Nutrient cycling in coastal and enclosed waters along the Oder outflow

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Sophie Kache
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Gutachter:

Gutachter*in 1:	Prof. Dr. Maren Voß Leibniz Institut für Ostseeforschung Warnemünde maren.voss@io-warnemuende.de
Gutachter*in 2:	Dr. Ugo Marzocchi Aarhus Universitet ugomar@bio.au.dk

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Abbreviations

AOA	Ammonium-oxidising archaea
AOB	Ammonium-oxidising bacteria
C	Carbon
Chl *a*	Chlorophyll *a*
CO_2	Carbon dioxide
DE	Denitrification efficiency
DIC	Dissolved inorganic carbon
DIN	Dissolved inorganic nitrogen
DNR	Denitrification rate
DNRA	Dissimilatory nitrate reduction to ammonium
$DNRA_n$	Nitrification-coupled dissimilatory nitrate reduction to ammonium rate
$DNRA_{tot}$	Total dissimilatory nitrate reduction to ammonium rate
$DNRA_w$	Water-borne nitrate - dissimilatory nitrate reduction to ammonium rate
DNR_n	Nitrification-coupled denitrification rate
DNR_{tot}	Total denitrification rate
DNR_w	Water-borne nitrate - denitrification rate
DON	Dissolved organic nitrogen
DWD	Deutscher Wetterdienst (German Meteorological Service)
GB	Greifswalder Bodden
H_2	Hydrogen
H_2S	Hydrogen sulphide
IRMS	Isotope ratio mass spectrometer
K_m	half saturation constant (Michaelis-Menten enzyme kinetics)
LOD	Limit of detection
LUNG	Landesamt für Umwelt, Naturschutz und Geologie Mecklenburg-Vorpommern (State Agency for the Environment, Nature Conservation and Geology, Mecklenburg–Western Pomerania)
N	Nitrogen
N_2	Di-nitrogen
N_2O	Nitrous oxide
NH_3	Ammonia
NH_4^+	Ammonium
NO	Nitric oxide
NO_2^-	Nitrate
NO_3^-	Nitrate
NOB	Nitrite-oxidising bacteria
NO_x	Nitrite plus nitrate

NR	Nitrification rate
O_2	Oxygen
OM	Organic matter
P	Phosphorus
PB	Pomeranian Bay
PO_4^{3-}	Phosphate
POC	Particulate organic carbon
POM	Particulate organic matter
PON	Particulate organic nitrogen
PP	Primary production
RDL	Rate detection limit
r-ITP	reverse isotope pairing technique
SL	Szczecin Lagoon
WRT	Water residence time

Summary

Eutrophication is one of the greatest threats to aquatic ecosystems, expressed by an increase in primary production, resulting in oxygen depletion from biomass recycling and changes in biodiversity. Coastal and Shelf Seas are particularly affected as they are the primary recipient of riverine nutrient loads, containing for example dissolved inorganic nitrogen (DIN). However, nutrient export from rivers can be mitigated by the filtering function of coastal systems, which usually describes nutrient reduction based on microbial processes along a terrestrial-marine gradient. In addition to the permanent nutrient removal, nutrients can also be retained in the coastal zone, thereby prolonging their availability to organisms in the coastal zone through repeated recycling. While removal processes, especially denitrification, have been extensively studied, they only alter a fraction of the riverine DIN loads reaching the coast. Therefore, the role of retention processes and the balance and coupling between retention and removal processes in estuarine ecosystems, such as the outflow region of the Oder River, needs to be investigated. This is essential to assess the relevance of the coastal filter function to the environment.

The outflow area of the Oder River is one of the largest tributaries to the southern Baltic Sea. There, with a focus on the marine N-cycle, nutrient concentrations and process rates such as DIC and DIN uptake rates, nitrification rates and sedimentary NO_3^- reduction rates were measured. Samples were taken over a seasonal cycle at three stations in the outflow region, each with different geomorphological and physical characteristics. In addition to water column measurements, oxygen and nutrient fluxes across the sediment-water interface were determined with a bottom chamber lander and from pore water nutrient profiles. Particle drift experiments provided data on the water residence time along the outflow.

In the Lagoon and Bodden, DIN concentrations, primary production and DIN uptake rates are high compared to the open coastal station, especially during the spring months. The data suggest efficient nutrient retention, with the majority of riverine nutrients being trapped in phytoplankton biomass (85%), preferring NH_4^+ over NO_3^- uptake. The high assimilation rates of DIN in the Lagoon and Bay are supported by long water residence times of around 180 days and a shallow water column (4 – 8 m). This is in contrast to the open coast, where productivity is limited due to continuous dilution of riverine nutrients by transport processes along the coast. Effective retention is reflected in the remineralisation of biomass and subsequent assimilation of the produced nutrients in the water column. In addition, the sediment periodically serves as a nutrient source for processes in the water column and may be responsible for the occurrence of hypoxic bottom waters, especially in the enclosed Lagoon. Surprisingly, nitrification as the key process linking retention with removal processes was very low in the entire

outflow region, probably due to high competition with phytoplankton for ammonium. In the end, the intense recycling in the water column and the close coupling of water and sediment facilitate a tight coupling of retention and removal processes, resulting in high N removal via coupled nitrification-denitrification in the sediment. Overall, N retention processes in the Oder outflow region are several times higher than N removal processes. This illustrates that retention processes are an important component of the coastal filter function, as they alter the quality of riverine nutrients and thereby provide substrate for nutrient removal.

1. Introduction

1.1 Eutrophication

In a world with a continuously growing human population, it was the production of artificial nitrogen (N) fertilisers in the first decade of the 20th century, which enabled mankind to produce more food than had previously been possible. Since 1913 the Haber-Bosch process produces ammonia (NH_3) for, e.g., agricultural fertiliser, from hydrogen (H_2) and di-nitrogen gas (N_2) under high temperature and pressure. Due to intensive use of these fertilisers, mostly applied by farmers in wealthier countries, the natural dynamics of the global N cycle were changed (Nixon 1995). The total global natural sources of fixed N (203000 kt N yr^{-1}) are almost equal to the total global anthropogenic N sources (210000 kt N yr^{-1}) (Fowler et al. 2013). The excess of artificial N on agricultural land was soon found in aquatic ecosystems like lakes, rivers and oceans (Gustafsson et al. 2012) because the fertilisers were washed out from fields during rainfall. In fact, 40000 - 66000 kt of total N (TN) enter the coastal zone each year (Galloway et al. 2004, Voss et al. 2013). On average, riverine inputs consist of 44% dissolved inorganic nitrogen (DIN), 32% particulate nitrogen (PN) and 25% dissolved organic nitrogen (DON) (Seitzinger et al. 2010). While submarine groundwater discharge (4000 kt N yr^{-1} (Voss et al. 2013)), NO_x ($NO_3^- + NO_2^-$) production by lightning over the ocean (1100-5000 kt N yr^{-1} (Levy et al. 1996, Tie et al. 2002)) and atmospheric deposition of N to the marine environment (33000 kt N yr^{-1} (Galloway et al. 2004)) are noteworthy sources of N to the ocean, nitrogen fixation by diazotrophic microorganisms is the largest natural source of N to the ocean (121000 - 140000 kt N yr^{-1} (Galloway et al. 2004, Deutsch et al. 2007, Fowler et al. 2013, Voss et al. 2013)).

The coastal zones of the oceans, particularly in Asia, Europe and South and North America (Seitzinger et al. 2010), are the primary recipients of these N-containing nutrients, mostly of anthropogenic origin, discharged from rivers as well as from urban sewage, industrial wastes and the burning of fossil fuels (Galloway et al. 2004). In Europe, the Seine, Loire and Elbe are amongst the biggest rivers concerning their discharge of 110.41, 106.13, and 80.39 kt N yr^{-1} (average 2015-2019), respectively (Axe et al. 2023). In the Baltic Sea, the Vistula, the Oder and the Nemunas have the highest discharge of 73.79, 45.58 and 31.07 kt N yr^{-1} (average of 2017-2021), respectively (HELCOM 2024).

This artificial fertilisation of the water can lead to eutrophication, i.e. an increase in the rate of organic matter (OM) supply to a system (Nixon 1995). The origin of the OM can be outside the ecosystem, e.g. from rivers (allochthonous material), or it can be produced within the ecosystem (autochthonous material), e.g. by primary production (PP) (Nixon 1995). In aquatic ecosystems, an increased rate of PP due to the enhanced supply of nutrients is the most common form of eutrophication (Nixon 1995). Due to the high abundance of primary producers in form of phytoplankton (possibly harmful algal blooms, HAB's), the turbidity in the water column increases, resulting in death and subsequent decomposition of benthic macrophytes and seagrass (Schiewer 1997). The loss of submerged aquatic vegetation increases the mobility of the sediment and thereby further enhances turbidity.

During the decomposition of macrophytes, and eventually the phytoplankton cells at the end of a bloom cycle, heterotrophic microorganisms deplete oxygen (O_2). The results are large scale hypoxic (O_2 concentration ≤ 2 mL L^{-1} or ≤ 89.3 µmol L^{-1}; Hansson & Viktorsson 2023) and anoxic areas (O_2 concentration ~ 0 mL L^{-1} or ~ 0 µmol L^{-1}; Hansson & Viktorsson 2023), often above the sediment where the decomposing OM has accumulated. This leads to shifts in the depth of the oxic-anoxic interface, in the water or in the sediment. Together with the increased supply of OM at the sediment surface, benthic microbial processes are severely altered (Jørgensen 1996, Cloern 2001), e.g. from aerobic to anaerobic metabolism, resulting in the release of iron-bound phosphate. Beside the shift in biogeochemistry, spreading hypoxia and anoxia in the sediment and water column as well as increased harmful algal blooms lead to the death of benthic fauna and fish. However, fish (e.g. dabs, flounder), are able to escape developing hypoxia when the O_2 saturation falls to 15% (Gray et al. 2002) because the area of their habitat and feeding grounds shrink and benthic food sources diminish (Cloern 2001, Diaz & Rosenberg 2008). Not only the abundance, also the diversity of marine communities is changed on all trophic levels (Rabalais et al. 2001), from phytoplankton to invertebrates and fish up to sea birds (Gray et al. 2002, Brauer et al. 2012). Eventually, the ecosystem structure and function is altered or lost under persistent anoxia (Rabalais 2002).

Coastal seas like the brackish Baltic Sea are strongly affected by eutrophication. Macrophyte coverage decreased due to eutrophication (Krause-Jensen et al. 2021), e.g. in the Greifswalder Bodden in the southern Baltic Sea, from 90% to 15% (Seifert 1938, Messner & Von Oertzen 1990). Especially in shallow areas of the southern and central Baltic Sea eutrophication leads to a shift from a macrophyte-dominated to a phytoplankton-dominated ecosystem (Schiewer 1997, Cloern 2001, Munkes 2005, Savage et al. 2010). Since the 1960s, a widespread decline in O_2 concentrations (Karlson et al. 2002) and Secchi depths (Sandén & Håkansson 1996, Kahru et al. 2022) was noted, coinciding with increased N and phosphorous (P) concentrations (e.g. Wulff et al. 1990, Bonsdorff et al. 1997). In 2022, 13% of the volume of the Baltic Proper (largest basin of the Baltic Sea) was permanently anoxic and 21% was hypoxic (Hansson & Viktorsson 2023). In addition to eutrophication, the basin structure of the Baltic Sea, stable stratification and the lack of major inflows of oxygenated water result in not only frequent but eventually persistent hypoxic and anoxic conditions (Karlson et al. 2002, Diaz & Rosenberg 2008).

The biggest impact of eutrophication in the Baltic Sea can be found in lagoons, bays and river-dominated estuaries (e.g. Bonsdorff et al. 1997, Savage et al. 2010, Carstensen et al. 2020), i.e. shallow coastal areas which are subject to greater input of nutrients. In contrast to bays and open estuaries, lagoons have a much lower water exchange with the open sea, potentially leading to the high accumulation and turnover of nutrients (Pastuszak et al. 2005). However, these ecosystems also prevent high nutrient export from land to the open sea because they are areas of intense biogeochemical cycling and removal processes (Asmala et al. 2017, Carstensen et al. 2020), which are referred to as coastal filter function. Thereby the filter function alleviates anthropogenic pressures on the sea.

1.2 The coastal filter concept

According to the coastal filter concept of Asmala et al. (2017) (with adjustments), nutrients can pass through (I), be retained (II) or be removed (III) within these ecosystems. The **passage of nutrients** (I) describes the undisturbed transport of riverine nutrients from land to sea, whereby the nutrients can remain in their original chemical form or be transformed. The "coastal filter" is thus bypassed, and the riverine nutrients reach the sea. During **retention processes** (II), the chemical structure is altered while the quantity of nutrients is unchanged, and they remain bioavailable. N **removal processes** (III), on the other hand, eliminate reactive N permanently from the ecosystem, resulting in little to no transport of riverine nutrients to the open ocean and the nutrients being no longer bioavailable. Overall, in the concept of retention processes, and to a certain degree removal processes, nutrients remain longer in the coastal zone or estuary than the river water itself, i.e. the mean nutrient residence time is higher than the mean water residence time (Asmala et al. 2017).

When the coastal filter concept is applied to the nitrogen (N) cycle (Fig. 1), the retention processes (II) are assimilation (uptake and incorporation of inorganic nutrients and DON into biomass), ammonification (mineralisation of organic N compounds into NH_4^+), nitrification (oxidation of ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-)), and DNRA (dissimilatory nitrate reduction to ammonium). Because the nutrients remain in the coastal zone for a longer period, they can be consumed by phytoplankton, thus potentially leading to blooms and eutrophication. Consequently, the open sea or ocean receives fewer dissolved nutrients but more organic matter than it would without the retention processes (Vybernaite-Lubiene et al. 2017).

As they will be of great importance in this thesis, N-assimilation, ammonification, and nitrification will be explained in detail in the following paragraphs, while DNRA will be explained briefly. This is followed by descriptions of removal processes.

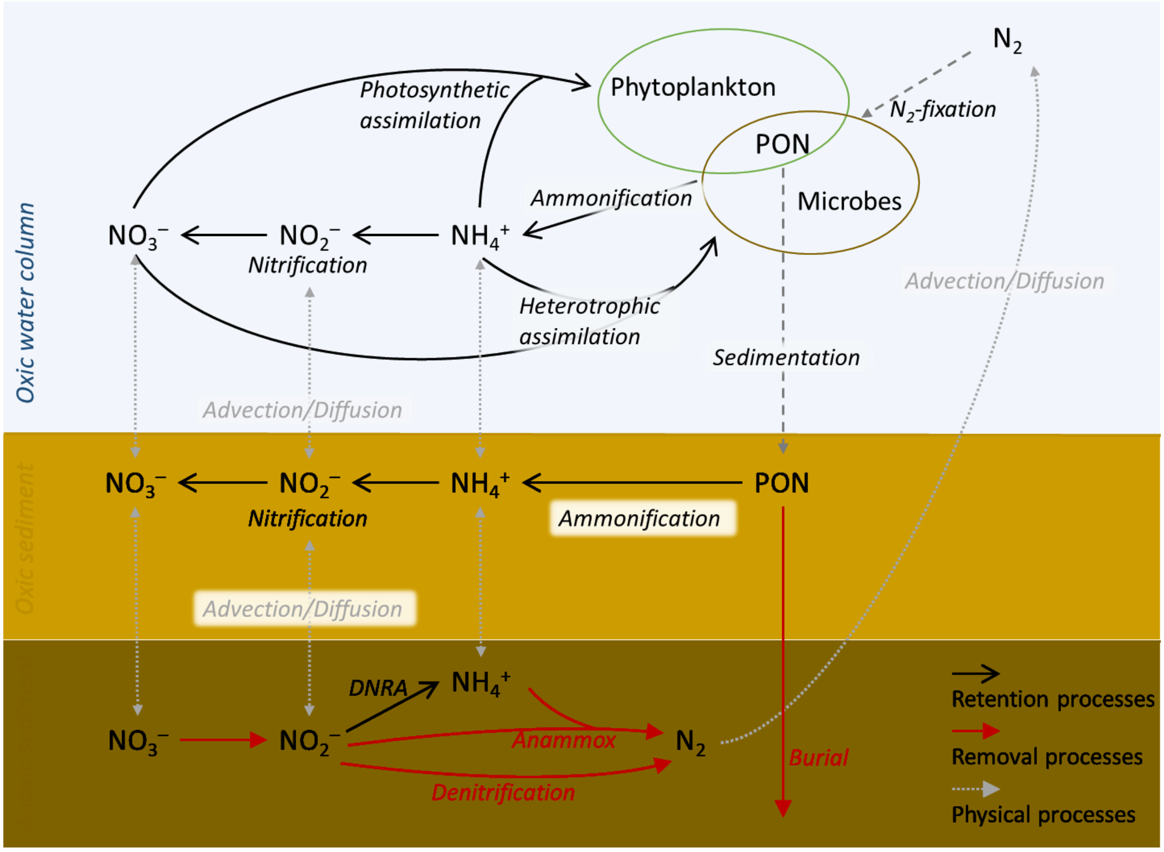

Figure 1. Overview of estuarine N cycling processes. Black arrows show retention processes, red arrows show removal processes, and dashed grey arrows show physical processes. Adapted from Damashek & Francis (2018)

Assimilation

Different types of dissolved N are assimilated by photo- and chemotrophic organisms (e.g. Brown et al. 1974, Glibert 1982), which incorporate these nutrients into the amino functional group, building amino acids and proteins. Assimilated N can further be used for building cell compartments like membranes (N-containing phospho- and glycolipids) and basic genomic structures like nucleic acids. The activity of phototrophic organisms, for instance phytoplankton, is limited to the euphotic zone as uptake rates depend on the irradiance level and decrease in the dark (Riegman et al. 2000). Constantly changing light conditions like in turbulent river waters, can lead to imbalances in the nutrient uptake dynamics of phytoplankton cells (Glibert et al. 2016). In ecosystems with high turbidity, such as coastal systems with high PP, resuspension or riverine particle load, not the access to nutrients but to light becomes the primary limiting factor (Sommer 1989, Passarge et al. 2006, Hautier et al. 2009, Brauer et al. 2012). Special pigments, like the phycobilin pigments in cyanobacteria, enable effective light harvesting and therefore phytoplankton to grow with limited light (Tilzer 1987). On the other hand, assimilation by chemotrophs like bacteria and archaea can be found throughout the water column and sediment. Interestingly, also benthic foraminifera and diatoms can survive in dark, anoxic sediments without O_2 and NO_3^- for long periods of time because they consume intracellular NO_3^- while producing NH_4^+ via DNRA (see below) (Risgaard-Petersen et al. 2006, Piña-Ochoa et al. 2010, Kamp et al. 2011). By now, it is well known that, beside inorganic N forms such as ammonium and nitrate, small organic N-compounds (DON), e.g. urea, can be taken up by phytoplankton (Bronk & Glibert 1993, Bronk et al. 2007) and bacteria (Hoch & Kirchman 1995) as well. In general, NH_4^+ is preferentially assimilated because of its similarity in structure to the target form, the amino functional group (Mccarthy et al. 1977, Glibert 1982, Glibert et al. 2016). NO_3^-, on the other hand, needs to be transformed before it can be used for various cellular metabolic processes, which consumes considerable amounts of energy (Syrett 1956). In fact, NO_3^- uptake is prevented or delayed when NH_4^+ is sufficiently supplied, whereby sufficient NH_4^+ concentrations reach from 1 – 2 µmol L^{-1} (McCarthy et al. 1975) up to 10 µmol L^{-1} (Wilkerson et al. 2006). To be precise, the inhibitory NH_4^+ concentration threshold depends on the environmental conditions, to which the cells have been exposed to (Lomas & Glibert 1999a), resulting in higher thresholds for cells from nutrient-rich environments to inhibit NO_3^- uptake.

Ammonification

When cells of phytoplankton and other microorganisms die, their organic compounds are degraded and NH_4^+ is produced. This process is referred to as ammonification. In the transformation enzymatic processes break down N-containing polymers into their soluble monomers via deamination reactions or a complex series of metabolic steps involving a number of hydrolytic enzymes. The following schematic illustrates the reaction (enzymes involved in *italic*):

Protein – *proteinases* → Peptides – *peptidates* → amino acids – *deamination* → organic acid + NH_4^+

Ammonification can occur under oxic and anoxic conditions (aerobic decomposition of OM or anaerobic fermentation) in the water column (e.g. Glibert 1982, Klawonn et al. 2015) and the sediment (Nixon 1981b). Remineralisation of OM is often positively correlated to temperature (Gardner & McCarthy 2009) and/or OM availability (Nixon et al. 2009). While ammonification in the open ocean is mostly happening in the water column, in estuaries and the coastal zone a high portion of OM is degraded in the sediment after its deposition. The quality of the OM determines the time frame of remineralisation processes depending on whether the material is labile or rather refractory as well as its origin (phytoplankton derived, allochthonous material, humic substances etc.). For instance, the detritus of seagrass, a common plant in the coastal zone of the Baltic Sea, contains 25-30% fibre and ca. 9% lignin (Herbert 1999), leading to a low mineralisation rate compared to phytoplankton cells which contain mostly labile

N-derived compounds. In coastal ecosystems with a relatively shallow water column, OM is quickly deposited, resulting in a high fraction of labile compounds when the degradation on and in the sediment starts (Nixon 1981a). As all OM consists of N-containing macromolecules e.g. nucleic acids, proteins and polyamino-sugars, they are the substrate for decomposing organisms and will eventually be degraded into NH_4^+, which can be released into the water and sustain a large portion of phytoplankton N-demand (Blackburn & Henriksen 1983) when benthic-pelagic coupling is distinctive. In addition, NH_4^+ can also be oxidised by nitrifiers. As a result, there is a close interaction between ammonifiers and nitrifiers, which populate degrading organic aggregates simultaneously as NH_4^+ producer and oxidiser (Kache et al. 2021).

Nitrification

NH_4^+ from remineralisation can be oxidised to NO_3^- during nitrification. The two-step process is considered of fundamental importance in the N cycle because it is the only biological oxidative process that links oxidised and reduced N species. First, ammonium is oxidised to nitrite with hydroxylamine as an intermediate. This is also the rate-limiting step (Ward 2008). During the second step nitrite is oxidised to nitrate, which makes up the largest pool of fixed N in the ocean and in coastal waters. Mostly, each of these steps is carried out by functionally distinct aerobic chemolitotrophic microorganisms. Ammonium-oxidising bacteria (AOB) e.g. *Nitrosomonas*, *Nitrosococcus* and *Nitrosospira* were long thought to be the only ammonium oxidisers. After the first detection of sequences associated with the marine group 1 *Crenarchaeota* in nitrifying cultures from coastal environments and aquariums (Könneke et al. 2005), ammonium-oxidising archaea (AOA) were intensely studied. They were found to be ubiquitous in both terrestrial (e.g. Schleper et al. 2005, Treusch et al. 2005) and marine environments (e.g. Francis et al. 2005, Wuchter et al. 2006, Mincer et al. 2007, Beman et al. 2008, Church et al. 2010, Pedneault et al. 2014) and seem to be the major nitrifiers in the open ocean (Karner et al. 2001, Francis et al. 2005). Interestingly, in coastal and estuarine ecosystems AOB can be the dominant nitrifier group (Magãlhaes et al. 2009, Kache et al. 2021), probably because they are better adapted to enhanced NH_4^+ concentrations (Prosser 1990, Bollmann et al. 2002) than AOA, which are well adapted to oligotrophic conditions (Martens-Habbena et al. 2009). The produced NO_2^- is then converted to NO_3^- by nitrite oxidising bacteria (NOB). The two processes, ammonium and nitrite oxidation, can be spatially and temporally decoupled (Bristow et al. 2015, Heiss & Fulweiler 2016, Schaefer & Hollibaugh 2017) which can lead to an accumulation of nitrite (Beman et al. 2013, Schaefer & Hollibaugh 2017). Recently, it was found that also single organisms can conduct both oxidation steps in a complete nitrification (Daims et al. 2015). Commamox bacteria of the genus *Nitrospira* encode all enzymes necessary for ammonia and nitrite oxidation in their genome (Van Kessel et al. 2015). In the last decade it has been demonstrated that nitrifiers can use organic compounds such as urea and cyanate as N, C and energy sources in addition to the 'classical' use of NH_4^+ as N and energy source and CO_2 as C source (Alonso-Saez et al. 2012, Bayer et al. 2016, Tolar et al. 2017, Kitzinger et al. 2019). All nitrifying microbes fill an unique niche due to their chemoauto- and heterotrophic skill set which on the other site leads to slow growth and restricted flexibility in their nutrient requirements (Ward 2008). Nitrification produces oxidised NO_3^- required for denitrification and, hence, is an essential component of the N cycle. Nitrification and denitrification are often coupled along the redoxcline of stratified waters and in sediments when NO_3^- is produced via nitrification in the oxic layer which is subsequently reduced to N_2 via denitrification in the anoxic compartment.

Dissimilatory nitrate reduction to ammonium, DNRA

In addition to denitrification, the NO_3^- produced during nitrification can also be used in DNRA, which is an anaerobic two-step reaction and the reverse process of nitrification as NO_3^- is first reduced to NO_2^- and then to NH_4^+. The process is conducted in sediments (Hellemann et al. 2020) and shallow pelagic areas with strong benthic-pelagic coupling (Broman et al. 2021) by heterotrophic or autotrophic bacteria, using OM or sulphide (Caffrey et al. 2018) as electron donors. It is also carried out by diatoms, which reduce intracellular NO_3^- to NH_4^+ in dark, anoxic sediments (Kamp et al. 2011). Both DNRA and denitrification compete for NO_3^- and OM as substrate because both processes are carried out by facultative anaerobes which are occupying the same environmental niches. In eutrophic ecosystems DNRA is favoured over denitrification (Jäntti & Hietanen 2012, Hylén et al. 2022) when there is a surplus in electron donors, e.g. in coastal areas like lagoons and estuaries where the concentrations of OM (Tiedje 1988) or hydrogen sulphide (H_2S) are high (An & Gardner 2002, Caffrey et al. 2018). The sediment type also appears to play a role, as the contribution of DNRA to total NO_3^- reduction was higher in muddy sediments than that of denitrification in sandy sediments of the coastal Baltic Sea (Hellemann et al. 2020). Such enhanced DNRA activity is relevant for coastal management because, unlike denitrification, bioavailable N remains in the system and can further contribute to eutrophication (Jäntti & Hietanen 2012, Murphy et al. 2016, Yin et al. 2017, Hellemann et al. 2020).

When the coastal filter concept is applied to the N cycle, N removal processes (III, Fig. 1) are denitrification (reduction of NO_3^- to dinitrogen-gas (N_2)), anammox (oxidation of NH_4^+ with NO_2^- to N_2) and burial. As denitrification is of great interest in this thesis, it will be explained in detail, while anammox and burial will be introduced briefly.

Denitrification

Heterotrophic denitrification is the key process (Nixon et al. 1996) for removing up to 92% (Almroth-Rosell et al. 2016) of bioavailable N from coastal ecosystems and helps mineralise OM under low oxygen conditions. In various steps NO_3^- is reduced N_2.

$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$

Depending on the denitrifying microbial species (e.g. *Pseudomonas* spp. or *Paracoccus denitrificans*) and the environmental conditions, one, several or all steps of the process are carried out (van Spanning et al. 2007). One intermediate and by-product is N_2O (Zumft 1997), a highly potent greenhouse gas (275 time higher warming potential than CO_2) (Wan et al. 2023, Forster et al. 2023), which escapes into the atmosphere. Additionally to facultative anaerobic bacteria, archaea (Zumft 1997), and certain fungi (Kobayashi et al. 1996), marine benthic foraminifera can also use NO_3^- as an electron acceptor, leading to denitrification (Risgaard-Petersen et al. 2006). For a long time, denitrification was believed to be strictly anaerobic as the necessary enzymes and transporters are only produced when the ambient oxygen concentration drops to anoxic and suboxic conditions ($\leq 7.5\%\ O_2$) (Hernandez & Rowe 1988, van Spanning et al. 2007). However, slurry incubations of North Sea surface sediments revealed that N_2 production via denitrification can start at oxygen concentrations of around 90 µmol L^{-1} (Gao et al. 2010), as is found in surface sediments. As the water column in estuaries and coastal systems is often well oxygenated, denitrification takes place at the oxic-anoxic interface in sediments. In strongly stratified waters, denitrification was found at the pelagic redoxcline, for example in the Baltic Sea (Rönner & Sörensson 1985, Brettar & Rheinheimer 1992, Dalsgaard et al. 2013, Bonaglia et al. 2016), the Black Sea (Ward & Kilpatrick 1991) and in upwelling areas (Dugdale et al. 1977, Ward et al. 2009). High NO_3^- concentrations stimulate denitrification (Middelburg et al. 1996). The highest denitrification rates (DNR) were measured in ecosystems with an N surplus, e.g. polluted streams and estuaries. NO_3^- can originate from the water column and diffuse into the pore water (DNR_w) but also from nitrification (coupled nitrification-denitrification (DNR_n), see above). As most denitrifiers are heterotrophs, a sufficient supply of and low competition over labile carbon is beneficial (Middelburg et al. 1996). Thereby the origin, quality and quantity of the OM influence denitrification (Eyre et al. 2013). Salinity indirectly determines the distribution of denitrification, especially along estuarine gradients, where DNR are highest in brackish and freshwater regions compared to marine areas (Rysgaard et al. 1999, Dong et al. 2009). The influence is only indirect because the changing salinity is associated with changes in for example NO_3^- and O_2 concentrations.

Anaerobic ammonium oxidation – Anammox

Another N_2-producing process is the anaerobic ammonium oxidation. Anammox can be found in estuarine continental shelf sediments (Thamdrup & Dalsgaard 2002b, Trimmer et al. 2003) and in anoxic water columns (Dalsgaard et al. 2003a, Kuypers et al. 2003). In the latter, anammox is expected to remove up to 35% of the fixed N from the system (Dalsgaard et al. 2003b). The oxidation of NH_4^+ with NO_2^- to N_2, with hydrazine and hydroxylamine as intermediates, is conducted by bacteria belonging to the *Planctomycetales* (Strous et al. 1999). Anammox bacteria appear to be strictly anaerobic, but process inhibition after exposure to O_2 seems to be reversible (Strous et al. 1997, Jetten 1998). However, in euxinic (water is both anoxic and sulphidic) systems with a high productivity, such as the Baltic Sea and the Black Sea, anammox can be inhibited by sulphide (Jensen et al. 2008). Sedimentary anammox is highest when the organic loading of the sediment is low, namely in systems with a deep water column, where anammox outperforms denitrification in terms of N_2 production (Thamdrup & Dalsgaard 2002, Dalsgaard et al. 2005 and references therein). It has been suggested that this is the case because the environmental conditions are more stable at greater depths, favouring the slow-growing anammox bacteria. However, the anammox bacteria probably prevail because they are autotrophic and do not depend on OM like denitrifiers. Therefore, high OM concentrations may hinder anammox in productive and eutrophic environments, as evidenced by the negative correlation of anammox rates with sedimentary remineralisation (Thamdrup & Dalsgaard 2002a, Hietanen & Kuparinen 2008, Jäntti et al. 2011).

Burial

Nutrients are also permanently removed when they are buried, i.e. when they are trapped in sediments for longer periods of time (Asmala et al. 2017). The burial is defined as non-permanent when, for example, nutrients are recycled in the sediment and subsequently released, or when the sediment and nutrients therein are resuspended into the water column by wind and wave force or dredging (Jansen et al. 2003). This is often the case in shallow and coastal ecosystems, where wind mixing can influence the sediment down to 10 cm depth (Leipe et al. 1998). From the analysis of sediment cores in the Chesapeake Bay and its tributaries, Boynton et al. (1995) concluded that sediments deposited one year prior to sampling are not ideal for investigating nutrient burial because resuspension events and bioturbation affect more than just the top few centimetres. Usually, PON of different origin (phytoplankton, faeces, dead plants and animals) settles on the sediment surface in depositional areas, i.e. areas with low turbulences and sheer stress, like the deep basins of the Baltic Sea. In shallow ecosystems, the disturbances just mentioned lead to an overall lower burial in fine sediments (Alongi et al. 2007). In comparison to denitrification, burial of N removes only single-digit percentages (6 – 10%) (Nixon et al. 1996 and references therein, Humborg et al. 2000, Almroth-Rosell et al. 2016). For the shelf sediments of the NW Atlantic, Nixon et al. (1996) calculated that 2 – 12% of N from land and atmosphere are buried. In ecosystems with a long WRT, high riverine particle load and high trophic potential (meso- to eutrophic), like Chesapeake Bay and the Patuxent River estuary (Maryland), up to 53% of the total inputs from land and atmosphere are buried in the sediments (Boynton et al. 1995, 2008).

