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ORIGINAL PAPER

Climate and de-eutrophication affect abundance of benthos-feeding waterbirds in the Wadden Sea during stop-over

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Abstract
Habitat quality such as food availability and physical structures impacts the abundance of bird species. During 1987–2019, we studied long-term changes in the quality of the habitat of 13 waterbird species in the Wadden Sea, an important stop-over site on the East Atlantic Flyway between arctic breeding areas and wintering grounds in Western Europe and Africa. Monitoring of waterbirds revealed that several species increased or remained stable in the northern and southern sections of the Wadden Sea, while their abundance mainly decreased in more central areas. The Wadden Sea is influenced by freshwater discharge from rivers draining a large part of central Europe, by geomorphological dynamics driven by the tidal cycle and by sea level rise and climate. We hypothesized that the abundance of waterbirds that are dependent on intertidal flats for feeding is influenced by (a) regime shifts in the southern North Sea, (b) climate affecting riverine discharge (the amount of nutrients) from rivers in the Wadden Sea area, (c) climate affecting breeding conditions at arctic and boreal breeding grounds, (d) changes in geomorphology, (e) sea level rise and (f) biomass of macrozoobenthos. The results reveal that the abundance of staging waterbirds in the Wadden Sea is affected by (i) regime shifts and the North Atlantic Oscillation index (NAO), (ii) annual discharge of nutrients (total N and total P have both positive and negative effects) and (iii) biomass of macrozoobenthos. Accretion or erosion of intertidal flats and sea level rise caused local displacements of waterbirds. In a broader context, we found that waterbirds in the Wadden Sea are influenced by a complex array of variables including de-eutrophication due to improved wastewater treatment and a reduced use of fertilizer in central Europe, regime shifts in the southern North Sea including the Wadden Sea (partly driven by the Gulf Stream) and changes in climate conditions, which may affect the breeding conditions of waterbirds in Northern Europe as well as precipitation in Central Europe.

Keywords Climate change · East Atlantic flyway · Nutrients · Geomorphology · Population changes · Sea level rise

Introduction

Waterbirds in the Wadden Sea have been monitored regularly since 1987, and the results show that the species using the intertidal flats for feeding have mostly been generally declining (Kleefstra et al. 2022). In addition, changes in bird numbers differed between the sections of the Wadden Sea, with most species stable or increasing in the northern and southern areas while decreasing in numbers in the central part (Ens et al. 2009; Van Roomen et al. 2012).

Habitat quality determines the abundance of birds and their fitness (Goss-Custard 1996; Gunnarsson et al. 2005; Ma et al. 2010). With regard to waterbirds in the non-breeding season, the amount of food and availability of suitable feeding areas at stop-over sites are among the most important factors for increasing fitness (Madsen 1998; Stillman et al. 2005; Fox and Kahlert 2000). Accessibility of food determines body condition, reproduction and survival and hence is fundamentally important in the life cycle of waterbirds (Stephens et al. 2007; Rakhimberdiev et al. 2018). However, food is a limiting factor in most habitats (Newton 1994), and its abundance is often dependent on growing conditions that are affected partly by nutrients, substrate and climate

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(Karlson et al. 2002; Philippart et al. 2017; Moreno and Møller 2011; Van Beusekom et al. 2019; Singer et al. 2023). In the marine environment, nutrients such as nitrogen and phosphorus stimulate the growth of phytoplankton, zooplankton, macrozoobenthos, fish and birds (Nielsen and Richardson 1996; Nixon and Buckley 2002; Rintala et al. 2022). The amount of riverine nutrients in the marine environments increased in Western Europe during the 1960 s and 1970 s, but massive efforts to purify huge amounts of wastewater from cities and regulate the use of fertilizer by farmers reduced nutrient loads discharged into the marine environment after the 1980 s (Riemann et al. 2016). Effects of the decreasing nutrient loads on coastal ecosystems, such as lower amounts of phytoplankton, zooplankton and birds, were reported (Møller et al. 2015; Riemann et al. 2016; Philippart et al. 2017), although these effects are debated (Drent et al. 2017). In the Wadden Sea, riverine nutrients influence biological activity in several tidal basins eastwards and northwards of the river estuaries due to the prevailing coastal stream in the North Sea moving from south to north along the Wadden Sea islands (Van Beusekom et al. 2019).

Climate and regime shifts affect sediments, macrozoobenthos and bird populations. Geomorphology is driven by wind, water current and tidal amplitude (Reineck 1983). Climate phenomena such as the North Atlantic Oscillation Index (NAO) affect bird species across their life cycle from timing of migration, physiological conditions and survival (Jenouvrier 2013; Rakhimberdiev et al. 2018; Dunn and Møller 2019; Illes and Jenouvrier 2019). Furthermore, the NAO index may affect reproduction in waders (Meltofte et al. 2007; Petersen et al. 2023). Regime shifts can be connected with the Gulf Stream and are defined as sudden changes in temperature and/or physical conditions that influence several trophic levels and their interactions (Moreno and Møller 2011; Philippart et al. 2017). In the southern North Sea and in the Wadden Sea, regime shifts have occurred a couple of times since the late 1970 s (Weijerman et al. 2005; Dippner et al. 2012; Kröncke et al. 2013). To analyse changes in waterbird numbers, we used indirect information of habitat quality, such as amount of nutrients, geomorphology and climate, which have effects on the amount of food, feeding conditions and reproduction of birds.

We hypothesized for the Wadden Sea that the changes in abundance of waterbirds depending on intertidal flats for feeding were influenced by changes in external and internal factors. The external factors considered included (a) regime shifts in the southern North Sea; (b) climate conditions such as NAO affecting riverine discharge to the Wadden Sea and (c) climate conditions affecting reproduction of waterbirds at northern European breeding grounds; and (d) nutrient enrichment of rivers due to agriculture and wastewater. Internal factors considered were changes in (e) geomorphology (accretion or erosion of intertidal flats), (f) sea level rise and (g) biomass of macrozoobenthos. From these hypotheses, we expected (a) that regime shifts would cause both positive and negative changes in waterbird numbers; (b) that increases in precipitation (high NAO values) would increase river discharge to the Wadden Sea due to increases in precipitation in Central Europe; (c) that increases in NAO values (e.g. mild winters and large amounts of precipitation) would improve breeding conditions of waterbirds at the northern breeding grounds due to increases in breeding conditions after mild winters with subsequently more birds staging in the Wadden Sea during autumn and winter; (d) that decreasing amounts of riverine nutrients, nitrogen and phosphorus would have negative effects on the abundance of waterbirds in the Wadden Sea due to lower biomass production; (e) that changes in geomorphology would affect waterbird numbers both positively and negatively; (f) that sea level rise would have negative effects on the abundance of waterbirds; and (g) increasing benthic biomass would have positive effects on waterbird numbers. We tested these hypotheses by use of coordinated, synchronous counts of 13 migratory waterbird species during 1987–2019 in 38 tidal basins in the Wadden Sea.

