Exploring Contrasting Trends of Migratory Waterbirds in the Wadden Sea

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Colophon

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Contents

Summary

A high number of waterbirds show declining trends in the Wadden Sea (for trend details see Blew *et al.* (2007)). While some species show a similar trend in all Wadden Sea countries, a sizable number of bird species shows different trends in different Wadden Sea countries. It is these contrasting trends that are the focus of this exploratory study.

A first step was to assemble a list of hypotheses that could potentially explain these contrasting trends. Our list contains no less than 20 different hypotheses, which can be classified into 5 main categories: climate change, eutrophication, human activities/impacts, changes in the biological community and population changes having their reason outside the Wadden Sea. So far all relevant and reasonable hypotheses are included in the list. As such, it can serve as a checklist for future studies.

Apart from formulating hypotheses, also a conceptual framework to derive one or more testing variables for each hypothesis was developed, which could be correlated with changes in bird numbers. Thus, to test a particular hypothesis, a trend in the test variable should correlate to a trend in bird numbers. Usually, one or more unequivocal testing variables for a given hypothesis were derived, but sometimes this proved difficult. For example for eutrophication, there is discussion whether nitrogen or phosphorus is the limiting nutrient.

As this study was of an exploratory nature, it was impossible to try to obtain data on all hypotheses and testing variables. Instead, we focused on those hypotheses and testing variables that experts judged to be most relevant.

Subsequently, many difficulties in assembling appropriate data sets on even this limited set of testing variables were encountered. For each species of bird, we calculated trends per Wadden Sea country for the period 1986/1987-2005/2006. Thus, we tried to obtain data on the selected testing variables that allowed us to do the same. This proved difficult for a variety of reasons:

1. There were simply no data available for particular variables in one or more countries. For instance, cockle stocks are not monitored in Germany.
2. Data are available, but only for a single survey or a short interval of the period under investigation, so that no reliable trend could be calculated. This is the case for instance for high quality data on salt marsh vegetation stored in the TMAP database.
3. Data are available in the form of time series spanning the entire period, but it is not clear how representative these time series are for the Wadden Sea country where the data were collected. This is the case for sampling transects on benthic animals for instance. In the Dutch Wadden Sea, sampling effort on the Balgzand area is high, but few samples are taken in other parts of the Dutch Wadden Sea.

Statistical analysis indicated that bird trends were most similar in Niedersachsen and Schleswig-Holstein, and differed strongly with bird trends in the other two countries. Except for bird species feeding on fish (which increased everywhere), or for species feeding on mussels, which decreased nearly everywhere, many bird trends were negative in the two German countries and positive elsewhere.

We used Principal Component Analysis (PCA; indirect gradient analysis) to infer possible causes for the observed contrasting trends. The data set contained 26 bird species, 19 testing variables and 4 samples (representing the Wadden Sea countries). Testing variables related to eutrophication, winter severity, salt marsh grazing regime, shellfish fishery and stocks of macrozoobenthos. The analysis did not yield a clear answer. In fact, all variables appeared equally important in explaining differences in species trends between countries.

There are many reasons why our analysis did not come to clear results, of which we consider the following to be the most important:

- The four Wadden Sea countries are used as sample units in the analyses. However, having only four sample units, but 19 testing variables (all relating to clear functional hypotheses), strongly restricts the potential of any statistical analysis.
- On top of that, we know that trends in individual species numbers and in individual testing variables often strongly differ between sites within a country (see JMMB report 2009, in prep.). This intra-country variation could not be taken into account, but may be very important in explaining the processes behind the contrasting trends. Although some parameters may act on a country level (e.g. management practices with regard to salt marsh management or fisheries), the majority will act on a different, often smaller, subdivision (e.g. eutrophication with regard to estuaries, or salt marsh management, which may even differ within a single salt marsh).
- Although the trends in bird numbers reflect the situation in the entire country (total population counts), testing variables regularly

consist of data from separate transects or areas within a country. In such cases there is no information about the representativeness of each transect or area for the entire country.

- Data on testing variables contain relatively many missing values, for which it is not yet possible to account.
- This study focused on causes of long-term trends in bird numbers, and therefore we used linear trends in both bird numbers and testing variables. However, trends are often far from linear, and smoothed trends may give a better description of the actual trends.

Since this study was of an exploratory nature, it can provide information for the next steps further investigating these contrasting trends. Our listing of hypotheses identified many human activities as potential causes of contrasting trends. Knowing the actual impact of these various activities on bird numbers, is very important for the effective management of the Wadden Sea as a nature area. Stakeholders, policy makers and managers have a shared interest in developing a tool to assess the probable impact of the various human activities on bird numbers. Our exploration helped us to identify the most effective next steps that must be taken to develop the combined monitoring of birds and testing variables and statistical analysis into such a tool:

- New analyses should focus on bird numbers on more meaningful, often smaller, spatial scales, both for statistical reasons and because bird numbers vary on much smaller spatial scales than by country.
- Smaller spatial scales require that data on testing variables is also available on a smaller spatial scale. It is the shared responsibility of stakeholders, policy makers and managers to fill the gaps in the monitoring scheme.
- Instead of relating trends in bird numbers to trends in testing variables, an alternative might be to start with analyzing the distribution pattern of birds in the international Wadden Sea:
  - o This requires an inventory of the hypotheses explaining this variation in distribution that will probably end up with many of the same explanatory variables.
  - o For an analysis of distribution patterns, we do not need time series, but one good estimate per spatial unit. Thus, more data may be available.
- By focussing on contrasting trends we may have missed out on hypotheses explaining an overall increase or decrease in the number of waterbirds using the international Wadden Sea. In a follow-on project, these hypotheses should be addressed as well and it might be worthwhile to compare developments in the international Wadden Sea to developments in other estuaries in Western Europe.

