 % of the global N-pool (Junk and Svec, 1958). Through variability in the distribution of nitrogen isotopes and due to isotopic fractionation, the abundance of ^{14}N and ^{15}N in nitrogen-containing molecules is dynamic and gives insight on nitrogen processes in systems of interest. As the absolute quantity of ^{15}N is low, analysis of quantitative differences in the isotope composition is impractical, thus, the ratio between ^{14}N and ^{15}N is used instead. This ratio between ^{14}N and ^{15}N is displayed in delta (δ) -values and postulated to be the ‰-difference to atmospheric N_2 with a constant $^{14}N/^{15}N$ ratio of 272 ± 0.3. The $\delta^{15}N$-value in the sample is then determined as followed (Eq. 1):

$$\delta^{15}N(vs.\,air) = ((\tfrac{^{15}N}{^{14}N})_{sample} / (\tfrac{^{15}N}{^{14}N})_{air} - 1) \times 1000 \tag{1}$$

The δ-value displays the ‰-difference to a commonly accepted reference standard, thus, the δ-value is then calculated by determining the isotope ratios (R) of the sample and the reference standard (Eq. 2):

$$\delta^{15}N = \frac{R_{sample}}{R_{standard}\ -1} \times 1000 \tag{2}$$

The ^{15}N-tracer method modifies under controlled conditions the isotopic composition in the system of interest through ^{15}N-enrichment or "-labeling". The advantage of this approach is, that the tracer method requires only little manipulation during the experiment and is practical for temporary incubations with comprised amount of isolated samples (Ryabenko 2013). Also, the isotopic signal collected is highly sensitive to smallest changes in $\delta^{15}N$ values which can be detected thanks to continuous flow systems consisting of an elemental analyzer (EA) and isotope ratio mass spectrometer (IRMS). The EA gives information about the elemental composition in the sample, whilst the IRMS measures the difference between the two ratios in the sample and the standard (e.g. IAEA standards) which is calibrated to atmospheric dinitrogen. Nowadays, the ^{15}N- tracer method is a routine analysis, however, it demands various considerations during the rate determination, such as the natural abundance in the sample, ambient concentration of the ^{15}N-tracer (typically 10 %), the length of the incubation/ turnover rate, and detection limits of the analytical methods.

1.4.2 Calculations of N-cycling rates

In this dissertation, the determination of the nitrogen fixation rates was achieved with help of the ^{15}N–N_2 gas method, where a bubble was injected into an incubation bottle containing water with an airtight syringe to the samples (bubble method; Montoya et al., 1996; more detailed description in section 2.1.3). Calculation of N_2 fixation rates (NF; Eq. 3) is based on Montoya et al. (1996):

$$NF = \frac{(A_{PN}^{final} - A_{PN}^{t=0})}{(A_{N2} - A_{PN}^{t=0})} \times \frac{[PN]}{\Delta t} \tag{3}$$

Here, "A" is the atom% ^{15}N in the particulate organic nitrogen (PN) at the end (final) and the start (t=0) of the incubation and in the dissolved N_2 pool (N_2).

For the determination of nitrification and ammonium assimilation rates the ^{15}N-NH_4^+ tracer method was used (Damashek et al., 2016; Veuger et al., 2013; more detailed description in section 3.1.3). The calculation of the nitrification rates (NR; Eq. 4) followed Veuger et al. (2013):

$$NR = [^{15}N - NO_x^-] \times \frac{[NH_4^+]_{tot}}{[^{15}N - NH_4^+]_{add}} / \Delta t \tag{4}$$

Here, $[^{15}N - NO_x^-]$ is the excess concentration of ^{15}N in both NO_2^-- and NO_3^-, $[NH_4^+]_{tot}$ presents the total amount of ammonium consisting of the initial and added ammonium concentrations, $[^{15}N - NH_4^+]_{add}$ is the concentration of the added $^{15}N - NH_4^+$ tracer, and Δt is the incubation time in hours (Veuger et al., 2013). The excess ^{15}N concentration in NO_x^- is the difference in the ^{15}N-content (in atom%) of the t_1 and t_0 sample.

For the ammonium assimilation rates, the ^{15}N-PON content was determined at the end of the experiment. We calculated the assimilation rates (AR; Eq. 5) following Dugdale and Wilkerson (1986):

$$AR = V_m \times [PON_m] \tag{5}$$

where V_m represents the mean specific ^{15}N-uptake rate and $[PON_m]$ the mean of the beginning and final PON concentrations. Calculation of V_m also incorporates the ^{15}N-PON content of the t_0 and the t_1 sample.

1.4.3 Dissolved nutrient analysis

Inorganic nutrient concentrations (ammonium, nitrite, nitrate, phosphate; µmol L^{-1}) were measured colorimetrically with a continuous segmented flow analyzer (QuAAtro, Seal Analytical) following the methods of Grasshoff et al. (1999). The analytical accuracy was ± 5 %, except for ammonium measurements, which was ± 5-10 %. The detection limit was 0.1 µmol L^{-1} for phosphate (PO_4^{3-}), 0.05 µmol L^{-1} for nitrite (NO_2^-), 0.2 µmol L^{-1} for nitrate (NO_3^-), and 0.5 µmol L^{-1} for ammonium (NH_4^+).

1.5 The aims of this thesis

This PhD thesis investigated and quantified rates of nitrogen-related processes in sediments of the southern Baltic coastline and in an episodically-flooded coastal peatland of NE-Germany to gain a better understanding on the nitrogen cycle and the dissolved nutrient pools in marine-terrestrial transects of the Baltic. As the (open and) coastal areas of the Baltic Sea are affected by seasonal eutrophication, additional nitrogen sources such as sediment-associated nitrogen fixation during resuspension may be harmful and contribute to the toxic nutrient overload in upper waters. Hence, as first aim of this thesis benthic nitrogen fixation in coastal sediments of the Baltic Sea (which likely experience resuspension) was quantified to determine its contribution to the pelagic nitrogen pool.

Low-lying freshwater peatlands of NE-Germany are prone to experience Baltic floodings, and the intrusion of brackish seawater may disturb microbial processes associated with the nitrogen cycle. As these peatlands were (often) cultivated in the past, additional nitrogen is still left in the soil and may influence nitrogen cycling and/ or the nutrient pool in surface waters of the peatland. For this reason, the second aim of this thesis was to monitor nitrification, ammonium assimilation rates, and the dissolved nutrient pool in a peatland after a flooding event. The intrusion of saline water into the peatland may also induce nitrogen-leaching through the soil due to cation exchange between seawater salt (here: sodium) and ammonium. Thereby, the excess nitrogen detaching from the soil may pollute ground- and coastal waters. Thus, the third aim was to measure ammonium loss from peat and mineral soils of a flooded peatland during seawater exposure. In the following, the main questions (Q) and hypotheses (H) are summarized:

1. **Q**: Is sediment-associated nitrogen fixation a major source of reactive nitrogen to the pelagic layers of the Baltic Sea during resuspension?
   H: Sediment-associated nitrogen fixation contributes to the reactive nitrogen pool in the pelagic during resuspension, because specialized non-cyanobacterial diazotrophs are resilient towards hydraulic stress and inhabit this niche.

2. **Q**: Are heterotrophic nitrification and ammonium assimilation in a formerly-freshwater peatland disturbed by seawater intrusion?
   H: The salinization of the peatland stresses the *in situ* communities and impedes nitrogen cycling.

3. **Q**: Are soils of coastal peatlands prone to ammonium-loss during flooding events?
   H: Formerly-cultivated peatlands are a source of nitrogen during flooding, since cation exchange between seawater-ions (sodium) and ammonium releases soil-attached ammonium.

Chapter 2

N_2-fixing SRB in coastal sediments under simulated resuspension

This chapter includes sections from the publication Liesirova et al. (2023) entitled: "N_2-fixing sulfate reducing bacteria in shallow coastal sediments under simulated resuspension" accepted by "Estuarine coastal and shelf sciences" on November 25, 2022. Co-authors are Tobias Aarenstrup-Launbjerg, Søren Hallstrøm, Meriel J. Bittner, Lasse Riemann and Maren Voss. I omitted all the molecular work as this was done by my co-authors, otherwise I wrote the chapters entirely myself.

2.1 Methods and materials

2.1.1 Sampling

The study sites were located along the southern Baltic coastline (Figure 2.1) and were selected to represent the typical sediments of the coastline based on grain size and organic matter (OM) content. Sediment samples were obtained from the Schnatermann and Hütelmoor Beach in May 2019, off Poel St. 1 and Poel St. 2 in August 2019, and off Warnemünde in October 2019 (Table 2.1) at water depths <1 m. In addition, one deep site in the Bay of

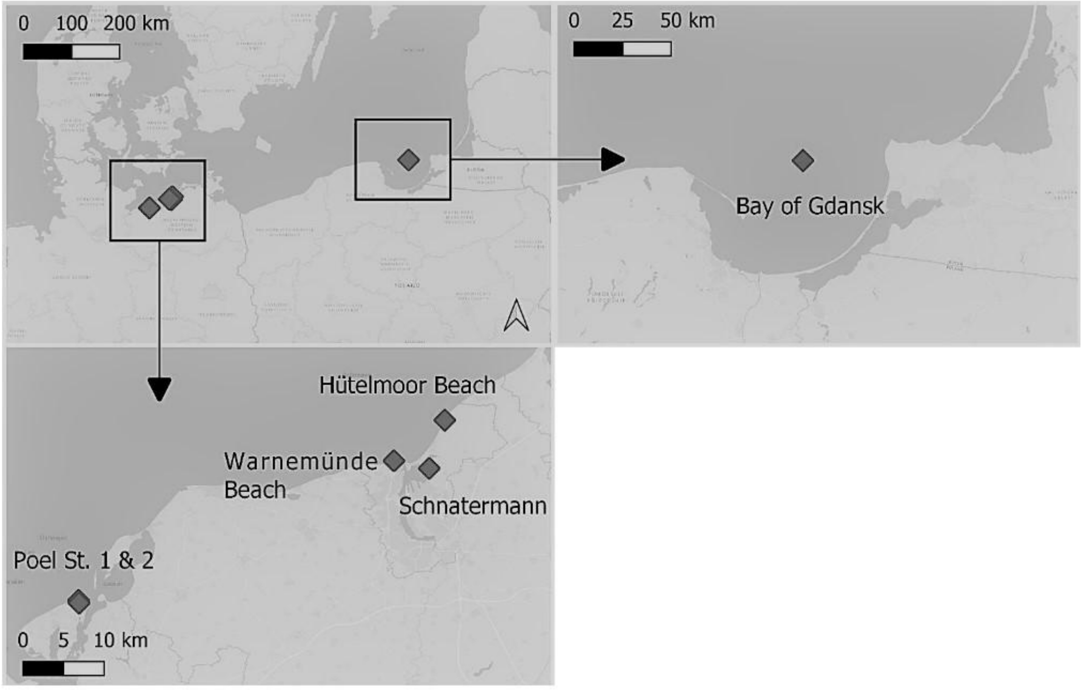


FIGURE 2.1: Map of the 5 shallow (<1 m depth) sampling sites along the southern Baltic coastline and one site at the Bay of Gdansk (109 m depth).

Gdansk (109 m) was sampled in October 2019 with expected anaerobic conditions and heterotrophic nitrogen fixers. At the shallow sites, *in situ* variables (temperature, oxygen, salinity) were measured above the sediments using a HQ40D portable multimeter (Hach). Sediment samples were collected using Plexiglas tubes (6 cores per site, length: 30 cm, diameter: 5 cm) that were pushed into the sediments, closed at the top with a plug, and carefully pulled out. From the deep site, sediment cores were collected with a multicorer during a cruise onboard RV Elisabeth Mann Borgese (EMB 233, Oct. 4^{th}, 2019). Environmental conditions were measured via a CTD system equipped with Seabird 911+ sensors. Immediately after sampling, subsamples from the sediment cores were filled in sterile Eppendorf tubes, frozen in liquid nitrogen, and stored frozen until DNA extraction. During the transport to the laboratory (2–6 h), the cores were kept dark and cool. Since the transport of the cores from the deep site lasted two days, the overlying water in the cores was aerated and the cores kept at in situ temperature. In the laboratory, the six sediment cores from each site were sliced into two depth strata (0–5 cm sediment depth and 0–10 cm sediment depth) in triplicates, and homogenised. From this material, 2 × 5 g sediment was dried at 50 °C for organic matter and grain size analyses (described below). Seawater for the slurry incubations was obtained at Warnemünde (0.5 m depth) in May, August, and October 2019 respectively (Table 2.1).

Date	Location	Sampling depth (m)	Benthic seawater*			Grain size composition		
			Temperature (°C)	Salinity	Oxygen (mg/L)	Clay (%)	Silt (%)	Sand (%)
27.05.2019	Schnatermann (54.17241°N, 12.14259°E)	1	16.1	10.77	9.34	0	3.5 - 3.9	94.5 - 95.5
27.05.2019	Hütelmoor Beach (54.2255°N, 12.17185°E)	1	14.7	10.77	9.6	0.3 - 1.4	2.8 - 5.6	92.4 - 96.7
01.08.2019	Poel St. 1 (54.02661°N, 11.48224°E)	1	22.3	11.42	6.93	0.8	7.35	87.3
01.08.2019	Poel St. 2 (54.02349°N, 11.48314°E)	1	21.6	11.88	5.04	0 - 0.8	0 - 10.1	89 -100
04.10.2019	Bay of Gdansk (54.8648°N, 19.28339°E)	109	7.73	12.61	0.07	24 - 24.6	39 - 53.8	21.5 - 35.7
06.10.2019	Warnemünde Beach (54.18078°N, 12.07619°E)	1	14	14.41	9.75	0	0 - 1.4	97.9 - 99.1

Date	Location	Sampling depth (m)	Pelagic seawater**			Dissolved inorganic nutrients	
			Temperature (°C)	Salinity	Oxygen (mg/L)	DIN (µmol/L)	DIP (µmol/L)
27.05.2019	Warnemünde Beach (54.18078°N, 12.07619°E)	0.5	14.7	10.77	9.7	0.34	0.18
01.08.2019			19	9.36	9	2.8	0.23
06.10.2019			14	14.41	9.75	2.5	0.45

*seawater conditions in the overlying water from sampling sites
**seawater conditions in the incubation medium

TABLE 2.1: Environmental conditions in bottom water during sampling and the grain size composition in the sediments. DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorus.

2.1.2 Slurry setup to simulate sediment resuspension

Prior to the incubations, 40 L of seawater from Warnemünde (Table 2.1) were filtered sequentially through a GF/F (Whatman, SigmaAldrich) and an acetate filter (Sartorius; 0.2 μm). All slurry incubations were done in acid washed 1.2 L polycarbonate Nalgene® bottles, which were subsequently filled with filtered sea water. To imitate the conditions of sediments resuspended in the water column, we aimed for a low sediment-to-water ratio (modified setup of Pedersen et al., 2018), thus, each bottle was amended with 10 g of wet, homogenised sediment (either from 0 to 5 cm or 0–10 cm depth). The incubations of these sediment depths represent different strengths of resuspension (0–5 cm: weak resuspension; Sarkar et al., 2021; 0–10 cm: strong resuspension; Kersten et al., 2005). The choice of these depths were based on previous studies along the southern Baltic coastline where geological features (ripples) indicated sediment redistribution patterns in the upper 5 cm under ordinary conditions (Sarkar et al., 2021), but down to 10 cm under a storm event (Kersten et al., 2005). All bottles were acclimated overnight in the dark (May and October: 15 °C; August: room temperature). To determine the importance of diazotrophic SRB for N_2 fixation, a parallel bottle series was amended with the SRB-specific inhibitor sodium molybdate (Oremland and Capone, 1988) the next day. The parallel series received sodium molybdate to achieve a final concentration of 0.02 M, then all bottles were filled up to full capacity with the filtered seawater and closed with septum caps. Triplicate bottles with seawater, but no added sediment served as control for potential N_2 fixation occurring in the filtered water. All incubations were done in the dark to exclude any potential light induced N_2 fixation. It needs to be mentioned that seawater (from Warnemünde) used in our incubations may have influenced sediment communities in the slurries and thereby affected the measured N_2 fixation rates. However, this would have mostly influenced communities of Bay of Gdansk, that rarely experience environmental changes at 109 m depth (Table 2.1). In contrast, for the remaining sites, local physio-chemical conditions were similar to those at Warnemünde (Table 2.1).

2.1.3 ^{15}N-incorporation to determine nitrogen fixation rates

Into each bottle, 1 ml of ^{15}N–N_2 gas (98 %, Campro Scientific lot # EB1169V) was injected with an airtight syringe to achieve a final labelling of approximately 10 % (Montoya et al., 1996). Emerging overpressure of air in the bottles was discharged via a cannula. Thereafter, the bottles were shaken thoroughly by hand for 2 min to reach isotopic equilibrium and placed in the dark on a shaker (60 rpm) at 15 °C (May and October) and 20 °C (August) for 48 h. After incubation (t_1), samples were filtered onto pre-combusted GF/F filters (Whatman, Sigma-Aldrich; 450 °C), which were subsequently dried at 50 °C, packed into tin capsules, and pelletized before analysis. The concentration of organic carbon (OC) and total nitrogen (TN) and the isotopic composition ($\delta^{13}C$; $\delta^{15}N$) was measured using an IRMS (Delta V Advantage - Thermo Fisher Scientific) connected to a FLASH 2000 Elemental Analyzer (Thermo Scientific) via ConFlo IV Universal Continuous Flow Interface (Thermo Fisher Scientific). Calibration was done with isotopic (IAEA Standards N1, N2, and N3) and elemental standards (peptone, acetanilide; ®Merck). Reference gases were ultrapure N_2 and CO_2 gas from bottles calibrated against IAEA reference standards. The equilibration of $^{15}N_2$ gas with the dissolved nitrogen gas in the sample takes several hours and the percentage label increases slowly over this period of time (Wannicke et al., 2018). However, since rate calculations assume immediate isotope equilibrium an underestimate of the final rates may occur. This underestimate depends on the volume of the incubated sample, water temperature, and the potential diurnal cycle of N_2 fixation (Wannicke et al., 2018). Since we applied a rough shaking after the $^{15}N_2$ gas addition and a total incubation time of 48 h, we consider this underestimate negligible. A critical point in the rate calculation is the information on the natural abundance of ^{15}N values in the sediment samples at the start of the incubation (t_0). According to Montoya et al. (1996), a 5‰ change in the initial particulate nitrogen-t_0 (*in situ* ^{15}N-PN) is conservatively assumed, which is the minimum difference between the unlabeled PN-t_0 or substrate sample and the labelled filter after the incubation. Since we lacked an estimate of the natural variability of the sediment stable isotope values (t_0 δ^{15}N values) we used data from 63 surface sediment samples from the coastal Bay of Gdansk (taken from the study by Thoms et al., 2018) that include coarse and fine grained sediments and are representative for the sediment types in our experiments. The standard deviation was 1.99‰ and we applied two standard deviations (4‰) as necessary minimum difference between our t_0 and t_1 values after the 48 h incubation. All ^{15}N-PN samples that were 4‰ or less enriched in ^{15}N at the end of the experiment were not considered as significantly different to t_0 and no rate was calculated.

2.1.4 Calculation of nitrogen fixation and limit of detection

As described earlier (Chapter 1.4.2), the calculation of N_2 fixation rates is based on Montoya et al. (1996) and includes the solubility of dinitrogen based on Weiss (1970) and the defined difference between initial and final atom percentage of 0.00146 % (or ca. 4‰). Calculated N_2 fixation rates in the slurries are the means ± standard deviation of six samples, averaging the two depth units (3× 0–5 cm; 3× 0–10 cm) per site.

The limit of detection (LOD) was determined as described in Montoya et al. (1996). IRMS determine the stable isotope ratios as $\delta^{15}N$ values with an error of less than 0.2‰, which would principally allow the determination of much lower rates. However, the natural variability of substrates should be considered in the calculation and is usually much higher than the instrumental error. The difference between initial (before incubation) and final atom percentage (after incubation) was defined as 0.00146 % (or ca. 4‰; Montoya et al., 1996). For each sample a limit of detection was calculated (Eq. 6) which varies depending on the PN of the respective sample,

$$^{min}A_{PN} \times [PN] \times (A_{N2})^{-1} \tag{6}$$

$^{min}A_{PN}$ = difference between initial and final atom percentage
PN = concentration of PN in each sample
A_{N2} = initial atom% of dissolved pool

2.1.5 Inorganic nutrients

Inorganic nutrient concentrations were determined in filtered water of each slurry in filtered water of each slurry (t_1) as described in Chapter 1.4.3 x.

2.1.6 Grain size analysis

Grain size analysis was performed with a Mastersizer 3000 (Malvern Instruments). Prior to measurement, sediment (5 g) was treated with hydrogen peroxide and sodium pyrophosphate to remove organic material (Harada and Inoko, 1977). Cobbles (>2000 μm) were picked out manually. During measurement, sonication (integrated treatment in the Mastersizer 3000) was performed to prevent agglomeration and clumping of particles. Sediment classification was done based on Shepard's classification scale (Shepard, 1954).

2.1.7 Data display and analysis

To create the map and the tables, the open source software QGIS 3.14.1. and the online LaTeX editor 'Overleaf' were used, respectively. RStudio Desktop (version April 1, 1106) was employed for data analysis and plotting of the graphs was performed via the ggplot2-package (v. 3.3.3; Wickham, 2016). The Shapiro-Wilk test was used to determine normality of the data. "Pearson's-method" was employed to identify linear correlations between N_2 fixation and relevant environmental variables, and ANOVA to determine if groups differed significantly among each other: Tested groups included "location", "SRB-inhibition", and "0–5 cm vs. 0–10 cm depth (weak vs. strong resuspension)". For the analysis between weak and strong resuspension, we compared all N_2 fixation rates of slurries filled with the 0–5 cm sediment layer with the rates of the slurries filled with the 0–10 cm sediment layer. Bay of Gdansk was left out from this generalised "depth-analysis" since sediments from Bay of Gdansk are deposited too deep (109 m) to be naturally affected by resuspension (80 m in the Baltic Sea; Almroth-Rosell et al., 2011) and showed no significant difference in N_2-fixing activity between 0-5 cm and 0–10 cm.

2.2 Results

2.2.1 *In situ* conditions

Temperature varied between 14.0 and 22.3 °C according to season, while the salinity remained between 10.00 and 14.41 (Table 2.1). Dissolved oxygen was present in the overlying water of all stations, but was only 0.07 mg O_2 L^{-1} in the Bay of Gdansk (Table 2.1). Sediments consisted mainly of unsorted, sandy sediment with low organic carbon (OC < 0.65 % dry weight) and total

Location	OC 0–5 cm (% d.w.)	OC 0–10 cm (% d.w.)	TN 0–5 cm (% d.w.)	TN 0–10 cm (% d.w.)	C/N 0–5 cm	C/N 0–10 cm
Bay of Gdansk	6.8	4.14	0.84	0.47	8	8.9
Poel St. 1	0.09	0.09	0.01	0.01	9	9
Poel St. 2	0.65	0.57	0.05	0.03	13	19
Schnatermann	0.29	0.27	0.02	0.03	14.5	9
Hütelmoor Beach	0.48	0.39	0.03	0.04	16	9.75
Warnemünde Beach	n.d.	n.d.	n.d.	n.d.		

TABLE 2.2: Organic carbon (OC) and total nitrogen (TN) content (% dry weight = % d.w.; n.d. = non-detected) in the 0–5 cm and 0–10 cm sediment strata of the respective sites (n = 1). C/N ratios are given as molar ratios.

nitrogen (TN < 0.05 % dry weight; Table 2.2) content. In contrast, sediment from Bay of Gdansk consisted mostly of clay and silt (Table 2.1), with an OC of 6.8 % dry weight and a TN of 0.84 % dry weight (Table 2.2). At all stations, OC concentrations were higher in the 0–5 cm section than in the 0–10 cm section (Table 2.2), with exception of Poel St. 1, where OC content was similar in the sections.

2.2.2 Dark nitrogen fixation rates in slurry incubations

N_2 fixation rates in the Bay of Gdansk were 7.66 ± 9.04 nmol N $g^{-1}d^{-1}$ (n = 6), thereby displaying high variability from 0 to 23.7 nmol N $g^{-1}d^{-1}$ (Figure 2.2). All other significant rates were two orders of magnitude lower. Second highest N_2 fixation rate was measured at Poel St. 2 with 0.72 ± 0.33 nmol N $g^{-1}d^{-1}$ (n = 6). Hütelmoor Beach and Schnatermann reached 0.27 ± 0.14 nmol N $g^{-1}d^{-1}$ (n = 6) and 0.21 ± 0.15 nmol N $g^{-1}d^{-1}$ (n = 6), respectively. In sediments of Poel St. 1 and Warnemünde, N_2 fixation rates were below detection. At three sampling sites (Hütelmoor Beach, Schnatermann, Poel St. 2), the 0–5 cm sediment section reached on average higher N_2 fixation rates than the 0–10 cm section (Figure 2.3). This was not the case for the Bay

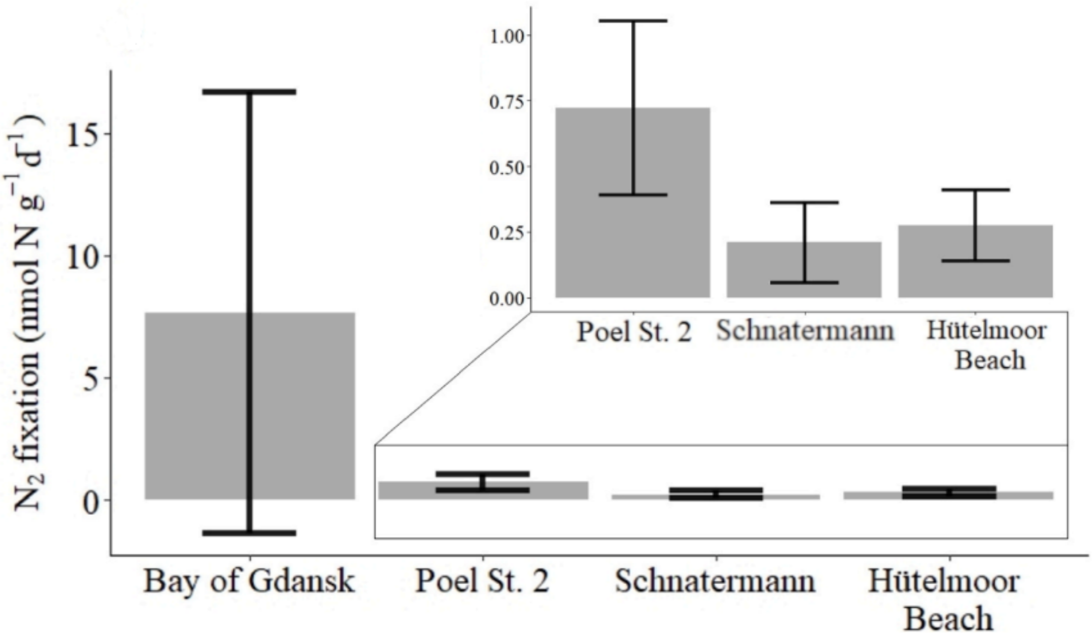


FIGURE 2.2: Barplot displaying N_2 fixation rates in the sediments, averaged from the 0–5 cm and 0–10 cm depth strata per site (n = 6 per site). Warnemünde Beach and Poel St. 1 displayed no N_2-fixing activity and are not included.

of Gdansk, where sediments showed no significant difference in N_2- fixing activity with depth (0–5 cm: 0–11.4 nmol N $g^{-1}d^{-1}$; 0–10 cm: 2.9–23.7 nmol N $g^{-1}d^{-1}$). The SRB-inhibitor reduced N_2 fixation in the samples from the Bay of Gdansk to 0.5 ± 1.2 nmol N $g^{-1}d^{-1}$ (n = 6) and at Poel St. 2 to 0.02 ± 0.07 nmol N $g^{-1}d^{-1}$ (n = 6), corresponding to a 93 % and 97 % reduction relative to incubations without inhibitor. At Hütelmoor Beach and Schnatermann, no N_2 fixation was detected in the inhibitor-treated slurries, which equals to a reduction of 100 %.