Materials and methods

Waterbird numbers

Since 1987, staging waterbird populations in the Wadden Sea have been monitored on a regular and systematic basis under the Trilateral Monitoring and Assessment program (Van Roomen et al. 2012; Kleefstra et al. 2022). In the current work, we focused on 13 common and widespread waterbird species that use the intertidal flats for feeding: common shelduck *Tadorna tadorna* (hereafter shelduck), Eurasian oystercatcher *Haematopus ostralegus* (hereafter, oystercatcher), pied avocet *Recurvirostra avosetta* (hereafter, avocet), great ringed plover *Charadrius hiaticula* (hereafter, ringed plover), grey plover *Pluvialis squatarola*, red knot *Calidris canutus* (hereafter, knot), Dunlin *Calidris alpina*, bar-tailed godwit *Limosa lapponica*, Eurasian curlew *Numenius arquata* (hereafter, curlew), common redshank *Tringa totanus* (hereafter, redshank), common greenshank *Tringa nebularia* (hereafter, greenshank), common black-headed gull *Chroicocephalus ridibundus* (hereafter, black-headed gull) and common gull *Larus canus*. For these species, data were extracted from the Joint Monitoring of Migratory Bird Database for 38 tidal basins in the Wadden Sea for the period 1987–2019 (Fig. 1). For a number of individuals of species, imputed numbers were used to account for missing counts. These counts were estimated by use of a statistical program, UINDEX (Bell 1995) taking site,

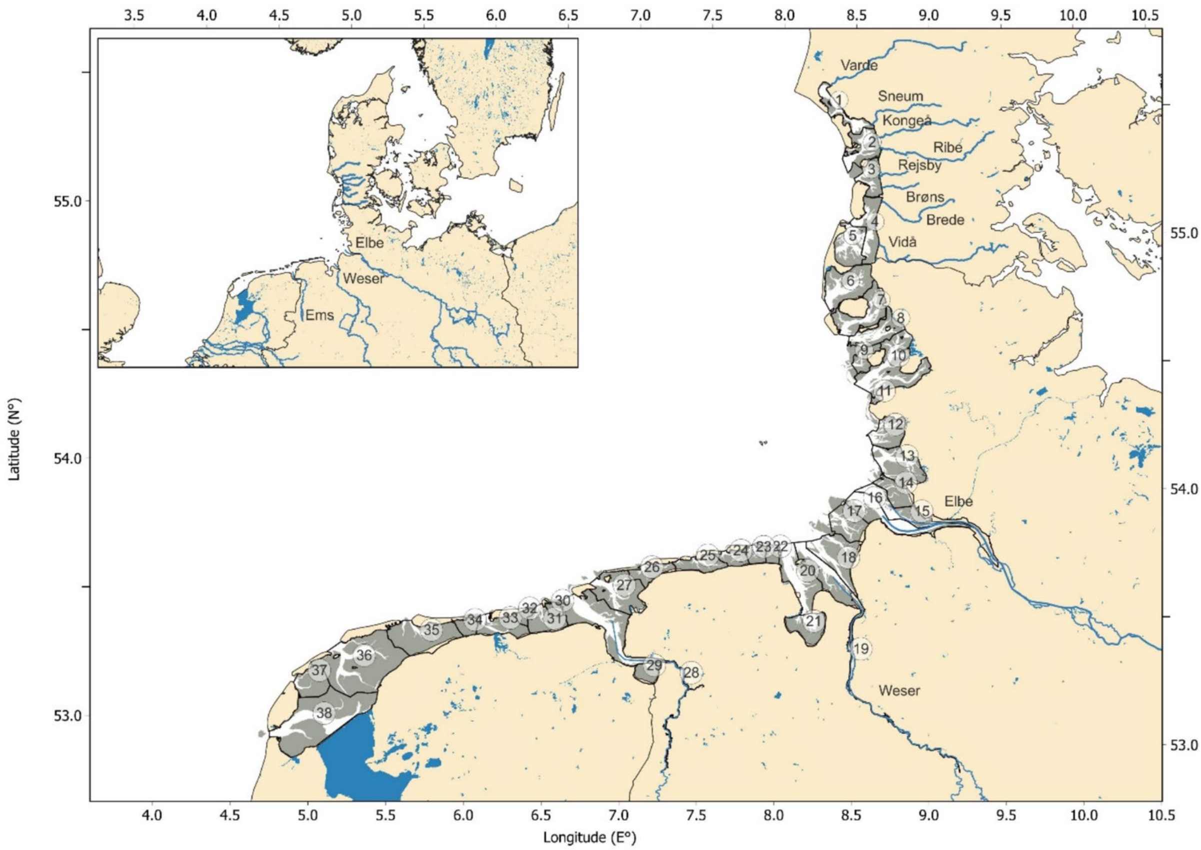

Fig. 1 The Wadden Sea with major rivers. Tidal basins are shown together with basin numbers (no. 1–38). Intertidal flats are shown in grey

year and month factors into account. If the percentage of imputed numbers was > 90% for a tidal basin, the figures were excluded (Kleefstra et al. 2022). Excluded numbers accounted for 8–18% of the data and were lowest for abundant species such as oystercatcher and dunlin and highest for less abundant species such as ringed plover and greenshank. The poorly covered tidal basins were especially tidal basins no. 11, 16, 17 and 18 (Fig. 1). If > 50% of the counts were missing for a species in a tidal basin and the remaining counts were not evenly distributed over the period, the figures were excluded to avoid incorrect estimations. Missing values were not replaced since they constitute a small part of the total data set (< 10%).