1.3 Factors influencing the productivity of the coastal zone

All transformation processes within the coastal filter (Fig. 1) are influenced by a variety of abiotic and biotic variables such as redox conditions, temperature, salinity, light regime, the microbial and phytoplankton community composition or the presence of benthic fauna. Briefly, the topography and morphology of coastal ecosystems play a distinctive role in shaping other influencing factors. The redox conditions, the distribution of oxic and anoxic regions and the interface between them, shape the distribution of microbial processes. In general, process rates are higher at elevated temperatures due to increased microbial growth (e.g. Nydahl et al. 2013, Bååth & Kritzberg 2024) and activity (e.g. Thamdrup & Fleischer 1998, Rysgaard et al. 2004, Bonaglia et al. 2014), but the lack of substrate or unfavourable redox conditions, presumably caused by high temperatures and respiration, can hinder microbial activity (Damashek & Francis 2018 and references therein). At the land-sea continuum, and particularly in estuaries, salinity often indirectly shapes the distribution and intensity of biogeochemical processes as substrate concentrations, redox conditions and microbial communities change along the estuary. Details of the regulatory mechanisms of each variable on N transformation processes can be found in the abovementioned process descriptions. The following section will focus on the role of sediment composition, benthic fauna, WRT, nutrient availability and light on coastal filter N processes.

In the Baltic Sea, a brackish shelf sea stretching from 54°N to 65.8°N and from 9.5°E to 30°E, the coastal ecosystems show a great morphological diversity, ranging from estuaries and lagoons to open bights, archipelagos and open coastal zones. This heterogeneity leads to differences in the functioning of coastal regions in terms of bottom topography, WRT, nutrient turnover and removal (Asmala et al. 2017, Carstensen et al. 2020).

In hard bottom areas, which are often found in archipelagos, nutrient removal via denitrification is negligible due to the dominance of barren rocks and the lack of sediments with suitable redox conditions (Deutsch et al. 2010). In sandy sediments, which are a prominent feature along wide stretches of shelf seas and the open coast, low N removal was found (Deutsch et al. 2010, Zilius et al. 2018). Often, these low denitrification rates in sandy sediments are attributed to a little microbial activity due to low OM content (Keil et al. 1994) and deep oxygen penetration in relation to fine/muddy sediments. This theory was dismissed in studies investigating the sandy sediments of the North Sea. There, permeable sediments, i.e. sediments with a permeability of ≥ 10^{-12} m^2 (Forster et al. 1996, 2003, Huettel et al. 1996, Huettel & Rusch 2000), are responsible for considerable N removal associated with advective pore water flow (Gao et al. 2012, Marchant et al. 2014). Such permeable sandy sediments are common in the southern Baltic Sea (Forster et al. 2003). Currents and wind waves force OM-, nutrient- and O_2-rich water into the permeable sediment (Reimers et al. 2004), where remineralisation and subsequent microbial transformation (Huettel et al. 2003, 2014) by a diverse microbial community (Boudreau et al. 2001) occur. In particular, deposition of OM at the sediment surface has been identified as the driving force of benthic N cycling (Jensen et al. 1990, Lohse et al. 1993). Hence, the heterotrophic denitrifiers are sufficiently supplied with OM and even the rapidly changing conditions regarding the distribution of O_2 in the upper centimetres of the sediment do not inhibit denitrification, as aerobic denitrification can occur (Rao et al. 2007, Gao et al. 2010). In the Wadden Sea, for example, this results in the removal of up to 50 - 75% of the NO_3^- pool by denitrification in the sandy sediment (Marchant et al. 2014). Such effective removal is facilitated by the shallow water depths in coastal waters compared to the open ocean, resulting relatively fast settling of OM due to the close proximity of the productive photic zone and the sediment. However, in the Baltic Sea, a review of denitrification across various coastal types with different sediment structure revealed higher DNR in muddy cohesive sediments than in sandy sediments (Asmala et al. 2017). It should be noted that most of the data included in the review are from measurements designed for sediments influenced by diffusive transport processes, such as incubation of intact cores with ^{15}N-NO_3^- additions (e.g. Sundbäck et al. 2006, Hietanen & Kuparinen 2008, Jäntti et al. 2011, Bonaglia et al. 2014, Broman et al. 2021). It is possible that other incubation techniques, such as flow-through reactors (Rao et al. 2007) or slurry incubations (Gao et al. 2010), may give different results. There are also mixed results on the influence of the sediment type on benthic nitrification rates, with the O_2 penetration depth (Henriksen et al. 1981, Hansen et al. 1981) and the size of the benthic NH_4^+ pool (Jäntti et al. 2011) being identified as drivers. However, the intensity of benthic N removal and retention processes depends on sediment characteristics and may vary between coastal ecosystem types independently of spatial proximity.

In addition, the coastal filter function is strongly affected by the abundance (Pennifold & Davis 2001) and diversity (Blackburn & Henriksen 1983) of benthic fauna species, which are in turn impacted by grain size, water depth and salinity (Rousi et al. 2011, Gogina et al. 2016, Thoms et al. 2018). Deep-burrowing polychaetes such as *Corophium volutator* or *Hediste diversicolor* or various amphipod species facilitate bioturbation and thus nutrient turnover processes in the sediment (Thoms et al. 2018). Bioturbation by fauna brings particles and OM to deeper layers of the sediment where these organic materials are degraded (Ouellette et al. 2004) and enhances the NH_4^+ fluxes from the sediment to the overlying water (Pennifold & Davis 2001, Karlson 2007). Bioturbation also stimulates denitrification and coupled nitrification-denitrification due to the fauna-induced inflow of NO_3^- and NH_4^+, respectively, from the overlying water into the burrows and sediment (Gilbert et al. 1998). Thus, in addition to the physical effects, the benthic fauna plays a role in benthic-pelagic coupling by enhancing the turnover and transport of nutrients at the sediment-water interface. However, the knowledge on the interaction between these dynamics and the processes within the coastal filter, as well as their ultimate influence on the coastal filter function, can be improved, especially in estuarine ecosystems.

The WRT also regulates the magnitude of N turnover processes, whereby N removal in estuarine and coastal systems is positively related to the WRT (Nixon et al. 1996, Dettmann 2001, Seitzinger et al. 2006). Likewise, a higher WRT results in a lower percentage of riverine N being exported from the ecosystem (Dettmann 2001). Based on analyses of 11 North American and European estuaries, the same author estimated a shift in the system from export as the major N loss pathway to internal, biogeochemical N removal processes as the major N loss pathway at a residence time of about 3.3 months (Dettmann 2001). The WRT determines the time available for biological processes to occur within an aquatic ecosystem (Middelburg & Nieuwenhuize 2000a, Dettmann 2001). A long WRT enables repeated cycles of N uptake by phytoplankton and subsequent OM sedimentation, which in turn facilitates sedimentary denitrification (or coupled nitrification/denitrification) (Seitzinger et al. 2006). Consequently, open coastal ecosystems with a short WRT have a low deposition rate of OM, resulting in reduced benthic biogeochemical turnover, namely DNR (Seitzinger et al. 2006). In general, the WRT is defined by geomorphological and hydrodynamic characteristics of an aquatic ecosystem, including the extent of water discharge in an estuary and tidal flushing at open coasts. More precisely, shallow lagoons have a longer WRT than deep drowned river valley estuaries. For example the shallow back-barrier lagoon Hog Island Bay (Virginia, USA) has a WRT of 15 days (Fugate et al. 2006) whereas the WRT of Chesapeake Bay ranged from 110 to 264 days (average of 180 days) between 1980 and 2012 (Du & Shen 2016). Due to the large variations in the WRT and thus in biogeochemical cycling between ecosystem types, it is crucial to assess both, residence time and N transformation processes, when studying the coastal filter function.

In most aquatic systems, nutrient availability is the primary factor limiting PP and, consequently, phytoplankton growth (Tilman 1977, 1985). There is a considerable debate among researchers whether the ratio of the growth-limiting nutrients or the absolute nutrient loads are the determining factor in phytoplankton competition and PP (Brauer et al. 2012). The original 'resource-ratio hypothesis' by Tilman (1985) states that the ratio of resources, like nutrients and light, limit growth and thereby determine which species dominate during competition. He illustrated his hypothesis in experiments with phytoplankton (Tilman 1977), and others demonstrated it in entire ecosystems (Sommer 1989). On the other hand, absolute nutrient concentrations, which are for example enhanced in eutrophic ecosystems, can lead to shifts in entire phytoplankton communities (Schiewer 2008). Eventually, as a consequence of the enhanced PP typical for eutrophication, turbidity is elevated and light often becomes one of the key limiting factors (Sommer 1989, Passarge et al. 2006, Hautier et al. 2009, Brauer et al. 2012). Furthermore, the intensity of mixing processes affects the competition for light between buoyant and sinking phytoplankton species (Huisman et al. 2004). This can, for example, lead to long-lasting alterations in the annual phytoplankton succession, as evidenced by observations in the Darss-Zingst Bodden Chain (Schiewer 2008). There, cyanobacteria and green algae are present in high numbers throughout the year, whereas the former is dominant in spring and autumn and the latter is dominant in the summer months. Both groups are best adapted to changing light conditions, with intense irradiance at the surface and limitation below (Schubert et al. 1995a b). Originally, diatoms were more important in the Darss-Zingst Bodden Chain, especially in spring, as is typical for the Baltic Sea phytoplankton succession (Wasmund et al. 1998). There are numerous examples of light limitation in coastal waters and estuaries, for example in the Cape Fear River Estuary (USA) or along the southern Baltic Sea (Mallin et al. 1997, Schiewer 2008).

In general, photosynthesis limits active phytoplankton growth to the euphotic zone of the ocean, where the light of low wavelengths (blue, ~ 460 – 490 nm) is most efficiently absorbed, leading to high growth of phytoplankton communities (Hintz et al. 2021). The medium wavelengths (green, ~ 490 – 570) are barely used and, when applied alone, result in significantly lower growth rates (Hintz et al. 2021). In addition to the ubiquitous Chl *a*, taxon-specific quantities, combinations and types of accessory pigments are found in phytoplankton, e.g. phycobillin in cyanobacteria. When the light quality changes, chlorophytes and chromophytes, for example, adjust the quantity of their pigment rather than their relative composition. Only a broad spectral range, without disturbances of for example cDOM (responsible for the "browning" of the water), facilitates the coexistence of different phytoplankton groups, whereas restricted light spectra can exclude species commonly found in white light and reduce species richness (Hintz et al. 2021). Phytoplankton cells also become richer in pigments when the blooms develop and self-shading increases, as occurs in eutrophic ecosystems, enabling them to become light saturated faster (lower E_k value) (Sakshaug et al. 2009). Overall, the influence of light on the structure and distribution of phytoplankton communities has been studied extensively.

Surprisingly, the influence of light on nitrification has not yet been investigated in the coastal zone, only in the open ocean. The low nitrification rates observed in sunlit oceanic waters (Ward 1985, Ward & Zafiriou 1988, Bianchi et al. 1999, Beman et al. 2012, Santoro et al. 2013) have been attributed to the intense competition between nitrifiers and phytoplankton for the substrate NH_4^+ (Smith et al. 2014). The phytoplankton metabolism exhibits a rapid response to NH_4^+ pulses from degradation or upwelling, despite the dominant nitrifier group, AOA, having a low K_m (Michaelis constant, half-saturation constant) of 0.133 µmol L^{-1} (Martens-Habbena et al. 2009). This low K_m indicates they can perform at half their maximum reaction rate at low NH_4^+ concentrations. In contrast, the K_m of phytoplankton in eutrophic waters is ~ 1.3 µmol NH_4^+ L^{-1} (Eppley et al. 1969). Nitrification increases in the ocean surface waters during the night or in deeper waters (Smith et al. 2014), illustrating the preference for a dark environment where phytoplankton is growth limited. Moreover, Wan et al. (2018) demonstrated that the ambient NO_3^- concentration influences the nutrient preference of phytoplankton. Specifically, a low NO_3^- concentration increases the affinity of phytoplankton towards NH_4^+, outcompeting nitrifiers, and vice versa. It is essential to identify these mechanisms specifically in the coastal zone, in order to gain insights into the regulatory mechanisms of nitrification as a nitrogen retention process in the coastal filter.

1.4 Previous focus on removal processes

To date, the majority of scientific work assessing the efficiency of coastal filters has focused on removal processes, in particular denitrification (Asmala et al. 2017, Hellemann et al. 2017, Carstensen et al. 2020), as it counteracts eutrophication and therefore plays a vital role in ecosystem management. Especially coastal and shelf sediments have been the focus of studies that ascribe them the role of natural N filters. In West Atlantic shelf sediments, up to 75% of the N remineralised in the sediment is removed by denitrification (Laursen & Seitzinger 2002b, Rao et al. 2007), and in the Baltic Sea, 48 – 73% of external N inputs are denitrified in the sediment (Deutsch et al. 2010). Denitrification has also been shown to be twice as high in eutrophic estuaries compared to oligotrophic estuaries (Seitzinger 1988, Bartl et al. 2019). In the Baltic Sea, the highest DNR were determined in lagoons, a prominent feature along the Baltic coastline, because they receive large NO_3^- and OM inputs (Carstensen et al. 2020) from the biggest rivers entering the Baltic Sea (HELCOM 2021). Anammox tends to occur in deep waters (see above), but can contribute significantly to N loss (Crowe et al. 2012), while burial is of minor importance (Humborg et al. 2000). Consequently, denitrification is not only the most studied but also the dominant benthic N removal pathway (Middelburg et al. 1996, Dettmann 2001, Seitzinger et al. 2006).

Different approaches are used to estimate N removal from an ecosystem. DNR are determined per sediment area (e.g. with the stable isotope tracer ^{15}N) and subsequently estimated for the area of the entire ecosystem, sometimes including the distribution of different sediment types (e.g. Hietanen & Kuparinen 2008, Deutsch et al. 2010, Marchant et al. 2014). The same approach is used for anammox (e.g. Dalsgaard et al. 2003a, Crowe et al. 2012), which helps to directly compare anammox with denitrification rates (Dalsgaard et al. 2005) and calculate their contribution to total N_2 production (Thamdrup & Dalsgaard 2002a). In estuaries, the difference in for example nutrient concentrations between two or more stations along the estuarine gradient can be calculated and attributed to nutrient retention or removal (e.g. Voss et al. 2010, Korth et al. 2013). Furthermore, the isotopic composition of NO_3^-, namely the ^{15}N and ^{18}O isotopic values of NO_3^-, and their relationship to each other can provide insight into processes such as nitrification, assimilation and denitrification (Fry 2006, Korth et al. 2013).

It is important to note that within the scientific and coastal management communities, the permanent elimination of N from a system is described using a variety of expressions. While the coastal filter concept of Asmala et al. (2017), which is also used in the present work, and some others (Nixon et al. 1996) use the term 'removal', the majority of published work uses the term 'retention' (Voss et al. 2010). In addition to the actual 'removal' of nutrients, it also describes the amount of riverine or terrestrial N that does not reach the open ocean. The term 'nitrate removal' has also been used to describe the overall removal of nitrate specifically from the water column, encompassing assimilation, DNRA and denitrification (Burgin & Hamilton 2007, Mulholland et al. 2008, Lunau et al. 2013). In the context of the coastal filter, it can be confusing to deal with the different terms and misunderstandings should be avoided by using defined terms.

1.5 Underrepresented retention processes

In agreement with findings of studies about the N removal efficiency of coastal areas, the majority of riverine nutrients entering the southern Baltic Sea remain within the coastal zone. This is due to the fact that the currents flow parallel to the southern coastlines, which facilitates intense N transformation in the coastal sediments (Radtke et al. 2012). However, on average, only 16% of the total N input is actually removed via denitrification in the coastal zone, with the extent of the removal capacity varying between coastal types, where lagoons and open coastal zones together account for 76% of the N removal in the coastal zone of the Baltic Sea (Asmala et al. 2017). The fate of the remaining 84% remains unresolved.

It is evident that investigations with a primary focus on retention processes are underrepresented in coastal filter studies. For instance, there are missing facts regarding DNRA in different ecosystems. What is currently known is that the magnitude of DNRA rates appears to be influenced by sediment grain size, organic carbon content, and season (Jäntti et al. 2011, Bonaglia et al. 2014, Hellemann et al. 2020). In Danish estuaries, nutrient uptake into phytoplankton and macrophytes was identified to store nutrients in the estuary (Conley et al. 2000). In stratified estuaries in the Baltic Sea, Bartl et al. (2019) identified retention processes such as nitrification and heterotrophic NH_4^+ assimilation, which follow OM sedimentation and denitrification, as important steps towards permanent nutrient removal. All processes benefit from long WRT or alongshore transport (Bartl et al. 2019). However, the OM that reaches the sediment can also simply be remineralised and released back into the water column (e.g. Thoms et al. 2018) instead of being denitrified, making the sediment another nutrient source for pelagic retention processes.

Hence, work needs to be done focusing on the role of retention processes in the costal filter. In fact, Jäntti et al. (2011) demonstrated that nitrification is often the most prominent controlling factor of DNR, making a retention process the key regulator of N removal. The possible close coupling of retention and removal processes can be illustrated by their control mechanisms. Both N removal and retention processes are strongly impacted by the seasonality of nutrient inputs, the ambient oxygen regime and temperature shifts. In some coastal ecosystems, O_2 consumption rates and coupled nitrification-denitrification are highest in summer, when temperatures are high and NH_4^+ is available in the sediment, increasing metabolic activity and stimulating nitrification (Piña-Ochoa & Álvarez-Cobelas 2006, Bonaglia et al. 2014). In addition, assimilation and ammonification are responsible for the supply of fresh labile organic carbon, facilitating denitrification in sediments along the Baltic Sea coastline (Hellemann et al. 2017, 2020). Recycling processes can dominate in summer and autumn, when an ecosystem is strongly impacted by seasonal hypoxia or anoxia, while N removal by denitrification is highest in winter, when temperatures are lowest but the sediment surface is reoxygenated, allowing coupled nitrification-denitrification (Kemp et al. 2005, Bonaglia et al. 2014).

Furthermore, in contrast to the high discharge and nutrient input in spring, the low discharge in summer results in low riverine N inputs and low DIN concentrations in the water column, which can limit N removal via denitrification (Seitzinger et al. 1984, Nielsen et al. 1995). However, if the majority of NO_3^- is supplied by OM remineralisation in the sediment and subsequent nitrification (Seitzinger 1988, Broman et al. 2021), sufficient N removal may be independent of the DIN pool above the sediment.

Consequently, a tight coupling of retention/recycling and removal processes could result in the most efficient N removal. Further observations of retention processes in ecosystems with different sediment types, nutrient availability and morphology will improve our understanding of their role in the coastal filter and their link to removal processes.

1.6 The Oder outflow region

The interaction of retention and removal processes as well as influencing factors such as the sediment and light availability were investigated in the outflow region of the Oder River (Fig. 3). Entering the southern Baltic Sea, the Oder River delivers the highest per area TN concentration (HELCOM 2021) to the Baltic Sea (discharge in 2021: 511 m^3 s^{-1} freshwater, 44 kt total N) (Fig. 2) after passing through a densely populated catchment area (~ 120 000 km^2) (HELCOM 2021). 89% of the catchment area are located in the republic of Poland, representing 50% of the entire Baltic agricultural land (Pastuszak et al. 2012).

Specifically, the Oder River discharges into a shallow estuarine lagoon system, the Szczecin Lagoon (Fig. 3 and 4), which is divided juristically by the German-Polish border. The Lagoon is connected to the Baltic Sea, specifically the Pomeranian Bay, by three waterways, whereby the majority of Oder river water is exported through the Swina (Mohrholz & Lass 1998). In the west, the Lagoon is connected via the Peenestrom to the Greifswalder Bodden, which has a wide connection to the Pomeranian Bay. Continuously high riverine nutrient loads from the Oder but also from smaller rivers, draining agriculture dominated catchments, are responsible for a strongly eutrophied outflow system since decades (Humborg et al. 2000). The poor ecological status of the Szczecin Lagoon is evident in low Secchi depths (high turbidity) and high chlorophyll *a* (Chl *a*) concentrations (Friedland et al. 2019). The enhanced turbidity led to a decrease in macrophyte coverage of about 66% in the Lagoon (potential historical maximum coverage was 36% of the bottom area, Schernewski et al. 2023) and 83% in the Greifswalder Bodden (historical maximum coverage was 90% of the bottom area, Munkes 2005). Cyanobacteria, including nitrogen-fixing species (diazotrophs), are prominent features in the outflow region during the summer months (Schiewer (2008), LUNG monitoring data), hinting towards N limitation. Thereby, abundant and toxic cyanobacteria like *Microcystis aeruginosa* pose a threat to tourism, pets and livestock

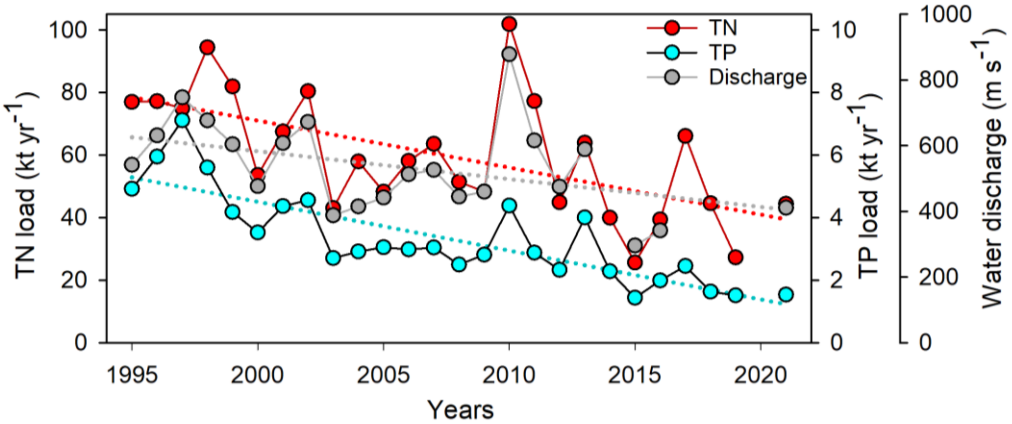

Figure 2. Annual Oder River discharge of total nitrogen (red, TN), total phosphorus (blue, TP) and water (grey). Dotted lined represent linear regression for each variable with the respective colour.

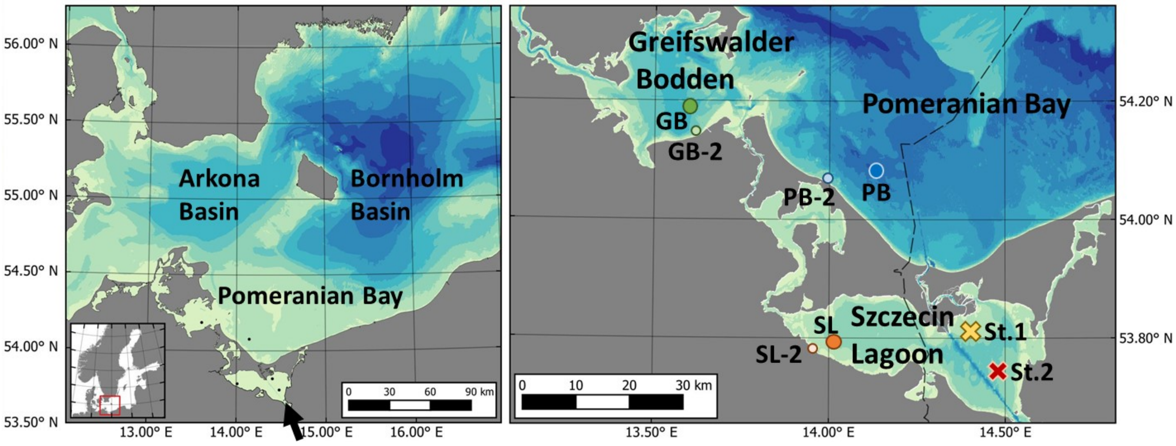

Figure 3. Location of the Oder Outflow region in the western Baltic Sea; the arrow indicates the entry of the Oder River (left panel; depth contours in 10 m intervals). Map of the Oder Outflow Region showing the sampling areas Szczecin Lagoon, Greifswalder Bodden and Pomeranian Bay and all sampled stations (right panel; depth contours in 2 m intervals).

farming (Schiewer 2008). It is suggested that a large internal nutrient pool and the periodic release of phosphate from the sediment into the water column are responsible for the continuing poor status of the ecosystems (Schernewski & Wielgat 2001, Bangel et al. 2004, Munkes 2005, Friedland et al. 2019), despite the reduction of nutrient input from the Oder river (Pastuszak et al. 2018) (Fig.1).

However, it seems that at least the open Baltic Sea is protected from those drastic eutrophication effects. In general, over one third of Polish river waters flow through coastal lakes or lagoons prior to entering the Baltic Sea coast (HELCOM 1993). Those ecosystems, due to the long WRT of weeks to months, promote the reduction of nutrients and pollutants being transported to the open sea, which makes actual estimates of export to the Baltic Sea difficult to impossible (HELCOM 1993). Previous studies in the Oder outflow region found a nutrient reduction between the entry and exit of the Szczecin Lagoon (Voss et al. 2010), suggesting a coastal filter function of the lagoon. According to mass budget calculations including the Lagoon and the Bay, 45% of the total N loads from the Oder river do not reach the Baltic Sea, whereby 85% of the retention and/or removal processes took place in the Szczecin Lagoon due to its long WRT (Pastuszak et al. 2005). The authors further concluded that denitrification in the sediment has the greatest contribution to the loss of N in the outflow region. In the Pomeranian Bay, the retention and removal capacity is rather limited due to the short WRT and frequent transport of depositional material from terrestrial sources to deep basins of the Baltic Sea (Christiansen et al. 2002, Emeis et al. 2002). However, analysis of NO_3^- isotopic data from spring in 2009 suggested rapid consumption of riverine NO_3^- along the coastline of the Pomeranian Bay during the spring bloom, followed by sedimentation of particulate N and subsequent sequestration in the sediment (Korth et al. 2013). As only NO_3^- uptake rates were determined and only in the Pomeranian Bay, nutrient transformation processes in the outflow region could be explained only to some extent. Furthermore, precise calculations of the N export from the lagoon to the Pomeranian Bay do not exist yet, even though those nutrients have a major influence on the productivity of the bay (Pastuszak et al. 1996).

1.7 Open questions and aims

Based on the existing knowledge outlined above, the objective of my thesis is to provide a better understanding of the balance between and coupling of retention and removal processes in estuarine ecosystems, as exemplified by the Oder outflow region. As part of the BMBF-financed project "Blue Estuaries – Developing estuaries as habitable sustainable ecosystem despite climate change and stress", I investigate the following thematic groups and address the following questions:

- Can the coastal filter function of the Oder outflow region regarding input from the Oder River be confirmed by process rate measurements? What is the importance of retention processes (especially N-assimilation, ammonification and nitrification) in the Oder outflow region and how are these processes related to removal processes? How efficient are retention and removal processes respectively and their coupling in reducing riverine N export to the Baltic Sea?
- How does the sediment, in particular the exchange of nutrients and O_2 across the sediment surface, impact the coastal filter processes and the overall filter function?
- Given the influence of light on the productivity of eutrophic ecosystems, does it have a similarly strong effect on nitrification as the crucial link between retention and removal processes?

Based on these questions, I studied stations in the Oder outflow region with different hydrological and morphological characteristics. I am the first to measure primary production (PP), DIN uptake rates, nitrification rates (NR) and sedimentary nutrient and O_2 fluxes, covering all seasons. The WRT in the coastal filter function of the region is assessed with a physical-biogeochemical model, which also estimates the transport between the Szczecin Lagoon and the Pomeranian Bay. Finally, the implications of the results for the open Baltic Sea are assessed.

2. Materials and Methods

2.1 Site description

The Oder River flows into the southern Baltic Sea at the German-Polish border. After crossing the Szczecin Lagoon (Fig. 3), the river water enters the Pomeranian Bay (Baltic Sea) via three river arms: the Peenestrom, the Swina (main shipping channel, deepened to 14.5 m) and the Dziwna (from W to E), whereby 60-70% of the water from the Szczecin Lagoon is transported through the Swina towards the Baltic Sea (the other two around 15% each) (Mohrholz & Lass 1998). As part of the project "Blue Estuaries", three areas in the Oder outflow region were chosen to be investigated: the enclosed Szczecin Lagoon as the primary recipient of the Oder river water; the seaward-open Greifswalder Bodden receiving both fresh- and Baltic Sea water; and the Pomeranian Bay with an open coastal structure and only limited river influence.

A - Szczecin Lagoon

The Szczecin Lagoon (area: 687 km^2) (Fig. 4) is divided into the Great Lagoon on the Polish side (Wielki Zalew, 410 km^2) and the Small Lagoon (277 km^2) on the German side (Kleines Haff) and is separated from the open Baltic Sea in the North by the islands of Usedom and Wolin. The islands are separated by the Swina, one of three connecting waterways to the Baltic Sea (see section above). The Small Lagoon is connected to the Greifswalder Bodden via the Peenestrom, a circa 20 km long strait with several bends and bays. The Lagoon is a shallow coastal ecosystem with an average depth of 3.8 m whereby the shipping channel connecting Szczecin and Świnoujście was deepened to 14.5 m. The shallowness of the lagoons leads to frequent mixing of the total water column. This results in no monitored occurrence of hypoxia (minimum O_2 concentration between 2011 and 2021 is 237 µmol L^{-1}) and maximum surface water temperatures of 24°C. In addition to the Oder entering the Lagoon in the South, several smaller rivers flow into the Small Lagoon of which Zarow and Uecker on the German side are the biggest. Due to the high freshwater inflow from the rivers and the limited exchange with the Baltic Sea, the water of the lagoon has a salinity of ~ 1.6 (median of 231 measurements, LUNG monitoring data). The river water transports large amounts of nutrients into the Lagoon (in 2021: 44393 tons total N and 1540 tons total P from the Oder) resulting in severe eutrophication of the ecosystem, which is visible in the generally low water transparency (Secchi depth between 0.1 and 2 m in the years 2011 to 2021, LUNG monitoring data). The eutrophic status is further facilitated by a long water residence time of 1-2 months (Mohrholz & Lass 1998, Grelowski et al. 2000, Friedland et al. 2019) and a limited water exchange. 54% of the bottom area are

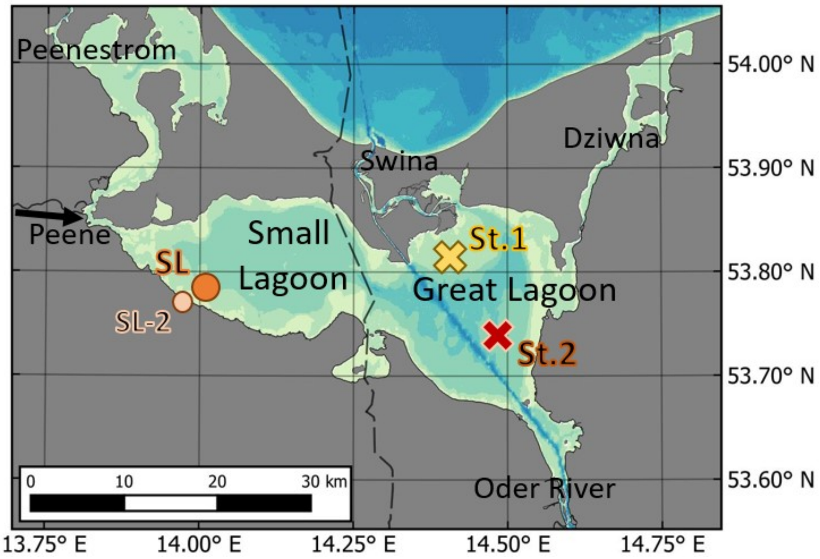

Figure 4. Map of the Szczecin Lagoon with inlet Oder River and outlets. The sampling locations are marked: orange circle for station SL (light colour for land-based sampling) and yellow and red cross for benthic stations St.1 and St.2.

covered by fine sediments (silt, silty sand), mostly deeper areas below 3.5 m (Osadczuk & Wawrzyniak-Wydrowska 1998).