2.2.3 Concentrations of inorganic nutrients in the slurries

At the end of the incubation, the dissolved nitrogen concentrations in the slurries of the different sites (Figure 2.4) were elevated, compared to seawater from Warnemünde (Table 2.1), which likely originated from the pore water of the sediments. Amongst the sites, inorganic nitrogen concentrations were on

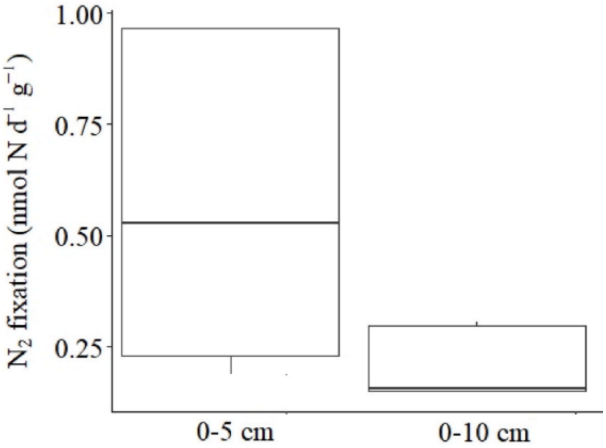


FIGURE 2.3: Boxplot of averaged N_2 fixation rates of all stations per depth strata of the sandy sites (Poel St. 2, Schnatermann, and Hütelmoor Beach).

average several magnitudes lower at Hütelmoor Beach (0.77 $\mu mol\ L^{-1}$) and Schnatermann (0.9 $\mu mol\ L^{-1}$), than at the other stations (3.8–8.53 $\mu mol L^{-1}$). Dissolved inorganic phosphorus (DIP) concentrations were low at Hütelmoor Beach, Schnatermann, and Poel St. 2 (0.1 $\mu mol\ L^{-1}$; Figure 2.5). In contrast, DIP was slightly higher at Bay of Gdansk, Warnemünde, and Poel St. 1 (0.17–0.35 $\mu mol\ L^{-1}$).

2.2.4 Environmental variables and dark nitrogen fixation

Organic carbon in the sediment dry weight is positively correlated to the respective percentage of clay and silt added together (r = 0.6; $p < 0.05$) in the sediments. Clay and silt content were positively correlated to N_2 fixation (clay; r = 0.5; $p < 0.05$; silt; r = 0.4; $p < 0.05$), however, there was no correlation between OC and N_2 fixation. At the sandy sites with detectable N_2 fixation (Poel St. 2, Hütelmoor Beach, Schnatermann), low inorganic phosphorus concentrations were measured in the slurries at the end of the experiment (0.1 $\mu mol\ L^{-1}$; Figure 2.5), while the sandy sites without N_2 fixation (Poel St.1, Warnemünde) showed higher DIP concentrations (Figure 2.5). This may display a trend of P-consumption during diazotrophic activity, however, no statistical significance between N_2 fixation and DIP was found ($p > 0.05$).

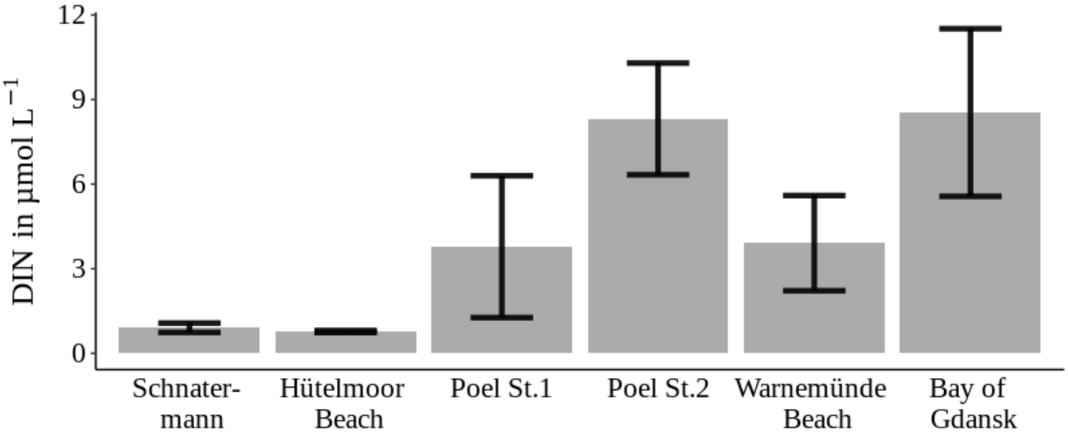


FIGURE 2.4: DIN in the slurries at the end of the experiment (means ± standard dev.; n = 6).

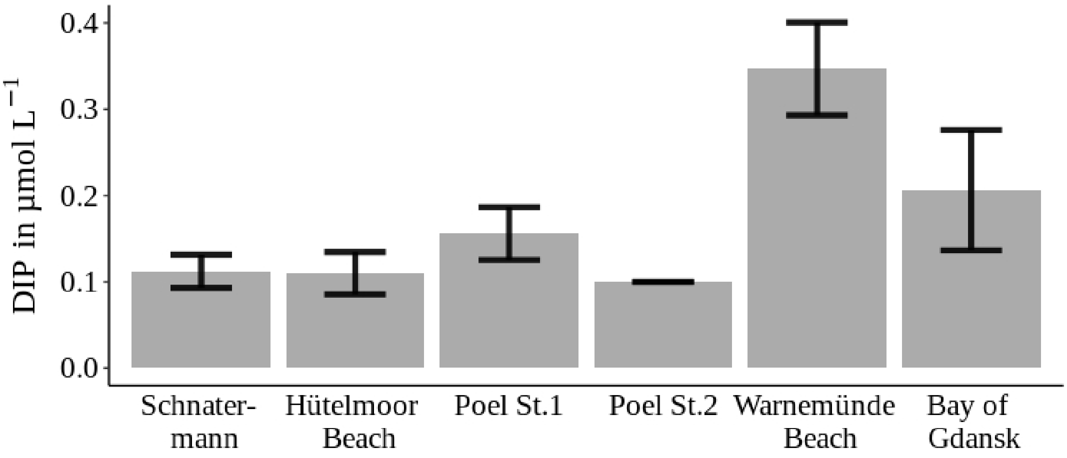


FIGURE 2.5: DIP in the slurries at the end of the experiment (means ± standard dev.; n = 6).

2.3 Discussion

2.3.1 Preferred niches of N_2 fixation in coastal sediments of the Baltic

This study investigated sediment-associated N_2 fixation by NCDs in nearshore sediments along the southern Baltic and in the Bay of Gdansk. Preferred niches of NCD are thereby, organic matter rich sediments with hypoxic conditions (Spinette et al., 2019). These conditions (hypoxia, organic matter rich) are common for muddy deap-sea sediments (Middelburg, 2019) like Bay of Gdansk. As expected, the N_2 fixation rates from the Bay of Gdansk were highest (Figure 2.2) since it displayed low oxic concentrations (Table 2.1) and high organic matter content (Table 2.2). Moreover, the rates were comparable to findings from Eckernförde Bay in northern Germany (>8 nmol N cm^{-3} d^{-1} ; Bertics et al., 2013). In contrast, the rates at our sandy deposits were low, probably due to the oxygenated and organic-poor conditions (Table 2.1; 2.2). Nevertheless, certain diazotroph species can adapt to environmental stressors such as organic matter depletion and oxic conditions, which may be true for our sites (Chapter 2.3.2). As seen in Liesirova et al. (2023), one of the dominating species in this study belonged to *Deltaproteobacteria*, including the sulfate reducing order *Desulfobacterales* (clusters I). *Desulfobacterales* is a well known species inhabiting sediments globally (Burns et al., 2002; Bertics et al., 2010; Dekas et al., 2018; Jabir et al., 2021) and also found in Eckernförde Bay (Germany) (Bertics et al., 2013). *Desulfobacterales* from Eckernförde Bay were reported to form symbiotic relationships with anaerobic methanotrophs, or ANME (Meulepas et al., 2009). Through symbiosis, both *Desulfobacterales* and ANME gain competitive advantage, as *Desulfobacterales* supply reactive nitrogen to ANME, whilst *Desulfobacterales* receive carbon from ANME in return. Interestingly, certain ANME feed on on methane as sole carbon source

(Roalkvam et al., 2011) and can therefore thrive even in carbon-poor sediments (Pohlman et al., 2013). Due to the occurrence of methane hotspots along the southern Baltic coastline, NCD like *Desulfobacterales* may also engage in symbiosis with ANME at carbon-poor deposits comparable to our sites (Table 2.1; Heyer and Berger, 2000). However, results from the sandy sites from Germany rather suggest that organic matter availability plays an important role for our NCD: the rates in the 0-5 cm sediment unit were higher than in the 0-10 cm unit (Figure 2.3; Poel St. 2, Hütelmoor Beach, Schnatermann) and OM content may be responsible for that (Table 2.2). It can be speculated, that seasonally increased deposition of pelagic phytoplankton (labile organic matter) at the sediment-water interface stimulated benthic N_2 fixation. The seasonal impact could also explain the higher rates at Poel St. 2 compared to the other sites (with exemption of Bay of Gdansk). Nevertheless, we found no correlation between N_2 fixation and organic matter, meaning organic matter does not automatically reassure high NCD-activity. Similar observations were made by Gandy and Yoch (1988), who reported that diazotrophy was stimulated in surface sediments (0-5 cm) by glucose amendment, but not in deeper sediment layers (>5 cm). Gandy and Yoch (1988) suggested that the microbial community compositions changed with depth and subsequently the nutritional requirements of the respective communities changed, too. As reported in Liesirova et al. (2023), there was no significant community change in our sediment cores. Nevertheless, vertical gradients in nutrient availability and demand may still have affected N_2-fixing communities during the experiment. This includes phosphate, as it is a well-known limiting factor for NCD. The pore waters in coastal sediments off the Bay of Gdansk contained up to $\mu mol\ P\ L^{-1}$ in surface sediments (Thoms et al., 2018), thus, the nutritional demand was probably met for N_2 fixation and enabled NCD activity. Phosphate demand and subsequent consumption by NCDs would also explain the low phosphate content in slurries of Poel St. 2, Schnatermann and Hütelmoor Beach (where we detected N_2 fixation) at the end of the experiment. Since phosphate content in sediment pore waters can increase with depth, it can be speculated that phosphate mobilisation and diffusion from deeper sediments may provide sufficient phosphate to upper sediment and water layers, and N_2 fixation may be supported. Still, no N_2 fixation was detected in surface sediments of Warnemünde and Poel St. 1, albeit phosphate availability in the slurries (Figure 2.5) and genetic potential for N_2 fixation (Liesirova et al., 2023). Therefore, we suggest, phosphate only positively influences N_2 fixation in combination with organic matter, as displayed at Bay of Gdansk (Table 2.2; Figure 2.5). Organic matter availability, however, usually also promotes dissolved inorganic nitrogen concentrations in sediments as a result of organic matter mineralization (Joshi et al., 2015), thereby, DIN has an inhibiting effect on N_2 fixation (Zehr, 2011). Lately, this assumption has been challenged though, as studies reported on NCD-activity despite DIN-availability in sediments (Bertics et al., 2010; Bentzon-Tilia et al., 2015; Newell et al., 2016). Our results confirm that NCD can perform N_2 fixation regardless of DIN. Still, we mostly detected low rates (Figure 2.2), and it cannot be excluded that N_2 fixation was influenced by DIN. For instance DIN-availability may have increased competition against other microorganisms which favour similar niches as diazotrophs (Andersson et al., 2014). However, other mechanisms may be responsible for NCD activity, as diazotrophs might have been pressured to perform N_2 fixation under P-availability to counter the low N:P ratio, as seen for pelagic diazotrophs (Glibert et al., 2013; Bhavya et al., 2016). Also, N_2 fixation allows certain bacteria to maintain their redox balance by acting as electron sink (Joshi and Tabita, 1996; Tichi and Tabita, 2000), so bioavailable DIN may be unrelated to diazotrophy altogether. In summary, sediment-associated N_2 fixation occurs in sediments of the southern Baltic coastline, despite inorganic nitrogen availability. Thereby, predominately fine grained deposits with high organic matter and phosphate content seem to be preferred niches for NCD.

2.3.2 N_2 fixation under resuspension

The NCD-activity was at the lower spectrum when compared to sediment-associated N_2 fixation under resuspension from the Swedish coastline (3.4 mmol N m^{-2} d^{-1} ; Andersson et al., 2014). However, the rates corresponded to heterotrophic N_2-fixing rates from pelagic water layers (3–41 m depth) of the Baltic (0.7–6 nmol N $L^{-1} d^{-1}$; Reeder et al., 2022). The results propose therefore, reduced microbial activity (here N_2 fixation) on resuspended sediment particles (Saint-Béat et al., 2014) for sandy, nearshore sediments of the southern Baltic. Even though Bay of Gdansk scored higher N_2-fixing rates than the other sites (Figure 2.2) and represents a favorable habitat for NCD (hypoxic, organic matter rich), these muddy sediments were deposited at great depth (Table 2.1). It would require strong storm events to induce sufficient resuspension at this depth, yet, storms in the Baltic reach "only" down to 52 m (Dreier et al., 2021). Therefore, it seems unlikely that resuspended sediments of Bay of Gdansk can contribute to the pelagic nitrogen pool. Still, 25 % of the entire Baltic seafloor is mud, and mud also frequently occurs along the Baltic shorelines (e.g. bay between Rügen and Greifswald; Leipe et al., 2017). It can be speculated that these coastal mud deposits may be crucial for sediment-associated N_2 fixation under resuspension. Nevertheless, the exposure to oxygenated water might trouble benthic communities which are used to oxygen-depleted conditions. Here it needs to be noted though, that certain species can adapt to exposure to dissolved oxygen, including species of diazotrophic SRB. The sodium molybdate technique revealed, that the dominant N_2 fixers at our sites were SRB (93 – 100%). The dominance of diazotrophic SRB had been already reported in intertidal sand flats of North

Carolina (64%; Steppe and Paerl, 2002), muddy sands in Catalina Habor (86-98%; Catalina Harbor, California; Bertics et al., 2010), diverse estuarine systems (Newwell and Aziz, 1980; Gandy and Yoch, 1988; Welsh et al., 1996; Jabir et al., 2021) and is confirmed by this study for various coastal deposits of the Baltic Sea which spans a wide range sediment types (fine to coarse grained) in shallow and deeper marine environments. As seen in Liesirova et al. (2023), one of the dominating species belonged to *Deltaproteobacteria*, including the sulfate reducing Order *Desulfovibrio* (clusters III), a well known species inhabiting sediments globally (Burns et al., 2002; Bertics et al.,2010; Dekas et al., 2018; Jabir et al., 2021), as well as in Eckernförde Bay (Germany) (Bertics et al., 2013). *Desulfovibrio spp.* is able to gain energy by reducing oxygen to water (Cypionka, 2000; Lumppio et al., 2001). This means *Desulfovibrio spp.* cannot only tolerate dissolved oxygen concentrations, but benefit energetically from it. The reduction of oxygen to water is thereby probably advantageous (in our slurry incubations and) during resuspension events, where sediments are massively in contact with oxic waters. Overall, resuspension of shallow sandy deposits will not significantly contribute to pelagic N_2 fixation. However, diazotrophic SRB have possibly the means to overcome resuspension-induced stressors, and enable sediment-associated N_2 fixation during resuspension events.

Chapter 3

Nitrogen processes in an episodically flooded fen

3.1 Methods and materials

3.1.1 Sampling

Sampling sites within Hütelmoor were selected with increasing distance to the coastal protection dune and named as “Heiligensee”, “Mid-peatland”, “Channel”, “Eastern Peatland”, and “Prahmgraben” (Figure 3.1). “Prahmgraben” was the southernmost sampling point and connects to the Warnow River. Sampling was undertaken throughout 2019 (Prahmgraben from March 2019) and once in March 2020. In the first 180 days, we sampled biweekly, from July (2019) on, we reduced the number of sites (Heiligensee, Prahmgraben) and sampled on a monthly basis due to access restrictions of the nature reserve authorities.

3.1.2 Environmental variables and dissolved nutrients

In situ variables (temperature, salinity, and dissolved oxygen) were measured in the surface water above the peat (later called “peatwater”) at 0.5 m depth using a HQ40D portable multimeter (Hach). For the analysis of dissolved nutrients, one polycarbonate bottle (500 ml) was filled to full capacity (no

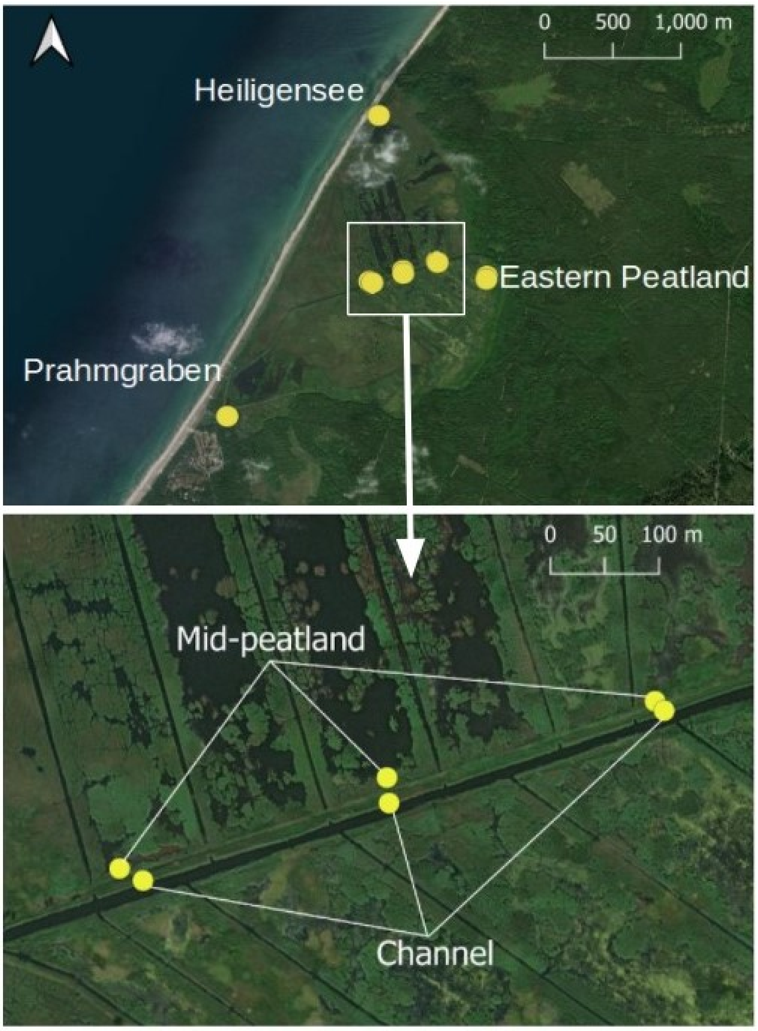


FIGURE 3.1: Map of sampling sites. Note: Mid-peatland and Channel are three "sub-sites" combined respectively.

overhead) with peatwater, and kept cool and dark while transported (ca. 2-6 h) to the lab. Immediately after return, 50 ml of sampled peatwater from each station was filtered (GF/F whatman) in the lab and subsequently frozen in Falcon tubes, and stored at - 20 °C. Dissolved nutrient analysis followed later as described in Chapter 1.4.3.

3.1.3 Dark nitrification and ammonium assimilation in slurry incubations

Three polycarbonate bottles (1 L) from each site were filled to full capacity with peatwater from the study sites (Heiligensee, Mid-peatland, Prahmgraben) and transported to the lab under the same conditions described above. In the lab, the water was filtered through a 3 mm sieve to remove large particles, and then homogenized by stirring the filtrate. As mentioned earlier (Chapter 1.4), for the determination of nitrification and N-assimilation rates, we applied the ^{15}N-NH_4^+ tracer method (Damashek et al., 2016; Veuger et al., 2013). For this, we filled the homogenized water into six polycarbonate bottles (325 ml) and sealed them airtight with a butyl septum and a perforated lid, to inject the tracer into the bottle. The water samples were enriched with ^{15}N-NH_4Cl (98 atom% ^{15}N, SigmaAldrich). From January to March 2019, a minimum enrichment was added resulting in 0.05 µmol L^{-1} of tracer addition. Thereafter, enrichment was calculated to equal 10 % of the in situ NH_4^+ concentrations in the sampled water. After the enrichment, the bottles were shaken firmly by hand. Three bottles were then immediately filtered (GF/F Whatman; precombusted for 3 h at 450 °C) to serve as t_0 value. The other three bottles were stored overnight in a dark, climate controlled room (15 °C). The next day, the incubation of the remaining triplicates was terminated by filtration of the bottle volume through precombusted GF/F Whatman filters. Both the filtrate and the filters of t_0 and t_1 were frozen at -20 °C for later analysis of delta ^{15}N-PON (N-assimilation) and ^{15}N-$NO_{2/3}$ (nitrification rates), respectively. For the measurement of nitrification rates, the denitrifier method was used (Casciotti et al., 2002; Sigman et al., 2001). Thereby, we measured the labelled nitrate only, as we did not differentiate between NH_4^+-oxidation and NO_2^--oxidation. In brief, the denitrifier method uses the bacterium *Pseudomonas chloroaphis* (ATTC 13985), which converts NO_3^- to nitrous oxide (N_2O), as it lacks the gene required for nitrous oxide reduction to dinitrogen. N_2O was extracted by a PAL autosampler, purified by a Finnigan GasBench II, and measured with a Delta V advantage continuous flow isotope ratio mass spectrometer (Thermo). Isotope standards (IAEA-N3 and USGS 34) were simultaneously analysed as references. The accuracy of the isotope measurements accounted for ± 0.16 ‰.

3.1.4 Statistical analysis and software application

RStudio (V2021.09.0) was used for the calculation and display of the statistical analysis. Data were checked for normal distribution (Shapiro-test) and differences of the means (Student's t-test (n > 20) or "Wilcoxon-Mann-Whitney"-test (n < 20)). Correlations were determined by Spearman's method (confidence interval = 0.95, significance level = 0.05), and plotted by using the corrplot package (https://github.com/taiyun/corrplot). The scatter- and barplots were made with help of ggplot2 (Wickham, 2016). The maps were created with QGIS Desktop (3.14.1), which included the basemap material from Esri. FAPROTAX ("Functional Annotation of Prokaryotic Taxa"; Version: 1.2.4; Copyright (c) 2020, Stilianos Louca) was utilized to identify relevant microbial taxa.

3.2 Results

3.2.1 Salinity and dissolved oxygen fluctuations

The seawater inflow occurred in the north of the Hütelmoor close to the Heiligensee (Figure 3.2) from where seawater spread out across the peatland (Gutekunst et al., 2022). After the inflow, salinities varied between >1 and 10 ppt within the whole peatland and underwent strong variability at each site

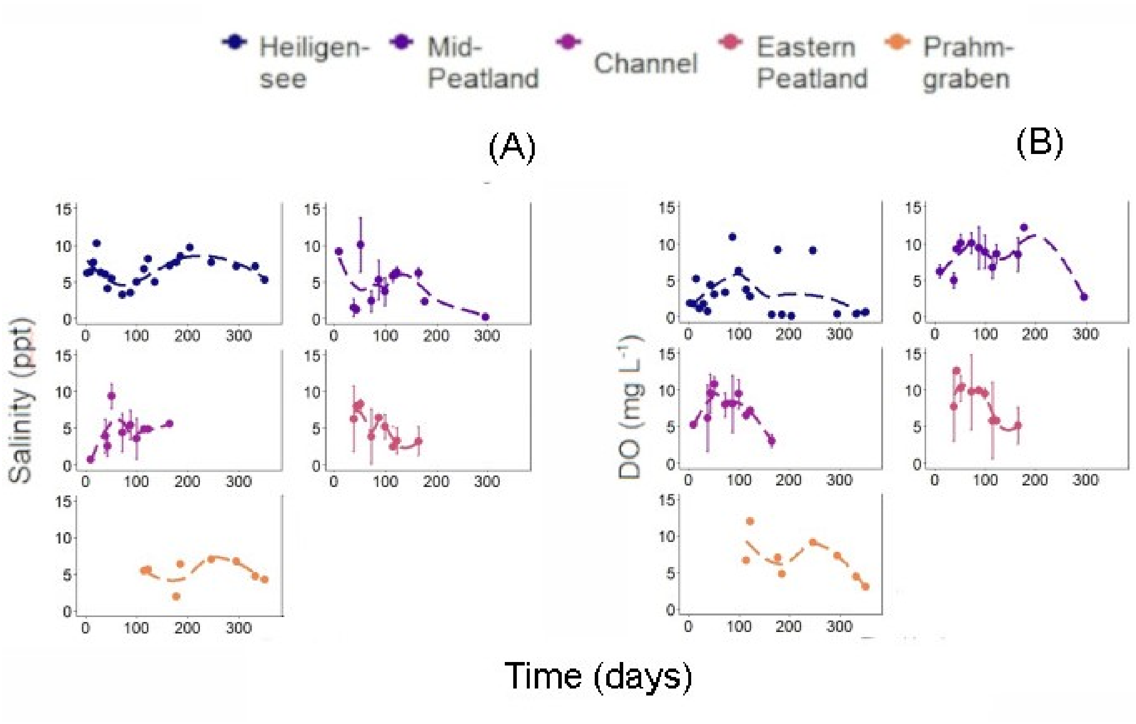


FIGURE 3.2: Lineplots of (A) salinity (ppt) and (B) dissolved oxygen ($mg\ L^{-1}$) fluctuations over time (days) in Hütelmoor (2019).

throughout 2019 (Figure 3.2). All sites had constant oxic conditions (Figure 3.2). However, the median DO-value at Heiligensee was lower than at the inner peatland sites, still with large DO-spreading (Figure 3.3).

