

Efficiency of the coastal filter: Nitrogen and phosphorus removal in the Baltic Sea

Eero Asmala ^{1,*} Jacob Carstensen ¹ Daniel J. Conley ² Caroline P. Slomp ³
Johanna Stadmark ² Maren Voss ⁴

¹Department of Bioscience, Aarhus University, Roskilde, Denmark

²Department of Geology, Lund University, Lund, Sweden

³Department of Earth Sciences, Utrecht University, Utrecht, The Netherlands

⁴Department Biological Oceanography, Leibniz Institute for Baltic Sea Research, Warnemünde, Germany

Abstract

An important function of coastal ecosystems is the reduction of the nutrient flux from land to the open sea, the coastal filter. In this study, we focused on the two most important coastal biogeochemical processes that remove nitrogen and phosphorus permanently: denitrification and phosphorus burial. We compiled removal rates from coastal systems around the Baltic Sea and analyzed their spatial variation and regulating environmental factors. These analyses were used to scale up denitrification and phosphorus burial rates for the entire Baltic Sea coastal zone. Denitrification rates ranged from non-detectable to 12 mmol N m⁻² d⁻¹, and correlated positively with both bottom water nitrate concentration and sediment organic carbon content. The rates exhibited a strong decreasing gradient from land to the open coast, which was likely driven by the availability of nitrate and labile organic carbon, but a high proportion of non-cohesive sediments in the coastal zone decreased the denitrification efficiency relative to the open sea. Phosphorus burial rates varied from 0.21 g P m⁻² yr⁻¹ in open coastal systems to 2.28 g P m⁻² yr⁻¹ in estuaries. Our analysis suggests that archipelagos are important phosphorus traps and account for 45% of the coastal P removal, while covering only 17% of the coastal areas. High burial rates could partly be sustained by phosphorus import from the open Baltic Sea. We estimate that the coastal filter in the Baltic Sea removes 16% of nitrogen and 53% of phosphorus inputs from land.

Inputs of nitrogen and phosphorus from land and the atmosphere to coastal environments have stimulated the autochthonous production of organic material by aquatic primary producers, leading to eutrophication (Nixon 1995). The Baltic Sea is no exception to the global trends (Gustafsson et al. 2012) and the consequences of large-scale eutrophication are evident: reduced water transparency, oxygen depletion and changes in aquatic food webs (Bonsdorff et al. 1997; Karlson et al. 2002; Carstensen et al. 2014).

Coastal ecosystems alter nutrient pools on their passage from headwaters to the sea through multiple biogeochemical

processes, which transform, retain or remove terrigenous nutrients permanently from the reach of aquatic organisms (McGlathery et al. 2007; Nelson and Zavaleta 2012). This “coastal filter” function of the coastal zone reduces the anthropogenic impact on the marine environment (Bouwman et al. 2013). Coastal ecosystems are characterized by the continuous flow of freshwater mixing gradually with seawater, and the time it takes for any water parcel to travel through the coastal zone, i.e., the residence time (Monsen et al. 2002), is considered the most important factor regulating the processing of nutrients and organic matter (Borum 1996; Nixon et al. 1996). Generally, coastal areas with a short residence time have lower sedimentation rates and thus reduced nutrient and organic matter deposition rates, causing lower benthic biogeochemical processing rates (Seitzinger et al. 2006).

There are four major pathways for nutrient processing in the coastal zone (Fig. 1). Some nutrient forms leave the system in the same form as they entered, without being intercepted by organisms or geochemical processes, thus bypassing the coastal filter. Parts of the nutrient pool are transformed on

*Correspondence: eeas@bios.au.dk

Additional Supporting Information may be found in the online version of this article.

Special Issue: Headwaters to Oceans: Ecological and Biogeochemical Contrasts Across the Aquatic Continuum

Edited by: Marguerite Xenopoulos, John A. Downing, M. Dileep Kumar, Susanne Menden-Deuer, and Maren Voss

GLOSSARY

Key terms describing coastal filter functioning

Nutrient bypassing (#1, gray arrow)

Transporting nutrients unaltered from land to sea.

$$\tau_N = \tau_W$$

Nutrient transformation (#2, gray spiral arrow)

Changing the chemical composition of nutrients during transport, e.g., from dissolved inorganic to particulate organic via biosynthesis.

$$\tau_N = \tau_W$$

Nutrient retention (#3, white arrows)

Slowing down the nutrient flow from land to sea by incorporating nutrients into biomass or non-living particles.

$$\tau_N > \tau_W$$

Nutrient removal (#4, red arrows)

Directing the nutrients permanently outside the coastal ecosystem, e.g., through denitrification or burial.

$$\tau_N = \text{mean nutrient residence time in system.}$$

$$\tau_W = \text{mean water residence time in system.}$$

their passage through the coastal ecosystem, which changes the chemical composition of the processed nutrients. Common to the nutrient bypassing and transformation pathways is that processes operate at the same time scale as physical mixing of water (nutrient residence time = freshwater residence time). Nutrients can be retained and will remain available to organisms within the aquatic system for periods of time longer than the freshwater residence time, albeit at shorter time scales than those associated with permanent removal. Biological processes contribute to the temporary nutrient retention by assimilating nutrients into biomass and remineralizing biomass into bioavailable nutrient forms again. This nutrient turnover is faster if carried out by short-lived organisms rather than long-lived ones (Ensign and Doyle 2006), acknowledging that the biological availability of nutrient inputs from land is gradually reduced with each cycle of nutrient turnover, that also produces nutrient forms more amenable to permanent burial (Benitez-Nelson and Buesseler 1999; Welsh 2003; Jørgensen et al. 2014). Finally, nutrients are considered permanently removed from the coastal zone if processed to a gaseous form that evades the system (such as N_2) or stored in the sediments for time scales longer than those relevant from an anthropogenic perspective (burial). Permanent removal in effect moves nutrients beyond reach for the organisms within the aquatic system. The focus of this study is on processes permanently removing nutrients from coastal ecosystems in the Baltic Sea.

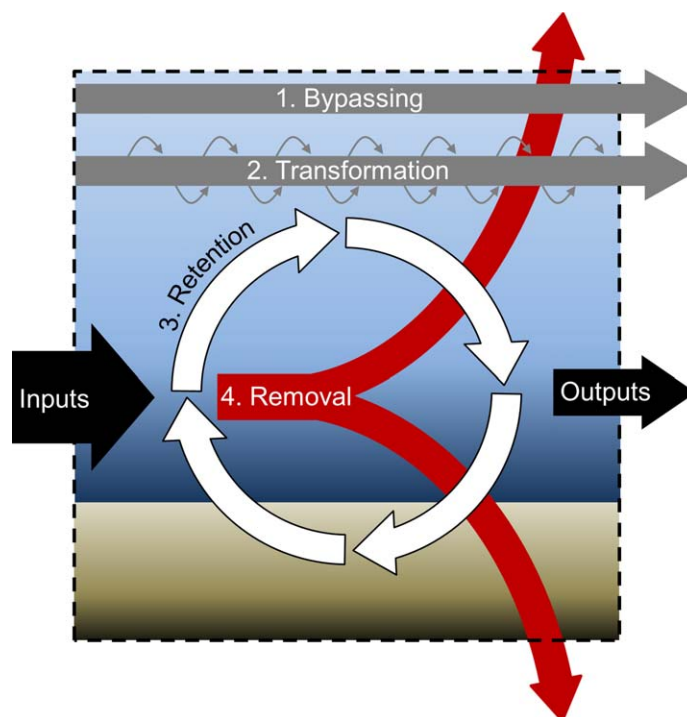


Fig. 1. Conceptual figure of nutrient pathways in the coastal filter. Dashed line indicates the system boundaries of the coastal ecosystem, and arrows different processes affecting the nutrient status within the system. [Color figure can be viewed at wileyonlinelibrary.com]

Only few processes contribute significantly to permanent removal of nutrients in coastal areas: phosphorus is trapped and buried in sediments, and nitrogen is removed through denitrification and sediment burial. Not all sediment burial is permanent, as biological activity within the sediment surface layers may drive recycling of the nutrients, but permanent burial can occur in locations with net sediment accumulation (Mort et al. 2010). However, coastal erosion and episodic sediment translocations may cause sporadic interferences to sediment accumulation (Jonsson and Carman 1994; Nuorteva and Kankaanpää 2016). Other processes contributing to nutrient removal within the coastal zone, such as extraction of living resources (e.g. from fisheries) are of minor importance (Boynton et al. 1995; Hjerne and Hansson 2002).

Nutrient inputs from land and atmosphere to the Baltic Sea have increased threefold over the last century reaching approximately 770 ktons N yr⁻¹ and 45 ktons P yr⁻¹ in recent years (Gustafsson et al. 2012). Cyanobacteria, a prominent feature of the open waters during summer, fix an additional substantial amount of nitrogen (Gustafsson et al. 2012). Model results for the entire Baltic Sea suggest that nutrient removal rates have increased in parallel to the rising external inputs, removing 87% and 12% of nitrogen inputs by denitrification and burial, respectively, and 78% of phosphorus inputs by burial (Gustafsson et al. 2012). Deutsch

et al. (2010) extrapolated measured denitrification rates and estimated that 48–73% of the nitrogen input from land and atmosphere (not including nitrogen fixation) was removed by denitrification in the sediments of the open Baltic Sea; however, denitrification in the water column is probably of similar magnitude (Dalsgaard et al. 2013). Thus, nutrient removal in the Baltic Sea is high relative to external inputs, but how efficient is the coastal filter in removing nutrients from land before they reach the open Baltic Sea?

We will address this question by analyzing nutrient removal rates in coastal ecosystems obtained from the literature and unpublished sources, and use this analysis for extrapolation across the entire Baltic Sea coastal zone. Our study focuses on the two most important removal processes: denitrification and phosphorus burial. Our objectives are to (1) to explore differences in denitrification and phosphorus burial rates among different coastal zones in the Baltic Sea, (2) analyze the potential drivers of these processes, and (3) extrapolate these removal rates across the entire Baltic Sea coastal zone.

Coastal ecosystems around the Baltic Sea

One major challenge of assessing nutrient removal in the Baltic Sea is the large spatio-temporal variability of the processes, both within and among coastal ecosystems. This heterogeneity of the environmental and biological factors causes differences in the functioning of the coastal filter, and the scale of heterogeneity in the coastal zone spans from microscopic to regional. Accounting for this variability is challenging (Sundbäck et al. 2004). So-called “hot spots” and “hot moments” can be used to gain mechanistic understanding of this heterogeneity, by identifying the patches and short periods of disproportionately high biogeochemical processing rates relative to the surrounding matrix or to longer time periods (McClain et al. 2003). The coastal zones around the Baltic Sea are very diverse in terms of their biological components, the importance of riverine inputs, the chemical composition of the freshwater input, salinity of the receiving water and bottom water redox conditions (Conley et al. 2011). Added complexity arises from sediment patchiness, as e.g., sediment structure, organic content and sedimentation rates may vary significantly even on a local scale (Holland and Elmore 2008). Rivers in the southern part have high nutrient concentrations and elevated N : P ratios, whereas rivers in the northern part are generally low in nutrients but high in dissolved organic matter (Voss et al. 2011). Furthermore, coastal salinity increases from ~ 2–3 in the north (Bothnian Bay) to ca. 25 in the southwest (Danish Straits). Hence, the coastal zones of the Baltic Sea allow for investigating retention processes across a broad span of environmental conditions.

We used national definitions of coastal water bodies according to the European Water Framework Directive to

Table 1. Ecosystem classification used in this study with the number of coastal ecosystems, their average depth and area.

