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Wadden Sea Eutrophication: Long-Term Trends and Regional Differences

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The Wadden Sea is a shallow intertidal coastal sea, largely protected by barrier islands and fringing the North Sea coasts of Netherlands, Germany, and Denmark. It is subject to influences from both the North Sea and major European rivers. Nutrient enrichment from these rivers since the 1950s has impacted the Wadden Sea ecology including loss of seagrass, increased phytoplankton blooms, and increased green macroalgae blooms. Rivers are the major source of nutrients causing Wadden Sea eutrophication. The nutrient input of the major rivers impacting the Wadden Sea reached a maximum during the 1980s and decreased at an average pace of about 2.5% per year for total Nitrogen (TN) and about 5% per year for total Phosphorus (TP), leading to decreasing nutrient levels but also increasing N/P ratios. During the past decade, the lowest nutrient inputs since 1977 were observed but these declining trends are leveling out for TP. Phytoplankton biomass (measured as chlorophyll a) in the Wadden Sea has decreased since the 1980s and presently reached a comparatively low level. In tidal inlet stations with a long-term monitoring, summer phytoplankton levels correlate with riverine TN and TP loads but stations located closer to the coast behave in a more complex manner. Regional differences are observed, with highest chlorophyll a levels in the southern Wadden Sea and lowest levels in the northern Wadden Sea. Model data support the hypothesis that the higher eutrophication levels in the southern Wadden Sea are linked to a more intense coastward accumulation of organic matter produced in the North Sea.

Keywords: eutrophication indicators, Wadden Sea, North Sea, nutrients, long-term trends, phytoplankton, submersed vegetation, sediments

INTRODUCTION

Increased nutrient fluxes to the coastal ocean are one of the main drivers for coastal change, having a pronounced impact on phytoplankton biomass and primary production, harmful algae blooms, seagrass, green macroalgae blooms, and water transparency (Cloern, 2001; Boesch, 2002; Orth et al., 2006; Smetacek and Zingone, 2013). Given the continuous increase in anthropogenic nitrogen fixation and increasing needs for nitrogen fertilizers (Battye et al., 2017), a further increase in the above mentioned eutrophication symptoms can be expected (e.g., Breitburg et al., 2018). First signs of coastal eutrophication like enhanced algae blooms were already observed in the 1950s and in Europe. Decisions to combat eutrophication were taken since the 1970s and 1980s (de Jong, 2007). Decreasing eutrophication trends have been observed for instance in European waters like the North Sea, Danish coastal waters or in the Baltic (e.g., Carstensen et al., 2006; Emeis et al., 2015; Andersen et al., 2017) during the 2000s or in Chesapeake Bay (Harding et al., 2016; Lefcheck et al., 2018) showing that a reversal of eutrophication is possible.

In the present paper, we will describe and compare the eutrophication levels and trends of the international Wadden Sea, a shallow coastal sea along the Dutch, German and Danish North Sea coast, based on long-term observations on nutrients and phytoplankton biomass (chlorophyll a). Since the earliest nutrient measurements in the Wadden Sea during the mid-20th century (Postma, 1954, 1966; Hickel, 1989) a strong increase in nitrogen and phosphorus concentrations has been documented (e.g., de Jonge and Postma, 1974; Hickel, 1989) reaching maximum values during the 1980s and 1990s (Jung et al., 2017) and decreasing since (e.g., van Beusekom et al., 2001, 2009; Cadée and Hegeman, 2002). Among the regularly occurring negative effects associated with the increased nutrient inputs are an increased import of organic matter from the North Sea to the Wadden Sea (de Jonge and Postma, 1974), more intense *Phaeocystis*-blooms (Cadée and Hegeman, 1986), a decline in seagrass distribution (de Jonge and de Jong, 1992), and increased green macroalgal cover (Reise and Siebert, 1994). Measures were taken during the 1970s and 1980s to address eutrophication (de Jong, 2007) through a reduction of riverine nutrient inputs to the North Sea.

Several studies have described local changes in Wadden Sea nutrient dynamics with a focus on the Dutch Wadden Sea (e.g., de Jonge and Postma, 1974; Cadée and Hegeman, 2002; Philippart et al., 2007) and the Northfrisian Wadden Sea (e.g., Hickel, 1989; van Beusekom et al., 2009). A comparison of available data for the entire Wadden Sea on phytoplankton and nutrients was only carried out within the framework of so-called Wadden Sea Quality Status Reports (e.g., van Beusekom et al., 2017). In these reports, the international scientific Wadden Sea community regularly compiles data on the ecological status of the North Sea (see for instance Wolff et al., 2010), showing among others a general decline in eutrophication levels.

Special attention will be given in the present study to long time series and regional differences in eutrophication levels covering the entire Wadden Sea. We will use two previously developed and tested eutrophication proxies (e.g., van Beusekom et al., 2001, 2009; van Beusekom and de Jonge, 2002) to describe temporal trends and regional differences. The proxies include autumn values of $NH_4 + NO_2$ as an indicator of organic matter turnover and summer phytoplankton chlorophyll a as an indicator of phytoplankton growth potential.

One of the processes responsible for the high productivity of Wadden Sea ecosystem is import of organic matter from the North Sea (Verwey, 1952; Postma, 1954). van Beusekom et al. (1999) compiled organic matter budgets from the Wadden Sea supporting the heterotrophic nature of the Wadden Sea with a primary production level of around 200–300 g C m^{-2} y^{-1}, remineralization levels of about 300–450 g C m^{-2} y^{-1}, and an annual import of about 100 g C m^{-2} y^{-1}. This import is an important driver of nutrient availability in the Wadden Sea (e.g., de Jonge and Postma, 1974; van Beusekom et al., 1999, 2012; van Beusekom and de Jonge, 2002). The import mechanism is as follows (e.g., van Beusekom et al., 2012): Transport of particles (both inorganic and organic) from the North Sea to the Wadden Sea is induced by residual, baroclinic circulation similar to estuarine circulation (e.g., Burchard et al., 2008; Flöser et al., 2011; Hofmeister et al., 2017) with bottom currents directed on average toward the coast, and surface currents directed toward the sea. This traps sinking particles from a large part of the coastal North Sea, transports them toward the Wadden Sea and prevents particles to escape from the Wadden Sea to the North Sea. By the same token, dissolved nutrients, released after organic matter remineralization and not taken up within in the Wadden Sea, can be transported back to the North Sea (e.g., Grunwald et al., 2010). As light conditions are generally much better outside the Wadden Sea, these nutrients can be taken up by phytoplankton, and are transported back into the Wadden Sea after settling into deeper water layers (e.g., Postma, 1981; Maerz et al., 2016). Hofmeister et al. (2017) demonstrated with a model that the transport of sinking phytoplankton and detritus toward the Wadden Sea is able to keep up a nutrient gradient between the North Sea and the Wadden Sea.

We will use a biogeochemical North Sea model (Kerimoglu et al., 2017) to investigate regional differences in the import of organic matter from the North Sea to the Wadden Sea. Model approaches are needed because available budgets are too coarse to resolve regional differences. Also, no recent carbon budgets are available that demonstrate changes in Wadden Sea eutrophication levels. We will show that with the two proxies -summer chlorophyll a and autumn $NH_4 + NO_2$, a general decrease in eutrophication can be linked to decreasing riverine nutrient loads. We will further show that high organic matter import rates in the southern part of the Wadden Sea lead to higher eutrophication level than in the northern part of the Wadden Sea.

MATERIALS AND METHODS

Area Description

The Wadden Sea is a shallow intertidal coastal sea along the Dutch, German, and Danish North Sea coast (**Figure 1**). Tidal range is about 1 m at the northern and western end and increases to more than 3 m in the central part. At tidal ranges below 3 m, barrier islands can be formed (e.g., Hayes, 1975; Oost and de Boer, 1994), protecting the southern and northern Wadden Sea, but are absent in the central part. About 50% of the sediments emerge during low tide. Sediments are mostly sandy in the more exposed parts, whereas in the more protected parts muddy sediments prevail. Major nutrient discharges directly into the southern Wadden Sea are the IJsselmeer and the Ems river. Major rivers entering the central Wadden Sea are the Weser and

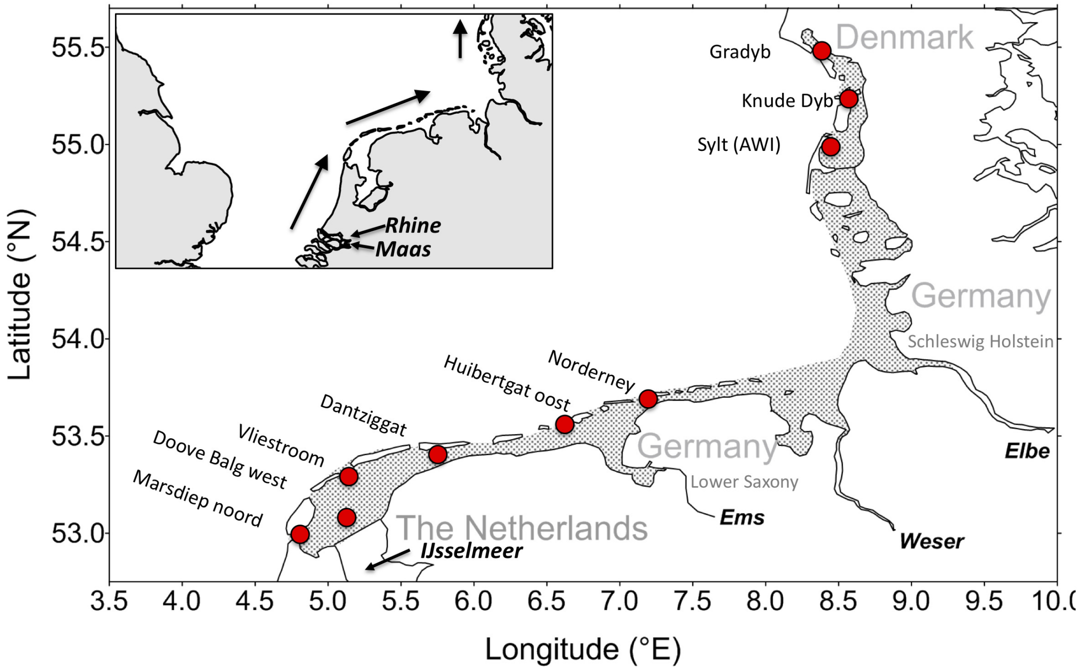

FIGURE 1 | Map of the Wadden Sea with stations having long time series starting before 1990. The Southern Wadden Sea includes the Dutch and Lower Saxonian part, the northern Wadden includes the Schleswig Holstein and the Danish part. The inset show the position of the rivers Rhine and Maas as well as the general circulation pattern along the Wadden Sea.

