

RESEARCH ARTICLE

Seagrass recovery trajectories and recovery potential in relation to nutrient reduction

Marieke M. van Katwijk¹  | Justus E. E. van Beusekom^{2,3,4}  | Eelke O. Folmer⁵  | Kerstin Kolbe⁶ | Dick J. de Jong⁷ | Tobias Dolch³ 

¹Department of Environmental Science, Radboud Institute of Biological and Environmental Sciences, Radboud University, Nijmegen, The Netherlands;

²Department of Nutrient Cycles, Institute of Carbon Cycles, Helmholtz-Zentrum Hereon, Geesthacht, Germany; ³Wadden Sea Station Sylt, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, List, Germany; ⁴Computing and Data Center, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany; ⁵Ecospace, Ecological Research and Environmental Informatics, Lemmer, The Netherlands; ⁶Lower Saxony Water Management, Coastal Protection and Nature Conservation Agency, Norden, Germany and ⁷Rijkswaterstaat Sea and Delta, Ministry of Infrastructure and Water Management, Middelburg, The Netherlands

Correspondence

Marieke M. van Katwijk

Email: marieke.vankatwijk@ru.nl

Funding information

HORIZON.2.6—Food, Bioeconomy Natural Resources, Agriculture and Environment, Grant/Award Number: 101060418

Handling Editor: Sarah Faye Harpenslager

Abstract

1. Seagrass recovery has been reported across the globe where previously eutrophied waters have become less nutrient-rich. In the European Wadden Sea, different recovery trajectories were found after riverine nutrient loads decreased, namely full, temporary and no recovery. We compiled intertidal seagrass presence (*Zostera noltei* and *Z. marina*) and eutrophication data for 1930–2020, to relate the seagrass trajectories and regional eutrophication differences to riverine nutrient loads, and inferred prospects for seagrass recovery.
2. Seagrass fully recovered in the less eutrophic North Frisian region. The recovery trajectory was tightly coupled to riverine nutrient load reduction. Relative seagrass area (meadow area/region area) dropped from 10% prior to eutrophication to 2% during the eutrophication peak, increased to 7% during the nutrient reduction period and subsequently expanded to 13%. Colonization of marginal habitats was observed, indicating propagule spillover from neighbouring meadows.
3. The more eutrophic southern regions showed no or only temporary seagrass recovery. Prospects for (limited) recovery are good in only two out of four southern regions, provided that riverine nutrient loads are further reduced by ~40% (reference: 2010–2017). Without this reduction, seagrasses may only temporarily recover and will remain vulnerable to erratic disturbances like macroalgae accumulation or storms.
4. Historical evidence and application of habitat suitability models suggest that the potential relative seagrass area in the southern regions is low: less than 0.2% in the western Dutch region and maximum 2.4% in the Ems-Jade region.

Marieke M. van Katwijk and Justus E. E. van Beusekom—Equal contribution.

Dick J. de Jong—Retired.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Author(s). *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

5. *Synthesis and applications.* Within a large seascape (15,000 km²) the least eutrophicated region showed seagrass recovery upon nutrient reduction. We translated the critical riverine nutrient loads for this recovery, via regional eutrophication indicators, to loads that may enable a sustained recovery in the other regions. This technique is applicable in other complex systems, provided sufficient historical data are available. Propagule spillover exerts a positive feedback at metapopulation scale leading to acceleration of recovery. Occupied and potential seagrass habitat (e.g. assessed by the maximum recorded area in the past) are thus important landscape selection criteria for restoration, particularly when eutrophication is not yet sufficiently reduced.

KEYWORDS

eutrophication, historical baseline, mass effect, metapopulation, propagule spillover, Wadden Sea, *Zostera marina*, *Zostera noltei*

1 | INTRODUCTION

Seagrasses continue to decline worldwide, and with it many ecosystem services such as coastal protection, carbon sequestration, biodiversity, support of global fish stocks and water purification (Lamb et al., 2017; Nordlund et al., 2016; Unsworth et al., 2019). Eutrophication is one of the major factors compromising seagrass meadows (e.g. Burkholder et al., 2007; Orth et al., 2006). Restoration efforts generally fail when eutrophication is not reduced sufficiently (van Katwijk et al., 2016 and references therein). On the other hand, worldwide, scattered recoveries are reported after nutrient reduction (de los Santos et al., 2019; Lefcheck et al., 2018; McCrackin et al., 2017; Riemann et al., 2016; Sherwood et al., 2017).

In the Wadden Sea, the largest coherent tidal flat system in the world, located along the North Sea coasts of the Netherlands, Germany and Denmark (northwestern Europe), a remarkable recovery of intertidal seagrass occurred merely in the northern region (North Frisia) during the last two decades. Meadows even expanded to marginal habitats (Dolch et al., 2013, 2017). The recovery mainly involved intertidal *Zostera noltei*, the dominant species in the Wadden Sea, but intertidal, annual *Z. marina* recovered as well. In the Ems-Jade and Elbe-Weser region (German coast), after a recovery between 2008 and 2013, intertidal seagrass declined again (Dolch et al., 2017; KÜFOG GmbH et al., 2020). In the western and eastern Dutch region, no natural recovery of intertidal seagrass has been recorded. The spatial differences in nutrient concentrations and eutrophication levels are often mentioned as a potential explanation for the regional differences in seagrass development and abundance in the Wadden Sea (e.g. Dolch et al., 2013, 2017; Folmer et al., 2016; van Beusekom et al., 2019; van Katwijk et al., 2000, 2009). However, up until now, a comprehensive assessment of seagrass distribution trends in connection to eutrophication across all Wadden Sea regions has not been carried out.

In this study, we analyse intertidal seagrass recovery trajectories and recovery potential in the international Wadden Sea in

relation to eutrophication status (after van Beusekom et al., 2019) and reduction in nutrient loading. Specifically, we compile and reconstruct available seagrass and nutrient data of all Wadden Sea regions to further examine the relationship between recovery trajectories and riverine nutrient loading. From this, we infer, for each region, if and to which levels nutrient loading should be reduced to allow for seagrass recovery. To explore the prospects for seagrass recovery, we assess the maximum seagrass area per region as recorded in our time series, as well as seagrass area per region predicted by habitat suitability models. We will discuss the role of propagule spillover potentially speeding up recovery at a landscape scale.

2 | STUDY AREA

2.1 | Study area—Geographical setting, regions and monitoring

The Wadden Sea is a shallow intertidal coastal sea along the Dutch, German and Danish North Sea coast (Figure 1) and a World Heritage because of its globally unique geological and ecological values. It consists of saltmarshes, intertidal and subtidal areas, drainage gullies, channels and deeper inlets. The semidiurnal tidal wave travels along the Wadden Sea from west to north-east and drives water exchange between the Wadden Sea and the North Sea through the tidal inlets between the barrier islands. The tidal range is about 1 m at the northern and western ends and increases to more than 3 m in the central part. At tidal ranges below 3 m, barrier islands and high sands are formed (e.g., Hayes, 1975; Oost & de Boer, 1994), protecting the tidal flats in the southern and northern Wadden Sea, but such islands are absent in the central part. About 50% (range: 30%–96%) of the tidal basin areas emerge during low tide. Tidal currents and exposure to waves strongly differ between regions due to differences in tidal range, geomorphology, fetch

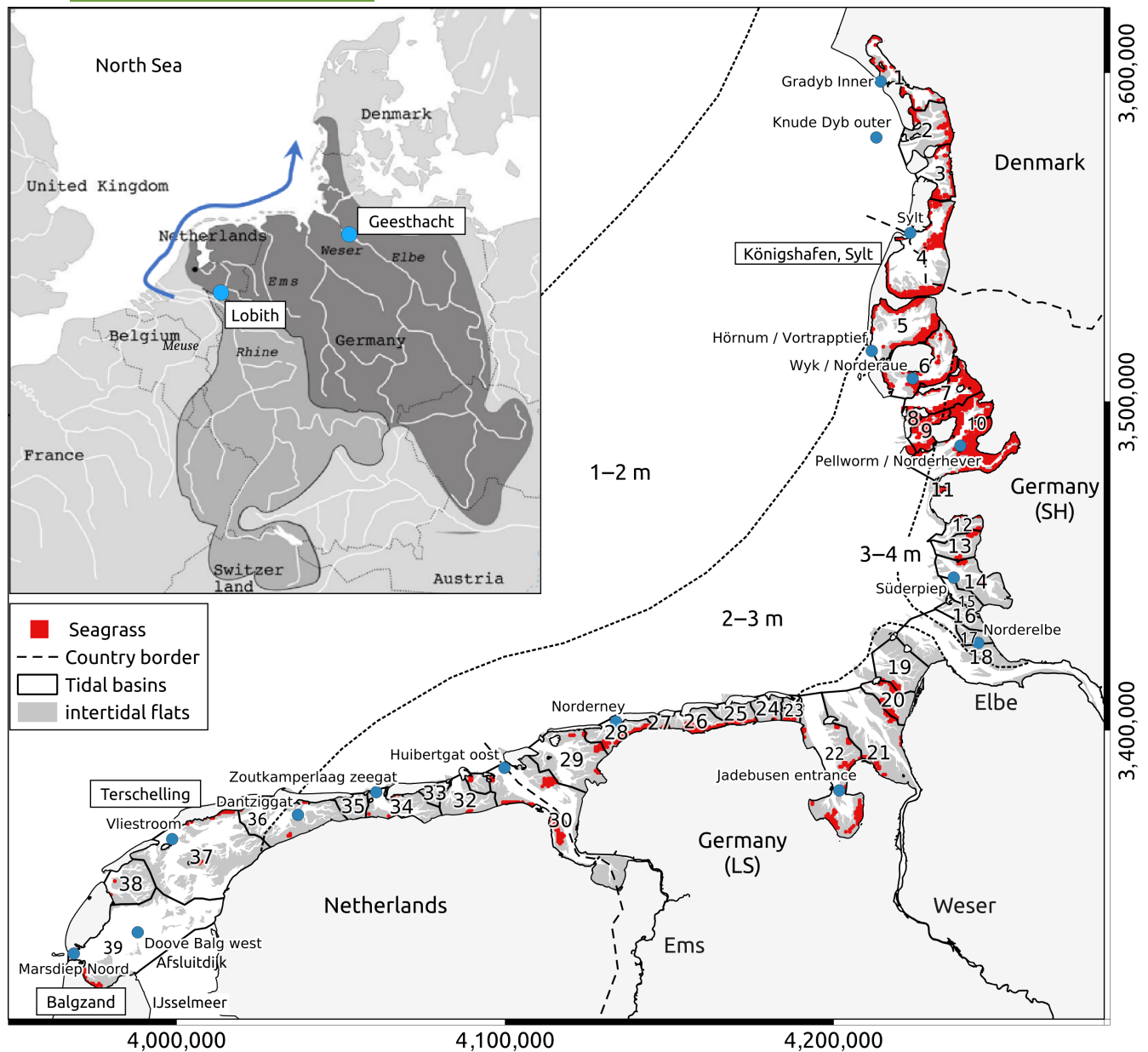


FIGURE 1 Wadden Sea consists of 39 tidal basins (numbered in ascending order from north-east to south-west), which are clustered in six regions, see Table 1. Tidal ranges at spring tide (redrawn from Wiersma et al., 2009) are presented with dotted lines. Intertidal seagrass meadows recorded in the period 1970–2015 are shown in red; they are drawn larger than their actual extents to increase visibility of the small seagrass meadows in The Netherlands and Lower Saxony (LS). SH=Schleswig-Holstein. Blue dots refer to water quality monitoring stations and their names are printed next to them. Inlay: The nutrient loads in the Wadden Sea are influenced directly by Lake IJssel, Ems, Weser and Elbe (catchment dark grey shading), and indirectly by the river Rhine and Meuse (catchment Rhine in Lobith: light grey shading). The water trajectory from Rhine and Meuse through the North Sea is indicated with a blue arrow.

and the presence of barrier islands. Geomorphology and sediment composition are strongly influenced by tidal currents and wind-driven waves. Sediments are mostly sandy in the more exposed parts, whereas in the more protected parts, muddy sediments prevail (Folmer et al., 2023). Seagrass occurs only in areas that are sheltered from large wind waves and where the tidal currents are relatively weak (Folmer et al., 2016).

We distinguish six regions (Table 1). The Wadden Sea can be further divided into 39 tidal basins which are loosely defined

hydrological units demarcated by tidal inlets, tidal divides and the mainland (e.g. Folmer et al., 2016; van Beusekom et al., 2010; Figure 1).

2.2 | Study area—Seagrass

In the Wadden Sea, the seagrass species *Z. marina* and *Z. noltei* are present and very incidentally *Ruppia maritima* has been recorded

TABLE 1 Regions in the Wadden Sea, based on geomorphological and governance (monitoring) considerations.

Region	Country/state	Tidal basins (see Figure 1)	%Intertidal/total area	Monitoring	Recovery (this study)
Danish (northern Wadden Sea)	Denmark	1–4 (half)	54%	Limited time series	Unknown
North Frisian (northern Wadden Sea)	Germany/Schleswig-Holstein	4 (half)–11	64%	Long time series (includes the well-investigated 'Königshafen, Sylt')	Full recovery
Elbe-Weser (central Wadden Sea)	Germany/Schleswig-Holstein Lower Saxony and Hamburg	12–21	59%	Long time series with large intervals ^a	Temporary recovery at low levels
Ems-Jade (southern Wadden Sea)	Germany/Lower Saxony	22–30 (half)	66%	Long time series with large intervals ^a	Temporary recovery
Eastern Dutch (southern Wadden Sea)	The Netherlands	30 (half)–36	61%	Long time series, no historical data	No recovery
Western Dutch (southern Wadden Sea)	The Netherlands	37–39	43%	Long time series (includes the well-investigated 'Balgzand' in the utmost west)	No recovery

Note: Recovery trajectories concern mid-intertidal seagrass, mostly *Z. noltei*, but annual *Z. marina* occurs as well. Species often mix spatially or occur directly next to each other, and no distinction between species is made during monitoring in Germany and Denmark. Meadow areas are monitored in all three countries.

^aAdditionally, six selected locations are annually monitored.