3.2.2 Dissolved inorganic nitrogen in Hütelmoor after flooding

NH_4^+ concentrations in spring 2019 were not significantly different from those measured in 2017 (prior to flooding; Appendix Table 1;), as the standard deviations overlap. The DIN (NH_4^+, NO_2^-, NO_3^-) concentrations during the flooding event were increased in the southern end of Heiligensee and the eastern part of the Hütelmoor (Figure 3.4; Figure 3.5), whilst the Baltic seawater (opposite of Heiligensee) had ammonium concentrations of < 5µmol L^{-1} (measurement from 3^{rd} of January; data not shown). In the first 45 days after the inflow we observed elevated DIN (NH_4^+, NO_2^-, and NO_3^-; Figure 3.4) at

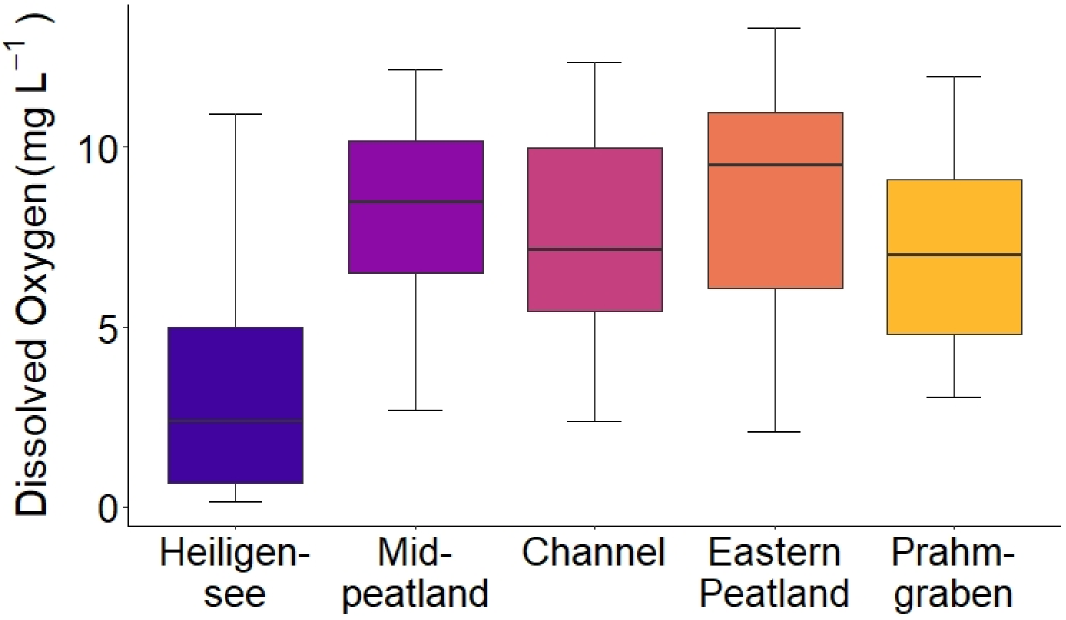


FIGURE 3.3: Boxplot of dissolved oxygen concentrations in Hütelmoor (2019).

all sites except Prahmgraben. Afterwards, we recorded no more NH_4^+ peaks comparable to the one from January 2019, whilst NO_2^-, and NO_3^- underwent further fluctuations. The sites did not differ significantly in dissolved inorganic nitrogen (DIN), represented in the NH_4^+, NO_2^-, and NO_3^- values.

3.2.3 Nitrification and heterotrophic ammonium assimilation

Nitrification rates declined from north to south(west): at Heiligensee nitrification rates were between non-detectable and 8.3 nmol N $L^{-1}d^{-1}$. In the Mid-peatland station, nitrification rates ranged between non-detectable and 0.6 nmol N $L^{-1}d^{-1}$, and at the Prahmgraben between non-detectable and 0.2 nmol N $L^{-1}d^{-1}$ (Figure 3.6). The heterotrophic NH_4^+ assimilation rates displayed large spreading, and thus, we detected rates at Heiligensee between non-detectable to 236 nmol N $L^{-1}d^{-1}$, at Mid-peatland between non-detectable to 86 nmol N $L^{-1}d^{-1}$, and at Prahmgraben between non-detectable to 110 nmol N $L^{-1}d^{-1}$ (Figure 3.6).

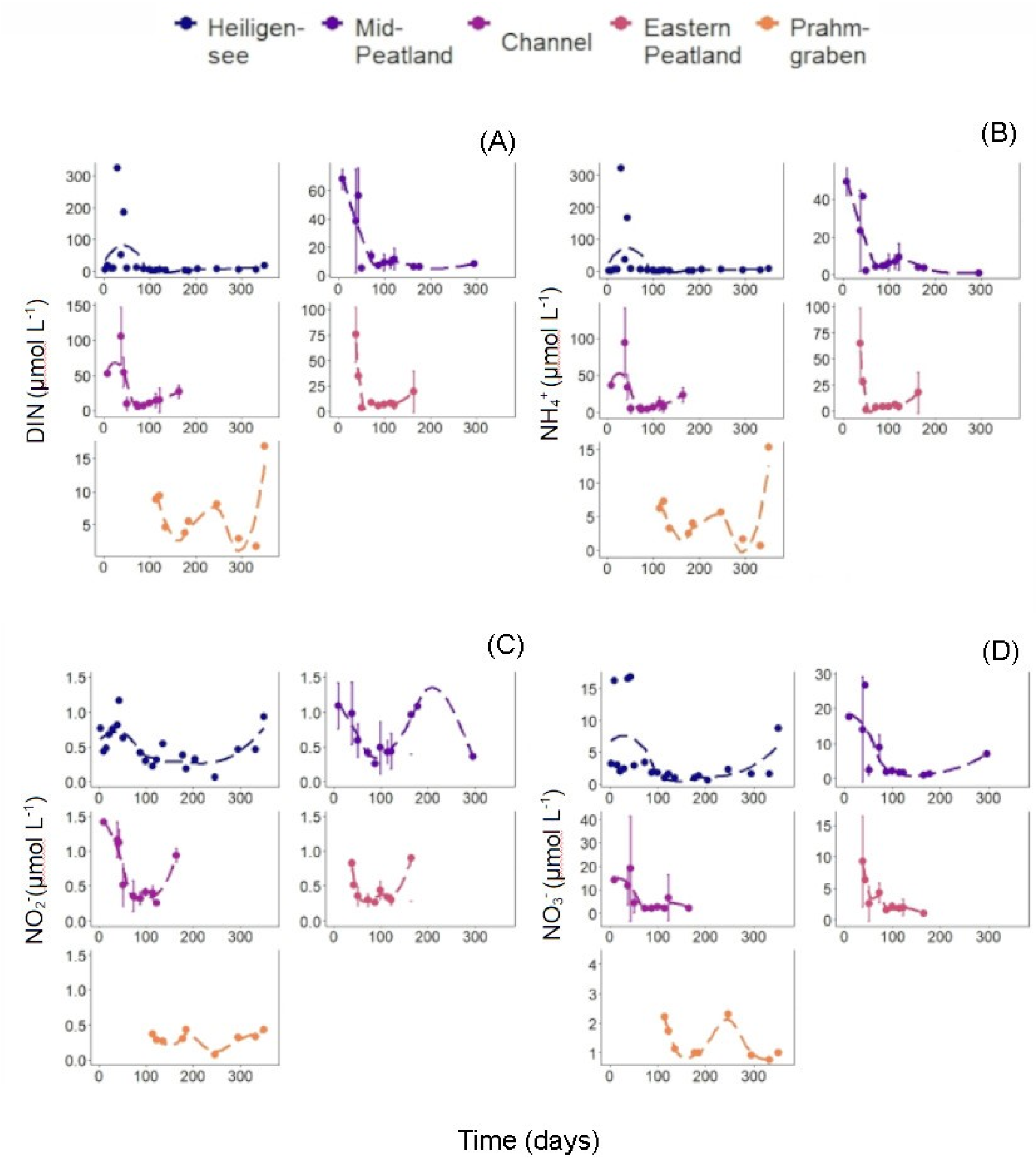


FIGURE 3.4: Lineplots of (A) DIN, (B) ammonium, (C) nitrite, and (D) nitrate fluctuations ($\mu mol\ L^{-1}$) over time (days) in Hütelmoor (2019). Note: individual y-axis

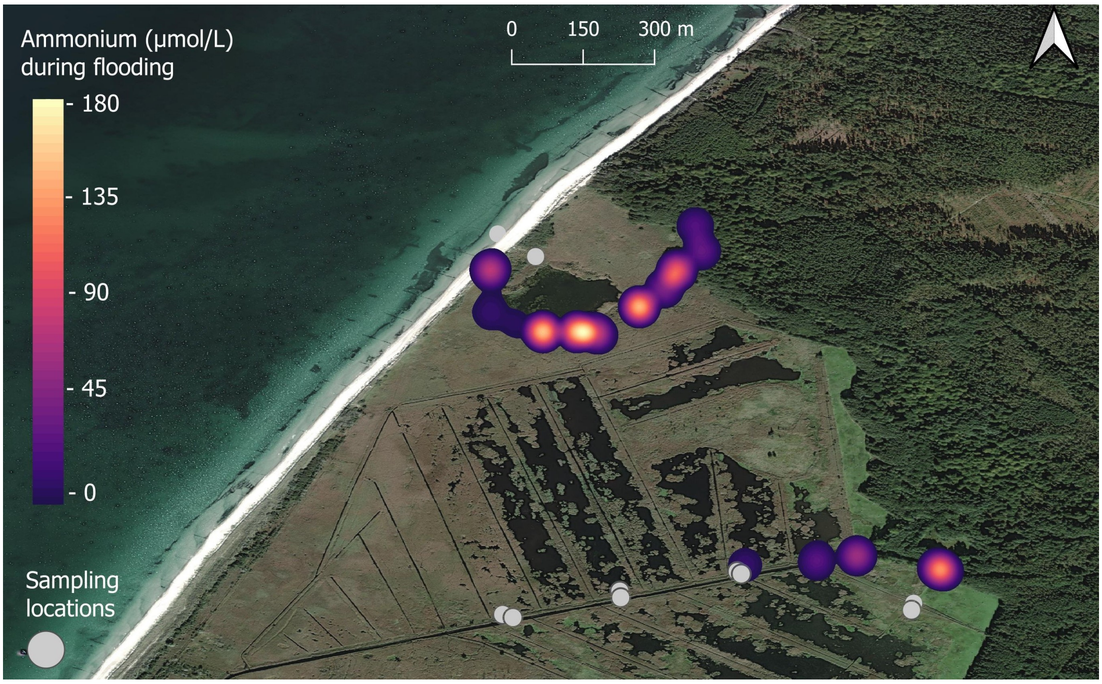


FIGURE 3.5: Heatmap displaying ammonium concentrations during the flooding event (1.-3.01.2019) in Hütelmoor. Sampling by F. Koebsch. Ammonium determination at IOW.

3.2.4 Non-linear relationships

Nitrification did not correlate with any environmental variables (salinity, temperature, DO; Figure 3.7). Ammonium assimilation negatively correlated with salinity ($p < 0.05$; n = 13; r = -0.97) and positively with the water height (WH; pers. comm. M. Janssen) controlled only by precipitation and evaporation respectively ($p < 0.05$; n = 13; r = 0.68; Figure 3.7). Ammonium was negatively correlated with DO (n = 110; $p < 0.05$; r = -0.34), and nitrite was negatively correlated with salinity (n = 110; $p < 0.05$; r = -0.42). Lastly, salinity fluctuations at Heiligensee were negatively correlated to the calculated water level ($p < 0.05$; n = 23; r = -0.9; not shown; pers. comm. M. Janssen).

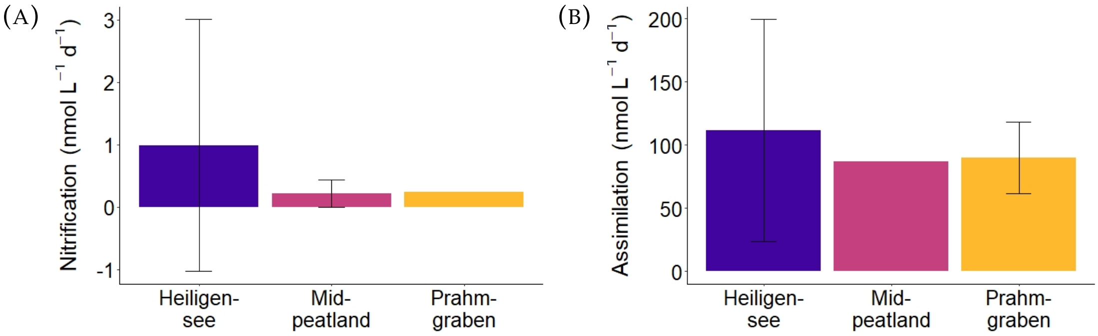


FIGURE 3.6: Barplot of averaged (A) nitrification and (B) ammonium assimilation rates (*mean* ± *s.d.*) per site in 2019.

3.3 Discussion

3.3.1 Salinity distribution in Hütelmoor after flooding

So far our findings suggest that the ditches across the peatland (Figure 1.2, Introduction) are mostly still intact (Miegel et al., 2016), thus, we expected that horizontal surface flows within Hütelmoor would eventually flow into smaller ditches and ultimately into the Prahmgraben, the main ditch as it has been shown by Toro et al. (2022) for a similar system. The salinity fluctuations after the inflow event suggest that the areas north of the Prahmgraben are hydrologically detached from the more southern parts (Figure 3.2). This is supported by the finding, that nearby dip wells north and south of the Prahmgraben showed considerable differences in water level (pers. comm. G. Jurasinksi and M. Janssen).

In January 2019, Heiligensee - located behind the dune - was the first site experiencing seawater intrusion (22 mS cm^{-1} or ca. 13 ppt; Gutekunst et al., 2022), which raised salinity in the surface layer of the lake to 7.5 ppt by mid-January (Figure 3.2). Around March, the salinity started to slowly increase in the lake, but declined again during autumn. Evaporation and dilution likely were responsible for these salinity fluctuations at Heiligensee, as salinities rose during phases of warming (spring/summer) and fell during phases of

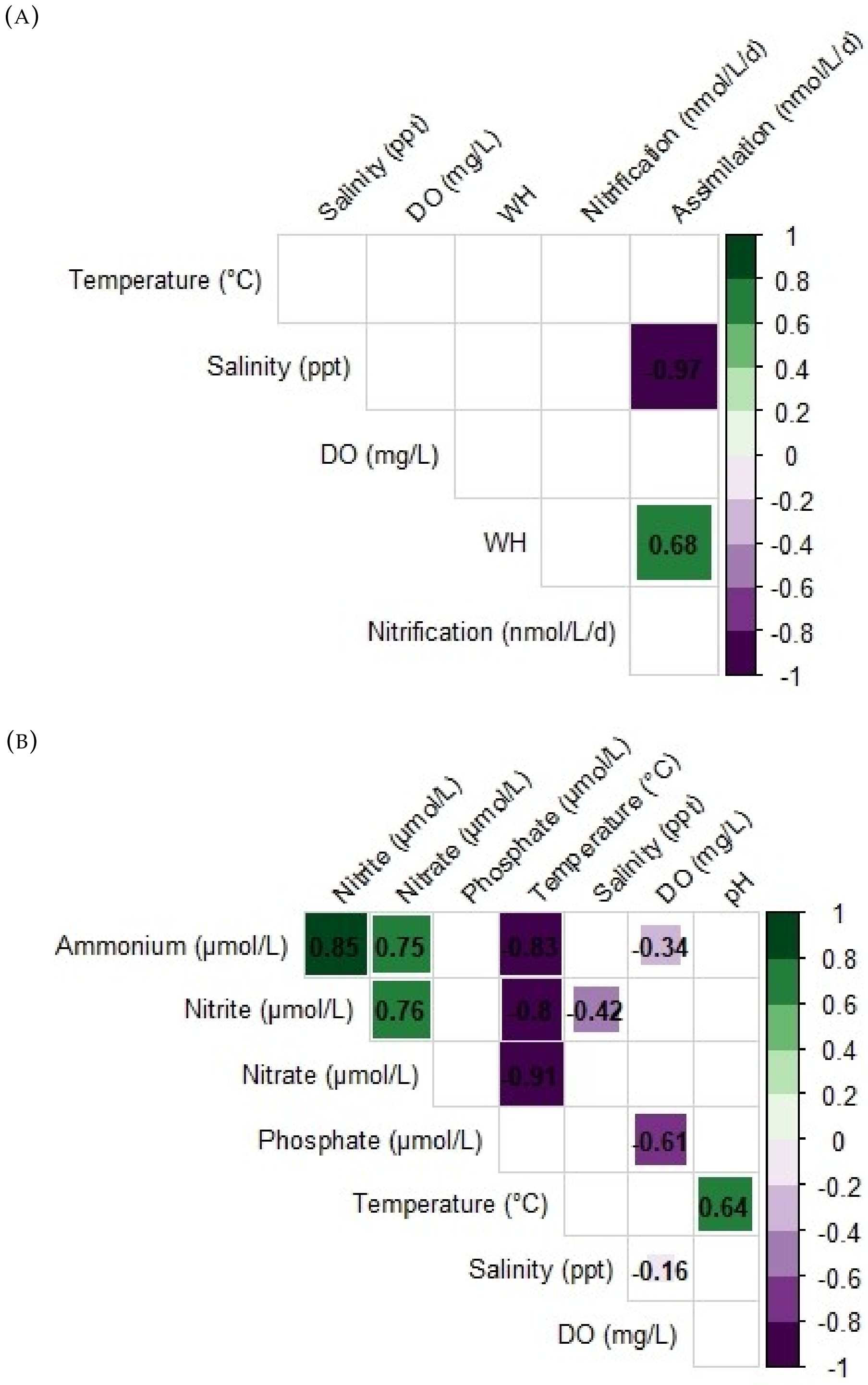


FIGURE 3.7: Corrplots showing significant correlations ($p < 0.05$) between abiotic variables and (A) nitrification and assimilation, and (B) dissolved nutrients. Blank fields mean no correlation between variables was found. WH: water height; DO: dissolved oxygen.

higher precipitation (autumn/winter) (pers. comm. E. Racasa). This indicates that the salinity in the lake is mostly controlled by atmospheric deposition (rain) during seasons, but not by other terrestrial water sources (e.g. groundwater, ditches/ channels; Bohne and Bohne 2018).

Evaporation and precipitation likely impacted salinity concentrations at all sites in Hütelmoor (Miegel et al., 2016), which could explain the simultaneous salinity rise in mean values around day 100 at Mid-peatland, Channel, and possibly Eastern peatland. However, unlike Heligensee, the central sites (Mid-peatland, Channel, Eastern peatland, Prahmgraben) are connected by ditches and channels with active input from other water sources (e.g. groundwater from elevated areas; Bohne and Bohne, 2008) affecting their salinity. We assume, that the seawater infiltrating the central parts of the fen probably mixed with pre-existing freshwater masses which lead to the recorded large range of salinity values. Shortly after flooding, salinities at Mid-peatland were slightly higher than at Heilgensee (10 ppt). This aligns with Gutekunst et al. (2022) documenting that the Baltic seawater quickly spread across the peatland already during flooding. It is likely that the Heiligensee was infiltrated and partly flushed by inflowing Baltic Sea water with a considerably higher salinity than the bottom water of the lake. Lower salinities in the lake compared to Baltic Sea water can be explained by dilution effect of the freshwater in the lake. At sites in the Mid-peatland the flood may have pushed freshwater from the water tables further south and only little dilution took place.

Moreover, the "pushed-out" freshwater from Mid-peatland probably flew partly southwestwards (Figure 1.2, Introduction) across the Channel, where internal mixing with freshwater would explain the low salinities there during the temporary flooding (< 2.5 ppt). Gutekunst et al. (2022) reported decreasing salinity gradients towards the forest in the north-east suggesting that some of the freshwater was pushed into direction of the forest (Figure

1.2, Introduction). After the inflow ended, the freshwater from the elevated terrain may have (partly) returned to the Mid-peatland, and consequently the salinity fell there within 50 days (Figure 3.2). Interestingly, salinities at Eastern peatland - the station where the influence of the inflow seem to have ended (Gutekunst et al., 2022) - salinities remained relatively high (ca. 7 ppt) and only subsequently declined below 5 ppt within 180 days after the inflow. We assume that this site is poorly connected to the central parts of the fen during warm periods, but received a constant and slow supply of freshwater from higher forest terrain (Bohne and Bohne, 2008) which could explain the gradual salinity decline. The freshwater supply also affected lower elevations within the Hütelmoor, which contributed to the overall salinity decline in the peatland throughout 2019. Freshening from central sites of the peatland may have been connected to vertical water flows transporting some saline water into deeper soil layers (Koebsch et al., 2013; Jurasinksi et al., 2018), but this was not further assessed in this study.

Interestingly, the salinity fluctuation at Prahmgraben coincides with the fluctuation of Heiligensee, thus, increased precipitation during autumn/winter is probably also responsible for the freshening at Prahmgraben. Recent findings even suggest (pers. comm. G. Jurasinksi), that Prahmgraben is - similar like Heiligensee - largely disconnected from the rest fen.

3.3.2 Heiligensee as inorganic nitrogen source in the Hütelmoor

We detected increased dissolved inorganic nitrogen values in the study area in January and February when compared to data from spring 2017 (Appendix Table A1). However, the increased N values were only temporary, and mean ammonium values in spring 2019 did not significantly differ from spring 2017 (Table A1, Appendix). For this reason, it seems unlikely that any excess nitrogen was released from the topsoil due to cation exchange from seawater in 2019, which confirms findings of Gosch et al. (2019). Instead, the surface layers of Hütelmoor had probably experienced earlier nutrient loss due to aerobic (Jurasinksi et al., 2018) and anaerobic (Gosch et al., 2019) peat degradation and any excess N from the topsoil may have been already detached. Interestingly, during flooding NH_4^+ concentrations were elevated (up to 179 µmol L^{-1}) at the southern end of Heiligensee (Figure 3.5), but the Baltic Sea water had only low concentrations of about 4 µmol L^{-1} (data not shown). For this reason, the only plausible N-source, which has lead to the increased DIN in the central parts of the fen, can be the water from the Heiligensee. Since the Heiligensee is located right behind the dune breach, and the seawater intrusion infiltrated the lake, bottom water could have easily been pushed southward (analog to salinity spreading in Gutekunst et al., 2022) into the peatland. As mentioned earlier, Heiligensee appears to be a decoupled system (no connection to ditches or channels) and is not connected to terrestrial water sources, but is only fed by rain. For this reason, Heiligensee may even display chemical stratification, since the surrounding elevated area isolates the lake from strong winds preventing internal mixing (Klerk et al., 2016) and may develop low-oxic conditions in the lake and bottom waters (Figure 3.3). These low oxic conditions favor NH_4^+ accumulation, as nitrification is inhibited.

3.3.3 Nitrifier species composition in Hütelmoor

Rapidly induced salt stress can lead to a species shift (Li et al., 2021b, 2021a) and we expected a varying community composition between 2014 (prior flooding) and 2019 (post flooding). However, microorganisms can overcome stress-momentum and acclimatize to new environmental conditions (here salinity) (Chase, 2003; Leibold et al., 2004), sometimes even within days (Shade et al., 2011). Since data from 2019 were sampled in autumn (months after the flooding event), species recovery due to their robustness (and freshening of the peatwater during autumn) may have occurred. Nevertheless, salinization introduced habitat-specific preferences for halophile or halotolerant microbes in the Hütelmoor and may have shifted selective pressure to their advantage. Halotolerant nitrifying species like *Nitrosomonas* (Cui et al., 2016), *Nitrosopumilus* (Nacke et al., 2017) or *Nitrospira* (Liu et al., 2020) were present in the Hütelmoor (Gutekunst et al., 2022). *Nitrosopumilus* is a commonly known marine nitrifier and has been also identified in another flooded soil earlier (Nacke et al., 2017). *Nitrosomonas* has only been investigated in wastewater treatments so far (Cui et al., 2016) and is, thus, a novel finding for flooded peatland ecosystems. Whilst *Nitrosomonadaceae* occurs abundantly both in 2014 and 2019, *Nitrosopumilus* was more abundant in 2014 (Gutekunst et al., 2022), which suggests that the flooding actually pressured *Nitrosopumilus*. Previously, *Nitrosopumilus* demonstrated inhibition under high ammonia concentrations (Di et al., 2010; Zhang et al., 2012). Since increased ammonium was released during flooding (see Figure 3.4 and 3.5), *Nitrosopumilus* may have subsequently declined in abundance. In contrast, *Nitrospira* was slightly more abundant in 2019 than in 2014 (Gutekunst et al., 2022), which confirms recent studies which reported about *Nitrospira* in saline estuarine sediments (Liu et al., 2020) and ecosystems with strongly fluctuating salinities (Daebeler et al., 2020). Interestingly, the genus of *Nitrospira* is a nitrite oxidizer (Sakoula et al., 2021), but it is also known to perform the complete ammonium oxidation (comammox), which enables a single bacterium to undertake complete nitrification (Daims et al., 2016, 2015; van Kessel et al., 2015). This potentially makes *Nitrospira* an important player for nitrification in an episodically flooded coastal peatland during strong salinity fluctuations. Altogether though, the microbial community composition was clearly dominated by freshwater taxa (Gutekunst et al., 2022), which was probably promoted by the low salinity prior to flooding (1 ppt; Koebsch et al., 2013) and declining salinity concentrations throughout 2019 (Figure 3.2). Furthermore, no distinctive community change occurred between 2014 (prior flooding) to 2019 (post flooding) in the Hütelmoor (Gutekunst et al., 2022) which confirms reports that community responses to environmental disturbances likely depend on the community robustness (Woodward et al., 2015), and probably the length of exposure to the stressor (Cocks, 2003). Past flooding events that are reported for the site in approximately 20 year intervals suggest that microbial communities in the Hütelmoor may have adapted to their initial state after a disturbing event (Chase, 2003; Leibold et al., 2004) followed by a rapid recovery of the community composition (Shade et al., 2011). With these means, we conclude that the freshwater nitrifiers in the study site are robust and can endure episodic salt-stress, and/or are able to recover rapidly from salt driven stress, however with no indication on their respective activity (see 3.6). Still, findings of *Nitrosomonas* and *Nitrospira* are an important documentation of possibly key halo-tolerant nitrifiers in rewetted coastal peatlands.

3.3.4 Nitrification and DIN after seawater flooding

Nitrification rates in the Hütelmoor were low (Figure 3.6), and we did not find any correlation between nitrification and the considered abiotic variables (temperature, pH, dissolved oxygen; Fig. 3.7). Interestingly though, the location (Heiligensee) with the single highest nitrification rates (8 nmol N $L^{-1}d^{-1}$) also had the lowest water clarity. Low water clarity is usually associated with a high content of dissolved and /or suspended particulate matter (SPM), which can favor nitrification as 1) particles release NH_4^+ during degradation and 2) provide low oxygen environments (Kache et al. 2021;

Kholdebarin and Oertli, 1977). The increasing impact of SPM is particle size-dependent and decreasing particle size has a negative impact on nitrification (Xia et al., 2017); particles > 0.7 µm may be even irrelevant for nitrification (Goldberg and Gainey 1955). However, since our experimental setup did not target particle size distribution and the nitrification rates at Heiligensee spread widely (Figure 3.6), the findings of prior studies cannot be confirmed. For a short period of time nitrification rates appeared largely unaffected by the increasig salinity caused by seawater intrusion. However, it is well known that sodium chloride (NaCl) —the most abundant seawater compound— is a strong and rapid nitrification-inhibitor (Guo et al., 2022; Souri, 2010) explaining our low rates after the flooding event. NaCl increases the osmotic pressure on freshwater microbes (here nitrifiers) and thus, disturbs their activity (Darrah et al., 1987; Golden et al., 1981; McGuire et al., 1999). NaCl-induced inhibition of nitrification has also been reported for estuarine sediments (Rysgaard et al., 1999), soils (Huang and Huang, 2009), and culture studies (Cortés-Lorenzo et al., 2015; Ilgrande et al., 2018; Moussa et al., 2006). Moreover, NaCl concentrations of 10 ppt (equaling the mean salinity of the Baltic Sea off the study area) already reportedly inhibited nitrification (Moussa et al., 2006; Rysgaard et al., 1999). In addition to NaCl, other seawater compounds such as sulfide (H_2S) may also have a strong negative impact on nitrification. Sulfide is known to disturb biogeochemical cycles (Setia et al., 2010; Weston et al., 2011) and is toxic to nitrifiers already after brief exposure (Joye and Hollibaugh, 1995). For instance was sulfide the decisive seawater compound that inhibited nitrification in a tidal oligohaline wetland (3.5 ppt; South Carolina, USA; Noe et al., 2013), and even though we have no tidal influence in our study site, Hütelmoor can also be characterised as an oligohaline wetland (Batistel et al., 2022).