Elbe. Residual currents along the Wadden Sea follow the anti-clockwise circulation of the North Sea. Thus, nutrient loads of the Rhine and Maas are carried northward and westward toward the Wadden Sea especially impacting the southern Wadden Sea. The Weser and Elbe nutrient loads are carried northward especially impacting the northern Wadden Sea (**Figure 1**).

Salinity ranges in most tidal inlets on average between about 27 and 31. A clear seasonality is observed with lowest values in winter and highest values in summer (e.g., van Aken, 2008a; van Beusekom et al., 2008; Grunwald et al., 2010). Deviations from long-term means are related to freshwater discharge (e.g., van Beusekom et al., 2008). Closer to the mainland, and especially near fresh water sources, lower salinities prevail (e.g., van Aken, 2008a; Grunwald et al., 2010).

Temperature ranges on average between minimum values of around 3°C in February and around 18°C in July/August (e.g., Diederich et al., 2005; van Aken, 2008b; Grunwald et al., 2010) with an increasing trend (Martens and van Beusekom, 2008).

Phytoplankton shows a clear seasonal cycle, mainly due to light limitation in winter (e.g., Loebl et al., 2009). The spring phytoplankton bloom is dominated by diatoms (e.g., Cadée, 1986; Loebl et al., 2007), mainly occurs during April, but can be earlier during cold winters (van Beusekom et al., 2009). It is often followed by a *Phaeocystis*-bloom during early summer (e.g., Cadée and Hegeman, 2002; Loebl et al., 2007).

Nutrient seasonal cycles reflect nutrient uptake by primary producers, but the shape depends on the nutrient species. Silica (H_4SiO_4) and nitrate (NO_3) show a simple cycle with highest values during winter and low values during summer due to uptake by phytoplankton (e.g., van Bennekom et al., 1974; van Beusekom et al., 2008; Leote et al., 2016). Ammonium (NH_4) and nitrite (NO_2) also show high winter and low summer values but with a clear autumn maximum (e.g., Postma, 1966; van Beusekom and de Jonge, 2002; Loebl et al., 2007; Reckhardt et al., 2015). Phosphate (PO_4) reaches lowest values during spring and early summer, but concentrations already increase during May/June (e.g., de Jonge and Postma, 1974; Loebl et al., 2007; Grunwald et al., 2010; van Beusekom and de Jonge, 2012). An overview of mean seasonal nutrient cycles in the Wadden Sea until the mid 1990s is given in van Beusekom et al. (2001).

Data Compilation

Riverine Input Data

Riverine nutrient input data were compiled by Lenhart and Pätsch (2004) and updated to 2017. Total nitrogen (TN) and total phosphorus (TP) concentrations, taken from stations within the freshwater part of the estuary near the river mouth, were linearly interpolated between observations (mostly about every 2 weeks) to achieve estimates of daily concentrations. These nutrient concentrations estimates were then multiplied with daily discharges values taken from the last tidal free gauge station to derive daily loads. Data are available through https://wiki.cen.uni-hamburg.de/ifm/ECOHAM/DATA_RIVER.

Dutch Wadden

For the Dutch Wadden Sea, a coherent observational program with methods applicable to the Wadden Sea is carried out by the Dutch governmental agency Rijkswaterstaat since 1977.

Frequency of the sampling is fortnightly and samples are taken between 2 h before or after high tide. Water samples are filtered and analyzed for dissolved nutrients according to CEN/ISO guidelines and intercalibrated. Chlorophyll is measured by HPLC and is intercalibrated. During the past decades, the number of stations that are regularly sampled has decreased and at present five stations are continuously monitored (**Figure 1**). All Dutch monitoring data can be downloaded from the internet[1].

Lower Saxonian Wadden Sea (Norderney, Germany)

Nutrients and phytoplankton are monitored at the island of Norderney since 1987. The exact position of the sampling station has changed during the time series within a radius of 2 km around Norderney harbor. Sampling was carried out at high tide, but includes a period with additional sampling at low tide from 2005 to 2014. Differences in chlorophyll a and $NH_4 + NO_2$ between these samplings is small (~1 μg chla/l or ~6% and ~2–3 μmol/l or ~22% for $NH_4 + NO_2$; compare van Beusekom et al., 2017). In this study, we have combined the data. Nutrients were filtered (0.4 μm), originally analyzed after Grasshoff et al. (1976, 1983) and later using continuous flow analysis (CFA) using German standard (DIN) methods. Labs are quality assured through interlaboratory comparisons: LÜRV (nationally) and Quasimeme (internationally). Data cannot be retrieved from a public data base but all data can be requested from NLWKN.

Northfrisian Wadden Sea (Sylt, Germany)

Regular sampling in the List tidal basin (Northfrisian Wadden Sea) was started in 1984 by the Biologische Anstalt Helgoland, now part of the Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung (AWI). Two stations (one in the main channel and one in the entrance to the Königshafen bay) were sampled twice weekly irrespective of the tidal phase. Until 1998, unfiltered nutrient samples were analyzed, afterward water samples were filtered through 0.4 Nuclepore polycarbonate filters and stored frozen until analysis. The impact of filtration on nutrient concentrations was not investigated systematically, but except for phosphate no clear shifts were observed in the time series. Nutrients were analyzed manually (NO_3 with CFA) after Grasshoff et al. (1983) and intercalibrated (Quasimeme). Chlorophyll was analyzed spectrophotometrically after Jeffrey and Humphrey (1975) and intercalibrated. Data are deposited in the Pangaea database (www.pangaea.de). Details can be found in van Beusekom et al. (2009).

Danish Wadden Sea

The Danish Wadden Sea has been monitored since 1989. All measurements are according to Danish standards[2]. In short, chlorophyll was extracted with ethanol and the absorbance is measured spectrophotometrically. Nutrients were filtered (GF/F or Advantec GF75) and analyzed using standard wet chemical techniques. In contrast to the other time series, NO_2 is not assessed separately. Labs must participate in quality assurance programs (Quasimeme) to assure comparability of results. Data are accessible[3].

Model Data

We use simulation data from Kerimoglu et al. (2017) to discuss the mechanisms controlling the cross-shore gradients between the North Sea and the Wadden Sea. The three-dimensional coupled model describes the biogeochemical processes within the southeastern North Sea, coupled to the General Estuarine Transport Model (Burchard and Bolding, 2002), defined on a curvilinear grid of 1.5–4 km and terrain-following 20 vertical layers. For the period 2000–2010, his model showed high skill in reproducing the spatial and temporal distribution of salinity, nutrients and chlorophyll; and in particular, capturing the steep cross-shore gradients between the North Sea and the Wadden Sea (Kerimoglu et al., 2017). We extracted transects of particulate organic nitrogen (PON), salinity and residual, cross-shore currents between the ~40 m depth contour and the Wadden Sea for the summer (May – September) of 2010 near the long-term stations, and present here the temporal average results.

Data Handling

In order to have an equal distribution of data over time, we binned data into monthly means. Handling and statistics were done with R (R Core Team, 2016), using the graphical package ggplot2 (Wickham, 2016). Processing and plotting of the model data was performed with nco[4] and Python 2.7.

Eutrophication Proxies and Drivers

Two eutrophication proxies were used: summer chlorophyll a and autumn levels of the $NH_4 + NO_2$. Summer chlorophyll a levels were the mean of the monthly means for May – September. We did not include spring values, as the intensity of the spring bloom at least in the northern Wadden Sea is closely related to temperature, with highest biomasses after cold winters (van Beusekom et al., 2009) probably due to low grazer activity. Autumn $NH_4 + NO_2$ levels were the mean of the monthly means for September to November. As for the Danish time series, no NO_2 values were reported and we estimated the NO_2 contribution as 25% of the NH_4 levels based on the nearby AWI time series from the Northfrisian Wadden Sea. The proxies are based on earlier work (e.g., van Beusekom et al., 2001; van Beusekom and de Jonge, 2002). Support for the usefulness of these proxies was given by van Beusekom and de Jonge (2012), who showed good correlations between summer dissolved organic phosphorus concentrations and the above eutrophication proxies.