(e.g. van Katwijk et al., 2006). Both *Zostera* species grow in the intertidal zone, where *Z. noltei* has a perennial life history and *Z. marina* predominantly an annual life history. In the past, a robust, subtidal form of *Z. marina* also occurred which had a perennial life history, that covered 70–150 km² or more in the subtidal western Dutch region. This morphotype also occurred in North Frisian region and it may have occurred in the Ems-Jade region, but all to a more limited extent (see Appendix S1.1 in Supporting Information). The subtidal, robust morphotype of *Z. marina*, has gone extinct in the western Dutch region in the 1930s due to a combination of wasting disease and major infrastructural works (closing of the former Zuiderzee by the Afsluitdijk in 1932, e.g. Giesen et al., 1990; Reise, 1994) and later also in the other regions (see Appendix S1.1). Historically, the robust morphotype of *Z. marina* was economically important in the western Dutch Wadden Sea (at that time including the Zuiderzee) where it covered more than 70 km² in 1869 (Oudemans et al., 1870), approximately 150 km² around 1915 (van Goor, 1919), and approx. 120 km² around 1931 (Reigersman et al., 1939) (see Appendix S1.1).

2.3 | Study area—Nutrients

Continental northwest European rivers are the main sources of anthropogenic nutrient loads to the Wadden Sea (Figure 1; van Beusekom et al., 2012, 2019). Major sources of nutrients that discharge directly into the southern Wadden Sea are Lake IJssel (fed by a branch of the Rhine) and the Ems river. Major rivers entering the central Wadden Sea are the Weser and Elbe. Indirect loads originate from the northward transport of river water (mainly Rhine and Meuse) with the residual currents along the Wadden Sea following the anti-clockwise circulation of the North Sea. Nutrient loads of the Rhine and Meuse are especially impacting the southern Wadden Sea. The central and northern Wadden Sea are especially impacted by the northward-directed nutrient loads from the rivers Weser and Elbe (Figure 1). Higher riverine nutrient loads increase eutrophication throughout the Wadden Sea causing intensified nutrient dynamics, higher phytoplankton densities and altered community composition (e.g. Cadée & Hegeman, 2002; de Jonge & Postma, 1974; van Beusekom et al., 2001). Local nutrient loads by small rivers and sluices play a secondary role (van Beusekom et al., 2001).

Eutrophication of the Wadden Sea is also driven by the import of particulate matter from the North Sea consisting of inorganic particles, phytoplankton and phytoplankton detritus from the coastal zone adjacent to the Wadden Sea. The heterotrophic nature of the Wadden Sea was already recognized in the early days of Wadden Sea research (Linke, 1939; Verwey, 1952; Wohlenberg, 1937) and further elaborated by Postma (e.g. Postma, 1981, 1984, see also van Beusekom & de Jonge, 2002; van Beusekom et al., 1999). Between the 1950s and 1970s, the increasing river nutrient loads caused nutrient-enhanced phytoplankton production in the North Sea (de Jonge & Postma, 1974; Postma & van Bennekom, 1974) which in turn increased the organic matter supply from the North Sea to the Wadden Sea.

The import of material from the North Sea to the Wadden Sea is regulated by hydrodynamics (e.g. Postma, 1981; van Beusekom et al., 2019). The freshwater discharge from the European continent to the North Sea causes density gradients which induce estuarine circulation in the coastal North Sea with a bottom current directed towards the Wadden Sea (e.g. Eisma, 1993; van Beusekom et al., 2012; Visser et al., 1991), driving the import of organic matter and maintaining nutrient gradients between the North Sea and the Wadden Sea (Hofmeister et al., 2017). Zones of maximum phytoplankton sedimentation rates are located in the North Sea adjacent to the Wadden Sea (Maerz et al., 2016; Neumann et al., 2019). Any sinking material (including decaying phytoplankton) in the North Sea adjacent to the Wadden Sea has a large probability to accumulate in the Wadden Sea keeping up the gradient of suspended particle matter between the Wadden Sea and the North Sea (Hofmeister et al., 2017; Postma, 1981). Within the Wadden Sea, suspended matter is retained by hydrodynamic factors like vertical density differences and tidal asymmetry (Burchard et al., 2008), tidal differences in settling and erosion (van Straaten & Kuenen, 1958), filter feeders (e.g. Cadée & Hegeman, 1974), stabilizing organisms (e.g. Reise, 2002) or particle retention in permeable sandy sediments (de Beer et al., 2005).

The winter dissolved inorganic nitrogen (DIN) concentration is more or less similar among the tidal basin entrances (40–80 μM), suggesting that the river influence is equally spread over the Wadden Sea, except for the tidal basins in the mouth of the Elbe, which show higher values, that is 200 μM average January–March 2004–2008 (van Beusekom et al., 2017). However, the levels of eutrophication (as measured by two eutrophication indicators, summer chlorophyll primarily representing productivity, and autumn $\text{NH}_4 + \text{NO}_2$ concentration primarily representing remineralization, as will be explained below in Section 3.2), differ strongly between the tidal basins and regions. This can be explained by: (1) the import of organic matter from the adjacent North Sea being higher in the south than in the north (van Beusekom et al., 2019) and (2) broader basins (like Hörnum tidal basin in the North Frisian region and the western Dutch tidal basins) spreading the imported organic matter over a larger area as opposed to narrow basins like the Ems-Jade or eastern Dutch basins, thus leading to a lower eutrophication level in the broader tidal basins (Schwichtenberg et al., 2017; van Beusekom et al., 2012).

Eutrophication levels for each of the regions within the Wadden Sea can be assessed by two indicators that strongly relate to riverine total nitrogen (TN) loads: summer chlorophyll and autumn $\text{NH}_4 + \text{NO}_2$. These indicators were chosen because they strongly relate to riverine TN loads (van Beusekom et al., 2001, 2009, 2019). They reflect a multitude of factors related to nutrient loading, such as nutrients for algae growth and organic matter import (from nutrient-enhanced phytoplankton growth in the adjacent North Sea) and remineralization. But the indicators also reflect factors that are not directly related to nutrients, like shellfish and zooplankton grazing, light limitation from suspended particles (e.g. Thompson et al., 2008) or hydrodynamical impacts on organic matter import influencing import

efficiency, all contributing to the observed variability in their relation with riverine nutrient loads.

3 | MATERIALS AND METHODS

3.1 | Seagrass monitoring

The extents of intertidal seagrass meadows prior to the eutrophication peak, that is in the 1930s, in the 1950s–1960s, or both, were documented for the western Dutch, Ems-Jade and North Frisian region (see Appendix S1.1 and van Katwijk et al., 2024). Pre-eutrophication data for the eastern Dutch, Elbe-Weser and Danish regions are lacking, to our knowledge. Since the 1990s, seagrass population development was monitored in programmes that differed between countries with respect to frequency and length of the time series as well as methodology (methods, see Appendix S1.2). For comparison, we used the meadow area of both species combined. Only meadows where seagrass % cover is >5% (in the Netherlands and Germany) or >20% (in Denmark and the historical assessment of the Ems-Jade region 1936–1939) are included in the monitoring data. To extrapolate from cover >20% to cover >5%, we multiplied the areas by 1.37. This multiplication factor is based on the cover classes in the North Frisian region where meadows >20% cover represent 73% of the meadow area >5% (std 20%, $n=189$; T. Dolch, unpublished data) and $100/73=1.37$. This value is similar in the western Dutch Wadden Sea for *Z. noltei*: 77% (std 19%, $n=12$ years monitoring of one meadow in Terschelling; Dutch Ministry of Infrastructure and Water Management). We used the conversion factor of 1.37 derived from North Frisia meadows because the western Dutch value is based on only one meadow located in atypical compact clay sediments.

To explore the prospects for seagrass recovery, we compiled for each region: (a) the historical maximum seagrass extent recorded and (b) the maximum potential seagrass extent predicted by a habitat suitability model of the Wadden Sea based on geomorphology, hydrodynamics and grain size (Folmer et al., 2016). Large discrepancies between the historically observed and predicted maxima may point at factors missing in the habitat suitability model, or incomplete seagrass data.

To compare seagrass presence between regions, the relative seagrass area (RSA) was calculated by dividing seagrass areas by the total area of the region. To tentatively assess which minimal seagrass extent may suffice to allow for recovery, we also extracted the minimum historical seagrass extent from our time series.

It should be noted that for all regions, the seagrass time series are incomplete, and particularly, historical data are largely missing, so interpretations should be cautiously made. Furthermore, it should be noted that there might have been meadows that were never monitored. Still, contemporary experts indicate that the non-mapped areas in the western and eastern Dutch region only had minor seagrass areas during the 1950s–1970s (Polderman & den Hartog, 1975;

van den Hoek et al., 1979), which may also hold for the 1930s and before (see Appendix S1, Table S1).

The maximum potential seagrass extent predicted by habitat suitability was calculated using the model of Folmer et al. (2016). In this model, the mean fraction of time that the seabed is exposed to the air, mean bottom shear stress due to tidal currents, slope, fraction of sediment <63 μm and median grain size were used as predictors. Exposure to air and mean bottom shear stress were calculated using a three-dimensional open-source model (GETM; Burchard & Bolding, 2002). The slope was calculated from bathymetry data generated by governmental agencies in the three countries and grain size was obtained from the German Federal Maritime and Hydrographic Agency, where missing data for Denmark were imputed. (Folmer et al., 2016). The habitat suitability model was refined for the western and eastern Dutch Wadden Sea by Folmer (2019), by incorporating wave energy data (orbital velocity) from the wave model SWAN (Donker, 2015), and the density of large lugworms obtained from a large Dutch monitoring programme (SIBES; Compton et al., 2013). Because these data were only available for the western and eastern Dutch region, the refinement was limited to these regions (Folmer, 2019). The continuous score of habitat suitability was classified into the classes 'unsuitable', 'marginal' and 'suitable' using the continuous Boyce index (Folmer et al., 2016). In our study, we used only two classes: suitable and unsuitable (which includes the original classes 'unsuitable' and 'marginal').

3.2 | Nutrients

Nutrient dynamics in the Wadden Sea are strongly linked to riverine nutrient loads (interpolated daily concentration \times daily discharge), and the impact of these loads on the eutrophication status depends on local factors like organic matter import from the North Sea (van Beusekom et al., 2019, see also Section 2.3). Nutrient monitoring programmes in the Wadden Sea started between the late 1970s and 1990. Thus, for the long-term studies starting before the 1970s, only riverine nutrient loads were used, whereas for regional comparisons and changes after the 1970s, we used the riverine nutrient loads and eutrophication indicators as developed by van Beusekom et al. (2001, 2019).

To examine the long-term (from the 1930s to the present) relationship between historical seagrass area, decline and recovery in North Frisia and eutrophication, and to identify a critical nutrient load for seagrass return in this region, we use riverine nutrient loads from the Elbe and Rhine. We focus on N rather than P as N is directly related to one of the regional eutrophication indicators (autumn $\text{NH}_4 + \text{NO}_2$, see next paragraph), but note that riverine P loads also correlate with the regional eutrophication indicators (van Beusekom et al., 2019). For a historical reconstruction of the TN loads in the Rhine, we used and extended the study by van Bennekom and Wetsteijn (1990) based on monitoring data at the Dutch-German border (Lobith, Figure 1) available since 1952. We reconstructed TN loads from 1952 to 1966 based on DIN (Dissolved Inorganic

Nitrogen) measurements and estimated TN based on correlations (1966–1990) between NH_4 and Total Kjeldahl Nitrogen, used TN measurements from 1966 to 2017, and included estimates for the 1930s based on Clarke (1924). For a historical reconstruction of the TN loads in the Elbe, we estimated riverine TN loads from 1954 to 1979 based on DIN measurements and estimated organic N from correlations between NH_4 and organic N (using data from 1979 to 1990). After 1979, we used measured TN monitoring data. All data are from a station just upstream of the weir at Geesthacht (Figure 1). We further included estimates for the 1930s based on Clarke (1924), (details on the reconstruction and estimates are provided in see Appendix S1.4).

To assess regional differences in eutrophication levels and explore how they compare to a critical eutrophication threshold for seagrass return, we used the eutrophication indicators as developed by van Beusekom et al. (2001) and recently applied by van Beusekom et al. (2019). More specifically, with these indicators we (1) document decreasing eutrophication in the international Wadden Sea in response to decreasing nutrient loads, (2) identify regional differences and (3) translate the critical riverine nitrogen load for seagrass recovery to a critical eutrophication threshold at a regional level. The indicators are summer chlorophyll (average of monthly means over May–September; spring values were excluded as winter temperature may have a strong impact on spring bloom intensity, e.g. van Beusekom et al., 2009) and autumn $\text{NH}_4 + \text{NO}_2$ (average of monthly means over September–November). Data for these two indicators were available over a wide geographical area over the period 2008–2016. It should be noted that several factors influence the relationship between these indicators and riverine nutrient loads: summer phytoplankton may be impacted by interannual differences in the import of organic matter (hydrodynamics, off-shore phytoplankton blooms, van Beusekom et al., 2001), by copepods or microzooplankton grazing (e.g. Loebel & Van Beusekom, 2008), by benthic filter feeders (Asmus & Asmus, 1991; Cadée & Hegeman, 1974; Ehrnsten et al., 2020; Hulot et al., 2020) or light limitation of algal growth as a consequence of high suspended matter concentrations (Colijn, 1982; Loebel et al., 2007, 2008; Thompson et al., 2008). Similarly, the autumn $\text{NH}_4 + \text{NO}_2$, a remineralization product, depends on summer import and summer productivity, autumn phytoplankton blooms, hydrodynamics (storms) and temperature (e.g. van Beusekom et al., 2001). The multitude of processes affecting the eutrophication indicators explains the variability in their relationships with river nutrient loads (van Beusekom et al., 2001, 2009, 2019). Note that the river load data used in these studies are from river monitoring stations closer to the Wadden Sea than the ones we had to use for the historical analysis for data availability reasons (Rhine–Meuse: Haringvliet and Maassluis, Weser: Intschede, Elbe: Teufelsbrück/Seemannshöft; for details: Pättsch & Lenhart, 2022). River loads are not annual loads but the loads from December–August (Rhine–Meuse) or January–August (Weser–Elbe) as loads after August will not impact the summer phytoplankton blooms. As a starting point for the Rhine–Meuse loads, we used December

as this gave a stronger correlation with the eutrophication indicators. As the Rhine Maas outflow is further away from the Wadden Sea than the Elbe-Weser, we choose a shorter period for the Elbe-Weser. For details, see van Beusekom et al. (2001) and van Beusekom et al. (2009).

The description of recent regional differences in eutrophication in the Wadden Sea is based on van Beusekom et al. (2019) and, for a better spatial resolution, supplemented with data from Zoutkamperlaag zeegat (eastern Dutch Wadden Sea, monitored until 2010), Jadebusen Entrance (Lower Saxony Wadden Sea, monitored since 2000) and the stations Süderpiep, Wyk/Norderaue and Hörnum /Vortrapptief (northern Wadden Sea, monitored since 2000). All stations are close to the tidal inlets (Figure 1).

As a critical eutrophication threshold, we used the range between the minimum and maximum levels of the eutrophication indicators in the North Frisian region (Sylt) during the 4 years preceding the year that recovery started to accelerate (the year 2000), that is the maximum of summer chlorophyll levels during 1997–2000 and the autumn $\text{NH}_4 + \text{NO}_2$ levels during 1997–2000.