Since the flooding introduced both H_2S and NaCl to the Hütelmoor (Gutekunst et al., 2022), a strong seawater-induced inhibition may have been the reason for the overall low nitrification rates recorded. In addition, both sulfide (Sears et al., 2004) and chloride (Guo et al., 2022; Laura, 1977; Pathak and Rao, 1998) have a long-lasting retardation effect on nitrification. This means that exposure to sulfide and chloride may not only rapidly inhibit nitrification, but also prolong reactivation of nitrifiers (Guo et al., 2022; Sears et al., 2004). For this reason, episodes of lower salinity (Figure 3.2) may decrease salt-stress on nitrifiers temporarily in the Hütelmoor, but they could still remain inactive. The disturbing effects of seawater-salts on nitrification may also explain the non-correlation between NH_4^+ and the measured nitrification rates; a phenomenon similar to previous observations (Verhagen et al., 1992). Even though our results indicate that strongly increased NH_4^+ concentrations (300 µmol L^{-1} at Heiligensee in February 2019; Figure 3.5) positively affect nitrification, large DIN-fluctuations and a wide range of nitrification values may have disabled the direct link between NH_4^+ and nitrification in the study site.

Interestingly, culture studies investigating the individual impact of NaCl and H_2S on nitrification found disproportionally high inhibiting effects of NaCl (Ilgrande et al., 2018; Moussa et al., 2006) and H_2S (Bejarano Ortiz et al., 2013) on NH_4^+- and NO_2^--oxidation respectively. For instance Moussa et al. (2006) reported that NaCl addition (10 g) reduced NH_4^+-oxidation by 36 %, while NO_2^--oxidation was only reduced by 11 %. Bejerano Ortiz et al (2013) documented that sulfide-supply (3.1 - 112 mg L^{-1}) reduced NH_4^+-oxidation by 51 - 92 %, and NO_2^--oxidation by 77 - 97 %. Whether AOM or NOB are more sensitive towards seawater salt depends on multiple variables such as type of salt ions, temperature, as well as NH_4^+ and NO_2^- availability (Sudarno et al., 2011). The matter is still debated, as some studies indicate higher salt-sensitivity of AOM (Coppens et al., 2016; Moussa et al., 2006) whereas others report NOB to be more sensitive (Bassin et al., 2012; Pronk et al., 2014).

Nevertheless, disproportional inhibition of NH_4^+- and NO_2^--oxidation may provide an explanation for the absent linear relationship between NH_4^+ concentrations and nitrification rates in the Hütelmoor samples. The episodical accumulation of nitrite was previously reported to be associated with salt-induced disproportional inhibition, since NO_2^--production (NH_4^+-oxidation) and NO_2^--consumption (NO_2^--oxidation) are not balanced (Bejarano Ortiz et al., 2013; Delgado Vela et al., 2018; Moraes, 2014). We observed nitrite accumulation — and, thus, relatively higher NH_4^+-production/ oxidation - during phases of low salinity (Figure 3.2). This suggests, that the AOM we found were more sensitive towards seawater salinity than the NOB as it has been reported from other sites as well (Coppens et al., 2016; Moussa et al., 2006) and that AOM are more active during decreased salinity than NOB. Disproportional inhibition of NH_4^+- of NO_2^--oxidation can also be caused by light. Photosensitivity (specifically against blue light) may inhibit nitrification in the upper water column leading to retardation of the nitrifying activity (Lu et al., 2020), meaning, that AOM are also more vulnerable to light changes than NOB (Guerrero and Jones, 1996). The peatwater at our sites was exposed to daylight until sampling. Since daylight was constant in our experiment and we observed nitrite fluctuations in the *in situ* water, photosensitivity can hardly be the determining variable explaining our results. Still, we found the highest nitrification rates at Heiligensee (Figure 3.6), where the low water clarity may have reduced light-depletion in the water (Bernardo et al., 2019). Therefore, light exposure may have been at least contributing to the low nitrification rates we recorded. Instead, nitrification was probably directly inhibited by oxygen depletion (negative correlation; Figure 3.7), as ammonium accumulated during low oxic conditions (Figure 3.4). This confirms the general assumption that nitrifiers are highly sensitive microbes (Juliastuti et al., 2003; Radniecki and Ely, 2008) and that NH_4^+-oxidation was probably the rate-limiting step for total nitrification (Kurisu et al., 2007; Yao et al., 2022) in the Hütelmoor.

In summary, our results suggest that the seawater flooding in January 2019 and the rising salinity in the peatwater of the Hütelmoor probably disturbed the nitrifying activity. Waters with high particle loads like those in the Heiligensee may be favorable locations for nitrifiers in comparison to illuminated sites with higher clarity. Nevertheless, high sulfide and chloride concentrations probably lead to the rapid inhibition of nitrification, thereby, AOM appear to be more sensitive towards salt than NOB. In spite of low nitrification, critical amounts of inorganic nitrogen did not accumulate, but it remains uncertain if disturbed nitrification resulted in increased formation of by-products like nitrous oxide.

3.3.5 Dark ammonium assimilation

NH_4^+ assimilation occurred in the peatwater of the Hütelmoor under dark conditions (Figure 3.6), however at low rates. Phases of increased salinity had a direct negative influence on NH_4^+ assimilation (Figure 3.7). This is similar to the findings of a single-factor study by Middelburg and Nieuwenhuize, (2000), where dark NH_4^+ assimilation by bacteria was reduced by increased salinity and almost completely inhibited (72 nmol N $L^{-1}d^{-1}$) at a salinity of 10. Still, NH_4^+ assimilation was performed at low rates in the Hütelmoor, although the salt stress probably led to reduced metabolic efficiency and enzyme activity (Rietz and Haynes, 2003), probably no cell lysis/ death occurred (Tan and Thanh, 2021).

The highest dark NH_4^+ assimilation rates were measured at Heiligensee which was expected since the lake displays low water clarity and little light penetration and competitive light-dependent NH_4^+ assimilation are unlikely (Bernardo et al., 2019; Vila et al., 1998). Therefore, the inhibiting effect of salt on dark NH_4^+ assimilation may play predominately a role in turbid waters of the lake and not in illuminated layers of the Hütelmoor. Consequently inhibited NH_4^+ assimilation under salt stress may contribute to the lake's increased ammonium loading (Chapter 3.3.2), thus, our findings give important insight into nitrogen dynamics in wetland depressions, which are often nitrogen-rich after previous cultivation (Zak and Gelbrecht, 2007). In terms of the importance of bacterial NH_4^+ assimilation to the nitrogen cycle, recently NH_4^+ assimilation was linked to aerobic denitrification (Sun et al., 2017). Aerobic denitrification describes the conversion of ammonium directly to dinitrogen under aerobic conditions (Hao et al., 2022). The results of lab studies suggest that co-occurring bacterial NH_4^+ assimilation and aerobic denitrification can double total N-removal (Sun et al., 2017). This means, salinity-induced inhibition of bacterial NH_4^+ assimilation may impair an additional nitrogen removal pathway (next to anaerobic denitrification), which may play a role in formerly cultivated surface soils with high nitrogen loads and aerated conditions.

In summary, salinity negatively affected dark NH_4^+ assimilation in the Hütelmoor, however, this may only affect aquatic bodies with low light penetration like the Heiligensee, and could contribute to DIN-accumulation in the water.

3.3.6 Summary

Our results showed low nitrogen cycling rates in a coastal peatland after a flooding event and suggest that rewetting projects should be monitored with respect to biogeochemical cycling and nutrient dynamics, which may ultimately disturb the ecosystem functioning. Nevertheless, no increased DIN-accumulation occurred in this study with exception of Heiligensee, which indicates that water-filled landscape depressions within a peatland may have a different ecology from the rest of the ecosytem. After the flooding, *Nitrosomonas* was one of three halophile species which were found in the Hütelmoor and represents a novelty finding for flooded peatlands. Altogether though, freshwater species dominated and suggest, that these species are more robust towards episodic salinity-stress than expected. Still, N-cycling rates were low and potential retardation of microbial activity may have long-lasting effects on the ecosystem.

Chapter 4

Impact of salinity on ammonium release in a coastal fen

This chapter is based on experimental work with Miaorun Wang (Faculty of Agriculture and Environmental Sciences of the University of Rostock). I did all the nitrogen related-work, while she determined the soil physical variables. The chapter I have written by myself.

4.1 Materials and methods

4.1.1 Sampling

Soils were sampled from two locations in the Hütelmoor. One was located close to Heiligensee (in the following referred to as natural peatland: 54°13′31.5"N, 12°10′24.9"E) the other was located towards the center of the largest fen area, close to the Moorhof (in the following referred to as rewetted peatland: 54°12′55.3"N, 12°10′49.0"E; Figure 4.1). At sampling location Heiligensee, the pH value of groundwater is 7.51. pH values of surface water and peat water at Moorhof are 7.67 and 5.99, respectively (pers. comm. Erwin Don Racasa). The annual average water level at Moorhof is 0.30 m above the ground. At each location an area of 1 m × 1 m was determined to extract undisturbed soil cores plexiglass tubes (diameter: 4.2 cm; length: 10

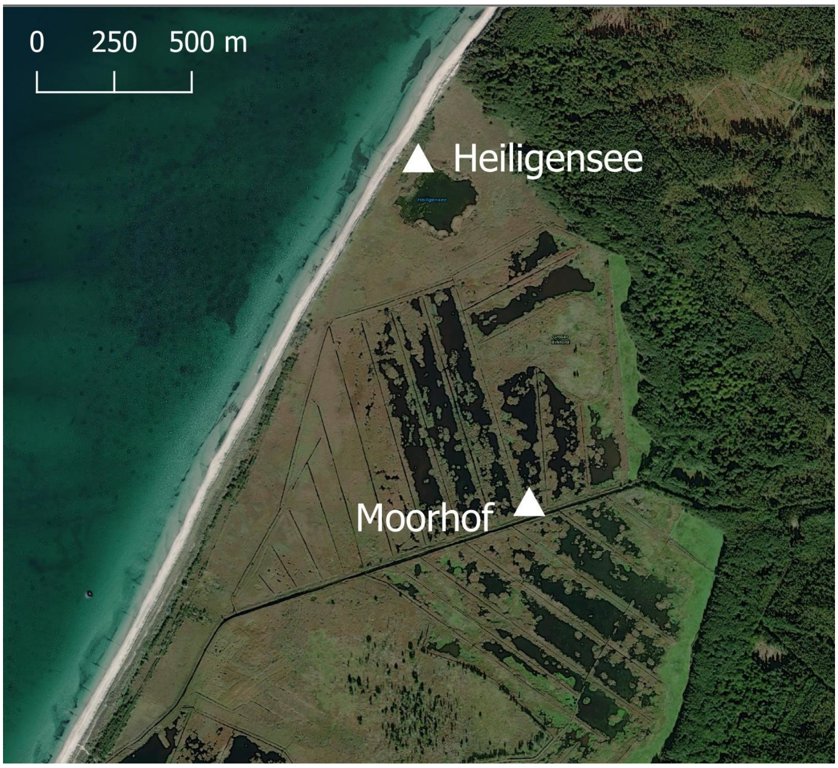


FIGURE 4.1: Map of sampling sites called natural site (Heiligensee) and rewetted site (Moorhof).

cm). 18 cores were obtained per location, with nine cores containing surface soil (0–10 cm) and nine cores containing deep-soil (30–40 cm), respectively. Immediately after sampling, the soil cores were sealed on both sides with lids and tape, and transported back to the soil physics laboratory in a cooling box.

4.1.2 Nutrient extraction experiment

The nutrient leaching in our cores was simulated with help of a Flow-through reactor (FTR; Kleimeier et al., 2017). For this, we modified the setup of Gosch et al. (2018). The FTR flushed the cores in triplicates with artificial water which imitated groundwater conditions (< 1ppt), sea water of the southern Baltic Sea (10 ppt), or mean seawater salinity (35 ppt). Groundwater and Baltic Sea water conditions simulated natural conditions which can induce nutrient leaching from the soil in Hütelmoor. The 35 ppt-treatment was undertaken to investigate a hypothetical extreme salinization event.

FTR-Setup

The salinity concentration in the solutions was adjusted by diluting sodium chloride with deionized water (gas content: 2.3 mg O_2 L^{-1}) to ultimately correspond to electric conductivities (EC) of 75 μS cm^{-1}, 18 mS cm^{-1}, and 55 mS cm^{-1}. Afterwards, the lids of the cores were removed and replaced with Whatman GF/F filters (47 mm; Sigma-Aldrich; pre-combusted at 450 °C for 4 h) at both ends of the cores. These cores were then placed upside-down into the FTR (surface soil at the lower end and bottom soil of the core at the top of the FTR). The background solutions were pumped from surface soil to bottom soil using a peristaltic pump with a constant flux of q = 0.650 cm h^{-1} for 24 hours. The leachate was sampled every 30 minutes for the first 6 hours of the experiment, thereafter hourly. There was a night-break of approximately 6 hours. The leachate was immediately used for ammonium analysis. We determined the ammonium content with the indophenol-blue method according to Hansen and Koroleff (1999) (detection limit: 0.65 μmol L^{-1}) and subsequently converted the values to mg L^{-1}. During the night break, we collected the entire leach (overnight sample). In these overnight samples we measured additionally to NH_4^+, the total carbon (TC) and total nitrogen (TN) content. For the TC and TN-analysis the overnight samples were filtered through a syringe with pore size 0.45 μm and then measured on a Continuous Flow Analyzer (CFA, Seal Analytical GmbH, Norderstedt, Germany).

4.1.3 Soil physical properties of soil

After the leaching experiment, the soil physical properties were measured. The determination and calculation of the soil physical properties followed standard measurements (e.g. ISO 11272:1998 for dry bulk density measurement; ISO 17892-3:2004 for particle density measurement). The soil physical properties included saturated hydraulic conductivity (K_s, cm h^{-1}), which describes the capability of pores of saturated soil to transmit water. Further bulk density (BD; g cm^{-1}) is measured as an indicator for soil compaction (dry weight/ soil volume). BD is determined through the thermogravimetric method where samples are dried in an oven at 105 °C for 24 h. Next, total porosity (volume or vol %; ratio) is measured, which describes the volume of void space to the total volume of sample. The detection of total porosity is based on the bulk density and gravimetric water content at saturation. Further, macroporosity (volume or vol %) is measured, which describes the proportion of large pores in the soils ($>$ 60 microns). Lastly, soil organic matter (SOM; weight or wt %). is measured through loss of ignition (4 h of incineration at 550 °C).

4.1.4 Statistical analysis and software application

All statistical analyses were conducted using the analytical tools in RStudio (V2021.09.0). We examined the impact of soil sampling location, depths and their interaction on different soil physical parameters individually with two-way ANOVA (Student-Newman-Keuls q-test; SNK-q test) and used t-tests to identify the significant differences in sampling locations and depths of each soil parameter. The correlation among soil physical properties and between the total amount of ammonium and soil properties were described by Pearson´s correlation coefficient (alpha = 0.05). For the graphs and maps, RStudio (V2021.09.0; “Ghost Orchid” and packages “ggplot2”) and QGIS (V3.24 “Tisler”; Map material from ESRI) were utilized respectively.

4.2 Results

4.2.1 Soil physical properties

Correlation between soil physical properties

SOM was negatively correlated with the bulk density ($p < 0.05$; $r = –0.97$) and increasing depth ($p < 0.05$; $r= -0.95$), whilst positively correlated with total porosity ($p < 0.05$; $r = 0.98$). Total porosity was negatively correlated with bulk density and increasing depth ($p < 0.05$; $r= -0.99$ respectively). Bulk density was positively correlated with increasing depth ($p < 0.05$; $r= -0.99$). Saturated hydraulic conductivity (K_s; data not shown) was positively correlated to macroporosity ($p < 0.0001$; $r = 0.68$; pers. comm. M. Wang).

Major differences between sites and depths

The soil physical properties of the natural and the rewetted site and their respective depths were distinctively different from each other (Figure 4.2). The natural site had significantly higher macroporosity than the rewetted site (both layers; $p < 0.05$; $r = -0.92$). Due to the positive correlation between K_s and macroporosity, the K_s values were probably also higher at the natural site than at the rewetted site. Comparing the peat layers (0-10 cm) of both sites, the SOM content and total porosity of the natural site was higher than at the rewetted site ($p < 0.05$; $r = -0.99$ respectively), whilst bulk density was higher at the rewetted site than at the natural site ($p < 0.05$; $r = 0.99$). Comparing the mineral layers (30-40 cm) of both sites, the SOM was significantly higher at the rewetted site than at the natural site ($p < 0.05$; $r = 0.99$), whilst bulk density was higher at the natural site than at the rewetted site ($p < 0.05$; $r = -0.97$).

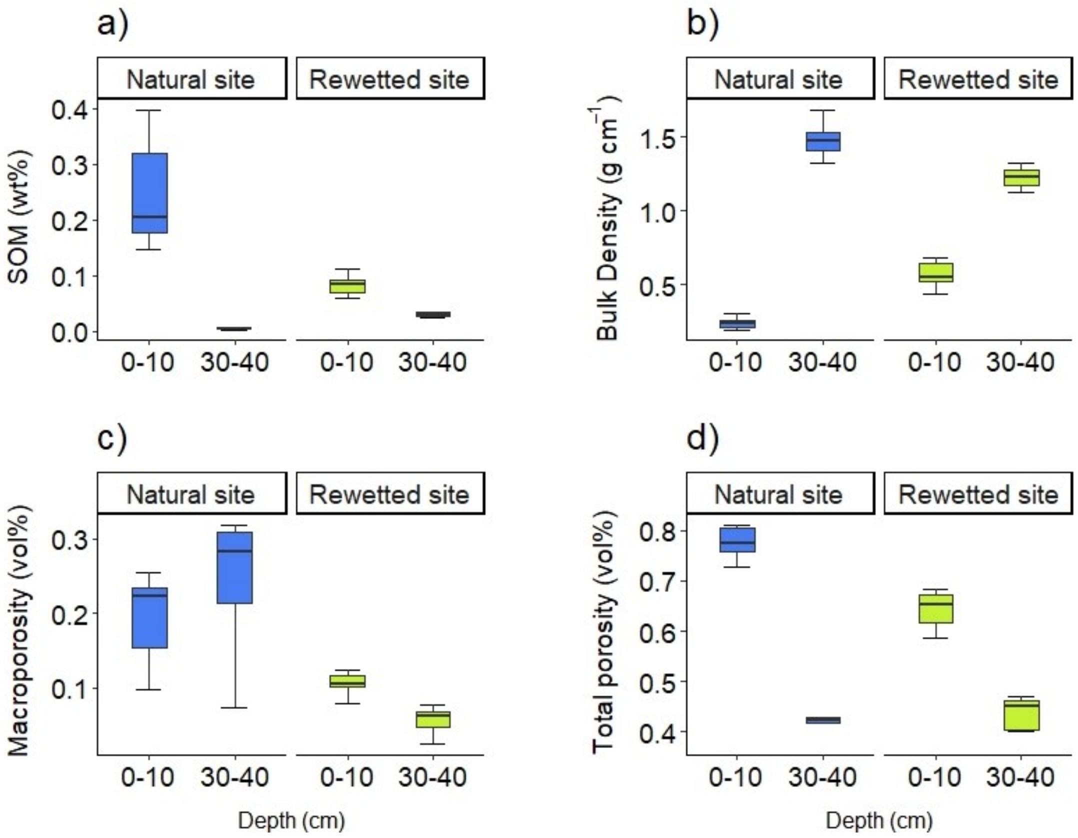


FIGURE 4.2: Boxplot of soil physical properties (n=9) of the normal and rewetted site showing a) soil organic matter, b) bulk density, c) macroporosity, d) total porosity. x-axis presents the different soil depths.

4.2.2 Ammonium release and correlation to soil physical variables

At both sites the ammonium concentrations declined throughout the 24 h experiment (Figure 4.3; note: peat intrusion in one replicate of the mineral layer at the natural site probably caused high ammonium release during 10 ppt treatment). The mean extracted ammonium from both sites and depths under all salinity treatments were not significantly different ($p > 0.05$).

Since no significant differences between salinity treatments were found, we henceforth disregarded the distinction between salinity concentrations, and instead combined all our results of the respective site and depth, and identified correlations between "ammonium extraction", "sites", "depths", and the soil physical properties. The total amount of ammonium extracted was

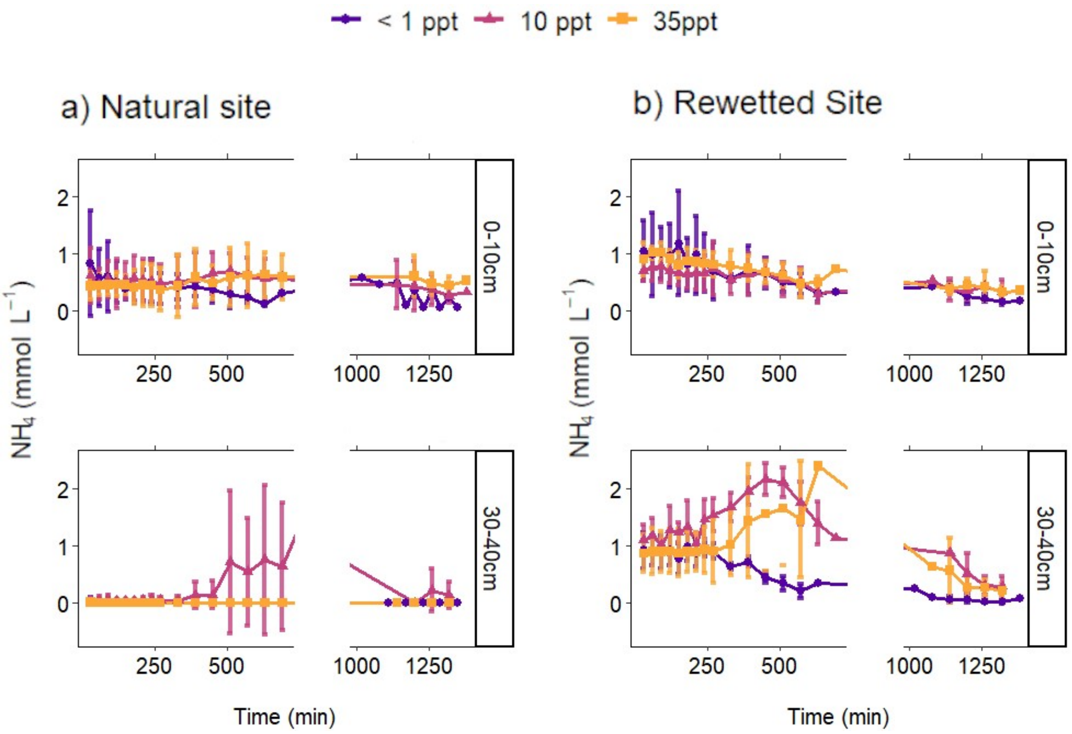


FIGURE 4.3: Lineplots of ammonium extraction (mmol L^{-1}) per site ("Natural"; "Rewetted") and depth (0-10 cm; 30-40 cm) (mean ± sd; n = 3). Salinity treatments distinguished by colour: < 1 ppt (dark purple), 10 ppt (red), and 35 ppt (yellow). x-axis break represents the night break.

higher at the rewetted site than at the natural site ($p < 0.05$; $r = 0.81$). Furthermore, the total amount of ammonium extracted correlated negatively with macroporosity of the soils ($p < 0.05$; $r = -0.85$). Considering only the peat layers (0-10 cm) of both sites, there was no correlation between soil physical properties and ammonium extraction. Considering only the mineral layers (30-40 cm) of both sites, the amount of ammonium extracted correlated positively with SOM ($p < 0.05$; $r = 0.98$) and negatively with bulk density ($p < 0.05$; $r = -0.99$). At the natural site, the ammonium extracted was positively linked to total porosity ($p < 0.05$; $r = 0.93$), and negatively with bulk density ($p < 0.05$; $r = -0.93$) and depth ($p < 0.05$; $r = -0.92$). At the rewetted site, ammonium extraction did not correlate to any soil physical properties.

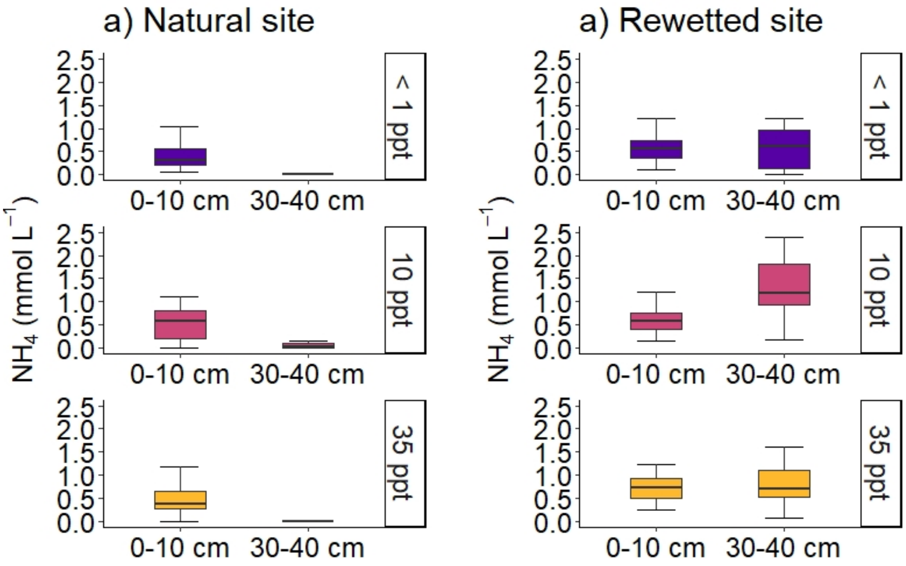


FIGURE 4.4: Boxplot of ammonium concentrations (mmol L^{-1}) at < 1 ppt, 10 ppt and 35 ppt at a) the natural site (left) and at b) the rewetted site (right).