Salt Marsh
(Photo: K. Janke)

1 Introduction

Oystercatchers
(Photo: J. v.d. Kam)

Systematic counts of waterbirds have been conducted since the 1960s in the various countries of the international Wadden Sea. Recently, a lot of progress has been made with regard to data storage and data analysis, allowing a meaningful analysis and comparison of trends in the various regions of the Wadden Sea; for details on methods and trends see Blew & Südbeck, 2005; Blew et al., 2007. The JMMB has carefully calculated and further described the waterbird trends (Blew & Südbeck, 2005). An alarming number of trends is negative. An assessment of these negative trends has suggested several potential causes, including: changes in the breeding or overwintering areas, changes in the food supply in the Wadden Sea, changes in the size of Wadden Sea population and/or the proportion of biogeographical population. However, these assessments were of a purely descriptive nature. The habitat use of barnacle and brent goose has been described by Koffijberg & Günther (2005), effects of hunting regimes on curlew by Laursen (2005) and a particular assessment of shellfish-eating birds has been conducted Scheiffarth & Frank (2005). The quality of high-tide roosting sites and potential impacts on these has been described by Koffijberg et al. (2003).

Apart from many trends being negative, some of the trends show remarkable differences between countries[1]. For instance, bar-tailed godwit increases in The Netherlands, shows a stable development in Lower Saxony, but decreases in Schleswig-Holstein and Denmark. Similarly, dunlin increases in The Netherlands, shows a stable development in Lower Saxony and Denmark, but decreases in Schleswig-Holstein. In contrast, oystercatcher declines nearly everywhere, except for Denmark, where it increases. Both from a conservation and management perspective, and from a scientific perspective, it is important to understand the cause, or causes, of these different trends. This led to the current project. The goal is to identify a more or less complete set of hypotheses and name explanatory variables for these hypotheses. Collection of the variables most likely to have an explanatory value and a statistical analysis should help to build understanding of some of the forces behind the different trends. Consequently, results should help to point at or advise on management options and to further focus our attention and efforts for improved data collection and management in the international Wadden Sea.

1 It should be noted that the trends refer to the number of birds averaged over the entire season. Thus, higher numbers can be due to more birds visiting the area and/or birds staying longer in the area.

Grey Plovers
(Photo: J. v.d. Kam)

2 Hypotheses

We started with reviewing the literature and questioning experts on the possible hypotheses explaining these differences in trends. This led to what we consider a reasonably complete list of hypotheses. For each hypothesis we subsequently inferred which explanatory variables should be included in a statistical analysis.

2.1 Determinants of the site choice of an individual bird

This study deals with birds that exploit the Wadden Sea during the non-breeding season (Meltofte et al., 1994; Blew et al., 2007). At any one time the number of such non-breeding birds in a given area of the Wadden Sea depends on the total population size frequenting the area and the fraction of the population that has decided to stay there during the time interval. Thus, the number of birds depends on both demographic processes and the behavioural choices of the individual birds to move to the area and stay there. The choice of an individual to stay for a given amount of time in an area will depend on the rate of food intake, the rate of energy expenditure, risk of predation and other factors. These variables are called the "decision" variables in this report, while other authors name them driving variables (Grimm & Railsback, 2005). The decision variables influence fitness components. In the case of non-breeding birds, the affected fitness component will often be survival. However, reproduction may be affected during the non-breeding season via carry-over effects; for instance, if a bird catches a non-lethal disease during the non-breeding season that has a negative impact on reproduction during the subsequent breeding season. Such carry-over effects may well be much more common than previously thought (Norris, 2005). Either way, decision variables impact fitness components and thereby influence demography and the total population size. It is assumed that individuals seek to maximize fitness. Thus, if a high rate of food intake has a positive effect on survival (which seems likely), it is expected that birds will prefer areas with a high rate of food intake over areas with a low rate of food intake (all else being equal). This preference will lead to higher survival and an increase in the size of the population. In this study, it is assumed that values for decision variables that have a positive influence on the decision of the birds to move to an area will also have a positive influence on the number of birds frequenting this area in the long run via demography. In our analysis we only look at the number of birds, so we cannot tell whether an increase in number is caused by the decision of many individuals to stay longer in the area, to suddenly move to the area from another area, or because population size has increased. We generally expect demographic changes to operate on a longer time scale than behavioural responses, but it is impossible to distinguish between demographic changes and changes in distribution on the basis of counts alone when counts include only part of the population. Thus, this analysis will focus on the direction of change and differences in the direction of change and not on the speed of change. The speed of change in the trend curve can be measured as the inclination or as a certain increase or decrease during a given time interval. However, the problem is that we do not have a prediction whether the speed of change should be quick or slow. As a result, we cannot make use of the speed of change in our hypothesis testing. We can only make use of the direction of change, and, perhaps, the absolute magnitude of the change.

The decision variables themselves are influenced by what are called the "governing" variables in this report (Table 1). We need these governing variables to infer how hypotheses put forward to explain contrasting trends actually determine the local number of birds (Figure 1).

Table 1 does not include "social status" and "local knowledge" of the food supply and predators. Such experience variables may make an individual return to an area it has visited before. As a result, a time lag between a change in conditions and the

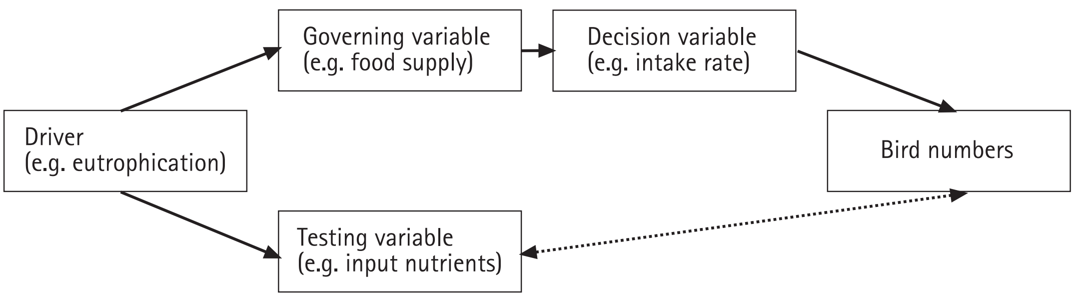


Figure 1: Conceptual scheme depicting the relationship between the various kinds of variables. Hypotheses explain how a driver influences a governing variable and how this impacts bird numbers via decision variables. The hypotheses are tested by testing for correlations between bird numbers and testing variables derived from the driver (stippled bidirectional arrow).

Table 1:
List of "decision" variables that influence the choice of an individual bird to stay in an area and the related "governing" variables that directly influence the "decision" variables.