We projected the riverine nutrient loads that may lead to seagrass recovery in other regions using a cautious approach because of the large environmental variability. We only used monitoring stations that have long time series and are located near tidal inlets: Sylt (North Frisian region, which is the reference region for recovery, data: 1984–2016), Marsdiep and Vlietstroom (western Dutch Wadden Sea, data: 1978–2017) and Norderney (Ems-Jade region, data: 1985–2016). We only used summer chlorophyll as it shows comparable variability patterns and significant correlations with riverine TN loads in North Frisia (Sylt), the western Dutch Wadden Sea and Ems-Jade region (compare van Beusekom et al., 2019). We did not use autumn $\text{NH}_4 + \text{NO}_2$ because this indicator only correlated significantly with riverine N loads in the southern Wadden Sea (Marsdiep, Vlietstroom and Norderney), but not in the northern Wadden Sea (Sylt) but note that the general levels of summer chlorophyll and autumn $\text{NH}_4 + \text{NO}_2$ show comparable regional patterns (van Beusekom et al., 2001, 2019). For the projection, (1) we used the year that recovery accelerated, that is 2000, and calculated the 4-year averaged riverine TN load preceding seagrass recovery, that is 1997–2000 (Elbe-Weser); (2) we deduced the maximum of summer chlorophyll at Sylt (North Frisian region) corresponding with these TN loads using the upper line of the two lines that envelop the observations (manually drawn); note that this is slightly more precise than the method we used to compare all regional stations described above, though the outcome is nearly the same; (3) we projected this chlorophyll maximum on the relation between river loads (Rhine–Meuse) and summer chlorophyll at the other stations, that is Marsdiep and Vlietstroom for the western Dutch Wadden Sea and Norderney for the Ems-Jade region; and (4) compared this deduced TN load to the recent TN loads (i.e. 2010–2017). To determine the sensitivity of the results to choices made, we additionally calculated the critical summer chlorophyll range in the year 2003 (when recovery was setting through) in addition to the year 2000 (when recovery started to accelerate), the 3- and 5-year averages in addition to

the 4-year average, and we used the average levels in addition to maximum levels, in total yielding 11 additional scenarios.

A permission for fieldwork was not needed as monitoring was performed on behalf of the environmental authorities and/or concern open source data.

4 | RESULTS

4.1 | Seagrass long-term dynamics

Intertidal seagrass abundance in the North Frisian region in the northern Wadden Sea has recovered and surpassed the levels as in the 1930s (Figure 2). Recovery accelerated between 2000 and 2011. Since 2011 the levels have remained high and relatively stable, with further expansions in 2018–2020. Danish data are scarce; P.B. Madsen observed a slow decline between 1974 and 1991 (de Jong et al., 1993). In 1991, values are high in the Danish region (also in North Frisia), which is likely due to a notable spread of *Z. marina* throughout the 1980s, followed by a return to smaller meadows and strong dominance of *Z. noltei* as observed also in the 1970s in the North Frisian region (Reise et al., 2005). The values may be an overestimation as during the survey in 1991 green algal mats attained peak coverage, and confounded the estimate (Reise & Kohlus, 2008). It could also be that seagrass abundance was actually very high in this particular year, because it was preceded by three dry years with low riverine nutrient loads in the Elbe (Figure 3).

In the southern Wadden Sea, the seagrass coverage is presently stagnating at a low level with some indications of temporary increase in the Ems-Jade region and the Elbe-Weser region (Figure 2). In the eastern and western Dutch Wadden Sea regions, seagrass has not recovered. Note that the time series for the Ems-Jade and Elbe-Weser region have a lower temporal resolution than the other regions (Figure 2); however, annual investigations at six selected key locations generally show a peak between 2009 and 2013 and a decline since (Dolch et al., 2017), which suggests that the presented data are representative for the general trends in these two regions.

The maximum recorded intertidal seagrass area in the Wadden Sea regions varied between 1 km² in the eastern Dutch region and 186 km² in the North Frisian region (Figure 2; Table 2). This corresponded to relative seagrass areas (RSA) of 0.11% and 13.3%, respectively (Table 2). Recovery trajectories in the Wadden Sea comprised expansions from 4.9 to 27.9 km² (Ems-Jade region, temporary recovery), from 1.5 to 11 km² (Elbe-Weser region, temporary recovery) and from 30 to 186 km² (North Frisian region, full recovery), which correspond to an increase of factor 5.7, 7.6 and 6.3 respectively (Table 2).

In the North Frisian region, RSA dropped to about 2% during the eutrophication peak and increased to 7% during the period of continuously decreasing nutrient loads, that is to circa 2007 (Figures 2 and 4), after which it expanded to 13%, colonizing even marginal habitats (Table 2). In the region with temporary recovery, the Ems-Jade region, RSA never dropped below 0.6% during the highest levels of

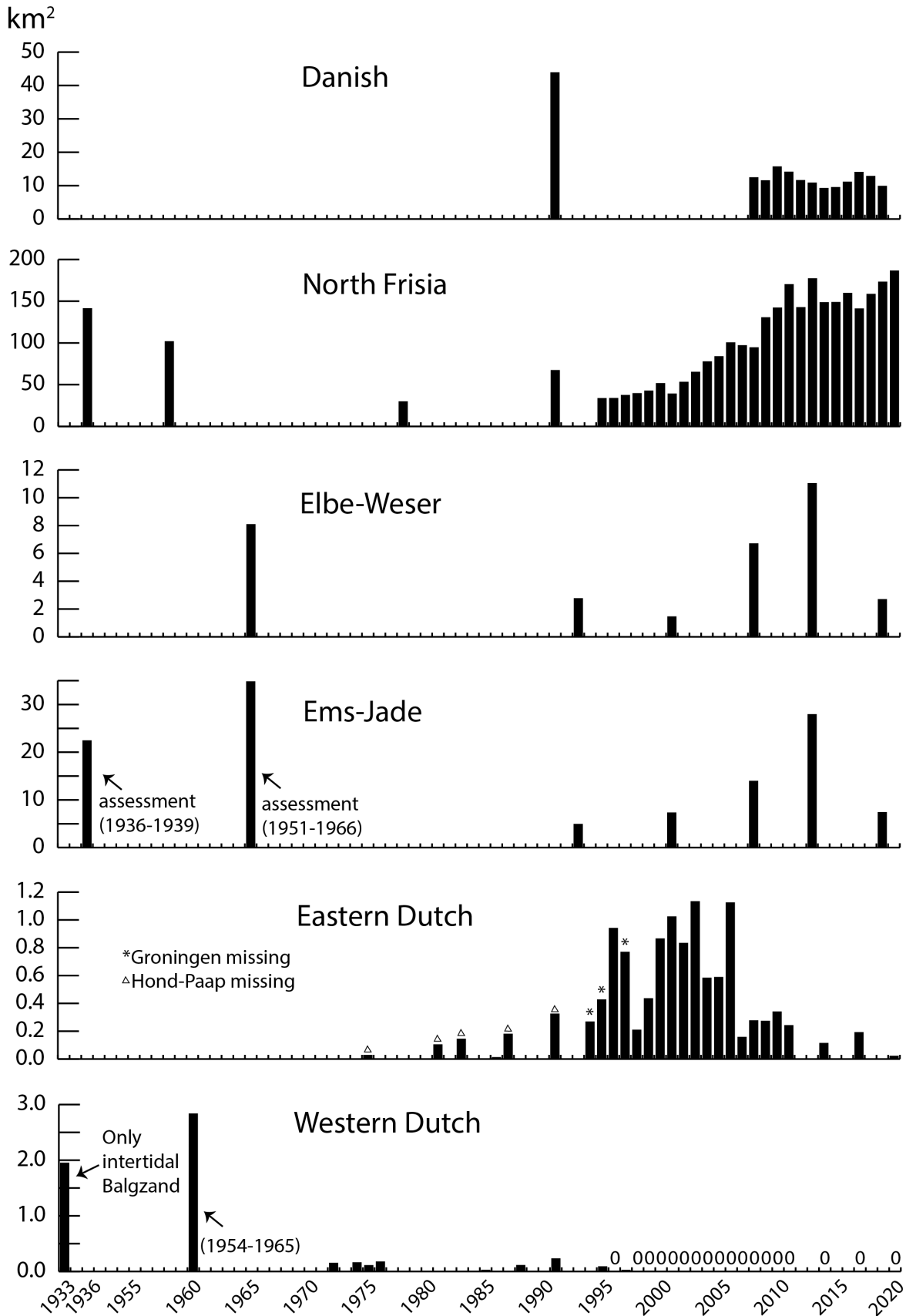


FIGURE 2 Seagrass long-term dynamics in six Wadden Sea regions. Only meadows with cover >5% are included. Data, explanations and sources are presented in van Katwijk et al. (2024). Information on species and lower cover categories are available for Dutch meadows (see Appendix S1.3). The assessment for 1936–1939 for Ems-Jade is based on a new analysis of aerial photographs (see Appendix S1.1). Triangles: monitoring of Hond-Paap is missing; stars: monitoring of Groningen is missing.

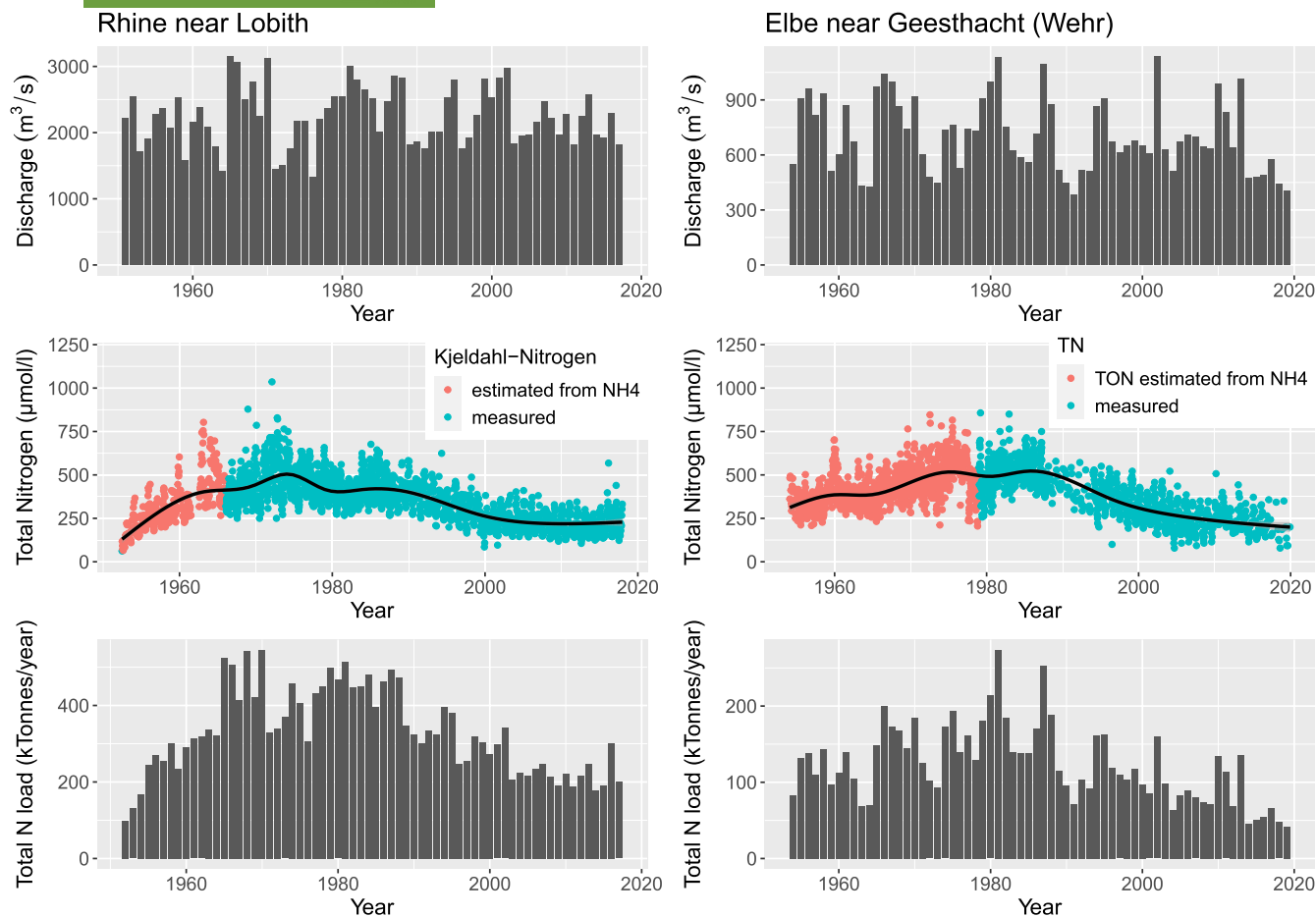


FIGURE 3 Historical discharges, total nitrogen (TN) concentrations and TN loads in the rivers Rhine (measured at Lobith; panels at the left) and Elbe (measured near Geesthacht; panels at the right).

eutrophication and recovered to 1.9% around 2013 after which it dropped to 0.5% in 2019. The maximum RSA in this region was 2.4% prior to eutrophication. In the Elbe-Weser region, also a region with temporary recovery, RSA never dropped below 0.08% during eutrophication, and temporarily recovered to 0.6% around 2013 (Table 2). In the western and eastern Dutch regions, prior to the eutrophication peak, around 1960, recorded RSA was maximally 0.2% (Table 2). Historical subtidal *Z. marina* in the western Dutch region occupied approximately 5% of the area (assuming 120 km² seagrass meadows and a total area including a part of the Zuiderzee of 2400 km²).

The habitat suitability model predicts 11.3% and 14.2% of potential suitable habitats in the Ems-Jade region and the eastern Dutch region, respectively. This is much higher than the observed maxima RSA of 2.4% and 0.1% prior to eutrophication. It is therefore likely that some other factors than those included in the habitat suitability model also limit the seagrass distribution. A habitat suitability model including waves for the western and eastern Dutch Wadden Sea (Folmer, 2019, not available for other regions) showed considerably less suitable habitats, but still nearly 7% in the Eastern Dutch Wadden Sea (Table 3) thus still leaving a portion of 'unexplained' absence of seagrass even prior to eutrophication.