B - Greifswalder Bodden

Along the German coastline, the Greifswalder Bodden (510 km^2) (Fig. 5) is the biggest Bodden, whereby the term Bodden describes a shallow marginal water in old North German dialect. It is on average 5.8 m deep, resulting in frequent wind-induced mixing of the entire water column and no pronounced stratification. But still, in summer, the surface water can reach temperatures of 23°C (2011-2021, LUNG monitoring data). On average, the O_2 concentration is 324 µmol L^{-1}, but can drop to 192 µmol L^{-1} when the mixing of the water column is weak (2011-2021, LUNG monitoring data). The salinity fluctuates between 5.7 and 9.1 in the years 2022 to 2021 with an average of 7.5 (2011-2021, LUNG monitoring data). The Greifswalder Bodden is connected with the Szczecin Lagoon via the 30 km long Peenestrom (Fig. 5). In contrast to the Lagoon, the freshwater entry only accounts for 0.3% of the total inflow (Schiewer 2008). Beside the wind-driven transport from the Strelasund in the west, exchange processes with the Pomeranian Bay in the east dominate transport over a broad but shallow sill (water depth ≥ 2 m). Due to intensive exchange with the Baltic Sea, abiotic factors like salinity, temperature and oxygen are almost identical in the Greifswalder Bodden and Pomeranian Bay. However, similar to the Lagoon, the Bodden is strongly eutrophied even though the input of nutrient was reduced over the last decades. The eutrophic status is visible in Secchi depths ranging from 0.6 to 4.5 m (2011-2021, LUNG monitoring data). Nutrients from the Oder and Peene reach the Bodden only when SE or E winds prevail, hence diffuse nutrient sources from land and the sediment are

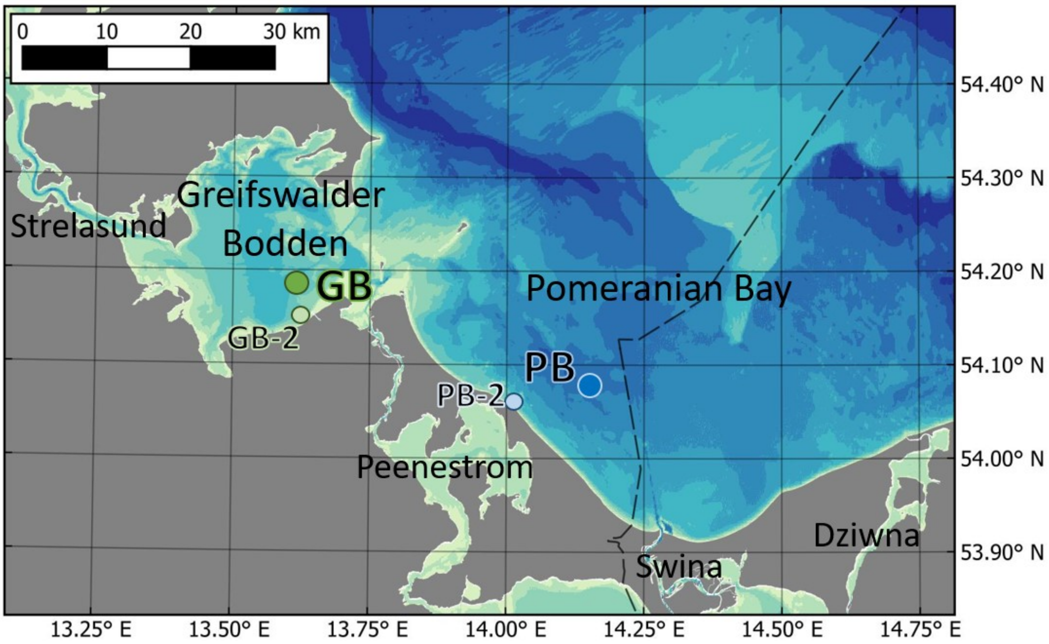

Figure 5. Map of the Pomeranian Bay and Greifswalder Bodden. BluEs sampling locations are marked: green circle for Greifswalder Bodden and Blue circle for Pomeranian Bay (lighter colour for land-based sampling)

probably responsible for the majority of the nutrient input. In the eastern part of the Bodden, sandy sediments are prevalent while in the western parts muddy sediments can be found, resulting from increasing eutrophication (Schiewer 2008).

C - The Pomeranian Bay

The Pomeranian Bay connects the Arkona Sea in the North-West to the Bornholm-Basin in the North-East (Fig. 3). To the south, the Pomeranian Bay is surrounded by the German and Polish coastline (Fig. 5). Overall, it covers 5500 km^2 and is, on average, 13.2 m deep with mostly sandy sediments covering the bottom. Due to its open coastal structure, the WRT of 8-10 days is rather low compared to GB and SL (Mohrholz & Lass 1998) and wind-induced transport is the main dynamical process. The salinity ranges between 6 and 8 (median of 215 measurements from LUNG monitoring), typical for that part of the Baltic Sea. The water column is well oxygenated throughout the year but periods with low winds and high temperatures can lead to stratification and hypoxia in the bottom water, especially near the coast (Pastuszak et al. 2003, Leibniz Insitute for Baltic Sea Reasearch Warnemünde 2023). 89.5% of the freshwater input and the majority of the nutrient input originate from SL via the Swina but frequently the river plume, characterised of low-salinity, low oxygen and nutrient rich water, flows eastwards along the polish coast during the prevailing W/SW winds (Pastuszak et al. 1996, 2003, Mohrholz & Lass 1998). During easterly winds, river waters flows westwards along the coast of Usedom and due to Ekman offshore currents (due to the Coriolis effect, sea water moves at a 90° angle from the direction of the winds on the sea surface) upwelling can occur (Pastuszak et al. 2003). The discharge of nutrients and organic matter from the Oder is varying between seasons and years and has a pulsating nature, depending on the hydrological and meteorological situation in the Lagoon and the Bay (Pastuszak et al. 1996). Additionally, eutrophic waters from the Greifswalder Bodden can influence the western part of the Pomeranian Bay (Pastuszak et al. 1996). This can lead to reduced water transparency (minimum Secchi depth of 1.2 m) which increases again in the winter months (maximum Secchi depth of 7 m).

2.2 Sampling of water and sediment

In the three areas, one station each was selected for water column and sediment sampling and the Chamber Lander deployment: SL in the Small Lagoon (4 m deep, 53.782983° N 14.010500° E), GB in the Greifswalder Bodden (8 m deep, 54.185252° N 13.607864° E) and PB in the Pomeranian Bay (13 m deep, 54.076972° N 14.143947° E). In addition, benthic NO_3^- reduction processes were characterised by Mindaugas Zilius at two stations in the Great Lagoon (St. 1 – 2.5 m depth, 53.816389° N 14.403611° E; St. 2 – 5 m depth, 53.742222° N 14.479167° E) (Fig. 3). All stations represent contrasting sites in terms of eutrophication and residence time.

In 2021 and 2022, several field campaigns covering all seasons took place (Tab. 1). The table of the precise dates can be found in the supplements. A small catamaran (*RV Klaashahn,* length 7.5 m, width 2.55 m) was used to sample stations SL and GB, while PB was sampled from the *RV Elisabeth Mann Borgese*. The benthic stations St.1 and St.2 were also sampled from a small boat. Abiotic variables across the water column of SL and GB were obtained using a Sea & Sun CTD system equipped with sensors for temperature, salinity, pressure and dissolved oxygen concentration. In PB, abiotic measurements of the water column were done with a Seabird CTD system, equipped with sensors for temperature, salinity, dissolved oxygen concentration, fluorescence (Chl *a* proxy), turbidity and PAR. PAR intensities in the surface and bottom water of SL and GB were measured with a spherical underwater quantum sensor (LI-COR, USA) No abiotic data are available from the benthic stations St.1 and St.2. Due to bad weather conditions, all sampling in February 2022 and sampling of GB in August 2021 was conducted from land, using the closest onshore sampling location to the original stations: the pier in Koserow (PB-2) and Lubmin (GB-2) and the jetty in Mönkebude (SL-2). During those "manual" sampling campaign, abiotic variables were measured using a HACH multimeter equipped with dissolved oxygen, pH, temperature, and conductivity sensors, with precisions of ± 6 µmol L^{-1}, ± 0.02, ± 0.3°C and ± 0.1, respectively. At each station, water samples were taken at the surface and the bottom of the water column (in February 2022 and August 2021 in GB only surface samples were taken). For logistical reasons the water was stored in canisters (in the dark, temperature-isolated, approx. three hours) until further processing in the lab. If remineralisation processes take place during the three-hour period, nutrient concentrations may be overestimated, while PON and POC concentrations may be underestimated. Usually, samples from SL and GB were processed in a lab of the University of Greifswald and PB samples on board of the research vessel (exceptions see supplements, Table S2).

Sediment cores for pore water analysis were collected when sampling was conducted by the catamaran and *RV Elisabeth Mann Borgese*. Using the Frahm Lot (MacArtney Germany GmbH), an instrument specifically designed for collecting cores from muddy sediments, cores of 20 – 30 cm length were taken at SL and GB. Sediment at OB had a higher sand content hence, cores were collected using a HAPS corer with a vibration unit (KC Denmark). Vibrations drive the core liner in the sediment, producing 10 – 20 cm long cores. Pore water samples were then taken from the cores through predrilled holes in the acrylic core liners by inserting rhizons (Rhizosphere Research Products B.V., Netherlands) into the sediment as described by Seeberg-Elverfeldt et al. (2005). Rhizons were inserted at 1 – 2 cm intervals for the top 10 cm of the core, increasing intervals with depth (up to 10 cm between insertions). As the tip of the rhizon, which enters the sediment horizontally, consists of a 5 cm long, porous membrane, the water is already filtered and can be collected in a tube. After disposing of the first millilitre sampled water (rinse by-product), 2 mL filtered pore water was collected and frozen for later nutrient analysis.

Additionally, in summer 2022, nine intact sediment cores (inner diameter 8 cm, length 30 cm) were collected by Mindaugas Zilius, University Klaipeda (Lithuania), and colleagues using a hand corer at St. 1 and 2 in the Great Lagoon (coordinates see above). St. 1 has sandy sediments and St. 2 has muddy sediments. Bottom water temperature was 22.5°C. In addition, 170 L of bottom water were collected for core transport and incubation in the laboratory.

Wind data were provided by the German Meteorological Service (DWD – Deutscher Wetterdienst). The daily average of the mean wind speed at a height of approximately 10 m (in m s^{-1}) was analysed for the station Ueckermünde (ID 5142).

2.3 Sample Analysis and Rate Determination

The water was filtered through precombusted (450°C, 3 h) glass fibre filters (GF/F, Whatman) prior to the determination of nutrients. The filters were used for the determination of particulate organic nitrogen (PON), particulate organic carbon (POC) and chlorophyll *a* concentrations (Chl *a*).

Nutrient concentrations (NH_4^+, NO_3^-, PO_4^{3-}) were measured on a continuous segmented flow analyser (QuAAtro, Seal Analytical) according to the methods of Grasshoff et al. (1999) (detection limits of 0.5, 0.2 and 0.1 µmol L^{-1}, respectively). If the concentrations were below the limit of detection (LOD), values of 0.5 * LOD were used for statistical analysis (USEPA 2000).

Filters for PON and POC determination (served also as t_0 values for uptake rates) were dried at 60°C, packed into tin caps, pressed into pellets and put in an elemental analyser (Isolink CN, Thermo Scientific), which uses a flash combustion at 1800°C. The instrument had been calibrated before each sample run with acetanilide (Merck) for both C and N analysis and an internal standard (peptone, Merck) was run after every fifth sample.

Chlorophyll *a* filters were left for extraction with 10 mL of 90% ethanol for 3 hours, followed by fluorometric measurement at 670 nm wave length using a Turner fluorometer (TURNER 10-AU-005, Turner Designs, USA) and a correction for phaeopigments (detection limit: 0.009 mg m^{-3}, accuracy: ± 3%) (Wasmund et al. 2006).

Nutrient and Chl *a* concentrations are compared to long-term monitoring data obtained by the LUNG (State Agency for the Environment, Nature Conservation and Geology, Mecklenburg–Western Pomerania). They collect samples monthly at stations along the coastline and acquire data on Secchi depth, temperature, oxygen levels, salinity and nutrient concentrations, following the guidelines of the European Water Framework Directive (LUNG 2016). For comparison to SL, GB and PB the LUNG stations OMMVKHM (53.83° N 14.10° E), OMMVGB19 (54.21° N 13.57° E) and OMMVO14 (54.11° N 14.12° E) were used. Average data of the variables listed above have been calculated for the period 2011 to 2021 to check that the data obtained in this study are within the range of the standard deviation of the 10-year median of the monitoring data.

Nutrient uptake and net primary production (determined as dissolved inorganic carbon (DIC) uptake) rates were determined in triplicate, for both surface and bottom water samples, using ^{15}N and ^{13}C tracer incubations after Dugdale & Wilkerson (1986). Transparent polycarbonate bottles were filled with 1 L of the water sample (with headspace). 10% of the ambient nitrogen and 1% of the ambient carbon concentration were added to the bottles in the form of $^{15}N–NH_4^+$, $^{15}N–NO_3^-$ and $^{13}C–HCO_3$ (98 atom% ^{15}N and ^{13}C, Sigma-Aldrich, Merck). This equals additions of 0.05 to 0.1 µmol L^{-1} of $^{15}N-NH_4^+$, 0.05 to 4 µmol L^{-1} of $^{15}N-NO_3^-$ and 17 to 40 µmol L^{-1} of $^{13}C–HCO_3$, depending on the ambient concentrations. The bottles with samples from PB were incubated at ambient light and temperature conditions (according to the conditions on the sampling spot) for 2 - 3 hours in on-deck incubators. Bottles with samples from SL and GB were incubated in lab-incubators which emitted 37 - 40 µmol photons m^{-2} s^{-1}. Further details on the two incubators can be found in the supplements. Ambient light ratios (based on PAR measurements) between surface and bottom water were recreated using light-screening with different light absorption intensities. The incubation was terminated by filtering the bottles through precombusted glass fibre filters (GF/F, Whatman) and freezing the filters (-20°C) until analysis. The ^{15}N and ^{13}C were measured following the same protocol as for the PON and POC filters (see above), where the elemental analyser was coupled to an IRMS (Isotope ratio mass spectrometer, Delta V advantage, Thermo Scientific) via a Conflo IV interface (Thermo Scientific). The delta values $\delta^{15}N$ and $\delta^{13}C$ are reported relative to atmospheric N_2 gas and Vienna PeeDee Belemnite (VPDB), respectively. The following reference materials were used: IAEA-N1, IAEA-N2, IAEA-N3, NBS 22, IAEA-CH-3 and IAEA-CH-6. Again, acetanilid was used for calibration and peptone served as an internal standard (run after every fifth sample). For both stable isotopes, the analytical precision was below ± 0.2‰ in samples with $\delta^{15}N$ or $\delta^{13}C$ values of up to 250‰ and ± 10‰ in samples with $\delta^{15}N$ or $\delta^{13}C$ values > 250‰.

To calculate the N and C uptake rates, the labelled excess concentration has to be calculated first (after Dugdale & Wilkerson 1986).

$$\text{(Eq. 1)} \quad {}^{15}N \; or \; {}^{13}C_{\;excess} = {}^{15}N \; or \; {}^{13}C_{\;sample} - F$$

${}^{15}N$ *or* ${}^{13}C_{excess}$ describes the difference between the natural ^{15}N value of PON or ^{13}C value of POC (*F*) and the ^{15}N-PON or ^{13}C-POC value of the sample after the incubation (${}^{15}N$ *or* ${}^{13}C_{sample}$) in atom percent (at%).

Subsequently, the specific uptake rate V (h^{-1}) is calculated differently for N and C uptake.

The specific N uptake rates are calculated as follows (Dugdale & Wilkerson 1986):

$$\text{(Eq. 2)} \quad V = \frac{{}^{15}N_{\;excess}}{({}^{15}N_{\;enrichment} - {}^{15}N_{\;sample})*t}$$

where ${}^{15}N_{enrichment}$ is the ^{15}N content in the initially labelled fraction (NH_4^+, NO_3^-), ${}^{15}N_{sample}$ is the ^{15}N value of the incubated sample (in at%) and t is the incubation time (in hours). In the case of NO_3^- and NH_4^+ uptake rates, V is calculated as the mean (V_m) of V_t and V_0, where V_t is based on the ^{15}N signal of PON at the end of the incubation and V_0 is based on the ^{15}N signal at the start of the incubation. As mentioned above, each incubation was performed in triplicate. Taking the mean of V_t and V_0 reduces the possibility of over- or underestimating uptake rates (Dugdale & Wilkerson 1986).

The specific C uptake rates are calculated as follows (Slawyk et al. 1977, Slawyk 1979):

$$\text{(Eq. 3)} \quad V = \frac{{}^{13}C_{\;excess} \;/t}{{}^{13}C_{\;enrichment} - {}^{13}C_{\;excess}}$$

Finally, V of N and C uptake is multiplied by the PON or POC concentration to obtain the transport rate ρ (nmol L^{-1} h^{-1}), whereby ρ_N uses the mean (PON_m) of PON concentrations before and after the incubation (n = 3), and ρ_C uses the natural POC concentration before the incubation (PON_0):

$$\text{(Eq. 4)} \quad \rho_N = V_m \; * PON_m$$

$$\text{(Eq. 5)} \quad \rho_C = V \; * PON_0$$

Nitrification rates (NR) were determined in triplicate using the stable isotope ^{15}N-NH_4^+ as a tracer (Ward 2005, Damashek et al. 2016, Bartl et al. 2018, Kache et al. 2021). To obtain in situ NR, a maximum addition of 10% of the ambient NH_4^+ concentration or a minimum of 0.05 µmol L^{-1} was added when nutrient concentrations were at the detection limit (Ward 2011). Transparent polycarbonate bottles (total volume: 315 mL) were completely filled using the overflow technique and sealed with an airtight butyl rubber septum. The tracer, in the form of $^{15}N\text{-}NH_4Cl$, was added to the sample through the septum using a syringe. The bottles were incubated, according to the method, in the dark at in situ temperature and additionally at ambient light conditions. Three bottles, used as t_0, were filtered immediately after tracer addition. The incubation time for the remaining bottles was 6 to 20 hours and was terminated by filtering the samples through precombusted glass fibre filters (GF/F, Whatman) and the filtrate was frozen at -20°C until further analysis (t_{end} samples). The ^{15}N content in the produced NO_2^- and NO_3^- was measured according to the denitrifier method (Sigman et al. 2001, Casciotti et al. 2002) using the denitrifying bacterium *Pseudomonas chlororaphis*, cultivated as described by Weigand et al. (2016). The isotopic value of the sample was then analysed in an IRMS (Delta V advantage, Thermo Scientific) after purification in a GasBench II system (Thermo Scientific). Internal standards (IAEA-N3 and USGS-34) were measured alongside the samples. The precision of the measurements was ± 0.16‰.

The NR were calculated according to Veuger et al. (2013). First, the excess concentration of ^{15}N in the product NO_{2+3}^- is calculated, where $^{15}N_{end}$ and $^{15}N_{t0}$ are the $\delta_{15}N$ values of t_{end} and t_0 samples, and $[NO_{2+3}^-]$ is the sum of the NO_2^- and NO_3^- concentrations.

$$\text{(Eq. 6)}\ {}^{15}N_{excess} = \frac{{}^{15}N_{end} - {}^{15}N_{t0}}{100} * \left[NO_{3+2}^-\right]$$

The NR is calculated as follows:

$$\text{(Eq. 7) NR} = \frac{{}^{15}N_{excess} * \frac{[NH_4^+]_{total}}{[{}^{15}N - NH_4^+]_{added}}}{\Delta t}$$

Where $[NH_4^+]_{total}$ is the sum of in situ and added NH_4^+ concentrations, $[{}^{15}N\text{-}NH_4^+]_{added}$ is the concentration of added NH_4^+ and Δt is the incubation time in hours. As hourly NR showed no significant difference between light and dark incubation (Fig. 15, further information see chapter 4.4), daily NR were calculated by multiplying the NR with 24 hours. NR includes both ammonium and nitrite oxidation, as the ^{15}N content of NO_2^- and NO_3^- was measured simultaneously.

The rate detection limits (RDL) were calculated individually for each uptake rate and day as a 0.4 or 20‰ increase in the target pool (PON, POC) from the initial value. The increase is twice the precision of the measurement (Santoro et al. 2013), which was ± 0.2‰ for samples with $\delta^{15}N$ or $\delta^{13}C$ values < 250‰ and ± 10‰ for samples with $\delta^{15}N$ or $\delta^{13}C$ values > 250‰. This increase corresponds to the excess concentration (see equation 1) and can therefore be used in the subsequent calculations of N and C uptake rates. The RDL for NH_4^+ uptake rates, NO_3^- uptake rates and PP ranged from 0.03 – 22.18, 0.004 – 6.11 and 1.9 – 134.62 nmol L^{-1} h^{-1}, respectively. For NR, instead of fixed values, the standard deviation of the IAEA standards run with each batch of measurements (n = 25 NR samples + 14 standards) was used. It varied between 0.06 and 0.53‰ (Ø = 1.63‰). They are then used to calculate the excess concentration according to equation 6, where $^{15}N_{end}$ is set to zero and $^{15}N_{t1}$ is the IAEA standard deviation. The RDL for NR ranged from 0.001 – 2.73 nmol L^{-1} h^{-1}. All RDLs depend on the substrate pool and therefore differ between stations and sampling days. Rates below the RDL were set to zero before the extrapolation to daily rates.

Surface and bottom water samples were used to integrate all uptake and nitrification rates over the depth of the total water column using the trapezoid integration.

Benthic NO_3^- reduction rates by denitrification and DNRA were measured by Mindaugas Zilius using the revised isotope pairing technique (r-IPT, Risgaard-Petersen et al. 2003). This technique allows the separation of denitrification and DNRA processes of NO_3^- diffusing into anoxic sediments from the overlying water column (D_w and $DNRA_w$, respectively), as well as the coupling of denitrification and ammonification with nitrification (D_n and $DNRA_n$, respectively) (Bonaglia et al. 2014). Briefly, $^{15}N\text{-}NO_3^-$, added to the water above the sediment, diffuses into the sediment and leads to the production of $^{15}N\text{-}N_2$ (via denitrification or anammox) and $^{15}N\text{-}NH_4^+$ (via DNRA), which can be determined despite high background concentrations of N_2. All retrieved cores were spiked with $^{15}NO_3^-$ tracer (20 mmol L^{-1} $Na^{15}NO_3$, 98 atom% ^{15}N, Sigma Aldrich) in triplicates to a final concentration of approximately 5, 15 and 25 µmol L^{-1}. The different $^{15}NO_3^-$ concentrations were used to validate the IPT assumptions. The cores were then capped and incubated in the dark for 3 – 7 hours as described by Zilius et al. (2022). At the end of the incubation period, the water and sediment were gently mixed to form a slurry. 20 mL aliquots of the slurry were then transferred to 12 mL exetainers (Labco Ltd) and fixed with 200 µL of 7 M $ZnCl_2$ for later $^{29}N_2$ and $^{30}N_2$ analyses. An additional 40 mL subsample was collected, transferred to 50 mL falcon vials and treated with 2 g KCl for determination of the exchangeable NH_4^+ pool and the $^{15}NH_4^+$ fraction. Samples for $^{29}N_2$ and $^{30}N_2$ production were analysed by gas chromatography-isotopic ratio mass spectrometry (GC-IRMS, Thermo Delta V Plus, Thermo Scientific) at the University of Southern Denmark following the protocol described by De Brabandere et al. (2015). Samples for $^{15}NH_4^+$ production were analysed by the same GC-IRMS after conversion of NH_4^+ to N_2 by the addition of an alkaline hypobromite reagent (Warembourg 1993). Denitrification and DNRA rates were calculated according to the r-IPT (Risgaard-Petersen et al. 2003) and extrapolated to daily rates by multiplying with 24.

2.4 Water Residence Time

The WRT was estimated by Johannes Pein (Hereon, Geesthacht) as part of the project 'Blue Estuaries'.

To estimate the residence time, drift experiments with Langrian particles are used, which based on the flow fields of a hydrodynamic simulation of the Oder river basin with the Semi-implicit Cross-scale Hydroscience Integrated System Model (SCHISM). SCHISM solves the Reynolds-averaged Navier-Stokes equations on an unstructured grid allowing a variable spatial resolution (Zhang et al. 2016). Here, the shallow water areas were resolved at about 250 m, the channels between the Szczecin Lagoon and the Baltic Sea at about 50 m, and the Pomeranian Bay at about 300 m. At the open edge in the Baltic Sea, the resolution is 2 km. Here, the model was driven by reanalysis data from the DMI model (available for download at CMEMS), which contains daily salinity, temperature and current fields as well as water levels. The atmospheric forcing is based on hourly reanalysis data from the DWD, and the discharges of the Oder River and smaller tributaries are from the responsible state authorities. For details on the model configuration and validation, see Pein & Staneva (2024). For the purpose of this study, the model was integrated for 15 months from 1. October 2020 and hourly water levels and 3D flow fields were stored. Based on this dataset, virtual particles were initialised in the areas of Greifswalder Bodden and Szczecin Lagoon on a 500 m x 500 m grid at a water depth of two metres. The particles were then advected by the current with an assumed neutral gravity. For each time step, the number of particles still present in the initial area was determined. The residence time was defined as the time when 67% of the particles had left the initial area (Liu et al. 2011). This process was carried out for the months of January to September 2021, with particles being tracked for up to 180 days.

2.5 Transport Model

The transport of solutes and particles was also estimated by Johannes Pein (Hereon, Geesthacht) as part of the project 'Blue Estuaries'.

For the estimation of nutrient fluxes between the Szczecin Lagoon and the Pomeranian Bay, the model simulation was carried out in the coupled hydrodynamics-ecosystem dynamics mode. The model framework SCHISM-FABM-ECOSMO was applied, which has already been used to study the nitrogen turnover in the Elbe estuary (Pein et al. 2021). In preparation for the coupled simulations, discharge and nutrient loads of the Oder River and smaller tributaries were requested and compiled. In addition to the framework conditions mentioned in the previous section, nutrient fields, dissolved oxygen and planktonic biomass concentrations from hindcast simulations with the ECOSMO model (Daewel & Schrum 2013, 2017) were processed for ecological forcing. The coupled model simulation was initially integrated for a one-year spin-up period from 1. January 2012 and then re-run for two years after the hot start (for details see Pein & Staneva (2024)). During the model run, volume fluxes and nutrient transports were stored perpendicular to predefined transects at the 120 s time step level.

2.6 Lander incubations

A Mini Chamber Lander System (Unisense, Denmark) was deployed at stations SL, GB and PB (not at benthic stations St. 1 and St. 2) to measure in situ benthic nutrient and oxygen fluxes across the sediment-water interface for around 4 h at SL and GB, and 6 - 7 h at PB. For logistical reasons only one deployment per station was possible. A detailed description of the Lander design can be found in Thoms et al. (2018). Briefly, a Teflon-coated metal chamber (30 x 30 x 35 cm) penetrates the sediment to a depth of about 3 - 5 cm, resulting in an incubated water volume of ~ 23 L. In contrast to smaller chambers or core incubations, larger chambers have a lower inaccuracy for O_2 uptake measurements (Glud & Blackburn 2002). The chamber lid closed automatically after the lander was placed on the sediment surface. The water inside the chamber was then stirred at 10 rpm by a cross shaped stirrer attached to the lid to ensure homogeneous samples (minimum 5 min stirring, Thoms et al. 2018). Nutrient fluxes over the 900 cm^2 sediment area were calculated from the change in nutrient concentrations in the incubated water volume within the chamber. 12 nutrient samples were taken from the chamber with 60 mL syringes at pre-determined times (a small valve in the chamber lid equalised the pressure), filtered through syringe GF filters and subsequently analysed as described above (Sample analyses section). NO_2^- fluxes were negligible and are not shown here. Oxygen concentrations in the chamber were monitored with an AADI Oxygen Optode 4835 (Aanderaa). The change in O_2 and nutrient concentrations over time and incubation area was used to calculate oxygen and nutrient fluxes, which were extrapolated to a daily rate (in mmol m^{-2} d^{-1}). The calculation (Eq. 8) requires the slope of the regression of nutrient concentrations against time (positive slope for nutrient efflux and negative slope for nutrient influx) and the depth of penetration of the chamber into the sediment.

$$\text{(Eq. 8)} \quad F = \frac{slope * (chamber\ volume)}{chamber\ area}$$

The chamber area is 0.09 m^2 and the chamber volume is the product of the edge length minus the penetration depth (z_P).

$$\text{(Eq. 9)} \quad V(chamber) = 0{,}3 * 0{,}3 * (0{,}35 - z_P)$$

2.7 Pore water fluxes

The nutrient pore water profiles were used to calculate diffusive fluxes according to Fick's first law of diffusion (Eq. 10), as presented in Schulz & Zabel (2006), which states that a solute flux is proportional to the concentration gradient, i.e. a substance diffuses from an area of high concentration to an area of low concentration.

$$\text{(Eq. 10)} \quad J = -D_s \frac{c_1 - c_0}{z_1 - z_0}$$

J is the flux of the respective nutrient in mmol m^{-2} d^{-1}, D_s is the diffusion coefficient for the respective nutrient, c is the nutrient concentration in the pore water at a certain sampling depth (z). Since depth z is defined as negative, a positive flux is equivalent to a flux from the sediment into the overlying water. If oscillation of the pore water nutrient profile is strong, a 1-2-1 filter was applied to the data to obtain a stable profile. The diffusion coefficient was calculated for each measured nutrient (Eq. 11), taking into account the temperature at the time of sampling and the porosity of the sampled sediment.

$$\text{(Eq. 11)} \quad D_s = \frac{D_0}{1 - \ln(\Phi^2)}$$

D_0 is the diffusion coefficient in free solution for seawater at the respective in situ temperature (Schulz 2006) and Φ is the porosity for fine (SL and GB) and coarse sediments (PB) according to Forster et al. (2003).

2.8 Statistical analysis

Statistical analyses were performed using the software 'SigmaPlot 13'.

Normal distribution was tested using the Shapiro-Wilk test. Correlation analyses were performed using the Spearman Rank Oder analysis. In order to determine the factors influencing N turnover rates, correlation analyses were performed separately for each station and for all stations combined. To determine whether two groups were significantly different from each other, a t-test was used if the data were normally distributed. If the data were not normally distributed, the Mann-Whitney Rank Sum Test was applied to compare two groups of data. Comparisons between three or more groups were done with an analysis of variance (ANOVA) if the data were normally distributed. If the data were not normally distributed, an ANOVA on ranks was performed (Kruskal-Wallis Test). In the case of significant differences between groups, Post-Hoc tests for pairwise comparisons were applied to identify which groups correlated with each other. ANOVA and ANOVA on Ranks were used to assess the variability between the three stations for each variable.

3. Results

3.1 Environmental conditions

The Szczecin Lagoon exhibited the anticipated lower salinity levels, indicating an oligohaline environment (≤ 2 PSU), which is in contrast to the Greifswalder Bodden and Pomeranian Bay (Fig. 6), which are typically characterised by mesohaline conditions (8 PSU). The stations displayed no significant differences in temperature ranges (t-test, n = 9, p = 0.754), but the PB station showed a higher range of values (Table 1). Due to the high turbidity in SL, visible in the low Secchi depths (Fig. 6), a large portion of the water column is seasonally aphotic. During our sampling campaigns, the water at SL and GB was always fully oxygenated due elevated wind speed on the day of sampling or the two previous days. The same can be found for the PB, except for summer when the CTD profile showed enhanced stratification, leading to the lowest O_2 saturation measured during all sampling campaigns of 52%.