Decision variables for the individual	Governing variables
Rate of food intake	1. Quality of the feeding area 1a. Size of the stocks of food 1b. Quality of the food stocks 1c. Availability of the food
Rate of energy expenditure	2. Weather (temperature and wind) 3. Quality of the roost 3a. Distance to feeding grounds 3b. Extent of natural and human disturbance 4. Quality of the feeding area 4a. Extent of natural and human disturbance
(Perceived) risk of predation	5. Quality of the roost 5a. Density of predators 5b. Attack success of predators* 5c. Density of alternative prey for predators 5d. Hunting pressure 6. Quality of the feeding area 6a. Density of predators 6b. Attack success of predators 6c. Density of alternative prey for predators
Risk of parasitism and diseases	7. Quality of the feeding area 7a. Density of infected prey 8. Density of infected conspecifics

*The attack success of predators is determined by the species of predator and the hunting strategy of the predator and also by properties of the terrain. Is it easy to hide from predators and/or do the birds have a good view of approaching predators so they can flee in time?

numbers of birds visiting the area might be visible. For instance, adult oystercatchers are well known for their extreme site fidelity (Ens & Cayford, 1996). As a result, the number of birds in an area may stay high for many years despite a decrease in the quality of this area (Atkinson et al., 2003; Verhulst et al., 2004). The same may well apply to many other long lived species. In this case, the time lag is due to a behavioural decision and it is the demographic process (the site faithful adults must die out and the newly born recruits must settle according to the new conditions) that must "restore" the link between the number of birds and the quality of the habitat. Since we cannot distinguish in our analysis between demography and site choice, as already argued, it is not useful to include the variables "social status" and "local knowledge" in Table 1. However, as noted before, when interpreting the results of the analyses in hand the possibility of time lags should be taken into account.

Furthermore, Table 1 also does not include the risk of falling victim to pollution (like oil pollution) as a decision variable. Oil pollution may cause high mortality among birds, but from an evolutionary perspective it is of very recent origin. Thus, birds may not yet have evolved behavioural strategies to avoid heavily polluted areas.

2.2 Processes determining the variables governing demography and the site choice of individual birds

In this section, various hypotheses that may explain contrasting trends are listed. It was tried to organize them in logical groups. Each hypothesis consists of a "driver" and an associated list of governing variables (see above) that may be impacted by the "driver". This list of governing variables is important, because if there is no impact on one or more governing variables, we do not expect an impact on one or more decision variables (see Table 1; the numbers in Table 2 correspond to the numbers in Table 1) and hence no effect on site choice and fitness expectations of the individual birds. However, to investigate the hypothesis "testing" variables are necessary that allow us to investigate (1) if there is regional variation in the testing variable, (2) if this regional variation can be linked to the regional differences in trends of the waterbirds. If possible, testing variables should be unique for a given hypothesis, but this is not always the case. For instance, the hypsometric curve is not only affected by sea level rise, but also by land claim and soil subsidence due to gas extraction. The testing variables identified are listed in the third column of Table 2. If possible, the hypotheses are couched in precise and quantitative terms. The hypotheses only concern the Wadden Sea. For instance, climate change is likely to also impact breeding and wintering habitats elsewhere along the migration route, but these impacts fall outside the scope of this investigation. That should not be taken to mean that we consider these hypotheses unimportant. On the contrary, we think these hypotheses to be very important as they may explain the overall trends in the numbers of waterbirds visiting the Wadden Sea.

Table 2: Hypotheses to explain contrasting trends in waterbirds in the Wadden Sea. Listed are the "drivers", the associated "governing" variables that may be impacted and the "testing" variables. Numbers refer to the numbers in Table 1.

Driver	Governing variables that may be impacted	Testing variables
Climate change		
Sea level rise	• Available feeding and roosting area (1, 3)	Change in hypsometric curve
Global warming	• Decreased energy expenditure (2) • Changes in quality and quantity of food stocks(1) • Mismatch in timing of food sources in the Wadden Sea and migration routes (1c)	• Temperature data • Phenological data
Decreased frequency severe winters	• Changed feeding conditions in winter (2) • Changes in quality and quantity of benthic prey (decreased frequency of good spatfalls) (1)	• Frequency of occurrence of severe winters in different regions
Changes in wind direction and storm frequency	• Energy expenditure (2) • Available feeding time (1c)	• Data on wind direction and storms • Data on exposure time of the tidal flats
Eutrophication		
Changes in eutrophication	• Stocks and quality of food (1)	• Nutrient inputs (N and P) • Primary production
Human activities and impacts		
Hunting	• Rate of energy expenditure (3b, 4a) • (perceived) risk of predation (5a, 5b, 6a, 6b)	• Hunting bags • Hunting policy (and changes in policy)
Shrimp fishery	• Stocks and quality of shrimps (1a, 1b) • Stocks and quality of non-target prey (1a, 1b) • Availability of non-target prey – discards (1c)	• Shrimp landings • Closed areas for shrimp fishery
Mussel fishery	• Stocks and quality of mussels (1a, 1b) • Stocks and quality of non-target prey (1a, 1b)	• Mussel landings • Area and biomass of mussel beds • Closed areas for mussel fishery
Cockle fishery	• Stocks and quality of cockles (1a, 1b) • Stocks and quality of non-target prey (1a, 1b) • Sediment composition (1c)	• Cockle landings • Cockle stocks • Quality of cockles • Sediment composition • Closed areas for cockle fishery
Land claim and coastal engineering	• Direct habitat loss (1, 3, 4) • Delayed impact on morphology and sediment composition (due to past embankments) (1, 3, 4)	• Area lost to reclamation in past 50 years (?) • Hypsometric curve • Changes in sediment composition
Increased turbidity due to dredging	• decrease in productivity ecosystem (1)	• turbidity measurements (Secchi disk etc) • dredging activity
Saltmarsh management	• Quality of roosting site (5) • Quality of feeding area (geese) (1)	• Management regime • Vegetation data
Soil subsidence due to extraction of gas or salt	• Available feeding time (1c)	• Hypsometric curve
Disturbance from recreation, military exercises and civilian air traffic	• Available feeding area (4a) • Quality roosting areas (3a)	• Actual data on recreation • Recreation management • Intensity and type of military exercises • Intensity of civilian air traffic • Area of SPA or other protection levels