Despite seagrass being near absent in the western and eastern Dutch Wadden Sea, seeds were available throughout the area, as we deduce

from the following evidence: firstly, low density meadows have been present for prolonged periods of times, for example along the southern shore of Terschelling in the western Dutch region, and fringing the mainland shore of the eastern Dutch region (see Appendix S1.3); secondly, in the utmost western part of the western Dutch region at Balgzand, solitary *Z. noltei* plants and small patches were continuously observed during the 1970s to 1990s by J.J. Beukema (quoted in Philippart & Dijkema, 1995), and during 1990s–2010s by M.M. van Katwijk; thirdly, *Z. marina* (and to a lesser extent *Z. noltei*) was frequently introduced in the western and eastern Dutch region from 1991 to present in a series of restoration programmes (Govers et al., 2022; Gräfnings, 2022; van Duren & van Katwijk, 2015; van Katwijk et al., 2009, see Appendix S1.5 for a review of seagrass restoration activities).

4.2 | Eutrophication

4.2.1 | Riverine nutrient loads

In the river Rhine, for the 1930s we estimated TN concentrations of about 80 µM and about 60 µM in 1952. Given the few available measurements and the uncertainty in estimating TN, we assume that no big changes occurred prior to 1952. After 1952, concentrations

TABLE 2 Seagrass meadow area prior to, during and after the peak of eutrophication as recorded (and assessed, see footnote c) in time series of the Wadden Sea regions, and corresponding RSA (% meadow area/total area).

Regions		Western Dutch Wadden Sea	Eastern Dutch Wadden Sea	Ems-Jade Wadden Sea	Elbe-Weser Wadden Sea	North Frisian Wadden Sea	Danish Wadden Sea ^a
Total area ^b	km ²	1525	1054	1466	1902	1398	628
1930s	km ² (%)	2.0 ^b (0.13%)	Anecd	22.4 ^c (1.5) ^c	n.a.	141.0 (10.1%)	n.a.
1950s–1960s	km ² (%)	2.83 ^e (0.19%) ^e	Anecd	28.3–34.8 ^d (1.93%–2.4%) ^d	8.1 (0.42%)	101.7 (7.3%)	n.a.
1970–2000	km ² (%)	0.0–0.2 (0.0%–0.02%)	0.03–0.9 (0.00%–0.09%)	4.9 (0.33%)	2.76 (0.14%)	29.6–67.1 ^f (2.1%–4.8%) ^f	43.84 ^f (7.0%) ^f
2001–2020	km ² (%)	0.0 (0.00%)	0.02–1.13 (0.00%–0.11%)	7.3–27.9 (0.50%–1.90%)	1.5–11.0 (0.1%–0.6%)	39.0–186.4 (2.8%–13.3%)	9.2–15.7 (1.5%–2.5%)
Current	km ² (%)	0.00 (0.00%)	0.02 (0.00%)	7.4 (0.50%)	2.7 (0.14%)	186.4 (13.3%)	9.8 (1.5%)
		(2020)	(2020)	(2019)	(2019)	(2020)	(2019)

Note: Ranges are minimum and maximum recorded. Each meadow has >5% seagrass cover. Anecd=anecdotal evidence available (see Appendix S1, Table S1).

Abbreviation: n.a., not available.

^aMeadow areas and percentages were multiplied by 1.37 to convert cover >20% to cover >5% (see Section 3.1).

^bIncomplete, only intertidal *Z. marina* at Balgzand.

^cAssessed from a new analysis of aerial photographs from 1936 to 1939 (see Appendix S1, Table S2).

^dThe first number was from mapping 1939–1970 (Michaelis et al., 1971); the second number was assessed from a new analysis of aerial photographs from 1951 to 1966 (see Appendix S1, Table S2).

^eThis is the sum of meadow areas estimated between 1954 and 1965, that is Balgzand and east Terschelling; expert judgement was that other location may only have had minor seagrass presence (Polderman & den Hartog, 1975; van den Hoek et al., 1979). We assume that 2/3 of the meadow area of 425 ha concerns cover >5%, based on the cover distribution in comparable meadows.

^fThis was recorded in an exceptional year: 1991, see text.

^gTotal area of the region was calculated by summing the areas of the separate tidal basins. The areas of tidal basins of Sylt-Rømø and Ems Estuary each belong to two regions, their areas were equally divided between both regions.

rose to a maximum of up to around 500 μM in the 1970s. Between the mid-1980s and 2000, the concentrations decreased and remained on a level between about 125 and 375 μM since (Figure 3). Annual loads show a similar pattern (Figure 3). In the river Elbe, TN concentrations during the 1930s were estimated at 37 μM (see Appendix S1.4). They sharply increased during the 1950s and 1960s, reaching a maximum in the 1970s and 1980s of 700–800 μM and decreased since the 1980s to presently reach maximum concentrations of about 350 μM (Figure 3). Despite a small decrease in annual discharge (van Beusekom et al., 2019), annual loads show the same pattern (Figure 3). Note that the TN loads actually reaching the North Sea may have been lower due to estuarine processes like denitrification. Denitrification is presently less dominant than in the past, since the organic matter loads have been strongly reduced during the 1980s (Dähnke et al., 2008).

4.2.2 | Relation between annual riverine nitrogen loads and seagrass abundance in North Frisia

Seagrass abundance in the North Frisian region is tightly related to the TN loads of both the Rhine and the Elbe (Figure 4), with seagrass abundance decreasing until the 1980s during a period of increasing

loads, and increasing during the period of decreasing loads since the 1990s. Recovery started to accelerate around the year 2000. That seagrass abundance correlates well with the TN loads of both rivers is not a surprise since N loads of river Rhine and Elbe are significantly correlated ($p < 0.0001$; $R^2 = 0.60$), probably due to a similar climate, and comparable agricultural and industrial land use developments in their respective catchments.

4.2.3 | Regional differences in Wadden Sea eutrophication

The eutrophication indicators, summer chlorophyll and autumn $\text{NH}_4 + \text{NO}_2$ concentrations show similar regional patterns during the period 2008–2016 (Figure 5). Lowest concentrations are observed in the North Frisian region (Pellworm–Sylt, locations see Figure 1) slightly increasing to the north in the narrower Danish region (Knude Dyb, Gradyb) and towards the Elbe estuary. The highest concentrations are found in the southern Wadden Sea but there, regional differences are large. Within the southern Wadden Sea the lowest concentrations are found in the broader western Dutch region (Marsdiep–Doove balg west) and the highest concentrations in the narrow eastern Dutch region

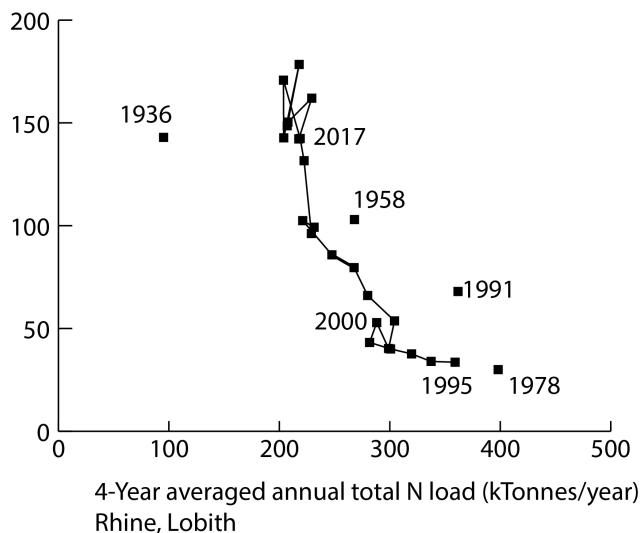
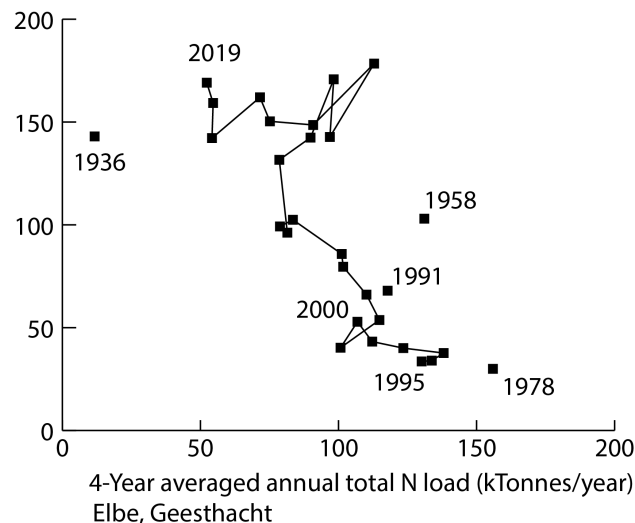
Seagrass area
(km²)Seagrass area
(km²)

FIGURE 4 Relation between 4-year averaged riverine total nitrogen load of the Rhine (left) and Elbe (right) and seagrass coverage in the North Frisian region.

(Danziggat–Zoutkamperlaag zeegat). The concentrations in the Ems-Jade region (Norderney, Jadebusen entrance) are intermediate. The critical eutrophication threshold ranges (the minimum and maximum value of the eutrophication indicators in the years preceding the acceleration of recovery in 2000, i.e. 1997–2000) are 4.0 and 8.2 $\mu\text{g chl a/L}$ summer chlorophyll and 3.8–7.5 μM autumn $\text{NH}_4 + \text{NO}_2$ (green belts in Figure 5).

4.2.4 | Projection of river load reduction that would allow for seagrass recovery

In the region where seagrass recovered (North Frisia), the riverine TN loads and summer chlorophyll concentrations are significantly correlated (van Beusekom et al., 2019). Most data (one exception) are enveloped by two straight lines with different slopes representing the expected range (approximately equivalent to a mean $\pm 40\%$) in summer chlorophyll concentrations at a certain TN load. The two lines have near-identical intercepts at zero river loads (Figure 6; 2 $\mu\text{g chl a/L}$, similar to the background values estimated by van Beusekom, 2005). The latter suggests that a certain background summer chlorophyll level seems to exist, independent of the riverine load (e.g. nutrient loads from the Atlantic Ocean). In the North Frisian region, seagrass recovery accelerated in the year 2000 (Figure 4). At this time, 4-year averaged river Elbe/Weser loads reached levels of about 122 kTonnes TN/year. This load corresponds to summer chlorophyll levels ranging between 4.0 and 8.6 $\mu\text{g chl a/L}$ (Figure 6).

In Figure 7, the relationship between river loads and summer chlorophyll levels is depicted for those stations that have sufficiently long time series and are situated near a tidal inlet similar to the Sylt station, that is monitoring stations Norderney in the Jade-Ems region, and Marsdiep Noord and Vlietstroom in the western

Dutch region. The relationships between river TN loads (Rhine/Meuse for these regions) and summer chlorophyll levels are similar to the relationship in the North Frisian region (Figure 6). In all graphs depicted in Figures 6 and 7, the upper and lower lines are about 40% higher or lower than the average (both at high and low TN load) showing that the variability of the chlorophyll concentrations increases with increasing TN loads. This variability in chlorophyll values reflects the suite of factors like grazing, light limitation or import efficiency that may impact phytoplankton growth during summer. The predictions shown in Figure 7 suggest that near Norderney in the Jade-Ems region, and in the western Dutch region the critical summer chlorophyll levels for seagrass recovery can be expected at Rhine/Meuse loads of about 86 and 92 kTonnes per year (December–August), respectively. These summer chlorophyll concentrations are presently only observed in the western Dutch Wadden Sea in very dry years with a low riverine TN load. Compared with the average TN loads 2010–2017 (150 kTonnes/year (December–August)), we suggest that a further reduction in TN loads with approximately 40% (34%–46%) is required for seagrass recovery in the Ems-Jade Wadden Sea and in the western Dutch region (Table 4). For the Elbe-Weser and Danish region, no long-term data are available that allow a similar analysis as carried out above. For the eastern Dutch region, a significant correlation existed only for the autumn $\text{NH}_4 + \text{NO}_2$, but not for the summer chlorophyll concentration and river nutrient loads (van Beusekom et al., 2019).

5 | DISCUSSION

The earliest records from the 19th and early 20th century provide us with an incomplete but consistent picture of historical seagrass

TABLE 3 Potential seagrass area (km²) and RSA (%) assuming full occupation of the habitat area that is predicted by a habitat suitability model based on geomorphology, shear stress from currents and sediment grain size properties (Folmer et al., 2016), and the same model but additionally based on wave energy and Arenicola densities (only for the western and eastern Dutch region, Folmer, 2019).

Regions	Western Dutch Wadden Sea	Eastern Dutch Wadden Sea	Ems-Jade Wadden Sea	Elbe-Weser Wadden Sea	North Frisian Wadden Sea	Danish Wadden Sea
Habitat suitability (not accounting for waves)	71.9 (4.7%)	149.2 (14.2%)	165.2 (11.3%)	10.4 (0.5%)	122.3 (8.8%)	60.3 (9.6%)
Habitat suitability (accounting for waves)	27.4 (1.8%)	69.6 (6.6%)	n.a.	n.a.	n.a.	n.a.

Note: Eutrophication level was not included in the models.

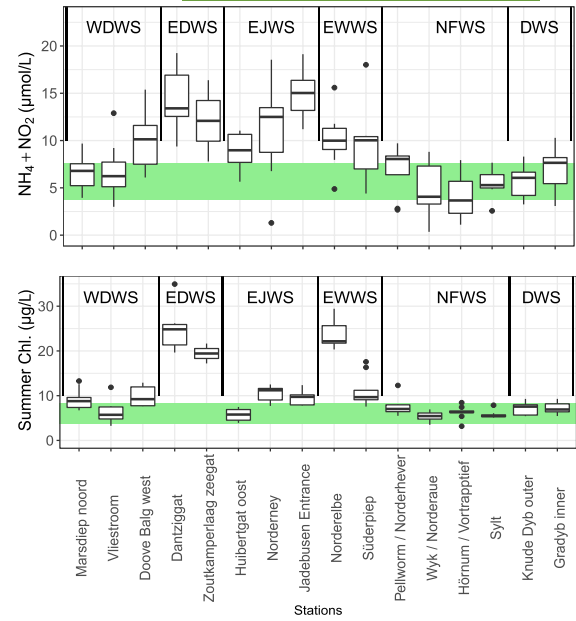


FIGURE 5 Regional difference in the eutrophication indicators summer chlorophyll (top) and autumn NH₄ + NO₂ (bottom) for the years 2008–2016. Summer Chlorophyll is the mean of the monthly means in May–September. Autumn NH₄ + NO₂ is the mean of the monthly means in September–November. DWS, Danish Wadden Sea; EDWS, eastern Dutch Wadden Sea; EJWS, Ems-Jade; EWWS, Elbe-Weser; NFWS, North Frisia; WDWS, western Dutch Wadden Sea. The green bar depicts the eutrophication threshold, that is the range between the minimum and maximum prevailing concentrations when seagrass recovery started to accelerate in the North Frisian region. Zoutkamperlaagzeegat: only 2008 and 2009.

abundance in the Wadden Sea. The long-term dynamics of intertidal seagrass in the Wadden Sea are characterized by a decrease since the 1950s and a minimum during the 1980s–2000s. Full recovery was only observed in the North Frisian region, first signs of (temporary) recovery in the Ems-Jade and Elbe-Weser region. In the latter regions, the seagrass areas increased by a factor 6–8 (after which they declined again). There were no signs of recovery in the western and eastern Dutch regions. For the Danish region there were insufficient data to be able to assess the development of seagrass over the long term but since 2008, the total seagrass area has remained relatively stable.