Coastal type	<i>n</i>	Mean depth (m)	Mean area (km ²)
Open coast	308	13.8	250
Archipelago	588	8.2	33
Embayment	59	7.1	121
Estuary	43	5.3	69
Lagoon	19	2.2	246

delineate 1017 coastal ecosystems and addressed their heterogeneity by grouping them into five distinct categories (Table 1). The categorization employed was based on a slight modification of HELCOM’s coastal types (GIS service at <http://www.helcom.fi>). Furthermore, the sediment distribution (sand, silt/mud, hard) for the 1017 coastal ecosystems was obtained from EUSeaMap (<http://www.emodnet.eu/sea-bed-habitats>).

Nitrogen removal by denitrification

In the denitrification process, denitrifying bacteria reduce nitrate (NO₃[−]) via nitrite (NO₂[−]), nitric oxide (NO) and nitrous oxide (N₂O) to non-reactive dinitrogen gas (N₂) with organic carbon as the main electron donor. Denitrification rates are controlled by multiple environmental factors, such as nitrate and oxygen concentrations, labile organic carbon availability, and temperature (Piña-Ochoa and Álvarez-Cobelas 2006). Anaerobic ammonium oxidation to N₂ (anammox) also removes nitrogen from coastal systems, but the dominant pathway is denitrification (Hietanen and Kuparinen 2008).

We collected denitrification rates and associated supplementary data (mostly nitrate concentrations in the overlying water and the sediment organic carbon content) from the literature and other sources (data and references in Supporting Information Table S1). We analyzed denitrification data determined by the isotope pairing method only (Nielsen 1992), as denitrification measurements with the acetylene method has reported shortcomings, mostly because of the blocking of the coupled nitrification-denitrification process (Seitzinger et al. 1993; Steingruber et al. 2001). The combined dataset comprised of 22 individual coastal systems around the Baltic Sea, totaling 720 rate measurements (Fig. 2). In some studies replicated cores (typically 3 but up to 12 cores) were sampled at the same site and time (*n* = 446), whereas other studies used single cores at multiple sites (*n* = 274). Most of the measurements originated from estuaries and archipelagos, whereas open coasts, embayments and lagoons had a smaller representation (Supporting Information Fig. S1). There were many observations from Denmark, where estuaries and embayment coastal types dominate, whereas archipelagos are only found in Sweden and Finland.

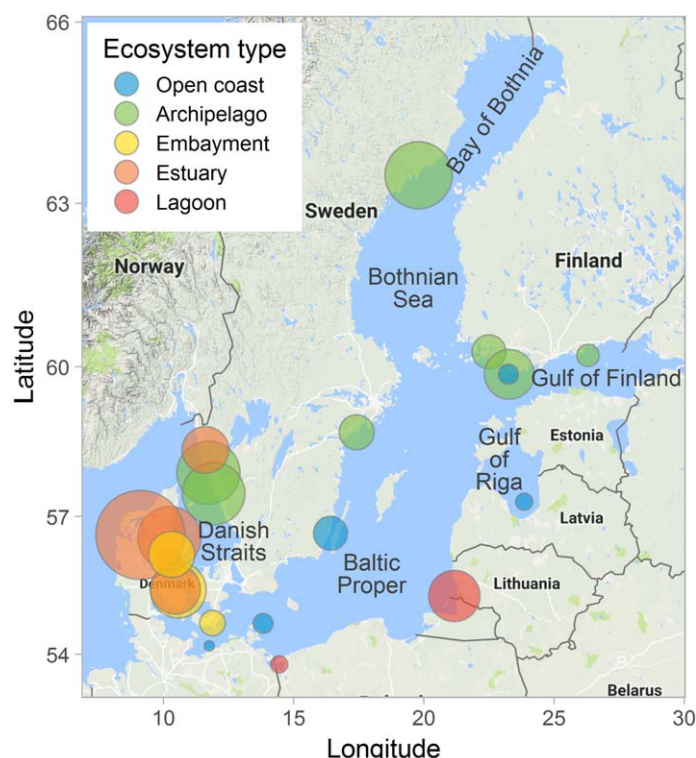


Fig. 2. Map showing locations of coastal ecosystems with denitrification measurements. Size of the circle is proportional to the number of measurements from given location, ranging continuously from $n = 4$ in Fehmarn Belt to $n = 135$ in Skive Fjord. Full list of references is provided in Supporting Information Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

Lagoons are only found in the southern Baltic Sea and were represented by two of the largest, Oder and Curonian. Open coasts are found all around the Baltic Sea and the denitrification studies were geographically distributed to provide an adequate representation of this type. Denitrification was measured more frequently during summer months (Supporting Information Fig. S1). Finally, we investigated the description of the sediment types in each of the supplied data sets and categorized these in either of two categories: sand ($n = 29$) and silt/mud ($n = 691$). Sandy sediments were only examined at two locations; Kalmarsund on the Swedish east coast and Curonian Lagoon in Lithuania.

Our combined dataset had a large variation in denitrification rates across coastal zones of the Baltic Sea ranging from non-detectable (typically below $10 \mu\text{mol N m}^{-2} \text{d}^{-1}$) to $12,000 \mu\text{mol N m}^{-2} \text{d}^{-1}$ (Supporting Information Table S1). Some coastal systems had a low number of observations (< 10), but for the majority of coastal systems 10–100 denitrification measurements were available. The highest average denitrification rate was measured in the Oder (Szczecin) Lagoon ($5246 \mu\text{mol N m}^{-2} \text{d}^{-1}$); a system characterized by high nutrient loadings from the Oder River and narrow opening to the Pomeranian Bay in the southern Baltic Sea

(Pastuszak et al. 2005). The lowest average denitrification rate was measured in Valda ($32 \mu\text{mol N m}^{-2} \text{d}^{-1}$); a system in southwestern Sweden with low nitrate concentrations year round and low sediment organic carbon content (Sundbäck et al. 2000). For the statistical analyses below, denitrification rates were log-transformed using $\log(X + 10)$, since variation in rates scaled with the mean level and the constant employed in the transformation (representing an approximate value for the lower detection limit) allowed for transformation of zero observations.

The five coastal types displayed increasing nitrate concentrations in the bottom water from the open coast and archipelagos toward estuaries and lagoons (Fig. 3), paralleling as expected a proximity to nitrate-rich freshwater sources. Sediment organic carbon content did not exhibit similar spatial trends and was more likely driven by a combination of local physical perturbation and redox conditions. Grain size was linked to sediment OC content, which averaged only 0.18% in sandy sediments, and 4.6% in silt/mud sampling sites. Organic carbon is not directly controlled by fluxes from land, but instead is a result of multiple processes both in the water column and sediment (Thornton and McManus 1994).

Environmental factors regulating denitrification in the Baltic Sea

Given the large variation among both sites and ecosystem types, it is apparent that there are other than typological drivers of denitrification in the coastal zone of the Baltic Sea. In a review by Piña-Ochoa and Álvarez-Cobelas (2006), six key factors affecting denitrification were identified: (1) oxygen concentration, (2) nitrate concentration, (3) pore water dissolved organic carbon concentration, (4) total phosphorus concentration, (5) light regime, and (6) plant occurrence. Paucity of data only allowed systematic examination of one of these factors, nitrate. Additionally, we looked into the role of sediment organic carbon content, as many studies have indicated that it has an influence on denitrification (e.g., Trimmer and Nicholls 2009; Deutsch et al. 2010).

In our data, nitrate concentrations ranged from non-detectable to $1110 \mu\text{mol L}^{-1}$. Open coast and archipelago ecosystems had average NO_3^- concentrations below $5 \mu\text{mol L}^{-1}$, whereas the other ecosystems closer to the shoreline had 10-fold higher average concentrations, around $40\text{--}50 \mu\text{mol L}^{-1}$. We found significant linear relationships between nitrate concentration and denitrification from three ecosystem types; open coasts, embayments, and estuaries (Fig. 4a). Positive relationships between nitrate concentrations and denitrification rates can be assumed below the saturation concentration, as the higher NO_3^- concentrations will allow higher diffusion rates, thus accelerating the denitrification efficiency of the microbial community (Christensen et al. 1990). Half-saturation constants have typically been used as a threshold below which limitation occurs (Arango et al. 2007), and in coastal seas, nitrate half-saturation constants

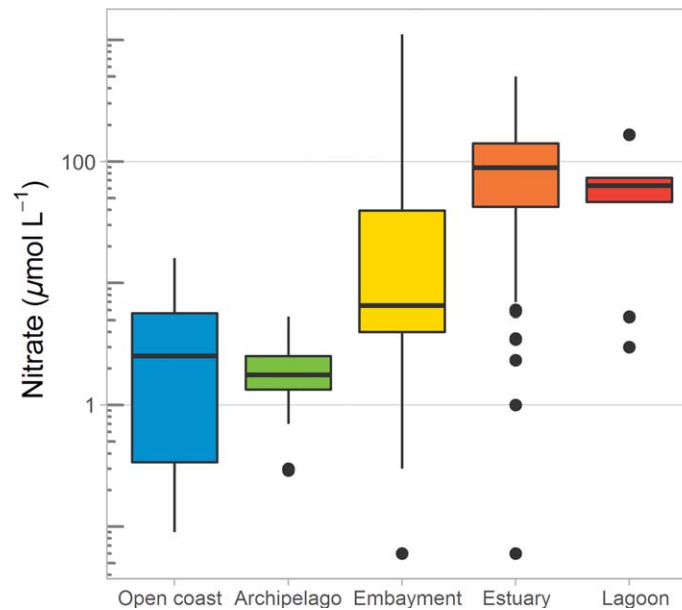


Fig. 3. Differences among coastal ecosystems in nitrate (NO_3^-) concentrations in bottom water associated to denitrification measurements ($n = 364$). [Color figure can be viewed at wileyonlinelibrary.com]