Driver	Governing variables that may be impacted	Testing variables
Ecological light pollution	• Food availability (1c) • Quality of roosting areas (3) • Attack success of predators (5b, 6b)	• Extent and intensity of artificial night lighting
Pollution (pesticides, industrial chemicals, oil)	• Change in stocks and quality of benthic prey (1a, 1b) • Risk of falling victim to pollution event?	• Levels of pollutants • Frequency of major as well as minor oil spills
Changes in the biological community		
Changes in the population of natural predators	• (Perceived) risk of predation during feeding (6) • (Perceived) risk of predation during roosting (5)	• Populations of natural predators frequenting the Wadden Sea • Prey choice of these predators
Changes in parasites and diseases	• Risk of parasitism and disease (7, 8)	• Intensity of infection with parasites or diseases
Invasion exotic species (Pacific oyster, Ensis, Crepidula, Gracilaria)	• Change in quality and stocks of benthic prey (1)	• Occurrence of exotic species
Externally mediated population changes		
Change in the total population size of a bird species, or the fraction using the international Wadden Sea	• Differential change in use of optimal and suboptimal parts of the Wadden Sea (1-8)	• Total size of the population using the Wadden Sea

Mussel bed
(Photo: H. Marencic)

2.2.1 Climate change

Climate change has several impacts on the Wadden Sea ecosystem. The two most obvious impacts are an increase in temperature (including a decreased frequency of severe winters) and a rise in sea level. Other impacts include changing river discharges and changes in wind direction and storminess (Essink et al. 2005).

2.2.1.1 Sea level rise

Sea level rise impacts the geomorphology of the subtidal and intertidal area. When sea level rise is large, emersion time of tidal flats may decrease (in the extreme case the tidal flats may even disappear) and salt marshes may erode. This reduces the feeding time for birds feeding on tidal flats and reduces the foraging area for birds feeding on salt marshes. However, when sea level rise does not exceed a critical rate, the geomorphology may be able to adapt. During the past thousand years sea level rise has varied between 5 and 30 cm per century and during the past century it amounted to 20 cm in the Dutch Wadden Sea (Louters & Gerritsen, 1994). The geomorphology of most tidal basins in the Dutch Wadden Sea is able to cope with this rate of sea level rise (Louters & Gerritsen, 1994). In fact, 20 cm per century amounts to 4 cm during the past 20 years, i.e. the period for which bird counts are available. This change is so small that very little impact is expected, let alone measurable differences in impact between different regions within the international Wadden Sea during the past 20 years. In fact, measurements on the hypsometric curve indicate that sedimentation has exceeded sea level rise during the past 20 years in most tidal basins in the Dutch Wadden Sea (Hoeksema et al., 2004). On the basis of the above, sea level rise is an unlikely candidate to explain the observed contrasting trends in the number of waterbirds. K. Reise (pers. comm.) agrees that it is very unlikely that sea level rise may explain contrasting trends during the past two decades. However, for future developments the possibility should be considered that some tidal basins will not be able to keep up with sea level rise and might start losing tidal flats. If so, this would clearly have a large impact on the birds feeding on these tidal flats.

2.2.1.2 Global warming and decreased frequency of cold winters

There is doubt that ambient temperature has increased in the Netherlands during the past 20 years (Verbeek, 2003) and this is also true for the sea water temperature in the western Dutch Wadden Sea (van Aken, 2003). The increase in temperature is especially apparent in winter and spring. These changes are thought to influence the ecosystem in several ways:

1. Higher temperatures decrease energy expenditure of the birds and when mudflats are less likely to freeze this also positively affects the feeding conditions of the birds during winter. It was shown for waders wintering in the United Kingdom that warmer winters led to a shift from wintering on the west coast (where winters are mild, but food is poor), to wintering on the east coast (where winters are generally more severe, but food supplies are higher) (Austin & Rehfisch, 2005). The shift was especially clear in the smaller species and these are the species that suffer most from energy stress when temperatures are low (Kersten & Piersma, 1987). A more recent analysis of waders wintering in Europe confirmed a shift in the centre of the distribution to the Northeast during the last 30 years, in line with milder temperatures in these areas (Maclean et al., 2008). For the Wadden Sea it has already been described that more birds remain to winter in the eastern part during mild winters and they may also depart at an earlier date to their northern breeding grounds when springs are warm (Bairlein & Exo, 2007).
2. Temperature influences the quality and the quantity of the food stocks as well as the availability. When winter temperatures are high, shellfish lose more body mass than when winter temperatures are low (Honkoop & Beukema, 1997). Severe winters cause high mortality among many invertebrates on the tidal flats, but subsequently, there is often a good spatfall (Beukema, 1982, 1992). The relationship between spatfall and temperature is complex and may involve the timing of spawning of the invertebrates and the timing of the predators of the newly settled spat (Philippart et al., 2003). Recent declines in recruitment success of various species of shellfish in the western Wadden Sea are thought to result from climate change (Beukema & Dekker, 2005).
3. Freezing of mud flats may be especially critical. When mud flats are frozen, birds cannot reach their food and also many benthic animals die. In the last decades of the previous millennium, the frost boundary ran somewhere through the Wadden Sea with often no ice in the Dutch Wadden Sea and ice-cover in

the Schleswig-Holstein and Danish Wadden Sea (Wim Wolff, pers. comm.).

In conclusion, recent temperature changes may have affected the feeding conditions for the birds in the Wadden Sea. Since average temperatures differ between different regions within the Wadden Sea (the north-east being the coldest in winter), it is certainly possible that temperature changes have also had a different impact in different regions of the international Wadden Sea. Perhaps more birds decide to spend the winter in the Dutch Wadden instead of moving south. Due to the many complex interactions it is difficult to formulate precise predictions. The most profitable course of action seems therefore to start with investigating the change over the years of the temperature regime in different regions. In The Netherlands increasing temperatures are mainly due to increasing temperatures in winter and spring (Verbeek, 2003). Thus, the change in temperature must be investigated per season. In addition it is worthwhile to investigate if temperature changes have been transferred to quality of prey and the success and timing of recruitment (more generally whether there have been changes in the phenology of the benthic prey in different areas, i.e. when do benthic animals spawn, when do they start growing and so on).