4.2.3 Total organic carbon and total nitrogen and correlation to soil physical variables

At the natural site, the TOC values from each treatment were alike (Figure 4.5), whilst at the rewetted site, the < 1ppt treatment released higher maximum TOC values (2.6 mmol C L^{-1}) than the 10 ppt treatment and the 35ppt treatment. The TN concentrations extracted at the natural site (Figure 4.5) appear to be higher during the 35 ppt treatment than during the other salinity amendments. At the rewetted site highest TN-concentrations were extracted in the < 1 ppt treatment. Due to large variations in TOC and TN concentrations respectively (and the small sample size), there were no analytically significant differences between “salinity”, “sites” and “depth”.

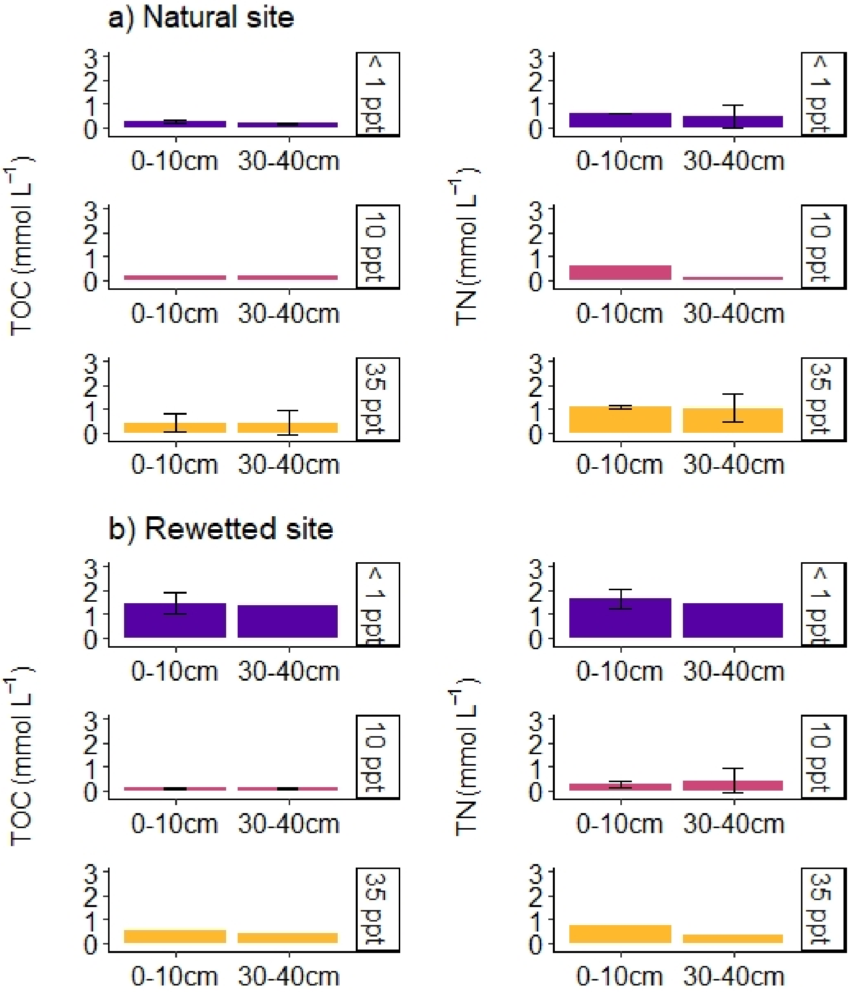


FIGURE 4.5: Barplot from a) natural site and b) rewetted site, showing TOC (left) and TN values (right; $mmol\ L^{-1}$) from overnight samples (mean ±sd; n=2 or n=1) distinguished by salinity treatment (< 1ppt; 10 ppt; 35 ppt).

4.3 Discussion

4.3.1 Differences between the natural and rewetted site

Our study targeted the peat and mineral soils of two sites in an episodically-flooded fen in NE-Germany, which receive different land management practices (natural or rewetted conditions). Our findings revealed major differences between the natural site (Heiligensee) and the rewetted site (Moorhof) (Figure 4.2), which confirms that differing land management practices of the past and presence individually shape the soils in the peatland (Jursasinski et al., 2018). Further, we found (as expected) distinctive differences between the peat and mineral layers (Figure 4.2) with regards to SOM content, bulk density, saturated hydraulic conductivity (pers. comm. M. Wang), marco- and total porosity. With these means, our study is able to give valuable insight on ammonium leaching of different soils under consideration of multiple soil physical properties and state of rewetting, but still within the same peatland.

4.3.2 The impact of varying salinity on ammounium extraction

Here we show, that NH_4^+ is released from the peat (0-10 cm) and mineral layers (30-40 cm) from both the natural and rewetted site when treated with solutions of different salinities (< 1 ppt, 10 ppt, 35 ppt). Further, the ammonium concentrations decline throughout the short term experiment (Figure 4.3), thus, the ammonium leaching appears to be only temporary, which aligns with previous findings (Liu and Lennartz, 2019). Interestingly though, the amount of ammonium extracted during the salinity treatments was not significantly different between sites and and soil types (Figure 4.4). Since increased salinity (10 ppt; 35 ppt) did not induce higher ammonium extraction in comparison to < 1 ppt treatment, cation exchange between NH_4^+ and Na^+ was not a dominant process in the Hütelmoor.

The results stand in contrast with earlier findings (Baldwin et al., 2006; Liu and Lennartz, 2019; Steinmuller and Chambers, 2018), where supply of NaCl-containing solutions induced higher ammonium extraction. Here we suggest, the availability of "competitive" soil cations which can act as cation exchange partners to Na^+ may have masked NH_4^+-mobilisation in our samples under Na^+ amendment (Evangelou and Phillips, 2005; Wada and Weerasooriya, 1990). Alkaline pH in Hütelmoor (up to 7.67) is an indicator for increased presence of "competitive" cations over ammonium, as base cations (e.g. calcium) increase soil pH, whilst ammonium-ions are acidic and reduce soil pH (Rayment and Higginson, 1992). The concentrations of (base) cations in peatlands are controlled by the degree of peat decomposition and state of rewetting (Zak and Gelbrecht, 2007). For this reason, the quantities of "competitive" cations vary between peatlands, which needs to be taken into account when comparing our results to other peatland-studies (e.g. Liu and Lennartz, 2019) where land management practices and soil conditions probably differ. With these means, Na^+-induced cation exchange with soil cations may still be an important process in the Hütelmoor, but in this case ammonium was probably not main exchange partner Na^+.

With respect to soil physical properties, the mineral soil from the natural site released the least total ammonium under water exposure (Figure 4.4). This was expected from a soil which had lowest total porosity, highest maximum marcoporosity (Figure 4.2) and highest saturated hydraulic conductivity (pers. comm. M.Wang), as such a soil easily transmits solutes, but only retains little dissolved nutrients (Helliwell, 2011). Still, due to high variability in ammonium extraction between peat and mineral layers (Figure 4.3) the ammonium release between all soils was altogether not significantly different. This was unexpected, since higher total porosity in the peatlayers implies higher ammonium retainment than in the mineral layers (Figure 4.2; Helliwell, 2011) - especially since it was hypothesized that rest nitrogen is still available in the upper peat layers due to previous cultivation (Zak and Gelbrecht, 2007). We therefore suggest, that either there were no increased amounts of nitrogen in the peat left (e.g. loss during previous drainage; Jurasinksi et al., 2018), pore-blockage in the peat occurred (Chapter 4.3.3), or that the ammonium extraction was inhibited in the upper soil layer by a characteristic peat structure called dual porosity. Dual porosity contains active and partially closed or dead-end pores (Liu and Lennartz, 2019;

Rezanezhad et al., 2016). In the active pores water and solute transport occurs (mobile soil water region), but in the partially closed pores solute transport is restricted to diffusion (immobile soil water region). Dual porosity is therefore a retardation factor controlling ion-adsorption on surfaces (Liu and Lennartz, 2019; Rezanezhad et al., 2012) and has the means to inhibit ammonium release. Indicators for dual porosity in our peat layers may be the high total porosity and low bulk density (Boelter, 1968; Rezanezhad et al., 2012), however, whether dual porosity inhibited ammonium release was not further assessed in this study. With respect to the mineral layers only, we found that the ammonium extraction at 30-40 cm depth was positively correlated with SOM content. SOM and extractable ammonium are linked through N-mineralization of organic matter (Steinmuller and Chambers, 2018), thus our findings indicate that in deeper (possibly oxygen-depleted) soil layers N-mineralization is an important process leading to ammonium-loss from the soil. Interestingly, Gosch et al. (2019) found also this link between SOM and anerobic mineralization in the soils of Hütelmoor under seawater-sulfate supply (acting as alternative terminal electron acceptor to oxygen). During previous drainage, our peat layers were aerated which possibly induced aerobic N-mineralization of SOM (Jurasinksi et al., 2018) and may have disabled a conclusive link between SOM and ammonium extraction in our study; however, deeper soil layers were saturated with water since 1990s (water tables 0.3 m below ground; Glatzel et al., 2011; Chapter 1.3) and SOM may have been partly "conserved". We speculate therefore, that the deeper, SOM-containing layers of the rewetted site (Figure 4.2) are a potential source for ammonium-loss through anaerobic SOM-mineralization. Thereby, SOM mineralization may be induced during flooding events under supply of terminal electrons such as seawater sulfate (Gosch et al., 2019). Next to SOM, also dissolved organic matter can lead to ammonium release in the Hütelmoor (Strehse et al., 2019). As we observed strong coloration of our leachates, it seems possible that coloured dissolved organic matter (cDOM) may have been present in our samples (Figure 4.6) which may have mineralized. DOM, however, was not directly measured in this study, still, DOM is closely related to TOC and TN (Gao et al., 2013), which was detected in the overnight samples of both sites (Figure 4.5). Thus, DOM may have factored ammonium extraction in this study as documented in Strehse et al. (2019), but DOM may have also flocculated under salinity exposure and retained ammonium (Chapter 4.3.3).

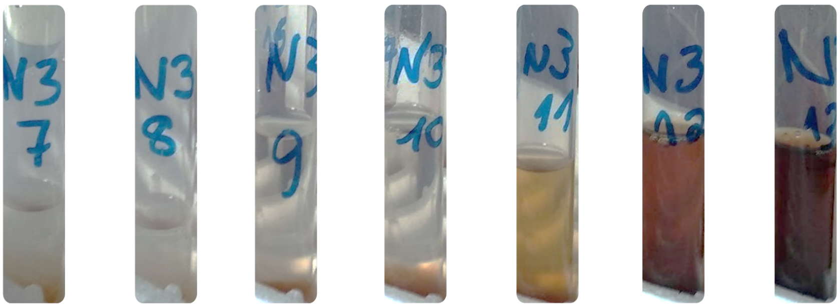


FIGURE 4.6: Leachates in order of sampling from left (first) to right (last) from the same core "N3". Orange precipitates formed at bottom of "older" samples (here: 7 to 10), whilst "fresher" samples (here: 11 to 13) are still strongly coloured. Picture taken by Miarun Wang.

4.3.3 Salinity-induced flocculation of dissolved organic matter

Reduced ammonium extraction may occur due to salinity-induced “pore blockage” which inhibits solute flow. Pore blockage may develop through coagulation and formation of organic flocs that (adsorb to and) clogg soil substrate (Michael-Kordatou et al., 2015). Coagulation is caused by increased ionic strength of the solution (here Na^+) which neutralizes surface charges between colliding molecules (e.g. humic acids) and enables the particles to stick and form “flocs” out of dissolved organic matter (Asmala et al., 2014; Gregory and O’Melia, 1989; Strehse et al., 2018). Salinity induced flocculation is known to effectively occur already at salinites 1 - 2 (Asmala et al., 2014). An indicator for coagulation of DOM is the reduction of extracted carbon concentrations (Strehse et al., 2018). In agreement, in both layers of the rewetted site the extraction of TOC and TN was lower under increased salinity (both 10 ppt and 35 ppt) than in the < 1ppt treatment (Figure 4.5). In addition to this, we observed aggregates developing in our leachates and subsequent gravitoidal settlement (orange precipitate; Figure 4.6), which hints towards the formation of flocs. With these means, coagulation and flocculation may have factored extraction of organic solutes at the rewetted site. Differing land management practices between natural and rewetted site may have favored DOM availability and flocculation at the rewetted site (McDowell et al., 1998; Yano et al., 2000), however, studies on this matter are inconsistent so far (Hu et al., 2013; Magill et al., 2004, 2000). Thus, determination of salinity-induced flocculation of DOM in Hütelmoor and whether this reduces the extraction of organic solutes to ground- and adjacent waters remains to be investigated.

4.4 Conclusion

The findings of this short-term experiment were connected to the salinity concentrations of the flushing solutes and the soil-physical properties from the peat and mineral layers of the natural and rewetted site. We investigated, if flooding events introducing saline waters into a coastal peatland induce increased ammonium leaching through cation exchange, which could affect the groundwater and adjacent coastline. The results of our simulation showed, that exposure to water engaged in temporarily increased ammonium release of the different soil layers. However, NH_4^+ mobilisation was not connected to cation exchange. Specific soil properties in the peat may retain/ retard ammonium release there (high total porosity or dual porosity, low saturated hydraulic conductivity). In contrast, N-mineralization of soil organic matter may be an important factor for ammonium release in deeper, oxygen-depleted layers under exposure of seawater (-sulfate). Availability of dissolved organic matter may both promote ammonium release (DOM-mineralization) or inhibit organic solute discharge (salinity-induced pore blockage) and remains to be closer investigated.

Chapter 5

References

Abadi, V. a. j. m., Sepehri, M., Rahmani, H. a., Dolatabad, H. k., Shamshiripour, M., Khatabi, B., 2021. Diversity and abundance of culturable nitrogen-fixing bacteria in the phyllosphere of maize. J. Appl. Microbiol. 131, 898–912. https://doi.org/10.1111/jam.14975

Aigle, A., Gubry-Rangin, C., Thion, C., Estera-Molina, K.Y., Richmond, H., Pett-Ridge, J., Firestone, M.K., Nicol, G.W., Prosser, J.I., 2020. Experimental testing of hypotheses for temperature- and pH-based niche specialization of ammonia oxidizing archaea and bacteria. Environ. Microbiol. 22, 4032–4045. https://doi.org/10.1111/1462-2920.15192

Aldunate, M., Henríquez-Castillo, C., Ji, Q., Lueders-Dumont, J., Mulholland, M.R., Ward, B.B., von Dassow, P., Ulloa, O., 2020. Nitrogen assimilation in picocyanobacteria inhabiting the oxygen-deficient waters of the eastern tropical North and South Pacific. Limnol. Oceanogr. 65, 437–453. https://doi.org/10.1002/lno.11315

Almroth-Rosell, E., Eilola, K., Hordoir, R., Meier, H.E.M., Hall, P.O.J., 2011. Transport of fresh and resuspended particulate organic material in the Baltic Sea — a model study. J. Mar. Syst. 87, 1–12. https://doi.org/10.1016/j.jmarsys.2011.02.005

Alonso-Sáez, L., Waller, A.S., Mende, D.R., Bakker, K., Farnelid, H., Yager, P.L., Lovejoy, C., Tremblay, J.-É., Potvin, M., Heinrich, F., Estrada, M., Riemann, L., Bork, P., Pedrós-Alió, C., Bertilsson, S., 2012. Role for urea in nitrification by polar marine Archaea. Proc. Natl. Acad. Sci. 109, 17989–17994. https://doi.org/10.1073/pnas.1201914109

Andersson, B., Sundbäck, K., Hellman, M., Hallin, S., Alsterberg, C., 2014. Nitrogen fixation in shallow-water sediments: Spatial distribution and controlling factors. Limnol. Oceanogr. 59, 1932–1944. https://doi.org/10.4319/lo.2014.59.6.1932

Asmala, E., Bowers, D.G., Autio, R., Kaartokallio, H., Thomas, D.N., 2014. Qualitative changes of riverine dissolved organic matter at low salinities due to flocculation. J. Geophys. Res. Biogeosciences 119, 1919–1933. https://doi.org/10.1002/2014JG002722

Baldwin, D.S., Rees, G.N., Mitchell, A.M., Watson, G., Williams, J., 2006. The short-term effects of salinization on anaerobic nutrient cycling and microbial community structure in sediment from a freshwater wetland. Wetlands 26, 455–464. https://doi.org/10.1672/0277-5212(2006)26[455:TSEOSO]2.0.CO;2

Baltic Marine Environment Protection Commission, 2003. The Fourth Baltic Sea Pollution Load Compilation (PLC-4)., Baltic Sea environment proceedings. Helsinki Commission, Baltic Marine Environment Protection Commission.

Bassin, J.P., Kleerebezem, R., Muyzer, G., Rosado, A.S., van Loosdrecht, M.C.M., Dezotti, M., 2012. Effect of different salt adaptation strategies on the microbial diversity, activity, and settling of nitrifying sludge in sequencing batch reactors. Appl. Microbiol. Biotechnol. 93, 1281–1294. https://doi.org/10.1007/s00253-011-3428-7

Batistel, C., Porsche, C., Jurasinski, G., Schubert, H., 2022. Responses of Four

Peatland Emergent Macrophytes to Salinity and Short Salinity Pulses. Wetlands 42, 67. https://doi.org/10.1007/s13157-022-01592-0

Bejarano Ortiz, D.I., Thalasso, F., Cuervo López, F. de M., Texier, A.-C., 2013. Inhibitory effect of sulfide on the nitrifying respiratory process. J. Chem. Technol. Biotechnol. 88, 1344–1349. https://doi.org/10.1002/jctb.3982

Bentzon-Tilia, M., Severin, I., Hansen, L.H., Riemann, L., 2015. Genomics and Ecophysiology of Heterotrophic Nitrogen-Fixing Bacteria Isolated from Estuarine Surface Water. mBio 6, e00929-15. https://doi.org/10.1128/mBio.00929-15

Berendt, J., Jurasinski, G., Wrage-Mönnig, N., 2022. Influence of rewetting on N2O emissions in three different fen types. Nutr. Cycl. Agroecosystems. https://doi.org/10.1007/s10705-022-10244-y

Berg, C., Vandieken, V., Thamdrup, B., Jürgens, K., 2015. Significance of archaeal nitrification in hypoxic waters of the Baltic Sea. ISME J. 9, 1319–1332. https://doi.org/10.1038/ismej.2014.218

Bernardo, N., do Carmo, A., Park, E., Alcântara, E., 2019. Retrieval of Suspended Particulate Matter in Inland Waters with Widely Differing Optical Properties Using a Semi-Analytical Scheme. Remote Sens. 11, 2283. https://doi.org/10.3390/rs11192283

Bertics, V., Sohm, J., Treude, T., Chow, C.-E., Fuhrman, J., Ziebis, W., 2010. Burrowing deeper into benthic nitrogen cycling: The impact of Bioturbation on nitrogen fixation coupled to sulfate reduction. Mar. Ecol. Prog. Ser. 409, 1–15. https://doi.org/10.3354/meps08639

Bertics, V.J., Löscher, C.R., Salonen, I., Dale, A.W., Gier, J., Schmitz, R.A., Treude, T., 2013. Occurrence of benthic microbial nitrogen fixation coupled to sulfate reduction in the seasonally hypoxic Eckernförde Bay, Baltic Sea. Biogeosciences 10, 1243–1258. https://doi.org/10.5194/bg-10-1243-2013

Bérubé, V., Rochefort, L., 2018. Production and decomposition rates of different fen species as targets for restoration. Ecol. Indic. 91, 105–115. https://doi.org/10.1016/j.ecolind.2018.03.069

Bhavya, P.S., Kumar, S., Gupta, G.V.M., Sudheesh, V., Sudharma, K.V., Varrier, D.S., Dhanya, K.R., Saravanane, N., 2016. Nitrogen Uptake Dynamics in a Tropical Eutrophic Estuary (Cochin, India) and Adjacent Coastal Waters. Estuaries Coasts 39, 54–67. https://doi.org/10.1007/s12237-015-9982-y

Björck, S. (1995). A review of the history of the Baltic Sea, 13.0-8.0 ka BP. Q. Int. 27, 19–40. doi: 10.1016/1040-6182(94)00057-C

Boelter, D., 1968. Important Physical Properties of Peat Materials. Proc Int Peat Conf Dublin 3.

Bohne, B., Bohne, K., 2008. Monitoring zum Wasserhaushalt einer auf litoralem Versumpfungsmoor gewachsenen Regenmoorkalotte – Beispiel Naturschutzgebiet„Hütelmoor“ bei Rostock., in: Aspekte der Geoökologie von Stüdemann, O. (2008). Weißensee Verlag, Berlin, pp. 313–338.

Bouskill, N., Tang, J., Riley, W., Brodie, E., 2012. Trait-Based Representation of Biological Nitrification: Model Development, Testing, and Predicted Community Composition. Front. Microbiol. 3.

Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D., 2013. Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. Nat. Clim. Change 3, 273–277. https://doi.org/10.1038/nclimate1781

Breitbarth, E., Oschlies, A., LaRoche, J., 2007. Physiological constraints on the global distribution of Trichodesmium ndash; effect of temperature on diazotrophy. Biogeosciences 4, 53–61. https://doi.org/10.5194/bg-4-53-2007

Brock, M.A., Nielsen, D.L., Crosslé, K., 2005. Changes in biotic communities developing from freshwater wetland sediments under experimental salinity and water regimes. Freshw. Biol. 50, 1376–1390. https://doi.org/10.1111/j.1365-2427.2005.01408.x

Buchfink, B., Xie, C., Huson, D.H., 2015. Fast and sensitive protein alignment using DIAMOND. Nat. Methods 12, 59–60. https://doi.org/10.1038/nmeth.3176

Burns, J.A., Zehr, J.P., Capone, D.G., 2002. Nitrogen-Fixing Phylotypes of Chesapeake Bay and Neuse River Estuary Sediments. Microb. Ecol. 44, 336–343.

Cabello, A.M., Turk-Kubo, K.A., Hayashi, K., Jacobs, L., Kudela, R.M., Zehr, J.P., 2020. Unexpected presence of the nitrogen-fixing symbiotic cyanobacterium UCYN-A in Monterey Bay, California. J. Phycol. 56, 1521–1533. https://doi.org/10.1111/jpy.13045

Caffrey, S.M., Voordouw, G., 2010. Effect of sulfide on growth physiology and gene expression of Desulfovibrio vulgaris Hildenborough. Antonie Van Leeuwenhoek 97, 11–20. https://doi.org/10.1007/s10482-009-9383-y

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nat. Methods 13, 581–583. https://doi.org/10.1038/nmeth.3869

Campbell, D.R., Duthie, H.C., Warner, B.G., 1997. Post-glacial development of a kettle-hole peatland in southern Ontario. Écoscience 4, 404–418.

Capone, D.G., Burns, J.A., Montoya, J.P., Subramaniam, A., Mahaffey, C., Gunderson, T., Michaels, A.F., Carpenter, E.J., 2005. Nitrogen fixation by Trichodesmium spp.: An important source of new nitrogen to the tropical and subtropical North Atlantic Ocean. Glob. Biogeochem. Cycles 19. https://doi.org/10.1029/2004GB002331

Capone, D.G., O'Neil, J.M., Zehr, J., Carpenter, E.J., 1990. Basis for Diel Variation in Nitrogenase Activity in the Marine Planktonic Cyanobacterium Trichodesmium thiebautii. Appl. Environ. Microbiol. 56, 3532–3536.

Caraco, N., Lampman, G., Cole, J., Limburg, K., Pace, M., Fischer, D., 1998. Microbial assimilation of DIN in a nitrogen rich estuary: Implications for food quality and isotope studies. Mar. Ecol.-Prog. Ser. - MAR ECOL-PROGR SER 167, 59–71. https://doi.org/10.3354/meps167059

Carpenter, E.J., Montoya, J.P., Burns, J., Mulholland, M.R., Subramaniam, A., Capone, D.G., 1999. Extensive bloom of a N 2 -fixing diatom/cyanobacterial association in the tropical Atlantic Ocean. Mar. Ecol. Prog. Ser. 185, 273–283.

Casciotti, K.L., Sigman, D.M., Hastings, M.G., Böhlke, J.K., Hilkert, A., 2002. Measurement of the Oxygen Isotopic Composition of Nitrate in Seawater and Freshwater Using the Denitrifier Method. Anal. Chem. 74, 4905–4912. https://doi.org/10.1021/ac020113w

Chase, J.M., 2003. Community assembly: when should history matter? Oecologia 136, 489–498. https://doi.org/10.1007/s00442-003-1311-7 Cocks, P.S., 2003. Land-use change is the key to protecting biodiversity in salinising landscapes. Aust. J. Bot. 51, 627–635. https://doi.org/10.1071/bt03004

Coppens, J., Lindeboom, R., Muys, M., Coessens, W., Alloul, A., Meerbergen, K., Lievens, B., Clauwaert, P., Boon, N., Vlaeminck, S.E., 2016. Nitrification and microalgae cultivation for two-stage biological nutrient valorization from source separated urine. Bioresour. Technol. 211, 41–50.

https://doi.org/10.1016/j.biortech.2016.03.001

Cortés-Lorenzo, C., Rodríguez-Díaz, M., Sipkema, D., Juárez-Jiménez, B., Rodelas, B., Smidt, H., González-López, J., 2015. Effect of salinity on nitrification efficiency and structure of ammonia-oxidizing bacterial communities in a submerged fixed bed bioreactor. Chem. Eng. J. 266, 233–240. https://doi.org/10.1016/j.cej.2014.12.083

Couwenberg, J., Thiele, A., Tanneberger, F., Augustin, J., Bärisch, S., Dubovik, D., Liashchynskaya, N., Michaelis, D., Minke, M., Skuratovich, A., Joosten, H., 2011. Assessing greenhouse gas emissions from peatlands using vegetation as a proxy. Hydrobiologia 674, 67–89. https://doi.org/10.1007/s10750-011-0729-x

Csonka, L.N., 1989. Physiological and genetic responses of bacteria to osmotic stress. Microbiol. Rev. 53, 121–147. https://doi.org/10.1128/mr.53.1.121-147.1989

Cui, Y.-W., Zhang, H.-Y., Ding, J.-R., Peng, Y.-Z., 2016. The effects of salinity on nitrification using halophilic nitrifiers in a Sequencing Batch Reactor treating hypersaline wastewater. Sci. Rep. 6, 24825. https://doi.org/10.1038/srep24825

Cypionka, H., 2000. Oxygen respiration by desulfovibrio species. Annu. Rev. Microbiol. 54, 827–848. https://doi.org/10.1146/annurev.micro.54.1.827

Daebeler, A., Kitzinger, K., Koch, H., Herbold, C.W., Steinfeder, M., Schwarz, J., Zechmeister, T., Karst, S.M., Albertsen, M., Nielsen, P.H., Wagner, M., Daims, H., 2020. Exploring the upper pH limits of nitrite oxidation: diversity, ecophysiology, and adaptive traits of haloalkalitolerant Nitrospira. https://doi.org/10.1101/2020.03.05.977850

Daims, H., Lebedeva, E.V., Pjevac, P., Han, P., Herbold, C., Albertsen, M., Jehmlich, N., Palatinszky, M., Vierheilig, J., Bulaev, A., Kirkegaard, R.H., von Bergen, M., Rattei, T., Bendinger, B., Nielsen, P.H., Wagner, M., 2015. Complete nitrification by Nitrospira bacteria. Nature 528, 504–509. https://doi.org/10.1038/nature16461

Daims, H., Lücker, S., Wagner, M., 2016. A New Perspective on Microbes Formerly Known as Nitrite-Oxidizing Bacteria. Trends Microbiol. 24, 699–712. https://doi.org/10.1016/j.tim.2016.05.004

Damashek, J., Casciotti, K.L., Francis, C.A., 2016. Variable Nitrification Rates Across Environmental Gradients in Turbid, Nutrient-Rich Estuary Waters of San Francisco Bay. Estuaries Coasts 39, 1050–1071. https://doi.org/10.1007/s12237-016-0071-7

Darrah, P.R., Nye, P.H., White, R.E., 1987. The effect of high solute concentrations on nitrification rates in soil. Plant Soil 97, 37–45. https://doi.org/10.1007/BF02149821

Dekas, A.E., Chadwick, G.L., Bowles, M.W., Joye, S.B., Orphan, V.J., 2014. Spatial distribution of nitrogen fixation in methane seep sediment and the role of the ANME archaea. Environ. Microbiol. 16, 3012–3029. https://doi.org/10.1111/1462-2920.12247

Dekas, A.E., Fike, D.A., Chadwick, G.L., Green-Saxena, A., Fortney, J., Connon, S.A., Dawson, K.S., Orphan, V.J., 2018. Widespread nitrogen fixation in sediments from diverse deep-sea sites of elevated carbon loading. Environ. Microbiol. 20, 4281–4296. https://doi.org/10.1111/1462-2920.14342

Delgado Vela, J., Dick, G., Love, N., 2018. Sulfide inhibition of nitrite oxidation in activated sludge depends on microbial community composition.