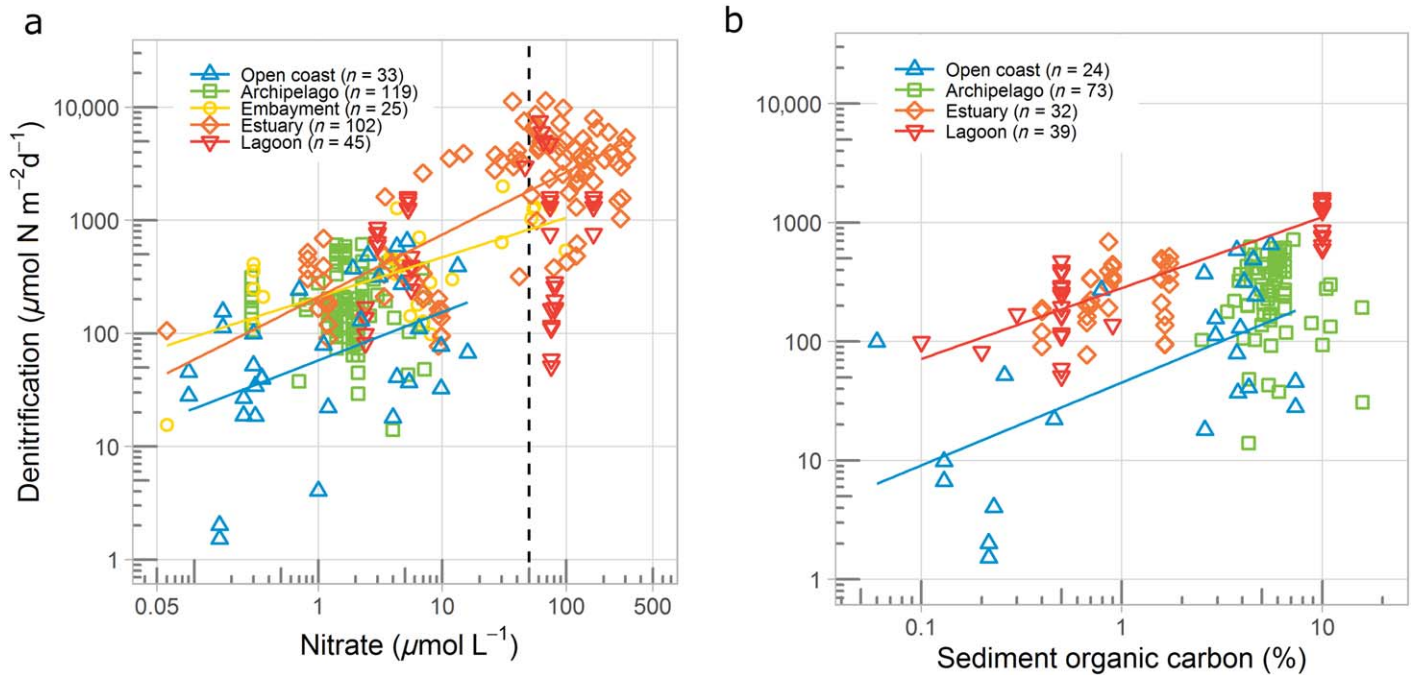


Fig. 4. Relationships between denitrification and (a) nitrate concentration ($n = 345$), and (b) sediment organic carbon content ($n = 176$) across coastal types in the Baltic Sea. The dashed line (in panel a) indicates the nitrate half saturation constant of $50 \mu\text{mol L}^{-1}$, considered as nitrate limitation threshold (Seitzinger 1988). Only significant linear relationships ($p < 0.05$) are shown. Equations for the linear regression between denitrification rate and NO_3^- : Open coast: $\log_{10}(y) = 1.76 + 0.43 \times \log_{10}(x)$, $r^2 = 0.180$; Embayment: $\log_{10}(y) = 2.32 + 0.35 \times \log_{10}(x)$, $r^2 = 0.422$; Estuary: $\log_{10}(y) = 2.32 + 0.55 \times \log_{10}(x)$, $r^2 = 0.529$. Equations for the linear regression between denitrification rate and sediment organic carbon content: Open coast: $\log_{10}(y) = 1.66 + 0.70 \times \log_{10}(x)$, $r^2 = 0.340$; Lagoon: $\log_{10}(y) = 2.45 + 0.60 \times \log_{10}(x)$, $r^2 = 0.793$. [Color figure can be viewed at wileyonlinelibrary.com]

of 50 $\mu\text{mol L}^{-1}$ have been used (Seitzinger 1988). Most of the observations in this study fall below that concentration, suggesting limitation or co-limitation by nitrate availability (Fig. 4a). However, when the nitrate concentrations are above the threshold, other factors are more important in limiting denitrification. One likely factor limiting (or co-limiting) denitrification rates is the availability of labile organic carbon (Arango et al. 2007).

Linkages between sediment organic carbon content and denitrification rates have been established (for a review, see Piña-Ochoa and Álvarez-Cobelas 2006), but this link seems to be quite weak and variable in our data. We found a significant relationship between the organic carbon content and denitrification only from open coast and lagoon ecosystems (Fig. 4b), where the lowest values for both sediment organic carbon content and denitrification rates were also observed. Organic carbon is needed for the denitrification process in a ratio close to 1 : 1 with nitrate (Taylor and Townsend 2010). As organic carbon is traditionally measured with combustion methods, the quality (biological lability) is not quantified. Thus, systems with similar organic carbon concentrations may actually have very different levels of bioavailable carbon for heterotrophic activity (Pusceddu et al. 2009). The bioavailability of sedimentary organic carbon is highly variable depending on the organic matter source and the extent of microbial processing (Fry et al. 1977; Kristensen 2000; Bianchi et al. 2002). The archipelago systems in the Baltic Sea receive relatively high inputs of organic material from land that is in general less bioavailable than autochthonous production (Hopkinson et al. 1998; Asmala et al. 2013). Combined with relatively low nitrate concentrations, this could explain the moderate denitrification rates in archipelagos. On the other hand, estuaries and lagoons maintained high denitrification rates despite relatively low organic carbon content (Fig. 4b), which could suggest that these systems have a high carbon turnover in the sediments.

As neither nitrate concentrations nor sediment organic carbon contents turned out as a satisfactory predictor to account for all the variation in the observed denitrification rates, we examined spatial and temporal patterns.

Spatial and temporal patterns of denitrification

Piña-Ochoa and Álvarez-Cobelas (2006) found that denitrification rates follow a seasonal pattern, peaking during the warm season. In our first analysis, we tested if seasonal variation was important in our combined data set. Only two coastal ecosystems had measured denitrification rates over multiple seasonal cycles (Kertinge Nor and Skive Fjord in Denmark), allowing for testing seasonal variations. Log-transformed denitrification rates were analyzed with a linear mixed model:

$$\log(\text{DN}+10) = \mu + m_i + Y_j(m_i) + S_k + e_{ijkl} \quad (1)$$

where m_i is a fixed categorical factor (up to 12 levels) describing the seasonal variations among month, $Y_j(m_i)$ is a random

factor describing changes in the seasonal variation among years, S_k is a random factor describing the spatial variation among sampling sites within the coastal area, and e_{ijkl} is the random variation between replicate cores within sampling sites. For both coastal ecosystems, the seasonal pattern was not significant relative to the other sources of random variation (Kertinge Nor: $F_{9,5.46} = 0.93$, $p = 0.5604$; Skive Fjord: $F_{11,13.3} = 0.73$, $p = 0.6972$; Supporting Information Table S2), despite monthly means varying by factors of 10 and 6, respectively (Supporting Information Fig. S2). Importantly, there was an apparent lack of synchrony in the seasonal variation between the two coastal ecosystems, suggesting that a common seasonal pattern cannot be imposed on all coastal systems. Denitrification in Kertinge Nor changes seasonally from coupled nitrification-denitrification in summer to become driven by nitrate in the water column during winter (Rysgaard et al. 1995). Nutrient inputs to Kertinge Nor are small and nitrate concentrations are mainly governed by exchanges with the open sea. On the other hand, the productive Skive Fjord receives large nutrient inputs from land and develops hypoxic/anoxic conditions during summer months, limiting coupled nitrification-denitrification (Supporting Information Fig. S2). In other systems, such as Aarhus Bight, denitrification driven by nitrate concentrations in the water dominates and they display higher rates during winter (Jensen et al. 1988). Consequently, the drivers of denitrification display different seasonal patterns leading to an overall lack of a common seasonal pattern for coastal denitrification.

Sundbäck et al. (2006) found higher denitrification rates in silt/mud sediments compared to sandy sediments. There were only two coastal ecosystems in our combined data set that had contrasting sediment types (Kalmarsund in Sweden and Curonian Lagoon in Lithuania). We analyzed differences between sand and silty/muddy sediments for these two systems using a linear mixed model

$$\log(\text{DN}+10) = \mu + t_i + M_j + T_i \times M_j + S_k + e_{ijkl} \quad (2)$$

where t_i describes the difference between sediment types, M_j describes the random temporal variation between two different sampling months (April and September for Kalmarsund; March and July for Curonian Lagoon), $T_i \times M_j$ describes the changes over time between sediment types, S_k is a random factor describing the spatial variation among sampling sites within the coastal area, and e_{ijkl} is the random variation between replicate cores within sampling sites. Our analysis suggested that denitrification rates in silty/muddy sediments were higher than in sandy sediments by factors of 3.1 and 6.8 (Supporting Information Fig. S3) for Kalmarsund and Curonian Lagoon, respectively, although these differences were overshadowed by the large random variation (Supporting Information Table S3) between measurements yielding low relative significance for the test (Kertinge Nor: $F_{1,2.54} = 1.42$, $p = 0.3329$; Skive Fjord: $F_{1,2.44} = 12.83$, $p = 0.0517$). The difference in denitrification

Table 2. Annual denitrification (DN) and phosphorus burial in the five coastal ecosystem types in the Baltic Sea. Denitrification is partitioned into sand and silt/mud sediments, whereas phosphorus burial only occurs for silt/mud sediments.

Ecosystem type	Area (km ²)	Silt/mud (%)	Sand (%)	Silt/mud DN (tons N yr ⁻¹)	Sand DN (tons N yr ⁻¹)	Total DN (tons N yr ⁻¹)	P burial (tons P yr ⁻¹)
Open coast	76,861	39%	27%	34,347	4861	39,208	6318
Archipelago	19,157	55%	5%	10,034	193	10,227	7578
Embayment	7139	35%	41%	4537	960	5497	585
Estuary	2965	60%	28%	9334	656	9990	387
Lagoon	4679	35%	54%	36,155	7886	44,040	1834
Entire coastal zone	110,800	42%	25%	94,406	14,556	108,963	16,701

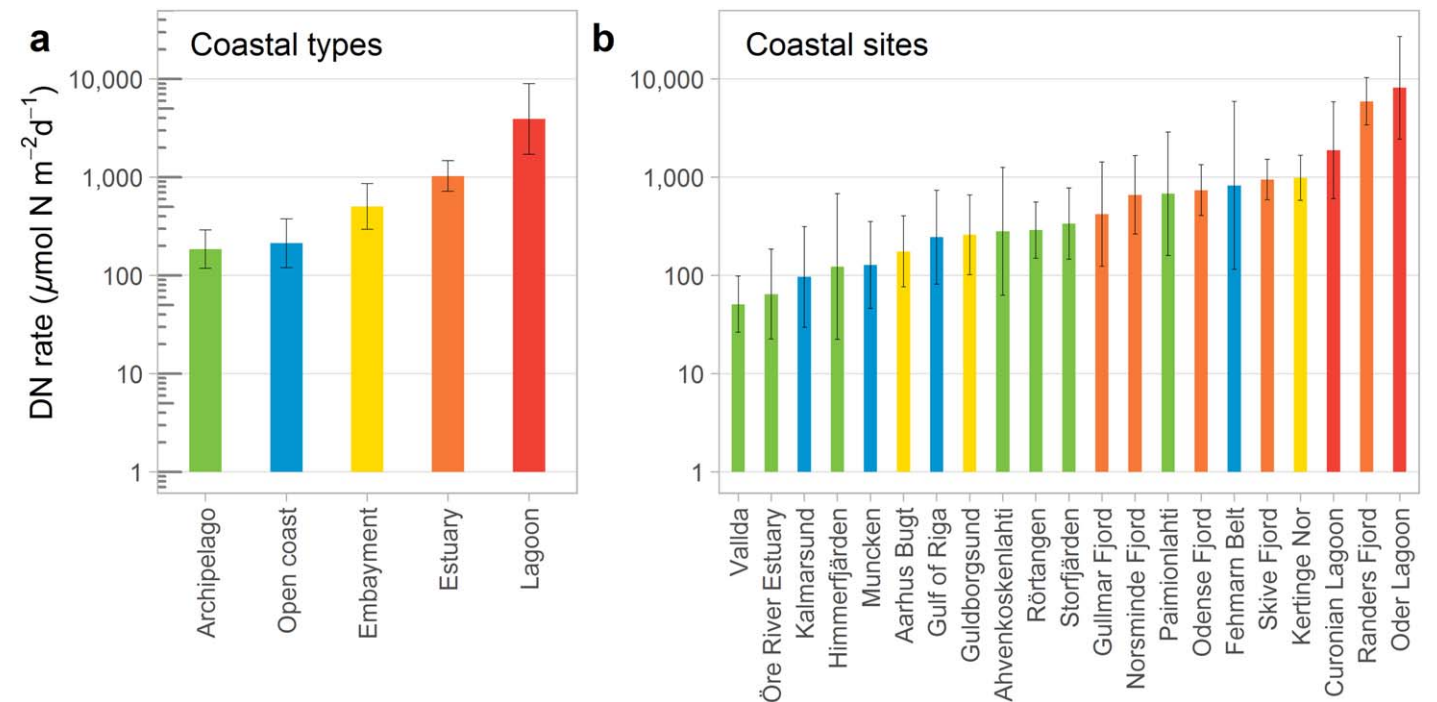


Fig. 5. Mean denitrification rates from Eq. 3 across (a) coastal ecosystem types and (b) coastal systems in the Baltic Sea. Error bars show the 95% confidence intervals for the mean estimates. Retransformation bias was accounted for using the variance estimates in Supporting Information Table S4. [Color figure can be viewed at wileyonlinelibrary.com]

rates between the two sediment types is mainly driven by differences in sediment organic carbon content, which on average was 0.40% for sand and 5.12% for silt/mud sediments. Although the effect of organic carbon content on denitrification has a more continuous nature (Fig. 4b), this categorization on sediment type allowed for extrapolating rates to all the Baltic Sea coastal ecosystems (Table 2).