2.2.1.3 Changes in wind direction and storm frequency

Although it is generally predicted that climate change will increase the frequency of extreme events like storms, it appears that the number of storms in The Netherlands has actually decreased during the last 40 years (Verbeek, 2003). This relates to the number of storms during the whole year, but in a study of oystercatchers breeding on the salt marsh of Schiermonnikoog, it was found that extreme floods (caused by strong winds from the North-West) had significantly increased during the past 25 years (van de Pol, 2006). This suggests that storms may have increased during late spring – early summer, in contrast to other times of the year, and/or the general wind direction has changed increasing the risk of flooding. High winds increase energy expenditure and may decrease the time available for feeding. The impact of wind is especially large in areas with a small tidal range. The average tidal amplitude varies between more than 3.8 m in the central parts of Schleswig-Holstein to less than 2 m in the northern and western parts of the international Wadden Sea (Eisma, 1980). An analysis of storm-related sea level variations along the North Sea coast for the years 1958-2002 revealed a complicated geographical pattern; apart from a small section along the German and Danish coast line no significant increase was found (Weisse & Plüß 2006).

Compared to global warming, the evidence that wind patterns have changed and impacted the birds in the Wadden Sea differentially is much more equivocal. Nonetheless, it might be useful to collect data on wind direction and storm, as well as data on exposure time of the tidal flats in different regions of the Wadden Sea. We predict stronger declines, especially of bird species stressed for time, in areas where available feeding time has decreased most. In many areas water level is monitored continuously. As a first step we might define critical water levels from an ecological point of view and subsequently investigate the frequency with which these critical water levels are exceeded. For oystercatchers, good food supplies seem to be located below mean sea level (Zwarts et al., 1996b) and a digestive bottleneck prevents the birds from meeting their daily energy requirements in a single low water period (Zwarts et al., 1996a).

2.2.2 Eutrophication

Since the 1980s the input of nutrients (especially phosphorus and to a lesser extent nitrogen) into the Wadden Sea has declined (Essink et al., 2005). Time series analysis (Philippart et al., 2007) and model calculations (Brinkman & Smaal, 2004) indicate that stocks of filter feeding bivalves have declined as a result. The declining shellfish productivity may have led the fishermen to overfish the stocks of shellfish (Ens, 2006), thereby exacerbating food shortages for shellfish-eating shorebirds. In the Mondego Estuary in Portugal it was observed that declining eutrophication led to a decrease in the coverage of macroalgae and an increase in the abundance of dunlin, perhaps as a result of an increase in some of its prey items (Lopes et al.,2006). In the Dollard Estuary, a decline in eutrophication coincided with a decline in the majority of birds, a decrease in the worm Nereis diversicolor and an increase in the worm Marenzelleria as well as in increase in the crustacean Corophium volutator (Essink & Esselink, 1998). Thus, changes in eutrophication are likely to lead to changes in the quality and the stocks of benthic animals that serve as prey for the birds. The data analysis in the Quality Status Report of 2004 also highlights regional differences in eutrophication (Essink et al., 2005). Since eutrophication is one of many processes influencing the quality and the stocks of benthic prey, the analysis should focus on the regional differences in the changing nutrient inputs. The prediction is that shellfish-eating birds will have decreased more in areas with a stronger decrease in eutrophication. Unambiguous predictions for worm-feeding birds are more difficult to make, because the results of the study in the Mondego Estuary (Lopes et al., 2006) differ from those of the Dollard (Essink & Esselink, 1998). Preferably, the eutrophication analysis should target the productivity and not the standing stocks of the phytoplankton, the microphytobenthos and the zoobenthos, but this may be hard to achieve.

2.2.3 Human activities and impacts

The following human activities were considered to be too localized to warrant inclusion in Table 2:

- mechanized fishing for lugworms; 4 licensed machines on 5 small areas totalling 2,000 ha intertidal flats in the western Dutch Wadden Sea (Ens et al., 2004); locally, the ecological impact may be high (Reneerkens et al., 2005);
- manual (sometimes illegal) bait digging for different species of worms;
- fishery using fykes, artisanal fishery for mullet, beamtrawl fishery for flatfish;
- wind turbines are considered a major future threat (Reneerkens et al., 2005), but present numbers are small, so unlikely to have affected the observed trends in bird numbers

2.2.3.1 Hunting

Hunting has a direct negative impact on bird numbers, as birds are killed. Hunting may also have an indirect effect, as birds shy away from areas where hunting occurs (Fox & Madsen, 1997, 1998). Furthermore, there are differences in the extent of hunting allowed in different Wadden Sea countries and regulations have also been subject to change (Essink et al., 2005). Thus, differences in the hunting regime may well have contributed to the contrasting trends of some waterbird species. For instance in the Quality Status Report of 1999 it was noted that curlew, which is a notoriously shy species and which was previously rare in Denmark, increased in Denmark after hunting curlew was banned (de Jong et al., 2000) There are two obvious testing variables: the hunting regulations and the hunting bags, i.e. the number of waterbirds that were actually shot in a given area in a given year. The prediction is that numbers (of hunted waterbirds) will have increased more in areas with the strongest decline in hunting pressure, measured either via the hunting regulations or the hunting bags.

2.2.3.2 Shrimp fishery

In terms of the number of licenses, shrimp fishery is the biggest fishery in the Wadden Sea (Essink et al., 2005). Shrimp fishery takes mainly place in subtidal areas and in the North Sea coastal zone. Thus, it is unlikely to have a simple and direct effect on the birds feeding on the intertidal flats or on the salt marsh. Shrimp fishery has a lot of bycatch that is discarded and this attracts large numbers of gulls. Thus, it could have a positive influence on the food supply of these gulls (Walter & Becker, 1994). Shrimp fishery may have a negative impact on benthic fauna in the sublittoral zone (Buhs & Reise 1997; Reneerkens et al., 2005), but the birds that we study do not prey on that fauna. It occurs in all regions of the Wadden Sea and has slightly increased in recent years. However, the increase has occurred in all countries (Essink et al., 2005). Very recently, shrimp fishery in The Netherlands may have intensified due to a ruling of the Dutch Competition Authority which caused strongly enhanced competition between fishermen, lower prices and longer fishing hours. In all, it cannot be categorically said that shrimp fishery has no effect on the contrasting trends of waterbirds, but it does not seem very likely.