As a drivers of the Wadden Sea eutrophication we used riverine TN loads and TP loads as suggested by van Beusekom et al. (2001). Instead of annual loads we used the loads until August as later riverine input cannot impact the production of organic matter during Summer. In case of the rivers Rhine and Maas, we extended the time series to include the December loads of the previous year as suggested by van Beusekom et al. (2001),

[1] https://waterinfo.rws.nl

[2] http://bios.au.dk/raadgivning/fagdatacentre/fdcmarintny/gaeldendetekniskeanvisninger/#c236812

[3] https://arealinformation.miljoeportal.dk/html5/index.html?viewer=distribution

[4] https://github.com/nco/nco

among others based on the fact that the first high winter discharges are in December and on the longer distance between river mouth and Wadden Sea as compared to the Elbe and Weser. Riverine discharges directly into the Wadden Sea like the river Ems and lake IJsselmeer can have strong local effects (e.g., de Jonge and Postma, 1974; de Jonge, 1990; Jung et al., 2017), but less on the adjacent tidal basins. We therefore used only riverine TN and TP loads by the rivers Rhine/Maas as a common driver for the entire southern Wadden Sea. These two rivers dominate the riverine nutrient concentrations in the North Sea off the southern Wadden Sea. The rivers Rhine and Maas account for around 80% of the nutrient loads, with IJsselmeer, Ems and Noordzeekanaal representing 20%. Moreover, Rhine + Maas loads correlate with the combined loads of Rhine, Maas, IJsselmeer, Ems, and Noordzeekanaal with an $r^2 > 0.98$.

RESULTS

Riverine Input

We used the TN and TP loads by the rivers Rhine and Maas as the main driver of the southern Wadden Sea nutrient dynamics, and the TN and TP loads by the rivers Weser and Elbe as the main driver of the northern Wadden Sea nutrient dynamics. Discharge (**Figure 2**) has a major impact on the riverine loads showing a high interannual variability with highest discharges in the 1980s, and at least for the Rhine/Maas rivers a decreasing tendency of peak discharge. Riverine TN and TP loads reflect the annual discharge (**Figure 3**) but in addition show a clear decreasing trend in both river systems. As discharge during the 1980s was higher than present, riverine TN loads were up to three times higher and the riverine TP loads were up to five times higher than present levels. TP decreased faster than TN. In the Rhine/Maas, molar N/P ratios continuously increased from around 25 in the 1980s to about 80 during recent years. In the rivers Weser/Elbe, N/P molar ratios increased from 40 in the 1980s, to about 60–70 in the 1990s, decreasing to recent levels of about 45 (**Figure 4**). Flow-weighed TN concentrations (annual nutrient load/annual discharge, **Figure 5**) reached a maximum around 1985, regularly decreasing at a rate of around 2.5% per year until 2017. Flow-weighed TP was decreasing faster, with a rate of about 8% until 1990 in both system. Whereas in the Rhine/Maas this trend continues, the decrease in TP loads (2.5%) of the Weser/Elbe is much slower after ∼1990. Overall, we observed a decrease in flow-weighed concentrations of about 50% (TN) and 70–85% (TP), respectively.

Chlorophyll a

Mean summer chlorophyll a concentrations (Chl) in the southern part of the Wadden Sea ranged between 2.6 and 48 μg Chl /l (**Figure 6**) with a median of 11.8 μg Chl /l. Most Dutch time series showed a significant decrease over time (**Figure 6** and **Table 1**). The clearest trends were observed in the tidal inlet stations "Marsdiep Noord" (NL), Vliestroom (NL), and "Huibertgat oost" (NL). At the station "Doove Balg west" (NL) situated more closer to the coast, the trend was significant but

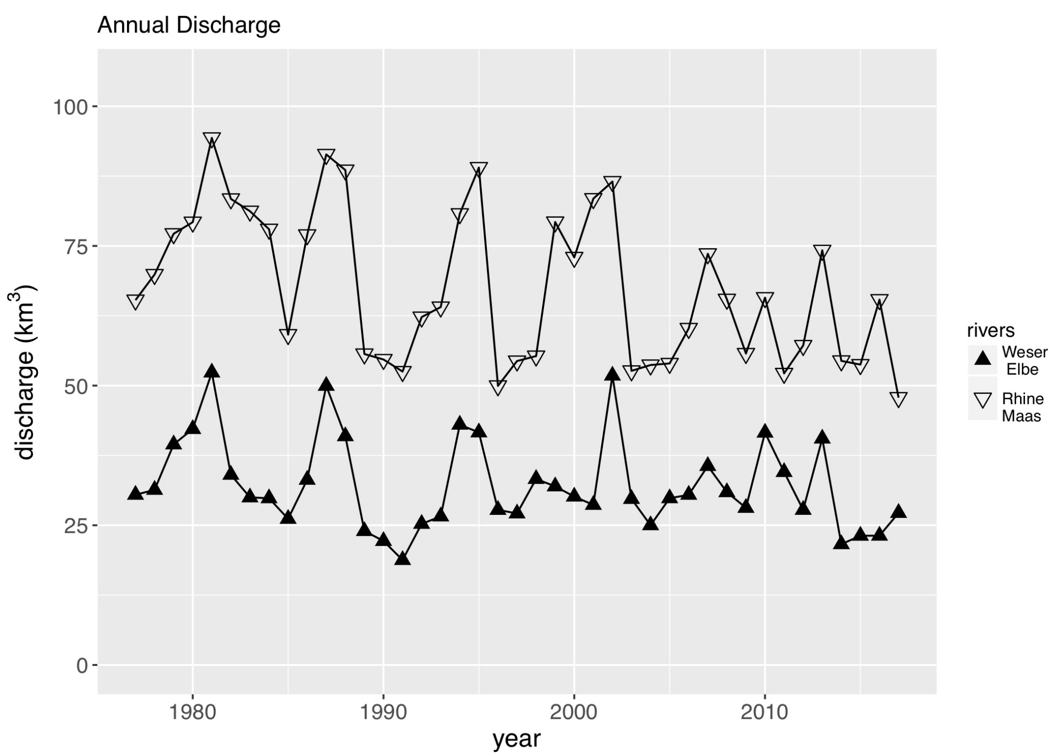

FIGURE 2 | Annual discharge of major rivers impacting the southern Wadden Sea (Rhine, Maas) and the Northern Wadden Sea (Weser, Elbe).

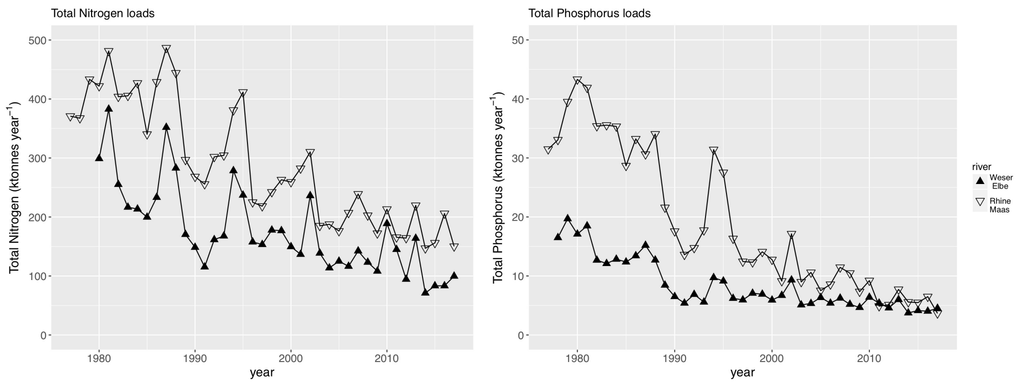

FIGURE 3 | Total nitrogen (TN) load and total phosphorus (TP) load of major rivers impacting the southern Wadden Sea (Rhine, Maas) and the northern Wadden Sea (Weser, Elbe).

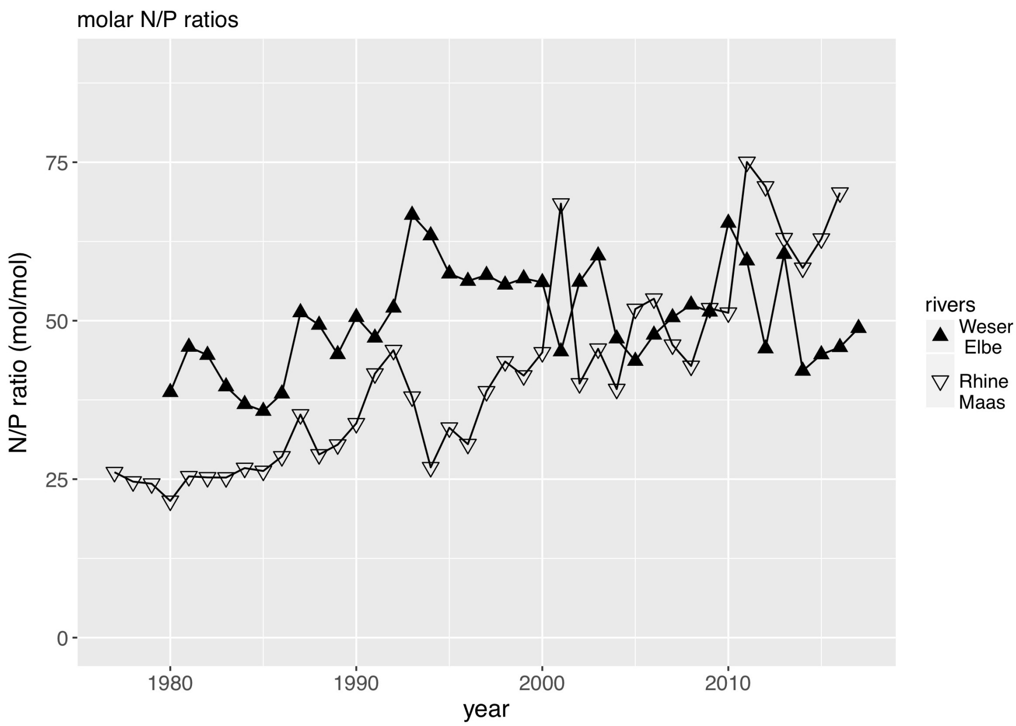

FIGURE 4 | Molar N/P Ratio of the major rivers impacting the southern Wadden Sea (Rhine, Maas) and the northern Wadden Sea (Weser, Elbe).

with a higher variability. The time series at Norderney (D) also showed a significant decrease. The combined time series of the four southern Wadden Sea tidal inlet stations with a decreasing trend (**Figure 7**) reveal a general pattern with initially increasing chlorophyll a levels peaking in 1987, decreasing afterward.