The spatial variation in denitrification rates was large among coastal ecosystems and we analyzed this variation using a linear mixed model for silt/mud sediments only

$$\log(\text{DN} + 10) = \mu + a_i + c_j(a_i) + T_j(c_j(a_i)) + S_k(c_j(a_i)) + e_{ijkl} \quad (3)$$

where a_i describes the variation among the five coastal ecosystem types (Table 2), $c_j(a_i)$ describes the variation among

coastal ecosystems within types, $T_j(c_j(a_i))$ and $S_k(c_j(a_i))$ describe the random temporal and spatial variation within coastal ecosystems, and e_{ijkl} is the random variation between replicate cores within sampling sites. We found significant differences among types ($F_{4,114} = 16.36$, $p < 0.0001$) and among coastal ecosystems within types ($F_{16,86} = 5.36$, $p < 0.0001$). Mean denitrification rates ranged from $185 \mu\text{mol m}^{-2} \text{d}^{-1}$ in archipelagos and open coasts to almost $4000 \mu\text{mol m}^{-2} \text{d}^{-1}$ in lagoons (Fig. 5a), but the variation among coastal ecosystems was even larger, ranging more than two orders of magnitude (Fig. 5b). This spatial trend across ecosystem types reflects a distinctive gradient of land connectivity in denitrification rates, increasing with the influence of nutrient inputs from land. The variation among coastal

Table 3. Annual denitrification (DN) and phosphorus burial in the coastal zone of the six major basins in the Baltic Sea. Denitrification is partitioned between sand and silt/mud sediments, whereas phosphorus burial only occurs for silt/mud sediments.

Coastal regions	Area (km ²)	Silt/mud (%)	Sand (%)	Silt/mud DN (tons N yr ⁻¹)	Sand DN (tons N yr ⁻¹)	Total DN (tons N yr ⁻¹)	P burial (tons P yr ⁻¹)
Bothnian Bay	16,181	19%	25%	3247	769	4016	636
Bothnian Sea	25,668	63%	38%	17,664	134	17,798	3406
Gulf of Finland	12,720	51%	11%	7331	317	7648	2336
Gulf of Riga	9040	35%	52%	3644	1119	4763	691
Baltic Proper	27,447	35%	38%	44,788	9775	54,564	7933
Danish Straits	19,744	41%	39%	17,732	2442	20,174	1700

ecosystems can be attributed to multiple factors, such as their geomorphological characteristics (depth, exchange with open sea; Dürr et al. 2011), the ratio between freshwater flow and estuarine area (Jickells et al. 2014), residence time and loading from terrestrial system (Nixon 1995). For example, lagoon systems in this study have high nitrogen loading, limited exchange with the coastal sea and relatively low discharge to area ratio (Pastuszak et al. 2005; Aleksandrov 2010), enabling high denitrification rates.

In addition to the large-scale spatial variation, there were significant random variations (i.e., variability that cannot be determined) in the denitrification rates (Supporting Information Table S4). Random variation among replicated cores was $\pm 84\%$ and in addition to this variation, denitrification rates among sampling sites varied by $\pm 42\%$ and sampling time varied by $\pm 105\%$. The spatial heterogeneity on the local scale arises primarily from variation in physical characteristics of the benthic environment, such as sediment grain size, vertical layering and patchiness, which can all vary within small spatial scales (Holland and Elmore 2008). Heterogeneous distribution of vegetation, macrofauna and even microbes further adds to the variability (Scala and Kerkhof 2000; Gray 2002; Healey and Hovel 2004). Seasonal changes in the water chemistry and in the flux of phytoplankton-derived organic into the sediment presumably contribute to the large temporal variation (Piña-Ochoa and Álvarez-Cobelas 2006).

Scaling up coastal denitrification

In spite of the large variability of rates, we assessed the coastal filter for the entire Baltic Sea by scaling up estimated mean denitrification rates for the five coastal types for each of the 1017 coastal ecosystems (Table 2). However, to account for the variable denitrification rates in sandy and silty/muddy sediments in each of these systems, the difference between the two sediment types was used for estimating denitrification rates in sandy sediments for the five coastal types. However, the data from sandy sediments may lack the impact of pore water flow through permeable sediments which have been suggested to be active sites of coupled nitrification-denitrification (Huettel et al. 2014).

It remains uncertain whether rates in these types of sediments could have been higher if other methods than closed core incubations had been applied (Rao et al. 2007). Comparable data was available from two systems (Kalmarsund and Curonian Lagoon) and used to quantify the difference in denitrification rates between sandy and silty/muddy sediments. Using this empirical relationship, we assumed that denitrification in sandy sediments was 13.7% of the rates in silt/mud sediments. Denitrification was set to zero for hard bottom habitats such as bedrock, boulder reefs, and gravel.

Scaling-up denitrification rates by the sediment areas with silt/mud and sand for each coastal ecosystem and aggregating these for the five different ecosystem types showed that lagoons are very important for the Baltic Sea coastal filter, accounting for 40% of total denitrification with only 4% of the total area (Table 2). Denitrification was of a similar magnitude along the more extensive open coast, together with lagoons accounting for 76% of the nitrogen removal by denitrification in the coastal zone. Further, our data shows that archipelagos, embayments, and estuaries were of almost equal importance for the entire Baltic Sea coastal filter.

The coastal region around the Baltic Proper accounted for 50% of the total denitrification, even though it contributed only 25% of the total area (Table 3). This was mainly due to the large denitrification in lagoons located in the southern Baltic Sea. Denitrification was lowest in the Bothnian Bay (4%), where hard bottoms were the dominant feature of the coastal zone, followed by Gulf of Riga (4%) and Gulf of Finland (7%). The Bothnian Sea and Danish Straits accounted for 16% and 19% of total denitrification, respectively, in comparison to contributing 23% and 18% of coastal area. Comparing coastal denitrification in the different Baltic Sea basins with nitrogen input from land (HELCOM 2015; Supporting Information Table S5), we found that the Bothnian Bay, Gulf of Finland, and Gulf of Riga only removed 5–7%, whereas the Bothnian Sea removed 38% of the nitrogen input (Fig. 6). The Danish Straits were slightly more efficient than the Baltic Proper (22% and 18%, respectively). In total, denitrification in the coastal zone removed approximately 16% of nitrogen inputs from land.

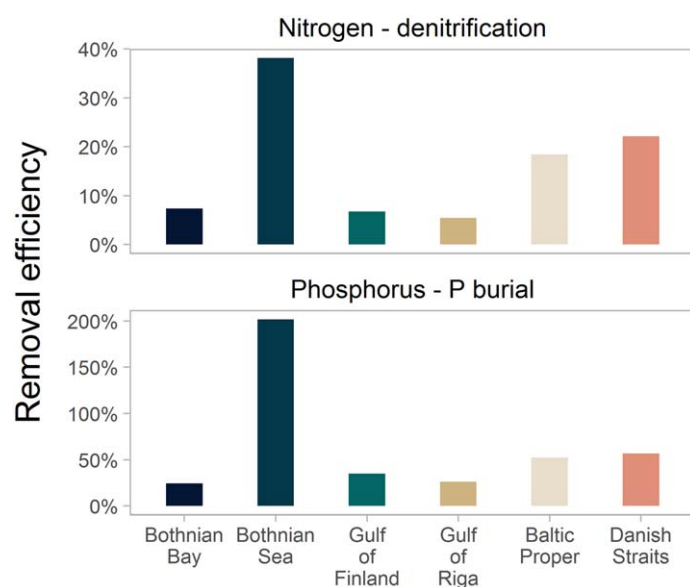


Fig. 6. Proportion of nutrient input from land (2007–2012; HELCOM 2015) removed by denitrification (upper panel) and phosphorus burial (lower panel) across the different regions of the Baltic Sea. [Color figure can be viewed at wileyonlinelibrary.com]

Removal of phosphorus in the coastal zone

Phosphorus burial mechanisms

The major pathway for removal of phosphorus (P) in estuaries is permanent burial into the sediment. This burial of phosphorus is generally variable on both spatial and temporal scales, and can range from less than 10% to more than 100% of the terrestrial phosphorus inputs in cases where estuaries trap large amounts of phosphorus from offshore areas (Howarth et al. 1996).

Three major forms of reactive (biologically available) phosphorus are considered to account for most burial of phosphorus in coastal environments (Ruttenberg, 2003). These forms are (1) organic phosphorus, (2) phosphorus bound to iron(Fe)-oxyhydroxides and (3) authigenic apatite, a calcium phosphate mineral. Most permanent burial of reactive phosphorus is assumed to occur in the form of authigenic apatite and organic phosphorus (Ruttenberg 2003), but in coastal environments with a low salinity, Fe-(oxyhydr)oxide bound P phases (Egger et al. 2015) or Fe(III)-P minerals may also act as a permanent burial sink (Ruttenberg 2003; Hyacinthe and Van Cappellen 2004). Recent work suggests that vivianite, an Fe(II)-P mineral (Ruttenberg 2003; Slomp 2011), may also play a quantitatively important role as a sink for phosphorus in coastal environments (Egger et al. 2015; Dijkstra et al. 2016; Reed et al. 2016), in particular in depositional settings where the inputs of Fe-(oxyhydr)-oxides are high. This makes P retention in the coastal zone a complex function of a range of factors besides salinity (Slomp 2011). Although the dominant forms of P burial vary across the Baltic Sea, we will consider the total P burial only for assessing the role of the coastal filter.

Phosphorus burial across the coastal Baltic Sea

Studies reporting phosphorus burial in Baltic Sea coastal sediments are few and have been estimated from either sediment cores or model approaches. For inclusion of phosphorus burial data from sediment cores, we had three criteria: (1) the sample site was located in the coastal zone of the Baltic Sea, (2) a sediment accumulation rate from dating was available, thereby allowing quantification of long-term net accumulation (e.g., not applicable to sediment trap data), (3) total phosphorus measurements were available for the same site to quantify permanent P burial. We also included model results, for which the major criterium was that a P budget for at least an entire year was available for the coastal system. Data and references are presented in Table 4. Burial rates were strongly related to sedimentation rates for these studies (Fig. 7), but net sedimentation rates were not available for coastal systems in general and could therefore not be used to extrapolate phosphorus burial more widely. Phosphorus burial estimated at four sites in the Stockholm Archipelago as well as in Gåsfjärden in southern Sweden ranged from $0.4 \text{ g P m}^{-2} \text{ yr}^{-1}$ to $2.8 \text{ g P m}^{-2} \text{ yr}^{-1}$, yielding an average of $1.83 \text{ g P m}^{-2} \text{ yr}^{-1}$ for archipelago systems (Table 4). These values may overestimate the P burial in the archipelagos of the Bothnian Bay and Bothnian Sea, where nutrient and chlorophyll concentrations are considerably lower (HELCOM 2009; Puttonen et al. 2014). Somewhat higher P burial rates have been measured in three estuaries (Kymijoki, Neva, and Paimionjoki) in the Gulf of Finland, averaging $2.28 \text{ g P m}^{-2} \text{ yr}^{-1}$. Three studies from the Oder Lagoon suggested a mean P burial rate of $0.98 \text{ g P m}^{-2} \text{ yr}^{-1}$, which was comparable to the Curonian Lagoon, and P burial in these two lagoons averaged $1.02 \text{ g P m}^{-2} \text{ yr}^{-1}$. Even though the lagoons receive high phosphorus inputs from land, they are also relatively shallow (Table 1) suggesting higher sediment mobilization and most likely relatively lower P burial compared to archipelagos and estuaries.