2.2.3.3 Mussel fishery and mussel culture

In former times mussel fishery directly targeted mussels of consumption size and transported them to the market. Nowadays, smaller mussels, often referred to as seed mussels, are fished from natural beds and transported to subtidal culture lots, where they grow to consumption size. It is only then that they are brought to the market. Fishery for (seed) mussels can take place on intertidal as well as subtidal beds. The transition from wild fishery to mussel culture differs between areas. Zeeland fishermen journeyed to the Wadden Sea for seed mussels already more than a century ago to stock their culture lots in the Zeeland estuaries (van Ginkel, 1991). In the Dutch Wadden Sea, culture plots were introduced in 1951 (Dijkema, 1997). In the Danish Wadden Sea, mussel fishery still directly target mussels of consumption size.

Mussel fishery on intertidal mussel beds reduces and in some instances entirely removes mussel beds that are an important habitat for birds feeding on mussels, like oystercatcher, and for birds that feed on associated fauna, like curlew. Overfishing of littoral mussel beds in the Dutch Wadden Sea around 1990 (Beukema, 1993; Beukema & Cadée, 1996), is thought to be the major cause of the decline in the number of wintering oystercatchers (Rappoldt et al., 2003; Ens, 2006). As a consequence of this, fishery on intertidal mussel beds has been greatly restricted in the Dutch Wadden Sea since 1993 (Ens et al., 2004). In contrast, fishery for mussels on intertidal flats is completely forbidden in Schleswig-Holstein since 1997, but fishing for seed mussels continues to be allowed in certain intertidal areas in Lower Saxony (Essink et al., 2005). Thus, fishery of intertidal mussel beds is a clear candidate to explain contrasting trends. The prediction is that birds that depend on mussel beds will have decreased more in areas with the highest impact of mussel fishery. The intensity of mussel fishery can be judged from landings, the capacity of the fishing fleet and management practices, like the extent of areas closed for mussel fishery. Since mussel fishery quite specifically targets mussel beds, this is a case where one might also consider the area of littoral mussel beds a testing variable.

Mussel fishery also occurs in the sublittoral zone, which is the area where the mussel cultures are located and where they grow to commercial size. There are clear regional differences in the extent of mussel fishery and mussel culture and the policies have changed during the study period as described above (see also Essink et al., 2005). Mussel fishery and mussel culture will have an impact on common eider (Camphuysen et al., 2002; Ens & Kats, 2004; Ens, 2006), but this impact can be both positive and negative. According to preliminary calculations, mussel culture increased the standing stock of sublittoral mussels by on average 15% during the 1990s (Bult et al., 2004) and therefore probably increased the food supply for common eider on average. However, it is likely that mussel culture actually decreases the stock of sublittoral mussels after two or more years without significant spatfall (Ens et al., 2007b), as happened around 1990 (Beukema, 1993; Beukema & Cadée, 1996). Shortage of sublittoral mussels is a prime determinant of mass mortality among common eider (Camphuysen et al., 2002; Ens et al., 2002; Ens & Kats, 2004), especially when alternative food sources are also scarce (Ens et al., 2006; Kats, 2007). Simulations with a population model built for another long-lived bird species like oystercatcher that feeds on large (short-lived) prey, indicate that the size of the population is primarily determined by these occasional severe food shortages. Thus, it is difficult to predict if numbers of common eider will increase or decrease when mussel culture in the sublittoral zone intensifies. The intensity of mussel culture in the sublittoral zone can be judged from the mussel landings, the area of culture plots and the extent of areas that are closed for mussel fishery. At present, we do not know if there are specific fish species associated with sublittoral mussel beds (although eelpout is suspected to favour mussel beds), nor do we know if these fish species are favoured by one or more of the fish-eating bird species in the Wadden Sea (Ens et al., 2007a).

2.2.3.4 Cockle fishery

Cockle fishery was and is only allowed on a large scale in the Dutch Wadden Sea. Mechanized cockle fishery was permanently closed as of 1 January, - 2005, but hand gathering of cockles continues (Essink et al., 2005). During the study period, the catches of cockles by hand gatherers were dwarfed by the catches by mechanized cockle boats (Kamermans et al., 2003b), so any impact of cockle fishery is almost certainly due to mechanized cockle fishery. There is little doubt that mechanized cockle fishery negatively impacted the stock of large cockles in the littoral zone and in this way had a negative impact on the number of wintering oystercatcher (Rappoldt et al., 2003; Ens et al., 2004). Cockles also occur in subtidal areas, but the stocks of subtidal cockles are minor compared to the stocks of cockles in the intertidal (Kamermans et al., 2003a). There is also evidence that mechanized cockle fishery has a negative impact on the quality of small cockles that serve as food for knot and thereby decreases the available food supply for these birds (van Gils et al., 2006). Finally, evidence has been presented that mechanized cockle fishery changes the composition of the sediment in such a way that the sediment loses the fine fraction (Piersma & Koolhaas, 1997; Zwarts et al., 2004) and as a result becomes less suitable for shellfish recruits (Piersma et al., 2001)[2]. This should have a negative impact on the birds feeding on shellfish on the intertidal flats. According to Kraan et al. (2004), mechanized cockle fishery may lead to increased densities of worms, thereby increasing the food supply for worm-feeding birds. However, Leopold et al. (2004) did not observe this general response, except for ragworm. Thus, the evidence that worm-feeding birds might benefit from mechanized fishing for cockles is equivocal. Testing variables include the area closed for

2 It should be noted though that Zwarts et al. (2004) concluded on the basis of an analysis covering the entire Dutch Wadden Sea, that suction dredging of cockles did indeed reduce the silt content of the sediment at both the short, medium and long time scales, but that this effect was masked by the fact that the cockle fishery had predominantly occurred in areas that had silted up during the study period.

mechanized cockle fishery, the cockle landings, the capacity of the fleet and the sediment composition. The latter variable is only indirectly linked to cockle fishery, and may be influenced by many other processes, so should not receive high priority during the data search. Since cockle fishery specifically targets cockles, the size of the cockle stocks and the quality of the cockles can also be used as testing variables.