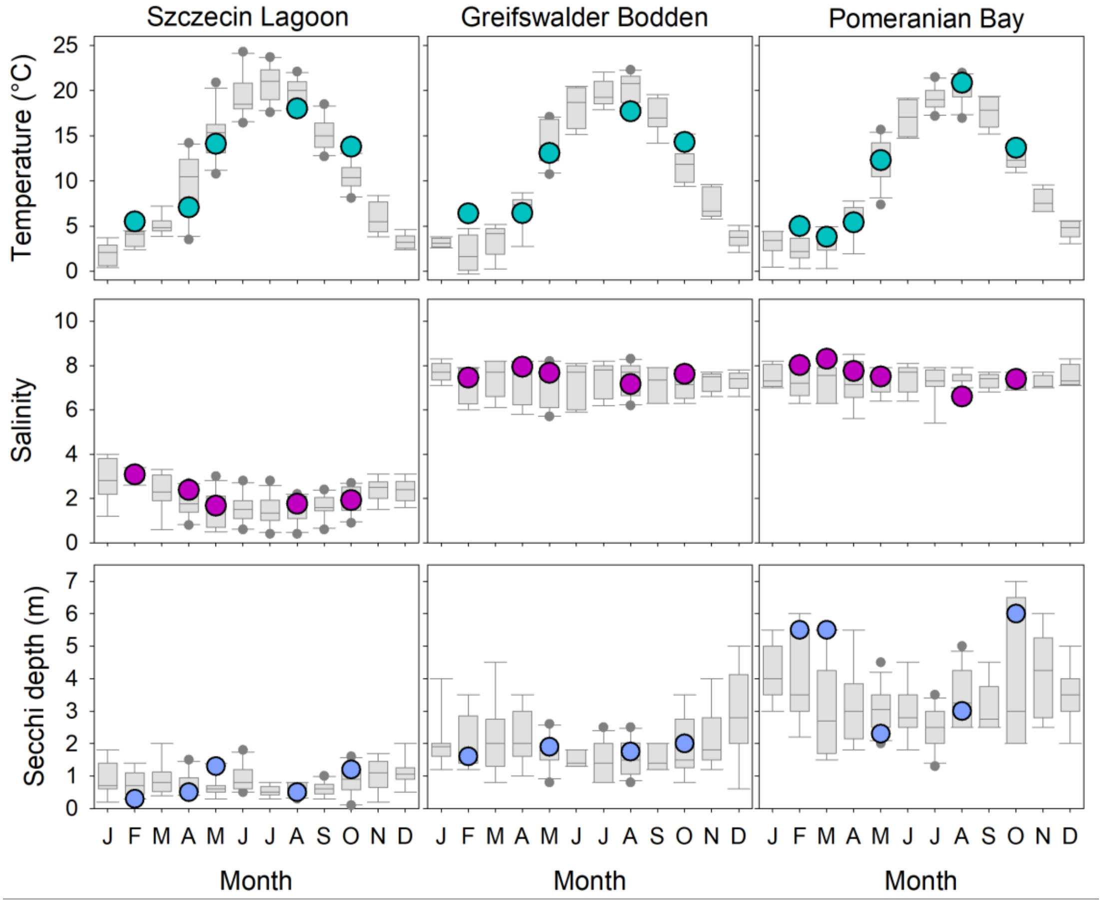

Figure 6. Temperature (in °C, turquoise), salinity (purple) and Secchi depth (in m, light blue) in the surface water from the sampling campaigns (coloured circles) of the Szczecin Lagoon (left panels), the Greifswalder Bodden (middle panels) and the Pomeranian Bay (right panels). Box-whisker plots show LUNG monitoring data (2011-2021) with median, lower and upper quartiles, extremes and outliers. Because the Secchi depth was not measured as part of this study, the coloured symbols in the lower panels show LUNG monitoring data of the months in which my sampling campaigns took place.

Table 1: Sampling dates and range of environmental data from the whole water column and air during the sampling campaigns. Mean values in brackets.

Variables	**Szczecin Lagoon**	**Greifswalder Bodden**	**Pomeranian Bay**
Sampling campaigns	2021: May, August, October; 2022: February, April, August	2021: May, August, October; 2022: February, April	2021: May, August, October; 2022: February, March, April
Depth (m)	4	8	14
Salinity (PSU)	1.7 – 3.1 (2)	6.7 – 8 (7.5)	7.3 – 8.4 (7.8)
Temperature (°C)	5.5 – 22.7 (14.1)	6.4 – 17.7 (11.4)	3.9 – 20.1 (10)
Oxygen concentration (μmol L^{-1})	299 – 415 (351)	277 – 460 (353)	122 – 407 (308)
Oxygen saturation (%)	96 – 112 (96)	96 – 119 (98)	52 – 104 (97)
pH	8.1 – 8.7 (8.4)	8.2 – 8.7 (8.4)	8 – 8.6 (8.4)
Wind speed (m s^{-1})	2.1 – 5.1 (3.6)	4.3 – 11.1 (7.8)	3.1 – 9.6 (7.3)

3.2 Nutrient, chlorophyll *a* and POM concentrations

A comparison of bottom and surface nutrient concentrations was made to see if there were differences between these water depths. As illustrated in Fig. 7, the concentrations of NO_3^-, NH_4^+, PO_4^{3-} and PON did not differ between samples taken at the surface and at the bottom of the water column. This finding was statistically supported by the t-tests performed (surface vs. bottom for each variable listed above), which showed no significant differences. This matches with observations of the abiotic variables, where not stratification can be found, i.e. I suggest that the water column is well mixed. Consequently, no continuous separation of data from the surface and the bottom water will be made in the following chapters of the thesis, except when it serves a specific purpose, for example to illustrate the effect of light on process rates.

Dissolved inorganic N (DIN) concentrations are compared to long-term measurements from 2011 to 2021 from the LUNG. The nutrient concentrations of the BluEs sampling campaigns are, with few exceptions, within the range of the standard deviation of the

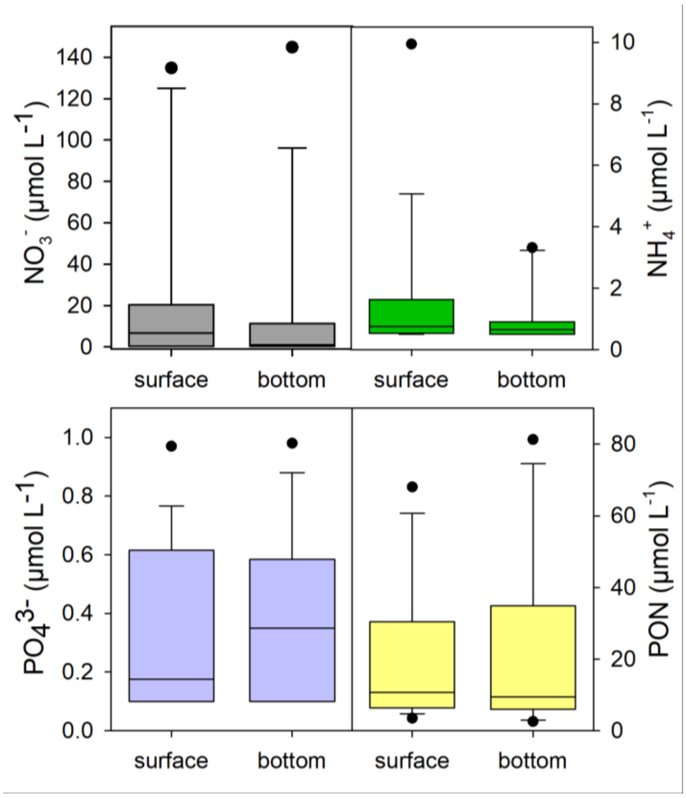

Figure 7. Nitrate (NO_3^-, top left panel, grey), ammonium (NH_4^+, top right panel, green), phosphate (PO_4^{3-}, bottom left panel, violet) and particulate organic nitrogen (PON, bottom right panel, yellow) concentrations (in µmol L^{-1}) of surface or bottom water column samples from all stations and sampling campaigns. Box-whisker plots show median, lower and upper quartiles, extremes and outliers.

11-year median of the monitoring data from 2011 to 2021 (Fig. 8 and 9). The nutrient concentrations are always highest in SL, followed by GB and lowest at PB. NH_4^+ concentrations in February (9.9 µmol L^{-1} in SL, 1.4 µmol L^{-1} in GB, 2.5 µmol L^{-1} in PB) decrease over the spring to barely detectable concentrations (around 0.5 µmol L^{-1}) in the summer at all stations. Only in June, a NH_4^+ peak is visible in the LUNG data of GB and especially in SL in several years (~ 9.1 µmol L^{-1} in SL, 0.8 µmol L^{-1} in GB). From September/October on, the LUNG data show increasing concentrations, reaching maximum values in November (15.1 ± 10.1 µmol L^{-1} in SL) and December (2.7 ± 1.4 µmol L^{-1} in GB, 2.3 ± 1.3 µmol L^{-1} in PB).

NO_3^- concentrations (Fig. 8) display a similar pattern to NH_4^+ concentrations and the highest values are measured at the beginning of the year: in March 77.7 ± 59.2 µmol L^{-1} in SL, and in February 20.8 ± 19.6 µmol L^{-1} in GB and 19.9 ± 13.5 µmol L^{-1} in PB. NO_3^- concentrations exceed the LUNG monitoring data in February (SL and GB) and April (SL) by up to 75% (Feb. in GB). After a decline in spring to values close to the detection limit, a slow increase starting in October leads to concentrations in December that are 20 – 40% of the highest annual values.

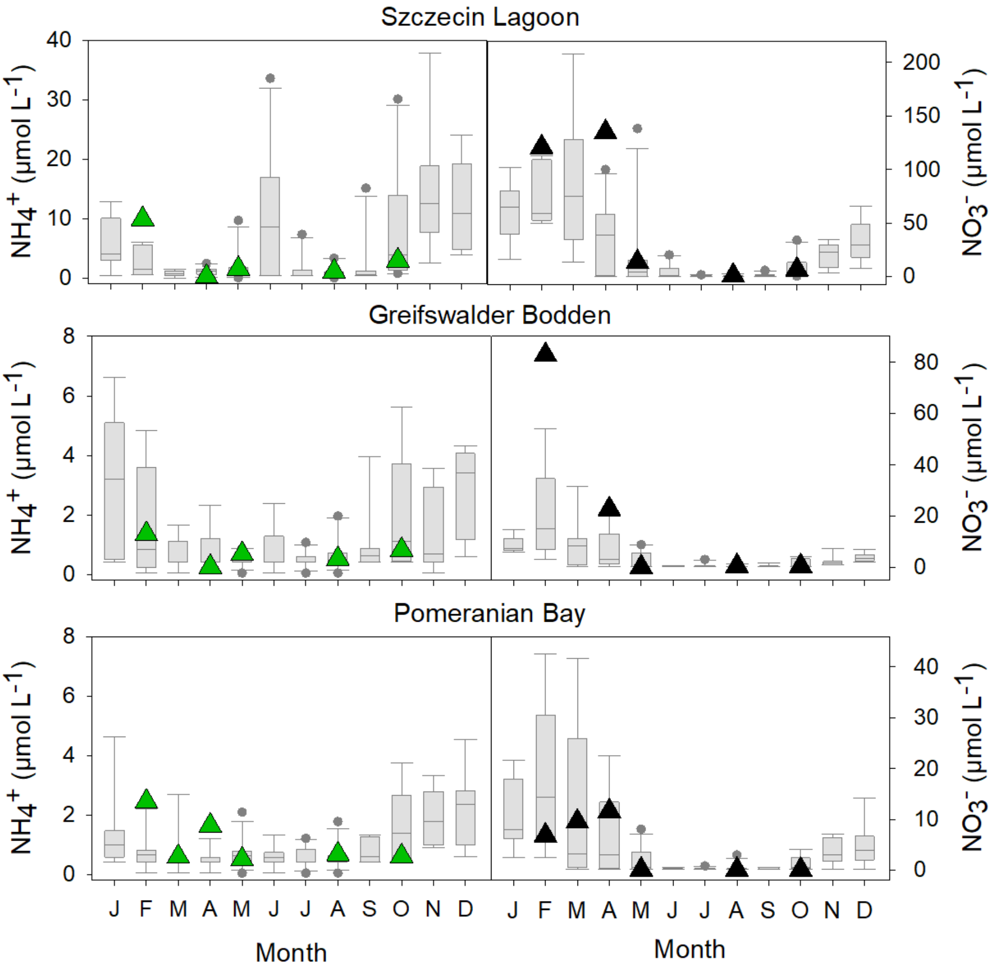

Figure 8. Ammonium (NH_4^+, green, left panels) and nitrate (NO_3^-, black, right panels) concentrations (µmol L^{-1}) from the sampling campaigns (triangles) in the surface water of the Szczecin Lagoon (top panels), the Greifswalder Bodden (middle panels) and the Pomeranian Bay (bottom panels) with axes covering different ranges. Box-whisker plots show LUNG monitoring data (2011-2021) with median, lower and upper quartiles, extremes and outliers.

Phosphate concentrations were consistently below 1 µmol L^{-1} and displayed different annual dynamics between stations (Fig. 9). In SL, the February concentration of 0.7 µmol L^{-1} declined to below the detection limit in April. According to the LUNG monitoring data, the annual concentration maximum occurs during the summer months. This was also observed in the present study, but the peak was rather small, with maximum PO_4^{3-} concentrations of 1 µmol L^{-1} in August. In the Bodden, phosphate was already depleted in February (not detectable between February and May) and started to increase again in August, reaching a maximum concentration of 0.7 µmol L^{-1} in October. In PB, the maximum PO_4^{3-} concentration in February (0.5 µmol L^{-1}) was followed by a decrease during the spring months. Concentrations were not detectable from April to August. In October, the concentrations increased again, a trend similar to the LUNG monitoring data.

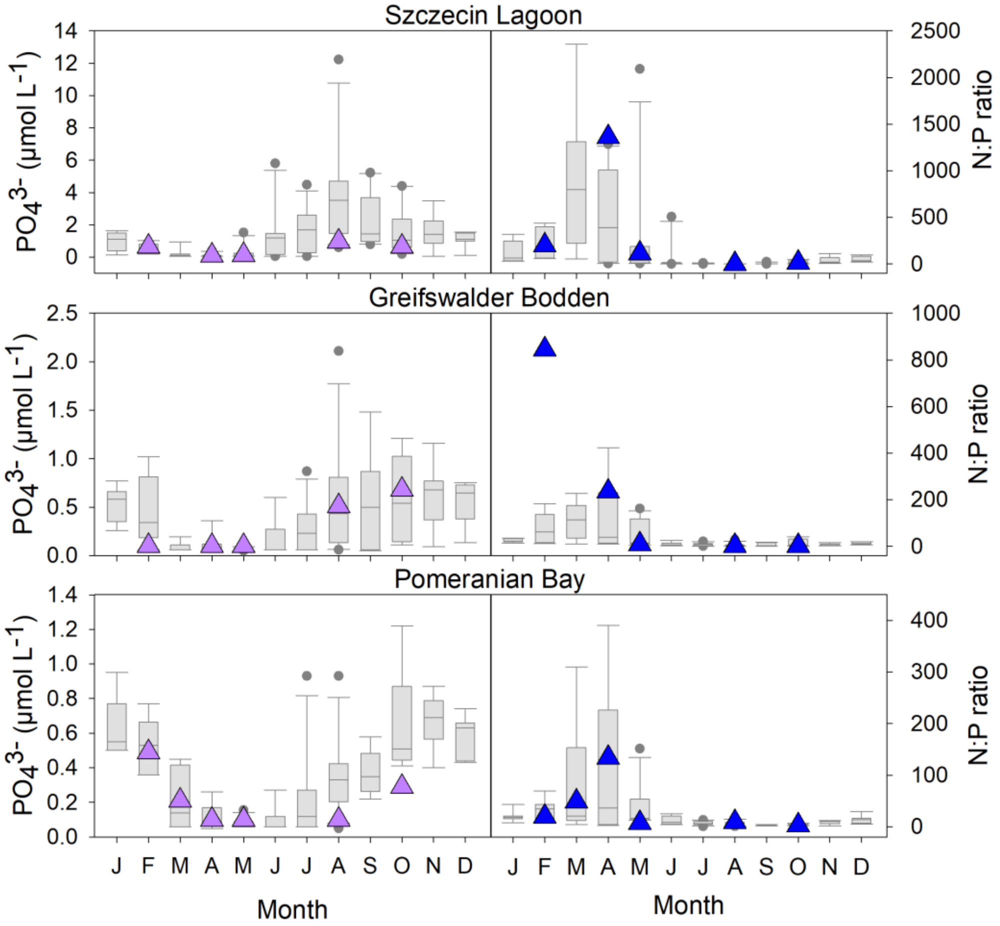

Figure 9. Phosphate concentrations (PO$_4^{3-}$, purple, left panels, in µmol L^{-1}) and ratio of DIN to PO$_4^{3-}$ (N:P ratio, blue, right panels) from the sampling campaigns (triangles) in the surface water of the Szczecin Lagoon (top panels), the Greifswalder Bodden (middle panels) and the Pomeranian Bay (bottom panels) with axes covering different ranges. Box-whisker plots show LUNG monitoring data (2011-2021) with median, lower and upper quartiles, extremes and outliers.

The ratio of DIN (NH_4^+ + NO_3^- + NO_2^-) to PO_4^{3-} (short N:P ratio) is an indicator for nutrient limitation (e.g. Turner 2002), whereby high ratios, usually above the Redfield ratio of 16:1, indicate P limitation and ratios below 16 indicate N limitation. The ratio thereby determines which species dominate the phytoplankton community (Conley 2000, Vrede et al. 2009). The biggest annual variation was determined in SL, with a difference of 1359 between April and August (Fig. 9). Overall, the highest ratios were determined in winter or spring, namely in February in GB (N:P of 845) and in April at stations SL (1362) and PB (134). Followed by a decline during the spring months, the N:P ratios were lowest in August (ranging between 1.3 and 9.3) and October (ranging between 2.1 and 15.3).

The majority of the chlorophyll *a* concentrations are below the median of the LUNG monitoring data, but remain within the range of the standard deviation of the 10-year median (Fig. 10). The Chl *a* concentrations measured here are highest in SL, and 4 to 8 times lower in GB and PB, respectively, reflecting the same gradient as observed for the nutrients.

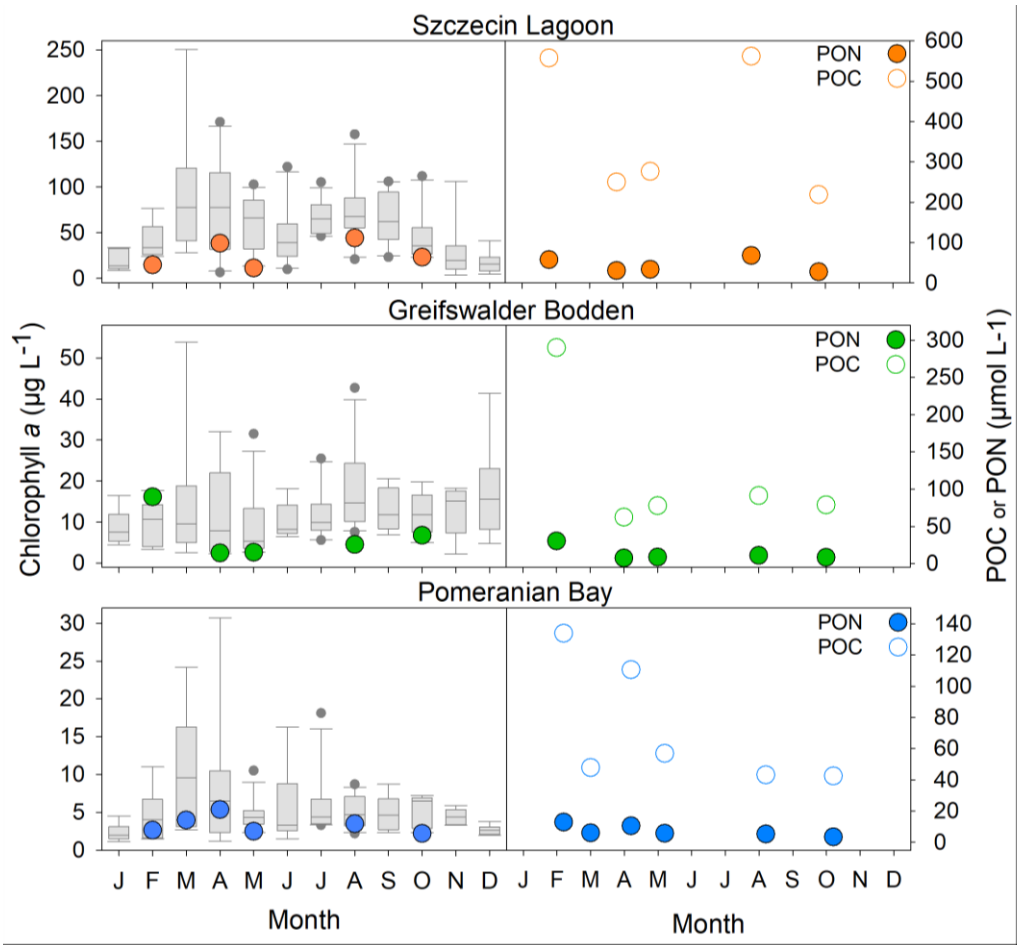

Figure 10. Chlorophyll *a* concentrations (in µg L^{-1}, left panels) and PON (closed symbols) and POC (open symbols) concentrations (in µmol L^{-1}, right panels) of surface water samples from the sampling campaigns (circles) in the Szczecin Lagoon (upper panel, orange), the Greifswalder Bodden (middle panel, green) and the Pomeranian Bay (lower panel, blue). Box-whisker plots show LUNG monitoring data (2011-2022) with median, lower and upper quartiles, extremes and outliers.

The highest concentrations were measured during spring at all stations (spring peak: 38.4 µg L^{-1} in SL, 16.2 µg L^{-1} in GB, 5.4 µg L^{-1} in PB) and again in summer in SL (44.2 µg L^{-1}) and PB (3.5 µg L^{-1}). A significant negative correlation (r^2 = -0.57 to -0.65, $p < 0.001$, n = 131-154) between the Chl *a* concentrations and the Secchi depth, a proxy for the light penetration depth, was found for all three stations (Fig. S1), implying that increased Chl *a* concentrations lead to decreasing Secchi and therefore light penetration depths. Similar to the nutrient and Chl *a* concentrations, the PON and POC concentrations (sum of PON & POC is POM) are highest in SL, and 3 and 5.5 times lower in GB and PB, respectively (Fig. 10). In SL, two peaks in the POM concentrations were measured during two sampling campaigns, in February (57.6 µmol L^{-1} PON, 557.5 µmol L^{-1} POC) and in August (68 µmol L^{-1} PON, 561.8 µmol L^{-1} POC), while only one peak was detected in GB (Feb.: 30.2 µmol L^{-1} PON, 289.9 µmol L^{-1} POC). In PB, on the other hand, PON and POC concentrations continuously decreased over the course of the year after the highest values were measured in February (12.9 µmol L^{-1} PON, 133.9 µmol L^{-1} POC).

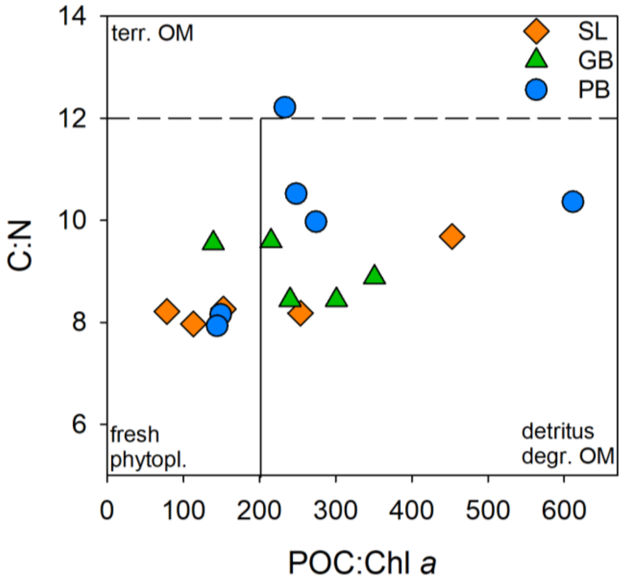

Figure 11. Relationship between the mass ratio of POC:Chl a and the molar POC:PON ratio (short C:N) of the surface water in the Szczecin Lagoon (orange), the Greifswalder Bodden (green) and the Pomeranian Bay (blue). A C:N ratio below 12 is representative for phytoplankton and above 12 for OM of terrestrial origin (dashed line). The solid vertical line represents the threshold between freshly produced phytoplankton (<200) and detrital or degraded OM (>200). For references see text.

POC:PON ratios (short C:N) were consistently higher than the Redfield ratio of 6.6:1 (Fig. 11). An increasing trend towards the open Baltic Sea was indicated by a shift of the mean ratio from 8.5 in SL, 9 in GB to 9.9 in PB. Values of PB exhibited the greatest variation over the annual cycle, ranging from 7.3 in March to 12.2 in October. The overall mean POC:PON ratio was 8.7. Most C:N ratios were found to be around or below 10, which indicates that the majority of the organic particles sampled along the Oder outflow was of phytoplankton origin (Savoye et al. 2003 and references therein). Only one ratio was slightly higher than 12 (October, PB), indicating terrestrial origin (Savoye et al. 2003).

The POC:Chla ratio gives insights into the freshness or degradation status of OM. The ratio ranges from 78.2 in SL in April to 611.6 in PB in March (Fig. 11). Ratios below 200 illustrate that the majority of POM consists of freshly produced phytoplankton, while ratios above 200 represent POM majorly consisting of detritus or degraded OM (Cifuentes et al. 1988, Savoye et al. 2003).

3.3 DIN uptake and primary production

Overall, the nutrient uptake rates and PP are highly variable throughout the year with no clear seasonality. However, differences between stations can be identified, where SL is the most and PB the least productive system. The productivity in the surface layer of the water column is higher than in the bottom water.

Primary production in SL shows great monthly variations (Fig. 12). While surface PP is < 25 µmol L^{-1} d^{-1} in February and May, it displays highest values of 560 µmol L^{-1} d^{-1} in

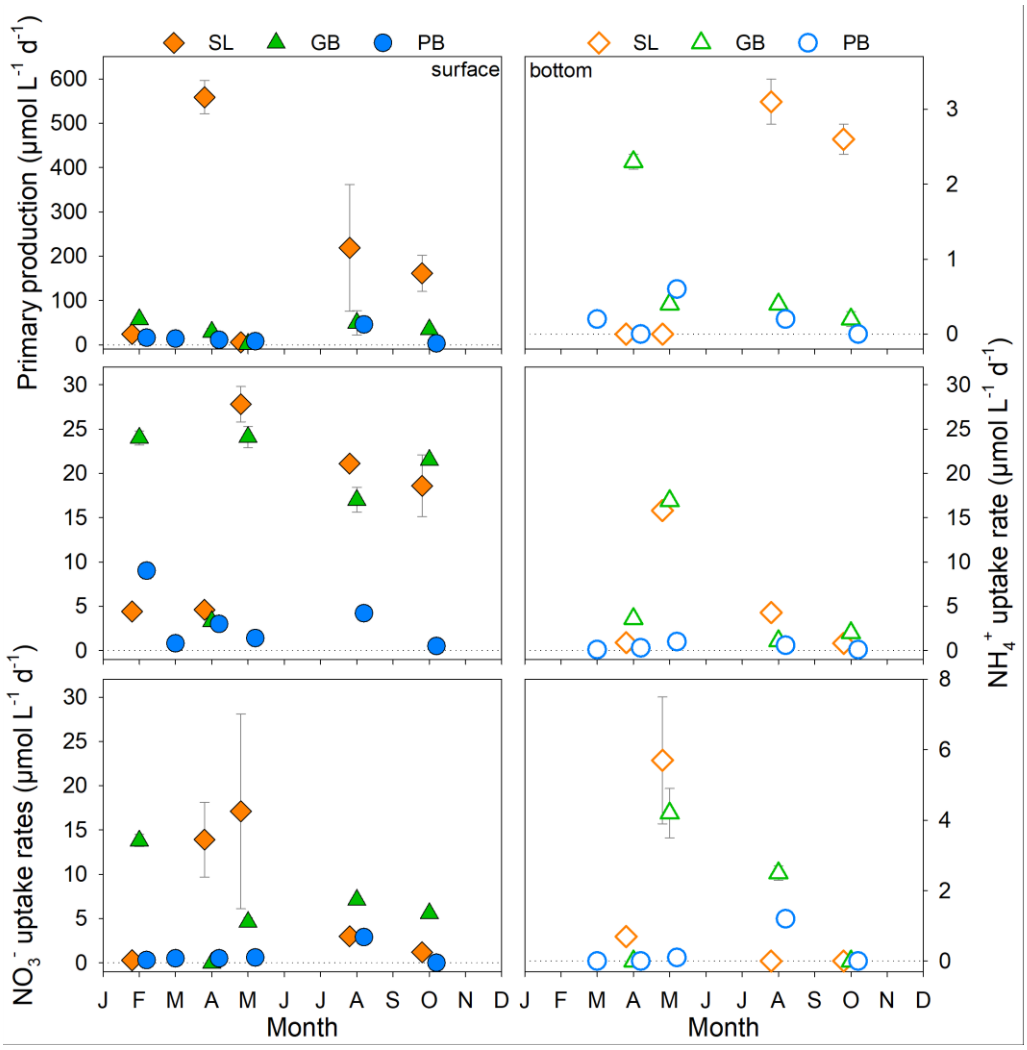

Figure 12. Primary production (upper panels), ammonium (middle panels) and nitrate uptake rates (lower panels) (all in µmol L^{-1} d^{-1}) of surface (filled symbols, left panels) and bottom water samples (open symbols, right panels) in the Szczecin Lagoon (orange diamonds), the Greifswalder Bodden (green triangles) and the Pomeranian Bay coast (blue circles). Data are presented as average and standard deviation (n=3). Note the different scales.

April. The second highest surface PP was measured in August (218.8 ± 142.9 µmol L^{-1} d^{-1}), followed by October. PP in the bottom water was only 0.6% of the surface rates, with the highest rates measured in August and October of ~ 3 µmol L^{-1} d^{-1}. In contrast to SL, the surface PP in the Bodden and the Bay never exceeded 60 and 50 µmol L^{-1} d^{-1}, respectively. The highest PP in GB was found in February (57.4 ± 6.2 µmol L^{-1} d^{-1}), whereas in PB the highest PP was measured in August (45.7 ± 3.7 µmol L^{-1} d^{-1}), followed by February (15.7 ± 0.6 µmol L^{-1} d^{-1}). In contrast to SL and PB, no August PP peak was measured in GB. Overall, the average surface PP in GB and PB is only 18 and 1% respectively of that SL. Bottom water PP in GB and PB was 1.9 and 1.1% of the surface rates, respectively, with rates always lower than in the Lagoon (≤ 2.3 µmol L^{-1} d^{-1}).

NH_4^+ uptake rates in the surface waters in SL and GB were similar in most months. In the Szczecin Lagoon the uptake was low in February and in March (around

4.5 µmol L^{-1} d^{-1}) and highest in May (27.8 ± 2 µmol L^{-1} d^{-1}) with a decreasing trend towards August and October (21.1 and 18.6 µmol L^{-1} d^{-1}, respectively) (Fig. 12). Throughout the year, surface NH_4^+ uptake rates in the Bodden fluctuate between 17 and 24.1 µmol L^{-1} d^{-1}, with April being the exception (3.3 ± 0.4 µmol L^{-1} d^{-1}). In the Bay, the surface rates alternated between months, ranging mostly from 0.5 to 4.2 µmol L^{-1} d^{-1}, except for the highest NH_4^+ uptake rate measured in February (9 ± 0.9 µmol L^{-1} d^{-1}). Bottom water rates in SL, GB and PB were always lower than surface water rates (Fig. 12), representing 28.5, 26.3 and 10.6% of the surface rates, respectively. The highest bottom water rates were determined in May at the stations SL and GB (~ 16 µmol L^{-1} d^{-1}).