Hence, the sparse literature suggests an increasing P burial from open coast ($0.21 \text{ g P m}^{-2} \text{ yr}^{-1}$) and embayments ($0.56 \text{ g P m}^{-2} \text{ yr}^{-1}$) to the shallow lagoons ($1.02 \text{ g P m}^{-2} \text{ yr}^{-1}$) and archipelagos ($1.83 \text{ g P m}^{-2} \text{ yr}^{-1}$) and deeper estuaries ($2.28 \text{ g P m}^{-2} \text{ yr}^{-1}$), applicable to coastal systems across the Baltic Sea. These different rates among coastal types seem reasonable given differences in phosphorus inputs from land and shallowness of the systems. Unfortunately, there are no studies on P burial in the coastal zone of the Bothnian Bay and Bothnian Sea, but the low nutrient input from land (HELCOM 2015) and low P concentrations in coastal waters (HELCOM 2009) suggest that P burial rates per m^2 are low. For the open Bothnian Bay and Bothnian Sea, reported maximum sedimentation ranges are $1.9\text{--}2.4$ and $1.9\text{--}3.7 \text{ mm yr}^{-1}$, respectively (Håkansson et al. 1996; Mattila et al. 2006), which are comparable to the Gulf of Riga (Table 4). Given that coastal-open sea gradients of nutrient and chlorophyll concentrations are weak in these two basins

Table 4. Total phosphorus burial and sedimentation rates in 15 different coastal systems of the Baltic Sea obtained from the literature. Burial rates in Oder and Curonian lagoons were recalculated from estimates of total P removal divided by the area of depositional bottoms (silt/mud).

Site	P burial (g P m ⁻² yr ⁻¹)	Sedimentation rate (mm yr ⁻¹)	Coastal type	Method	Reference
Gåsfjärden	0.4–1.1	4.5	Archipelago	Sediment cores	Ning et al. (2016)
Gälnan	1.7	9	Archipelago	Sediment cores	Rydin et al. (2011)
Pilkobbsfjärden	1.7	11	Archipelago	Sediment cores	Rydin et al. (2011)
Bulleröfjärden	2.2	12	Archipelago	Sediment cores	Rydin et al. (2011)
Torsbyfjärden	2.8	20	Archipelago	Sediment cores	Rydin et al. (2011)
Aarhus Bight	0.56	6.1	Embayment	Sediment cores	Jensen et al. (1995)
Kymijoki Estuary 1	1.4	7	Estuary	Sediment cores	Pitkänen (1994)
Kymijoki Estuary 2	1.3	5.8	Estuary	Sediment cores	Lukkari et al. (2008)
Neva Estuary	2.1	11	Estuary	Sediment cores	Pitkänen (1994)
Paimionjoki Estuary	4.3	24.6	Estuary	Sediment cores	Lukkari et al. (2008)
Oder Lagoon	0.30–0.95	N/A	Lagoon	Nutrient budget model	Lampe (1999)
Oder Lagoon	0.41	N/A	Lagoon	Nutrient budget model	Grelowski et al. (2000)
Oder Lagoon	1.89	N/A	Lagoon	Nutrient budget model	Humborg et al. (2000)
Curonian Lagoon	0.76–1.35	N/A	Lagoon	Inflow–outflow fluxes	Petkuvienė et al. (2016)
Gulf of Riga	0.21	2.2	Open coast	Sediment cores	Carman et al. (1996)

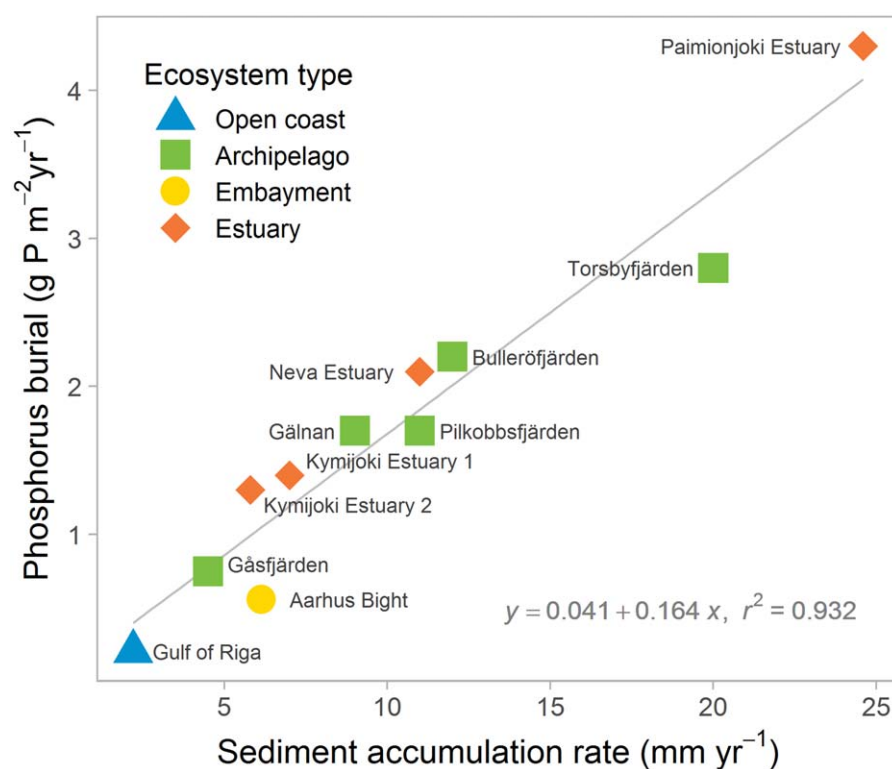


Fig. 7. Relationship between sedimentation accumulation rate and phosphorus burial in 11 study sites across the Baltic Sea. [Color figure can be viewed at wileyonlinelibrary.com]

(HELCOM 2009), it is realistic to assume sedimentation and phosphorus burial rates similar to the Gulf of Riga. This is also consistent with Slomp et al. (2013) estimating a

phosphorus burial rate of 0.24 g P m⁻² yr⁻¹ in the open Bothnian Sea (60–90 m depth). Consequently, for extrapolating phosphorus burial rates to coastal region of

the two basins we used the rate from the open coast ($0.21 \text{ g P m}^{-2} \text{ yr}^{-1}$).

Upscaling of the P burial rates to the coastal zone of the whole Baltic Sea suggests that P burial was largest in archipelagos, accounting for 45% of the total removal in the coastal zone (Table 2). Phosphorus removal was also important in the open coastal zone (38%) due to the large contributing area, whereas lagoons accounted for 11% of the total P burial and estuaries and embayments accounted for only 2% and 4%, respectively. These results suggest that archipelagos are highly efficient environments in trapping P. Archipelago systems are typically characterized by highly varied bottom water topography and strongly contrasting depositional environments at the seafloor. Sediment accumulation sites in archipelagos are typically organic rich and high in organic phosphorus, which is the dominant form of P buried (Lukkari et al. 2009; Puttonen et al. 2014).

Coastal systems in the Baltic Proper accounted for almost half of the total P removal in the coastal zone (47%), followed by the Bothnian Sea (20%), Gulf of Finland (14%), and Danish Straits (10%) (Table 3). Phosphorus removal in the coastal zones of the Bothnian Bay and Gulf of Riga was generally small ($\sim 4\%$ for both regions). When comparing the estimated P burial rates with inputs from land, the Bothnian Sea coastal zone removed twice the P input from land (Fig. 6). This implies that large amounts of P were imported from the bottom waters of the open Bothnian Sea and buried in coastal sediments. In this low salinity environment, P is likely mostly buried in the form of Fe-(oxyhydr)oxide bound P and vivianite (Egger et al. 2015). In the Baltic Proper and Danish Straits more than half of the phosphorus input from land was removed in the coastal zone, with authigenic apatite likely being a major sink (Jensen et al. 1995). In contrast, only 25–35% of the P input from land was removed in the coastal zone of the Bothnian Bay, Gulf of Finland, and Gulf of Riga. For the entire Baltic Sea the extrapolation approach suggests that 53% of the phosphorus input from land is removed in the coastal zone.

Synthesis

Our extrapolation approach suggests that the 16% of nitrogen inputs and 53% of phosphorus inputs from land are removed by denitrification and phosphorus burial in the coastal zone. For comparison, Gustafsson et al. (2012) estimated that the entire Baltic Sea removes 87% of nitrogen inputs by denitrification and 78% of phosphorus inputs by burial.

Given that the coastal zone comprises 27% of the total area of the Baltic Sea, denitrification in the coastal zone is apparently less efficient than the open Baltic Sea. This is consistent with Deutsch et al. (2010), who measured increasing denitrification rates from the coast ($\sim 12 \mu\text{mol m}^{-2} \text{ d}^{-1}$) toward the deeper basins ($\sim 690 \mu\text{mol m}^{-2} \text{ d}^{-1}$) of the

southern Baltic Sea. Their gradient also expressed a transition from sand to mud sediments. We also found reduced denitrification rates in sandy sediments (Supporting Information Fig. S3) and given that sandy sediments are an important feature of the coastal zone, particularly in shallow lagoons and embayments (Table 2), the coastal filter becomes less efficient for removing nitrogen, even though denitrification rates in lagoons can be ca. 10 times higher than in the open Baltic Sea. Furthermore, the coastal zone contains considerable areas with hard substrate where nutrient removal is negligible.

On the other hand, the coastal zone was more efficient in trapping phosphorus than the open Baltic Sea. This is mainly due to the relatively low phosphorus burial in the Baltic Proper ($\sim 0.23 \text{ g P m}^{-2} \text{ yr}^{-1}$; Mort et al. 2010), where widespread hypoxia reduces burial of iron-bound phosphate (Carstensen et al. 2014). Despite the potential release of phosphorus even during oxic conditions (Puttonen et al. 2016), our results suggest that archipelagos surrounding the Baltic Proper are hot spots (McClain et al. 2003) for phosphorus removal. The complex bathymetry of archipelagos with isolated depressions and generally low currents are likely to allow locally high sedimentation rates in these systems (Bonsdorff et al. 1997), enabling high phosphorus burial rates. Furthermore, phosphate-rich bottom water from the Baltic Proper spills into the archipelagos which combined with relatively high Fe-concentrations in Swedish rivers (Kritzberg et al. 2014) may facilitate high burial rates of iron-bound phosphate. High inputs of iron are also believed to be important for P burial in the Bothnian Sea (Egger et al. 2015). To support this Rydin et al. (2011) found that iron-bound P burial dominated in the inner Stockholm Archipelago, whereas organic forms were more important in the outer Stockholm Archipelago. This suggests that the high P burial rates in archipelagos are partly sustained by phosphorus imports from the Baltic Proper (Savchuk 2005). P burial in estuaries was also high, which could be associated with high inputs of organic material and coastal erosion driven by changes in fluvial inputs. Coastal erosion is also caused by the continuous land uplift in the northern part of the Baltic Sea, which further adds to the nutrient inputs to the coastal zone (Jonsson and Carman 1994).