5.1 | Eutrophication

In the Wadden Sea, seagrass abundance was at its lowest during the peak eutrophication period in the 1980s. After reduction in riverine nutrient loads the seagrass recovered only in North Frisia. There, seagrass presence is closely related to TN loads in the rivers Rhine and Elbe. In the other regions, seagrass has not recovered as the eutrophication levels are still above the identified threshold ranges in North Frisia (Figure 5). While reduced eutrophication levels are necessary for seagrass recovery, there could be other factors

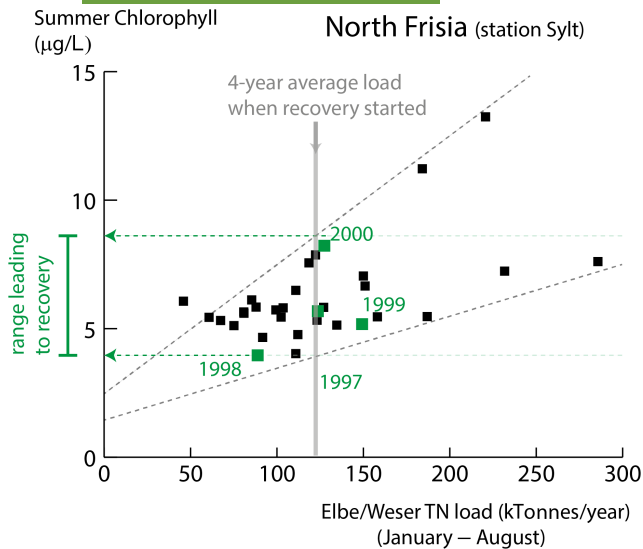


FIGURE 6 Summer chlorophyll concentration as an indicator for eutrophication at the long-term Station Sylt in the North Frisian region is related to the summed total nitrogen (TN) loads by the rivers Weser and Elbe (January–August 1984–2016). From this relationship, the critical summer chlorophyll range required for seagrass recovery (provided other habitat and seed availability requirements are met) is deduced (green vertical range). The grey broken lines envelop most of the data and are interpreted as the expected maximum and minimum values as a function of riverine TN load. The vertical grey line is placed at a TN load of 122 kTonnes/year, being the average of the loads during the years preceding seagrass recovery, that is 1997–2000 (Figure 4). The green points mark the single observations for the years 1997–2000.

preventing it. The lowest eutrophication levels are observed in the North Frisian and Danish region, and the highest levels in the eastern Dutch and the Elbe-Weser regions. Intermediate levels are found in the western Dutch region and in the Jade-Ems region. The difference between the western and eastern Dutch region can be explained by the broader basins in the west in which the imported organic matter is diluted over a larger volume (Schwichtenberg et al., 2017; van Beusekom et al., 2012). It is not immediately clear why the eastern Dutch region has a higher eutrophication level than the Ems-Jade region. We hypothesize that, in addition to the import from the North Sea, import over the tidal divide from west to east is an additional source of organic matter and nutrients contributing to the high eutrophication levels in the eastern Dutch Wadden Sea (Duran-Matute et al., 2014). Between the eastern Dutch and Ems-Jade region, part of this import is likely trapped by the Ems estuary situated between the two areas and acting as a particle and nitrogen sink (e.g. de Jonge et al., 2014; Schulz et al., 2022; van Beusekom & de Jonge, 1998), which may explain the lower eutrophication level in the Ems-Jade regions as compared to the eastern Dutch region.

We estimated that a further reduction in nutrient loads by about 40% (34%–46%) of the present (2010–2018) levels is required for the western Dutch region and the Ems-Jade region for a persistent seagrass recovery. Given this uncertainty, a reasonable management goal should aim at a reduction of at least 1/3 compared with

the levels of 2010–2017. The eutrophication indicators suggest that prevailing conditions already may lead to a recovery, as supported by the temporary recovery to RSA 1.9% in Ems-Jade, and by the recent restoration success from yearly supplementary seeding (mainly *Z. marina*) at one of the restoration sites in the western Dutch Wadden Sea (Griend) to a presence of >1 million plants scattered over an area of 6.5 km² in 2022 (Gräfnings, 2022). Two other sites in this region showed only temporary or no restoration success (Govers et al., 2022; van Duren & van Katwijk, 2015; van Katwijk et al., 2009), showing both the vulnerability and potential of seagrass in these regions. The eutrophication levels in the eastern Dutch and Elbe-Weser regions are far above the eutrophication threshold. Note that seagrass meadows that are located in lower salinity areas (e.g. salinity 22–28, e.g. in the Ems estuary) generally tolerate higher eutrophication levels because of enhanced growth rates (van Katwijk et al., 1999).

5.2 | Why enhanced nutrient loads lead to seagrass decline: Algae and habitat squeezing

Eutrophication negatively affects seagrasses by mechanisms that are largely indirect, via enhanced growth of phytoplankton, epiphytes or macroalgae or a combination of them. Algae shade and smother seagrasses, and their decay in autumn enhances anoxia with sulphide and ammonia toxicity (Burkholder et al., 2007; McGlathery et al., 2007; van Katwijk et al., 1997). Phytoplankton productivity in the Wadden Sea and adjacent North Sea plays a dominant role in the eutrophication process as is explained in Section 2.3. However, direct shading of seagrass by phytoplankton is not likely detrimental because the seagrasses grow in the mid-intertidal, being exposed to daylight about half of the time. Epiphytes negatively affect seagrass and may become dominant at relatively exposed sites; at sheltered sites, they are grazed (Schanz et al., 2002). In the Wadden Sea, several observations point at green macroalgae being a major threat to seagrass in the intertidal zone. The temporal and spatial macroalgae dynamics show similar patterns as the eutrophication indicators: On Sylt in the North Frisian region, a switch between seagrass dominance in the 1930s to green macroalgae dominance in the early 2000s was described by Reise et al. (2008) with mass developments of green macroalgae since 1979 (Reise, 1983). In August 1991, upon monitoring, hydrogen sulphide could even be smelled in the aircraft flying 150 m above the decaying macroalgae mass (Reise & Siebert, 1994). Since the mid-1990s, green macroalgae cover decreased to low levels (e.g. Dolch & Reise, 2021; van Beusekom et al., 2017) and seagrass recovered. Similarly, in the Jade-Ems region, macroalgae cover peaked during the early 1990s and decreased since. But in contrast to the North Frisian region, a high growth potential of green macroalgae is still clear in the Jade-Ems region, with peaks close to 50% of the maximum observed during the 1990s (e.g. van Beusekom et al., 2017). Interestingly, the seagrass recovery period around 2010 in the Ems-Jade region coincided with a transient

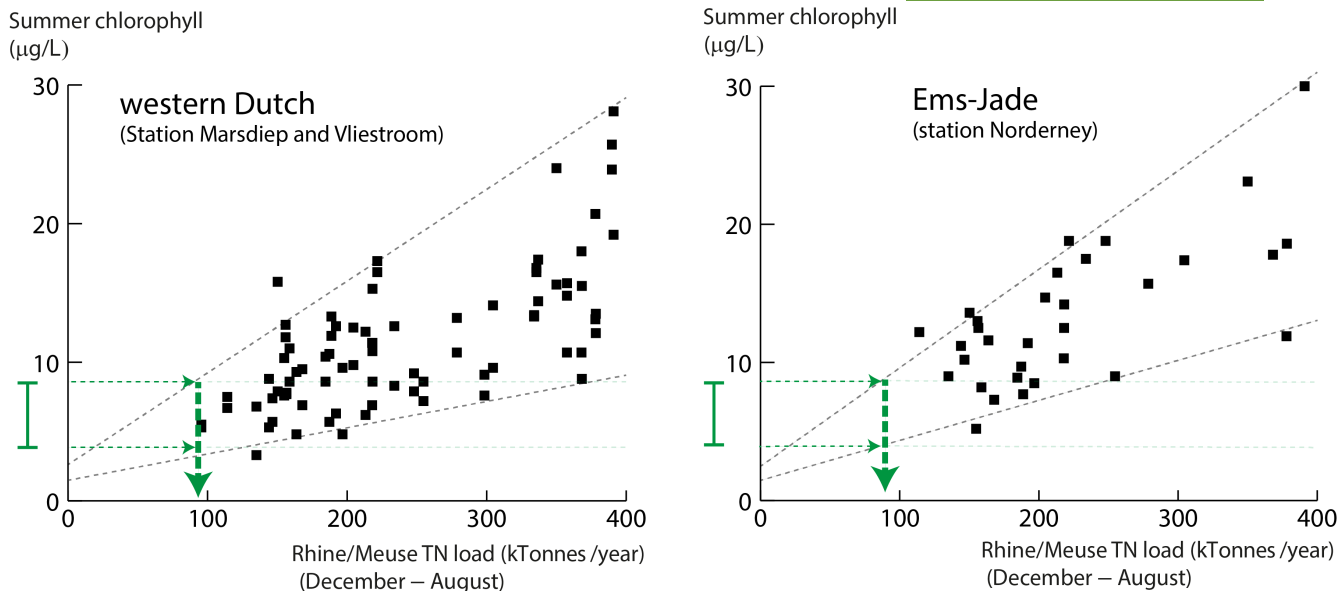


FIGURE 7 Relation between summer chlorophyll levels and TN loads by the rivers Rhine/Meuse from December–August, for the long-term Stations ‘Marsdiep noord’ and ‘Vliestroom’ in the western Dutch region, 1977–2017 (left) and at ‘Norderney’ in the Ems-Jade region, 1985–2016 (right), and the predicted riverine TN loads that lead to seagrass recovery—provided that other habitat and seed availability requirements are met for each region. The grey dotted lines envelop most of the data and can be interpreted as the maximum and minimum values to be expected at a certain riverine nutrient load. The critical summer chlorophyll concentration (vertical green range, its derivation is depicted in Figure 6) is projected on the river TN load of Rhine/Meuse to come to this prediction (green dotted arrows).

TABLE 4 Reduction in total nitrogen (TN) loads of the Rhine/Meuse required for seagrass recovery using 12 scenarios to derive thresholds: 3-, 4- and 5-year averaged TN loads, upper line and the average of the upper and lower lines in Figures 6 and 7, and the year 2000 as start of the acceleration and 2003 as the start of the recovery setting through (detailed outcomes are presented in Appendix S1.6).

Scenario	Western Dutch Wadden Sea stations Mardiep and Vliestroom	Ems-Jade Wadden Sea station Norderney
4-year averaged TN, year 2000, upper line	38%	43%
Minimum of all scenarios	34%	39%
Maximum of all scenarios	43%	46%

minimum in macroalgae cover. Finally, restoration success in the western Dutch region (Balgzand) was high after years with low macroalgal cover (van Katwijk et al., 2009), whereas in years with high macroalgal cover, the majority of the plants wasted away before the seeds were formed (van Katwijk et al., 2010).

When riverine nutrient loads are not sufficiently reduced, the densities of epiphytes and macroalgae will remain high. Whereas epiphytes exert a relatively constant stress during the growing season (Philippart, 1995), macroalgae will drift depending on tidal currents and wind, thus leading to unpredictable disturbances and local extinctions. Particularly, sheltered habitats are prone to the accumulation of macroalgae. Seagrass may then survive better at relatively exposed areas. However, as relatively exposed areas are more vulnerable to storms, this may lead to habitat squeezing: In tranquil years, seagrass may only survive in relatively exposed areas, whereas in stormy years, seagrass may only survive at the more sheltered sites.

5.3 | If nutrients are further reduced, can we expect seagrass recovery in the southern Wadden Sea?

Historical evidence suggests that—even prior to the eutrophication—the potential relative seagrass area in the southern regions is low: maximum 2.4% in the Ems-Jade region and less than 1% in the Elbe-Weser, eastern and western Dutch region. This indicates that seagrass habitat suitability is lower than in the North Frisian region and similar recovery trajectories are not to be expected even if nutrient loadings would be reduced. Per region application of habitat suitability models (Folmer, 2019; Folmer et al., 2016) suggest that hydrodynamics and geomorphology can fully explain low seagrass abundance prior to eutrophication for the Elbe-Weser region, but only partly for the western and eastern Dutch and Ems-Jade region. Maybe the alignment of the barrier islands (East-West) doesn't give as much shelter from westerly wind and wave energy as the high sands and barrier islands in the

northern Wadden Sea do (North–South aligned). The relatively high suitability and historical presence in the sheltered Jade Bay supports the important role of shelter. The central part of the Elbe-Weser region is even hardly protected by barrier islands, and wind-wave dynamics preclude persistent seagrass meadows.

Another part of the low habitat suitability in the southern regions could perhaps be explained by the abundant presence of clay and peat banks in the north, and not in the south acting as seagrass refuges. Clay and peat layers lying below the sandy surface may have enabled a strong anchorage of seagrass roots further stabilizing the local seagrass meadows under adverse conditions like heavy storms (Reise & Kohlus, 2008). It is illustrative that the scarce presence of seagrass in the Dutch Wadden Sea is limited to clay bank relicts from former saltmarshes and a harbour in the western Dutch region and artificial saltmarshes of former reclamation works in the eastern Dutch region. Also, the loss of suitable habitats due to progressive land reclamation over centuries may play a role (Lotze & Reise, 2005; Dolch et al., 2013; see Appendix S1.1). Seagrass recovery could also be constrained by alterations in the biotic community (e.g. Cronau et al., 2023; Sievers et al., 2022). In the Wadden Sea, it was for instance shown that ragworms could limit recruitment from seed (Kwakernaak et al., 2023). Interestingly, the temporal and spatial gradients in eutrophication in the Wadden Sea are reflected in faunal characteristics, which may therefore serve as an indicator for eutrophication, and as a predictor for seagrass recovery (e.g. Gräfnings et al., 2023; Singer et al., 2023).

5.3.1 | Subtidal seagrass

Subtidal seagrass was abundant in the western Wadden Sea prior to the 1930s, but not in other parts of the Wadden Sea. Prospects for recovery of subtidal *Z. marina* may be still low at the present eutrophication level of the western Wadden Sea. The subtidal form of *Z. marina* is perennial and may therefore be even more sensitive to eutrophication than the intertidal annual form of *Z. marina*, as was inferred from system-scale experiments in Lake Grevelingen (van Katwijk & van Tussenbroek, 2023). Large geomorphological changes and altered salinity regime (average higher salinity with more intense low salinity peaks) since the closure of the Zuiderzee limits the suitable area for subtidal seagrass in the western Wadden Sea (van der Heide et al., 2006, 2007).