Overall, surface NO_3^- uptake rates are lower than surface NH_4^+ uptake rates. However, for all stations, time periods of elevated NO_3^- uptake rates were detected (Fig. 12). In the Lagoon, the surface rates were highest in April and May (13.9 ± 4.2 and 17.1 ± 11 µmol L^{-1} d^{-1}, respectively) and low at the other sampling points (≤ 3 µmol L^{-1} d^{-1}). In the Bodden, surface NO_3^- uptake rates peaked in February (13.8 ± 0.7 µmol L^{-1} d^{-1}), alongside the PP and NH_4^+ uptake rate. For the rest of the year, the NO_3^- uptake rates were below 7 µmol L^{-1} d^{-1}. In the Bay, the surface rates were even lower than in GB. There, NO_3^- uptake rates peaked in August (2.9 µmol L^{-1} d^{-1}) and remained low otherwise (≤ 0.6 µmol L^{-1} d^{-1}). NO_3^- uptake rates of the bottom waters of SL, GB and PB were again always lower than surface water rates, representing 18, 21.4 and 27.2% of the surface rates, respectively. Similar to the NH_4^+ uptake rates, the highest NO_3^- uptake rates in the bottom waters were found in May in SL and PB (~ 5 µmol L^{-1} d^{-1}).

The ratios of DIC:DIN uptake rates (short: ratios of C:DIN uptake) are ranging from 0.1 in SL in May to 30.1 in SL in April (Fig. 13). Only 4 values are within the range of the POC:PON ratio determined for the Oder outflow (7.1 to 12.2). 68% of the ratios are below the range of PON:POC ratios, indicating a higher N uptake relative to C uptake.

3.4 Nitrification rates

Nitrification rates were always much lower than DIN uptake rates in the water column. At station SL, surface NR were very low (< 23 nmol L^{-1} d^{-1}) throughout the year (Fig. 14). Slightly lower NR were found in GB, where the highest rate was measured in February (6.9 nmol L^{-1} d^{-1}).

At PB, elevated surface NR were measured in February, March and April (56.6 ± 5.9, 8.6 ± 0.2 and 7 nmol L^{-1} d^{-1}, respectively) compared to the rest of the year, where surface rates were barely detectable (≤ 1 nmol L^{-1} d^{-1}). The annual mean NR of the bottom water in SL, GB and PB were 32.3, 58 and 12.7% lower than the surface rates.

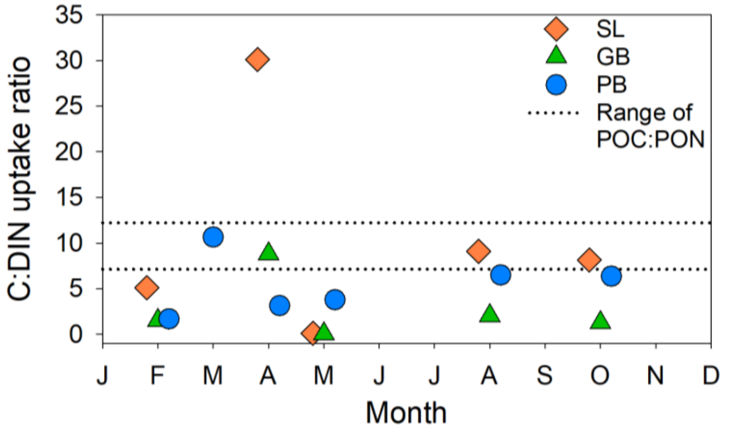

Figure 13. Ratio of DIC to DIN uptake rates of the surface water in the Szczecin Lagoon (orange diamonds), the Greifswalder Bodden (green triangles) and the Pomeranian Bay (blue circles). The range of POC:PON ratio in the Oder outflow is marked with dashed lines, ranging from 7.1 to 12.2.

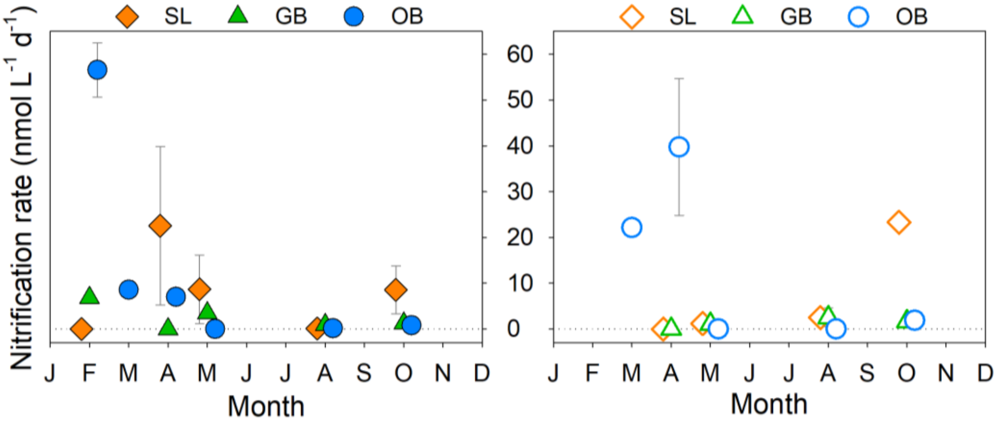

Figure 14. Nitrification rates (in nmol L^{-1} d^{-1}) of surface (filled symbols, left panels) and bottom water samples (open symbols, right panels) in the Szczecin Lagoon (orange diamonds), the Greifswalder Bodden (green triangles) and the Pomeranian Bay coast (blue circles). Data are presented as average and standard deviation (n=3). Note the different unit compared to PP and N uptake rates.

Specifically, bottom water NR were higher than surface water NR in almost half of the sampling campaigns at each station. However, the differences between bottom and surface water NR are not significant (n = 58, p = 0.463, Fig. 15). In addition, no significant differences between the incubation of nitrification samples in the ambient light or in the dark were found (n = 58, p=0.803, Fig. 15). When bottom water samples were exposed to light, the NR incubated in the light are slightly lower than the dark incubated NR. However, the differences between the two groups are not significant (n = 13, p = 0.896, Fig. 16). When the surface water samples were treated the same, NR in PB increased slightly in the dark while not effect of exposure to the dark was found for samples from SL and GB (Fig. 17). Again, all visible differences were not statistically significant.

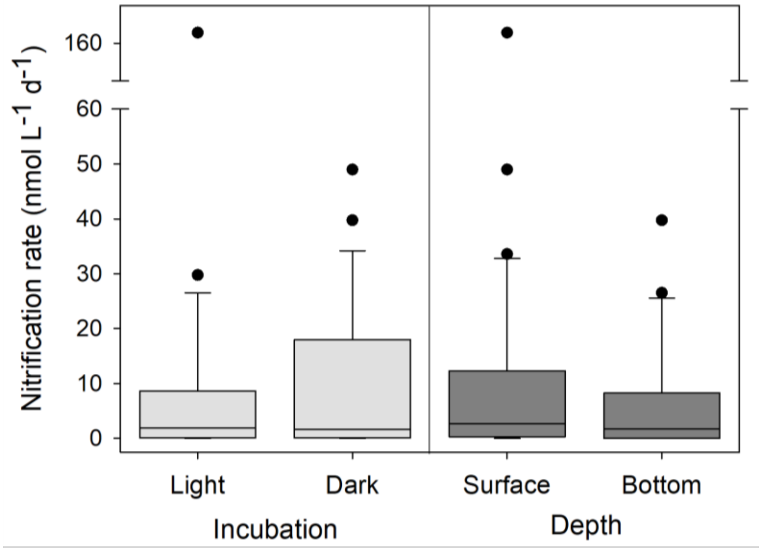

Figure 15. Nitrification rates (in nmol L^{-1} d^{-1}) incubated in ambient light or darkness (left, light grey) and of surface or bottom water column samples (right, dark grey) from all stations and sampling campaigns. Box-whisker plots show median, lower and upper quartiles, extremes and outliers.

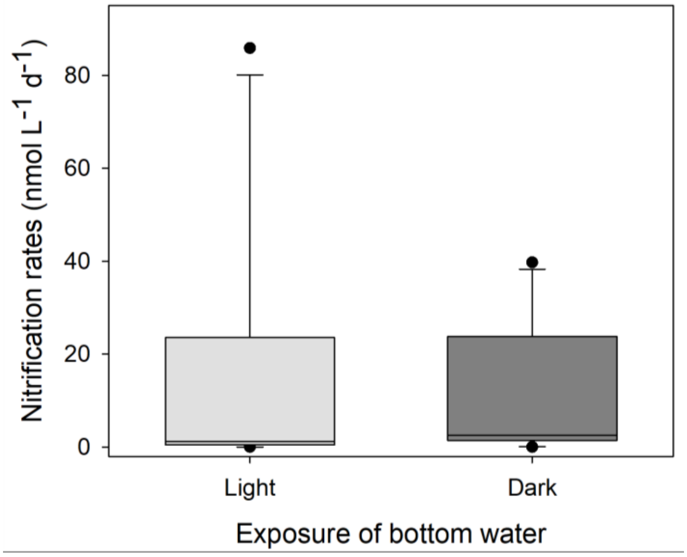

Figure 16. Bottom water nitrification rates (in nmol L^{-1} d^{-1}) incubated in the light (left box, light grey) or darkness (right box, dark grey) from all stations and sampling campaigns combined. Box-whisker plots show median, lower and upper quartiles, extremes and outliers.

NR were often not detectable because there was little transformation from $^{15}N\text{-}NH_4^+$ to $^{15}N\text{-}NO_x^-$ and the ^{15}N signal was too small to be measurable in the large natural $^{14}N\text{-}NO_x^-$ pool.

3.5 Nitrate removal rates

Benthic NO_3^- reduction processes (denitrification and DNRA) in the Szczecin Lagoon were primarily (70 – 90%) fuelled by NO_3^- produced within sediments via nitrification (Fig. 18). The contribution of NO_3^- diffusion from the overlaying bottom water (DNR_W and $DNRA_W$) was relatively low (23.8 – 2467.2 µmol m^{-2} d^{-1}), except in muddy areas

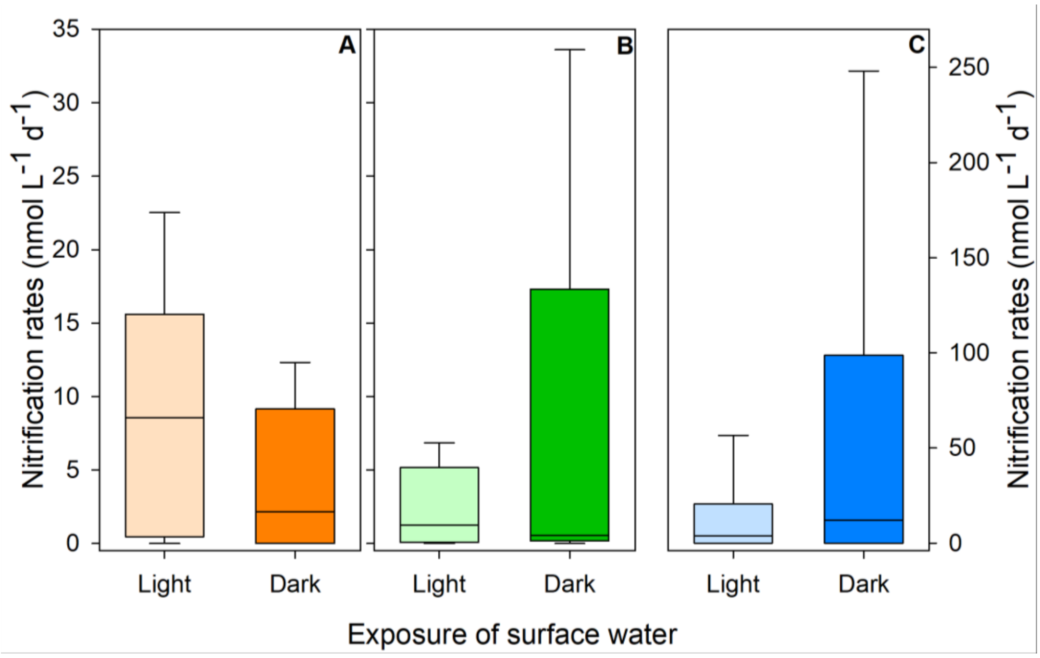

Figure 17. Surface water nitrification rates (in nmol L^{-1} d^{-1}) incubated in the light (left boxes, light colour) or darkness (right boxes, dark colour) of Szczecin Lagoon (orange, A), Greifswalder Bodden (green, B) and Pomeranian Bay (blue, C) during all sampling campaigns. Box-whisker plots show median, lower and upper quartiles, extremes and outliers.

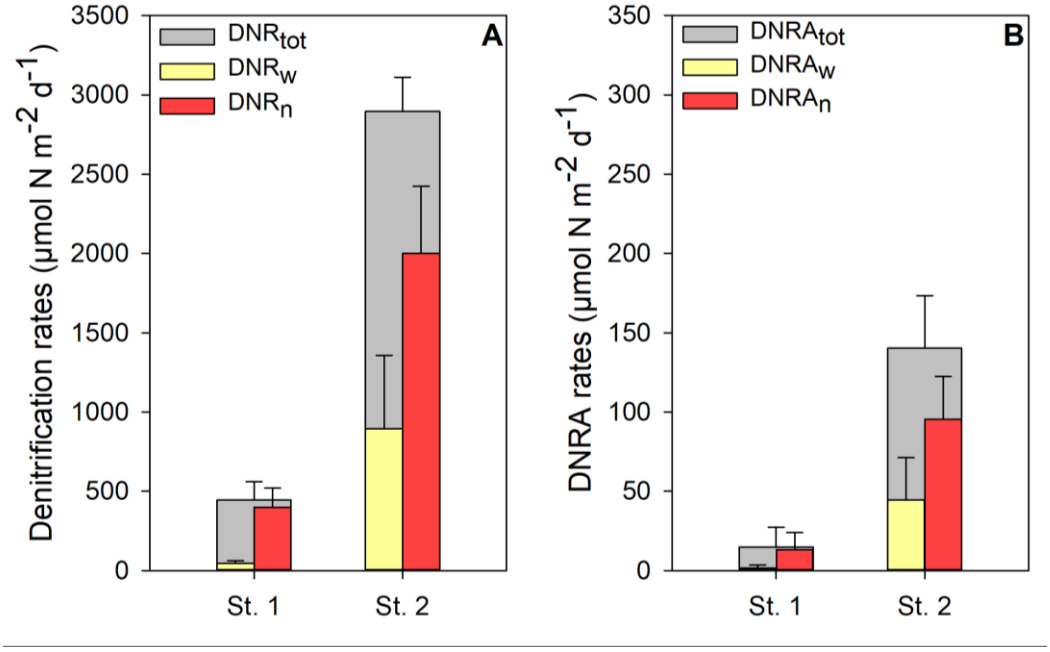

Figure 18. Sedimentary denitrification of water column NO_3^- (DNR_w), coupled nitrification-denitrification (DNR_n) and total denitrification (DNR_{tot}, A), and dissimilatory nitrate reduction to ammonium of water column NO_3^- ($DNRA_w$), coupled nitrification-DNRA ($DNRA_n$) and total DNRA ($DNRA_{tot}$, B) (in µmol m^{-2} d^{-1}) measured in whole core incubations at benthic stations St. 1 and St. 2. Data are presented as average and standard deviation (n=9). Data provided by Mindaugas Zilius (University Klaipeda).

(St. 2) that were flushed by the Odra River. DNR_n ranged from 220.8 to 2467.2 µmol N m^{-2} d^{-1}, with significantly higher rates observed in muddy sediments (t-test, $n = 9$, $p < 0.001$). DNRA accounted for 3 - 5% of the total measured NO_3^- reduction and ranged from 13.5 to 199.3 µmol N m^{-2} h^{-1}. Similar to denitrification, DNRA rates were significantly higher at muddy sites (t-test, $n = 9$, $p < 0.001$).

3.6 Water Residence Time

The WRT is overall high with several months according to the model results. In the Small Lagoon (157 ± 18 days) it is longer than in the Great Lagoon (96 ± 19 days) and similar to the Greifswalder Bodden (143 ± 26 days) (Fig. 19). Furthermore, the WRT in the Small Lagoon and GB have a seasonal influence from the variation of the river flow, with a higher residence time in spring and early summer than in winter and mid-summer, whereas no seasonality is visible in the Great Lagoon. The open coast station in the Bay, on the other hand, has a rapid exchange with the Baltic Sea compared to the Szczecin Lagoon and the Greifswalder Bodden (Pastuszak et al. 1996, 2003).

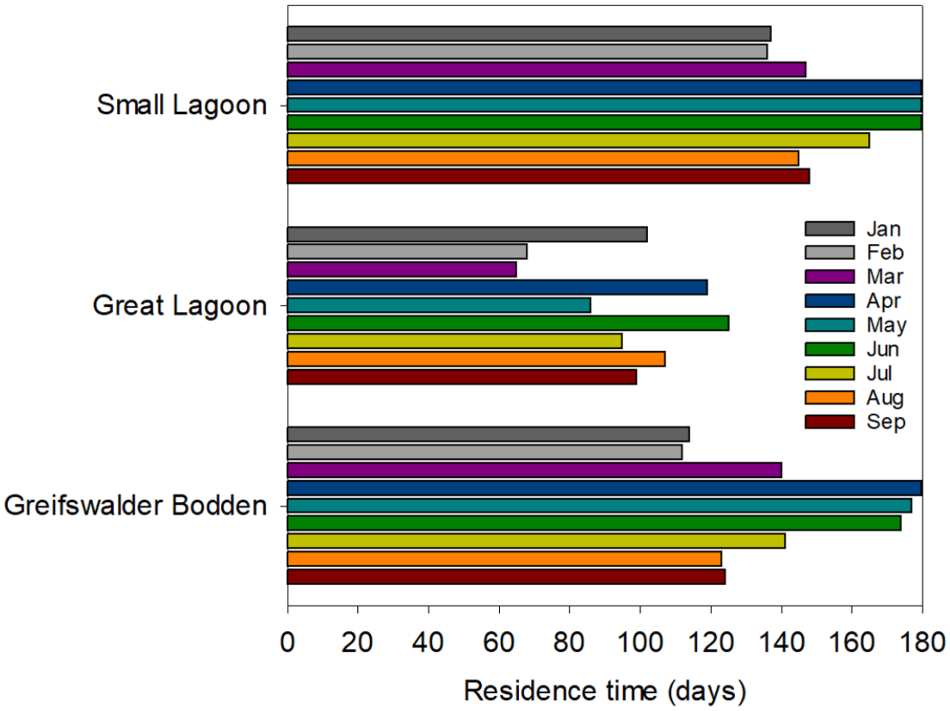

Figure 19. Water residence time in the Small and Great Lagoon (the two parts of the Szczecin Lagoon) and the Greifswalder Bodden (in days) from January to September 2021. The model run was terminated on 31 December 2021.

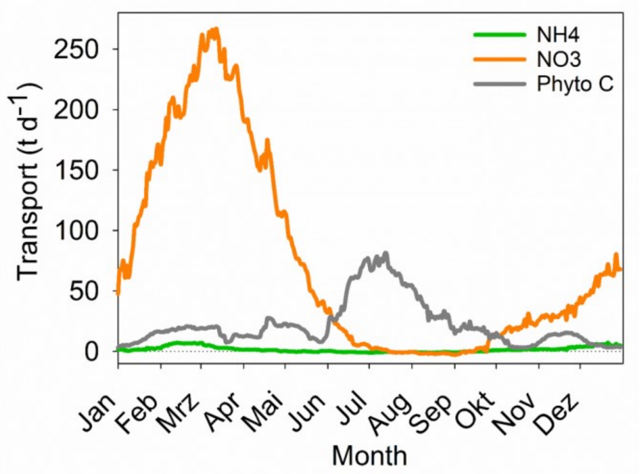

Figure 20. Modelled transport of ammonium, nitrate and phytoplankton-derived carbon in t d^{-1} through the Swina. Data used are from 2012 (see section 2.5).

3.7 Transport Model

The transport through the Swina was directed towards the Pomeranian Bay 44 days of the year (positive values) for NH_4^+, 306 days for NO_3^-, and every day of the year for phytoplankton-derived carbon (Phyto-C) (Fig. 20). NO_3^- was transported the most, showing a transport peak between February and May with the highest values measured in the first half of March (255 t d^{-1} on average). Between July and October, on the other hand, NO_3^- transport hardly ever happened (-2 to +2 t d^{-1}). NH_4^+ transport was always around zero, with a little peak between February and March, representing only 2% of NO_3^- transport. Phyto-C transport from the Lagoon to the Bay peaked in July with around 73 t d^{-1}. The rest of the year, Phyto-C transport values ranged from 3 to 25 t d^{-1}. Per year, 27.3 kt NO_3^-, 0.6 kt NH_4^+ and 8.2 kt Phyto-C are transported through the Swina. According to Mohrholz & Lass (1998), about 70% of the Lagoon water is transported through the Swina and 15% each through the Peenestrom and Dziwna. Assuming a similar annual distribution as in SL, 5.9 kt NO_3^-, 0.1 kt NH_4^+ and 1.8 kt Phyto-C would be transported through the Peenestrom and Dziwna, respectively, per year.

3.8 Fluxes from the sediment

The net O_2 flux across the sediment-water interface at all stations was always negative, suggesting oxygen consumption in the sediment (Fig. 21) throughout the year. The measured net NH_4^+, NO_3^- and PO_4^{3-} effluxes indicate that the sediments were a source of those nutrients for the overlying water. Most net nutrient and the O_2 fluxes varied seasonally, with the highest fluxes in the summer, followed by autumn and spring. The highest NH_4^+ (9.8 mmol m^{-2} d^{-1}) and NO_3^- efflux (1.4 mmol m^{-2} d^{-1}) from the sediment coincided with the highest net uptake of O_2 (–61.3 mmol m^{-2} d^{-1}) in August in SL. PO_4^{3-} fluxes were detectable only in PB (highest efflux of 0.2 mmol m^{-2} d^{-1} in August) during all sampling campaigns but never in SL. Average NH_4^+ and NO_3^- fluxes are lower

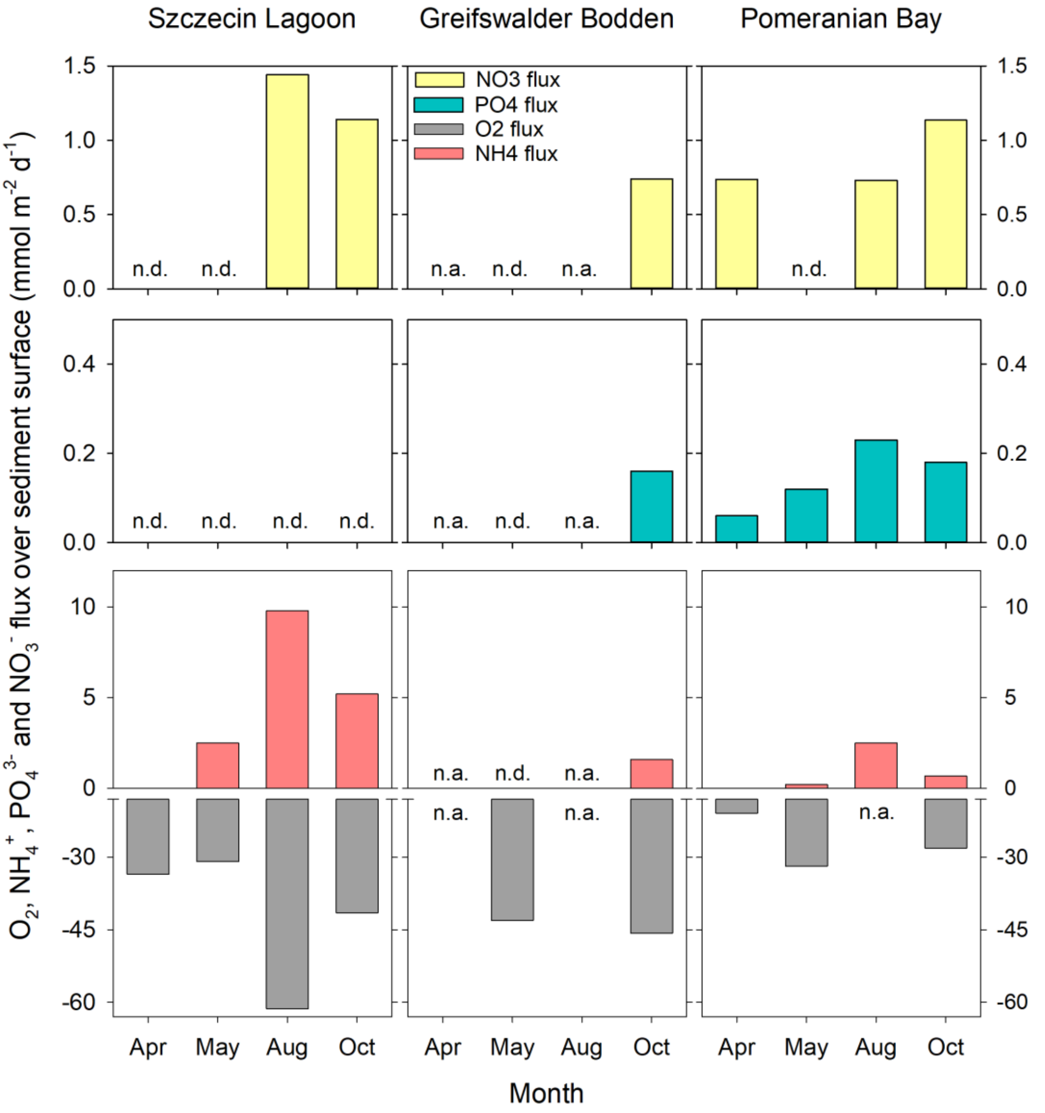

Figure 21. Bottom Chamber Lander fluxes of oxygen (grey bars), ammonium (rose bars), phosphate (turquoise bars) and nitrate (yellow bars) across the sediment-water interface (in mmol m^{-2} d^{-1}) in the Szczecin Lagoon (left column), the Greifswalder Bodden (middle column) and the Pomeranian Bay (right column) in 2021 and 2022. Positive fluxes represent fluxes out of the sediment and negative fluxes into the sediment. n.a. = not available; n.d. = not detectable. Note the different axis scales.

in GB and PB compared to SL. O_2 fluxes were up to 30% higher in GB than in SL (on the two sampling campaigns available for GB), while they were up to 2.5 times lower in PB than in SL.

Nutrient fluxes calculated from nutrient pore water profiles were always different from the fluxes derived from the chamber lander deployments (Fig. 22). On most sampling dates, NH_4^+ fluxes from the chamber lander deployment were higher. Specifically, the fluxes of the chamber lander deployment were up to 48 times higher. The same applies to fluxes of NO_3^- and PO_4^{3-}. Similar to the chamber lander data (see above), pore water fluxes show a seasonal trend with higher rates towards summer and autumn, especially visible in data from SL. Overall, the efflux of NH_4^+ was higher than of NO_3^- and PO_4^{3-}.

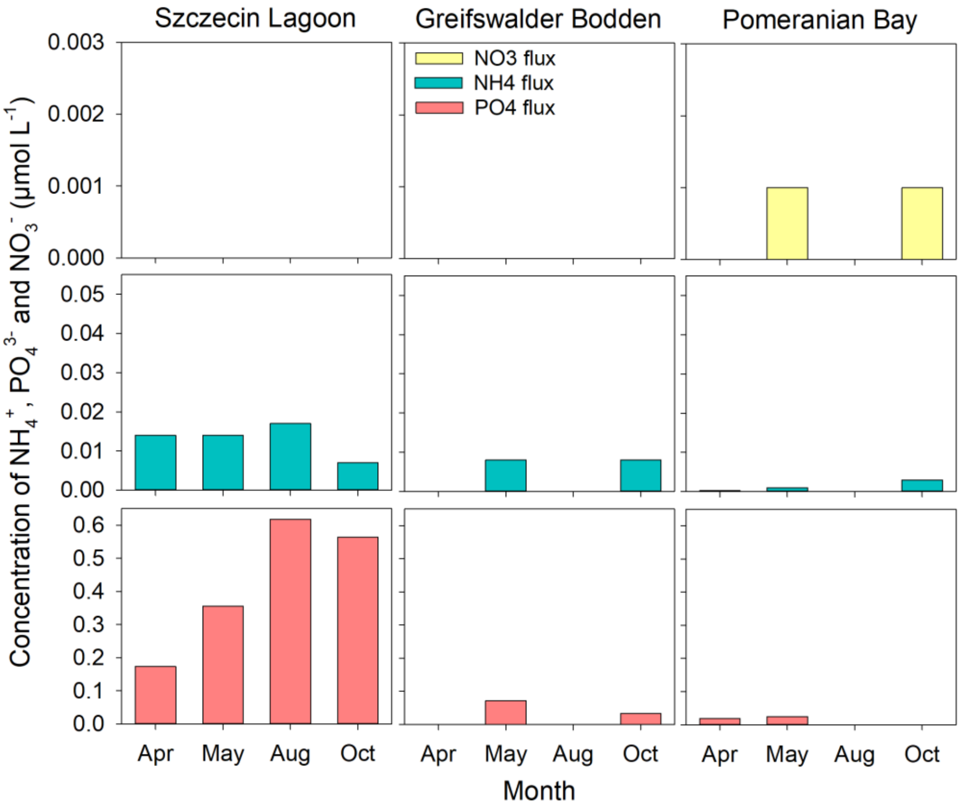

Figure 22. Pore water fluxes of ammonium (rose bars), phosphate (turquoise bars) and nitrate (yellow bars) across the sediment-water interface (in mmol m^{-2} d^{-1}) in the Szczecin Lagoon (left column), the Greifswalder Bodden (middle column) and the Pomeranian Bay (right column) in 2021 and 2022. Positive fluxes represent fluxes out of the sediment and negative fluxes into the sediment. n.a. = not available; n.d. = not detectable. Note the different axis scales.

The results clearly illustrate the strong differences in nutrient fluxes across the sediment-water interface depending on the method applied. The main difference between the two approaches is that the Chamber Lander incubates the sediment surface in situ, thereby including benthic macrofauna, whose activity has been shown to enhance the benthic fluxes of solutes (e.g. Thoms et al. 2018). Further discussion on the use of the two approaches can be found below in section 4.3.1.

3.9 Statistical analysis

Correlation analysis shows that PP is significantly correlated with the least and NH_4^+ uptake with the most abiotic variables (Tab. 2). PP is not correlated with any nutrient concentration and with N uptake rates only in PB. Neither PP nor N uptake rates are correlated with PON or POC concentrations. NR showed no relationship with any other process rate and only with a few abiotic variables. Surprisingly, only two correlations were found in the SL dataset. Overall, no abiotic variable or solute concentration has an influence on all process rates.

Table 2. Spearman rank order correlation matrix of environmental data and rates in the Oder outflow. Only significant ($p \leq 0.05$) correlations are shown. Negative correlations are underlined. The number of samples is 29 for the analysis of all three stations together, 9 for the Szczecin Lagoon, 9 for the Greifswalder Bodden and 11 for the Pomeranian Bay.

Variable	**Primary Production**	**NO_3^- uptake**	**NH_4^+ uptake**	**Nitrification**
Temp *(°C)*				$\underline{\text{PB}}$
Salinity				$\underline{\text{SL}}$ PB
O_2 *($\mu mol\ L^{-1}$)*	PB			
pH			$\underline{\text{GB}}$	
Chl *a* *($\mu g\ L^{-1}$)*		GB	all	
NO_3^- *($\mu mol\ L^{-1}$)*				PB
NH_4^+ *($\mu mol\ L^{-1}$)*			GB	all
PO_4^{3-} *($\mu mol\ L^{-1}$)*				
N:P ratio				PB
PON *($\mu mol\ L^{-1}$)*		GB	all	
POC *($\mu mol\ L^{-1}$)*		all GB	all PB	
PP *($\mu mol\ L^{-1}\ d^{-1}$)*	– – – –	– – – –	– – – –	
NO_3^- uptake *($\mu mol\ L^{-1}\ d^{-1}$)*	PB	– – – –	– – – –	
NH_4^+ uptake *($\mu mol\ L^{-1}\ d^{-1}$)*	all PB	all SL PB	– – – –	

SL is significantly different from GB and PB in terms of environmental conditions and nutrient concentrations (Tab. 3), implying similar abiotic conditions at GB and PB. However, SL and GB are both significantly different from PB when N uptake rates are used for the ANOVA, suggesting similar conditions at SL and GB.

Table 3. Analysis of significant differences between Szczecin Lagoon, Greifswalder Bodden and Pomeranian Bay for each variable using ANOVA and ANOVA on ranks. Significant differences with p-value ≤ 0.05, marked with asterisk. Pairwise significance was tested using post-hoc tests (see Materials and Methods section for details).