In contrast to the southern Wadden Sea, summer chlorophyll a levels were much lower in the northern Wadden Sea ranging, between 2.0 and 16.9 µg Chl /l and with median of 6.9 µg Chl /l. A significant decreasing trend was only observed for the longer Sylt (D) time series and no trends were found for the Danish Wadden Sea time series. The contrast between the Sylt and the southern tidal inlet stations of Netherlands and Lower Saxony is clearly shown in **Figure 7**. It is noteworthy, that with decreasing chlorophyll a levels during recent years, regional differences were becoming increasingly smaller.

Autumn Concentrations of NH_4 and NO_2

Seasonal dynamics of nitrogen-containing nutrients (NH_4, NO_2, and NO_3) in the Wadden Sea showed decreasing values during spring, low values in summer and increasing concentrations from September onward (e.g., van Beusekom and de Jonge, 2002; van Beusekom et al., 2009), due to decreasing light availability and subsequent decreasing nutrient uptake rates (see section "Area Description"). We used the summed autumn

FIGURE 5 | Flow-weighed TN Load (annual TN load/annual discharge) and Flow-weighed TP Load (annual TP load/annual discharge) of major rivers impacting the southern Wadden Sea (Rhine, Maas) and the Northern Wadden Sea (Weser, Elbe).

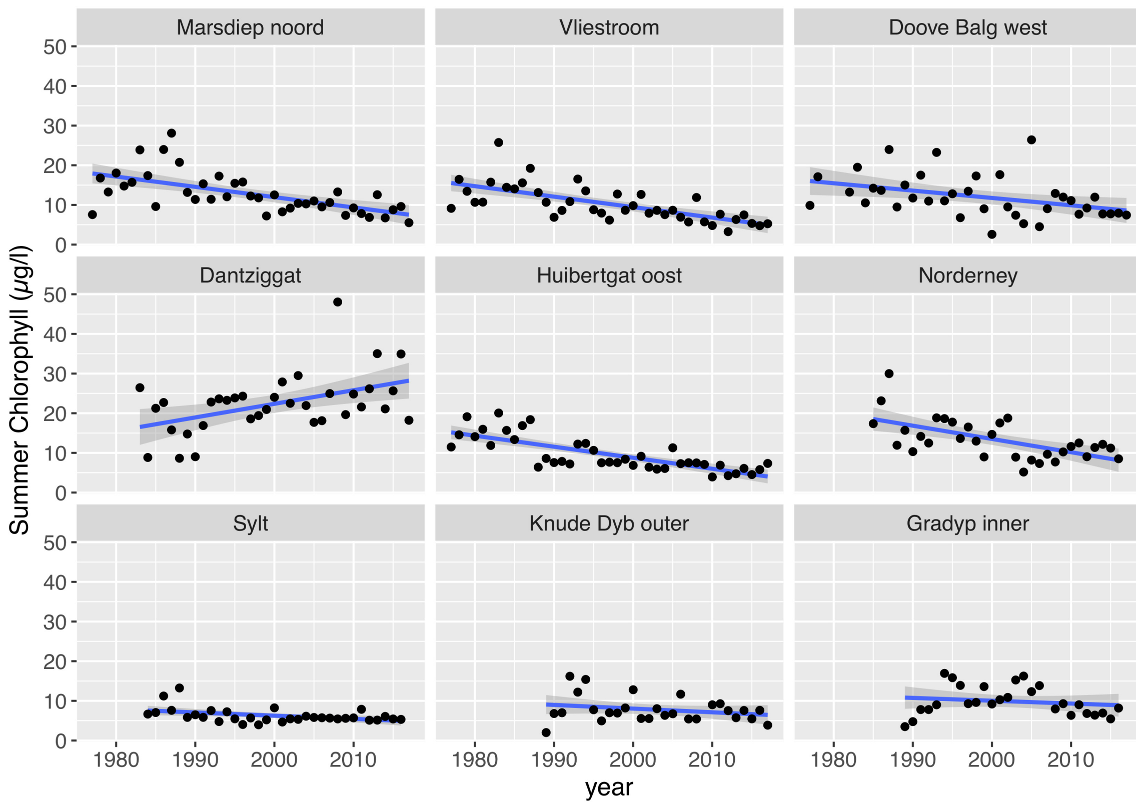

FIGURE 6 | Trends in mean summer chlorophyll-a (May – September).

concentrations of NH_4 and NO_2 as a proxy of organic matter turnover, as these compounds are mainly produced locally by degradation processes. We did use NO_3, although NO_3 is also produced locally by degradation processes and nitrification. However, in contrast to NH_4 and NO_2, NO_3 presently is the main form of nitrogen in rivers. Thus, both riverine input and local degradation processes may impact Wadden Sea NO_3 concentrations (van Beusekom and de Jonge, 2002). Autumn concentrations of $NH_4 + NO_2$ have decreased significantly at all southern Wadden Sea stations, whereas in the northern Wadden Sea a significant decrease was only observed at the Danish Wadden Sea station Grådyb (**Figure 8** and **Table 1**). As for chlorophyll a, the autumn $NH_4 + NO_2$ concentrations in the southern Wadden Sea (median: 11.9 µmol/l) were substantially higher than in the northern Wadden Sea (median: 6.0 µmol/l). It is important to note that at the Dutch Station Dantziggat, a significant decrease in autumn $NH_4 + NO_2$ was observed.

TABLE 1 | Summary statistics of the temporal trends in summer chlorophyll (May – September) and autumn (NH_4 and NO_2).

	Temporal trend in summer chlorophyll			Temporal trend in autumn $NH_4 + NO_2$		
	R^2	p	n	R^2	p	n
Marsdiep Noord (NL)	0.38	≪0.001	40	0.45	≪0.001	40
Vliestroom (NL)	0.48	≪0.001	40	0.40	≪0.001	39
Doove Balg west (NL)	0.16	<0.05	37	0.36	≪0.001	37
Dantziggat (NL)	0.22	<0.01	34	0.14	<0.05	34
Huibertgat oost (NL)	0.60	≪0.001	40	0.52	≪0.001	40
Norderney (D)	0.37	≪0.001	31		*n.s.*	31
Sylt (D)	0.18	<0.05	32		n.s.	32
Knude Dyb outer (DK)		n.s.	27		n.s.	27
Grådyb inner (DK)		n.s.	26	0.24	<0.01	26

Summer Chlorophyll a and Autumn $NH_4 + NO_2$: Two Independent Eutrophication Proxies

Most summer chlorophyll a time series showed significant correlations with riverine nutrient loads (**Figure 9**). It made no clear difference whether TN or TP was used as causative factor as evident by very similar r^2 values (**Table 2** for TN and **Table 3** for TP). As for the temporal trends, correlations between riverine loads and chlorophyll a are clearest for the tidal inlet stations of the southern Wadden Sea [Marsdiep noord (NL), Vliestroom (NL), Huibertgat oost (NL), and Norderney(D)], weak for Doove Balg west (NL), and absent for Dantziggat (NL). The northern Wadden Sea stations all show a weak but significant correlation with lower r^2 values. In most cases, riverine TN loads provided slightly better predictions than riverine TP loads. We also observed strong correlation between autumn $NH_4 + NO_2$ and riverine nutrient loads in the southern Wadden Sea (**Figure 10**), with no clear differences between TP, and TN as predictors. In the northern Wadden Sea, correlations between autumn $NH_4 + NO_2$ and riverine nutrient loads were not significant, except for TP in Grådyb (DK). Both proxies, summer chlorophyll a and autumn $NH_4 + NO_2$, were significantly correlated ($p << 0.001$, $r^2 = 0.26$), and both identify the southern Wadden Sea as having the highest eutrophication levels.

Model Data

Model results (see Kerimoglu et al., 2017) show, that within the regions where a thermohaline stratification occurs, PON concentrations at the bottom layers are slightly higher than at the surface layers within the deep (>20 m) regions (**Figure 11**). This, in combination with an estuarine-like circulation mentioned above, where the residual surface currents are directed toward off-shore and the bottom currents directed toward the shore, results in a net PON transport toward the shore, thus contributing to the eutrophication of the Wadden Sea. The efficiency of this transport mechanism varies between different regions: The intensity of the bottom transport is much higher along the southern Wadden Sea with average values of about 2 cm/s compared to the northern Wadden Sea (1 cm/s or less).