Two estimates of bird numbers were made: (a) the number of individuals for each species, tidal basins and year were estimated to analyse temporal changes, and (b) the slope of trend lines in 1987–2019 was estimated for each species and tidal basin to analyse spatial changes during the period (see Laursen et al. 2023). The slopes were estimated by a linear regression analysis. The number of individuals and slopes were standardized (standardized number = ((x_{mean}—x_{observed})/standard deviation)), giving mean = 0, standard deviation = 1) to compare temporal and spatial differences between species. For the standardized values of the number of individuals for each species and tidal basins in 1987–2019, the residual values were estimated as the differences between the linear regression line and the standardized values. In this way, a residual value was estimated for each species in each tidal basin for each year. The residual values were used in statistical tests.

Climate and riverine nutrients

As a proxy for climate in North-West Europe, including the Wadden Sea, we used the North Atlantic Oscillation Index (NAO) during winter (Fig. 2a; Hurrell and Trenberth 2010).

Riverine nutrient input data were compiled by Lenhart and Pätch (2004) and updated to 2019 (NL-G 2023). Total amount of nitrogen (total N) and total amount of phosphorus (total P) per year were measured continuously (Fig. 2b; Van Beusekom et al. 2019). Discharge into the Wadden Sea mainly comes from four large rivers in the Dutch and German sectors (1987–2019) and from eight smaller rivers in the Danish sector (1990–2019; DK 2023). Of these rivers, the Rhine-Maas in the Dutch sector (via the English Channel) and the Elbe-Weser in the German sector are by far the largest and drain major parts of central Europe (Fig. 1).

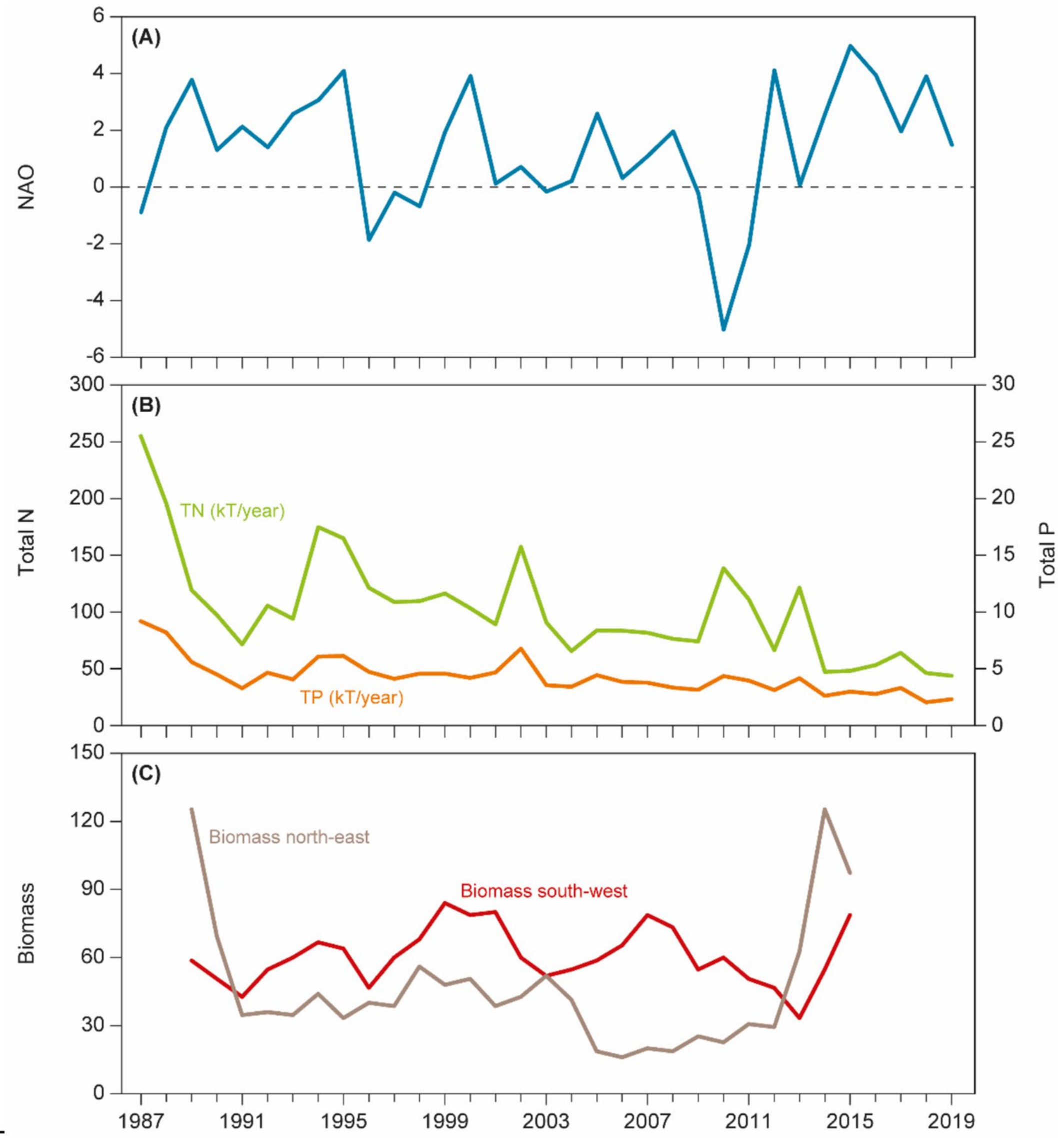

Fig. 2 **A** North Atlantic Oscillation index (NAO) during winter, December–February. **B** Annual outlet of total N (kT year^{-1}) and total P (kT year^{-1}) from the Dutch river Rhine-Maas. **C** Biomass of macrozoobenthos (g m^{-2}) estimated for the Northeastern and the Southwestern section of the Wadden Sea

The data on discharge and nutrients were standardized in the statistical tests.

Biomass and regime shifts

Biomass of macrozoobenthos (ash free dry mass, g m^{-2}) was estimated in 1989–2015 in the Northeastern and the Southwestern sections of the Wadden Sea (Fig. 2c; Drent et al. 2017). Data of biomass was transformed into $\log_{10}$. Regime shifts were identified in 1988–1989 and in 1999–2000 in the southern North Sea and the Wadden Sea (Weijerman et al. 2005; Dippner et al. 2012; Peperzak and Witte 2019).