Variable	**p-value**	**Pairwise significance**
Environmental conditions		
Temperature	0.291	
Salinity	< 0.001 *	SL-GB, SL-PB
Oxygen concentration	0.254	
pH	0.25	
Chl *a* concentration	< 0.001 *	SL-GB, SL-PB
Nutrient & POM concentrations		
NO_3^- concentration	0.038 *	SL-PB
NH_4^+ concentration	0.25	
PO_4^{3-} concentration	0.349	
PON	< 0.001 *	SL-GB, SL-PB
POC	< 0.001 *	SL-GB, SL-PB
Process rates		
NO_3^- uptake	0.012 *	GB-PB
NH_4^+ uptake	0.004 *	SL-PB, GB-PB
PP	0.492	
NR	0.691	

Note: Data from surface and bottom water samples have been used. Process rates are used according to in situ light conditions in surface and bottom water.

4. Discussion

4.1 Trophic state of the ecosystem

Eutrophication is a persistent problem in the Baltic Sea, ultimately leading to the so-called 'death zones' in the central Baltic Sea, which are hypoxic and anoxic areas in the deeper parts of the basins (Conley et al. 2009a, Carstensen & Conley 2019). The nutrients responsible are mostly land-derived and are transported via rivers and streams, passing coastal areas and especially estuaries, which themselves are often strongly eutrophied (HELCOM 2018). Another contribution to nutrient load comes from atmospheric deposition (Rolff et al. 2008, Berthold et al. 2019). However, there is no standardised definition of when an ecosystem is eutrophic considering all actors like scientists, policy makers and stakeholders. I have therefore used the data I have collected to assess the ecological status of the Szczecin Lagoon, the Greifswalder Bodden and the Pomeranian Bay, based on different definitions of eutrophication.

According to Nixon (1995) an ecosystem is oligotrophic, mesotrophic, eutrophic and hypertrophic if the organic C supply is < 100, 100-300, 301-500 and > 500 g C m^{-2} a^{-1}, respectively. Rates of daily PP were integrated over the water column and extrapolated to one year, resulting in an annual organic C supply of 1581, 544 and 449 g C m^{-2} a^{-1} in SL, GB and PB, respectively. In comparison to the annual PP of 591-648 and 140-280 g C m^{-2} a^{-1} for SL and GB, respectively, measured by Westphal & Lenk (1998), the values determined by me are high. Using Nixon's definition, the Lagoon and the Bodden are hypertrophic and Bay is a eutrophic ecosystem. The in situ organic C supply is likely even higher as I only considered organic C from PP and not from allochthonous sources. However, those values need to be interpreted cautiously as rates were determined in 5 single months and then extrapolated over several following months. Consistent monthly measurements of PP would give a more precise picture. Furthermore, incubating PP samples in on-deck incubators with natural light spectrum and intensity might further improve these data.

A second assessment approach considers the mean seasonal (May-September) Chl *a* concentrations. In order to assess the ecological status, the coastline along the Oder outflow was characterised according to the EU Water Framework Directive (WFD) and the LUNG as follows: The Lagoon is classified as B1a (oligohaline, 0.5-4 PSU), the Bodden as B2a (mesohaline, 5-10 PSU, enclosed bay) and the coastline of the Pomeranian Bay as B3a (mesohaline, 5-10 PSU, exposed coast). Following the reference values of Sagert et al. (2008), the Lagoon is in a poor ecological status as the mean seasonal Chl *a* concentration is 30.4 µg L^{-1}, which is above the threshold value of 21.5 µg L^{-1}. The Greifswalder Bodden (mean seasonal Chl *a* concentration of 4 µg L^{-1}) and the Bay as well (mean seasonal Chl *a* concentration of 3.46 µg L^{-1}) are in an unsatisfactory ecological state. This is in line with the latest follow-up assessment under the EU-WFD of 2021 (BMUV/UBA 2022), which showed an unsatisfactory status for all three ecosystems (according to the classification of very good, good, moderate, unsatisfactory, poor ecological status). Furthermore, no improvement in the ecological status was observed compared to the last assessment in 2015. Other assessments came to different conclusions, ranging from meso- and eutrophic in GB and PB to polytrophic in SL (Schiewer 2002, Bangel et al. 2004). They have mentioned several times that the water quality in GB is relatively good, due to, among other things, a high surface to catchment area ratio of 1:1 (SL has 1:188) and a good exchange with the Baltic Sea (Schiewer 2002, 2008).

For future assessments, I would recommend the determination of PP alongside the currently used productivity proxies Chl *a* and Secchi depth. In contrast to the PP, DIN uptake rates, as determined in this study, are not appropriate because heterotrophic bacteria also take up DIN (Middelburg & Nieuwenhuize 2000a), which would overestimate the trophic status of the ecosystem if only phytoplankton growth were considered. Cell- or species-specific metabolisms can also alter DIN uptake rates, such as the intracellular NO_3^- storage by diatoms (Lomas & Glibert 1999a) or the production of cell membrane NO_3^- or NH_4^+ transporters, the extent of which depends on the ambient nutrient concentrations (Eppley et al. 1969, Glibert et al. 2016 and references therein). In general, an ecological assessment should definitely include not one but several variables and measurements of e.g. PP, POM concentrations, Chl *a* concentrations, Secchi depth and O_2 concentration, the latter being crucial as hypoxia and anoxia have major effects on nutrient cycling and higher fauna (Rabalais et al. 2001, Conley et al. 2009b). The occurrence of HABs should also be monitored, as their occurrence increases with eutrophication and can have far-reaching consequences for marine fauna, mammals and seabirds (Anderson et al. 2002).

Significant correlations between the river inflow and productivity and bottom water O_2 depletion, as shown for large rivers such as the Po (Italy) and the Mississippi (USA) (Justić et al. 1993), lead to the conclusion that riverine nutrient inputs should be closely monitored. In the Baltic Sea region, this is overseen and data are collected by the HELCOM. Easy access to the data is provided via a webpage, but only annual discharge data are available, hindering the assessment of seasonal processes, as done in this study.

As frequent monitoring, in the rivers and affected coastal ecosystems, can be logistically challenging, long-term sensors and moorings can provide continuous data on critical variables such as O_2 concentration or saturation, turbidity/PAR or fluorescence/Chl *a*. Finally, remote sensing and satellite imagery can provide a low-cost, low-effort solution that has been successfully applied to estimate and predict coastal hypoxia in the Gulf of

Mexico (Li et al. 2023), where the eutrophication extends over the coastal zone and across the continental shelf (Turner & Rabalais 1994).

4.2 The Coastal Filter Function of the Oder Outflow

The sampling times were chosen according to weather conditions that would allow sampling at approximately 3-month intervals, but are not necessarily representative of the respective season. However, a comparison of the measurements at the three stations with long-term nutrient and Chl *a* concentrations confirms that the data are representative of an average seasonal cycle.

4.2.1 Primary Production as a Retention Process

As the Oder outflow is a highly productive system fuelled by the Oder river input, the production of organic matter and the associated nutrient uptake processes have the potential for nutrient retention.

A - Szczecin Lagoon

In general, phytoplankton in estuaries prefers NH_4^+ over NO_3^- as a source of N (Underwood & Kromkamp 1999) because cells must invest more energy to reduce NO_3^- to NH_4^+ prior to their incorporation into biomass (Syrett 1956). Additionally, essential genes for NO_3^- uptake are repressed by NH_4^+ (Zumft 1997). And yet, PP in SL in spring is mainly supported by NO_3^- as illustrated by the high NO_3^- uptake rates of ≥ 14 $\mu mol\ L^{-1}\ d^{-1}$ (Fig. 12). The same was previously shown in San Francisco Bay (Wilkerson et al. 2006). The preference for NO_3^- may be caused by the high ambient NO_3^- concentrations of over 134 $\mu mol\ L^{-1}$, leading to a higher capability for NO_3^- uptake than for NH_4^+ (Lomas & Glibert 1999a b, Glibert et al. 2016). Diatoms, being the most abundant phytoplankton group in spring (Bąk et al. 2006), were shown to prefer NO_3^- (Lomas & Glibert 1999a) and they can take up NO_3^- in excess for compensating energy imbalance during light harvesting (Lomas & Glibert 1999b). Additionally, increased NO_3^- concentrations result in a higher abundance of NO_3^- transporters in the cell membrane of phytoplankton, leading to enhanced uptake and reduction (Dugdale et al. 1981, Coruzzi & Bush 2001).

A preference for NO_3^- as a nutrient for PP was also shown in the Thames estuary (Middelburg & Nieuwenhuize 2000a), where NO_3^- uptake rates were similar to those in SL, even though measurements were done in winter, when phytoplankton activity is usually low. Due to the unfavourable growing conditions for phytoplankton in winter, Middelburg & Nieuwenhuize (2000a) suggested that up to 80% of the N uptake was performed by heterotrophic bacteria, which could be a possibility in SL as well. In another study, the same authors found the opposite preference of NH_4^+ over NO_3^- in other European estuaries, e.g. the Rhine, Seine and Scheldt (Middelburg &

Nieuwenhuize 2000b), illustrating the variability between estuaries even in the same climate zone.

In SL, two peaks of phytoplankton growth can be observed (Fig. 12), one in spring and one in summer (Schiewer 2008). In contrast to the literature and other lagoons (Zilius et al. 2024), I measured the highest PP in April, not in August. Slightly lower annual PP was determined in the Cochin estuary in India (65.9 to 126.5 µmol L^{-1} d^{-1}), which is also a lagoonal estuary (Bhavya et al. 2017). In the Baltic Proper, spring PP specifically (April-May 2013-2016) was ≤ 30 µmol L^{-1} d^{-1} (Spilling et al. 2019), only 5% of the PP in April in the lagoon. Despite the high NO_3^- uptake rates in spring, there was a high export of NO_3^- from SL to PB in spring, which is in line with previous estimates (Radtke et al. 2012). This shows that an active phytoplankton spring bloom in optimum environmental conditions is not able to retain the NO_3^- load from large rivers into the Baltic Sea when the discharge is high (Meyer & Lampe 1999).

In August, NH_4^+ was the preferred N source, although dissolved inorganic nitrogen (DIN) inputs from rivers are generally low during the summer months (Nausch et al. 1999) and DIN concentrations in the water column were close to the detection limit. Possibly, NH_4^+ originates from both mineralisation of organic matter in the water column and fluxes of NH_4^+ from the sediment, supporting the second highest PP measured in SL (Fig. 12). Considering the NH_4^+ flux from the sediment (9.8 mmol m^{-2} d^{-1}) (the NH_4^+ pool in the water column was negligible), 47.8 mmol NH_4^+ m^{-2} d^{-1} must be remineralised in the water column of the lagoon to maintain the observed NH_4^+ uptake rates, which corresponds to 396.5 mmol POC m^{-2} d^{-1}, using the average POC:PON ratio of 8.3:1. Therefore, 16% of the POC standing stock must be recycled per day, assuming a POC standing stock of 2520 mmol m^{-2} (integrated August POC concentration). This seems reasonable considering that 29% of the POC standing stock is produced per day during PP in August (727.1 mmol m^{-2} d^{-1}). Klawonn et al. (2019) showed in an experiment with Baltic Sea water that NH_4^+ turnover is very rapid, and that during one hour of phytoplankton degradation, enough NH_4^+ is produced to sustain the N demand for PP.

Efficient recycling of N via OM mineralisation and N assimilation during periods of limited N supply, has been demonstrated for the Curonian Lagoon (Zilius et al. 2018, Broman et al. 2021). In line with the data here, they measured low NH_4^+ concentrations but high NH_4^+ uptake rates, indicating a high turnover rate of NH_4^+ in the water column and low standing stock. The tight coupling of NH_4^+ remineralisation and uptake across a wide range of nutrient, light and temperature conditions was already illustrated by Glibert (1982), who concluded that phytoplankton can utilise NH_4^+ at the same rate as it is produced by heterotrophic processes. At the single-cell level, Klawonn et al. (2019) showed that ≥ 91% of ammonium production under N-limited conditions in summer came from regenerated sources (as also shown by Harrison 1978, Suttle et al. 1990), supporting 78-97% of PP. In addition, the POC:Chla ratios of all stations and seasons

(Fig. 11) were indicative of both freshly produced phytoplankton and detrial or degraded OM, without a clear temporal or spatial trend, whereby the mean C:N ratio of 8.7 excludes OM of terrestrial origin (Savoye et al. 2003). This further emphasises the close coupling of biomass production and degradation in the water column of the Oder outflow.

This indicates that during periods of limited N supply, nutrients are retained in the system through an efficient coupling of assimilation and recycling. Thus, only a limited amount of the nutrient stock in SL is available for export during the summer months and in the form of phytoplankton derived particles.

B - Greifswalder Bodden

In the Bodden, the highest annual NO_3^- concentrations have previously been measured in the first months of the year. For example, a maximum of 53.9 µmol L^{-1} was recorded in February 2011 (LUNG monitoring data), while ~ 12 µmol L^{-1} was measured in March 1993 (Hübel et al. 1995). The concentrations observed in February 2022 (82.8 µmol L^{-1}) were of an unprecedented magnitude and presumably originated from the Peene or smaller rivers entering the Bodden directly, not from the Oder river. Interestingly, this did not result in as strongly elevated PP as was observed in SL. Overall, the mean annual PP at station GB of 34.4 ± 19.2 µmol L^{-1} d^{-1} represents only 17% of the PP in SL. Simultaneous to the observed decline in DIN and PO_4^{3-} concentrations, a spring bloom occurs around March/April, according to Hübel et al. (1995) and Schiewer (2008a). However, not only is the PO_4^{3-} pool already depleted during my sampling campaign in February 2022, resulting in a P limitation during the spring months, but a pronounced PP peak was already measured in February. Elevated water temperatures could be an explanation: while February temperatures ranged between -0.4°C and 4.8°C in the years 1998 to 2021 (LUNG monitoring data), but the water was 6.4°C warm in 2022. According to the monitoring data, such temperatures would normally be reached at the earliest in April, the typical month for the spring bloom according to (Hübel et al. 1995, Munkes 2005). This finding is consistent with analyses of long-term monitoring data (Hjerne et al. 2019) and laboratory incubation experiments (Sommer et al. 2012), showing an earlier onset of the spring bloom at high temperatures, suggesting the frequent recurrence of early spring blooms in the climate change-affected future (Kahru et al. 2016).

The spring PP peak is then followed by several smaller summer peaks (Schiewer 2008), but due to the temporal distance between sampling campaigns only one summer peak in August was determined with the data. Because of a DIN:DIP ratio of around 2 in August (Fig. 9), illustrating the N limitation, cyanobacteria are likely the most abundant phytoplankton group as has been observed in the Curonian Lagoon (Zilius et al. 2014, Vybernaite-Lubiene et al. 2017). While the PP in August is only 14% lower than in

February, the Chl *a* concentration drops by 3.5 times. This can be due to the fact that the Chl *a* content of phytoplankton cells increases with ambient amount of nutrients (Riemann et al. 1989) and with low light conditions as found in February (Jones & Myers 1965, Brown & Richardson 1968, Fisher & Halsey 2016) and illustrates that PP determination via rate incubations are a better measure for PP than using Chl *a* concentrations as a proxy.

Both, spring and summer PP peaks coincide with elevated NH_4^+ and NO_3^- uptake rates, even though NO_3^- and NH_4^+ were depleted during summer in the Bodden. Like at the other stations, NH_4^+ uptake rates are several times higher (~ 3 times in GB) than NO_3^- uptake rates. In fact, the mean surface NH_4^+ uptake rate in GB (18 µmol L^{-1} d^{-1}) is slightly higher than of SL (15.3 µmol L^{-1} d^{-1}1), emphasizing the productivity of the Bodden. However, in contrast to SL and PB, the seasonal variations are very low, indicating its importance all year round. Overall, the N uptake rates in GB (annual mean of 6.2 µmol L^{-1} d^{-1}) are similar to rates in SL (annual mean of 7.1 µmol L^{-1} d^{-1}) despite the Lagoon being a much more productive system. In my view, there are four possible explanations for these low rates: (I) PP in SL is supported by additional N-sources such as DON, (II) a big fraction of the N taken up in GB is emitted again as NH_4^+ or DON, or (III) stored in cells, and finally (IV) a high fraction of N uptake by heterotrophic bacteria in GB.

(I) DON from allochthonous (e.g. plant degradation products and humic substances) and autochthonous (e.g. exudates from cyanobacteria (Wannicke et al. 2009)) sources, can serve as additional N-source for phytoplankton, especially in the coastal zone (Korth et al. 2012). Seitzinger et al. (2002) present increased phytoplankton production when DON is supplied additional to DIN, emphasising the possibility of enhanced PP through uptake of riverine and internally produced DON in the Lagoon.

(II) 25 to 41% of the NO_3^- and NH_4^+ taken up can be directly excreted by the phytoplankton cell in form of DON or NH_4^+ (Wannicke et al. 2009). The release of low molecular weight DON can happen already 30 min after the uptake of DIN (Bronk & Glibert 1991). The rates in GB may be so low because some of the initially taken up DIN was rapidly released as DON and was therefore no longer measurable in the PON fraction after the 2 h incubation period.

(III) The phytoplankton community in GB is dominated by diatoms (LUNG monitoring data) which have been shown to store NO_3^- internally (Lomas & Glibert 1999b). By reducing the incorporated NO_3^-, the diatom cells are able to regulate the energy flow of photosynthetic produced electrons, enabling them to thrive in temperate regions with elevated NO_3^- concentrations and turbulent mixing (Lomas & Glibert 1999b) such as the Oder outflow region. However, this stored NO_3^- is not used for biomass production.

(IV) Finally, enhanced bacterial N uptake would also result in high annual N uptake rates relative to annual PP (Hoch & Kirchman 1995, Middelburg & Nieuwenhuize 2000a). On the other hand, those bacteria can excrete DON, making them an N-source for phytoplankton.

In my opinion, the Greifswalder Bodden plays a similarly important role in the coastal filter of the Baltic Sea coast as the Szczecin Lagoon. Although the N uptake rates are lower a standing stock can already be built up after 2 days if NO_3^- uptake rates are taken as a basis. Thus, the amplitude of N assimilation is lower, but still illustrates the significance of assimilation as a major retention process.

C - Pomeranian Bay

In PB, the PP over the year is up to twice the rates measured in the Southeast Baltic Sea (10.4 to 381.9 nmol L^{-1} h^{-1}) (Kudryavtseva et al. 2011), half the rates of the Bodden and only 8% of the PP in the Lagoon. The modelled NO_3^- export from SL to PB in spring can explain the elevated NO_3^- concentrations of 10-20 µmol L^{-1} which are similar to spring concentrations in the off-shore waters of the Baltic Sea (Wasmund et al. 1998). Pein & Staneva (2024) could illustrate that the river plume of the Oder water entering the Baltic Sea through the Swina can in fact influence station PB, even though it is located west of the river mouth and during the prevailing wind direction W or NW the plume is diverted to the east. While in SL and GB the highest PP was measured in April and February, the highest PP in the Bay was determined in August, supposedly facilitated by diazotrophic cyanobacteria which are independent of DIN and the dominant phytoplankton group in vast parts of the Baltic Sea during the summer months (Niemistö et al. 1989). For non-diazotrophic phytoplankton species the nutrient export from SL may be the most important nutrient source. However, the export from SL is lowest during the summer months and dominantly in the form of organic particles (labelled as "Phyto-C", Fig. 20). To serve as a DIN-source, the particles need to be mineralised, which takes days to weeks (Newell et al. 1981) and contrasts the high PP. However, DON excreted by diazotrophic cyanobacteria (Wannicke et al. 2009) may act as an essential source of N, facilitating all phytoplankton growth and resulting in their high PP.

In contrast to SL and GB, no clear preference for NO_3^- versus NH_4^+ uptake can be identified in the PB over the course of the year. Instead NH_4^+ uptake rates are always higher than NO_3^- uptake rates, displaying the general affinity towards NH_4^+ (Underwood & Kromkamp 1999). In fact, the constantly low NH_4^+ concentration of 0.6 to 2 µmol L^{-1} during the productive season might reflect the continuous activity and production of NH_4^+ transporters in the cell membrane (Clarkson & Lüttge 1991). Additionally, diazotrophic cyanobacterial are independent of DIN but they also have a high affinity for NH_4^+ (Glibert & Berg 2009, Glibert et al. 2016), potentially explaining the high NH_4^+ uptake rates in summer.

Overall, NH_4^+ and NO_3^- uptake rates were 5% and 9% of SL and 6% and 8% of GB, respectively. Obviously, the productivity of PB is much lower than that of the inner coastal ecosystems SL and GB, but PP is closely coupled with the N uptake, as shown by the significant correlations between these variables (Table 2). With the possible presence of diazotrophic cyanobacteria (Meyer-Harms & von Bodungen 1997, Gromisz & Witek 2001), riverine nutrients may be much less important for PP. Interestingly, the Pomeranian Bay shows an elevated N uptake compared to the open Baltic Sea, i.e. N retention processes also take place in the open coastal zone.

D - Synthesis

The C:DIN uptake ratios in the Oder outflow were mostly within the range of the POC:PON ratio or below (Fig. 11), which is indicative for enhanced N uptake. This can result from an increased N demand due to continuous loss of DON shortly after DIN uptake (Bronk & Glibert 1991, Wannicke et al. 2009). During cell division, intracellular N-reserves are used extensively and need to be filled up again (Dauchez et al. 1991). As the Oder outflow is a very productive system, where recycled N supplies the phytoplankton N demand even during limited riverine N input, this cellular metabolism can cause high N uptake in relation to C uptake (PP), resulting in similar uptake and POC:PON ratios (Dauchez et al. 1991).

High C:DIN uptake ratios, as found in SL in April (Fig. 13), can be connected to C overconsumption due to DOC release (Ianson et al. 2003), or to uptake of DON (Carpenter & Dunham 1985, Seitzinger et al. 2002b), which was not measured in this study and would balance, when included, the C:N uptake ratio. When N is limited or sufficiently supplied, the uptake ratio can also increase (Eppley et al. 1977), but not likely due to high riverine input or internal recycling processes. Often, the C:N uptake ratios differ from POC:PON ratios because uptake is rather indicative for cellular metabolisms at the present time while POC:PON shows the time averaged results of this metabolism (Dauchez et al. 1991).

At all three stations, PP did not correlate with nutrient concentrations or abiotic variables (exception O_2 in PB) (Tab. 2). This illustrates the large variability of PP between stations and seasons in this data set and hints towards other influencing factors like the phytoplankton composition. The yearly dominance of cyanobacteria during the summer months (Schernewski & Dolch 2004, Munkes 2005), when the N:P ratio is low (Fig. 9), might explain the absence of correlations between nutrient concentrations and PP, as diazotrophic cyanobacteria do not depend on DIN. And indeed, in the Curonian Lagoon, N fixation has been measured (Zilius et al. 2021). This, however, remains speculative as factors like the effect of the N:P ratio on the phytoplankton composition and finally on the PP were not analysed. Additionally, PP during the summer and autumn months appears to be sustained by recycled DIN, and presumably DON, which cannot be included in the correlation analyses as it was not determined. The lack of correlation between PON, POC and C and N uptake rates displays nicely the discrepancy between biomass standing stock and biomass production. Hence, I support the recommendations to determine process rates at in situ conditions (Cloern et al. 2014) instead of proxies like POM or Chl *a* concentrations or pCO_2.

Most estuaries are heterotrophic environments where respiration dominates over PP and high proportions of DIC and N uptake rates can stem from bacterial and not from phytoplankton uptake. Heterotrophic bacteria can also account for a large fraction of the PO_4^{3-} uptake, ranging between 15% and 90% in rivers and estuaries (Kirchman 1994 and references therein). Especially in estuaries, those percentages can vary strongly along the salinity gradient (Middelburg & Nieuwenhuize 2000a b) and should always be considered when studying nutrient uptake by phytoplankton. The ratios of dark to light (D/L) PP across the three stations (in surface water), displayed in Table 4 were always ≤ 0.16, indicating inhibited uptake in the dark compared to the light. Thus, I conclude that the measured DIC uptake was mostly done by phytoplankton or heterotrophic bacteria, which use organic C compounds, and not by autotrophic bacteria, which would be able to take up DIC in the dark. Interestingly, the dark to light ratio of NH_4^+ and NO_3^- uptake rates were higher than those of PP, but only the differences between D/L of NH_4^+ uptake rates and PP were statistically significantly (ANOVA on Ranks, $n = 16$, $p<0.001$). In addition, the ratios of the three rates showed differences between the stations. Specifically, during each sampling campaign, D/L of NH_4^+ and NO_3^- uptake was highest in PB. Unfortunately, this trend was not statistically significant, only close to significance for D/L of NH_4^+ uptake (ANOVA on ranks, $n = 16$, $p=0.061$ for PB). Theoretically, this would indicate a high share of uptake in the dark, for example by heterotrophic bacteria. This trend of higher bacterial N uptake at the station with the highest salinity is in contrast to previous studies (Kirchman 1994, Middelburg & Nieuwenhuize 2000a), reporting highest bacterial N uptake in the freshwater area of estuaries, which often coincides with high concentrations of nutrients and particles (Middelburg & Nieuwenhuize 2000b), both able to facilitate microbial activity (Kache et al. 2021). Overall, if phytoplankton N uptake is of sole interest, bacterial uptake has to be inhibited e.g. with broad-spectrum antibiotics. Size-fractionated incubation of the samples in the light and in the dark may also reveal dynamics between phototrophic phytoplankton and bacteria, assuming that bacteria make out the majority of microorganisms in the small-size fraction, which is not always the case (Kirchman 1994).

In summary, the data confirm NH_4^+ uptake preferences over NO_3^-, while the absolute NH_4^+ uptake rates in SL and GB are surprisingly similar compared to other studies of estuarine ecosystems (e.g. Middelburg & Nieuwenhuize 2000b, Andersson et al. 2006).

While the uptake of NO_3^- may be subdued by cellular metabolic processes, it is still significant at all sites, especially when the ambient concentrations are high. High ambient nutrient concentrations also support high NH_4^+ uptake rates. How productivity is regulated in general remains unclear, as there is no statistical evidence of particular relationships between nutrient concentrations or abiotic variables.

Table 4. Ratio of dark to light primary production, NH_4^+ uptake rates and NO_3^- uptake rates of surface water samples of Szczecin Lagoon (SL), Greifswalder Bodden (GB) and Pomeranian Bay (PB). Presented as minimum – maximum (mean).

	Primary production	**NH_4^+ uptake**	**NO_3^- uptake**
SL	0.00 – 0.21 (0.06)	0.12 – 0.39 (0.24)	0.00 – 0.23 (0.12)
GB	0.01 – 0.16 (0.04)	0.1 – 0.23 (0.18)	0.01 – 0.16 (0.07)
PB	0.00 – 0.13 (0.04)	0.08 – 0.93 (0.5)	0.01 – 0.71 (0.34)

PP alongside N assimilation is often the first major retention process of riverine N as DIN is bound into organic particles. From there on, PON can be exported or undergoes further transformation (e.g. feeding or remineralisation) and be retained in the ecosystem.

4.2.2 Comparison of individual retention processes

Retention processes are an important component of the coastal filter because they provide the link between riverine inputs and biomass production, followed by ammonification and nitrification. Especially nitrification is essential in the estuarine and coastal N cycle as it connects OM input and N removal.

At all three stations NR were always much lower than NO_3^- and NH_4^+ uptake rates (Fig. 14). Nitrification contributes not even 2% to the total NH_4^+ consumption (annual mean percentage), illustrating a minor role of nitrification in the Oder outflow region. This is in contrast to previous studies in the area (NR of 10 - 7700 nmol L^{-1} d^{-1}, (Dahlke et al. 1997)) and other estuarine systems in the Baltic Sea area, e.g. the Curonian Lagoon, where nitrification in the water column and the sediment provides up to 95% of NO_3^- for pelagic community production and sedimentary denitrification, especially during summer (Broman et al. 2021, Zilius et al. 2024). However, I only determined pelagic nitrification, presumably underestimating the total nitrification activity of the ecosystem, as sedimentary nitrification often plays a major role (e.g. Macfarlane & Herbert 1984, Pauer & Auer 2000). According to the DNR_n in the Great Lagoon presented in this thesis (Fig. 18), nitrification in the sediment supplies up to 70% of the NO_3^- for denitrification (DNR_n of 2000.8 µmol m^{-2} d^{-1}). This would equal a sedimentary NR of 1400 µmol m^{-2} d^{-1}, which is almost the same to the sedimentary nitrification rates calculated by Broman et al. (2021) for the Curonian Lagoon (1590 µmol m^{-2} d^{-1}).

Pelagic nitrification rates can be low due to the competition of nitrifiers with phytoplankton over the ambient NH_4^+ as was shown in the open ocean (Smith et al. 2014, Wan et al. 2018). However, due to high turbidity with a Secchi depth of only 20 cm in August 2022 in SL, most of the water column was light-limited. The resulting lower photosynthetic activity of phytoplankton was assumed to weaken the competition between nitrifiers and photoautotrophic organisms (Smith et al. 2014). However, this assumption was disproved, as the high PP and coinciding high N demand of the phytoplankton in August causes a disadvantage for the nitrifiers and thus, low NR. A more detailed discussion on the factors influencing nitrification is presented in section 4.4.

Despite these conditions, the NR remained low. Consequently, assimilation of DIN seems to be the major retention process in the Oder outflow area, binding DIN in biomass, and therefore excluding it short-term from the phytoplankton-available pool. The average C:N ratio of ~ 8.7 (Fig. 11) also suggests, that the majority of POM is of phytoplankton origin. After sedimentation, OM is mineralised to NH_4^+, nitrified to NO_3^- and finally denitrified in organic-rich and anoxic sediments to be permanently removed from the system (Deutsch et al. 2010). This role of PON as an intermediate storage and transport form of N was previously shown in the Vistula estuary (Bartl et al. 2019), which has a much shorter WRT (Dippner et al. 2019) but is otherwise comparable to our study sites, and the Curonian Lagoon (Zilius et al. 2018).

Furthermore, ammonification (remineralisation of OM) seems to be an equally important retention process in the Oder outflow as it connects other retention processes, including assimilation and nitrification. High assimilation rates in summer are facilitated by the ammonification of OM, supporting up to 60% of the assimilatory N demand during a summer cyanobacteria bloom in the Curonian Lagoon (Zilius et al. 2018). They argued that remineralised N and fluxes from the sediment met only 12% of the demand, so that additional sources such as DNRA are required. High ambient NH_4^+ concentrations can enhance NR, but high rates have also been found in estuaries with low ambient NH_4^+ concentrations (Bianchi et al. 1999, Carini et al. 2010, Hsiao et al. 2014, Heiss & Fulweiler 2016, Tolar et al. 2016). The latter relationship suggests a tight coupling of NH_4^+ production by ammonification and nitrification, as demonstrated in cyanobacteria aggregates (Klawonn et al. 2015). However, in the Oder outflow, ammonification is closely coupled to assimilation, as phytoplankton outcompetes nitrifiers. Whether nitrifiers or phytoplankton ultimately have the best possible access to the remineralised NH_4^+ depends on various environmental factors such as the community composition of nitrifiers and phytoplankton or abiotic variables. A further discussion on the competition between nitrifiers and phytoplankton can be found in section 4.4.

The NH_4^+ production through DNRA in the water column was not measured in the present study, but the process may be relevant. The results of Broman et al. (2021), suggest that NH_4^+ regeneration through dissimilatory pathways in the oxygenated water column of the Curonian Lagoon is possible. This can be attributed to the presence of suspended particles that create anoxic microsites where bacteria thrive, that perform DNRA. Similar to the Curonian Lagoon, DNRA rates in the sediment of the Szczecin Lagoon are lower than denitrification, suggesting their negligible significance in providing NH_4^+ substrate (Broman et al. 2021). As DNRA can be influenced, e.g., by the accumulation of OM (An & Gardner 2002, Song et al. 2014, Yin et al. 2017), sulphides (Caffrey et al. 2018) or reduced metal forms (Kessler et al. 2019), its regulation is difficult to specify. Hellemann et al. (2020), on the other hand, were able to show a high share of DNRA in total NO_3^- reduction in sandy sediments of the northern Baltic Sea. In contrast, the share of DNRA in the total NO_3^- reduction was only 3-5% in the SL, emphasizing the spatial heterogeneity of NO_3^- reduction processes across various coastal forms (Asmala et al. 2017).