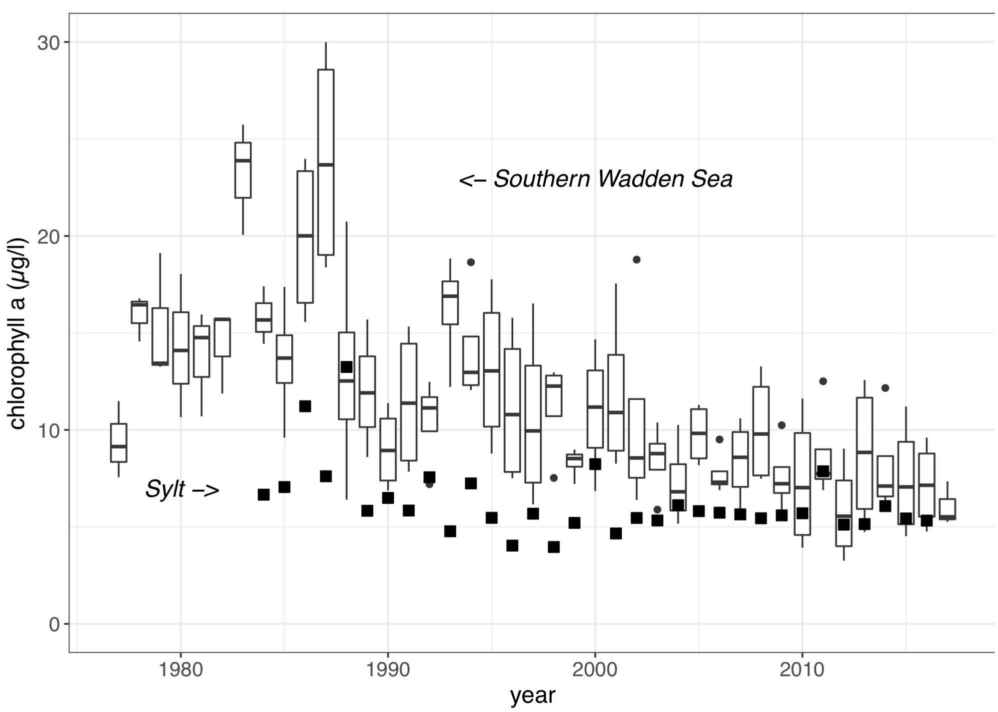

FIGURE 7 | Trends of summer chlorophyll a for long-term stations in the tidal inlets of the southern Wadden Sea [boxplot of Marsdiep noord (NL), Vliestroom (NL), Huibertgat oost, (NL) Norderney (D)], and in the northern Wadden Sea (Sylt, D).

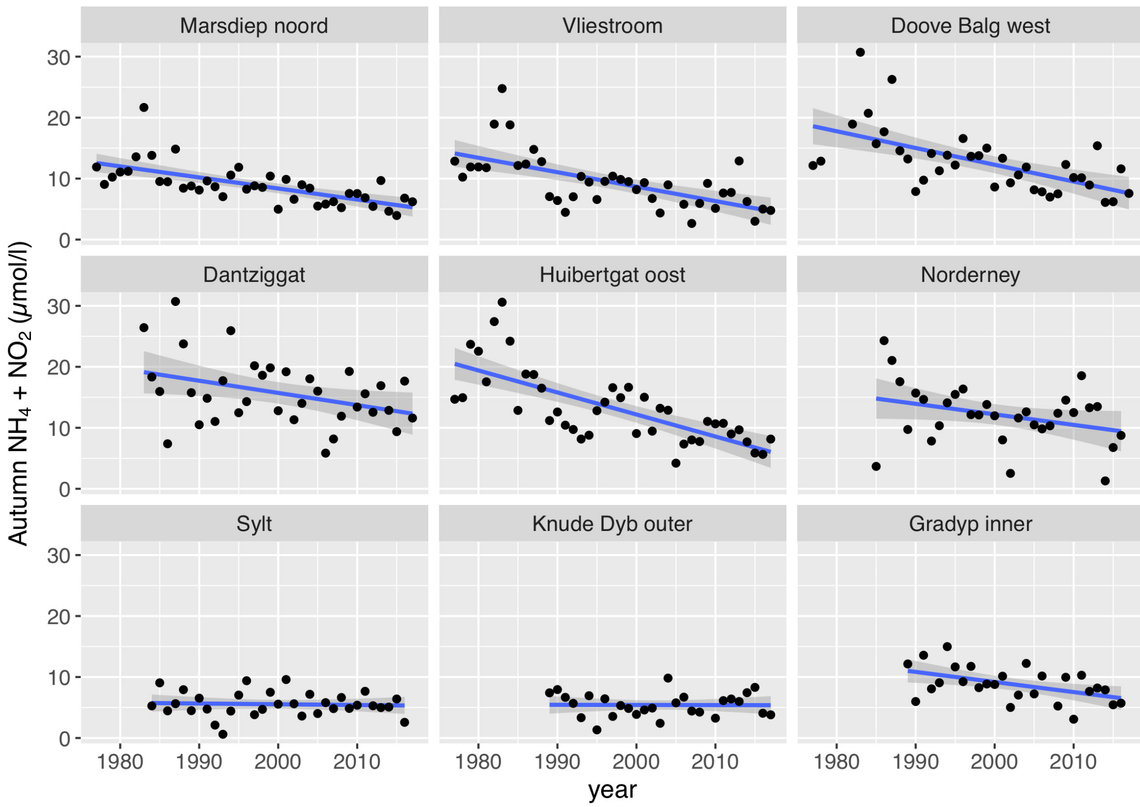

FIGURE 8 | Trends in autumn NH_4 + NO_2 (mean of September - November).

Also, the PON concentrations are in general higher along the southern Wadden Sea than along the northern Wadden Sea.

DISCUSSION

The Role of Sediments in Wadden Sea Nutrient Cycling

The present results show that riverine nutrients are a major driver of the long term phytoplankton and nitrogen dynamics in the Wadden Sea. An essential link is the primary production of organic matter in the North Sea, import of primary produced organic matter from the North Sea into the Wadden Sea and remineralization within the Wadden Sea (van Beusekom and de Jonge, 2002). Sediments are a major site of organic matter remineralization and constitute a significant sources of nutrients (e.g., Beck and Brumsack, 2012). In shallow coastal settings, benthic, and pelagic contribute about equally to the total organic matter turn-over (Heip et al., 1995). Wadden Sea carbon budgets support this (van Beusekom et al., 1999). Grunwald et al. (2010) estimated nutrient fluxes from the Lower Saxonian Wadden Sea to the North Sea based on high resolution water column nutrient measurement from an automatic measurement station. They concluded, that particulate nutrients have to be imported from the North Sea to balance the export of inorganic nutrients. Grunwald et al. (2010) further identified pore water discharge as a major nutrient source. The release of nutrients from organic matter remineralization in sediments may be fast in permeable sediments, when surface sediments are rapidly flushed (e.g., Huettel and Rusch, 2000; Ehrenhauss et al., 2004; de Beer et al., 2005). Sediments may also trap nutrients on longer time scales, if transport of pore water to deeper sediment layers is involved (e.g., Beck et al., 2008; Røy et al., 2008). This internal storage of nutrients may induce lag effects in the response of the Wadden Sea to changes in eutrophication levels. Jung et al. (2017) constructed a nutrient budget for the Western Dutch Wadden Sea based on long-term nutrient measurements. They explicitly accounted for sediment import from the North Sea as this part of the Wadden Sea has a sediment deficit due to the construction of a dike (Afsluitdijk) between the Wadden Sea and the former Zuiderzee (now IJsselmeer, see **Figure 1**). Jung et al. (2017) concluded that during the initial eutrophication phase (until 1981) P and N were imported. A net export of N was observed since 1981 and for P since 1992.

Despite the potential role of sediments to buffer nutrients, a rapid response to changing riverine N loads can be deduced from work by van Beusekom and de Jonge (2002). They showed that during wet years substantially more $NH_4 + NO_2$ is released in autumn than during dry years. Also phytoplankton dynamics respond quite fast to changes in riverine nutrient loads (compare **Figures 2**, **7**): During the 1980s, high riverine TN and TP

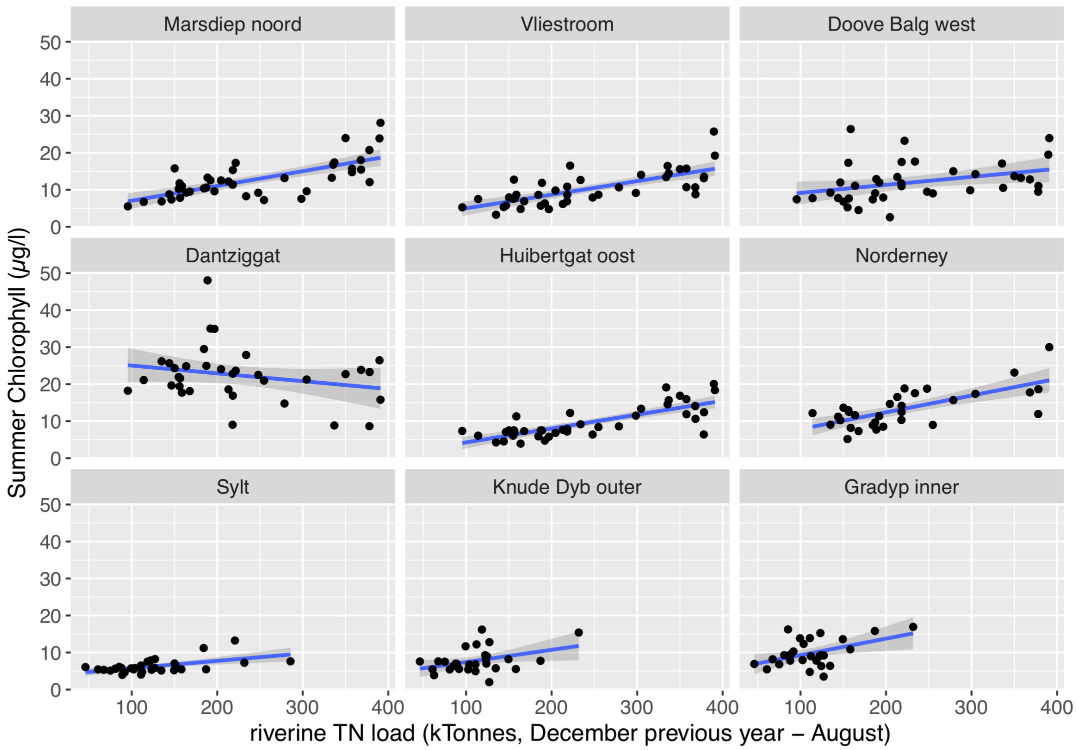

FIGURE 9 | Correlations between riverine TN loads and summer chlorophyll a (µg/l; May – September). For the southern Wadden Sea stations, Marsdiep noord (NL), Vliestroom (NL), Doove Balg west (NL), Dantziggat (NL), Huibertgat oost (NL) and Norderney (D), and the combined loads of the Rhine and Maas were used (December of the previous year until August of a given year). For the northern Wadden Sea stations, Sylt (D), Knude Dyb outer (DK), Grådyb inner (DK), and the combined loads of the Weser and Elbe were used (January – August).

concentrations and high discharges caused peak loads and high chlorophyll a levels during the late 1980s. This was followed by a period (1989–1993) of very low discharges, strongly reduced loads, and rapidly decreasing chlorophyll a levels. This suggests a rapid response of the phytoplankton to prevailing nutrient availability despite a potential nutrient buffering by sediments. Also, the present analysis does not suggests a major role of N and P legacies in sediments on the long term eutrophication levels, as the river loads (reflecting interannual dynamics) are a better predictor of the eutrophication level than a simple linear (smoothed) temporal trend. This is in line with the conclusions of Jung et al. (2017).