Coastal ecosystems around the Baltic Sea are very diverse in their hydromorphology, salinity, and nutrient levels. Consequently, denitrification and phosphorus burial removal rates vary broadly among systems and they appear disconnected (Fig. 8). For example, archipelagos have high P burial but relatively low denitrification, whereas lagoons have high denitrification but moderate P burial. Coastal denitrification rates displayed an increasing gradient from archipelagos to lagoons with high inputs from land, whereas P burial was strongly coupled to sedimentation rates (Fig. 7). In addition to these general patterns, other factors modulate denitrification and P burial.

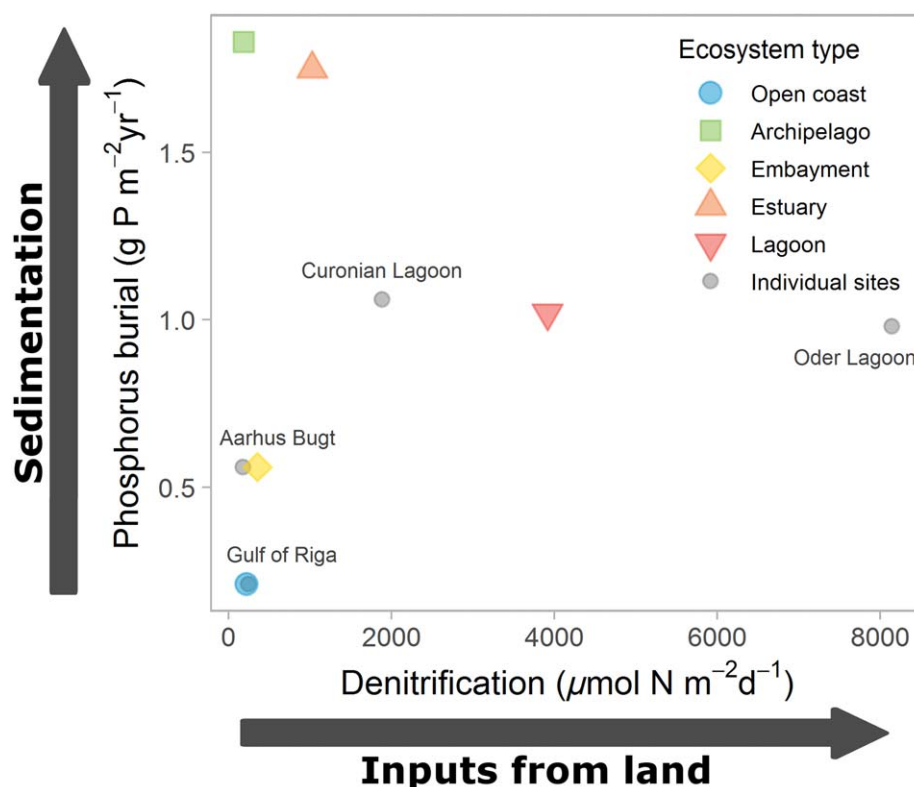


Fig. 8. Relationship between denitrification and phosphorus burial in the five Baltic Sea coastal ecosystems (colored circles), and in four individual sites (gray rectangles). The main environmental driver for both processes is marked with a solid gray arrow outside the plot area. [Color figure can be viewed at wileyonlinelibrary.com]

The variability among coastal systems in denitrification and P burial rates was large; more than two orders of magnitude for denitrification (Fig. 5b) and one order of magnitude for P burial (Table 4). Why was denitrification more variable? First of all, denitrification in silty/muddy sediment was on average seven times higher compared to denitrification in sandy sediments (Supporting Information Fig. S3). The organic content of the sediment (Fig. 4b) is likely a strong driver for this observed difference. Second, our analysis of denitrification rates suggests that availability of nitrate could explain the large span in denitrification rates (Fig. 4a) and hence, that variations in nitrogen inputs and their availability to the coastal ecosystem are the main factors driving this variability. On the other hand, variations in P burial were strongly linked to sedimentation rates (Fig. 7), so understanding the mechanisms affecting net sedimentation rates will also help to understand the dynamics of phosphorus burial. Phosphorus burial is partly governed by the amount of organic material produced in the system and subsequently reaching the sediment. However, the large variability among coastal ecosystems has implications, when extrapolating studies from a few sites (22 for denitrification and 15 for P burial) to 1017 different systems. We decreased the overall variation introduced by differences among studies by

partitioning them into five different ecosystem types, but even within these types variability in nutrient removal rates was large. Consequently, our nutrient removal estimates are associated with a considerable uncertainty. To reduce the uncertainty, it is important to obtain rates from other coastal systems around the Baltic Sea, particularly from the northern part.

To date, the role of the coastal filter has not yet been quantitatively considered in nutrient management plans, including the Baltic Sea Action Plan. Our results highlight the importance of coastal ecosystems in reducing nutrient inputs to the open Baltic Sea, but the efficiency of the coastal filter may have decreased over time. As an example, the diversion of the largest single nutrient source in the Baltic Sea, Vistula River outflow in the late 19th century (Cyberski et al. 2006), from passing through the Vistula Lagoon to discharging directly into the Baltic Sea enhanced the nutrient delivery to the open waters (Glasby and Szefer 1998). Today, many coastal systems in the Baltic Sea are affected by hypoxia (Conley et al. 2011). Low oxygen concentrations reduce the coupled nitrification-denitrification process, potentially limiting denitrification rates (Conley et al. 2009). Further, iron-bound phosphorus may be released from surface sediments during anoxic conditions (Mort et al. 2010).

Targeting coastal environments where hypoxia has eroded the nutrient filter capacity by reducing local nutrient inputs is an effective means to achieve the targets.

Salinity imposes natural boundaries to distribution ranges of many aquatic organisms (Zettler et al. 2007) and the diversity of the macrofauna community is strongly reduced from the saline Danish Straits toward the brackish coastal systems to the north and east (Bonsdorff 2006). The absence or even low diversity of bioturbating species, due to hypoxia or low salinity, can severely reduce denitrification and phosphorus burial (Karlson et al. 2007; Norkko et al. 2012; Carstensen et al. 2014). Also, mixing of freshwater and saline seawater in estuaries causes the riverine organic carbon to form sinking aggregates (Asmala et al. 2014), which adds to the sedimentation otherwise fueled by primary production, enhancing P burial potential. In general, the land-to-sea gradient of allochthonous carbon in the coastal zone stimulates heterotrophic activity, potentially providing also denitrifiers with a supply of labile organic carbon (Wikner et al. 1999). In addition to chemical properties of the coastal waters, residence time has been suggested to have a strong, positive relationship with nutrient retention in coastal systems (Nixon et al. 1996).

In this review, we synthesized data from several coastal studies in the Baltic Sea to obtain a coherent view of two major nutrient removal processes. We quantified the significance of the coastal zone in buffering nutrient inputs to the Baltic Sea from a broad span of coastal ecosystems. The coastal filter permanently removes more than half of the phosphorus entering the Baltic Sea and one-sixth of the nitrogen, leaving the remaining proportion to be utilized and recycled within the coastal system or transported to open waters. Given the substantial removal of nutrients taking place within the coastal zone, it is important that this filter effect is considered in management plans for the Baltic Sea.

Changes in land use and climate may increase the nutrient pressure on the coastal zone, affecting ecosystem services provided such as nutrient removal. Despite considerable progress in understanding the biogeochemical cycles of nitrogen and phosphorus in the Baltic Sea, it is evident that substantial knowledge gaps remain regarding the importance of different regulating factors, as well as describing the seasonal and spatial variability of nutrient removal processes. In particular, for the management of the entire Baltic Sea it is crucial to be able to predict the efficiency of the coastal filter in a future warmer and wetter climate with expected large shifts in nutrient inputs among regions (Hong et al. 2017).

References

Aleksandrov, S. 2010. Biological production and eutrophication of Baltic Sea estuarine ecosystems: The Curonian and Vistula Lagoons. *Mar. Pollut. Bull.* **61**: 205–210. doi:10.1016/j.marpolbul.2010.02.015

Arango, C. P., J. L. Tank, J. L. Schaller, T. V. Royer, M. J. Bernot, and M. B. David. 2007. Benthic organic carbon influences denitrification in streams with high nitrate concentration. *Freshw. Biol.* **52**: 1210–1222. doi:10.1111/j.1365-2427.2007.01758.x

Asmala, E., R. Autio, H. Kaartokallio, L. Pitkänen, C. Stedmon, and D. Thomas. 2013. Bioavailability of riverine dissolved organic matter in three Baltic Sea estuaries and the effect of catchment land use. *Biogeosciences* **10**: 6969–6986. doi:10.5194/bg-10-6969-2013

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

Benitez-Nelson, C. R., and K. O. Buesseler. 1999. Variability of inorganic and organic phosphorus turnover rates in the coastal ocean. *Nature* **398**: 502–505. doi:10.1038/19061

Bianchi, T. S., S. Mitra, and B. A. McKee. 2002. Sources of terrestrially-derived organic carbon in lower Mississippi River and Louisiana shelf sediments: Implications for differential sedimentation and transport at the coastal margin. *Mar. Chem.* **77**: 211–223. doi:10.1016/S0304-4203(01)00088-3

Bonsdorff, E. 2006. Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. *J. Exp. Mar. Biol. Ecol.* **330**: 383–391. doi:10.1016/j.jembe.2005.12.041

Bonsdorff, E., E. Blomqvist, J. Mattila, and A. Norkko. 1997. Coastal eutrophication: Causes, consequences and perspectives in the archipelago areas of the northern Baltic Sea. *Estuar. Coast. Shelf Sci.* **44**: 63–72. doi:10.1016/S0272-7714(97)80008-X

Borum, J. 1996. Shallow Waters and Land/Sea Boundaries, *In* B. B. Jørgensen, and K. Richardson [eds.], *Eutrophication in Coastal Marine Ecosystems*, American Geophysical Union, Washington, D. C., doi:10.1029/CE052p0179.

Bouwman, A., M. Bierkens, J. Griffioen, M. Hefting, J. Middelburg, H. Middelkoop, and C. Slomp. 2013. Nutrient dynamics, transfer and retention along the aquatic continuum from land to ocean: Towards integration of ecological and biogeochemical models. *Biogeosciences* **10**: 1–22. doi:10.5194/bg-10-1-2013

Boynton, W., J. Garber, R. Summers, and W. Kemp. 1995. Inputs, transformations, and transport of nitrogen and phosphorus in Chesapeake Bay and selected tributaries. *Estuaries* **18**: 285–314. doi:10.2307/1352640

Carman, R., J. Aigars, and B. Larsen. 1996. Carbon and nutrient geochemistry of the surface sediments of the Gulf of Riga, Baltic Sea. *Mar. Geol.* **134**: 57–76. doi:10.1016/0025-3227(96)00033-3

Carstensen, J., and others. 2014. Hypoxia in the Baltic Sea: Biogeochemical cycles, benthic fauna, and management. *Ambio* **43**: 26–36. doi:10.1007/s13280-013-0474-7