Sea level rise and sediment geomorphology

Data on sea level rise in the Wadden Sea (1993–2011) was given by Wang et al. (2013). Temporal changes of geomorphology (accretion or erosion, mm year^{-1}) of intertidal flats in tidal basins were compiled for the Danish section by Pedersen and Bartholdy (2006), for the German section by Benninghoff and Winter (2019) and for the Dutch section by Wang et al. (2018). Accretion or erosion was transformed into $\log_{10}$ after the figures were add by '5' to obtain positive values before transformation. See Appendix 1 for further details of material and methods.

Variables and statistical methods

Variables

Twelve variables were analysed in relation to (standardized residual) waterbird numbers. Of these, 11 were abiotic variables and one was biotic. The abiotic variables were regime shift, NAO_t, NAO_{t-1}, river discharge$_t$, total N_t, total P_t, river discharge$_{t-1}$, total $N_{t-1,}$ total P_{t-1}, accretion or erosion of intertidal flats and sea level rise. Of these 11 variables, the first nine were temporal variables and the last two were spatial variables. The one biotic variable was biomass of macrozoobenthos.

Statistical methods

Three statistical analyses were performed: The first analysis aimed to identify the most impactful variables using PCA (principal component analysis) and a correlation matrix, while the second and third analyses focused on temporal and spatial variables using linear ANOVA (analysis of variance) with GLM (generalized linear model) to identify those variables that show significant correlation with bird numbers.

First analysis

We used PCA and a correlation matrix to identify five variables with the greatest impact on waterbird numbers. These five variables were used in the following statistical test.

Second analysis

A linear ANOVA with GLM was used to analyse which of the five selected variables were statistically significantly correlated with bird numbers. These five variables included both temporal variables such as climate and nutrients and spatial variables such as sea level rise and geomorphology. In the first step of the statistical test, only abiotic variables were included, such as nutrients, climate and geomorphology. To obtain the final result of the test, the biotic variable, biomass of macrozoobenthos, was added as a second step.

Statistical procedure

First statistical analysis: using PCA, we selected five variables with the highest numeric values, one for each of the principal component 1 to principal component 5. In addition, we identified five variables with the highest numeric values using a correlation matrix. If there were differences in the variables between the two selection methods, the additional variable/s were included in the following test.

Second statistical analysis: in the first step of the linear ANOVA with GLM, we analysed the standardized numbers of individuals of the 13 waterbird species as dependent variable in relation to the five (or six) selected variables of temporal and spatial variables as quantitative variables. For the tidal basins, we used values of annual riverine discharge and nutrients from rivers situated west or south of the tidal basins (see below). To increase causality in the statistical analyses, we used residuals of the standardized numbers of riverine discharge and nutrients in the models. Due to correlations between (1) river discharge, total P and total N and (2) between NAO_t and NAO_{t-1}, only the variables with the highest correlation values from each of the two groups were retained in the model. Variables with p-values > 0.1 were successively removed from the model. Due to assumed interactions between nutrients and climate (through precipitation) and between temporal and spatial variables, cross-over effects of nutrients and NAO were added to the models together with cross-over effects of temporal variables (nutrients, NAO) and spatial variables (accretion or erosion and sea level rise) to account for polynomial functions. In the final model, we have identified the abiotic variables that have significant effects on numbers of waterbirds.

Second statistical analysis: in the second step of the linear ANOVA with GLM, we added the biotic variable, macrozoobenthos biomass in Northeastern and Southwestern Wadden Sea, to the final model of the second analysis step one. The statistics of biomass stayed in the model if $p < 0.1$. The results of the final models were not changed after biomass was included. In the final model of this analysis, we have identified the abiotic and biotic variables with significant correlations on waterbird numbers out of the initial 12 variables used in the analyses.

Third statistical analysis: this analysis was performed because the effects of spatial variables (accretion or erosion and sea level rise) could be suppressed in the statistical models by the temporal variables due to temporal values being available for all years (e.g. amounts of total N, total P and discharge were given for each year), whereas spatial variables were given for periods of years (e.g. one value of accretion or erosion was given for the entire period 1987–2019 for a section of tidal basins). Therefore, a linear ANOVA with GLM was employed to analyse standardized numbers of individuals of the 13 waterbird species as the dependent variable in relation to spatial variables, with accretion or erosion of tidal flats and sea level rise as quantitative variables and with the cross-over effect of the two variables to account for polynomial functions. This analysis would show if the spatial variables had significant effects on the distribution of waterbirds.

In the statistical analyses, SAS Enterprise Guide 7.1 was used (SAS 2017).

Results

Temporal trends in number of waterbirds

Mean number (se) of individuals of the 13 waterbird species in the Wadden Sea decreased significantly during 1987–2019 ($F = 43.98$, df = 1, 31, $p < 0.0001$, estimate (se) = −0.0209 (0.0031; Fig. 3)). Three periods of changes in waterbird numbers were identified: during 1987–1994, high increases in numbers were demonstrated in most years (mean (se) = 0.35 (0.08)); in 1995–2006, numbers showed a mixture of decreases and increases (mean (se) = −0.02 (0.04)); and in 2007–2019, there were large decreases in numbers in most years (mean (se) = −0.21 (0.03)). Mean number of waterbirds differed significantly between the three periods (one-way ANOVA: $F = 38.62$, df = 2,30, $p < 0.0001$). See Appendix 2 for more results.