Water Res. 138. https://doi.org/10.1016/j.watres.2018.03.047

Deutsch, C., Sarmiento, J.L., Sigman, D.M., Gruber, N., Dunne, J.P., 2007. Spatial coupling of nitrogen inputs and losses in the ocean. Nature 445, 163–167. https://doi.org/10.1038/nature05392

Di, H.J., Cameron, K.C., Shen, J.-P., Winefield, C.S., O'Callaghan, M., Bowatte, S., He, J.-Z., 2010. Ammonia-oxidizing bacteria and archaea grow under contrasting soil nitrogen conditions. FEMS Microbiol. Ecol. 72, 386–394. https://doi.org/10.1111/j.1574-6941.2010.00861.x

Di, H.J., Cameron, K.C., Shen, J.P., Winefield, C.S., O'Callaghan, M., Bowatte, S., He, J.Z., 2009. Nitrification driven by bacteria and not archaea in nitrogen-rich grassland soils. Nat. Geosci. 2, 621–624. https://doi.org/10.1038/ngeo613

Dreier, N., Nehlsen, E., Fröhle, P., Rechid, D., Bouwer, L.M., Pfeifer, S., 2021. Future Changes in Wave Conditions at the German Baltic Sea Coast Based on a Hybrid Approach Using an Ensemble of Regional Climate Change Projections. Water 13, 167. https://doi.org/10.3390/w13020167

Dugdale, R.C., Wilkerson, F.P., 1986. The use of 15N to measure nitrogen uptake in eutrophic oceans; experimental considerations1,2. Limnol. Oceanogr. 31, 673–689. https://doi.org/10.4319/lo.1986.31.4.0673

Empadinhas, N., Viete-Vallejo, O., 2008. Osmoadaptation mechanisms in prokaryotes: distribution of compatible solutes. Int. Microbiol. 151–161. https://doi.org/10.2436/20.1501.01.55

Enoksson, V., 1986. Nitrification Rates in the Baltic Sea: Comparison of Three Isotope Techniques. Appl. Environ. Microbiol. 51, 244–250. Evangelou, V.P., Phillips, R.E., 2005. Cation Exchange in Soils, in: Chemical Processes in Soils. John Wiley Sons, Ltd, pp. 343–410. https://doi.org/10.2136/sssabookser8.c7

Falony, G., Joossens, M., Vieira-Silva, S., Wang, J., Darzi, Y., Faust, K., Kurilshikov, A., Bonder, M.J., Valles-Colomer, M., Vandeputte, D., Tito, R.Y., Chaffron, S., Rymenans, L., Verspecht, C., De Sutter, L., Lima-Mendez, G., D'hoe, K., Jonckheere, K., Homola, D., Garcia, R., Tigchelaar, E.F., Eeckhaudt, L., Fu, J., Henckaerts, L., Zhernakova, A., Wijmenga, C., Raes, J., 2016. Population-level analysis of gut microbiome variation. Science 352, 560–564. https://doi.org/10.1126/science.aad3503

Fan, H., Bolhuis, H., Stal, L.J., 2015. Drivers of the dynamics of diazotrophs and denitrifiers in North Sea bottom waters and sediments. Front. Microbiol. 6. https://doi.org/10.3389/fmicb.2015.00738

Forchhammer, K., 2007. Glutamine signalling in bacteria. Front. Biosci.-Landmark 12, 358–370. https://doi.org/10.2741/2069

Fulweiler, R.W., Brown, S.M., Nixon, S.W., Jenkins, B.D., 2013. Evidence and a conceptual model for the co-occurrence of nitrogen fixation and denitrification in heterotrophic marine sediments. Mar. Ecol. Prog. Ser. 482, 57–68. https://doi.org/10.3354/meps10240

Gandy, E.L., Yoch, D.C., 1988. Relationship between nitrogen-fixing sulfate reducers and fermenters in salt marsh sediments and roots of Spartina alterniflora. Appl. Environ. Microbiol. 54, 2031–2036. https://doi.org/10.1128/aem.54.8.2031-2036.1988

Gao, Y., Hirose, K., Ohki, T., Osaki, M., Kohyama, T., Paneque-Gálvez, J., 2013. Estimation of dissolved organic carbon concentration in peat water using airborne hzmap image. https://doi.org/10.13140/2.1.3511.3923

Geets, J., Boon, N., Verstraete, W., 2006. Strategies of aerobic ammonia-oxidizing bacteria for coping with nutrient and oxygen fluctuations. FEMS Microbiol. Ecol. 58, 1–13. https://doi.org/10.1111/j.1574-6941.2006.00170.x

Geisler, E., Rahav, E., Bar-Zeev, E., 2022. Contribution of Heterotrophic Diazotrophs to N2 Fixation in a Eutrophic River: Free-Living vs. Aggregate-Associated. Front. Microbiol. 13.

Giebels, M., Beyer, M., Augustin, J., Minke, M., Juszczak, R., Serba, T., 2010. Seasonal Trace Gas Dynamics on Minerotrophic Fen Peatlands in NE-Germany.

Gier, J., Sommer, S., Löscher, C.R., Dale, A.W., Schmitz, R.A., Treude, T., 2016. Nitrogen fixation in sediments along a depth transect through the Peruvian oxygen minimum zone. Biogeosciences 13, 4065–4080.
https://doi.org/10.5194/bg-13-4065-2016

Gijzen, H., 2001. The nitrogen cycle out of balance. Water21 August 2001, 38–40.

Glatzel, S., Koebsch, F., Beetz, S., Hahn, J., Richter, P., and Jurasinski, G., 2011: Maßnahmen zur Minderung der Treibhausgasfreisetzung aus Mooren im Mittleren Mecklenburg, TELMA, 4, 85–106.
https://doi.org/10.23689/fidgeo-2976.

Glibert, P.M., Kana, T.M., Brown, K., 2013. From limitation to excess: the consequences of substrate excess and stoichiometry for phytoplankton physiology, trophodynamics and biogeochemistry, and the implications for modeling. J. Mar. Syst., Advances in Marine Ecosystem Modelling Research III 125, 14–28. https://doi.org/10.1016/j.jmarsys.2012.10.004

Goldberg, S.S. Gainey, P.L. (1995): Role of surface phenomena in nitrification. Soil Sei., 80, 43. Golden, D.C., Sivasubramaniam, S., Sandanam, S., Wijedasa, M.A., 1981. Inhibitory effects of commercial potassium chloride on the nitrification rates of added ammonium sulphate in an acid red yellow podzolic soil. Plant Soil 59, 364–364. https://doi.org/10.1007/BF02184209

Gorham, E., 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. Ecol. Appl. 1, 182–195. https://doi.org/10.2307/1941811

Gosch, L., Janssen, M., Lennartz, B., 2018. Impact of the water salinity on the hydraulic conductivity of fen peat. Hydrol. Process. 32, 1214–1222. https://doi.org/10.1002/hyp.11478

Gosch, L., Townsend, H., Kreuzburg, M., Janssen, M., Rezanezhad, F., Lennartz, B., 2019. Sulfate Mobility in Fen Peat and Its Impact on the Release of Solutes. Front. Environ. Sci. 7. https://doi.org/10.3389/fenvs.2019.00189

Grant, R.F., 1994. Simulation of ecological controls on nitrification. Soil Biol. Biochem. 26, 305–315. https://doi.org/10.1016/0038-0717(94)90279-8

Grasshoff, K., Kremling, K., Ehrhardt, M., 1999. Methods of Seawater Analysis, 3rd Completely Revised and Enlarged Edition | Wiley [WWW Document]. Wiley.com.
URL https://www.wiley.com/en-us/Methods+of+Seawater+Analysis%2C+3rd+Completely+Revised+and+Enlarged+Edition-p-9783527613991 (accessed 3.30.21).

Gregory, J., O'Melia, C.R., 1989. Fundamentals of flocculation. Crit. Rev. Environ. Control 19, 185–230. https://doi.org/10.1080/10643388909388365

Groß-Schmölders, M., Klein, K., Birkholz, A., Leifeld, J., Alewell, C., 2021. Rewetting and Drainage of Nutrient-Poor Peatlands Indicated by Specific Bacterial Membrane Fatty Acids and a Repeated Sampling of Stable Isotopes ($\delta^{15}N$, δ^{13}C). Front. Environ. Sci. 9.

Guerrero, M.A., Jones, R.D., 1996. Photoinhibition of marine nitrifying bacteria. I. Wavelength-dependent response. Mar. Ecol. Prog. Ser. 141, 183–192.

Guo, Y., Becker-Fazekas, S., Mühling, K.H., 2022. Impact of different chloride salts and their concentrations on nitrification and trace gas emissions from a sandy soil under a controlled environment. Soil Use Manag. 38, 861–872. https://doi.org/10.1111/sum.12713

Gutekunst, C.N., Liebner, S., Jenner, A.-K., Knorr, K.-H., Unger, V., Koebsch, F., Racasa, E.D., Yang, S., Böttcher, M.E., Janssen, M., Kallmeyer, J., Otto, D., Schmiedinger, I., Winski, L., Jurasinski, G., 2022. Effects of brackish water inflow on methane-cycling microbial communities in a freshwater rewetted coastal fen. Biogeosciences 19, 3625–3648. https://doi.org/10.5194/bg-19-3625-2022

Hahn, J., Köhler, S., Glatzel, S., Jurasinski, G., 2015. Methane Exchange in a Coastal Fen in the First Year after Flooding - A Systems Shift. PLoS ONE 10, e0140657. https://doi.org/10.1371/journal.pone.0140657

Hallstrøm, S., Benavides, M., Salamon, E.R., Evans, C.W., Potts, L.J., Granger, J., Tobias, C.R., Moisander, P.H., Riemann, L., 2021. Pelagic N2 fixation dominated by sediment diazotrophic communities in a shallow temperate estuary. Limnol. Oceanogr. n/a. https://doi.org/10.1002/lno.11997

Hansen, H.P., Koroleff, F., 1999. Determination of nutrients, in: Methods of Seawater Analysis. John Wiley & Sons, Ltd, pp. 159–228. https://doi.org/10.1002/9783527613984.ch10

Hao, Z.-L., Ali, A., Ren, Y., Su, J.-F., Wang, Z., 2022. A mechanistic review on aerobic denitrification for nitrogen removal in water treatment. Sci. Total Environ. 847, 157452. https://doi.org/10.1016/j.scitotenv.2022.157452

Harada, Y., Inoko, A., 1977. The oxidation products formed from: Soil organic matter by hydrogen peroxide treatment. Soil Sci. Plant Nutr. 23, 513–521. https://doi.org/10.1080/00380768.1977.10433069

Helliwell, J., 2011. An assessment of the nitrate leaching risk for different buffer strip establishments. Biosci. Horiz. Int. J. Stud. Res. 4, 79–89. https://doi.org/10.1093/biohorizons/hzr010

Herrero, A., Flores, E., Imperial, J., 2019. Nitrogen Assimilation in Bacteria, in: Reference Module in Life Sciences. Elsevier, p. B9780128096338207000. https://doi.org/10.1016/B978-0-12-809633-8.20680-8

Heyer, J., Berger, U., 2000. Methane Emission from the Coastal Area in the Southern Baltic Sea. Estuar. Coast. Shelf Sci. 51, 13–30. https://doi.org/10.1006/ecss.2000.0616

Hill, B.M., Siegel, D.I., 1991. Groundwater flow and the metal content of peat. J. Hydrol. 123, 211–224. https://doi.org/10.1016/0022-1694(91)90091-U

Hink, L., Lycus, P., Gubry-Rangin, C., Frostegård, Å., Nicol, G.W., Prosser, J.I., Bakken, L.R., 2017a. Kinetics of NH3-oxidation, NO-turnover, N2O-production and electron flow during oxygen depletion in model bacterial and archaeal ammonia oxidisers. Environ. Microbiol. 19, 4882–4896. https://doi.org/10.1111/1462-2920.13914

Hink, L., Nicol, G.W., Prosser, J.I., 2017b. Archaea produce lower yields of N_2O than bacteria during aerobic ammonia oxidation in soil. Environ. Microbiol. 19, 4829–4837. https://doi.org/10.1111/1462-2920.13282

Hoag, R.S., Price, J.S., 1997. The effects of matrix diffusion on solute transport and retardation in undisturbed peat in laboratory columns. J. Contam. Hydrol. 28, 193–205. https://doi.org/10.1016/S0169-7722(96)00085-X

Hoggart, S., Hanley, M., Parker, D., Simmonds, D., Bilton, D., Filipova-Marinova, M., Franklin, E., Kotsev, I., Penning-Rowsell, E., Rundle, S., Trifonova, E., Vergiev, S., White, A.C., Thompson, R.C., 2014. The consequences of doing nothing: The effects of seawater flooding on coastal zones. Coast. Eng. 169–182, 169–182. https://doi.org/10.1016/j.coastaleng.2013.12.001

Höper, H., 2002. Carbon and nitrogen mineralisation rates of fens in Germany used for agriculture. A review, in: Broll, G., Merbach, W., Pfeiffer, E.-M. (Eds.), Wetlands in Central Europe: Soil Organisms, Soil Ecological Processes and Trace Gas Emissions. Springer, Berlin, Heidelberg, pp. 149–164. https://doi.org/10.1007/978-3-662-05054-5_8

Horak, R.E.A., Qin, W., Schauer, A.J., Armbrust, E.V., Ingalls, A.E., Moffett, J.W., Stahl, D.A., Devol, A.H., 2013. Ammonia oxidation kinetics and temperature sensitivity of a natural marine community dominated by Archaea. ISME J. 7, 2023–2033. https://doi.org/10.1038/ismej.2013.75

Howarth, R., Marino, R., 2006. Nitrogen as the Limiting Nutrient for Eutrophication in Coastal Marine Ecosystems: Evolving Views over Three Decades. Limnol. Oceanogr. 51, 364–376. https://doi.org/10.4319/lo.2006.51.1_part_2.0364

Hu, Y.-L., Jung, K., Zeng, D.-H., Chang, S.X., 2013. Nitrogen- and sulfur-deposition-altered soil microbial community functions and enzyme activities in a boreal mixedwood forest in western Canada. Can. J. For. Res. 43, 777–784. https://doi.org/10.1139/cjfr-2013-0049

Huang, L., Chakrabarti, S., Cooper, J., Perez, A., John, S.M., Daroub, S.H., Martens-Habbena, W., 2021. Ammonia-oxidizing archaea are integral to nitrogen cycling in a highly fertile agricultural soil. ISME Commun. 1, 1–12. https://doi.org/10.1038/s43705-021-00020-4

Huang, Q., Huang, G., 2009. Effect of NaCl salt on mineralization and nitrification of a silt loam soil in the North China Plain. Int. J. Agric. Biol. Eng. 2. https://doi.org/10.3965/j.issn.1934-6344.2009.02.014-023

Hudson, R.C., Ruttersmith, L.D., Daniel, R.M., 1993. Glutamate dehydrogenase from the extremely thermophilic archaebacterial isolate AN1. Biochim. Biophys. Acta 1202, 244–250. https://doi.org/10.1016/0167-4838(93)90011-f

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M.B., Treat, C., Turetsky, M., Voigt, C., Yu, Z., 2020. Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. Proc. Natl. Acad. Sci. U. S. A. 117, 20438–20446. https://doi.org/10.1073/pnas.1916387117

Humborg, C., Danielsson, Å., Sjöberg, B., Green, M., 2003. Nutrient land–sea fluxes in oligothrophic and pristine estuaries of the Gulf of Bothnia, Baltic Sea. Estuar. Coast. Shelf Sci. 56, 781–793. doi:10.1016/S0272-7714(02)00290-1

Ibello, V., Cantoni, C., Cozzi, S., Civitarese, G., 2010. First basin-wide experimental results on N2 fixation in the open Mediterranean Sea. Geophys. Res. Lett. 37. https://doi.org/10.1029/2009GL041635

Ilgrande, C., Leroy, B., Wattiez, R., Vlaeminck, S.E., Boon, N., Clauwaert, P., 2018. Metabolic and Proteomic Responses to Salinity in Synthetic Nitrifying Communities of Nitrosomonas spp. and Nitrobacter spp. Front. Microbiol. 9.

Jabir, T., Vipindas, P.V., Jesmi, Y., Divya, P.S., Adarsh, B.M., Nafeesathul Miziriya, H.S., Mohamed Hatha, A.A., 2021. Influence of environmental factors on benthic nitrogen fixation and role of sulfur reducing diazotrophs in a eutrophic tropical estuary. Mar. Pollut. Bull. 165, 112126.

https://doi.org/10.1016/j.marpolbul.2021.112126

Jia, Z., Conrad, R., 2009. Bacteria rather than Archaea dominate microbial ammonia oxidation in an agricultural soil. Environ. Microbiol. 11, 1658–1671. https://doi.org/10.1111/j.1462-2920.2009.01891.x

Joosten, H., 2009. The Global Peatland CO2 Picture: peatland status and drainage related emissions in all countries of the world. undefined.

Joosten, H., Clarke, D., 2002. Wise use of mires and peatlands: background and principles including a framework for decision-making. International Peat Society; International Mire Conservation Group, Jyväskylä: Greifswald.

Joshi, H.M., Tabita, F.R., 1996. A global two component signal transduction system that integrates the control of photosynthesis, carbon dioxide assimilation, and nitrogenfixation. Proc. Natl. Acad. Sci. 93, 14515–14520. https://doi.org/10.1073/pnas.93.25.14515

Joshi, S., Kukkadapu, R., Burdige, D., Bowden, M., Sparks, D., Jaisi, D., 2015. Organic Matter Remineralization Predominates Phosphorus Cycling in the Mid-Bay Sediments in the Chesapeake Bay. Environ. Sci. Technol. 49. https://doi.org/10.1021/es5059617

Joye, S.B., Hollibaugh, J.T., 1995. Influence of Sulfide Inhibition of Nitrification on Nitrogen Regeneration in Sediments. Science 270, 623–625. https://doi.org/10.1126/science.270.5236.623

Juliastuti, S.R., Baeyens, J., Creemers, C., Bixio, D., Lodewyckx, E., 2003. The inhibitory effects of heavy metals and organic compounds on the net maximum specific growth rate of the autotrophic biomass in activated sludge. J. Hazard. Mater. 100, 271–283. https://doi.org/10.1016/s0304-3894(03)00116-x

Junk, G., Svec, H.J., 1958. The absolute abundance of the nitrogen isotopes in the atmosphere and compressed gas from various sources. Geochim. Cosmochim. Acta 14, 234–243. https://doi.org/10.1016/0016-7037(58)90082-6

Jurasinski, G., Ahmad, S., Anadon-Rosell, A., Berendt, J., Beyer, F., Bill, R., Blume-Werry, G., Couwenberg, J., Günther, A., Joosten, H., Koebsch, F., Köhn, D., Koldrack, N., Kreyling, J., Leinweber, P., Lennartz, B., Liu, H., Michaelis, D., Mrotzek, A., Negassa, W., Schenk, S., Schmacka, F., Schwieger, S., Smiljanić, M., Tanneberger, F., Teuber, L., Urich, T., Wang, H., Weil, M., Wilmking, M., Zak, D., Wrage-Mönnig, N., 2020. From Understanding to Sustainable Use of Peatlands: The WETSCAPES Approach. Soil Syst. 4, 14. https://doi.org/10.3390/soilsystems4010014

Jurasinski, G., Janssen, M., Voss, M., Böttcher, M.E., Brede, M., Burchard, H., Forster, S., Gosch, L., Gräwe, U., Gründling-Pfaff, S., Haider, F., Ibenthal, M., Karow, N., Karsten, U., Kreuzburg, M., Lange, X., Leinweber, P., Massmann, G., Ptak, T., Rezanezhad, F., Rehder, G., Romoth, K., Schade, H., Schubert, H., Schulz-Vogt, H., Sokolova, I.M., Strehse, R., Unger, V., Westphal, J., Lennartz, B., 2018. Understanding the Coastal Ecocline: Assessing Sea–Land Interactions at Non-tidal, Low-Lying Coasts Through Interdisciplinary Research. Front. Mar. Sci. 5. https://doi.org/10.3389/fmars.2018.00342

Kache, S., 2021. Influence of organic particle addition on nitrification rates and ammonium oxidiser abundances in Baltic seawater. Mar Ecol Prog Ser 14.

Karl, D.M., Michaels, A.F., 2001. Nitrogen Cycle, in: Steele, J.H. (Ed.), Encyclopedia of Ocean Sciences. Academic Press, Oxford, pp. 1876–1884. https://doi.org/10.1006/rwos.2001.0275

Karlsson, A.E., Johansson, T., Bengtson, P., 2012. Archaeal abundance in relation to root and fungal exudation rates. FEMS Microbiol. Ecol. 80, 305–311. https://doi.org/10.1111/j.1574-6941.2012.01298.x

Keiser, A.D., Knoepp, J.D., Bradford, M.A., 2016. Disturbance decouples biogeochemical cycles across forests of the southeastern US. Ecosystems 19, 50–61. https://doi.org/10.1007/s10021-015-9917-2

Kerby, N.W., Rowell, P., Stewart, W.D.P., 1987. Cyanobacterial ammonium transport, ammonium assimilation, and nitrogenase regulation. N. Z. J. Mar. Freshw. Res. 21, 447–455. https://doi.org/10.1080/00288330.1987.9516240

Kholdebarin, B., Oertli, J.J., 1977. Effect of Suspended Particles and Their Sizes on Nitrification in Surface Water. J. Water Pollut. Control Fed. 49, 1693–1697.

Kits, K.D., Sedlacek, C.J., Lebedeva, E.V., Han, P., Bulaev, A., Pjevac, P., Daebeler, A., Romano, S., Albertsen, M., Stein, L.Y., Daims, H., Wagner, M., 2017. Kinetic analysis of a complete nitrifier reveals an oligotrophic lifestyle. Nature 549, 269–272. https://doi.org/10.1038/nature23679

Kleimeier, C., Karsten, U., Lennartz, B., 2014. Suitability of degraded peat for constructed wetlands — Hydraulic properties and nutrient flushing. Geoderma, Properties, processes and ecological functions of floodplain, peatland, and paddy soils 228–229, 25–32. https://doi.org/10.1016/j.geoderma.2013.12.026

Kleimeier, C., Rezanezhad, F., Van Cappellen, P., Lennartz, B., 2017. Influence of pore structure on solute transport in degraded and undegraded fen peat soils. Mires Peat 19. https://doi.org/10.19189/MaP.2017.OMB.282

Klerk, A., De Klerk, L., Oberholster, P., Ashton, P., Dini, J., Holness, S., 2016.

A review of depressional wetlands (pans) in South Africa, including a water quality classification system. https://doi.org/10.13140/RG.2.2.28486.06723

Koch, H., van Kessel, M.A.H.J., Lücker, S., 2019. Complete nitrification: insights into the ecophysiology of comammox Nitrospira. Appl. Microbiol. Biotechnol. 103, 177–189. https://doi.org/10.1007/s00253-018-9486-3

Koch, S., Jurasinski, G., Koebsch, F., Koch, M., Glatzel, S., 2014. Spatial variability of annual estimates of methane emissions in a Phragmites australis (Cav.) Trin. ex Steud. dominated restored coastal brackish fen. Wetlands 34, 593–602.

Koebsch, F., Glatzel, S., Hofmann, J., Forbrich, I., Jurasinski, G., 2013. CO2 exchange of a temperate fen during the conversion from moderately rewetting to flooding. J. Geophys. Res. Biogeosciences 118, 940–950. https://doi.org/10.1002/jgrg.20069

Koebsch, F., Winkel, M., Liebner, S., Liu, B., Westphal, J., Schmiedinger, I., Spitzy, A., Gehre, M., Jurasinski, G., Köhler, S., Unger, V., Koch, M., Sachs, T., Böttcher, M.E., 2019. Sulfate deprivation triggers high methane production in a disturbed and rewetted coastal peatland. Biogeosciences 16, 1937–1953. https://doi.org/10.5194/bg-16-1937-2019

Kreuzburg, M., Ibenthal, M., Janssen, M., Rehder, G., Voss, M., Naumann, M., Feldens, P., 2018. Sub-marine Continuation of Peat Deposits From a Coastal Peatland in the Southern Baltic Sea and its Holocene Development. Front. Earth Sci. 6.