All in all, the relatively low NR observed in the Oder outflow region were unexpected, given the favourable abiotic environmental conditions. This suggests that the production of NO_3^- via pelagic nitrification is insignificant. Conversely, the remineralisation of OM via ammonification is of significant importance in this ecosystem, as it supports PP during periods of depleted DIN concentrations in the water column. While it facilitates the retention of N in the system, it also contributes to the ongoing eutrophication of the environment. In addition, the remineralised NH_4^+ may be a favoured N-source of HABs, which have been observed in SL and GB (Munkes 2005, Overlingė et al. 2020), and can pose risks for humans and animals. Cyanobacteria also preferably use NH_4^+ (Takamura et al. 1987) as there are many non-diazotrophic species, e.g. *Microcystis aeruginosa*, which is very abundant in SL.

4.2.3 The role of removal processes

The DNR were only measured in the Great Lagoon of SL. Since it is well proven that denitrification is closely linked to the OM content of the sediments (Deutsch et al. 2010), I will extrapolate the rates to the entire Szczecin Lagoon, assuming that ~ 54% of the bottom area is covered in muddy sediments (corresponding to St. 2) and ~ 46% is covered in sandy sediments (corresponding to St. 1) (Osadczuk & Wawrzyniak-Wydrowska 1998). As literature data from the Bodden and Bay are sparse, the Lagoon will be the focus of this chapter.

Denitrification in the sediment is the most intensely studied N removal process in the Baltic Sea. DNR in the muddy sediments of the Lagoon (DNR_{tot} of 2897 ± 214.9 µmol m^{-2} d^{-1}) were much higher (Tab. 5) than rates determined in the Curonian Lagoon (Broman et al. 2021, Zilius et al. 2024), in the fine sediment of the

Gulf of Finland (Hietanen & Kuparinen 2008, Jäntti & Hietanen 2012, Hellemann et al. 2020) and the Himmarfjärden (Bonaglia et al. 2014). According to Dahlke et al. (1997), DNR in GB are much lower than in SL, but in the Peenestrom, where the organic content of the sediment and the riverine NO_3^- input from the Peene are high, the rates are only slightly lower.

Table 5. Reference values of denitrification rates (DNR) in muddy and sandy sediments.

Sediment type	**Ecosystem**	**DNR (in µmol m^{-2} d^{-1})**	**Reference**
Muddy	Szczecin Lagoon, Baltic Sea	2897 ± 215	This thesis
	Greifswalder Bodden	~ 120	(Dahlke et al. 1997)
	Peenestrom	≤ 2088	
	Curonian Lagoon, Baltic Sea	950 ± 60	(Broman et al. 2021)
		1161 ± 62	(Zilius et al. 2024)
	Gulf of Finland, Baltic Sea	263	(Hellemann et al. 2020)
		≤ 600	(Hietanen & Kuparinen 2008)
		46 – 1619	(Jäntti & Hietanen 2012)
	Himmarfjärden (Baltic Sea)	≤ 420	(Bonaglia et al. 2014)
Sandy	Szczecin Lagoon	444.7 ± 116	This thesis
	Wadden Sea, North Sea	≤ 2256	(Marchant et al. 2016)
		~5700	(Gao et al. 2012)
	Kalmar Sound, Baltic Sea	≤ 96	(Sundbäck et al. 2006)

In the sandy sediment of SL, with a DNR_{tot} of 444.7 ± 116 µmol m^{-2} d^{-1}, the denitrification is 6.5 times lower than in the muddy sediments of the Lagoon. While DNR in the Kalmar Sound are lower (Tab. 5) than in SL (Sundbäck et al. 2006), rates in the sandy sediment of the North Sea exceeds the sandy rates of SL by a factor of 12 (Gao et al. 2012, Marchant et al. 2016). Surprisingly, the DNR of the muddy sediment in SL, an ecosystem dominated by diffusive transport processes across the sediment water interface, are comparable to rates measured by Marchant et al. (2016) in the permeable sediments of the North Sea (≤ 2256 µmol m^{-2} d^{-1}), a system dominated by advective pore water transport that was shown to increase process rates (Huettel et al. 2003, 2014).

Similar dynamics in NO_3^- reduction rates and in nutrient fluxes over the sediment water interface were measured in the Curonian Lagoon (Zilius et al. 2018, 2024) and the Kalmarsund (Sweden) (Sundbäck et al. 2006). In those studies, the DNR in sands was 13.7% of the DNR in mud (Asmala et al. 2017), which is close to the differences between sites in SL, where sandy DNR were 15.4% of the DNR found in muddy sediments.

Such differences between sediment types are mostly driven the OM content (Asmala et al. 2017, Carstensen et al. 2020), which is often low in sandy sediments (Thoms et al. 2018). In the muddy sediment of SL, the organic C and N content was 10 and 1.3%, respectively. In addition, temperature, O_2 concentrations and NO_3^- availability can influence DNR (Piña-Ochoa & Álvarez-Cobelas 2006, Hietanen & Kuparinen 2008, Deutsch et al. 2010).

The Denitrification Efficiency (DE), calculated according to (Eyre & Ferguson 2009) indicates the percentage of the total DIN released from the sediment as denitrified N_2. Whether N efflux from the sediment is bioavailable, e.g. NH_4^+, NO_3^- or DON, or not bioavailable, e.g. N_2, has important implications for the trophic and ecological status of the ecosystem. In muddy sediments of SL, the DE is around 20%, i.e. 80% of the DIN release from the sediment is NH_4^+, NO_3^- or NO_2^- efflux. This illustrates the dominance of degradation and recycling processes resulting in an efflux of N into the water column instead of loss of N_2. It has been shown that DE decreases with increasing sediment carbon decomposition rates, due to elevated C input, i.e. eutrophication (Eyre & Ferguson 2002, 2009). As the Oder outflow system is eutrophic to hypertrophic (see section 4.1), a low DE can be expected. Using this relationship between DE and trophic status, Eyre & Ferguson (2009) defined a trophic scheme in which oligotrophic, mesotrophic, eutrophic and hypertrophic ecosystems are characterised by a median DE of 68, 40, 18 and 8%, respectively. Consequently, the DE of 20% for the eutrophic to hypertrophic Szczecin Lagoon aligns well with my previous trophic classification and is similar to the DE of 22% measured in the Curonian Lagoon (Broman et al. 2021), a comparable ecosystem to SL. Benelli et al. (2024) calculated lower DE for the Vistula estuary and found a decreasing trend from spring to summer and from deep to shallow coastal waters, representing a shift from high to low sedimentary OM content.

In the Curonian Lagoon, Zilius et al. (2018, 2024) showed an influence of the phytoplankton composition on sedimentary denitrification. In spring, when a diatom-dominated bloom was deposited, it was immediately remineralised, stored or nitrified and ultimately denitrified. Conversely, only a minor portion of the cyano-bacteria-dominated summer bloom settled on the sediment due to high buoyancy, resulting in lower denitrification. The authors concluded that the majority of riverine DIN is likely to be denitrified in winter and spring, not during the summer months. The phytoplankton community composition in SL is comparable to that of the Curonian Lagoon, with a high abundance of diatoms observed in spring and cyanobacteria in the summer months, when the buoyant species *Microcystis aeruginosa* and *Dolichospermum sp.* are dominant. Consequently, the same temporal pattern of denitrification being higher in winter and spring and lower in summer might be expected. This would result in even higher DNR in winter and spring than were currently measured in August. This is in contrast to other studies which demonstrate a seasonal fluctuation with elevated denitrification rates during the summer months or at times of high temperatures (Piña-Ochoa & Álvarez-Cobelas 2006, Skiba 2008), also for the Baltic Sea (Jäntti et al. 2011). It can be reasonably assumed that sedimentary nitrification, which represents the primal source of NO_3^- for denitrification, exhibits a similar temporal pattern, with the highest rates occurring during the summer months (Jäntti et al. 2011). This is supported by findings in the Narraganset Bay, USA, (Seitzinger et al. 1984) as well as in the Tay estuary in Scotland (Macfarlane & Herbert 1984). The data from the Chamber Lander support this further because NO_3^- is released from the sediment in SL in August (Fig. 21), despite the high consumption by denitrification. This correlation of NO_3^- efflux and sedimentary nitrification was also found in the sediments of Danish waters in the Belt area, Kattegat and Skagerrak (Blackburn & Henriksen 1983). Interestingly, both theories on the major influencing factors and the time periods of peak denitrification are plausible and can be applied to the Lagoon, resulting in an inconclusive picture of the seasonality of denitrification in the Lagoon. Therefore, it is necessary to conduct seasonal, if not monthly, measurements of DNR in order to identify the driving factors.

In general, riverine NO_3^- as well as NO_3^- from sedimentary nitrification are used for denitrification during periods of high discharge, i.e. during the winter and spring months. Once the riverine NO_3^- input decreases and the NO_3^- concentration in the water column has been depleted, typically by May (according to LUNG monitoring data), sedimentary nitrification becomes the sole source of NO_3^- (coupled nitrification-denitrification). Consequently, the DNR becomes dependent on coupled nitrification-denitrification. Since nitrification in the water column of the SL was negligible, nitrification in the sediment provided nearly 70% of the NO_3^- for denitrification (DNR_n) and DNRA ($DNRA_n$) (Fig. 18). Specifically, a high sedimentary DNR_{tot} of 2897 ± 214.9 $\mu mol\ m^{-2}\ d^{-1}$ was measured in SL in August 2022, mostly driven by coupled nitrification-denitrification. Thereby, the nitrification was driven by a high sedimentary NH_4^+ pool of 273.6 $mmol\ m^{-2}$, according to the pore water concentrations in SL in August. In contrast, the NO_3^- pool in the sediment comprised only 1.3 $mmol\ m^{-2}$ (calculated from pore water profiles and thereby excluding activity of macrofauna), illustrating the dependence of denitrification on nitrification. Surprisingly, due to the low overall DNR_w, only 6% of the annual riverine NO_3^- input of 2022 to the Great Lagoon (sum of discharge from Oder, Uecker, Zarow) is directly removed from the water column over a year, which is comparable to previous estimates for the Oder outflow region (7%, Dahlke et al. 1997). The overall high DNR illustrate that not river-borne but rather NO_3^- from nitrification is removed during denitrification in SL. Hence, N assimilation, mineralisation and subsequent coupled nitrification-denitrification are probably tightly linked in the Lagoon. This ultimately leads to efficient N removal, as 33% of the riverine input are removed in the Lagoon, when both DNR_n and DNR_w are included in the calculation. This agrees with mass balance calculations of Pastuszak et al. (2005), who estimated the N loss of around 30% of inputs. In comparison, the average annual N removal in the total Baltic Sea coastal zone is 16% (Asmala et al. 2017). Even in the Curonian Lagoon, a comparable ecosystem to the Szczecin Lagoon, only 11% of the total N input is removed via denitrification in summer (Broman et al. 2021), demonstrating the high potential for N removal after previous recycling in SL.

Surprisingly, our data further suggest that nearly 85% of the annual DIN input in 2022 was initially assimilated in SL via NO_3^- and NH_4^+ uptake (low NR were considered negligible), followed by remineralisation and recycling processes. Thus, N retention in the Szczecin Lagoon is processing several times the amount compared to N removal (considering NH_4^+ and NO_3^- uptake vs. denitrification). This demonstrates the important role of retention processes as a critical factor in the coastal filter of lagoons.

Lastly, Humborg et al. (2000) estimated that 5.4% of the annual N load coming from the Oder River was removed via burial of organic N, whereas they did not take into account the littoral zones and the removal of sediment during dredging of the shipping channel. Leipe et al. (1998) estimated a retention of particulate N of around 6% of the total N input from the Oder. Additionally, Lampe (1999) postulated that only a small fraction of riverine N is permanently buried in the sediments of SL as frequent dredging activities and sediment resuspension result in the flushing of particles into the Baltic Sea (Leipe et al. 1998). There is no information on burial in PB and GB, but calculations for the Swedish coast suggest that less than 8% of the land-derived N are buried (Almroth-Rosell et al. 2016), representing a small fraction of N removal (Gustafsson et al. 2012), similar to SL.

All in all, the results illustrate that N retention processes, including assimilation and remineralisation, are the primary drivers of the transformation of riverine DIN. In contrast, denitrification of riverine NO_3^- from the water column (DNR_w) plays a relatively minor role. Ultimately, the N retention processes facilitate the successful N removal via denitrification in the sediment (DNR_n). This is because the assimilation is followed by deposition on the sediment surface, remineralisation and nitrification. Denitrification may be the ultimate objective in the concept of the coastal filter function, as it counteracts eutrophication. But, the effectiveness of denitrification can be substantially reduced in the absence of efficient recycling/retention processes prior to this.

4.2.4 Influence of WRT on nutrient turnover

Schiewer (2002) and Pastuszak et al. (2003) stated that the short residence time of river-dominated estuaries, such as the Szczecin Lagoon, results in a diminished efficiency to act as bioreactors and thus, coastal filters. Conversely, initial estimates with a water age module yielded higher residence times for the Lagoon and the Greifswalder Bodden than previously published (e.g. Mohrholz & Lass 1998, Grelowski et al. 2000, Friedland et al. 2019). Hence, the period of Lagrangian particle advection for the estimation of the residence time was extended to 180 days, producing the novel results (Table 6). They are based on robust validated numerical model simulations that resolve the channels between SL and the Baltic Sea (Pein & Staneva 2024).

A positive relationship between WRT and N removal via denitrification was shown for various aquatic ecosystems such as lakes, rivers, estuaries and continental shelfs (Kelly et al. 1987, Nixon et al. 1996, Dettmann 2001, Laursen & Seitzinger 2002a, Seitzinger et al. 2006). Overall, the WRT directly controls the N processing time in an ecosystem, and hence the proportion of N inputs that are retained or removed. The riverine N input on the other hand is determining the amount of N available for microbial processes (Seitzinger et al. 2006). Thus, a long WRT of ≥ 180 days provides optimum conditions for both efficient N retention and N removal. Interestingly, Peierls et al. (2012) demonstrated that the phytoplankton biomass in shallow (< 5 m), micro-tidal estuaries is at its maximum when the flushing time (the average time that freshwater spends in the estuary) is only approximately 10 days. When the flushing time is less than 10 days, the accumulation of biomass is limited by the dilution of the phytoplankton community. At longer flushing times, the biomass growth rate is limited by the nutrient supply (Peierls et al. 2012). However, in SL, the relatively long WRT likely facilitates the close coupling of assimilation of N in phytoplankton, OM mineralisation and subsequent assimilation of the produced NH_4^+, as described above, making it a reactor which increases the productivity of the system. Furthermore, effective OM mineralisation, subsequent N release from the sediment, and NH_4^+ accumulation in the water column facilitated high August PP as well.

The same was described for the Curonian Lagoon (water renewal time of 150 d) (Umgiesser et al. 2016), where OM mineralisation followed by nitrification provided sufficient NO_3^- supply for denitrification in summer when N river loads are low (Zilius et al. 2018, Broman et al. 2021). In the shallow Norsminde Fjord, Denmark, with low water residence times of 1.5 to 13 d, the removal of annual N inputs was only 2% to 3% (Nielsen 1992). In SL, the estimated annual N removal of 33% of the total DIN input is higher than in the Norsminde Fjord, although the N load to the Fjord was larger,

Table 6. Compilation of previously published residence times in the Oder outflow region.

Ecosystem	Residence time	Reference
Szczecin Lagoon	55 days	(Schiewer 2008)
	53 days	(Pastuszak et al. 2005)
	~ 2 months	(Mohrholz & Lass 1998, Grelowski et al. 2000)
Small Lagoon	~ 157 days	This study
	60 days	(Friedland et al. 2019)
	~ 3 months	(Schernewski et al. 2023)
	3-6 months	(Meyer & Lampe 1999)
Great Lagoon	~ 96 days	This study
	0.5-2 months	(Meyer & Lampe 1999)
	~ 1 months	(Schernewski et al. 2023)
Greifswalder Bodden	~ 143 days	This study
	36 days	(Schiewer 2008)
Pomeranian Bay	21 days	(Pastuszak et al. 2005)

demonstrating a less efficient costal filter in the Fjord compared to estuarine lagoons like SL. Likewise, in Puck Bay, a high residence time was calculated, enhancing nutrient cycling (Dippner et al. 2019). These findings emphasise that higher WRT are able to retain and process larger amounts of nutrients from rivers (Dettmann 2001). However, a long WRT might be responsible for the phytoplankton dominance in eutrophic ecosystems as they outcompete benthic algae by increasing turbidity during the bloom phase and, hence, shading macrophytes.

The WRT of PB was not estimated as part of this study, but it was stated before that the exchange with other parts of the Baltic Sea is mostly driven by wind and density (Mohrholz & Lass 1998, Lass et al. 2001). For the Bay of Gdansk, a WRT of 53-60 days was estimated (Dippner et al. 2019), which could be transferred to PB as depths and bottom morphology are similar. According to the relationship of WRT and N removal, a high portion of the incoming N from the Swina and Greifswalder Bodden will be exported (Dettmann 2001) and the retention and removal capacity of the open coastal zone will be lower than of the inner costal ecosystems. However, studies from the North Sea demonstrated that sandy sediments along the open coastal zone have a high removal capacity (Marchant et al. 2016) because the advective transport of nutrient and OM into the sediment facilitates N turnover and N removal processes (Huettel et al. 2003, Precht

& Huettel 2003). Therefore, the coastal filter efficiency of the Pomeranian Bay should not be underestimated, although it probably is overall lower than in SL and GB.

4.2.5 The coastal filter of the Oder outflow - Summary

In conclusion, the coastal filter function of the Oder outflow region is driven by the tight coupling of retention and removal processes. Up to 85% of the annual riverine DIN input is assimilated initially. Thereby, the differing hydro-morphological characteristics of the three ecosystems determine their coastal filter efficiency: the long WRT and shallow water depths of SL facilitate the efficient assimilation and recycling of N, while the wind-forced currents in PB lead to a fast dilution of nutrients and DIN independent phytoplankton, like diazotrophic cyanobacteria. Due to the effective link between assimilation and remineralisation in SL and GB, continuously producing the nutrients to support PP, the Lagoon and the Bodden are strongly eutrophic. However, when remineralisation of OM takes place in the sediment, it provides the basis for effective N removal, as NH_4^+ from ammonification is nitrified, subsequently leading to the denitrification of ~ 33% of the riverine N input in the sediment. Hence, the high productivity of the Oder outflow region can be understood as two sides of the same coin: it promotes eutrophication by repeated remineralisation of nutrients that support high PP, but it also provides the organic matter and nutrients for efficient N removal once the OM produced reaches the sediment, where it can finally and efficiently be denitrified. It is noteworthy that these dynamics appear to be a distinctive feature of estuarine lagoons in the Baltic Sea, as Broman et al. (2021) observed the same functioning in the Curonian Lagoon, where more N is recycled than denitrified.

4.3 Role of the sediment in the Oder outflow

In shallow coastal ecosystems, the sediment can alter pelagic processes due to the tight coupling of the water column and the sediment, including deposition of OM, sediment resuspension and the release of inorganic nutrients (Griffiths et al. 2017). Especially in shallow ecosystems, where wind-driven mixing prevails, sediments are the only compartment where anoxic conditions are found, which are mandatory for removal processes such as denitrification.

4.3.1 Comparison of nutrient flux determination methods

A number of techniques are available for measuring solute exchange across the sediment-water interface in an ex situ setting. These include pore water extraction via rhizons (Seeberg-Elverfeldt et al. 2005) or from sediment slurries (Serruya et al. 1974), whole core incubations (Allert & Mackin 1989, Choisnard et al. 2023) and measurements of dissolved gas concentrations such as O_2 using microelectrodes (Revsbech et al. 1980). In situ sampling involves the deployment of lander systems on the sediment, which are equipped with microelectrodes (Ahmerkamp et al. 2017), pore water samplers (Seeberg-Elverfeldt et al. 2005) or incubation chambers (Thoms et al. 2018). Each method considers different abiotic and biotic influential factors that may regulate the fluxes and measurements.

As part of this study, a benthic Chamber Lander was used for in situ assessments, and nutrient fluxes were additionally calculated from pore water profiles of sediment cores, which were measured from pore water samples obtained with rhizons. When fluxes were obtained by both methods, i.e. sampling on the same day and station, nutrient fluxes measured with the chamber lander were frequently higher than the fluxes calculated from the pore water profiles (Fig. 22). While the O_2 and nutrient fluxes derived from the Chamber Lander incubations are estimated as changes in concentrations over a designated time period, pore water nutrient profiles enable the calculation of fluxes over a depth horizon, whereby the calculation is based on the change in concentration over a specific depth, according to Fick's Law (for further details, please refer to Material and Methods 2.7). Lavery et al. (2001) showed that that predicted nutrient release, calculated according to Fick's First Law, was close to 100% of the respective observed fluxes in coarse sediments (grain size 0 - 3 mm). In fine sediments (grain size < 0.01 mm), calculated nutrient fluxes were overestimated by up to 40% in comparison to observed fluxes, probably caused by unfavourable oxygen conditions influencing chemical and microbial processes. The authors conclude that Fick's First law is useful to estimate a baseline nutrient flux but should be applied cautiously in unfavourable redox conditions (Lavery et al. 2001). Hence, the theoretical basis of the methods and the calculations is different, and a direct comparison must be approached with caution.

The second reason for the discrepancy may be attributed to the fact that the Chamber Lander is deployed on the sampling site, measuring in situ fluxes and thus including the activity of the benthic fauna. Benthic fauna often increases fluxes over the sediment-water interface due to their activity, namely movement, ventilation, and the building of burrows. Sediments influenced by this bioturbation exhibit an enhanced efflux of nutrients and other substances into the water column (Karlson 2007) in comparison to sediments without fauna activity. Furthermore, benthic fauna excrete NH_4^+, thereby enlarging the sedimentary NH_4^+ pool (Gardner et al. 1993), which is primarily supplied from the degradation of organic matter in the sediment. Moreover, bioturbation by benthic fauna may also promote the adsorption and subsequent precipitation of P by oxidising deeper sediment layers and buffering DIP release (Lewandowski et al. 2005, Karlson 2007).

During the degradation of OM, O_2 is consumed by heterotrophic microorganisms and fauna, resulting in a diffusive influx of O_2 into the sediment. Oxygen is further consumed by microorganisms during oxidation reactions, such as nitrification. In addition, bioirrigation occurs, a process in which tube-burrowing fauna, for example polychaetes, pump oxic bottom water through their tubes. As a result, the sediment surface of the tunnels becomes oxic, while the sediment surrounding the tunnels remains anoxic. This enlarges the oxic-anoxic interface and thus increases several redox-dependent biogeochemical processes, including coupled nitrification-denitrification (Pelegri et al. 1994, Gilbert et al. 1998, Zilius et al. 2022) and DNRA (Bonaglia et al. 2013). In fact, when the O_2 uptake of the sediment is divided in diffusion mediated and fauna mediated, the latter can account for up to 70% of the total O_2 uptake (Archer & Devol 1992, Glud & Blackburn 2002).

Hence, benthic fauna plays an active role in altering the distribution of oxygen in the sediment and enhancing the efflux of nutrients and metabolites produced in remineralisation processes. This provides a reasonable explanation for the higher fluxes that have been measured with the Chamber Lander compared to the calculations that have been made from pore water profiles.

In contrast to the Chamber Lander, concentration profiles of nutrients in the sediment pore water provide information about the nutrient pool stored inside the sediment. These nutrients could potentially be supplied to the overlying water, for example during strong resuspension or dredging. Then, the emitted nutrients can fuel uptake and transformation processes in the water column (Schallenberg & Burns 2004). It is therefore important to know the theoretical amount of nutrients to be released. The size of benthic nutrient pools can influence, and itself be influenced by, the degree of benthic microbial processes such as nitrification and denitrification (Middelburg et al. 1996, Fennel et al. 2009). For example, while the sedimentary NO_3^- pool in SL in summer was low (1.3 mmol m^{-2}), the NH_4^+ pool was large enough (273.6 mmol m^{-2}) to support the high rates of coupled nitrification-denitrification that were measured in SL in August.

However, nutrient fluxes calculated using Fick's Law, represent only theoretical fluxes of nutrients based on the theory of diffusion, excluding the influence of fauna and advection. Using the chamber lander, one measures the amount of nutrients actually reaching the overlying water, based on diffusion as well as fauna reworking. Nonetheless, small scale concentration changes are more difficult to assess with the chamber lander as the released nutrients are diluted in the water volume of the chamber (in my case 27 - 29 L, depending on the penetration depth of the chamber). For this reason, for example changes in PO_4^{3-} concentrations were not detectable using the chamber lander, but were calculated using pore water profiles. Overall, both methods seem to be most sensitive towards different nutrient species. While NH_4^+ fluxes were not detectable from the pore water profiles, incubations with the chamber lander showed a significant concentration increase at most sampling days and locations. This is most likely associated to fauna activity. PO_4^{3-} on the other hand was barely detectable using the chamber lander. As the water in the chamber was oxic over the whole course of the incubation period, I suspect that the little amount of PO_4^{3-} which was released from the sediment was at some point reacting with Fe(III)-ions to iron phosphate, excluding it from the dissolved pool (Froelich et al. 1982).

Altogether, the chamber lander is better suited to estimate the in situ flux of nutrients from the sediment to the water column as it includes the benthic fauna and aims for a concentration change at the target location, not the source. Unfortunately, the chamber excludes any physical impact such as currents and wave action. This leads to strongly altered assumptions of in situ nutrient fluxes, especially in shallow coastal ecosystems with sediment of high permeability like in the Pomeranian Bay. Specifically, in PB currents and wave action can lead to advective pore water flux in its sandy sediments of high permeability (compared to fine sediments in SL and GB) where water and solutes are actively transported into the sediment, overpowering diffusive pore water flux by several orders (Huettel et al. 1996). Advective pore water exchange can result in the shift of redoxclines in the sediment as anoxic pore water is released and the O_2 consumption in the sediment is increased (Huettel & Gust 1992). This will affect redox-sensitive biogeochemical processes in the sediment such as nitrification and denitrification which in turn influence nutrient fluxes over the sediment water interface. Only when those forces are included in the measurements, real in situ fluxes can be determined. Chamber Landers like *Sandy* were developed to include advective pore water exchange by adjusting the speed of the stirrer inside the chamber to establish pressure gradients and thereby advective flow similar to in situ conditions (Janssen et al. 2005a b). Unfortunately, even the highest stirring speed in the Chamber Lander I used did not result in advective pore water flow, as it was not aimed to be used for such investigations. In SL and GB, large parts of the Lagoon and Bodden are dominated by diffusive fluxes and covered in fine sediments whereas advective pore water transport is assumed to be restricted to shallow, sandy sediments. Hence, the Chamber Lander is sufficient for studies of solute exchange in the inner coastal ecosystems such as lagoons where physical forcing has a minor impact on exchange processes across the sediment water interface.

4.3.2 Influence of sediment on the coastal filter

Sediments have the capacity to store nutrients via burial (Leipe et al. 1998). For example, estuarine sediments can have a large storage pool of NH_4^+ as the available oxidants are limited, resulting in the accumulation of NH_4^+ and other reduced ions in the anoxic sediment. But, sediments can also release nutrients, e.g. PO_4^{3-} and NH_4^+, into the water column above (Janssen et al. 2005a, Niemistö et al. 2018, Thoms et al. 2018), which I quantified in the chamber incubations, whose results will be discussed here. NH_4^+ is a product of OM degradation at the water sediment interface (Waugh & Aller 2021), representing an important nutrient source. Due to frequent wind-induced mixing, NH_4^+ from the bottom water will be easily mixed with the upper water layers and supports high uptake rates, as shown in August in SL. In Danish coastal waters, for example, Blackburn & Henriksen (1983) estimated that 30 - 82% of the DIN requirements of the phytoplankton could be supplied by the flux of NH_4^+ and NO_3^- from the sediment, illustrating the significant role of the sediment for pelagic processes. In SL, an assessment of the NH_4^+ uptake rates in the water column and the NH_4^+ fluxes from the sediment indicates that the sedimentary NH_4^+ fluxes could potentially support a maximum of 17.2% of the pelagic uptake rates, whereby the highest estimates were calculated for August and October (7 - 17.2%). It can thus be concluded that the primary source of DIN for pelagic phytoplankton productivity is not the sediment but riverine DIN during the spring months and remineralised NH_4^+ during the summer months.

The measured O_2 consumption in the sediment (30.9 - 61.3 mmol m^{-2} d^{-1}) of SL (Fig. 21) is similar to that in other lagoons (De Vittor et al. 2012, Zilius et al. 2012, 2014, 2022). Assuming a 1 molar ratio between CO_2 and O_2 as the respiratory quotient and a sedimentary C/N molar ratio of 8.86 (mean of upper 10 cm in SL), then the theoretical ammonification rates would be 3.5 - 6.9 mmol N m^{-2} d^{-1}, which are close to the NH_4^+ fluxes obtained in the chamber incubations in the Lagoon (0.01 - 9.8 mmol N m^{-2} d^{-1} in August). The high O_2 consumption measured during August (61.3 mmol m^{-2} d^{-1}) indicates that fresh organic matter inputs had a significant impact on respiration (Zilius et al. 2012, 2014).

Surprisingly, O_2 consumption in the sandy sediments of PB (17.4 - 31.9 mmol m^{-2} d^{-1}) is only slightly lower than in SL (Fig. 21), suggesting a comparable degree of OM degradation, possibly due to high OM input and subsequent enhanced remineralisation caused by advective transport processes (Forster et al. 1996, Huettel et al. 1996, 2003). Indeed, the O_2 consumption rates at PB are comparable to those observed in the permeable shelf sands of the German Bight (31.2 ± 18.2 mmol m^{-2} d^{-1}, Janssen et al. 2005b) and to other Baltic Sea estuaries, such as the Himmerfjärden in Sweden (5.6 - 30.3 mmol m^{-2} d^{-1}, Bonaglia et al. 2014) and the Curonian Lagoon in Lithuania (13.7 - 46.8 mmol m^{-2} d^{-1}, Zilius et al. 2012). Specifically, the highest O_2 consumption in SL was measured in August during the highest NH_4^+ flux of 9.8 mmol N m^{-2} d^{-1}. The elevated O_2 demand in sediments may ultimately result in the depletion of O_2 concentrations in bottom waters, which could potentially lead to the development of hypoxia or anoxia. In contrast, model simulations indicate that in the Lagoon and in extensive areas of the Bodden, the bottom water O_2 concentrations are not strongly influenced by O_2 respiration during high WRT (Pein & Staneva 2024) and that the shallow waters experience frequent wind-induced mixing of the water column. The model results are supported by LUNG monitoring data, which did not record any hypoxic or anoxic conditions. In contrast, Bangel et al. (2004) measured short-term anoxia in the Lagoon, induced by stable, short-term stratification, which induced P release from the sediment.

Since the LUNG monitoring takes place on a monthly basis, and hypoxia and anoxia can occur within days, as proven by Bangel et al. (2004), previous measurements may have missed these occasions. In fact, the O_2 consumption rate, as measured with the Chamber Lander, indicates that anoxia in SL can occur after only 4.12 days of calm weather when the wind speed is < 3 m s^{-1}. According to meteorological data from the German Meteorological Service, such conditions occurred on 77 occasions in 2021 and 2022. In other words, the data indicate that during the summer months of June, July, and August, when the highest O_2 consumption can be expected, there were 12 (2021) and 21 (2022) events when the wind speed was < 3 m s^{-1} for 4 consecutive days. Hence, bottom-water anoxia is a real and probable threat in SL. In PB, monitoring data from the MARNET station "ODAS Oder Buoy" show five events since 2000 when the bottom water was hypoxic or anoxic (Leibniz Insitute for Baltic Sea Research Warnemünde 2023, https://odin2.io-warnemuende.de/). Besides eutrophication, an enhanced stratification of the water column resulting from climate change (IPCC, Bindhoff et al. 2019) can increase the risk of bottom water oxygen deficiency. In fact, according to Rabalais et al. (2002), stratification of the water column and decomposition of OM are the two most important factors leading to the development and persistence of hypoxia and anoxia. The first isolates the oxygenated surface water from the bottom water, leaving diffusion as the sole transport process over the oxycline. At the same time, decomposition of OM in the bottom water and sediment consumes O_2, lowering the overall O_2 concentration. Increased phytoplankton biomass production due to eutrophication therefore provides ideal conditions for the formation of hypoxia. This, in turn, can lead to the release of phosphorus (P) from the sediment.