Spatial number of waterbirds

In the tidal basins of the Wadden Sea, four sections have been identified based on the mean slope of waterbirds showing changes in waterbird numbers over the years. The slopes were positive in the Northeastern and Southwestern tidal basins and negative in the central tidal basins (Fig. 4). The four groups of slopes identified were as follows: tidal basins

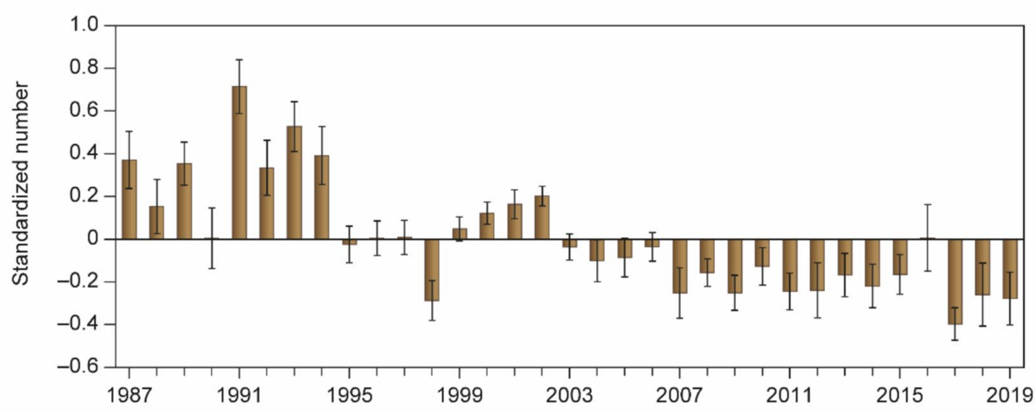

Fig. 3 Average (± se) of standardized number of 13 waterbird species in 38 tidal basins (data pooled) in the Wadden Sea during 1987–2019

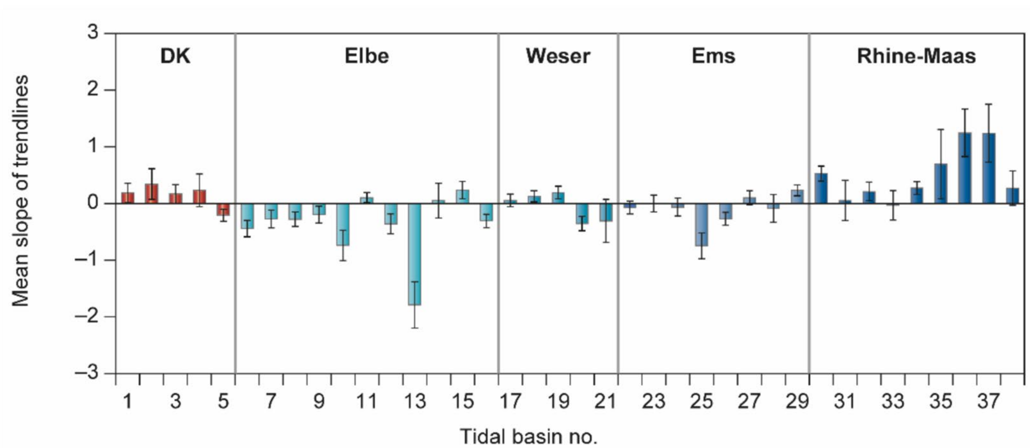

Fig. 4 Average (± se) of slope values of trend lines estimated for 13 waterbird species in 38 tidal basins. Trend lines were estimated for each species for each tidal basin based on the number of birds counted during 1987–2019. At the top: indications of groups of tidal basins influenced by discharge from specified rivers. In Denmark (DK), the Wadden Sea receives discharge from eight rivers

no. 1–4 slopes increased (mean (se) = 0.23 (0.049)); basins no. 5–13 slopes decreased (mean (se) = − 0.46 (0.18)); basins no. 14–33 both positive and negative slopes occurred (mean (se) = − 0.02 (0.08)); and basins no. 34–38 the slopes increased (mean (se) = 0.74 (0.16)). The mean slopes were significantly different in the four groups of tidal basins (one-way ANOVA: $F = 11.65$, df = 1,34, $p < 0.0001$).

Analysis of spatial, temporal and biomass relationships with waterbird numbers

The final ANOVA model with GLM of waterbird numbers during 1987–2019 and temporal and spatial variables in tidal basins in the Wadden Sea showed that all species except common gull were significantly correlated with nutrients (total N and total P) and NAO, or a combination of these three variables (Table 1, Fig. 5). Nine out of 13 waterbird species were significantly correlated with the annual amount of nutrients (total N or total P) from rivers in the current year (total N: two species versus total P: one species) or after a delay of 1 year (total N: three species versus total P: three species). Out of the nine species showing correlations with the amount of nutrients, four effects were positive and five negative. There was a tendency for the effect of nutrients on species in the current year to be positive (three positive effects versus none negative), while the effects of nutrients with the effects of nutrients after a delay of one year were negative (five negative effects versus one positive). Eight species were significantly correlated with NAO (six positive effects versus two negative, Table 1). Of these, four species were correlated with NAO in the current year and four species after a delay of 1 year. Cross-over effects of nutrients and NAO were significant for four species, three of which were among those commented on above and the fourth species was ringed plover, the only species that was increasing or stable in numbers in all sections of the Wadden Sea (Kleefstra et al. 2022). Regime shifts, accretion or erosion and sea level rise combined were correlated with five species (including cross-over effects). The amount of annual macrozoobenthos biomass estimated for Northeastern and Southwestern areas of the Wadden Sea was significantly correlated with seven species (six positive and one negative correlation). The annual biomass in the Northeastern and Southwestern Wadden Sea was significantly positively correlated with total P_{t-1} from river discharge (Appendix 2). The range (mean) of r^2-values of the models in Table 1 that included temporal and spatial variables was 0.01–0.05 (0.03), and the range (mean) with biomass included was 0.01–0.06 (0.04).

Analyses of the spatial variables revealed significant effects on bird numbers of the cross-over effects of accretion or erosion of sediment on the intertidal flats and of sea level rise (Table 2).

Discussion

Regime shift

Three phases of changing numbers of waterbirds could be identified: 1987–1994, 1995–2002 and 2003–2019 (Fig. 3). For the German sector of the Wadden Sea, Laursen et al. (2023) found a shift in population size of six wader species in 1992, initiated by regime shifts in 1989 or 1988/1989 that had a delayed effect. In the current study, a downward shift in population size was identified in 1994/1995. The difference in results between the two studies (1992 vs. 1994/1995) was probably caused by more species or a larger area being included in the current study, which may have increased variation. We found another downward shift in population size in 2002/2003, which could be caused by a regime shift in 1999–2000, with a delay of 2–3 years (Peperzak and Witte 2019). Alternatively, the suggested effect of the regime shifts on the ecosystem in the Wadden Sea in 1988 could have been influenced by 4 years with low riverine discharges from the Rhine-Maas and Elbe rivers and in 2003 by three years with low discharges from the Rhine-Maas (Van Beusekom et al. 2019).