TABLE 2 | Summary statistics of the correlation between riverine Total Nitrogen loads and summer chlorophyll (May – September) and autumn (NH_4 and NO_2).

	Correlation between TN loads and summer chlorophyll			Correlation between TN loads and autumn $NH_4 + NO_2$		
	R^2	*p*	*n*	R^2	*p*	*n*
Marsdiep noord (NL)	0.50	≪0.001	40	0.55	≪0.001	40
Vliestroom (NL)	0.52	≪0.001	40	0.44	≪0.001	39
Doove Balg west (NL)	0.13	<0.05	37	0.48	≪0.001	37
Dantziggat (NL)		n.s.	34	0.27	<0.01	34
Huibertgat oost (NL)	0.61	≪0.001	40	0.48	≪0.001	40
Norderney (D)	0.48	≪0.001	31	0.14	<0.05	31
Sylt (D)	0.30	<0.001	32		n.s.	32
Knude Dyb outer (DK)	0.16	<0.05	27		n.s.	27
Grådyb inner (DK)	0.22	<0.05	26		n.s.	26

For the southern Wadden Sea Stations Marsdiep noord (NL), Vliestroom (NL), Doove Balg west (NL), Dantziggat (NL), Huibertgat oost (NL), and Norderney (D) the combined loads of the Rhine and Maas were takten (months 12 of the previous year until month 8 of a given year). For the northern Wadden Sea stations Sylt (D), Knude Dyb outer (DK), and Grådyb inner (DK) the combined loads of the Weser and Elbe were taken (month 1 – month 8).

Nutrient ratios in rivers impacting the Wadden Sea have increased toward high N/P ratios clearly above the Redfield ratio, with potential consequences for the coastal food webs (see below). Wadden Sea sediments play an important role in lowering (and thus improving) these ratios in the Wadden Sea and adjacent North Sea: On the one hand, denitrification rates are high (e.g., Gao et al., 2009; Deek et al., 2012) removing significant amounts of N, on the other hand, sediments have a high capacity to bind and buffer PO_4 (e.g., Leote and Epping, 2015).

Limiting Factors of Phytoplankton Growth in the Wadden Sea

Phytoplankton dynamics in the Wadden Sea are governed by a multitude of factors including zooplankton grazing (e.g., Loebl and van Beusekom, 2008), macrobenthos filter feeder activity (e.g., Cadée and Hegeman, 1974; Asmus and Asmus, 1993), light

TABLE 3 | Summary statistics of the correlation between riverine total phosphorus loads and summer chlorophyll (May – September) and autumn (NH_4 and NO_2).

	Correlation between TP and summer chlorophyll			Correlation between TP and autumn $NH_4 + NO_2$		
	R^2	*p*	*n*	R^2	*p*	*n*
Marsdiep noord (NL)	0.43	$\ll$0.001	40	0.50	$\ll$0.001	40
Vliestroom (NL)	0.45	$\ll$0.001	40	0.44	$\ll$0.001	39
Doove Balg west (NL)		n.s.	37	0.44	$\ll$0.001	37
Dantziggat (NL)		n.s.	34	0.21	<0.01	34
Huibertgat oost (NL)	0.64	$\ll$0.001	40	0.54	$\ll$0.001	40
Norderney (D)	0.42	$\ll$0.001	31	0.14	<0.05	31
Sylt (D)	0.40	<0.001	32		n.s.	32
Knude Dyb outer (DK)		n.s.	27		n.s.	27
Grådyb inner (DK)	0.18	<0.05	26	0.18	<0.05	26

For the southern Wadden Sea Stations Marsdiep noord (NL), Vliestroom (NL), Doove Balg west (NL), Dantziggat (NL), Huibertgat oost (NL), and Norderney (D) the combined loads of the Rhine and Maas were taken (months 12 of the previous year until month 8 of a given year). For the northern Wadden Sea stations Sylt (D), Knude Dyb outer (DK), and Grådyb inner (DK) the combined loads of the Weser and Elbe were taken (month 1 – month 8).

availability (Colijn, 1982), nutrient limitation (Loebl et al., 2008), or interactive effects of light limitation and nutrients (Colijn and Cadée, 2003; Loebl et al., 2009). We will discuss, whether trends in these three factors -grazing, light limitation and nutrient limitation- may have impacted the overall decreasing trends observed in the Wadden Sea during the last 3 decades.

Grazing by benthic filter feeders or (micro)zooplankton may have a large impact on phytoplankton dynamics. However, the observed recent decline in phytoplankton biomass is most probably not due to an increase in grazing pressure: For Wadden Sea zooplankton, only one time series is available since 1984 as part of the AWI-Sylt time series. Long term trends show a longer copepod season, an increase in *Acartia* sp. in April-May but no clear overall trend in copepod abundance (Martens and van Beusekom, 2008). This is in line with observations from the Helgoland road time series, even showing an overall decline in zooplankton densities (Boersma et al., 2015). Macrozoobenthos densities in the Wadden Sea have been relatively stable during the past decades (Drent et al., 2017) or even decreased in the adjacent coastal zone (Meyer et al., 2018). Philippart et al. (2007) did not observe a clear decrease in macrobenthos biomass in the western Dutch Wadden Sea but did observe a decrease in filter capacity by the macrobenthos. Taken together, no convincing evidence exists to support that recent long-term phytoplankton decline is driven by an increased top-down control. Whereas the long term trend in summer phytoplankton biomass is not driven by top-down control, short term dynamics, and interannual difference in summer phytoplankton biomass can be related to grazer-phytoplankton interactions. The tight coupling between phytoplankton growth rates and microzooplankton grazing rates in summer was demonstrated by Loebl and van Beusekom (2008). In the inner German Bight (Helgoland), Wiltshire et al. (2015) concluded that zooplankton grazing may control phytoplankton dynamics.

There has been a debate whether light, N or P limit phytoplankton dynamics in the Wadden Sea (e.g., de Jonge, 1990; Colijn and Cadée, 2003; Philippart et al., 2007). Colijn and Cadée (2003) used a method by Cloern (1999) to derive from time series, whether phytoplankton growth is limited by nitrogen or light and concluded that light is the dominating limiting factor, especially at Wadden Sea stations close to the coast like in the Dollard (inner part of the Ems estuary), with some N-limited periods during summer at Marsdiep, Norderney, Ems, and Büsum Mole (52.12°N, 8.86°E). Loebl et al. (2009) extended this analysis to also cover Si and P. They also concluded that during most of the year light is limiting, followed by Si during most of the growth season for diatoms, P limitation during the summer, and N limitation toward the end of the growth season.

The decreasing trend in phytoplankton biomass could potentially be caused by an decrease in light availability. Available evidence, however, suggests increasing light availability in the Wadden Sea and North Sea. Philippart et al. (2013) analyzed 4 decades of Secchi depth reading and concluded no overall change. Long-term trends (their **Figure 7**) suggest a slight decrease in light availability in the western Dutch Wadden Sea between the mid-1970s until the mid-1990s followed by an increase. This is in line with de Jonge and de Jong (2002) describing a general increase in annual suspended matter concentrations in the Western Dutch Wadden Sea from the 1950s to the mid 1980s, then decreasing until the 2000s. de Jonge and de Jong (2002) related changes in suspended matter concentrations to dredging activities in the Rhine Estuary and Rhine discharge. In the German Bight, Gebuhr et al. (2009) described a general increase in Secchi depth from the mid 1970s. In general, light conditions in the coastal North Sea and Wadden Sea apparently improved rather than deteriorated, suggesting that light is not the dominant factor in the long-term phytoplankton decrease observed in most of the Wadden Sea. Thus, the observed correlation between summer chlorophyll a levels and riverine nutrient loads supports that nutrients are a dominant factor in the long-term decline of phytoplankton. The low correlation coefficients do indicate, however, that many other factors and their interactions modulate the long-term phytoplankton dynamics. For instance, better light conditions would also increase microphytobenthos activity, possibly leading to reduced nutrient fluxes from the sediment (e.g., Sundbäck et al., 2000).