Kreyling, J., Tanneberger, F., Jansen, F., van der Linden, S., Aggenbach, C., Blüml, V., Couwenberg, J., Emsens, W.-J., Joosten, H., Klimkowska, A., Kotowski, W., Kozub, L., Lennartz, B., Liczner, Y., Liu, H., Michaelis, D., Oehmke, C., Parakenings, K., Pleyl, E., Poyda, A., Raabe, S., Röhl, M., Rücker, K., Schneider, A., Schrautzer, J., Schröder, C., Schug, F., Seeber, E., Thiel, F., Thiele, S., Tiemeyer, B., Timmermann, T., Urich, T., van Diggelen, R., Vegelin, K., Verbruggen, E., Wilmking, M., Wrage-Mönnig, N., Wołejko, L., Zak, D., Jurasinski, G., 2021. Rewetting does not return drained fen peatlands to their old selves. Nat. Commun. 12, 5693. https://doi.org/10.1038/s41467-021-25619-y

Krüger, J.P., Leifeld, J., Glatzel, S., Szidat, S., Alewell, C., 2015. Biogeochemical indicators of peatland degradation – a case study of a temperate bog in northern Germany. Biogeosciences 12, 2861–2871. https://doi.org/10.5194/bg-12-2861-2015

Küpper, H., Šetlík, I., Seibert, S., Prášil, O., Šetlikova, E., Strittmatter, M., Levitan, O., Lohscheider, J., Adamska, I., Berman-Frank, I., 2008. Iron limitation in the marine cyanobacterium Trichodesmium reveals new insights into regulation of photosynthesis and nitrogen fixation. New Phytol. 179, 784–798. https://doi.org/10.1111/j.1469-8137.2008.02497.x

Kurisu, F., Kurisu, F., Sakamoto, Y., Yagi, O., 2007. Effects of ammonium and nitrite on communities and populations of ammonia-oxidizing bacteria in laboratory-scale continuous-flow reactors. FEMS Microbiol. Ecol. 60, 501–512. https://doi.org/10.1111/j.1574-6941.2007.00307.x

Kyveryga, P.M., Blackmer, A.M., Ellsworth, J.W., Isla, R., 2004. Soil pH Effects on Nitrification of Fall-Applied Anhydrous Ammonia. Soil Sci. Soc. Am. J. 68, 545–551. https://doi.org/10.2136/sssaj2004.5450 Lamers, L.P.M., Vile, M.A., Grootjans, A.P., Acreman, M.C., van Diggelen, R., Evans, M.G., Richardson, C.J., Rochefort, L., Kooijman, A.M., Roelofs, J.G.M., Smolders, A.J.P., 2015. Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. Biol. Rev. 90, 182–203. https://doi.org/10.1111/brv.12102

Lampe, R., Naumann, M., Meyer, H., Janke, W., Ziekur, R., 2011. Holocene Evolution of the Southern Baltic Sea Coast and Interplay of Sea-Level Variation, Isostasy, Accommodation and Sediment Supply, in: Harff, J., Björck, S., Hoth, P. (Eds.), The Baltic Sea Basin, Central and Eastern European Development Studies (CEEDES). Springer, Berlin, Heidelberg, pp. 233–251. https://doi.org/10.1007/978-3-642-17220-5_12

Lång, K., Lehtonen, M., Martikainen, P.J., 1993. Nitrification potentials at different ph values in peat samples from various layers of a drained mire. Geomicrobiol. J. 11, 141–147. https://doi.org/10.1080/01490459309377946

Laura, R.D., 1977. Salinity and nitrogen mineralization in soil. Soil Biol. Biochem. 9, 333–336. https://doi.org/10.1016/0038-0717(77)90005-0 Laws, E.A., Harrison, W.G., DiTullio, G.R., 1985. A comparison of nitrogen assimilation rates based on 15N uptake and autotrophic protein synthesis. Deep Sea Res. A 32, 85–95. https://doi.org/10.1016/0198-0149(85)90018-4

le Gall, J., Postgate, J.R., 1973. The Physiology of Sulphate-Reducing Bacteria, in: Rose, A.H., Tempest, D.W. (Eds.), Advances in Microbial Physiology. Academic Press, pp. 81–133.
https://doi.org/10.1016/S0065-2911(08)60087-9

Lea, P.J., 1985. Ammonia assimilation and amino acid biosynthesis, in: Coombs, J., Hall, D.O., Long, S.P., Scurlock, J.M.O. (Eds.), Techniques in Bioproductivity and Photosynthesis (Second Edition), Pergamon International Library of Science, Technology, Engineering and Social Studies. Pergamon, pp. 173–187. https://doi.org/10.1016/B978-0-08-031999-5.50024-8

LeCorre, P., Wafar, M.V.M., Helguen, S.L., Maguer, J.F., 1996. Ammonium assimilation and regeneration by size-fractionated plankton in permanently well-mixed temperate waters. J. Plankton Res. 18.

https://doi.org/10.1093/plankt/18.3.355

Lehtimaki, J., Moisander, P., Sivonen, K., Kononen, K., 1997. Growth, Nitrogen Fixation, and Nodularin Production by Two Baltic Sea Cyanobacteria. Appl. Environ. Microbiol. 63, 1647–1656.

Lehtovirta-Morley, L.E., 2018. Ammonia oxidation: Ecology, physiology, biochemistry and why they must all come together. FEMS Microbiol. Lett. 365, fny058. https://doi.org/10.1093/femsle/fny058

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Leifeld, J., Wüst-Galley, C., Page, S., 2019. Intact and managed peatland soils as a source and sink of GHGs from 1850 to 2100. Nat. Clim. Change 9, 945–947. https://doi.org/10.1038/s41558-019-0615-5

Leipe, T., Naumann, M., Tauber, F., Radtke, H., Friedland, R., Hiller, A., Arz, H.W., 2017. Regional distribution patterns of chemical parameters in surface sediments of the south-western Baltic Sea and their possible causes. Geo-Mar. Lett. 37, 1–14. https://doi.org/10.1007/s00367-017-0514-6

Leppänen, J.-M., Niemi, A., Rinne, I., 1988. Nitrogen Fixation of Cyanobacteria (Blue-Green Algae) and the Nitrogen Cycle of the Baltic Sea Symbiosis, 181–194.

Lespinat, P.A., Berlier, Y.M., Fauque, G.D., Toci, R., Denariaz, G., LeGall, J., 1987. The relationship between hydrogen metabolism, sulfate reduction and nitrogen fixation in sulfate reducers. J. Ind. Microbiol. 1, 383.

Li, X., Wan, W., Zheng, L., Wang, A., Luo, X., Huang, Q., Chen, W., 2021a. Community assembly mechanisms and co-occurrence patterns of nitrite-oxidizing bacteria communities in saline soils. Sci. Total Environ. 772, 145472. https://doi.org/10.1016/j.scitotenv.2021.145472

Li, X., Wang, A., Wan, W., Luo, X., Zheng, L., He, G., Huang, D., Chen, W., Huang, Q., 2021b. High Salinity Inhibits Soil Bacterial Community Mediating Nitrogen Cycling. Appl. Environ. Microbiol. 87, e01366-21. https://doi.org/10.1128/AEM.01366-21

Li, Y., Xu, J., Liu, B., Wang, H., Qi, Z., Wei, Q., Liao, L., Liu, S., 2020. Enhanced N_2O Production Induced by Soil Salinity at a Specific Range. Int. J. Environ. Res. Public. Health 17, 5169. https://doi.org/10.3390/ijerph17145169

Liesirova, T., Aarenstrup-Launbjerg, T., Hallstrøm, S., Bittner, M.J., Riemann, L., Voss, M., 2023. Nitrogen-fixing sulfate reducing bacteria in shallow coastal sediments under simulated resuspension. Estuar. Coast. Shelf Sci. 280, 108165. https://doi.org/10.1016/j.ecss.2022.108165

Liikanen, A., Silvennoinen, H., Karvo, A., Rantakokko, P., Martikainen, P., 2009. Methane and nitrous oxide fluxes in two coastal wetlands in the northeastern Gulf of Bothnia, Baltic Sea. Boreal Environ. Res. 14, 351–368.

Liu, H., Lennartz, B., 2019. Short Term Effects of Salinization on Compound Release from Drained and Restored Coastal Wetlands. Water 11, 1549. https://doi.org/10.3390/w11081549

Longhurst, A.R., Glen Harrison, W., 1989. The biological pump: Profiles of plankton production and consumption in the upper ocean. Prog. Oceanogr. 22, 47–123. https://doi.org/10.1016/0079-6611(89)90010-4

Lu, S., Liu, X., Liu, C., Cheng, G., Shen, H., 2020. Influence of photoinhibition on nitrification by ammonia-oxidizing microorganisms in aquatic ecosystems. Rev. Environ. Sci. Biotechnol. 19. https://doi.org/10.1007/s11157-020-09540-2

Lu, X., Taylor, A.E., Myrold, D.D., Neufeld, J.D., 2020. Expanding perspectives of soil nitrification to include ammonia-oxidizing archaea and comammox bacteria. Soil Sci. Soc. Am. J. 84, 287–302. https://doi.org/10.1002/saj2.20029

Lumppio, H.L., Shenvi, N.V., Summers, A.O., Voordouw, G., Kurtz, D.M., 2001. Rubrerythrin and Rubredoxin Oxidoreductase inDesulfovibrio vulgaris: a Novel Oxidative Stress Protection System. J. Bacteriol. 183, 101–108. https://doi.org/10.1128/JB.183.1.101-108.2001

Luo, Y.-W., Doney, S.C., Anderson, L.A., Benavides, M., Berman-Frank, I., Bode, A., Bonnet, S., Boström, K.H., Böttjer, D., Capone, D.G., Carpenter, E.J., Chen, Y.L., Church, M.J., Dore, J.E., Falcón, L.I., Fernández, A., Foster, R.A., Furuya, K., Gómez, F., Gundersen, K., Hynes, A.M., Karl, D.M., Kitajima, S., Langlois, R.J., LaRoche, J., Letelier, R.M., Marañón, E., McGillicuddy Jr., D.J., Moisander, P.H., Moore, C.M., Mouriño-Carballido, B., Mulholland, M.R., Needoba, J.A., Orcutt, K.M., Poulton, A.J., Rahav, E., Raimbault, P., Rees, A.P., Riemann, L., Shiozaki, T., Subramaniam, A., Tyrrell, T., Turk-Kubo, K.A., Varela, M., Villareal, T.A., Webb, E.A., White, A.E., Wu, J., Zehr, J.P., 2012. Database of diazotrophs in global ocean: abundance, biomass and nitrogen fixation rates. Earth Syst. Sci. Data 4, 47–73. https://doi.org/10.5194/essd-4-47-2012

Ma, S., Huang, S., Tian, Y., Lu, X., 2022. Heterotrophic ammonium assimilation: An important driving force for aerobic denitrification of Rhodococcus erythropolis strain Y10. Chemosphere 291, 132910. https://doi.org/10.1016/j.chemosphere.2021.132910

Magill, A.H., Aber, J.D., Berntson, G.M., McDowell, W.H., Nadelhoffer, K.J., Melillo, J.M., Steudler, P., 2000. Long-Term Nitrogen Additions and Nitrogen Saturation in Two Temperate Forests. Ecosystems 3, 238–253. https://doi.org/10.1007/s100210000023

Magill, A.H., Aber, J.D., Currie, W.S., Nadelhoffer, K.J., Martin, M.E., McDowell, W.H., Melillo, J.M., Steudler, P., 2004. Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. For. Ecol. Manag., The Harvard Forest (USA) Nitrogen Saturation Experiment: Results from the First 15 Years 196, 7–28. https://doi.org/10.1016/j.foreco.2004.03.033

Malone, T.C., Newton, A., 2020. The Globalization of Cultural Eutrophication in the Coastal Ocean: Causes and Consequences. Front. Mar. Sci. 7.

Martens-Habbena, W., Berube, P.M., Urakawa, H., de la Torre, J.R., Stahl, D.A., 2009. Ammonia oxidation kinetics determine niche separation of nitrifying Archaea and Bacteria. Nature 461, 976–979. https://doi.org/10.1038/nature08465

Martín-Nieto, J., Herrero, A., Flores, E., 1991. Control of Nitrogenase mRNA Levels by Products of Nitrate Assimilation in the Cyanobacterium Anabaena sp. Strain PCC 7120 1. Plant Physiol. 97, 825–828.

Masclaux-Daubresse, C., Reisdorf-Cren, M., Pageau, K., Lelandais, M., Grandjean, O., Kronenberger, J., Valadier, M.-H., Feraud, M., Jouglet, T., Suzuki, A., 2006. Glutamine synthetase-glutamate synthase pathway and glutamate dehydrogenase play distinct roles in the sink-source nitrogen cycle in tobacco. Plant Physiol. 140, 444–456. https://doi.org/10.1104/pp.105.071910

McDowell, W.H., Currie, W.S., Aber, J.D., Yang, Y., 1998. Effects of Chronic

Nitrogen Amendments on Production of Dissolved Organic Carbon and Nitrogen in Forest Soils, in: Wieder, R.K., Novák, M., Černý, J. (Eds.), Biogeochemical Investigations at Watershed, Landscape, and Regional Scales: Refereed Papers from BIOGEOMON, The Third International Symposium on Ecosystem Behavior; Co-Sponsored by Villanova University and the Czech Geological Survey; Held at Villanova University, Villanova Pennsylvania, USA, June 21–25, 1997. Springer Netherlands, Dordrecht, pp. 175–182. https://doi.org/10.1007/978-94-017-0906-4_17

McGuire, M.J., Lieu, N.I., Pearthree, M.S., 1999. Using chlorite ion to control nitrification. J. AWWA 91, 52–61. https://doi.org/10.1002/j.1551-8833.1999.tb08715.x

McMurdie, P.J., Holmes, S., 2013. phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. PLOS ONE 8, e61217. https://doi.org/10.1371/journal.pone.0061217

Meulepas, R.J.W., Jagersma, C.G., Khadem, A.F., Buisman, C.J.N., Stams, A.J.M., Lens, P.N.L., 2009. Effect of Environmental Conditions on Sulfate Reduction with Methane as Electron Donor by an Eckernförde Bay Enrichment. Environ. Sci. Technol. 43, 6553–6559. https://doi.org/10.1021/es900633c

Michael-Kordatou, I., Michael, C., Duan, X., He, X., Dionysiou, D.D., Mills, M.A., Fatta-Kassinos, D., 2015. Dissolved effluent organic matter: Characteristics and potential implications in wastewater treatment and reuse applications. Water Res. 77, 213–248. https://doi.org/10.1016/j.watres.2015.03.011

Middelburg, J., 2019. Carbon Processing at the Seafloor. pp. 57–75. https://doi.org/10.1007/978-3-030-10822-9_4

Middelburg, J.J., Nieuwenhuize, J., 2000. Nitrogen uptake by heterotrophic bacteria and phytoplankton in the nitrate-rich Thames estuary. Mar. Ecol.

Prog. Ser. 203, 13–21.

Miegel, K., Graeff, T., Selle, B., Salzmann, T., Franck, C., Bronstert, A., 2016. Investigation of a renaturated fen on the Baltic Sea coast of Meckelenburg - Part I: System description and basic hydrological characterisation. Hydrol. Wasserbewirtsch. 60, 242–258. https://doi.org/10.5675/HyWa_2016,4_1

Mokhele, B., Zhan, X., Yang, G., Zhang, X., 2012. Review: Nitrogen assimilation in crop plants and its affecting factors. Can. J. Plant Sci. 92, 399–405. https://doi.org/10.4141/cjps2011-135

Monteverde, S., Healy, M.G., O'Leary, D., Daly, E., Callery, O., 2022. Management and rehabilitation of peatlands: The role of water chemistry, hydrology, policy, and emerging monitoring methods to ensure informed decision making. Ecol. Inform. 69, 101638. https://doi.org/10.1016/j.ecoinf.2022.101638

Montoya, J.P., Voss, M., Kahler, P., Capone, D.G., 1996. A Simple, High-Precision, High-Sensitivity Tracer Assay for N(inf2) Fixation. Appl. Environ. Microbiol. 62, 986–993.

Moore, C.M., Mills, M.M., Arrigo, K.R., Berman-Frank, I., Bopp, L., Boyd, P.W., Galbraith, E.D., Geider, R.J., Guieu, C., Jaccard, S.L., Jickells, T.D., La Roche, J., Lenton, T.M., Mahowald, N.M., Marañón, E., Marinov, I., Moore, J.K., Nakatsuka, T., Oschlies, A., Saito, M.A., Thingstad, T.F., Tsuda, A., Ulloa, O., 2013. Processes and patterns of oceanic nutrient limitation. Nat. Geosci. 6, 701–710. https://doi.org/10.1038/ngeo1765

Moore, T.R., Bubier, J.L., Bledzki, L., 2007. Litter Decomposition in Temperate Peatland Ecosystems: The Effect of Substrate and Site. Ecosystems 10, 949–963. https://doi.org/10.1007/s10021-007-9064-5 Moraes, B. de S., 2014. Shortcut Nitrification-Denitrification Coupled With Sulfide Oxidation In A

Single Reactor. J. Microb. Biochem. Technol. 06. https://doi.org/10.4172/1948-5948.1000127

Moussa, M.S., Sumanasekera, D.U., Ibrahim, S.H., Lubberding, H.J., Hooijmans, C.M., Gijzen, H.J., van Loosdrecht, M.C.M., 2006. Long term effects of salt on activity, population structure and floc characteristics in enriched bacterial cultures of nitrifiers. Water Res. 40, 1377–1388. https://doi.org/10.1016/j.watres.2006.01.029

Moynihan, M.A., 2020. NifHdada2 GitHub Repository. (Version v. 1.1.0). https://doi.org/10.5281/zenodo.3958370

Murray, C.J., Müller-Karulis, B., Carstensen, J., Conley, D.J., Gustafsson, B.G., Andersen, J.H., 2019. Past, Present and Future Eutrophication Status of the Baltic Sea. Front. Mar. Sci. 6. https://doi.org/10.3389/fmars.2019.00002

Mustamo, P., Hyvärinen, M., Ronkanen, A.-K., Kløve, B., 2016. Physical properties of peat soils under different land use options. Soil Use Manag. 32, 400–410. https://doi.org/10.1111/sum.12272

Nacke, H., Schöning, I., Schindler, M., Schrumpf, M., Daniel, R., Nicol, G.W., Prosser, J.I., 2017. Links between seawater flooding, soil ammonia oxidiser communities and their response to changes in salinity. FEMS Microbiol. Ecol. 93, fix144. https://doi.org/10.1093/femsec/fix144

Nedwell, D.B., Azni bin Abdul Aziz, S., 1980. Heterotrophic nitrogen fixation in an intertidal saltmarsh sediment. Estuar. Coast. Mar. Sci. 10, 699–702. https://doi.org/10.1016/S0302-3524(80)80097-1

Newell, S.E., McCarthy, M.J., Gardner, W.S., Fulweiler, R.W., 2016. Sediment Nitrogen Fixation: a Call for Re-evaluating Coastal N Budgets. Estuaries Coasts 39, 1626–1638. https://doi.org/10.1007/s12237-016-0116-y

Nie, S., Zhu, G.-B., Singh, B., Zhu, Y.-G., 2019. Anaerobic ammonium oxidation in agricultural soils-synthesis and prospective. Environ. Pollut. 244, 127–134. https://doi.org/10.1016/j.envpol.2018.10.050 Niu, Z., Yan, J., Guo, X., Xu, M., Sun, Y., Tou, F., Yin, G., Hou, L., Liu, M., Yang, Y., 2021. Human activities can drive sulfate-reducing bacteria community in Chinese intertidal sediments by affecting metal distribution. Sci. Total Environ. 786, 147490. https://doi.org/10.1016/j.scitotenv.2021.147490

Nixon, S.W., 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. Ophelia 41, 199–219. https://doi.org/10.1080/00785236.1995.10422044

Noe, G.B., Krauss, K.W., Lockaby, B.G., Conner, W.H., Hupp, C.R., 2013. The effect of increasing salinity and forest mortality on soil nitrogen and phosphorus mineralization in tidal freshwater forested wetlands. Biogeochemistry 114, 225–244. https://doi.org/10.1007/s10533-012-9805-1

Norton, J., Ouyang, Y., 2019. Controls and Adaptive Management of Nitrification in Agricultural Soils. Front. Microbiol. 10. Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2020. vegan: Community Ecology Package.

Olofsson, M., Klawonn, I., Karlson, B., 2020. Nitrogen fixation estimates for the Baltic Sea indicate high rates for the previously overlooked Bothnian Sea. Ambio 1–12. https://doi.org/10.1007/s13280-020-01331-x

Orellana, L.H., Chee-Sanford, J.C., Sanford, R.A., Löffler, F.E., Konstantinidis, K.T., 2018. Year-Round Shotgun Metagenomes Reveal Stable Microbial Communities in Agricultural Soils and Novel Ammonia Oxidizers Responding to Fertilization. Appl. Environ. Microbiol. 84, e01646-17.

https://doi.org/10.1128/AEM.01646-17

Ouyang, Y., Evans, S.E., Friesen, M.L., Tiemann, L.K., 2018. Effect of nitrogen fertilization on the abundance of nitrogen cycling genes in agricultural soils: A meta-analysis of field studies. Soil Biol. Biochem. 127. https://doi.org/10.1016/j.soilbio.2018.08.024

Päivänen, J., 1973. Hydraulic conductivity and water retention in peat soils. Acta For. Fenn. 1973 129 1-70 129. https://doi.org/10.14214/aff.7563

Pajares, S., Bohannan, B.J.M., 2016. Ecology of Nitrogen Fixing, Nitrifying, and Denitrifying Microorganisms in Tropical Forest Soils. Front. Microbiol. 7.

Papen, H., Bothe, H., 1984. The activation of glutamine synthetase from the cyanobacterium Anabaena cylindrica by thioredoxin. FEMS Microbiol. Lett. 23, 41–46. https://doi.org/10.1111/j.1574-6968.1984.tb01032.x

Parton, W.J., Holland, E.A., Del Grosso, S.J., Hartman, M.D., Martin, R.E., Mosier, A.R., Ojima, D.S., Schimel, D.S., 2001. Generalized model for NO x and N_2O emissions from soils. J. Geophys. Res. Atmospheres 106, 17403–17419. https://doi.org/10.1029/2001JD900101

Pathak, H., Rao, D.L.N., 1998. Carbon and nitrogen mineralization from added organic matter in saline and alkali soils. Soil Biol. Biochem. 30, 695–702. https://doi.org/10.1016/S0038-0717(97)00208-3

Pedersen, J.N., Bombar, D., Paerl, R.W., Riemann, L., 2018. Diazotrophs and N2-Fixation Associated With Particles in Coastal Estuarine Waters. Front. Microbiol. 9. https://doi.org/10.3389/fmicb.2018.02759

Pjevac, P., Schauberger, C., Poghosyan, L., Herbold, C.W., van Kessel, M.A.H.J., Daebeler, A., Steinberger, M., Jetten, M.S.M., Lücker, S., Wagner, M., Daims, H., 2017. AmoA-Targeted Polymerase Chain Reaction Primers for the Specific Detection and Quantification of Comammox Nitrospira in the Environment. Front. Microbiol. 8.

Pohlman, J., Riedel, M., Bauer, J., Canuel, E., Paull, C., Lapham, L., Grabowski, K., Coffin, R., Spence, G., 2013. Anaerobic methane oxidation in low-organic content methane seep sediments. Geochim. Cosmochim. Acta 108, 184–201. https://doi.org/10.1016/j.gca.2013.01.022

Pommerening-Röser, A., Koops, H.-P., 2005. Environmental pH as an important factor for the distribution of urease positive ammonia-oxidizing bacteria. Microbiol. Res. 160, 27–35. https://doi.org/10.1016/j.micres.2004.09.006

Pranzini, E., Williams, A., 2013. Coastal Erosion and Protection in Europe [WWW Document]. Routledge CRC Press. URL https://www.routledge.com/Coastal-Erosion-and-Protection-in-Europe/Pranzini-Williams/p/book/9781849713399 (accessed 5.9.22).

Pronk, M., Bassin, J.P., de Kreuk, M.K., Kleerebezem, R., van Loosdrecht, M.C.M., 2014. Evaluating the main and side effects of high salinity on aerobic granular sludge. Appl. Microbiol. Biotechnol. 98, 1339–1348. https://doi.org/10.1007/s00253-013-4912-z

Prosser, J.I., Nicol, G.W., 2012. Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. Trends Microbiol. 20, 523–531. https://doi.org/10.1016/j.tim.2012.08.001

Qin, W., Amin, S.A., Martens-Habbena, W., Walker, C.B., Urakawa, H., Devol, A.H., Ingalls, A.E., Moffett, J.W., Armbrust, E.V., Stahl, D.A., 2014. Marine ammonia-oxidizing archaeal isolates display obligate mixotrophy and wide ecotypic variation. Proc. Natl. Acad. Sci. U. S. A. 111, 12504–12509. https://doi.org/10.1073/pnas.1324115111

Racasa, E.D., Lennartz, B., Toro, M., Janssen, M., 2021. Submarine Groundwater Discharge From Non-Tidal Coastal Peatlands Along the Baltic Sea. Front. Earth Sci. 9.

Radniecki, T. s., Ely, R. l., 2008. Zinc chloride inhibition of Nitrosococcus mobilis. Biotechnol. Bioeng. 99, 1085–1095. https://doi.org/10.1002/bit.21672

Ray, S., Mukherjee, J., Mandal, S., 2015. Chapter 13 - Modelling nitrogen and carbon cycles in Hooghly estuary along with adjacent mangrove ecosystem, in: Park, Y.-S., Lek, S., Baehr, C., Jørgensen, S.E. (Eds.), Developments in Environmental Modelling, Advanced Modelling Techniques Studying Global Changes in Environmental Sciences. Elsevier, pp. 289–320. https://doi.org/10.1016/B978-0-444-63536-5.00013-2

Rayment, G.E., Higginson, F.R., 1992. Australian Laboratory Handbook of Soil and Water Chemical Methods. Inkata Press.

Reeder, C.F., Stoltenberg, I., Javidpour, J., Löscher, C.R., 2022. Salinity as a key control on the diazotrophic community composition in the southern Baltic Sea. Ocean Sci. 18, 401–417. https://doi.org/10.5194/os-18-401-2022

Reeve, A.S., Siegel, D.I., Glaser, P.H., 2001. Simulating dispersive mixing in large peatlands. J. Hydrol. 242, 103–114. https://doi.org/10.1016/S0022-1694(00)00386-3

Revsbech, N.P., Jacobsen, J.P., Nielsen, L.P., 2005. Nitrogen transformations in microenvironments of river beds and riparian zones. Ecol. Eng., Riparian buffer zones in agricultural watersheds 24, 447–455. https://doi.org/10.1016/j.ecoleng.2005.02.002

Rezanezhad, F., Price, J.S., Craig, J.R., 2012. The effects of dual porosity on transport and retardation in peat: A laboratory experiment. Can. J. Soil Sci.

92, 723–732. https://doi.org/10.4141/cjss2011-050

Rezanezhad, F., Price, J.S., Quinton, W.L., Lennartz, B., Milojevic, T., Van Cappellen, P., 2016. Structure of peat soils and implications for water storage, flow and solute transport: A review update for geochemists. Chem. Geol. 429, 75–84. https://doi.org/10.1016/j.chemgeo.2016.03.010

Rietz, D.N., Haynes, R., 2003. Effects of Irrigation-Induced Salinity and Sodicity on Soil Microbial Activity. Soil Biol. Biochem. 35, 845–854. https://doi.org/10.1016/S0038-0717(03)00125-1

Rigano, C., Rigano, V.D.M., Vona, V., Carfagna, S., Carillo, P., Esposito, S., 1996. Ammonium Assimilation by Young Plants of Hordeum vulgare in Light and Darkness: Effects on Respiratory Oxygen Consumption by Roots. New Phytol. 132, 375–382.