Nutrients

The number of waterbirds correlated with riverine nutrients and climate conditions or combinations of these variables. The temporal variables dominated the relationships while spatial variables such as accretion or erosion of tidal flats and sea level rise were of minor importance. Nutrients such as total N and total P had a significant effect on nine species. For five species, the effects of nutrients were positive and for four species negative. The positive effects occurred in the current year while most negative effects occurred in the following year. These results indicate that density-dependent effects may have taken place. If this is correct, bird numbers in the current year use the available resources that have a negative effect on bird numbers the following year (Gunnarsson et al. 2013). However, this is probably not the case for all parts of the Wadden Sea, because bird numbers increased in the Northeastern and Southwestern sections. The reasons for the difference between these two sections and the central parts could be that for the Northeastern part (e.g. the Danish section) of the Wadden Sea, the amount of total N and total P did not decrease in four out of six rivers in the Danish section (see Appendix 2). In addition, hunting was prohibited in most parts of the Danish Wadden Sea in 1992, and several hunted waterbirds as well as non-hunted waterbirds such as shelduck and six wader species increased in numbers in the mid-1990s (Laursen and Frikke 2013). Thus, increase in nutrients and cessation of hunting could have contributed to an increase in number of waterbirds in the Danish section.

Table 1 Final results of linear models (ANOVA with GLM) of relationships between residual of standardized numbers of 13 waterbird species, monitored in 1987–2019 in 38 tidal basins in the Wadden Sea, as dependent variable and regime shift, accretion or erosion of intertidal flats ($\log_{10+5}$ mm year^{-1}), sea level rise (mm), NAO_t, NAO_{t-1}, river discharge$_t$ (1000 m^3 year^{-1}), river discharge$_{t-1}$ (1000 m^3 year^{-1}), total N_t (tons year^{-1}), total N_{t-1}(tons year^{-1}), total P_t (tons year^{-1}) and total P_{t-1} (tons year^{-1}) as quantitative variables. Benthic biomass$_t$ ($\log_{10}$ g m^{-2}) was added to the final model. Values of river discharge and nutrients were estimated as residuals of standardized numbers. The five quantitative variables with the highest impact were selected for the initial statistical model by PCA; see the main text. r^2 values are given for the models and r^2 values in brackets for the models when biomass was included. p-values < 0.1 are shown. Bold font indicates statistically significant relationship ($p < 0.05$)

Species	Model r^2	F	df	p	Estimate (se)
Shelduck	0.04 (0.03)				
Total P_t		12.07	1, 1119	**0.0005**	0.1243 (0.0358)
NAO_{t-1}		29.22	1, 1119	**< 0.0001**	−0.1411 (0.0261)
(NAO_{t-1} × sea level)		15.94	1, 1119	**< 0.0001**	0.0260 (0.1443)
Biomass$_t$		6.221	1, 931	**0.0128**	0.3601 (0.1443)
Oystercatcher	0.05 (0.06)				
Regime shift		7.15	1, 1020	**0.0076**	−0.0731 (0−0274)
Total P_{t-1}		20.50	1, 1020	**< 0.0001**	−0.1285 (0.0284)
NAO_t		27.41	1, 1020	**< 0.0001**	0.0799 (0.0149)
(NAO_t × accretion-erosion)		14.24	1, 1020	**0.0002**	−0.00543(0.0014)
Biomass$_t$		3.28	1,867	0.0706	−0.2162 (0.1194)
Avocet	0.01 (0.02)				
Total N_t		5.38	1,948	**0.0205**	0.1081 (0.0466)
Accretion-erosion		2.76	1,948	0.0973	−0.0094 (0.0057)
(Total N_t × NAO_t)		4.53	1,948	**0.0335**	−0.0441 (0.0207)
Biomass		4.79	1,791	**0.0289**	0.3748 (0.1713)
Ringed plover	0.01 (0.01)				
Regime shift		2.93	1,1056	0.0874	0.0625 (0.0365)
(Total P_t × NAO_t)		9.00	1,1056	**0.0028**	−0.0546 (0.0182)
Biomass$_t$		2.82	1,873	0.0937	2.0751 (2.0751)
Grey plover	0.04				
Regime shift		5.02	1,990	**0.0253**	−0.0874 (0.0390)
Total N_{t-1}		14.08	1,990	**0.0002**	−0.0874 (0.0390)
NAO_t		14.60	1,990	**< 0.0001**	0.0541 (0.0142)
Accretion-erosion		6.92	1,990	**0.0087**	−0.0139 (0.0053)
Knut	0.02 (0.03)				
Regime shift		3.49	1,1001	0.0619	−0.0673 (0.0360)
Total P_{t-1}		8.75	1,1001	**0.0032**	−0.1092 (0.0369)
NAO_t		3.16	1,1001	0.0756	0.0232 (0.0130)
Biomass$_t$		5.10	1,842	**0.0242**	−0.3484 (0.0153)
Dunlin	0.03 (0.06)				
NAO_t		31.24	1,1089	**< 0.0001**	0.0668 (0.0139)
(Total P_{t-1} × NAO_t)		11.91	1,21,089	**0.0006**	−0.0484 (0.0140)
Biomass$_t$		18.72	1,923	**< 0.0001**	0.6079 (0.1905)
Bar-tailed godwit	0.02 (0.03)				
Total N_t		12.24	1,1183	**0.0005**	0.1147 (0.0328)
NAO_{t-1}		5.17	1,1183	**0.0231**	0.0259 (0.0114)
Biomass$_t$		19.01	1,898	**< 0.0001**	0.6047 (0.1387)
Curlew	0.03				
NAO_t		14.16	1,1102	**0.0002**	0.0437 (0.0116)
(Total P_{t-1} × NAO_t)		26.25	1,1102	**< 0.0001**	−0.0731 (0.0143)
Redshank	0.01 (0.04)				
Regime shift		7.68	1,1120	**0.0017**	−0.0832 (0.0300)
Total N_{t-1}		7.78	1,1120	**0.0054**	0.0301 (0.0101)
Greenshank	0.02 (0.02)				
Total N_{t-1}		6.76	1,906	**0.0095**	−0.2668 (0.1026)
NAO_t		4.82	1,906	**0.0284**	−0.0317 (0.0144)
(Total N_t × sea level)		4.38	1,906	**0.0367**	0.0548 (0.0262)
Biomass$_t$		27.15	1,762	**< 0.0001**	0.2810 (0.0539)
Black-headed gull	0.05 (0.05)				
Total P_{t-1}		24.88	1,1062	**< 0.0001**	0.1892 (0.0379)