2.2.3.5 Land claim and coastal engineering

Land claim not only leads to direct loss of habitat (salt marshes, intertidal flats, subtidal areas), but also changes tidal currents and sedimentation patterns. It may take decades, or even longer, before a new geomorphological equilibrium is reached. The Zuiderzee was closed in 1932, but there is increasing evidence that a new geomorphological equilibrium has not been reached yet in the western Dutch Wadden Sea (Elias, 2006). Similarly, the closure of the Lauwerszee in 1969 is probably still a major factor in sediment transports in the area north of Lauwersoog in the eastern Dutch Wadden Sea (Wang, 2007). In Germany, land claims are more recent (Meldorfer Speicherkoog in 1978 and Beltringharder Koog in 1987). Those land claims, both recent and at an earlier date, may be affecting local areas in the Wadden Sea and variation between areas is likely. Since it is difficult to formulate precise predictions about which birds will be affected in which way and since the hypsometric curve and sediment composition are also affected by other processes, it seems prudent to first make an inventory of the various land claims in the international Wadden Sea during the past 50 or 100 years, requiring an update of the data presented in report 11 of Wolff (1983). In Germany, recent embankments have disproportionately reduced muddy flats and therefore birds preferentially foraging in mud might show effects (K. Reise, pers. comm.).

Dredging in the rivers for better access to large harbours results in increased tidal amplitude, with lower low tides and higher high tides. This has occurred especially near and in the estuaries of the rivers Ems, Weser and Elbe (Wim Wolff, pers. comm.).

2.2.3.6 Increased turbidity due to dredging

In the Wadden Sea, dredging mainly takes place to keep the shipping lanes at sufficient depth. Especially in The Netherlands and in Schleswig-Holstein (for the island of Sylt), dredging also takes place in the North Sea for beach nourishment, which is part of coastal defence measures. The ecological impact of dredging gullies is expected to be very different from the impact of dredging for beach nourishment (K. Reise, pers. comm.). During the study period there were considerable differences in the amount of dredged material dumped between areas and there were also variations in time (Essink et al., 2005). Dredging and dumping of dredged material increases turbidity, which will decrease phytoplankton primary productivity. This decrease in productivity is expected to lead to lower stocks and/or production of the organisms that feed on the algae, including zooplankton and benthic organisms. The species composition of the various algae feeders may also be affected. Computer simulations for the Ems Estuary indicated that an increase in turbidity led to major declines in the standing stock of filter feeders, but did not affect zooplankton (DeGroodt & de Jonge, 1990). However, in an empirical study for the Tamar Estuary in the UK, no evidence was found that changes in the dredging activity affected intertidal benthic macrofauna, fishes or birds (Widdows et al., 2007). Two possible testing variables are measurements on turbidity and measures for the amount of dredging. The prediction would be that an increase in dredging and turbidity is correlated with a decrease in birds feeding on benthos. Among the benthos feeding birds it is not possible to predict which species will be affected most. We classify this as a likely impact that warrants investigation.

2.2.3.7 Salt marsh management

Shorebirds use the salt marsh as a high tide roost and herbivorous birds use it as a feeding area. Many salt marshes are grazed by livestock and this has an impact on the vegetation, which in turn will influence the birds. Salt marsh management differs regionally, both with regard to the dominant domestic grazers (horses, cattle or sheep) and with regard to the intensity of grazing. In addition, salt marsh management has also changed quite dramatically in some areas recently (Essink et al., 2005). Thus, salt marsh management is a good candidate to explain contrasting trends in waterbirds. Grazing by cattle and sheep reduces the height of the vegetation and makes it more suitable for geese (Bos et al., 2002). Thus, we predict that a reduction in the amount of grazing will lead to taller and differently structured vegetation and lower numbers of herbivorous birds on the salt marsh. With regard to the salt marsh as a roosting place, it must be noted that different species prefer different vegetation types to roost (Koffijberg et al., 2003). Thus, taller vegetation as a result of reduced grazing is predicted to have a negative effect on the species preferring to roost in short vegetation, when no suitable alternative areas with short vegetation (like arable lands which are typically used for roosting in Zeeland) are nearby.

2.2.3.8 Soil subsidence due to gas extraction

Gas extraction has been a major conservation issue in The Netherlands since it was generally believed that soil subsidence as a result of gas extraction would have severe negative consequences for the birds feeding on the tidal flats (Verbeeten, 1999). However, the magnitude of the subsidence is so small that scenario calculations make it unlikely that it has a measurable impact on the biomass of benthic animals (Beukema, 2002) or on the birds that feed on these animals (Brinkman & Ens, 1998). Studies on the impact of gas extraction underneath Ameland and the surrounding area found no evidence for a measurable impact on birds (Doornhof et al., 2005). In general, sediment transports into the Wadden Sea have been sufficiently high to compensate the extra sediment needs due to soil subsidence as a result of gas extraction (Hoeksema et al., 2004). Soil subsidence, which may also result from the extraction of salt from geological formations, may have a measurable impact in the future, but on the basis of the above it is concluded that soil subsidence is not a likely candidate to explain contrasting trends in bird numbers.

2.2.3.9 Disturbance from recreation

Tourism and recreational activities make an important contribution to the local economy of the Wadden Sea region (Essink et al., 2005). Tourism and recreation are also on the rise, but there are some suggestions that trends differ between different Wadden Sea countries (Essink et al., 2005). Tourists may disturb birds during feeding and roosting. We expect fewer birds when disturbance is high, although the quantitative details will depend on the species as reviewed by Krijgsveld et al. (2004); see also Drewitt (2007). Thus, disturbance from tourism and recreation is a good candidate to explain contrasting trends in waterbirds, even though Madsen (2007) considers it unlikely that increasing recreation is responsible in general for declining trends of waterbirds in the Wadden Sea. The logical testing variables are the number of people walking on the tidal flats and the salt marshes, and counts of leisure boats. Such data are partly available for sub-areas but it is unlikely that they are available for all areas. If available, they are based on expert judgement but are not expressed as time series (Koffijberg et al., 2003). As a result, it seems likely that we will have to use very indirect measurements on the extent of tourism (sluice passages, number of beds, and number of overnight stays) and management variables (areas closed for tourists, etc.).