5.4 | Delay in decline and recovery?

Declines and recoveries of seagrass meadows generally show some delay in response time. In the Wadden Sea, the high seagrass abundance in 1958 may suggest a delayed response to increasing eutrophication, but may also be due to an overestimation of TN loads from the estuaries to the North Sea because of the higher denitrification rates related to the high organic matter loads during this period (Dähnke et al., 2008).

The recovery observed in North Frisia started to accelerate in 2000, but slow recovery already started 10–15 years before. For the other regions this may imply that, upon partial reduction of nutrient

loads—and all other habitat requirements being met—a delayed, slow or only temporary recovery of seagrass, as observed in the Ems-Jade region, may be expected. Several processes could be responsible for delays in recovery. First, when the nutrient levels are reduced but still above the threshold values there may still be large yearly variability in (macro- and micro-) algal abundance or import of organic matter that may impair recovery. A delay may also result from low propagule availability and large-scale seeding may then accelerate the recovery process (Reynolds et al., 2016). Third, it could be argued that a period of eutrophication may lead to delayed nutrient delivery from the sediments. However, van Beusekom et al. (2001, 2009) show minor delay of nitrogen release from organic matter stored in the sediment in the Wadden Sea, and phosphorus concentrations in the Wadden Sea are generally only related to river phosphorus loads during the preceding year, or maximally two preceding years, suggesting that lag-effects (through inorganic adsorption to the sediment) are likely no more than 2 years (van Beusekom et al., 2001).

In addition, positive feedbacks may explain delays in decline and recovery. Several positive feedbacks have been described for *Z. noltei* and *Z. marina*. For example, sediment stabilization and alleviation of bioturbation by seagrass, support seagrass expansion (Eklöf et al., 2015; Philippart, 1994; Reise, 2002; Suykerbuyk, Bouma, et al., 2016; Suykerbuyk, Govers, et al., 2016; van Katwijk & Hermus, 2000). Desiccation in the upper intertidal zones is also partly alleviated by high densities of seagrass canopies retaining water, providing another positive feedback (Fox, 1996). The well-known feedback of seagrass trapping sediments and thereby improving light conditions (van der Heide et al., 2007) is probably not very relevant in the intertidal zones where most seagrass occurs in the Wadden Sea as they are directly exposed to daylight during the low tides. The positive feedback provided by the mutualism of seagrass with lucinid clams alleviating sulphide toxicity does not occur in the Wadden Sea as Lucinids are absent (van der Heide et al., 2012). All aforementioned feedbacks occur at the mm to 100m scale and may explain the delays in decline and recovery. However, they do not explain the new settlements beyond extant meadows which are at the base of the recoveries. Therefore, we propose feedback from propagule spillover as a feedback for seagrass operating at a landscape scale.

5.5 | A positive feedback operating at landscape scale: Propagule spillover

Propagule spillover is high in the Wadden Sea. For example, when seagrasses recovered from an RSA of 2.1% to the present 12%–13% in North Frisia, they were noticed to also cover marginal habitats (Dolch et al., 2013; T. Dolch, personal observations). High levels of propagule spillover are also suggested from the presented omnipresence of seagrass in the Wadden Sea in very low densities, and further supported by the high level of genetic connectivity (Coyer et al., 2004; Ferber et al., 2008; Olsen et al., 2004). Also, the recovery rates observed in North Frisia and temporary in the Ems-Jade region, are orders of magnitude larger than could be expected from clonal expansion rates only, further indicating propagule spillover.

Propagule spillover provides positive feedback at landscape scales that is well-described for metapopulations (rescue effect, Hanski, 1998), but not yet considered in seagrass recovery literature. In seagrass restorations, the importance of propagule spillover and abundance was suggested by (1) the larger environmental range covered by recovering seagrass when propagule abundance was higher (Dolch et al., 2013; Oreska et al., 2021), (2) higher success rates with increasing proximity of the donor populations (van Katwijk et al., 2016) and (3) disproportionately higher success of global restoration trials with increasing numbers of introduced propagules (van Katwijk et al., 2016). Propagule spillover operates at landscape scale (0.01–1000 km) and the suggested high levels may explain the acceleration in recovery observed in North Frisia. Rescue effects from propagule spillover will be particularly important when nutrient reduction is not yet complete and macroalgal blooms may still lead to local extinctions. Therefore, for restoration, occupied and potential seagrass habitat (e.g. assessed by the maximum recorded area in the past) should be an important landscape selection criterion.

Vectors for transport of propagules are water or birds. Dominant winds and the tidal wave run from west to east and from the Elbe onward to the north, making the western tidal basins a net source, and the most north-eastern basins net sinks of propagules. Transport modelling studies, which include wind effects, show that patterns of transport are highly variable over various timescales (Chrastansky & Callies, 2011; Duran-Matute et al., 2014; Erftemeijer et al., 2008). These studies imply that westward transport by water currents is possible but that it is less frequent and takes place over shorter distances than eastward transport. The propagules are usually seeds that are still attached to the seed-bearing shoots that are positive buoyant; single seeds are too heavy to travel far (e.g. Berkovic et al., 2014; Harwell & Orth, 2002). Waterfowl, particularly Brent Geese and Anas species, feed on seagrass and its seeds (Jacobs et al., 1981). The seeds can survive the gut and may contribute to dispersal (Loquès et al., 1988; Sumoski & Orth, 2012); the autumnal transport by waterfowl is usually from north to south (Clausen et al., 2002).

Propagule spillover may provide an important feedback also for other seagrass species. Most seagrass species have both short- and long-range propagule dispersal strategies, and propagules often travel in groups, for example through fruits or seed-bearing shoots (Kendrick et al., 2012; McMahon et al., 2014). The propagule spillover feedback generates (1) locally high densities for density-related feedbacks to operate and (2) frequent and locally spread propagule arrivals to employ the available windows of opportunity (see van Katwijk et al., 2016).

6 | CONCLUSIONS

6.1 | Recommendations for the Wadden Sea

The only areas in the Wadden Sea where seagrass is not threatened by eutrophication are the North Frisian and the Danish regions where present eutrophication levels are below thresholds for seagrass

recovery. In the Ems-Jade and Elbe-Weser region, temporary recovery has been observed, but the eutrophication status is probably still too high to enable sustained recovery. Further reductions in riverine nutrient loads by ~40% (compared with 2010–2018) are needed to enable a permanent seagrass recovery. For comparison, terrestrial nitrogen inputs—to meet EU policy targets regarding terrestrial biodiversity, aquatic ecosystems and drinking water standards—should reduce nitrogen run-off to surface water by 51% and 74% in Germany and The Netherlands, respectively (de Vries et al., 2021). In this context, a reduction of 40% of riverine nutrient loads is well within reductions needed to meet EU environmental policy targets.

6.2 | Seagrass prospects in the Wadden Sea

After a reduction in nutrient loads, seagrass abundance in the southern Wadden Sea will probably not reach higher levels than an RSA of approximately 2.4% in the Ems-Jade region, and in the western Wadden Sea not more than 0.2%. The Elbe-Weser region has a low suitability for seagrass for other reasons, that is no wind-wave protection by barrier islands (except the margins of the region), and in the eastern Dutch Wadden Sea, the nutrient levels are so high that a 40% reduction is not sufficient. The temporary recovery in Ems-Jade as well as recent restoration success at one out of three restoration sites in the western Wadden Sea (Govers et al., 2022; Gräfnings, 2022) show the vulnerability, but also the potential of seagrass in these regions.

6.3 | Landscape scale assessment of nutrient loads

Eutrophication in a half open tidal system is extremely complex (e.g. Ehrnsten et al., 2020; Thompson et al., 2008). Still, region-specific eutrophication indicators and their relation with riverine TN loads allowed us to deduce a tentative critical river TN load for seagrass recovery per region. We could only do this for those regions where the indicators correlated sufficiently tight with river nutrient loads to allow such projection. This may be a technique that can be applied in other (data-dense) landscapes in the land-ocean interface as well.

6.4 | Propagule spillover: A positive feedback at landscape scale

The seagrass dynamics observed in our study indicate high levels of propagule spillover. Propagule spillover provides a positive feedback at metapopulation scale (0.01–1000 km), which may also operate in other seagrass species worldwide. It implies that, when planning seagrass restoration, a site within a landscape with a high density of (potential, or—even better—occupied) habitat should be preferred over an isolated 'suitable' site.

AUTHOR CONTRIBUTIONS

Justus E. E. van Beusekom and Marieke M. van Katwijk conceived the ideas and designed the methodology. Marieke M. van Katwijk, Justus E. E. van Beusekom, Eelke O. Folmer, Kerstin Kolbe, Dick J. de Jong and Tobias Dolch collected and analysed the data. Marieke M. van Katwijk and Justus E. E. van Beuskom lead the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We would like to thank the Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein (LKN) and the Landesamt für Umwelt des Landes Schleswig-Holstein (LfU, former LLUR) for funding the seagrass monitoring in Schleswig-Holstein and for providing aerial photographs. Karsten Reise is greatly acknowledged for years of collecting seagrass data and valuable comments on this manuscript. The two reviewers are thanked for their constructive and helpful comments. We would like to thank Lasse Ørsted Jensen (Ministry of Environment DK, Environmental Protection Agency) for providing us with information about older Danish aerial pictures. Rijkswaterstaat is thanked for a financial contribution to Marieke van Katwijk and Eelke Folmer. Justus van Beusekom acknowledges support from the European Union's HORIZON.2.6—Food, Bioeconomy Natural Resources, Agriculture and Environment programme under grant agreement no. 101060418 (NAPSEA; <https://napsea.eu/>). Lucien Hanssen is thanked for fruitful discussions and feedback. Ketil Koop-Jakobsen is thanked for the Danish translation of the abstract.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data on the habitat suitability model results (Table 3), and data of seagrass long-term dynamics, river discharges, total nitrogen loads and eutrophication indicators (Figures 2, 3, 5, 6 and 7) are available via DANS Data Station Life Sciences <https://doi.org/10.17026/LS/TZYAGQ> (van Katwijk et al., 2024).

ORCID

Marieke M. van Katwijk <https://orcid.org/0000-0002-4482-5835>

Justus E. E. van Beusekom <https://orcid.org/0000-0001-6848-0811>

Eelke O. Folmer <https://orcid.org/0000-0001-7321-1085>

Tobias Dolch <https://orcid.org/0000-0001-6038-6695>

REFERENCES

- Asmus, R. M., & Asmus, H. (1991). Mussel beds: Limiting or promoting phytoplankton? *Journal of Experimental Marine Biology and Ecology*, 148, 215–232.
- Berkovic, B., Cabaço, S., Barrio, J. M., Santos, R., Serrao, E. A., & Alberto, F. (2014). Extending the life history of a clonal aquatic plant: Dispersal potential of sexual and asexual propagules of *Zostera noltii*. *Aquatic Botany*, 113, 123–129.
- Burchard, H., & Bolding, K. (2002). *GETM—A general estuarine transport model. Scientific documentation*. Technical Report EUR 20253EN.
- Burchard, H., Flüser, G., Staneva, J. V., Badewien, T. H., & Riethmüller, R. (2008). Impact of density gradients on net sediment transport into the Wadden Sea. *Journal of Physical Oceanography*, 38, 566–587.
- Burkholder, J. M., Tomasko, D. A., & Touchette, B. W. (2007). Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology*, 350, 46–72.
- Cadée, G. C., & Hegeman, J. (1974). Primary production of phytoplankton in the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, 3, 240–259.
- Cadée, G. C., & Hegeman, J. (2002). Phytoplankton in the Marsdiep at the end of the 20th century; 30 years monitoring biomass, primary production, and *Phaeocystis* blooms. *Journal of Sea Research*, 48, 97–110.
- Chrastansky, A., & Callies, U. (2011). Using a bayesian network to summarize variability in numerical long-term simulations of a meteorological-marine system: Drift climatology of assumed oil spills in the North Sea. *Environmental Modeling & Assessment*, 16, 1–14.
- Clarke, F. W. (1924). *The data of geochemistry, Bulletin 770*. Government Printing Office.
- Clausen, P., Nolet, B. A., Fox, A. D., & Klaassen, M. (2002). Long-distance endozoochorous dispersal of submerged macrophyte seeds by migratory waterbirds in northern Europe—A critical review of possibilities and limitations. *Acta Oecologica-International Journal of Ecology*, 23, 191–203.
- Colijn, F. (1982). Light absorption in the waters of the Ems-Dollard estuary and its consequences for the growth of phytoplankton and microphytobenthos. *Netherlands Journal of Sea Research*, 15, 196–216.
- Compton, T. J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Smith, J., Galama, Y., Brugge, M., van der Wal, D., van der Meer, J., van der Veer, H. W., & Piersma, T. (2013). Distinctly variable mudscapes: Distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *Journal of Sea Research*, 82, 103–116.
- Coyer, J. A., Diekmann, O. E., Serrao, E. A., Procaccini, G., Milchakova, N., Pearson, G. A., Stam, W. T., & Olsen, J. L. (2004). Population genetics of dwarf eelgrass *Zostera noltii* throughout its biogeographic range. *Marine Ecology-Progress Series*, 281, 51–62.
- Cronau, R. J. T., Telgenkamp, Y., de Fouw, J., van Katwijk, M. M., Bouma, T. J., Heusinkveld, J. H. T., Hoeijmakers, D., van der Heide, T., & Lamers, L. P. M. (2023). Seagrass is protected from ragworm pressure by a newly discovered grazer-ragworm interaction; implications for restoration. *Journal of Applied Ecology*, 60, 978–989.
- Dähnke, K., Bahlmann, E., & Emeis, K. (2008). A nitrate sink in estuaries? An assessment by means of stable nitrate isotopes in the Elbe estuary. *Limnology and Oceanography*, 53, 1504–1511.
- de Beer, D., Wenzhofer, F., Ferdelman, T. G., Boehme, S. E., Huettel, M., van Beusekom, J. E. E., Bottcher, M. E., Musat, N., & Dubilier, N. (2005). Transport and mineralization rates in North Sea sandy intertidal sediments, Sylt-Romo Basin, Wadden Sea. *Limnology and Oceanography*, 50, 113–127.
- de Jong, F., Bakker, J. F., Dankers, N., Dahl, W., Jäppelt, W., Madsen, P. B., & Kossmagk-Stephan, K. (1993). *Quality status report of the North Sea, subregion 10, the Wadden Sea*. The Common Wadden Sea Secretariat.
- de Jonge, V. N., & Postma, H. (1974). Phosphorus compounds in the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, 8, 139–153.
- de Jonge, V. N., Schuttelaars, H. M., van Beusekom, J. E. E., Talke, S. A., & de Swart, H. E. (2014). The influence of channel deepening on estuarine turbidity levels and dynamics, as exemplified by the Ems estuary. *Estuarine, Coastal and Shelf Science*, 139, 46–59.
- de los Santos, C. B., Krause-Jensen, D., Alcoverro, T., Marba, N., Duarte, C. M., van Katwijk, M. M., Perez, M., Romero, J., Sanchez-Lizaso, J. L., Roca, G., Jankowska, E., Perez-Llorens, J. L., Fournier, J., Montefalcone, M., Pergent, G., Ruiz, J. M., Cabaco, S., Cook, K.,