Table 1 (continued)

Species	Model r^2	F	df	p	Estimate (se)
NAO_{t-1}		23.21	1,1062	**< 0.0001**	0.0612 (0.0127)
$Biomass_t$		25.68	1,898	**< 0.0001**	0.7329 (0.1446)
Common gull	0.03 (0.04)				
$Discharge_t$		5.99	1,1063	**0.0146**	0.0728 (0.0297)
NAO_t		3.32	1,1063	0.0686	0.0236 (0.0129)

Increase in waterbird numbers in the Southwestern sections could be caused by a higher eutrophication status in this part of the Wadden Sea (Van Beusekom et al. 2019) indicated by higher phytoplankton biomass, higher primary production (Loebl et al. 2007), higher mud input (Alonso et al. 2024), higher organic matter turnover and thus more food available for birds.

Climate-NAO

NAO, the North Atlantic Oscillation index, affected the abundance of eight waterbird species, with most of these effects being positive (Table 1). The waterbirds that were affected by NAO included both arctic and boreal breeders. In addition, discharge from the river Elbe and the Danish rivers was correlated with NAO. The results reveal that NAO has at least two effects on bird numbers in the Wadden Sea. The first effect may be on bird reproduction at breeding grounds in Northern Europe, which are parts of the main breeding areas for waterbird populations using the East Atlantic Flyway (Van Roomen et al. 2022). Positive NAO values indicate mild, stormy and wet climatic conditions in North Europe that provide prime breeding conditions for boreal and arctic breeders (Petersen et al. 2023), whereas low temperatures and late snow melt reduce breeding conditions of wader species (Meltofte et al. 2007). The second effect of NAO may be an influence on precipitation in Central Europe, which is positively related to discharge from Danish rivers and the Elbe. This indicates that discharge from the rivers in the Northeastern sections of the Wadden Sea may be driven by climate conditions.

Macrozoobenthos

Macrozoobenthos biomass was correlated with seven waterbird species, with positive effects for most of these species. Several studies have documented relationships between macrozoobenthos biomass and the number of birds (Zwarts 1996; Ponsero et al. 2016; Horn et al. 2019; Rintala et al. 2022). Negative relationships are assumed to be caused by density-dependent interactions (Gunnarsson et al. 2013).

The low r^2-values of the models for the species (Table 1) reveal that only a small amount of the variance in bird numbers was explained by the statistical models (range = 1%–6%, mean = 4%). However, our results are within the magnitude of most ecological studies, which are between 2 and 5% (Moller and Jennions 2002). Separate statistical analyses for the different sections defined by the river discharge of the Wadden Sea (Fig. 4) could provide more detailed results of the processes in these areas, including the effect of the large amount of discharge from the Rhine-Maas and Elbe rivers compared to the other rivers. However, such analyses are outside the scope of this paper.

Geomorphology and sea level rise

Spatial variables such as accretion or erosion and sea level rise affected only a few species significantly when spatial and temporal variables were analysed together (Table 1). Separate analyses of spatial variables showed significant relationships with accretion or erosion of intertidal flats and sea level rise (Table 2). Changes in geomorphology were largest in the central part of the German Wadden Sea, where decreases in bird numbers were most pronounced (Laursen et al. 2023) and least in the Danish and Dutch parts (Kleefstra et al. 2022), where smaller geomorphological changes occurred (Pedersen and Bartholdy 2006; Wang et al. 2018; Benninghoff and Winter 2019). Sea level rise and accretion or erosion of intertidal flats both had negative effects on the abundance of waterbirds in the current study. For sea level rise analysed in the German section, Laursen et al. (2023) also found negative relationships with waterbird number.

East Atlantic Flyway

Most waterbird species that use the East Atlantic Flyway have increased in numbers since the first regional counts in the 1980 s to 1990 s (Schekkerman et al. 2022). This increase is especially so for species groups with larger body sizes, such as pelicans, ducks, herons and gulls, but terns have also increased in numbers, whereas wader numbers have decreased both in the long term and short term. These declines have occurred in several parts of the East Atlantic Flyway (Schekkerman et al. 2022). In the southern parts, suitable coastal habitats have deteriorated as a result of disturbance and degradation due to human activity. In the northern parts, wader species breeding in the Arctic region