Roalkvam, I., Jørgensen, S.L., Chen, Y., Stokke, R., Dahle, H., Hocking, W.P., Lanzén, A., Haflidason, H., Steen, I.H., 2011. New insight into stratification of anaerobic methanotrophs in cold seep sediments. FEMS Microbiol. Ecol. 78, 233–243. https://doi.org/10.1111/j.1574-6941.2011.01153.x

Rognes, T., Flouri, T., Nichols, B., Quince, C., Mahé, F., 2016. VSEARCH: a versatile open source tool for metagenomics. PeerJ 4, e2584. https://doi.org/10.7717/peerj.2584

Ruan, Z., Giordano, M., 2017. The use of NH_4^+ rather than NO_3^- affects cell stoichiometry, C allocation, photosynthesis and growth in the cyanobacterium Synechococcus sp. UTEX LB 2380, only when energy is limiting. Plant Cell Environ. 40, 227–236. https://doi.org/10.1111/pce.12858

Rütting, T., Schleusner, P., Hink, L., Prosser, J.I., 2021. The contribution of ammonia-oxidizing archaea and bacteria to gross nitrification under different substrate availability. Soil Biol. Biochem. 160, 108353. https://doi.org/10.1016/j.soilbio.2021.108353

Ryabenko, E., 2013. Stable Isotope Methods for the Study of the Nitrogen Cycle, Topics in Oceanography. IntechOpen. https://doi.org/10.5772/56105

Rysgaard, S., Thastum, P., Dalsgaard, T., Christensen, P.B., Sloth, N.P., 1999. Effects of salinity on NH4+ adsorption capacity, nitrification, and denitrification in Danish estuarine sediments. Estuaries 22, 21–30. https://doi.org/10.2307/1352923

Sakoula, D., Koch, H., Frank, J., Jetten, M.S.M., van Kessel, M.A.H.J., Lücker, S., 2021. Enrichment and physiological characterization of a novel comammox Nitrospira indicates ammonium inhibition of complete nitrification. ISME J. 15, 1010–1024. https://doi.org/10.1038/s41396-020-00827-4

Sanz-Alférez, S., del Campo, F.F., 1994. Relationship between nitrogen fixation and nitrate metabolism in the Nodularia strains M1 and M2. Planta 194, 339–345.

Schoephorster, D.B., 1974. Soils of the Juneau area, Alaska. Or., U.S. Soil Conservation Service].

Schwieger, S., Kreyling, J., Couwenberg, J., Smiljanić, M., Weigel, R., Wilmking, M., Blume-Werry, G., 2021. Wetter is Better: Rewetting of Minerotrophic Peatlands Increases Plant Production and Moves Them Towards Carbon Sinks in a Dry Year. Ecosystems 24, 1093–1109. https://doi.org/10.1007/s10021-020-00570-z

Sears, K., Alleman, J., Barnard, J., Oleszkiewicz, J., 2004. Impacts of Reduced

Sulfur Components on Active and Resting Ammonia Oxidizers. J. Ind. Microbiol. Biotechnol. 31, 369–78. https://doi.org/10.1007/s10295-004-0157-2

Serrano, R., 1996. Salt Tolerance in Plants and Microorganisms: Toxicity Targets and Defense Responses, in: Jeon, K.W. (Ed.), International Review of Cytology. Academic Press, pp. 1–52. https://doi.org/10.1016/S0074-7696(08)62219-6

Setia, R., Marschner, P., Baldock, J., Chittleborough, D., 2010. Is CO2 evolution in saline soils affected by an osmotic effect and calcium carbonate? Biol. Fertil. Soils 46, 781–792. https://doi.org/10.1007/s00374-010-0479-3

Severin, I., Stal, L.J., 2008. Light dependency of nitrogen fixation in a coastal cyanobacterial mat. ISME J. 2, 1077–1088. https://doi.org/10.1038/ismej.2008.63

Shade, A., Read, J.S., Welkie, D.G., Kratz, T.K., Wu, C.H., McMahon, K.D., 2011. Resistance, resilience and recovery: aquatic bacterial dynamics after water column disturbance. Environ. Microbiol. 13, 2752–2767. https://doi.org/10.1111/j.1462-2920.2011.02546.x

Shepard, F.P., 1954. Nomenclature based on sand-silt-clay ratios. J. Sediment. Res. 24, 151–158. https://doi.org/10.1306/D4269774-2B26-11D7-8648000102C1865D

Sigman, D.M., Casciotti, K.L., Andreani, M., Barford, C., Galanter, M., Böhlke, J.K., 2001. A Bacterial Method for the Nitrogen Isotopic Analysis of Nitrate in Seawater and Freshwater. Anal. Chem. 73, 4145–4153. https://doi.org/10.1021/ac010088e

Smith, C.J., Hespell, R.B., Bryant, M.P., 1980. Ammonia assimilation and glutamate formation in the anaerobe Selenomonas ruminantium. J. Bacteriol. 141, 593–602. https://doi.org/10.1128/jb.141.2.593-602.1980 Sohm, J.A., Hilton, J.A., Noble, A.E., Zehr, J.P., Saito, M.A., Webb, E.A., 2011. Nitrogen fixation in the South Atlantic Gyre and the Benguela Upwelling System. Geophys. Res. Lett. 38. https://doi.org/10.1029/2011GL048315

Souri, M.K., 2010. Effectiveness of Chloride Compared to 3,4-Dimethylpyrazole Phosphate on Nitrification Inhibition in Soil. Commun. Soil Sci. Plant Anal. 41, 1769–1778. https://doi.org/10.1080/00103624.2010.489139

Spinette, R.F., Brown, S.M., Ehrlich, A.L., Puggioni, G., Deacutis, C., Jenkins, B.D., 2019. Diazotroph activity in surface Narragansett Bay sediments in summer is stimulated by hypoxia and organic matter delivery. Mar. Ecol. Prog. Ser. 614, 35–50. https://doi.org/10.3354/meps12901

Stankiewicz, B.A., van Bergen, P.F. (Eds.), 1998. Nitrogen-Containing Macromolecules in the Bio- and Geosphere, ACS Symposium Series. American Chemical Society, Washington, DC. https://doi.org/10.1021/bk-1998-0707

Stein, L.Y., Nicol, G.W., 2018. Nitrification, in: ELS. John Wiley & Sons, Ltd, pp. 1–9. https://doi.org/10.1002/9780470015902.a0021154.pub2

Steinmuller, H.E., Chambers, L.G., 2018. Can Saltwater Intrusion Accelerate Nutrient Export from Freshwater Wetland Soils? An Experimental Approach. Soil Sci. Soc. Am. J. 82, 283–292. https://doi.org/10.2136/sssaj2017.05.0162

Steppe, T., Paerl, H., 2002. Potential N_2 fixation by sulfate-reducing bacteria in a marine intertidal microbial mat. Aquat. Microb. Ecol. - AQUAT MICROB ECOL 28, 1–12.
https://doi.org/10.3354/ame028001

Steppe, T.F., Paerl, H.W., 2005. Nitrogenase activity and nifH expression in a marine intertidal microbial mat. Microb. Ecol. 49, 315–324.
https://doi.org/10.1007/s00248-004-0245-x

Stoeva, M.K., Nalula, G., Garcia, N., Cheng, Y., Engelbrektson, A.L., Carlson, H.K., Coates, J.D., 2019. Resistance and Resilience of Sulfidogenic Communities in the Face of the Specific Inhibitor Perchlorate. Front. Microbiol. 10.

Stow, D.A.V. Fine-grained sediments in deep water: An overview of processes and facies models. Geo-Marine Letters 5, 17–23 (1985). https://doi.org/10.1007/BF02629792

Strehse, R., Bohne, H., Amha, Y., Leinweber, P., 2018. The influence of salt on dissolved organic matter from peat soils. Org. Geochem. 125. https://doi.org/10.1016/j.orggeochem.2018.10.001

Suberkropp, K., Chauvet, E., 1995. Regulation of Leaf Breakdown by Fungi in Streams: Influences of Water Chemistry. Ecology 76, 1433–1445. https://doi.org/10.2307/1938146

Sudarno, U., Winter, J., Gallert, C., 2011. Effect of varying salinity, temperature, ammonia and nitrous acid concentrations on nitrification of saline wastewater in fixed-bed reactors. Bioresour. Technol. 102, 5665–5673. https://doi.org/10.1016/j.biortech.2011.02.078

Sumi, T., Koike, I., 1990. Estimation of ammonification and ammonium assimilation in surficial coastal and estuarine sediments. Limnol. Oceanogr. 35, 270–286. https://doi.org/10.4319/lo.1990.35.2.0270

Sun, D., Tang, X., Zhao, M., Zhang, Z., Hou, L., Liu, M., Wang, B., Klümper, U., Han, P., 2020. Distribution and Diversity of Comammox Nitrospira in Coastal Wetlands of China. Front. Microbiol. 11.

Sun, Y., Liang, F., Li, A., Zhang, X., Yang, J., Ma, F., 2017. Ammonium assimilation: An important accessory during aerobic denitrification of Pseudomonas stutzeri T13. Bioresour. Technol. 234. https://doi.org/10.1016/j.biortech.2017.03.053

Swanson, D.K., Grigal, D.F., 1989. Vegetation Indicators of Organic Soil Properties in Minnesota. Soil Sci. Soc. Am. J. 53, 491–495. https://doi.org/10.2136/sssaj1989.03615995005300020031x

Tan, L.V., Thanh, T., 2021. The effects of salinity on changes in characteristics of soils collected in a saline region of the Mekong Delta, Vietnam. Open Chem. 19, 471–480. https://doi.org/10.1515/chem-2021-0037

Thoms, F., Burmeister, C., Dippner, J.W., Gogina, M., Janas, U., Kendzierska, H., Liskow, I., Voss, M., 2018. Impact of Macrofaunal Communities on the Coastal Filter Function in the Bay of Gdansk, Baltic Sea. Front. Mar. Sci. 5. https://doi.org/10.3389/fmars.2018.00201

Tichi, M.A., Tabita, F.R., 2000. Maintenance and control of redox poise in Rhodobacter capsulatus strains deficient in the Calvin-Benson-Bassham pathway. Arch. Microbiol. 174, 322–333. https://doi.org/10.1007/s002030000209

Toro, M., Ptak, T., Massmann, G., Sültenfuß, J., Janssen, M., 2022. Groundwater flow patterns in a coastal fen exposed to drainage, rewetting and interaction with the Baltic Sea. J. Hydrol. 615, 128726. https://doi.org/10.1016/j.jhydrol.2022.128726

Truu, M., Nõlvak, H., Ostonen, I., Oopkaup, K., Maddison, M., Ligi, T., Espenberg, M., Uri, V., Mander, Ü., Truu, J., 2020. Soil Bacterial and Archaeal Communities and Their Potential to Perform N-Cycling Processes in Soils of Boreal Forests Growing on Well-Drained Peat. Front. Microbiol. 11.

Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Laine, J., 1999. Restored cut-away peatland as a sink for atmospheric CO2. Oecologia 120, 563–574. https://doi.org/10.1007/s004420050891

Unger, V., Liebner, S., Koebsch, F., Yang, S., Horn, F., Sachs, T., Kallmeyer, J., Knorr, K.-H., Rehder, G., Gottschalk, P., Jurasinski, G., 2021. Congruent changes in microbial community dynamics and ecosystem methane fluxes following natural drought in two restored fens. Soil Biol. Biochem. 160, 108348. https://doi.org/10.1016/j.soilbio.2021.108348

van Genuchten, M.Th., Wierenga, P.J., 1976. Mass Transfer Studies in Sorbing Porous Media I. Analytical Solutions. Soil Sci. Soc. Am. J. 40, 473–480. https://doi.org/10.2136/sssaj1976.03615995004000040011x

van Kessel, M.A.H.J., Speth, D.R., Albertsen, M., Nielsen, P.H., Op den Camp, H.J.M., Kartal, B., Jetten, M.S.M., Lücker, S., 2015. Complete nitrification by a single microorganism. Nature 528, 555–559. https://doi.org/10.1038/nature16459

Venterea, R.T., Clough, T.J., Coulter, J.A., Breuillin-Sessoms, F., Wang, P., Sadowsky, M.J., 2015. Ammonium sorption and ammonia inhibition of nitrite-oxidizing bacteria explain contrasting soil N_2O production. Sci. Rep. 5, 12153. https://doi.org/10.1038/srep12153

Verhagen, F.J.M., Duyts, H., Laanbroek, H.J., 1992. Competition for Ammonium between Nitrifying and Heterotrophic Bacteria in Continuously Percolated Soil Columns. Appl. Environ. Microbiol. 58, 3303–3311.

Veuger, B., Pitcher, A., Schouten, S., Sinninghe-Damste, J., Middelburg, J., 2013. Nitrification and growth of autotrophic nitrifying bacteria and Thaumarchaeota in the coastal North Sea. Biogeosciences 10.
https://doi.org/10.5194/bg-10-1775-2013

Vigouroux, G., Kari, E., Beltrán-Abaunza, J.M., Uotila, P., Yuan, D., Destouni, G., 2021. Trend correlations for coastal eutrophication and its main local and whole-sea drivers – Application to the Baltic Sea. Sci. Total Environ. 779, 146367.
https://doi.org/10.1016/j.scitotenv.2021.146367

Vila, X., Abella, C.A., Figueras, J.B., Hurley, J.P., 1998. Vertical models of phototrophic bacterial distribution in the metalimnetic microbial communities of several freshwater North-American kettle lakes. FEMS Microbiol. Ecol. 25, 287–299. https://doi.org/10.1111/j.1574-6941.1998.tb00481.x

von Post, L., 1922. Sveriges Geologiska Undersöknings torvinventering och några av dess hittills vunna resultat. [WWW Document].
URL https://pub.epsilon.slu.se/8627/ (accessed 5.19.22).

Voss, M., Liskow, I., Pastuszak, M., Ruess, D., Schulte, U., Dippner, J.W., 2005. Riverine discharge into a coastal bay: A stable isotope study in the Gulf of Gdańsk, Baltic Sea. J. Mar. Syst. 57, 127–145.
doi:http://dx.doi.org/10.1016/j.jmarsys.2005.04.002

Voss, M., Bange, H.W., Dippner, J.W., Middelburg, J.J., Montoya, J.P., Ward, B., 2013. The marine nitrogen cycle: recent discoveries, uncertainties and the potential relevance of climate change. Philos. Trans. R. Soc. B Biol. Sci. 368, 20130121. https://doi.org/10.1098/rstb.2013.0121

Vymazal, J., 2007. Removal of Nutrients in Various Types of Constructed Wetlands. Sci. Total Environ. 380, 48–65.
https://doi.org/10.1016/j.scitotenv.2006.09.014

Wada, S.-I., Weerasooriya, J.D., 1990. Sodium-calcium, calcium-potassium, and potassium-sodium exchange equilibria on a montmorillonitic soil. Soil Sci. Plant Nutr. 36, 451–459. https://doi.org/10.1080/00380768.1990.10416913

Wallenstein, M.D., Hall, E.K., 2012. A trait-based framework for predicting when and where microbial adaptation to climate change will affect ecosystem functioning. Biogeochemistry 109, 35–47. https://doi.org/10.1007/s10533-011-9641-8

Wang, F., Liu, Y., Wang, J., Zhang, Y., Yang, H., 2012. Influence of growth manner on nitrifying bacterial communities and nitrification kinetics in three lab-scale bioreactors. J. Ind. Microbiol. Biotechnol. 39, 595–604. https://doi.org/10.1007/s10295-011-1065-x

Wang, H., Weil, M., Dumack, K., Zak, D., Münch, D., Günther, A., Jurasinski, G., Blume-Werry, G., Kreyling, J., Urich, T., 2021. Eukaryotic rather than prokaryotic microbiomes change over seasons in rewetted fen peatlands. https://doi.org/10.1101/2020.02.16.951285

Wang, Q., Quensen, J.F., Fish, J.A., Kwon Lee, T., Sun, Y., Tiedje, J.M., Cole, J.R., 2013. Ecological Patterns of nifH Genes in Four Terrestrial Climatic Zones Explored with Targeted Metagenomics Using FrameBot, a New Informatics Tool. mBio 4, e00592-13. https://doi.org/10.1128/mBio.00592-13

Wannicke, N., Benavides, M., Dalsgaard, T., Dippner, J.W., Montoya, J.P., Voss, M., 2018. New Perspectives on Nitrogen Fixation Measurements Using $^{15}N_2$ Gas. Front. Mar. Sci. 5. https://doi.org/10.3389/fmars.2018.00120

Ward, B.B., 2008. Chapter 5 - Nitrification in Marine Systems, in: Capone, D.G., Bronk, D.A., Mulholland, M.R., Carpenter, E.J. (Eds.), Nitrogen in the Marine Environment (Second Edition). Academic Press, San Diego, pp. 199–261. https://doi.org/10.1016/B978-0-12-372522-6.00005-0

Weiss, R.F., 1970. The solubility of nitrogen, oxygen and argon in water and seawater. Deep Sea Res. Oceanogr. Abstr. 17, 721–735. https://doi.org/10.1016/0011-7471(70)90037-9

Welsh, D., Wellsbury, P., Bourguès, S., De Wit, R., Herbert, R., 1996. Relationship between porewater organic carbon content, sulphate reduction and nitrogen fixation (acetylene reduction) in the rhizosphere of Zostera noltii. Hydrobiologia 329, 175–183. https://doi.org/10.1007/BF00034556

Weston, N.B., Vile, M.A., Neubauer, S.C., Velinsky, D.J., 2011. Accelerated microbial organic matter mineralization following salt-water intrusion into tidal freshwater marsh soils. Biogeochemistry 102, 135–151. https://doi.org/10.1007/s10533-010-9427-4

Wheeler, P.A., Kirchman, D.L., 1986. Utilization of inorganic and organic nitrogen by bacteria in marine systems1. Limnol. Oceanogr. 31, 998–1009. https://doi.org/10.4319/lo.1986.31.5.0998

Wickham, H., 2016. Create Elegant Data Visualisations Using the Grammar of Graphics [WWW Document]. URL https://ggplot2.tidyverse.org./ (accessed 1.12.22).

Widdison, P.E., Burt, T.P., 2008. Nitrogen Cycle, in: Jørgensen, S.E., Fath, B.D. (Eds.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 2526–2533. https://doi.org/10.1016/B978-008045405-4.00750-3

Winogradow, A., Mackiewicz, A., Pempkowiak, J., 2019. Seasonal changes in particulate organic matter (POM) concentrations and properties measured from deep areas of the Baltic Sea. Oceanologia 61, 505–521. https://doi.org/10.1016/j.oceano.2019.05.004

Woodward, G., Bonada, N., Feeley, H.B., Giller, P.S., 2015. Resilience of a stream community to extreme climatic events and long-term recovery from a catastrophic flood. Freshw. Biol. 60, 2497–2510. https://doi.org/10.1111/fwb.12592

Xia, X., Jia, Z., Liu, T., Zhang, S., Zhang, L., 2017. Coupled Nitrification-Denitrification Caused by Suspended Sediment (SPS) in Rivers: Importance of SPS Size and Composition. Environ. Sci. Technol. 51, 212–221. https://doi.org/10.1021/acs.est.6b03886

Yano, Y., McDowell, W.H., Aber, J.D., 2000. Biodegradable dissolved organic carbon in forest soil solution and effects of chronic nitrogen deposition. Soil Biol. Biochem. 32, 1743–1751. https://doi.org/10.1016/S0038-0717(00)00092-4

Yao, R., Li, H., Yang, J., Wang, X., Xie, W., Zhang, X., 2022. Ammonia Monooxygenase Activity Connects Nitrification Rate with Dominant Edaphic Properties Under Salinity Stress in Coastal Fluvo-aquic Soil. J. Soil Sci. Plant Nutr. https://doi.org/10.1007/s42729-022-00867-z

Yin, T., Feng, M., Qiu, C., Peng, S., 2022. Biological Nitrogen Fixation and Nitrogen Accumulation in Peatlands. Front. Earth Sci. 10. Zaidi, J., Pal, A., 2015. International journal of current research in chemistry and pharmaceutical sciences influence of temperature on physio-chemical properties of freshwater ecosytem of bundelkhand region of uttar pradesh, India. Int. J. Curr. Res. Chem. Pharm. Sci. 2, 1–8.

Zak, D., Gelbrecht, J., 2007. The mobilisation of phosphorus, organic carbon and ammonium in the initial stage of fen rewetting (a case study from NE Germany). Biogeochemistry 85, 141–151. https://doi.org/10.1007/s10533-007-9122-2

Zauft, M., Fell, H., Glaßer, F., Rosskopf, N., Zeitz, J., 2010. Carbon storage in the peatlands of Mecklenburg-Western Pomerania, north-east Germany 12.

Zehr, J., Mellon, M.T., Braun, S.T., Litaker, R., Steppe, T.F., Paerl, H., 1995. Diversity of heterotrophic nitrogen fixation genes in a marine cyanobacterial mat. Appl Environ Microbiol 61: 2527-2532. Appl. Environ. Microbiol. 61, 2527–32. https://doi.org/10.1128/AEM.61.7.2527-2532.1995

Zehr, J.P., 2011. Nitrogen fixation by marine cyanobacteria. Trends Microbiol. 19, 162–173. https://doi.org/10.1016/j.tim.2010.12.004

Zehr, J.P., Capone, D.G., 2020. Changing perspectives in marine nitrogen fixation. Science 368. https://doi.org/10.1126/science.aay9514

Zehr, J.P., McReynolds, L.A., 1989. Use of degenerate oligonucleotides for amplification of the nifH gene from the marine cyanobacterium Trichodesmium thiebautii. Appl. Environ. Microbiol. 55, 2522–2526. https://doi.org/10.1128/aem.55.10.2522-2526.1989

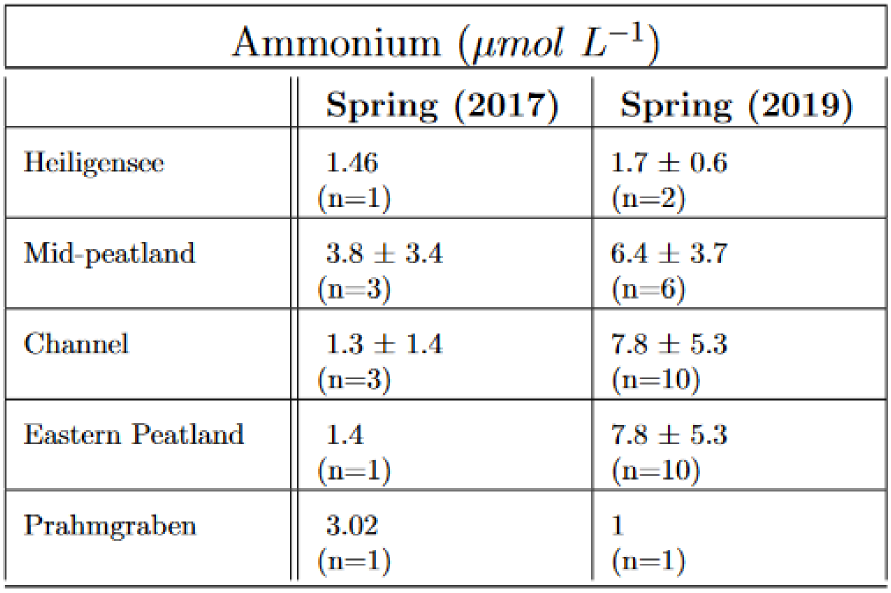
Zhang, L.-M., Hu, H.-W., Shen, J.-P., He, J.-Z., 2012. Ammonia-oxidizing archaea have more important role than ammonia-oxidizing bacteria in ammonia oxidation of strongly acidic soils. ISME J. 6, 1032–1045. https://doi.org/10.1038/ismej.2011.168

Zhang, W., Wang, C., Xue, R., Wang, L., 2019. Effects of salinity on the soil microbial community and soil fertility. J. Integr. Agric. 18, 1360–1368. https://doi.org/10.1016/S2095-3119(18)62077-5

Zilius, M., Samuiloviene, A., Stanislauskienė, R., Broman, E., Bonaglia, S., Meškys, R., Zaiko, A., 2021. Depicting Temporal, Functional, and Phylogenetic Patterns in Estuarine Diazotrophic Communities from Environmental DNA and RNA. Microb. Ecol. 81, 36–51. https://doi.org/10.1007/s00248-020-01562-1

Appendix A

Appendix



Ammonium ($\mu mol\ L^{-1}$)

	Spring (2017)	Spring (2019)
Heiligensee	1.46 (n=1)	1.7 ± 0.6 (n=2)
Mid-peatland	3.8 ± 3.4 (n=3)	6.4 ± 3.7 (n=6)
Channel	1.3 ± 1.4 (n=3)	7.8 ± 5.3 (n=10)
Eastern Peatland	1.4 (n=1)	7.8 ± 5.3 (n=10)
Prahmgraben	3.02 (n=1)	1 (n=1)

TABLE A.1: Overview of averaged ammonium concentrations at sampling sites prior (2017) and post flooding (2019). Data from spring (2017) supplied by M. Böttcher and M. Voss.

CV - TINA LIESIROVA

PERSONAL

tina.liesirova@gmail.com
Av. de la Renaissance 7, 1000 BXL (BE)
16.06.1993
Citizenship: GER & FIN

SKILLS

Professional Skills

Analytical skills	●●●●●
Data visualization	●●●●●
Presentation skills	●●●●●
Report writing	●●●●●
Problem solving skills	●●●●○
Project management	●●●●○

Software

MS Office	●●●●●
RStudio	●●●●○
QGIS	●●●●○
LaTeX	●●●●○
GIMP	●●●●○
Python	●○○○○

Languages

German (native)	●●●●●
English	●●●●●
Swedish	●●●●○
French	●●●○○
Danish	●●○○○
Finnish	●○○○○

Personality traits

Confident

Team player

Drive to learn

Critical thinker

Goal oriented

Creative

PERSONAL PROFILE

Specialized in geology and climate sciences during my studies. Main topics during my doctorate studies at the IOW were nitrogen related processes in marine and terrestrial environments of the southern Baltic Sea as part of Baltic TRANSCOAST.

WORK EXPERIENCE

11/2023 - ongoing International Organization of the Flavour Industry (BE)	Junior Regulatory Affairs and Sustainability Officer
03/2023 - 08/2023 European Chemical Agency in Helsinki (FIN)	Trainee (Data analysis, REACH)
01/2019 - 11/2023 Leibniz institute for Baltic Sea Research in Warnemünde (GER)	PhD candidate (Biogeochemistry)
02/2018 - 08/2018 NIOZ institute on Texel (NL)	Student research assistant (Marine Sciences)
03/2016 - 06/2016 DTU in Risø (DK)	Student research assistant (Aquatic Sciences)

DEGREES

08/2016 - 08/2018 University of Copenhagen (DK)	Master of Science, Climate Change
08/2014 - 08/2016 Lund University (SE)	Bachelor of Science, Geology
09/2012 - 01/2014 Heidelberg University (GER)	Studies in Geosciences

CERTIFICATES

06/2021 Graduate Academy, Rostock	Conflict management
06/2021 Graduate Academy, Rostock	Rhetorics and presentation style
11/2020 Graduate Academy, Rostock	Introduction to Python
02/2020 Graduate Academy, Rostock	Leadership training

SIGNATURE

CV - TINA LIESIROVA

PUBLICATION

- Nitrogen-fixing sulfate reducing bacteria in shallow coastal sediments under simulated resuspension (Estuarine coastal and shelf sciences)

CONFERENCES

- European Geoscience Union, Austria (2021); Presentation: Nitrogen-fixing sulfate reducing bacteria in shallow coastal sediments under simulated resuspension
- Baltic Earth, Poland (2020), Presentation: Nitrogen-fixing sulfate reducing bacteria in shallow coastal sediments under simulated resuspension