- Wilkes, R. J., ... Santos, R. (2019). Recent trend reversal for declining European seagrass meadows. *Nature Communications*, 10, 3356.
- de Vries, W., Schulte-Uebbing, L., Kros, H., Voogd, J. C., & Louwagie, G. (2021). Spatially explicit boundaries for agricultural nitrogen inputs in the European Union to meet air and water quality targets. *Science of the Total Environment*, 786, 147283.
- Dolch, T., Buschbaum, C., & Reise, K. (2013). Persisting intertidal seagrass beds in the northern Wadden Sea since the 1930s. *Journal of Sea Research*, 82, 134–141.
- Dolch, T., Folmer, E. O., Frederiksen, M. S., Herlyn, M., van katwijk, M. M., Kolbe, K., Krause-Jensen, D., Schmedes, P., & Westerbeek, E. P. (2017). Seagrass. In S. Kloepper, M. J. Baptist, A. Bostelmann, J. A. Busch, C. Buschbaum, L. Gutow, G. Janssen, K. Jensen, H. P. Jørgensen, F. de Jong, G. Lüerßen, K. Schwarzer, R. Stempel, & D. Thielges (Eds.), *Wadden sea quality status report 2017*. Common Wadden Sea Secretariat, 24 pp.
- Dolch, T., & Reise, K. (2021). *Vorkommen von Grünalgen und Seegrass im Nationalpark Schleswig-Holsteinisches Wattenmeer*. Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein—Nationalparkverwaltung, Tönning, Alfred Wegener Institute.
- Donker, J. J. A. (2015). *Hydrodynamic processes and the stability of intertidal mussel beds in the Dutch Wadden Sea*. No. 83 in Utrecht Studies in Earth Sciences—Thesis.
- Duran-Matute, M., Gerkema, T., De Boer, G. J., Nauw, J. J., & Grawe, U. (2014). Residual circulation and freshwater transport in the Dutch Wadden Sea: A numerical modelling study. *Ocean Science*, 10, 611–632.
- Ehrsten, E., Sun, X. L., Humborg, C., Norkko, A., Savchuk, O. P., Slomp, C. P., Timmermann, K., & Gustafsson, B. G. (2020). Understanding environmental changes in temperate coastal seas: Linking models of benthic fauna to carbon and nutrient fluxes. *Frontiers in Marine Science*, 7, 450.
- Eisma, D. (1993). *Suspended matter in the aquatic environment*. Springer.
- Eklöf, J. S., Donadi, S., van der Heide, T., van der Zee, E. M., & Eriksson, B. K. (2015). Effects of antagonistic ecosystem engineers on macrofauna communities in a patchy, intertidal mudflat landscape. *Journal of Sea Research*, 97, 56–65.
- Erfteemeijer, P. L. A., van Beek, J. K. L., Ochieng, C. A., Jager, Z., & Los, H. J. (2008). Eelgrass seed dispersal via floating generative shoots in the Dutch Wadden Sea: A model approach. *Marine Ecology-Progress Series*, 358, 115–124.
- Ferber, S., Stam, W. T., & Olsen, J. L. (2008). Genetic diversity and connectivity remain high in eelgrass *Zostera marina* populations in the Wadden Sea, despite major impacts. *Marine Ecology-Progress Series*, 372, 87–96.
- Folmer, E. O. (2019). *Update habitatkaart littoraal zeegrass voor de Nederlandse Waddenzee. Een aanscherping van de trilaterale zeegrass habitatkaart voor de Nederlandse Waddenzee op basis van een analyse van de effecten van golfwerking, sediment en wadpielen op zeegrass*. Ecospace.
- Folmer, E. O., Bijleveld, A. I., Holthuijsen, S., van der Meer, J., Piersma, T., & van der Veer, H. W. (2023). Space-time analyses of sediment composition reveals synchronized dynamics at all intertidal flats in the Dutch Wadden Sea. *Estuarine, Coastal and Shelf Science*, 285, 108308.
- Folmer, E. O., van Beusekom, J. E. E., Dolch, T., Grawe, U., van Katwijk, M. M., Kolbe, K., & Philippart, C. J. M. (2016). Consensus forecasting of intertidal seagrass habitat in the Wadden Sea. *Journal of Applied Ecology*, 53, 1800–1813.
- Fox, A. D. (1996). *Zostera* exploitation by Brent geese and wigeon on the Exe Estuary, southern England. *Bird Study*, 43, 257–268.
- Giesen, W. B. J. T., van Katwijk, M. M., & den Hartog, C. (1990). Temperature, salinity, insolation and wasting disease of eelgrass (*Zostera marina* L.) in the Dutch Wadden Sea in the 1930's. *Netherlands Journal of Sea Research*, 25, 395–404.
- Govers, L. L., Heusinkveld, J. H. T., Gräfnings, M. L. E., Smeele, Q., & van der Heide, T. (2022). Adaptive intertidal seed-based seagrass restoration in the Dutch Wadden Sea. *PLoS One*, 17(2), 1–17.
- Gräfnings, M. L. E. (2022). *Seed to meadow—Developing intertidal seagrass restoration*. Thesis, University of Groningen, The Netherlands.
- Gräfnings, M. L. E., Govers, L. L., Heusinkveld, J. H. T., Silliman, B. R., Smeele, Q., Valdez, S. R., & van der Heide, T. (2023). Macrozoobenthos as an indicator of habitat suitability for intertidal seagrass. *Ecological Indicators*, 147, 109948.
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396, 41–49.
- Harwell, M. C., & Orth, R. J. (2002). Long-distance dispersal potential in a marine macrophyte. *Ecology*, 83(12), 3319–3330.
- Hayes, M. O. (1975). Morphology and sand accumulations in estuaries. In L. E. Cronin (Ed.), *Estuarine research 2: Geology and engineering* (pp. 3–22). Academic Press.
- Hofmeister, R., Floser, G., & Schartau, M. (2017). Estuary-type circulation as a factor sustaining horizontal nutrient gradients in freshwater-influenced coastal systems. *Geo-Marine Letters*, 37, 179–192.
- Hulot, V., Saulnier, D., Lafabrie, C., & Gaertner-Mazouni, N. (2020). Shellfish culture: A complex driver of planktonic communities. *Reviews in Aquaculture*, 12, 33–46.
- Jacobs, R. P. W. M., den Hartog, C., Braster, B. F., & Carriere, F. C. (1981). Grazing of the seagrass *Zostera noltii* by birds at Terschelling (Dutch Wadden Sea). *Aquatic Botany*, 10, 241–259.
- Kendrick, G. A., Waycott, M., Carruthers, T. J. B., Cambridge, M. L., Hovey, R., Krauss, S. L., Lavery, P. S., Les, D. H., Lowe, R. J., Vidal, O. M. I., Ooi, J. L. S., Orth, R. J., Rivers, D. O., Ruiz-Montoya, L., Sinclair, E. A., Statton, J., van Dijk, J. K., & Verduin, J. J. (2012). The central role of dispersal in the maintenance and persistence of seagrass populations. *BioScience*, 62, 56–65.
- KÜFOG GmbH, K., Steuer, J., & Köritz, M. (2020). *Eulitorale Seegrassbestände im niedersächsischen Wattenmeer 2019*. Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN).
- Kwakernaak, C., Hoesjmakers, D. J. J., Zwartz, M. P. A., Bijleveld, A. I., Holthuijsen, S., de Jong, D. J., & Govers, L. L. (2023). Ragworms (*Hediste diversicolor*) limit eelgrass (*Zostera marina*) seedling settlement: Implications for seed-based restoration. *Journal of Experimental Marine Biology and Ecology*, 560, 151853.
- Lamb, J. B., van de Water, J., Bourne, D. G., Altier, C., Hein, M. Y., Fiorenza, E. A., Abu, N., Jompa, J., & Harvell, C. D. (2017). Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. *Science*, 355, 731–733.
- Lefcheck, J. S., Orth, R. J., Dennison, W. C., Wilcox, D. J., Murphy, R. R., Keisman, J., Gurbisz, C., Hannam, M., Landry, J. B., Moore, K. A., Patrick, C. J., Testa, J., Weller, D. E., & Batiuk, R. A. (2018). Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 3658–3662.
- Linke, O. (1939). Die Biota des Jadebusenwattes. *Helgoland Marine Research*, 1, 201–348.
- Loebl, M., Colijn, F., & van Beusekom, J. E. E. (2008). Increasing nitrogen limitation during summer in the List Tidal Basin (Northern Wadden Sea). *Helgoland Marine Research*, 62, 59–65.
- Loebl, M., Dolch, T., & van Beusekom, J. E. E. (2007). Annual dynamics of pelagic primary production and respiration in a shallow coastal basin. *Journal of Sea Research*, 58, 269–282.
- Loebl, M., & Van Beusekom, J. E. E. (2008). Seasonality of microzooplankton grazing in the northern Wadden Sea. *Journal of Sea Research*, 59, 203–216.
- Loquès, F., Caye, G., & Meinesz, A. (1988). Flowering and fruiting of *Zostera noltii* in Golfe-Juan (French Mediterranean). *Aquatic Botany*, 32, 341–352.
- Lotze, H. K., & Reise, K. (2005). Ecological history of the Wadden Sea. *Helgoland Marine Research*, 59, 1.

- Maerz, J., Hofmeister, R., van der Lee, E. M., Grawe, U., Riethmuller, R., & Wirtz, K. W. (2016). Maximum sinking velocities of suspended particulate matter in a coastal transition zone. *Biogeosciences*, 13, 4863–4876.
- McCrackin, M. L., Jones, H. P., Jones, P. C., & Moreno-Mateos, D. (2017). Recovery of lakes and coastal marine ecosystems from eutrophication: A global meta-analysis. *Limnology and Oceanography*, 62, 507–518.
- McGlathery, K. J., Sundback, K., & Anderson, I. C. (2007). Eutrophication in shallow coastal bays and lagoons: The role of plants in the coastal filter. *Marine Ecology-Progress Series*, 348, 1–18.
- McMahon, K., van Dijk, K. J., Ruiz-Montoya, L., Kendrick, G. A., Krauss, S. L., Waycott, M., Verduin, J., Lowe, R., Statton, J., Brown, E., & Duarte, C. (2014). The movement ecology of seagrasses. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140878.
- Michaelis, H., Ohba, T., & Tüxen, R. (1971). Die *Zostera*-Gesellschaften der Niedersaechsischen Watten. *Jahresbericht Forschungsstelle für Insel- und Küstenschutz, 1969(21)*, 87–100.
- Neumann, A., Hass, H. C., Mobius, J., & Naderipour, C. (2019). Ballasted flocc capture pelagic primary production and alter the local sediment characteristics in the coastal German Bight (North Sea). *Geosciences*, 9, 344.
- Nordlund, L. M., Koch, E. W., Barbier, E. B., & Creed, J. C. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS One*, 11, e0163091.
- Olsen, J. L., Stam, W. T., Coyer, J. A., Reusch, T. B. H., Billingham, M., Bostrom, C., Calvert, E., Christie, H., Granger, S., La Lumiere, R., Milchakova, N., Oudot-Le-Secq, M. P., Procaccini, G., Sanjabi, B., Serrao, E., Veldsink, J., Widdicombe, S., & Wyllie, E. S. (2004). North Atlantic phylogeography and large-scale population differentiation of the seagrass *Zostera marina* L. *Molecular Ecology*, 13, 1923–1941.
- Oost, A. P., & de Boer, P. L. (1994). Sedimentology and development of barrier islands, ebb-tidal deltas, inlets and backbarrier areas of the Dutch Wadden Sea. *Senckenbergiana Maritima*, 24, 65–115.
- Oreska, M. P. J., McGlathery, K. J., Wiberg, P. L., Orth, R. J., & Wilcox, D. J. (2021). Defining the *Zostera marina* (eelgrass) niche from long-term success of restored and naturally colonized meadows: Implications for seagrass restoration. *Estuaries and Coasts*, 44, 396–411.
- Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., & Williams, S. L. (2006). A global crisis for seagrass ecosystems. *BioScience*, 56, 987–996.
- Oudemans, C. A. J. A., Conrad, J. F. W., Maats, P., & Bouricius, L. J. (1870). Verslag der Staatscommissie inzake de wiermaayerij. *Verslag aan den Koning over de Openbare Werken in het Jaar 1869* (pp. 1–231). Van Weelden en Mingelen.
- Pätsch, J., & Lenhart, H. J. (2022). *Daily loads of nutrients, total alkalinity, dissolved inorganic carbon and dissolved organic carbon of the European continental rivers for the years 1977–2019*. University of Hamburg. <https://wiki.cen.uni-hamburg.de/ifm/COHAM/DATA>
- Philippart, C. J. M. (1994). Interactions between *Arenicola marina* and *Zostera noltii* on a tidal flat in the Wadden Sea. *Marine Ecology-Progress Series*, 111, 251–257.
- Philippart, C. J. M. (1995). Seasonal variation in growth and biomass of an intertidal *Zostera noltii* stand in the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, 33, 205–218.
- Philippart, C. J. M., & Dijkema, K. S. (1995). Wax and wane of *Zostera noltii* Hornem in the Dutch Wadden Sea. *Aquatic Botany*, 49, 255–268.
- Polderman, P. J. G., & den Hartog, C. (1975). De zeegrassen in de Waddenzee. *Wetenschappelijke Mededelingen Koninklijke Nederlandse Natuurhistorische Vereniging*, 107, 1–32.
- Postma, H. (1981). Exchange of materials between the North-Sea and the Wadden Sea. *Marine Geology*, 40, 199–213.
- Postma, H. (1984). Introduction to the symposium on organic matter in the Wadden Sea. *Netherlands Institute for Sea Research Publication Series*, 10, 15–22.
- Postma, H., & van Bennekom, A. J. (1974). Budget aspects of biologically important chemical compounds in the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, 8, 312–318.
- Reigersman, C. J. A., Houben, G. F. H., & Havinga, B. (1939). *Rapport omtrent den invloed van de wierziekte op den achteruitgang van de wierbedrijven, met Bijlagen*. Provinciale Waterstaat in Noord-Holland.
- Reise, K. (1983). Sewage, green algal mats anchored by lugworms, and the effects on Turbellaria and small polychaeta. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, 36, 151–162.
- Reise, K. (1994). Changing life under the tides of the Wadden Sea during the 20th century. *Ophelia*, 6, 117–125.
- Reise, K. (2002). Sediment mediated species interactions in coastal waters. *Journal of Sea Research*, 48, 127–141.
- Reise, K., Herre, E., & Sturm, M. (2008). Mudflat biota since the 1930s: Change beyond return? *Helgoland Marine Research*, 62, 13–22.
- Reise, K., & Kohlus, J. (2008). Seagrass recovery in the Northern Wadden Sea? *Helgoland Marine Research*, 62, 77–84.
- Reise, K., & Siebert, I. (1994). Mass occurrence of green algae in the German Wadden Sea. *Deutsche Hydrographische Zeitschrift*, 1, 171–180.
- Reise, K., van Katwijk, M. M., de Jong, D. J., Schanz, A., & Jager, Z. (2005). Seagrass. In H. Marencic (Ed.), *Wadden Sea quality status report 2005* (pp. 91–98). Common Wadden Sea Secretariat.
- Reynolds, L. K., Waycott, M., McGlathery, K. J., & Orth, R. J. (2016). Ecosystem services returned through seagrass restoration. *Restoration Ecology*, 24, 583–588.
- Riemann, B., Carstensen, J., Dahl, K., Fossing, H., Hansen, J. W., Jakobsen, H. H., Josefson, A. B., Krause-Jensen, D., Markager, S., Staehr, P. A., Timmermann, K., Windolf, J., & Andersen, J. H. (2016). Recovery of Danish coastal ecosystems after reductions in nutrient loading: A holistic ecosystem approach. *Estuaries and Coasts*, 39, 82–97.
- Schanz, A., Polte, P., & Asmus, H. (2002). Cascading effects of hydrodynamics on an epiphyte-grazer system in intertidal seagrass beds of the Wadden Sea. *Marine Biology*, 141, 287–297.
- Schulz, G., Sanders, T., van Beusekom, J. E. E., Voynova, Y. G., Schol, A., & Dahnke, K. (2022). Suspended particulate matter drives the spatial segregation of nitrogen turnover along the hyper-turbid Ems estuary. *Biogeosciences*, 19, 2007–2024.
- Schwichtenberg, F., Callies, U., & van Beusekom, J. E. E. (2017). Residence times in shallow waters help explain regional differences in Wadden Sea eutrophication. *Geo-Marine Letters*, 37, 171–177.
- Sherwood, E. T., Greening, H. S., Johansson, J. O. R., Kaufman, K., & Raulerson, G. E. (2017). Tampa Bay (Florida, USA). Documenting seagrass recovery since the 1980's and reviewing the benefits. *Southeastern Geographer*, 57, 294–319.
- Sievers, M., Brown, C. J., Buelow, C. A., Hale, R., Ostrowski, A., Saunders, M. I., Silliman, B. R., Swearer, S. E., Turschwell, M. P., Valdez, S. R., & Connolly, R. (2022). Greater consideration of animals will enhance coastal restoration outcomes. *BioScience*, 72, 1088–1098.
- Singer, A., Bijleveld, A. I., Hahner, F., Holthuisen, S. J., Hubert, K., Kerimoglu, O., Schaars, L. K., Kröncke, I., Lettmann, K. A., Rittweg, T., Scheiffarth, G., van der Veer, H. W., & Wurpts, A. (2023). Long-term response of coastal macrofauna communities to de-eutrophication and sea level rise mediated habitat changes (1980s versus 2018). *Frontiers in Marine Science*, 9, 2022.963325.
- Sumoski, S. E., & Orth, R. J. (2012). Biotic dispersal in eelgrass *Zostera marina*. *Marine Ecology Progress Series*, 471, 1–10.
- Suykerbuyk, W., Bouma, T. J., Govers, L. L., Giesen, K., de Jong, D. J., Herman, P., Hendriks, J., & van Katwijk, M. M. (2016). Surviving in changing seascapes: Sediment dynamics as bottleneck for long-term seagrass presence. *Ecosystems*, 19, 296–310.