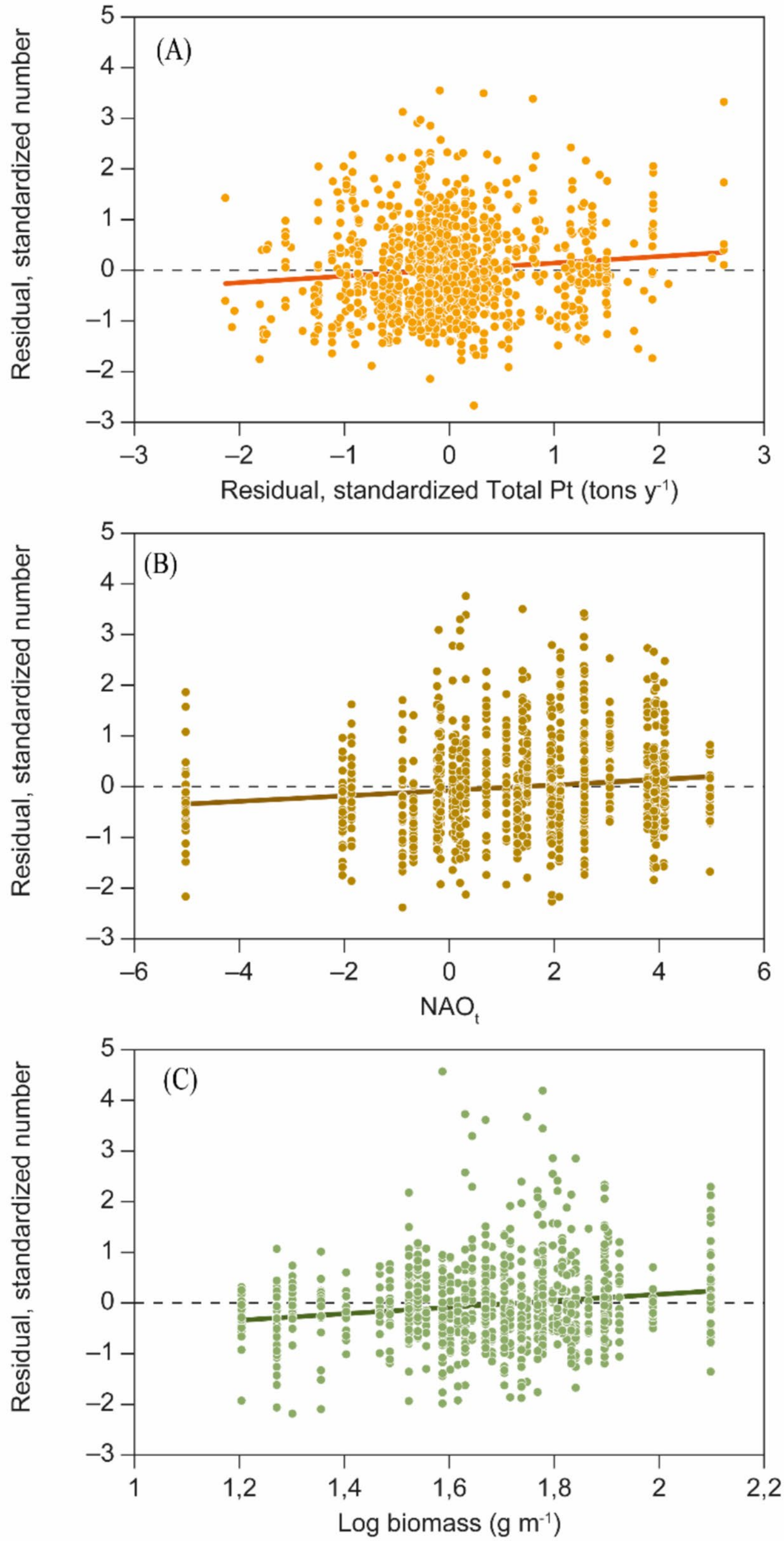

Fig. 5 Three examples of relationships between standardized residual numbers during 1987–2019 on a tidal basis in the Wadden Sea of **A** shelduck in relation to riverine total P_t (tons year^{-1}); **B** grey plover in relation to NAO_t; and **C** bar-tailed godwit in relation to biomass of macrozoobenthos ($\log_{10}$ g m^{-2}). Trend lines are shown for illustrative purposes

Table 2 Final results of linear models (ANOVA with GLM) of the relationship between the slope of trend lines of standardized numbers of 13 waterbird species monitored in 1987–2019 in 38 tidal basins in the Wadden Sea as the dependent variable (data pooled) and accretion or erosion of intertidal flats ($\log_{10+5}$ mm year^{-1}) and sea level rise (mm year^{-1}) as quantitative variables. Bold font indicates statistically significant relationships ($p < 0.05$). Model $r^2 = 0.045$

Variable	*F*	df	*p*	Estimate (se)
(Accretion-erosion × accretion-erosion)	11.49	1, 36	**0.0008**	−0.3278 (0.0967)
Sea level rise	11.42	1, 36	**0.0008**	−0.8297 (0.2456

have exhibited the largest decreases probably due to climate change. Since several of these species winter in the African area, they contribute to the declining numbers in this part. In addition to effects on breeding numbers, climate change may also cause a northward shift in non-breeding waterbirds, which provides them with the advantage of being closer to the breeding areas by reducing the migration distance. A northward movement has been shown for several waterbirds in the Netherlands and by duck species in the Baltic Sea (Pavòn-Jordàn et al. 2019; Hornman et al. 2020). However, extensive wetlands suitable for non-breeding waders are scarce north and northeast of the Wadden Sea and up to the breeding areas in Scandinavia and Russia. Thus, waders are probably not staying in the non-breeding season in larger numbers between the Wadden Sea and the breeding grounds in Scandinavia, Finland and Russia. On the other hand, some wader species have been leaving the Wadden Sea earlier in spring in recent years compared to decades ago (Laursen and Frikke 2013). However, these changes cannot explain the large decreases in waterbird numbers in the Wadden Sea described in the current study. Thus, de-eutrophication may be added to the list of threats to coastal sites along the East Atlantic Flyway. De-eutrophication now occurs in most European countries and is a consequence of political agreements to reduce the discharge of nutrients into the marine environment. Such reduction in nutrients does not only cause a reduction in numbers of benthos-eating waterbirds in the Wadden Sea but also benthos-eating duck species such as the eider *Somateria mollissima* and long-tailed duck *Clangula hyemalis* in the Baltic Sea (Morelli et al. 2021; Rintala et al. 2022).

Conclusions and management aspects

The overall decline in numbers of waterbirds in the Wadden Sea was affected by the North Atlantic Oscillation index (NAO), annual discharge of nutrients (N and P), regime shifts and biomass of macrozoobenthos. The spatial distribution in the Wadden Sea was affected by accretion or erosion of intertidal flats and by sea level rise, although the effects of these variables were of minor importance. From a management point of view, there is no easy way to return the decreasing trend of the benthos-eating bird species in the Wadden Sea. Both the EU Water Framework Directive and the targets of the Trilateral Wadden Sea program aim to lower the concentration of nutrients to reduce eutrophication (Van Beusekom et al. 2017). Further reduction of riverine nutrients to the Wadden Sea will probably diminish the biomass of macrozoobenthos which will lead to further reduction in the number of waterbirds. The Intergovernmental Panel on Climate Change (IPCC) stated that further increase at global warming of 1.5 °C will probably cause decrease in river discharges and increase in severe windstorms (IPCC 2021). Thus, future climate conditions will probably reinforce decreasing riverine discharge to the Wadden Sea and in addition affect geomorphology. Political decisions are required for the reduction of greenhouse gases to change these discouraging prospects for waterbird populations.

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Declarations

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