- Christensen, P. B., L. P. Nielsen, J. Sørensen, and N. P. Revsbech. 1990. Denitrification in nitrate-rich streams: Diurnal and seasonal variation related to benthic oxygen metabolism. *Limnol. Oceanogr.* **35**: 640–651. doi:[10.4319/lo.1990.35.3.0640](https://doi.org/10.4319/lo.1990.35.3.0640)
- Conley, D. J., and others. 2009. Hypoxia-related processes in the Baltic Sea. *Environ. Sci. Technol.* **43**: 3412–3420. doi:[10.1021/es802762a](https://doi.org/10.1021/es802762a)
- Conley, D. J., and others. 2011. Hypoxia is increasing in the coastal zone of the Baltic Sea. *Environ. Sci. Technol.* **45**: 6777–6783. doi:[10.1021/es201212r](https://doi.org/10.1021/es201212r)
- Cyberski, J., M. Grześ, M. Gutry-Korycka, E. Nachlik, and Z. W. Kundzewicz. 2006. History of floods on the River Vistula. *Hydrol. Sci. J.* **51**: 799–817. doi:[10.1623/hysj.51.5.799](https://doi.org/10.1623/hysj.51.5.799)
- Dalsgaard, T., L. De Brabandere, and P. O. Hall. 2013. Denitrification in the water column of the central Baltic Sea. *Geochim. Cosmochim. Acta* **106**: 247–260. doi:[10.1016/j.gca.2012.12.038](https://doi.org/10.1016/j.gca.2012.12.038)
- Deutsch, B., S. Forster, M. Wilhelm, J. Dippner, and M. Voss. 2010. Denitrification in sediments as a major nitrogen sink in the Baltic Sea: An extrapolation using sediment characteristics. *Biogeosciences* **7**: 3259. doi:[10.5194/bg-7-3259-2010](https://doi.org/10.5194/bg-7-3259-2010)
- Dijkstra, N., C. P. Slomp, and T. Behrends. 2016. Vivianite is a key sink for phosphorus in sediments of the Landsort Deep, an intermittently anoxic deep basin in the Baltic Sea. *Chem. Geol.* **438**: 58–72. doi:[10.1016/j.chemgeo.2016.05.025](https://doi.org/10.1016/j.chemgeo.2016.05.025)
- Dürr, H. H., G. G. Laruelle, C. M. van Kempen, C. P. Slomp, M. Meybeck, and H. Middelkoop. 2011. Worldwide typology of nearshore coastal systems: Defining the estuarine filter of river inputs to the oceans. *Estuaries Coast.* **34**: 441–458. doi:[10.1007/s12237-011-9381-y](https://doi.org/10.1007/s12237-011-9381-y)
- Enger, M., T. Jilbert, T. Behrends, C. Rivard, and C. P. Slomp. 2015. Vivianite is a major sink for phosphorus in methanogenic coastal surface sediments. *Geochim. Cosmochim. Acta* **169**: 217–235. doi:[10.1016/j.gca.2015.09.012](https://doi.org/10.1016/j.gca.2015.09.012)
- Ensign, S. H., and M. W. Doyle. 2006. Nutrient spiraling in streams and river networks. *J. Geophys. Res. Biogeosci.* **111**: 1–13. doi:[10.1029/2005JG000114](https://doi.org/10.1029/2005JG000114)
- Fry, B., R. S. Scalan, and P. L. Parker. 1977. Stable carbon isotope evidence for two sources of organic matter in coastal sediments: Seagrasses and plankton. *Geochim. Cosmochim. Acta* **41**: 1875–1877. doi:[10.1016/0016-7037\(77\)90218-6](https://doi.org/10.1016/0016-7037(77)90218-6)
- Glasby, G., and P. Szefer. 1998. Marine pollution in Gdansk Bay, Puck Bay and the Vistula lagoon, Poland: An overview. *Sci. Total Environ.* **212**: 49–57. doi:[10.1016/S0048-9697\(97\)00333-1](https://doi.org/10.1016/S0048-9697(97)00333-1)
- Gray, J. S. 2002. Species richness of marine soft sediments. *Mar. Ecol. Prog. Ser.* **244**: 285–297. doi:[10.3354/meps244285](https://doi.org/10.3354/meps244285)
- Grelowski, A., M. Pastuszek, S. Sitek, and Z. Witek. 2000. Budget calculations of nitrogen, phosphorus and BOD 5 passing through the Oder estuary. *J. Mar. Syst.* **25**: 221–237. doi:[10.1016/S0924-7963\(00\)00017-8](https://doi.org/10.1016/S0924-7963(00)00017-8)
- Gustafsson, B. G., and others. 2012. Reconstructing the development of Baltic Sea eutrophication 1850–2006. *Ambio* **41**: 534–548. doi:[10.1007/s13280-012-0318-x](https://doi.org/10.1007/s13280-012-0318-x)
- Håkansson, B., P. Alenius, and L. Brydsten. 1996. Physical environment in the Gulf of Bothnia. *Ambio* **8**: 5–12.
- Healey, D., and K. A. Hovel. 2004. Seagrass bed patchiness: Effects on epifaunal communities in San Diego Bay, USA. *J. Exp. Mar. Biol. Ecol.* **313**: 155–174. doi:[10.1016/j.jembe.2004.08.002](https://doi.org/10.1016/j.jembe.2004.08.002)
- HELCOM. 2009. Eutrophication in the Baltic Sea—an integrated thematic assessment of eutrophication in the Baltic Sea region. Baltic Sea Environmental Proceedings No. 115B. Helsinki Commission, 148 p. Available from www.helcom.fi
- HELCOM. 2015. Updated Fifth Baltic Sea Pollution Load Compilation (-5.5). Baltic Sea Environmental Proceedings No. 145, 143 p. Available from www.helcomPLC.fi
- Hietanen, S., and J. Kuparinen. 2008. Seasonal and short-term variation in denitrification and anammox at a coastal station on the Gulf of Finland, Baltic Sea. *Hydrobiologia* **596**: 67–77. doi:[10.1007/s10750-007-9058-5](https://doi.org/10.1007/s10750-007-9058-5)
- Hjerne, O., and S. Hansson. 2002. The role of fish and fisheries in Baltic Sea nutrient dynamics. *Limnol. Oceanogr.* **47**: 1023–1032. doi:[10.4319/lo.2002.47.4.1023](https://doi.org/10.4319/lo.2002.47.4.1023)
- Holland, K., and P. Elmore. 2008. A review of heterogeneous sediments in coastal environments. *Earth Sci. Rev.* **89**: 116–134. doi:[10.1016/j.earscirev.2008.03.003](https://doi.org/10.1016/j.earscirev.2008.03.003)
- Hong, B., D. P. Swaney, M. McCrackin, A. Svanbäck, C. Humborg, B. Gustafsson, A. Yershova, and A. Pakhomau. 2017. Advances in NANI and NAPI accounting for the Baltic drainage basin: Spatial and temporal trends and relationships to watershed TN and TP fluxes. *Biogeochemistry* **133**: 245–261. doi:[10.1007/s10533-017-0330-0](https://doi.org/10.1007/s10533-017-0330-0)
- Hopkinson, C. S., and others. 1998. Terrestrial inputs of organic matter to coastal ecosystems: An intercomparison of chemical characteristics and bioavailability. *Biogeochemistry* **43**: 211–234. doi:[10.1023/A:1006016030299](https://doi.org/10.1023/A:1006016030299)
- Howarth, R. W., G. Billen, D. Swaney, A. Townsend, N. Jaworski, K. Lajtha, J. A. Downing, R. Elmgren, N. Caraco, and T. Jordan. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: Natural and human influences, p. 75–139. In *Anonymous Nitrogen cycling in the North Atlantic Ocean and its watersheds*. Springer.
- Huetzel, M., P. Berg, and J. E. Kostka. 2014. Benthic exchange and biogeochemical cycling in permeable sediments. *Ann. Rev. Mar. Sci.* **6**: 23–51. doi:[10.1146/annurev-marine-051413-012706](https://doi.org/10.1146/annurev-marine-051413-012706)
- Humborg, C., K. Fennel, M. Pastuszek, and W. Fennel. 2000. A box model approach for a long-term assessment of estuarine eutrophication, Szczecin Lagoon, southern Baltic. *J. Mar. Syst.* **25**: 387–403. doi:[10.1016/S0924-7963\(00\)00029-4](https://doi.org/10.1016/S0924-7963(00)00029-4)
- Hyacinthe, C., and P. Van Cappellen. 2004. An authigenic iron phosphate phase in estuarine sediments: Composition,

- p formation and chemical reactivity.
- Mar. Chem.*
- 91**
- : 227–251. doi:10.1016/j.marchem.2004.04.006
- Jensen, H. S., P. Mortensen, F. Andersen, E. Rasmussen, and A. Jensen. 1995. Phosphorus cycling in a coastal marine sediment, Aarhus Bay, Denmark. *Limnol. Oceanogr.* **40**: 908–917. doi:10.4319/lo.1995.40.5.0908
- Jensen, M. H., T. K. Andersen, and J. Sørensen. 1988. Denitrification in coastal bay sediment: Regional and seasonal variation in Aarhus Bight, Denmark. *Mar. Ecol. Prog. Ser.* **48**: 155–162. doi:10.3354/meps048155
- Jickells, T., J. Andrews, D. Parkes, S. Suratman, A. Aziz, and Y. Hee. 2014. Nutrient transport through estuaries: The importance of the estuarine geography. *Estuar. Coast. Shelf Sci.* **150**: 215–229. doi:10.1016/j.ecss.2014.03.014
- Jonsson, P., and R. Carman. 1994. Changes in deposition of organic matter and nutrients in the Baltic Sea during the twentieth century. *Mar. Pollut. Bull.* **28**: 417–426. doi:10.1016/0025-326X(94)90127-9
- Jørgensen, L., S. Markager, and M. Maar. 2014. On the importance of quantifying bioavailable nitrogen instead of total nitrogen. *Biogeochemistry* **117**: 455–472. doi:10.1007/s10533-013-9890-9
- Karlson, K., R. Rosenberg, and E. Bonsdorff. 2002. Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic waters: A review. *Oceanogr. Mar. Biol. Ann. Rev.* **40**: 427–489. doi:10.1201/9780203180594.ch8
- Karlson, K., E. Bonsdorff, and R. Rosenberg. 2007. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *Ambio* **36**: 161–167. doi:10.1579/0044-7447(2007)36[161:TIOBMF]2.0.CO;2
- Kristensen, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* **426**: 1–24. doi:10.1023/A:1003980226194
- Kritzberg, E. S., A. B. Villanueva, M. Jung, and H. E. Reader. 2014. Importance of Boreal rivers in providing iron to marine waters. *PLoS One* **9**: e107500. doi:10.1371/journal.pone.0107500
- Lampe, R. 1999. The Odra Estuary as a filter and transformation area. *Acta Hydrochim. Hydrobiol.* **27**: 292–297. doi:10.1002/(SICI)1521-401X(199911)27:5 <292::AID-AHEH292>3.0.CO;2-Z
- Lukkari, K., M. Leivuori, and H. Hartikainen. 2008. Vertical distribution and chemical character of sediment phosphorus in two shallow estuaries in the Baltic Sea. *Biogeochemistry* **90**: 171–191.
- Lukkari, K., M. Leivuori, H. Vallius, and A. Kotilainen. 2009. The chemical character and burial of phosphorus in shallow coastal sediments in the northeastern Baltic Sea. *Biogeochemistry* **94**: 141–162. doi:10.1007/s10533-009-9315-y
- Mattila, J., H. Kankaanpää, and E. Ilus. 2006. Estimation of recent sediment accumulation rates in the Baltic Sea using artificial radionuclides ^{137}Cs and $^{239,240}\text{Pu}$ as time markers. *Boreal Environ. Res.* **11**: 95.
- McClain, M. E., and others. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems* **6**: 301–312. doi:10.1007/s10021-003-0161-9
- McGlathery, K. J., K. Sundbäck, and I. C. Anderson. 2007. Eutrophication in shallow coastal bays and lagoons: The role of plants in the coastal filter. *Mar. Ecol. Prog. Ser.* **348**: 1–18. doi:10.3354/meps07132
- Monsen, N. E., J. E. Cloern, L. V. Lucas, and S. G. Monismith. 2002. A comment on the use of flushing time, residence time, and age as transport time scales. *Limnol. Oceanogr.* **47**: 1545–1553. doi:10.4319/lo.2002.47.5.1545
- Mort, H. P., C. P. Slomp, B. G. Gustafsson, and T. J. Andersen. 2010. Phosphorus recycling and burial in Baltic Sea sediments with contrasting redox conditions. *Geochim. Cosmochim. Acta* **74**: 1350–1362. doi:10.1016/j.gca.2009.11.016
- Nelson, J. L., and E. S. Zavaleta. 2012. Salt marsh as a coastal filter for the oceans: Changes in function with experimental increases in nitrogen loading and sea-level rise. *PLoS One* **7**: e38558. doi:10.1371/journal.pone.0038558
- Nielsen, L. P. 1992. Denitrification in sediment determined from nitrogen isotope pairing. *FEMS Microbiol. Lett.* **86**: 357–362. doi:10.1016/0378-1097(92)90800-4
- Ning, W., A. Ghosh, T. Jilbert, C. P. Slomp, M. Khan, J. Nyberg, D. J. Conley, and H. L. Filipsson. 2016. Evolving coastal character of a Baltic Sea inlet during the Holocene shoreline regression: impact on coastal zone hypoxia. *J. Paleolimnol.* **55**: 319–338.
- Nixon, S. W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia* **41**: 199–219. doi:10.1080/00785236.1995.10422044
- Nixon, S., and others. 1996. The fate of nitrogen and phosphorus at the land-sea margin of the North Atlantic Ocean. *Biogeochemistry* **35**: 141–180. doi:10.1007/BF02179826
- Norkko, J., and others. 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. *Glob. Chang. Biol.* **18**: 422–434. doi:10.1111/j.1365-2486.2011.02513.x
- Nuorteva, J., and H. T. Kankaanpää. 2016. Relocation of soft mud deposits: An example from the Archipelago Sea, northern Baltic Sea. *Mar. Geol.* **380**: 148–162. doi:10.1016/j.margeo.2016.08.002
- Pastuszak, M., Z. Witek, K. Nagel, M. Wielgat, and A. Grelowski. 2005. Role of the Oder estuary (southern Baltic) in transformation of the riverine nutrient loads. *J. Mar. Syst.* **57**: 30–54. doi:10.1016/j.jmarsys.2005.04.005
- Petkuvienė, J., M. Zilius, I. Lubiene, T. Ruginis, G. Giordani, A. Razinkovas-Baziukas, and M. Bartoli. 2016. Phosphorus cycling in a freshwater estuary impacted by cyanobacterial blooms. *Estuaries Coast.* **39**: 1386–1402. doi:10.1007/s12237-016-0078-0