- Suykerbuyk, W., Govers, L. L., Bouma, T. J., Giesen, W., de Jong, D. J., van de Voort, R., Giesen, K., Giesen, P. T., & van Katwijk, M. M. (2016). Unpredictability in seagrass restoration: Analysing the role of positive feedback and environmental stress on *Zostera noltii* transplants. *Journal of Applied Ecology*, 53, 774–784.
- Thompson, J. K., Koseff, J. R., Monismith, S. G., & Lucas, L. V. (2008). Shallow water processes govern system-wide phytoplankton bloom dynamics: A field study. *Journal of Marine Systems*, 74, 153–166.
- Unsworth, R. K. F., Nordlund, L. M., & Cullen-Unsworth, L. C. (2019). Seagrass meadows support global fisheries production. *Conservation Letters*, 12, e12566.
- van Bennekom, A. J., & Wetsteijn, F. J. (1990). The winter distribution of nutrients in the southern bight of the North Sea (1961–1978) and in the estuaries of the Scheldt and the Rhine Meuse. *Netherlands Journal of Sea Research*, 25, 75–87.
- van Beusekom, J. E. E. (2005). A historic perspective on Wadden Sea eutrophication. *Helgoland Marine Research*, 59, 45–54.
- van Beusekom, J. E. E., Bot, P., Carstensen, J., Grage, A., Kolbe, K., Lenhart, H. J., Pätsch, J., Petenati, T., & Rick, J. (2017). Eutrophication. In S. Kloepper, M. J. Baptist, A. Bostelmann, J. A. Busch, C. Buschbaum, L. Gutow, G. Janssen, K. Jensen, H. P. Jørgensen, F. de Jong, G. Lüerßen, K. Schwarzer, R. Stempel, & D. Thielges (Eds.), *Wadden Sea quality status report*. Common Wadden Sea Secretariat, 20 pp.
- van Beusekom, J. E. E., Brockmann, U. H., Hesse, K. J., Hickel, W., Poremba, K., & Tillman, U. (1999). The importance of sediments in the transformation and turnover of nutrients and organic matter in the Wadden Sea and German Bight. *German Journal of Hydrography*, 51, 245–266.
- van Beusekom, J. E. E., Buschbaum, C., Loebel, M., Martens, P., & Reise, K. (2010). Long-term ecological change in the northern Wadden Sea. In F. Muller, C. Baessler, H. Schubert, & S. Klotz (Eds.), *Long-term ecological research: Between theory and application* (pp. 145–153). Springer.
- van Beusekom, J. E. E., Buschbaum, C., & Reise, K. (2012). Wadden Sea tidal basins and the mediating role of the North Sea in ecological processes: Scaling up of management? *Ocean and Coastal Management*, 68, 69–78.
- van Beusekom, J. E. E., Carstensen, J., Dolch, T., Grage, A., Hofmeister, R., Lenhart, H., Kerimoglu, O., Kolbe, K., Patsch, J., Rick, J., Ronn, L., & Ruiter, H. (2019). Wadden Sea eutrophication: Long-term trends and regional differences. *Frontiers in Marine Science*, 6, 370.
- van Beusekom, J. E. E., & de Jonge, V. N. (1998). Retention of phosphorus and nitrogen in the Ems estuary. *Estuaries*, 21, 527–539.
- van Beusekom, J. E. E., & de Jonge, V. N. (2002). Long-term changes in Wadden Sea nutrient cycles: Importance of organic matter import from the North Sea. *Hydrobiologia*, 475, 185–194.
- van Beusekom, J. E. E., Fock, H., de Jong, F., Diel-Christiansen, S., & Christiansen, B. (2001). *Wadden Sea specific eutrophication criteria*. Wadden Sea ecosystem no. 14. Common Wadden Sea Secretariat, Wilhelmshafen.
- van Beusekom, J. E. E., Loebel, M., & Martens, P. (2009). Distant riverine nutrient supply and local temperature drive the long-term phytoplankton development in a temperate coastal basin. *Journal of Sea Research*, 61, 26–33.
- van den Hoek, C., Admiraal, W., Colijn, F., & de Jonge, V. N. (1979). The role of algae and seagrasses in the ecosystem of the Wadden Sea, a review. In W. J. Wolff (Ed.), *Flora and vegetation of the Wadden Sea* (pp. 9–118). Wadden Sea Working Group, Report 3.
- van der Heide, T., Govers, L. L., de Fouw, J., Olff, H., van der Geest, M., van Katwijk, M. M., Piersma, T., van de Koppel, J., Silliman, B. R., Smolders, A. J. P., & van Gils, J. A. (2012). A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science*, 336, 1432–1434.
- van der Heide, T., van Katwijk, M. M., & Geerling, G. W. (2006). *Een verkenning van de groeimogelijkheden van ondergedoken Groot zee gras (Zostera marina) in de Nederlandse Waddenzee*. Radboud University.
- van der Heide, T., van Nes, E. H., Geerling, G. W., Smolders, A. J. P., Bouma, T. J., & van Katwijk, M. M. (2007). Positive feedbacks in seagrass ecosystems: Implications for success in conservation and restoration. *Ecosystems*, 10, 1311–1322.
- van Duren, L. A., & van Katwijk, M. M. (2015). *Herstelmaatregel Groot zee gras in de Nederlandse Waddenzee*. Report 1203892-000. Deltares, Ecoscience.
- van Goor, A. C. J. (1919). Het zee gras (*Zostera marina* L.) en zijn beteekenis voor het leven der visschen. *Rapporten en verhandelingen van het Rijksinstituut Visserij-onderzoek*, 1(4), 415–498.
- van Katwijk, M. M., Bos, A. R., de Jonge, V. N., Hanssen, L. S. A. M., Hermus, D. C. R., & de Jong, D. J. (2009). Guidelines for seagrass restoration: Importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. *Marine Pollution Bulletin*, 58, 179–188.
- van Katwijk, M. M., Bos, A. R., Kennis, P., & de Vries, R. (2010). Vulnerability to eutrophication of a semi-annual life history: A lesson learnt from an extinct eelgrass (*Zostera marina*) population. *Biological Conservation*, 143, 248–254.
- van Katwijk, M. M., Geerling, G. W., Rasín, R., van 't Veer, R., Bos, A. R., Hermus, D. C. R., van Wieringen, M., Jager, Z., Groeneweg, A. H., Erfteimeijer, P. L. A., van der Heide, T., & de Jong, D. J. (2006). Macrophytes in the western Wadden Sea: Monitoring, invasion, transplantations, dynamics and European policy. In K. Laursen & H. Marencic (Eds.), *Monitoring and assessment in the Wadden Sea. Proceedings from the 11. Scientific Wadden Sea symposium* (pp. 89–98). National Environmental Research Institute.
- van Katwijk, M. M., & Hermus, D. C. R. (2000). Effects of water dynamics on *Zostera marina*: Transplantation experiments in the intertidal Dutch Wadden Sea. *Marine Ecology-Progress Series*, 208, 107–118.
- van Katwijk, M. M., Hermus, D. C. R., de Jong, D. J., Asmus, R. M., & de Jonge, V. N. (2000). Habitat suitability of the Wadden Sea for restoration of *Zostera marina* beds. *Helgoland Marine Research*, 54, 117–128.
- van Katwijk, M. M., Schmitz, G. H. W., Gasseling, A. M., & van Avesaath, P. H. (1999). The effects of salinity and nutrient load and their interaction on *Zostera marina* L. *Marine Ecology-Progress Series*, 190, 155–165.
- van Katwijk, M. M., Thorhaug, A., Marba, N., Orth, R. J., Duarte, C. M., Kendrick, G. A., Althuisen, I. H. J., Balestri, E., Bernard, G., Cambridge, M. L., Cunha, A., Durance, C., Giesen, W., Han, Q. Y., Hosokawa, S., Kiswara, W., Komatsu, T., Lardicci, C., Lee, K. S., ... Verduin, J. J. (2016). Global analysis of seagrass restoration: The importance of large-scale planting. *Journal of Applied Ecology*, 53, 567–578.
- van Katwijk, M. M., van Beusekom, J. E. E., Folmer, E. O., & Dolch, T. (2024). Data with: Seagrass recovery trajectories and recovery potential in relation to nutrient reduction. *DANS Data Station Life Sciences*, <https://doi.org/10.17026/LS/TZYAGQ>
- van Katwijk, M. M., & van Tussenbroek, B. I. (2023). Facultative annual life cycles in seagrasses. *Plants-Basel*, 12, 102002.
- van Katwijk, M. M., Vergeer, L. H. T., Schmitz, G. H. W., & Roelofs, J. G. M. (1997). Ammonium toxicity in eelgrass *Zostera marina*. *Marine Ecology-Progress Series*, 157, 159–173.
- van Straaten, L. M. J. U., & Kuenen, P. H. (1958). Tidal action as a cause of clay accumulation. *Journal of Sedimentary Petrology*, 28, 406–413.
- Verwey, J. (1952). On the ecology and distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation and the source of their food supply. *Archives Néerlandaises de Zoologie*, 10, 172–239.
- Visser, M., de Ruijter, W. P. M., & Postma, L. (1991). The distribution of suspended matter in the Dutch coastal zone. *Netherlands Journal of Sea Research*, 27, 127–143.
- Wiersma, A., Oost, A. P., van der Berg, M., Vos, P., Marges, V., & de Vries, S. (2009). Geomorphology. In H. Marencic & J. de Vlas (Eds.), *Thematic Report 9* (pp. 1–22). Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group.

Wohlenberg, E. (1937). Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. *Helgoland Marine Research*, 1, 1–92.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Historic maps of subtidal and intertidal seagrass distributions.

Appendix S2: Monitoring since 1990s: Methods.

Appendix S3: Seagrass meadows in The Netherlands: Low and high cover meadows of *Zostera noltei* and *Z. marina* between 1972 and 2000.

Appendix S4: Calculation of Historic nutrient loads of Rhine and Elbe.

Appendix S5: Seagrass restoration activities (Dutch Wadden Sea).

Appendix S6: Eutrophication thresholds for recovery.

How to cite this article: van Katwijk, M. M., van Beusekom, J. E. E., Folmer, E. O., Kolbe, K., de Jong, D. J., & Dolch, T. (2024). Seagrass recovery trajectories and recovery potential in relation to nutrient reduction. *Journal of Applied Ecology*, 61, 1784–1804. <https://doi.org/10.1111/1365-2664.14704>