During anoxic and reduced conditions in the sediment, P can be released into the water column, as has been demonstrated in other coastal regions (Petkuviene et al. 2016). For the Greifswalder Bodden, Meyer et al. (1998) coupled nutrient data to a 2D-current model and concluded that the sediment might even represents a permanent P source, facilitated by internal release processes. For SL, models estimate an anoxic P release of up to 10 µmol m^{-3} d^{-1} (Schernewski & Wielgat 2001), which is comparable to the theoretical diffusive P efflux of 17 µmol m^{-2} d^{-1}, which I calculated from the August pore water profile. However, no P flux from the sediment was detected in SL using the Chamber Lander, which is reasonable, considering the continuously oxygenated bottom water. During periods of calm conditions and no mixing, pelagic respiration, in addition to stratification, can prevent the downward transport of O_2 to the bottom water, eventually resulting in hypoxia within hours (Zilius et al. 2014) and facilitating P release. Furthermore, P release can be spatially heterogenic, for instance when phytoplankton-derived aggregates settle on the sediment surface, which can induce local anoxia through the degradation of the aggregates (Marzocchi et al. 2018). Thus, P release from the sediment is a difficult to measure but productivity elevating process, which needs to be studied more closely in the future.

Additionally, the resuspension of solutes by ship propellers or wind can result in the efflux of nutrients into the overlying water. This transport of solutes from the pore water to the water column can be up to several orders of magnitude higher than the diffusive flux (Niemistö & Lund-Hansen 2019). However, redox-dependent nutrients such as P can initially be released only to subsequently be adsorbed and precipitated again. This occurs when oxygenated water is part of the resuspension process, resulting in the formation of iron oxyhydroxides (Niemistö et al. 2018). This phenomenon may explain the short-term P effluxes observed in SL. Interestingly, in the Gulf of Finland, NH_4^+ effluxes were not enhanced when the bottom water was oxygenated but O_2 consumption showed a 59% increase during resuspension (Almroth et al. 2009), which was associated with an enhanced oxidation of reduced inorganic compounds released from the sediment. In a model study, the intensity of the resuspension event (Almroth-Rosell et al. 2012) determines the extent to which nutrients from the pore water are transported to the water column, where they contribute to increased phytoplankton productivity. According to another model study, Friedland et al. (2019) the frequent occurrence of resuspension is the primary reason for the sustained eutrophic status of the Lagoon, specifically facilitated by the release of P. Ultimately, the re-establishment of submerged vegetation is essential for the stabilisation of the sediment, the reduction of sediment resuspension and the efflux of nutrients (Schernewski et al. 2023).

In summary, nutrients are not permanently stored in the sediment of the Oder outflow system but are eventually released into the waters above. Therefore, the sediment indirectly enhances the productivity of the ecosystem albeit to a small degree. On the other hand, NH_4^+ as a product of OM remineralisation in the sediment will eventually be nitrified under oxic conditions, thereby providing the substrate for denitrification and permanent removal.

4.4 Influence of light and other factors on nitrification rates in eutrophic coastal ecosystems

NR in the Oder outflow were low (Fig. 14), which is unexpected as riverine NH_4^+ can promote pelagic nitrification in estuaries (Lipschultz et al. 1986, Bianchi et al. 1999, Brion & Billen 2000, Hsiao et al. 2014, Damashek et al. 2016). However, pelagic nitrification can also be below detection, as was observed in a hypertrophic river system, probably linked to low nitrifier abundance in the water column, with sedimentary nitrification still being high (Pauer & Auer 2000).

Usually, NR from coastal ecosystems often show large variations along the estuarine gradient, for example in the Vistula estuary (13 - 397 nmol L^{-1} d^{-1} (Bartl et al. 2018)), the Chang Jiang River estuary (not detectable to 4600 nmol L^{-1} d^{-1} (Hsiao et al. 2014)) and the Amazon River plume (0 – 3238.4 nmol L^{-1} d^{-1} (Choisnard et al. 2024a), which was not the case in the Oder outflow. Often, abiotic factors like salinity as well as NH_4^+ and POM availability play a major role in the regulation of NR along an estuarine gradient (Andersson et al. 2006, Damashek et al. 2016, Bartl et al. 2018), for example by changing the microbial community composition (Bouskill et al. 2012, Tolar et al. 2013). Particles suspended in the water column are another abiotic factor with a typically strong estuarine gradient. They can enhance NR (Xia et al. 2004, Wang et al. 2010, Füssel et al. 2012, Hsiao et al. 2014, Zheng et al. 2017) by providing a habitat and, most importantly, they can be a direct substrate source for nitrifiers as other particle-associated microbial assemblages decompose the POM and produce NH_4^+ (Simon et al. 2002, Grossart & Tang 2010, Klawonn et al. 2015, Bayer et al. 2016, Bianchi et al. 2018). Experiments adding in situ and culture-derived POM to Baltic Sea water revealed higher rates of bulk nitrification (unaltered water samples), but not of free-living nitrifiers (water filtered prior to ^{15}N incubation), indicating a strong effect of organic particles on NR (Kache et al. 2021). As the PON and POC concentrations in the Oder outflow were always (SL) or sometimes (GB and PB) above the concentrations measured in Kache et al. (2021), nitrification should have been facilitated in the Oder outflow. Additionally, in this work the authors suggest that intense recycling of OM and production of NH_4^+ takes place during the summer months (see section 4.2.1). The degradation of POM should promote nitrifiers if they are directly attached to the particles as the source of NH_4^+, as previously shown. In fact, studies measuring both NH_4^+ production by degradation and nitrification have found high rates of both occurring simultaneously (Bronk et al. 2014). Surprisingly, the high POM concentrations in the Oder outflow did not enhance NR. In total, regulatory effects of physical/chemical variables on NR, e.g. NH_4^+ and POM concentrations, were ruled out as only few correlations of NR with these variables were found (Table 2).

In addition to the estuarine nutrient gradient, seasonal variations were shown to affect the distribution of rates (Berounsky & Nixon 1993, Bianchi et al. 1999). Similar to Bartl et al. (2018), I expected elevated NR during the productive, warm season (May – September) when there are large pools of fresh, labile phytoplankton-derived PON available which are regenerated into NH_4^+ due to high microbial activity at high temperature. Surprisingly, the highest NR in the Oder outflow were measured in winter/early spring (56.6 nmol L^{-1} d^{-1}), similar to the coastal North Sea, but these rates were much higher (984 - 5304 nmol L^{-1} d^{-1}; Veuger et al. 2013). Sedimentary potential nitrification rates from the Danish coast showed the same seasonal pattern (Hansen et al. 1981).

In order to assess the effect of light on nitrification rates in the Oder outflow area, water samples from the surface and the bottom of the water column were incubated at the ambient light conditions or in the dark. No significant difference between the light or dark incubated samples were found (Fig. 15), independent of sampling time and station. If the irradiance measured at the bottom of the water column was less than 0.1% of the surface water, samples were incubated in the dark but also with 100% light exposure. This can be considered a light exposure experiment, as nitrifiers adapted to darkness are suddenly exposed to light. This is consistent with Smith et al. (2014), who found no effect of light exposure per se, but in contrast to Ward (1985). Interestingly, these light-exposed bottom water NR are mostly lower (except SL in October) than the dark-incubated bottom water NR (Fig. 16), which can be interpreted as acclimation of the nitrifiers to the dark conditions and a stress-induced response to light exposure. However, as the differences between the two groups are not significant ($n = 13$, $p = 0.896$), the interpretation must be cautious. Conversely, when surface water samples were exposed to darkness, an enhancement of NR was only visible for PB samples. No effect was observed for GB and an inhibitory effect of darkness was found for SL samples. Again, no significant differences were found between light and dark incubation at any of the three stations. Lastly, no difference was found when in situ irradiance was included by comparing NR of surface and bottom waters (Fig. 15). Differences were expected based on previous culture experiments where photoinhibition was determined for AOA and AOB as well as *Commamox* cultures. Blue light close to the UV spectrum can cause complete growth inhibition for all nitrifier groups (Shears & Wood 1985, French et al. 2012, Ghimire-Kafle et al. 2023). As the blue colours of the visible light spectrum has a great penetration depth this inhibitory effect can reach beyond the very surface of the upper ocean. Furthermore, AOB show a linear relationship with increasing irradiance (Hooper & Terry 1974) and, unlike AOA, are able to recover from inhibition after transfer to darkness (French et al. 2012). Indeed, in my data set 61% of the surface NR were higher in the dark than in the light incubation, but the differences at each station were not significant (SL: $n = 10$, $p = 0.206$; GB: $n = 10$, $p = 0.841$; PB: $n = 12$, $p = 8.18$) (Fig. 17). Hence, I am not able to support the theory of recovery from photoinhibition at the stations I sampled. A seasonal trend according to annual changes in irradiance (or temperature) in temperate regions (high irradiance and temperature in summer, low in winter), as found in Bianchi et al. (1999), was also not found. NR at PB and GB were higher in February and March compared to the rest of the year, which could be explained by lower phytoplankton competition due to lower irradiance. However, the rates remained low thereafter, even in the autumn when irradiance levels drop again. Therefore, light is not a driving force for the extent of nitrification in the Oder outflow region.

Smith et al. (2014) concluded in their study of the influence of light on nitrification, that it is often not the light itself, but the light-induced activity of phytoplankton that limits nitrifying activity. Since abiotic factors were excluded as an explanation, competition with phytoplankton for NH_4^+ may be a reasonable explanation. During growth, phytoplankton take up N for biomass production, often preferring NH_4^+ to NO_3^- (Underwood & Kromkamp 1999, discussed further in 4.2.1 above). During periods of high NH_4^+ uptake by phytoplankton or heterotrophic bacteria, less NH_4^+ is available for nitrifiers, resulting in a negative linear relationship between NH_4^+ uptake and NR (Smith et al. 2014, Bartl et al. 2018). In the estuary of the Amazon River, (Choisnard et al. 2024b) were able to show that nitrification dominates in the nutrient rich and turbid river mouth while nutrient uptake by phytoplankton outcompeted nitrifiers as soon as the turbidity started to decrease and phototrophic activity was possible. No such relationship was found at any of Oder outflow stations (Tab. 2), although PP did show a seasonal trend, resulting in times of low phytoplankton NH_4^+ demand that could benefit nitrifiers. However, in February, when the highest NR were detected, NH_4^+ uptake rates were already elevated, indicating the beginning of the spring bloom. Sampling in December or January might give more insight into the dynamics of NR during low phytoplankton productivity.

Although no direct relationship between nitrification and PP was found, I suspect that nitrifiers are outcompeted by the dense phytoplankton community in the Oder outflow, especially in August and October when N is limited (Fig. 9). This has been shown in open ocean ecosystems e.g. in the euphotic zone of the north-west Pacific ocean (Xu et al. 2019) and in the Southern Ocean Surface Layer (Mdutyana et al. 2020). Coastal and estuarine ecosystems have not yet been in the focus of such investigations. Choisnard et al. (2024) have been one of the first to link nitrifier and phytoplankton activity in the estuarine Amazon River plume, but obtaining opposite results to my NR as they determined the highest NR in the river mouth, decreasing towards the open ocean. Such contrasting results mean that more research on the topic is needed.

Beside Smith, Wan et al. (2018, 2021) suspect an indirect influence of NO_3^- on the dynamics of the NR. They assumed that the phytoplankton community switches from NO_3^- to NH_4^+ assimilation when NO_3^- is depleted, resulting in elevated competition for NH_4^+ between phytoplankton and nitrifiers. In fact, the annual temporal development of NO_3^- concentrations (Fig. 8) and NR (Fig. 14) show a similar trend at all stations, with NR being highest in winter and early spring together with NO_3^- concentrations, and both variables being lowest in summer. Thus, I suspect that the depletion of NO_3^- by the spring phytoplankton bloom initiates the decrease in NR in the Oder outflow and the low NO_3^- river load in summer favours the progression of this competitive situation for NH_4^+ as N source for phytoplankton assimilation and nitrification. However, a significant correlation between the NO_3^- concentration and NR was found only in PB (Tab. 2). It must also be noted that this theory is only valid for SL, experiencing very high NO_3^- concentrations, as NH_4^+ uptake rates in February, March and April in GB and PB are higher than NO_3^- uptake rates.

In summer, when NO_3^- concentrations were barely detectable at all stations, phytoplankton were likely N-limited (Fig. 9) and, like nitrifiers, depended on the NH_4^+ recycled in the water column or emitted from the sediment. Under these conditions, transport rates of NH_4^+ into the phytoplankton cell have been found to be high (Flynn et al. 1999), as high affinity transporters at the cell surface are more active (Howitt & Udvardi 2000). Nevertheless, nitrifiers should be able to outperform phytoplankton due to the low K_m of AOA and AOB of 0.1 (Martens-Habbena et al. 2009) and 1 µmol L^{-1} (Bollmann et al. 2002, Prosser & Embley 2002), allowing them to be active at both low (AOA; Martens-Habbena et al. 2009) and high NH_4^+ concentrations (AOB; Magãlhaes et al. 2009). However, the slow growing nitrifiers show a growth lag phase of several days (AOB) to weeks (AOA) (French et al. 2012), resulting in a slower response to changes in ambient NH_4^+ concentration compared to phytoplankton, so that they get outcompeted.

Coastal areas and estuaries in particular can be subject to chemical pollution, for example from fertilisers and heavy metals, but also from emerging contaminants such as pharmaceuticals and antibiotics. Several heavy metals have a dual effect on microbial activity, acting as essential trace elements but also inhibiting nitrification, e.g. zinc (Zn) and copper (Cu). Experiments with wastewater and activated sludge showed that nitrification can be completely inhibited at concentrations between 0.16 and 1.2 mg L^{-1} Zn^{2+} and already at 0.01 - 1 mg L^{-1} Cu^{2+} (Kong et al. 1993, Juliastuti et al. 2003). Copper concentrations in the water column of the Oder outflow are always below 0.0015 mg L^{-1} (average concentration of 2021 and 2022, LUNG), i.e. below the inhibition threshold. The same applies to zinc with concentrations below 0.0025 mg L^{-1} (average concentration of 2021 and 2022, LUNG). Thus, I do not consider chemical pollution as an important factor on NR in this study.

Altogether, the low NR in the Oder outflow region are not caused by the inhibition due to light, as no direct relationship between the variables was found. I suspect that a combination of light and restricted nutrient availability indirectly hampers the activity of nitrifiers by facilitating phytoplankton activity. Due to frequent mixing of the shallow water column and the continuous supply of DIN through remineralisation, light and nutrient availability of phytoplankton is secured and metabolic advantages lead to the nitrifiers being outcompeted. As a result, pelagic NO_3^- production is negligible and coupled nitrification-denitrification restricted to the sediment or anoxic microsites.

5. Final Conclusions and Perspectives

With this work I illustrate the important role of retention processes in the coastal filter, which is summarised in Figure 23. Retention of riverine N via assimilation, where NH_4^+ is preferred over NO_3^-, is the first and most important step in N-processing of the Oder outflow, contrary to previous suggestions (Voss et al. 2010). It traps riverine N in biomass producing PON, which is subsequently either deposited on the sediment or remineralised. This process prevents the majority of the riverine N from being directly exported to the open Baltic Sea, thereby retaining it in the coastal zone. Besides assimilation, ammonification is the most important retention process, supplying NH_4^+ for PP during periods of reduced riverine input through the remineralisation of PON in the water column and the sediment. The latter then functions as an additional nutrient source, as N and P can be released from the sediment. These processes collectively contribute to the formation of highly productive coastal ecosystems, with the Szczecin Lagoon being the most productive and the Pomeranian Bay the least. Nitrification, an important retention process is surprisingly low in the water column. This can be attributed to the intense competition with phytoplankton for NH_4^+ (Smith et al. 2014), which is lost by the nitrifiers due to metabolic disadvantages. However, I suspect high NR in the sediment, fuelled by the high input of PON from the water column. In contrast to the sedimentary denitrification of riverine NO_3^- form the water column (DNR_w), coupled nitrification-denitrification (DNR_n) efficiently removes N from the water column (up to 85% of the annual riverine DIN input), as evidenced by high DNR in comparison to other Baltic Sea coastal systems (Asmala et al. 2017). This further illustrates the importance of retention processes, which is in contrast to the conclusions of Voss et al. (2010), who suggested that denitrification is the most important process in the coastal filter of the Oder outflow region. The different retention processes provide substrate for PP and removal processes, thereby sustaining both the productivity of the ecosystem and the removal of surplus riverine N. This close link between retention/recycling and removal processes appears to be a distinctive feature of shallow, estuarine lagoons along the Baltic Sea coastline (Broman et al. 2021). A characteristic attribute of enclosed coastal ecosystems, such as the Szczecin Lagoon and the Greifswalder Bodden, is the prolonged WRT, which fosters biogeochemical processes, notably denitrification (Dettmann 2001, Seitzinger et al. 2006). This renders the Oder outflow region an effective bioreactor and nutrient reservoir. It was demonstrated that coastal zones with diverse morphologic characteristics, e.g. open estuaries like the Vistula and Öre estuary, exhibit a lower N removal potential (Hellemann et al. 2017, Bartl et al. 2019) in comparison to lagoons or enclosed bays. DNR showed significant differences between coastal ecosystem types, with the lowest rates observed in archipelagos and open coasts (~ 185 $\mu mol\ m^{-2}\ d^{-1}$) and the highest rates documented in lagoons (almost

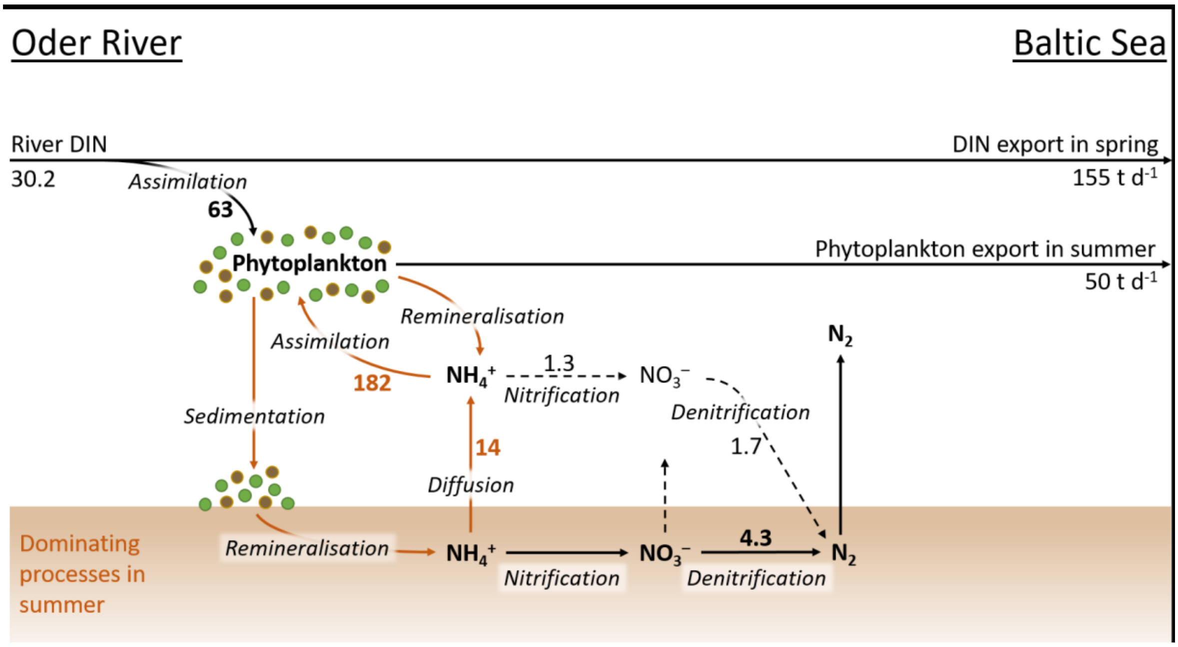

Figure 23. Schematic of major processes shaping the coastal filter of the Oder outflow. A transect from the Oder River mouth to the Baltic Sea is illustrated. Important processes of the coastal filter are highlighted with bigger arrows, process of minor importance with dashed arrows. Orange arrows represent processes, which dominate in summer. Numbers represent processes, fluxes and riverine input in kt per year, exemplified on data from the Szczecin Lagoon. Therefore, values for the Greifswalder Bodden and the Pomeranian Bay will differ. Pelagic process rates of the water column were calculated via trapezoid integration using the surface and bottom water rates. All rates and fluxes were extrapolated to the area of the Lagoon (687 km^2). Export numbers in t per day are from the transport model described above.

4000 µmol m^{-2} d^{-1}) (Asmala et al. 2017). Thus, depending on the morphologic ecosystem type, retention processes play a pivotal role in preventing the immediate export of riverine N, for instance by storing it in biomass (Bartl et al. 2019).

In the end, removal of riverine N is the major function of the coastal filter, reducing or even preventing the export of nutrients from rivers like the Oder to the eutrophic Baltic Sea. The successful functioning of the coastal filter is confirmed by this study, supporting the model of Radtke et al. (2012), who estimated that the majority of riverine total N does not reach the open Baltic Sea and is retained and transformed in the coastal zone. Vice versa, the coastal zone itself is strongly eutrophic due to the high nutrient turnover. The intense retention and recycling of nutrients in the coast facilitates not only removal processes but also high primary production, resulting in high autochthonous C input (Nixon 1995). As DIN and DON are most limiting for coastal productivity in temperate ecosystems, reducing N inputs is essential for improving the trophic status of coastal waters (Howarth & Marino 2006). Indeed, the flow-normalised total N input from the Oder river was reduced by ~ 20% between the mid-1990s and today (HELCOM 2024). However, when the input from small rivers and streams like Uecker, Zarow and Peene (UZP) are included, a reduction of only 2.3% can be found. In addition, the control of N inputs goes hand in hand with the control of P inputs, which were reduced by 67% in the Oder river and by only 4.3% when UZP are included (flow-normalised data, HELCOM

2024). This demonstrates that measures for nutrient input reductions are not yet effective enough in smaller rivers and streams with a mostly agriculture-based catchment area. Additionally, due to the pronounced retention processes and the long WRT, especially in SL and GB, internal nutrient cycling is well-established, and the removal or export of such internal nutrients is low (Munkes 2005, Friedland et al. 2019). Further measures are necessary to decrease the pressure on the Oder outflow region, such as the recolonization of macrophytes (Berthold et al. 2018, Schernewski et al. 2023) or the introduction of filter feeder aquaculture to increase water transparency (Schernewski et al. 2019). For Danish coastal waters, Riemann et al. (2016) compiled applied measures and their effectiveness: reduction of nutrient inputs from land resulted in decreased nutrient and Chl *a* (phytoplankton biomass) concentrations and increased coverage of macrophytes, resulting from improved water clarity. However, the authors alert against the impact of climate change on those positive trends, as enhanced temperature and stratification may hamper the improvement of bottom water O_2 conditions (Riemann et al. 2016). Other coastal lagoons face similar challenges in times of climate change, such as reduced water transparency and loss of macrophytes (Lloret et al. 2008). In the Oder outflow region, modelled climate change experiments suggest even greater phytoplankton biomass and therefore magnified eutrophication in the Szczecin Lagoon and intensified oxygen depletion in the Pomeranian Bay, where wind-induced mixing does not reach the bottom throughout the year (Pein & Staneva 2024) and enhanced stratification increases the overall risk of bottom water hypoxia (Rabalais et al. 2002, 2014). Additionally, the river flow to the Baltic Sea in the southern areas may decrease, especially during the summer months, according to hydrologic climate change models (Graham 2004). The corresponding decrease in the input of riverine nutrients may facilitate diazotrophic phytoplankton species, resulting in a possible reduction of N removal (Zilius et al. 2018, 2024) and increasing health risks for bathers and livestock due to cyanotoxins (Overlingė et al. 2020). However, contrasting models on the influence of climate change on river runoff were published (e.g. Saraiva et al. 2019, Gröger et al. 2019), estimating an increase in river runoff and nutrient input.

Even though these predictions are rather negative, analysis of the food web structure in the Oder outflow region paint a different picture. Stable isotope data of amino acids suggest that the present food web is surprisingly stable, implying a stable and well working ecosystem which is probably adjusted to the continuously eutrophic status of the system (pers. comm., Markus Steinkopf). This is in line with the hypothesis of the ecosystem being naturally eutrophic (Schernewski et al. 2023). How climate change will alter the communities of microbes, plankton and fauna has to be closely monitored in order to identify possible tipping points for the Oder outflow region. Those variables as well as uptake and transformation rates have to be measured monthly over several years in the water column and sediment to best evaluate all trophic levels and nutrient dynamics, while the ongoing monitoring of nutrients and abiotic variables by the LUNG is a great baseline for future work. Additionally, the station grid needs to be finer to consider spatial variations, specifically, including the Peenestrom as it is strongest eutrophic (Pein & Staneva 2024).

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Supplements

Sampling dates

Table S1. Sampling dates for each campaign in 2021 and 2022 to the Szczecin Lagoon, Greifswalder Bodden and Pomeranian Bay. Sampling conducted from land is marked with an asterisk.

Sampling campaigns	Szczecin Lagoon	Greifswalder Bodden	Pomeranian Bay
Winter	22.02.2022*	22.02.2022*	22.02.2022*
Spring			08.03.2022
	30.03.2022	31.03.2022*	10.04.2022
	18.05.2021	20.05.2021	28.05.2021
Summer	24.08.2021	25.08.2021*	13.07.2021
Autumn	05.10.2021	06.10.2021	14.10.2021

Light conditions during rate determination

Most samples from PB were incubated in on-deck incubators, being exposed to in situ light conditions. Some samples from PB and all samples from SL and GB were incubated in lab-incubators (Table S2).

Primary production depends on the light availability. Photosynthesis-irradiance (P-E) curves, describing this dependency, are produced from exposure experiments of marine phytoplankton species or assemblages to a controlled range of irradiance levels. This allows a comparison of photosynthetic characteristics of marine phytoplankton (Bouman et al. 2018). One of the characteristic variables is E_k, the light saturation parameter, describing the irradiance level at which half of the maximum photosynthetic capacity (V_{max}) is reached (in µmol photons m^{-2} s^{-1}). Previous studies in the Baltic Sea calculated E_k of 76 µmol photons m^{-2} s^{-1} (Carpenter et al. 1995) in the Gotland Basin and 85 (winter) and 73 (spring) µmol photons m^{-2} s^{-1} in the Darss-Zingst Bodden Chain (Schumann et al. 2005), a lagoon system similar to SL. Assuming that a double E_k is equivalent to the irradiance at which V_{max} is reached, these irradiances would be 152, 170 and 146 µmol photons m^{-2} s^{-1}, with an average of 156 µmol photons m^{-2} s^{-1}. Therefore, the uptake and nitrification rates determined under the lightning conditions stated above are extrapolated to 156 µmol photons m^{-2} s^{-1}. These calculated rates represent the metabolically maximum possible rates considering the photosynthetic characteristics of marine phytoplankton in the Baltic Sea.

Table S2: Characteristics of the two different lab-incubators used for incubation of samples for PP, NH_4^+ uptake and NO_3^- uptake rates, nitrification rates.

Location of incubator	**PAR photon flux (µmol photons m^{-2} s^{-1})**	**Samples**
University Greifswald	40.3 (n = 18)	SL & GB August 2021 SL & GB October 2021 SL & GB April 2022
Leibniz Institute for Baltic Sea Research Warnemünde	36.6 (n = 3)	SL & GB May 2021 SL, GB & PB February 2022

Furthermore, PP (Haro et al. 2019) and therefore N uptake (Cochlan et al. 1991) follow the diurnal light cycle, whereby uptake rates in the dark are negligible. Hence, the uptake rates were multiplied with the daylight lengths (in hours) of the respective sampling day to obtain daily rates. Nitrification rates on the other hand, can be light sensitive (see chapter 4.4) but no significant differences between light and dark incubation where found during this word. Thus, there is no need to include the factor light in the calculation of daily rates, which can simply be obtained by multiplying dark rates (determined according to method description, chapter 2.3) with 24 hours.

Supplementary figures

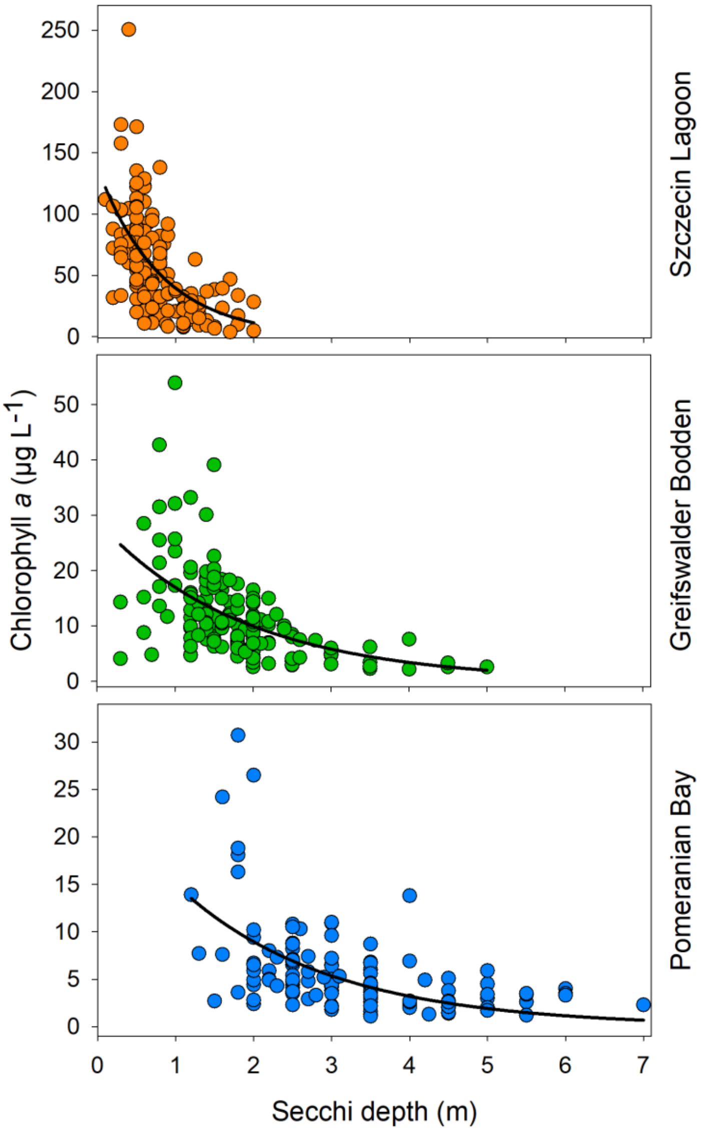

Figure S1. Relationship between Secchi depths (m) and chlorophyll *a* concentrations (µg L^{-1}) in the Szczecin Lagoon (orange), the Greifswalder Bodden (green) and the Pomeranian Bay (blue). LUNG data between 2006 and 2022 were used. Black lines show an exponential fit to the data.

Curriculum vitae

Work experience

Doctoral researcher – 06/2020 to 02/2024
Biological Oceanography
Leibniz Institute for Baltic Sea Research Warnemuende, Germany

Researcher – 06/2019 to 05/2020
Biological Oceanography
Leibniz Institute for Baltic Sea Research Warnemuende, Germany

Student Research Assistant – 02/2018 to 03/2018
Physical Oceanography
Leibniz Institute for Baltic Sea Research Warnemuende, Germany

Student Research Assistant – 10/2017 to 12/2017
Applied Ecology and Phycology
Institute for Biological Sciences, University Rostock, Germany

Student Research Assistant – 03/2017 to 04/2017
Applied Ecology and Phycology
Institute for Biological Sciences, University Rostock, Germany

Education

Dr. rer. nat. – 06/2020 to 12/2024
Institute for Biological Sciences, University Rostock, Germany

M.Sc. Marine Biology – 10/2016 to 05/2019
Institute for Biological Sciences, University Rostock, Germany

B. Sc. Biological Sciences – 10/2013 to 06/2016
Institute for Biological Sciences, University Rostock, Germany

Abitur – 07/2012
Europagymnasium “Richard von Weizsäcker” Thale, Germany

Declaration

Hiermit bestätige ich, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Hilfsmittel benutzt habe. Die Stellen der Arbeit, die dem Wortlaut oder dem Sinn nach anderen Werken entnommen sind, wurden unter Angabe der Quelle kenntlich gemacht.

Ort Datum Unterschrift