- Piña-Ochoa, E., and M. Álvarez-Cobelas. 2006. Denitrification in aquatic environments: A cross-system analysis. *Biogeochemistry* **81**: 111–130. doi:[10.1007/s10533-006-9033-7](https://doi.org/10.1007/s10533-006-9033-7)
- Pitkänen, H. 1994. Eutrophication of the Finnish coastal waters: Origin, fate and effects of riverine nutrient fluxes. National Board of Waters and the Environment.
- Pusceddu, A., A. Dell'Anno, M. Fabiano, and R. Danovaro. 2009. Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Mar. Ecol. Prog. Ser.* **375**: 41–52. doi:[10.3354/meps07735](https://doi.org/10.3354/meps07735)
- Puttonen, I., and others. 2014. Distribution and estimated release of sediment phosphorus in the northern Baltic Sea archipelagos. *Estuar. Coast. Shelf Sci.* **145**: 9–21. doi:[10.1016/j.ecss.2014.04.010](https://doi.org/10.1016/j.ecss.2014.04.010)
- Puttonen, I., T. Kohonen, and J. Mattila. 2016. Factors controlling phosphorus release from sediments in coastal archipelago areas. *Mar. Pollut. Bull.* **108**: 77–86. doi:[10.1016/j.marpolbul.2016.04.059](https://doi.org/10.1016/j.marpolbul.2016.04.059)
- Rao, A. M., M. J. McCarthy, W. S. Gardner, and R. A. Jahnke. 2007. Respiration and denitrification in permeable continental shelf deposits on the South Atlantic Bight: Rates of carbon and nitrogen cycling from sediment column experiments. *Cont. Shelf Res.* **27**: 1801–1819. doi:[10.1016/j.csr.2007.03.001](https://doi.org/10.1016/j.csr.2007.03.001)
- Reed, D. C., B. G. Gustafsson, and C. P. Slomp. 2016. Shelf-to-basin iron shuttling enhances vivianite formation in deep Baltic Sea sediments. *Earth Planet. Sci. Lett.* **434**: 241–251. doi:[10.1016/j.epsl.2015.11.033](https://doi.org/10.1016/j.epsl.2015.11.033)
- Ruttenberg, K. 2003. The global phosphorus cycle. In W. H. Schlesinger [ed.], *Treatise on Geochemistry*, Vol. 8. p. 682. doi:[10.1016/B0-08-043751-6/08153-6](https://doi.org/10.1016/B0-08-043751-6/08153-6)
- Rydin, E., J. Malmaeus, O. Karlsson, and P. Jonsson. 2011. Phosphorus release from coastal Baltic Sea sediments as estimated from sediment profiles. *Estuar. Coast. Shelf Sci.* **92**: 111–117. doi:[10.1016/j.ecss.2010.12.020](https://doi.org/10.1016/j.ecss.2010.12.020)
- Rysgaard, S., P. B. Christensen, and L. P. Nielsen. 1995. Seasonal variation in nitrification and denitrification in estuarine sediment colonized by benthic microalgae and bioturbating infauna. *Mar. Ecol. Prog. Ser.* **126**: 111–121. doi:[10.3354/meps126111](https://doi.org/10.3354/meps126111)
- Savchuk, O. P. 2005. Resolving the Baltic Sea into seven sub-basins: N and P budgets for 1991–1999. *J. Mar. Syst.* **56**: 1–15. doi:[10.1016/j.jmarsys.2004.08.005](https://doi.org/10.1016/j.jmarsys.2004.08.005)
- Scala, D. J., and L. J. Kerkhof. 2000. Horizontal heterogeneity of denitrifying bacterial communities in marine sediments by terminal restriction fragment length polymorphism analysis. *Appl. Environ. Microbiol.* **66**: 1980–1986. doi:[10.1128/AEM.66.5.1980-1986.2000](https://doi.org/10.1128/AEM.66.5.1980-1986.2000)
- Seitzinger, S. P. 1988. Denitrification in freshwater and coastal marine ecosystems: Ecological and geochemical significance. *Limnol. Oceanogr.* **33**: 702–724. doi:[10.4319/lo.1988.33.4part2.0702](https://doi.org/10.4319/lo.1988.33.4part2.0702)
- Seitzinger, S. P., L. P. Nielsen, J. Caffrey, and P. B. Christensen. 1993. Denitrification measurements in aquatic sediments: A comparison of three methods. *Biogeochemistry* **23**: 147–167. doi:[10.1007/BF00023750](https://doi.org/10.1007/BF00023750)
- Seitzinger, S., J. A. Harrison, J. Böhlke, A. Bouwman, R. Lowrance, B. Peterson, C. Tobias, and G. V. Dreht. 2006. Denitrification across landscapes and waterscapes: A synthesis. *Ecol. Appl.* **16**: 2064–2090. doi:[10.1890/1051-0761\(2006\)016\[2064:DALAWA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[2064:DALAWA]2.0.CO;2)
- Slomp, C. 2011. Phosphorus cycling in the estuarine and coastal zones biogeochemistry: Treatise on estuarine and coastal science, 5. Elsevier/Academic Press, Amsterdam, pp. 201–229. doi:[10.1016/B978-0-12-374711-2.00506-4](https://doi.org/10.1016/B978-0-12-374711-2.00506-4)
- Slomp, C. P., H. P. Mort, T. Jilbert, D. C. Reed, B. G. Gustafsson, and M. Wolthers. 2013. Coupled dynamics of iron and phosphorus in sediments of an oligotrophic coastal basin and the impact of anaerobic oxidation of methane. *PLoS One* **8**: e62386. doi:[10.1371/journal.pone.0062386](https://doi.org/10.1371/journal.pone.0062386)
- Steingruber, S. M., J. Friedrich, R. Gächter, and B. Wehrli. 2001. Measurement of denitrification in sediments with the 15N isotope pairing technique. *Appl. Environ. Microbiol.* **67**: 3771–3778. doi:[10.1128/AEM.67.9.3771-3778.2001](https://doi.org/10.1128/AEM.67.9.3771-3778.2001)
- Sundbäck, K., A. Miles, and E. Göransson. 2000. Nitrogen fluxes, denitrification and the role of microphytobenthos in microtidal shallow-water sediments: An annual study. *Mar. Ecol. Prog. Ser.* **200**: 59–76. doi:[10.3354/meps200059](https://doi.org/10.3354/meps200059)
- Sundbäck, K., F. Linares, F. Larson, A. Wulff, and A. Engelsen. 2004. Benthic nitrogen fluxes along a depth gradient in a microtidal fjord: The role of denitrification and microphytobenthos. *Limnol. Oceanogr.* **49**: 1095–1107. doi:[10.4319/lo.2004.49.4.1095](https://doi.org/10.4319/lo.2004.49.4.1095)
- Sundbäck, K., A. Miles, and F. Linares. 2006. Nitrogen dynamics in nontidal littoral sediments: Role of microphytobenthos and denitrification. *Estuaries Coast.* **29**: 1196–1211. doi:[10.1007/BF02781820](https://doi.org/10.1007/BF02781820)
- Taylor, P. G., and A. R. Townsend. 2010. Stoichiometric control of organic carbon–nitrate relationships from soils to the sea. *Nature* **464**: 1178–1181. doi:[10.1038/nature08985](https://doi.org/10.1038/nature08985)
- Thornton, S., and J. McManus. 1994. Application of organic carbon and nitrogen stable isotope and C/N ratios as source indicators of organic matter provenance in estuarine systems: Evidence from the Tay Estuary, Scotland. *Estuar. Coast. Shelf Sci.* **38**: 219–233. doi:[10.1006/ecss.1994.1015](https://doi.org/10.1006/ecss.1994.1015)
- Trimmer, M., and J. C. Nicholls. 2009. Production of nitrogen gas via anammox and denitrification in intact sediment cores along a continental shelf to slope transect in the North Atlantic. *Limnol. Oceanogr.* **54**: 577–589.
- Voss, M., J. W. Dippner, C. Humborg, J. Hürdler, F. Korth, T. Neumann, G. Schernewski, and M. Venohr. 2011. History and scenarios of future development of Baltic Sea eutrophication. *Estuar. Coast. Shelf Sci.* **92**: 307–322. doi:[10.1016/j.ecss.2010.12.037](https://doi.org/10.1016/j.ecss.2010.12.037)

- Welsh, D. T. 2003. It's a dirty job but someone has to do it: The role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. *Chem. Ecol.* **19**: 321–342. doi:[10.1080/0275754031000155474](https://doi.org/10.1080/0275754031000155474)
- Wikner, J., R. Cuadros, and M. Jansson. 1999. Differences in consumption of allochthonous DOC under limnic and estuarine conditions in a watershed. *Aquat. Microb. Ecol.* **17**: 289–299. doi:[10.3354/ame017289](https://doi.org/10.3354/ame017289)
- Zettler, M. L., D. Schiedek, and B. Bobertz. 2007. Benthic biodiversity indices versus salinity gradient in the southern Baltic Sea. *Mar. Pollut. Bull.* **55**: 258–270. doi:[10.1016/j.marpolbul.2006.08.024](https://doi.org/10.1016/j.marpolbul.2006.08.024)

Acknowledgments

We would like to thank Tage Dalsgaard, Dana Hellemann, Susanna Hietanen, Kristina Sundbäck, and Mindaugas Zilius for providing original denitrification data. This study was supported by the BONUS COCOA project (grant agreement 2112932-1), funded jointly by the EU and Danish Research Council and the BMBF (grant number FKZ 03F0683A).

Conflict of Interest

None declared.

Submitted 17 November 2016

Revised 13 April 2017

Accepted 19 June 2017

Associate editor: John Downing