As in most of the Wadden Sea phytoplankton biomass recently decreased, the increase at the station Danziggat in the Dutch Wadden Sea is striking. The increase can be due to an increased accumulation of phytoplankton, an increased growth potential or reduced loss factors in this part of the Wadden Sea. The decreasing trend in autumn $NH_4 + NO_2$ contrasts with the chlorophyll time series and suggests that increased nutrient availability was not responsible for the observed phytoplankton, but hints at improved growth condition e.g., due to increasing light conditions or decreasing grazing rates or filter rates. Suspended matter concentrations at Danziggat are higher than at the other western Dutch Wadden Sea stations (de Jonge and de Jong, 2002), suggesting stronger light limitation here than at the other Dutch long-term stations. Possibly, strong light limitation prevailed also during summer at this station during

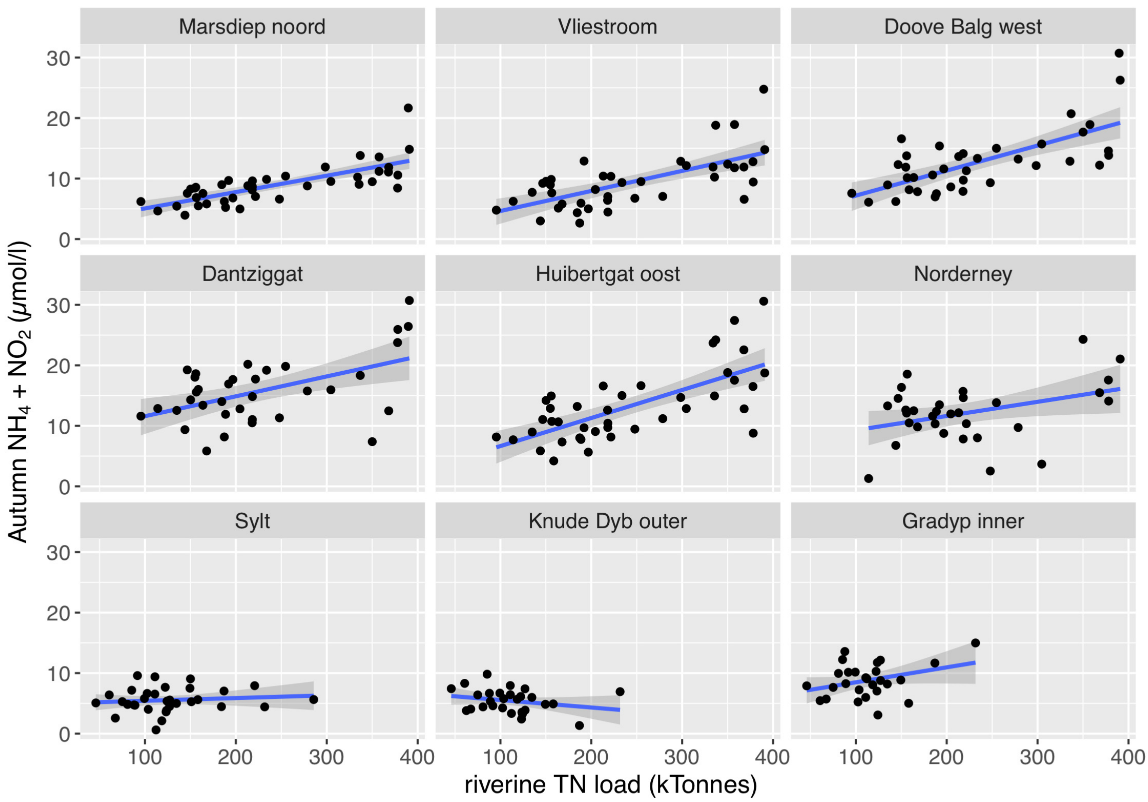

FIGURE 10 | Correlations between riverine TN loads and autumn NH_4 + NO_2 (µmol/l; September – November). For the southern Wadden Sea stations, Marsdiep noord (NL), Vliestroom (NL), Doove Balg west (NL), Dantziggat (NL), Huibertgat oost (NL) and Norderney (D), and the combined loads of the Rhine and Maas were used (December of the previous year until August of a given year). For the northern Wadden Sea stations, Sylt (D), Knude Dyb outer (DK), Grådyb inner (DK), and the combined loads of the Weser and Elbe were used (January – August).

the early 1980s. We hypothesize that improved light conditions since the 1980s (see section "Discussion") enabled enhanced phytoplankton production in this part of the Wadden Sea leading to increasing phytoplankton biomass (compare **Figure 6**).

Both riverine N and P loads have been used to explain long-term trends in phytoplankton biomass and primary production (e.g., de Jonge, 1990; van Beusekom et al., 2001). Our analyses show good correlations between summer chlorophyll a with both N and P. This indicates that N and P availability ultimately determine the eutrophication levels of the Wadden Sea. However, they do not provide conclusive indications whether N or P are ultimately limiting the phytoplankton dynamics.

Riverine P loads decreased faster than the N loads leading to high N/P ratios. Although no large differences were observed in the response of the phytoplankton biomass to decreasing loads of either riverine N or P, the changes of the N/P ratio may have implications on coastal communities. Malzahn et al. (2007) investigated food chain effects of N limited and P limited phytoplankton (*Rhodomonas* sp.) on Copepods (*Acartia* sp.) and fishlarvae (*Clupea harengus*). The P-limited food chain resulted in larval fish with a significantly poorer condition than N-limited or nutrient-sufficient food chains. Meunier et al. (2018) showed that long-term shifts in dissolved PO_4 concentration in the North Sea were closely linked to biomass trends of heterotrophic dinoflagellates and corroborated this experimentally. These results are interesting in the light of a study by Philippart et al. (2007) on the impact of nutrient reductions in the western Dutch Wadden Sea on phytoplankton, macrozoobenthos and estuarine birds. In their study, they used the IJsselmeer (see **Figure 1**) nutrient loads instead of the combined Rhine Maas loads used in the present study. They observed a weak correlation of P loads with the phytoplankton biomass but stronger correlations with macrozoobenthos and estuarine birds. Kerimoglu et al. (2018) studied the potential changes of phytoplankton in the North Sea under pre-industrial nutrient input scenario (about 30% of present levels) and suggested that the nutrient limitation led to disproportionately lower zooplankton biomass relative to the phytoplankton biomass (expressed as C content). This implied reduced grazing pressure, contributing in turn to a limited sensitivity of phytoplankton, and in certain regions, even to a slight phytoplankton increase under those lower nutrient input rates. Although we did not find support whether N or P was the ultimate limiting element for phytoplankton biomass formation, the impact of increasing N/P ratios on food quality definitely needs further attention.

Both proxies – summer phytoplankton and autumn NH_4 + NO_2 – are correlated, but with a large spread (r^2 = 0.26). This correlation does not necessarily reflect a causal relation between

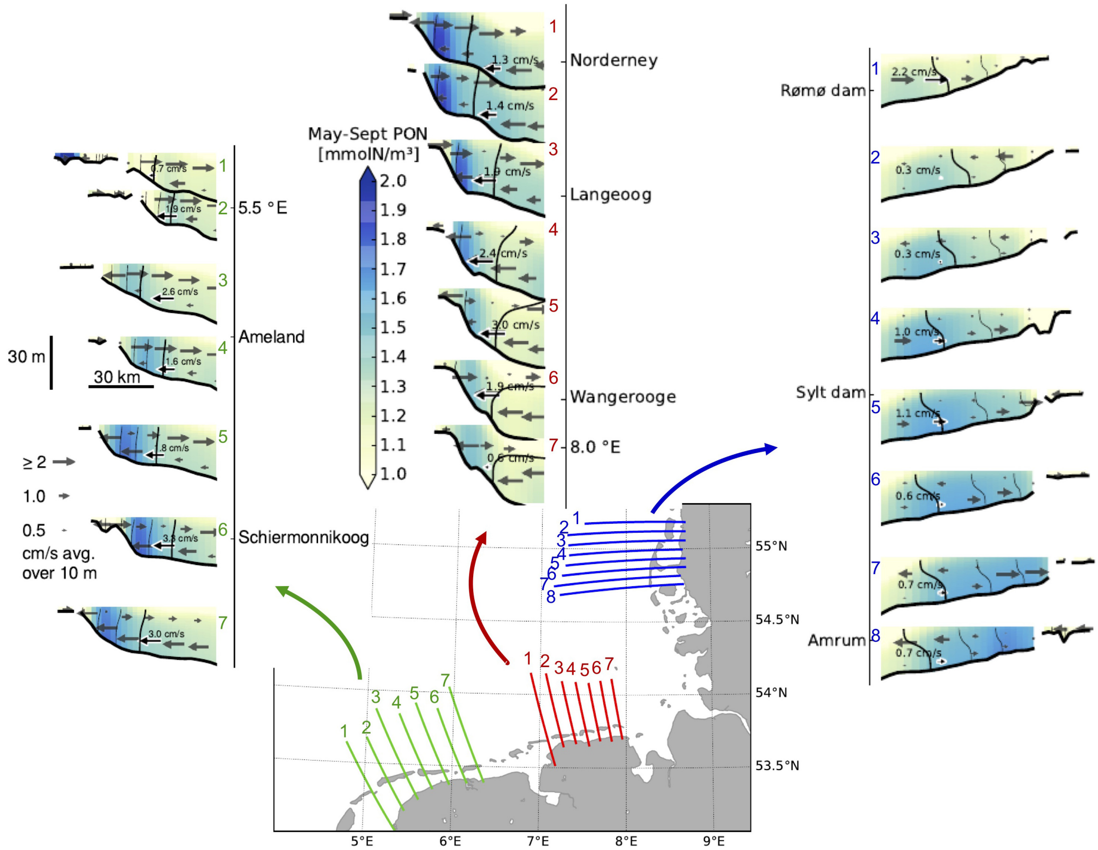

FIGURE 11 | Transects of mean currents (arrows) and particulate organic nitrogen (colors) and salinity (isolines; thicker isoline indicates 32 g/kg, thinner ones indicate each 1 g/kg lower increment) averaged over the period May – September 2010 for three areas along the Dutch Wadden Sea (green), along the Lower Saxonian Wadden Sea (red), and along the Schleswig-Holstein Wadden Sea (blue). For a better readability, to one arrow in each transect the current velocity was added.

the two proxies, but rather is the result of a common underlying driver: nutrient availability. Both proxies are impacted by different factors: Phytoplankton is positively influenced by light and nutrient availability but negatively by grazing. Autumn NH_4 + NO_2 is positively influenced by organic matter accumulation, but negatively by phytoplankton/microphytobenthos nutrient uptake and nitrification rates and high exchange with the North Sea during autumn. Only enhanced organic matter/nutrient availability is a common factor increasing both proxies. Other factors increasing the phytoplankton growth potential like better light conditions or decreasing grazing rates would lead to higher summer chlorophyll a levels but lower autumn levels of NH_4 + NO_2 due to increased phytoplankton nutrient uptake during autumn. Therefore, similar long-term trends of both proxies but no high correlation coefficient between the proxies is expected.

Based on the above discussion we suggest, that due to decreased riverine nutrient loads both summer chlorophyll a – as an indicator of the phytoplankton biomass and phytoplankton growth potential – and the autumn concentrations of NH_4 + NO_2 as an indicator of organic matter turnover intensity have declined over the entire Wadden Sea. Both proxies independently identify the southern Wadden Sea as having a higher eutrophication level than the northern Wadden Sea. Model data (**Figure 11**) support that import of organic matter from the North Sea to the Wadden Sea is larger along the southern Wadden Sea than along the northern Wadden Sea. An analysis of satellite data and *in situ* suspended matter data (Schartau et al., 2019) supports the model results by showing sharper gradients along the southern Wadden Sea than along the northern Wadden Sea. However, further model analyses including a quantification of transport rates based on multidecadal runs performed on higher resolution setups (see e.g., Gräwe et al., 2016; Androsov et al., 2019; Stanev et al., 2019) are needed to better understand the relative contribution of estuarine circulation and direct river inputs on the maintenance of horizontal gradients within the Wadden Sea.

Regional Differences in Eutrophication Indicators

Both model data and the eutrophication proxies identify the southern Wadden Sea as having a higher eutrophication level than the northern Wadden Sea. We will discuss, whether these patterns are also observed in other ecosystem components that respond to nutrient-enrichment like green macroalgae, seagrass, or benthic filter feeders.

Green macroalgae blooms can be due to coastal eutrophication with consequences for local economies, tourism, and the ecological state of coastal ecosystems (Fletcher, 1996; Smetacek and Zingone, 2013). In the Wadden Sea, green macroalgae blooms increased from the 1970s onward (Reise and Siebert, 1994; Kolbe et al., 1995; Schories et al., 1997), reaching a maximum during the 1990s (Kolbe et al., 1995; van Beusekom et al., 2017). Since the 1990s, a general decline to very low levels is observed for the northern Wadden Sea, but the decline in the German part of the southern Wadden Sea is less clear and a high growth potential is still present (van Beusekom et al., 2017). The decline in the northern Wadden Sea and remaining blooms in the southern Wadden Sea are in line with a higher eutrophication level in the southern Wadden Sea.

Seagrass is an important component of coastal ecosystems (e.g., Costanza et al., 1997; Orth et al., 2006), but globally declining at an increased rate (Waycott et al., 2009). Many factors have contributed to the seagrass decline in the entire Wadden Sea during the 20th century, including Wasting Disease, habitat destruction through embankment, increased turbidity, increased storminess, and eutrophication (e.g., Den Hartog, 1987; de Jonge and de Jong, 1992; Kastler and Michaelis, 1997; Dolch et al., 2013). Since the late 1990s, seagrass is clearly recovering in the northern Wadden Sea (Dolch et al., 2013) but not in the southern Wadden Sea (Dolch et al., 2017), where present seagrass distribution is less than expected on the basis of habitat preferences (Folmer et al., 2016). Although multiple stressors are involved, eutrophication probably has played a major role in seagrass decline (e.g., Bittick et al., 2018). Indeed, the recovery of Chesapeake Bay submerged vegetation is directly related to reduction in nutrient loads (Lefcheck et al., 2018). We hypothesize, that if riverine nutrient loads further decrease, seagrass occurrence in the Southern Wadden Sea will increase.

Recent distribution patterns of mussel beds also show regional differences, with the southern Wadden Sea having highest shares of tidal basin surface occupied by mussel beds (Folmer et al., 2014). The authors stress that many factors are involved, but ruled out temperature and extreme wind effects. Food availability is one of the factors involved and would be in line with the regional difference in organic matter and phytoplankton availability shown in this paper. In this context, it is important to note that macrozoobenthos biomass off the German southern Wadden Sea showed a clear decline, that was linked to a decrease in eutrophication (Meyer et al., 2018).

To summarize, more opportunistic macroalgae, a higher share of mussel beds and less seagrass in the southern Wadden Sea as compared to the northern Wadden Sea are all in agreement with a higher nutrient and organic matter availability in the southern Wadden Sea.

Whereas the overall regional distribution patterns of the eutrophication proxies are in agreement with other ecosystem components that respond to nutrient-enrichment, it should be borne in mind that part of the regional differences can be due to timing of sampling with regard to the tidal phase. Grunwald et al. (2010) reported higher nutrient concentrations at low tide than at high tide. Dutch monitoring stations are sampled around high tide, whereas the other stations [Grådyb (DK) and List tidal basin(D)] are sampled independently of the tidal phase. Since 2005, the Norderney (D) time series were sampled both during low and during high tide. Whereas differences for summer chlorophyll a were small (~6%), autumn $NH_4 + NO_2$ concentrations at high tide were about 22% (2–3 μmol/l) lower than at low tide. The overall effect would be that the Dutch eutrophication levels are slightly underestimated as compared to the other stations. The Norderney temporal trend is probably slightly underestimated due to slightly higher autumn values during recent years by including low tide values since 2005.

CONCLUSION

Long time series are pivotal for understanding how ecosystems respond to both man-made and natural changes. The long history of Wadden Sea eutrophication is described best by the work done at the Royal Netherlands Institute for Sea Research (NIOZ) with a focus on the western Dutch Wadden Sea. Available data suggest that eutrophication already started from the 1950s onward (e.g., de Jonge, 1990), culminating in the 1980s (e.g., Cadée and Hegeman, 2002). Our study extends the description of Wadden Sea eutrophication to the entire Wadden Sea. The longest time series on phytoplankton/chlorophyll a are available for the Dutch Wadden Sea. They document an increase in phytoplankton from the mid 1970s to the mid 1980s and a decrease since. The Norderney and Sylt time series starting in the 1980s document the decreasing trends, whereas the Danish time series starting at the end of the 1980s only weakly reflect the decreasing eutrophication levels. Riverine nutrient loads are important drivers of phytoplankton dynamics and correlated significantly with summer phytoplankton biomass (as chlorophyll a), but only explained about 30% of interannual variability, suggesting the importance of other factors. These may include both biological factors like the balance between grazing and growth, but also physical factors like the import of organic matter (as a source of nutrients) from the North Sea.

Given the high variability of phytoplankton in response to riverine nutrient loads, it is important to have additional proxies that indicate the intensity of organic matter turnover. We show that the mean autumn concentration of the remineralization products $NH_4 + NO_2$ in autumn (when decreasing light levels limit phytoplankton productivity) is a useful proxy. Especially in the southern Wadden Sea, this proxy is significantly linked to riverine nitrogen loads suggesting its driving role in Wadden Sea organic matter turnover. Both proxies – summer chlorophyll a and autumn $NH_4 + NO_2$– are significantly correlated. The best correlations between the eutrophication proxies and riverine nutrient loads are found for stations in tidal inlets, probably because of less stronger interactions with the sediment than at the shallower, more coastward stations.

Regional differences are apparent, with long-term summer chlorophyll levels and autumn $NH_4 + NO_2$– levels clearly higher in the southern Wadden Sea than in the northern Wadden Sea. The model by Kerimoglu et al. (2017) supports, that these differences are driven by a higher organic matter import from the North Sea into the Wadden Sea. These regional differences suggest a lower eutrophication potential in the northern Wadden Sea as evidenced by lower phytoplankton biomass, lower organic matter turnover (autumn release of NH_4 and NO_2), seagrass recovery and decreasing green algae blooms.

The present data show, that measures taken to reduce riverine nutrient loads have led to a decrease in phytoplankton biomass in the Wadden Sea and adjacent coastal zone, and contributed to an improved ecological status. However, long, well designed long time-series with a high temporal resolution are needed to derive statistically significant correlations due to complex physical and ecological interactions, resulting in a strong interannual variability. Given the world-wide increase in the use of fertilizers (Battye et al., 2017), it can be expected that eutrophication problems will increase world-wide. The present example of the Wadden Sea underlines that measures to reduce nutrient enrichment do lead to an improvement of the coastal ecological status.

AUTHOR CONTRIBUTIONS

This article is an extended version of a contribution to the Wadden Sea Quality Status Report on Eutrophication lead by JvB with contributions from JC, TD, AG, HL, KK, JP, HR, and JR. JvB conceived the study, analyzed the data, and wrote the first draft of the manuscript. JC, AG, LR, HR, and JR provided the chlorophyll and nutrient data. TD and KK specifically contributed to the discussion of seagrass and macroalgae. HL and JP provided the riverine input data. RH and OK contributed with the analysis of the model data. All authors contributed to the discussion of the manuscript.

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