2.2.3.10 Disturbance from military activities

The main centre of military activities is situated in the western part of the Dutch Wadden Sea, but military activities also occur in other areas (Essink et al., 2005). In recent years, the extent of military activities is on the decline, although the Juvre Dyb (DK) is still an active training area for flying fighters. The exercise area on Sylt (SH) was abandoned in 1992 and the exercise area on Terschelling (NL) was abandoned in 1995. As with disturbance from recreation, military activities may disturb birds during feeding and during roosting. We expect fewer birds with more military activity, although a possible confounding factor is that military areas are often closed to the general public. Thus the possibly negative effect of the military activity may be offset or even more than offset by the reduction in disturbance from recreational activities. Higher breeding densities were observed in dune areas on Vlieland closed to the general public (de Roos, 1972). Detailed studies on the impact of military exercises are lacking, but negative impacts cannot be excluded in many areas in the Dutch Wadden Sea (Heunks et al., 2007). Thus, disturbance from military activities is a potential candidate to explain contrasting trends in the number of waterbirds. To test this hypothesis we need information on the type and intensity of military activities in different areas, collected in such a way that these areas may be meaningfully compared.

2.2.3.11 Disturbance from civilian air traffic

Civilian air traffic may disturb birds and civilian airports are scattered throughout the Wadden Sea area. There is also a tendency for civilian air traffic to increase. According to one study, an increase in air traffic may actually decrease disturbance due to habituation (Smit, 2004), but this conclusion has been challenged. Disturbance from civilian air traffic is a potential candidate to explain contrasting trends in the number of waterbirds. To test this hypothesis we need information on the type and intensity of civilian air traffic in different areas of the Wadden Sea. Site based information is available based on expert judgement but not expressed as time series (Koffijberg et al., 2003).

2.2.3.12 Ecological light pollution

From an evolutionary perspective, humans have started to artificially light the night-time sky only very recently. Because animals (including man) and plants did not evolve under these artificial conditions, they are maladapted. As a result, night lighting may have serious negative consequences for the ecosystem, which made Longcore & Rich (2004) coin the term "ecological light pollution". Artificial night lighting can disturb development, activity patterns and hormone regulated processes, such as the internal clock mechanism (Rich and Longcore, 2006). Many bird species that migrate during night-time are attracted to and disoriented by sources of artificial light, a phenomenon called positive phototaxis. Depending on the circumstances, they can be strongly attracted to them and get trapped or disoriented (Verheijen, 1985). This may cause direct mortality, or may have indirect negative effects through the depletion of their energy reserves. There is evidence that nocturnal migrants are especially disoriented by red and white light (Poot et al., 2008). Reviewing the literature, Gauthreaux & Belser (2006) conclude that "all evidence indicates that the increasing use of artificial light at night is having an adverse effect on populations of birds, particularly those that typically migrate at night". However, it is also possible that birds feeding on mudflats find it easier to feed at night when these mudflats are lit. Similarly, artificial night lighting may influence the attack success of predators hunting the waterbirds. Thus, such lighting may impact birds in the Wadden Sea, but whether this is actually the case is not known. The extent of the effect is likely to vary between different regions in the Wadden Sea, so it is worthy of further investigation. The most logical testing variables are the extent and intensity of artificial night lighting in different regions of the Wadden Sea.

2.2.3.13 Area of SPA or protection levels

So far, we have looked at human activities that are likely to have a negative impact on the birds. However, some activities are specifically meant to improve conditions for the birds. In most cases this amounts to protecting the birds from human activities that may cause harm. With the exception of some major waterways, nearly all of the tidal flats and subtidal regions of the international Wadden Sea are designated as Wadden Sea Conservation Area, Particular Sensitive Sea Area (PSSA), Birds Directive Special Protection Area (SPAs), Habitats Directive Special Area of conservation (SAC) and Ramsar area (Essink et al., 2005). In terms of percentage area designated there is not much difference between the different regions (Koffijberg et al., 2003). However, there are clear differences in the level of protection. The most extreme form of protection is a zero-use area, but although zero-use areas have been designated in several Wadden Sea countries, the total surface is still only a very small fraction of the international Wadden Sea (Essink et al., 2005) and the different zero-use areas were designated at different moments in time (Essink et al., 2005). Furthermore, there are differences in the sizes of the core zones of the conservation areas. In The Netherlands, the core zones (formerly known as Article 17 areas of the Nature Protection Act) cover 5-10% of the Wadden Sea, whereas in the German national parks the core zones with comparable protection level occupy 40-50% of the area. Site-based information about protection status is available (Koffijberg et al., 2003). Summarizing, differences in general protective regimes may potentially explain contrasting trends. However, in case it is possible to relate contrasting trends to differences in protective regimes, our next step should be to find out which specific human activities are underlying these differences.

2.2.3.14 Pollution

Pollution has many faces. In the Wadden Sea Quality Status Report 2004, almost 60 pages are devoted to natural contaminants (metals, organic micropollutants), xenobiotics (PCBs, lindane, DDT, DDD, DDE, HCB, TBT, TPT), oil pollution and newly emerging xenobiotics (BFRs, PFOs, IRGAROL, alkylphenols, bisphenol-A, phtalates, polycyclic musk fragrances) (Essink et al., 2005). Thus, inclusion of the concentration levels of each specific pollutant as a testing variable is a tall order. The general picture that emerges from the Quality Status Report 2004 is that there are clear regional differences in pollution and that for many pollutants the level of pollution is declining. Thus, pollution is a good candidate to explain contrasting trends of waterbirds. Assuming that high levels of pollution have a negative effect on birds, we predict more steeply increasing bird numbers in areas where levels of pollution are declining more strongly. An implicit assumption is that the pollutants either affect the prey and/or have a more or less immediate effect on the birds. This applies to oil pollution and to the pesticides that strongly affected several breeding bird species in the 1960s in the Dutch Wadden Sea (Essink & Wolff, 1983). However, there are also pollutants that slowly accumulate in the birds over many years and only gradually impair their fitness. In that case the birds may experience the negative impact of the pollution on the breeding grounds (via reduced reproduction) or elsewhere along the migration route (via an increased mortality risk). For such "slow" pollutants, we will only be able to link contrasting trends to changes in pollution levels if the birds actively avoid heavily polluted areas.

2.2.4 Changes in biological community

The following changes in biological community were not included in Table 2 and Table 4:

- Toxic algal blooms. Such blooms are considered a risk for the future due to climate change, but there is no strong evidence that such blooms have regularly occurred in the past.

2.2.4.1 Natural predators

Use of pesticides, especially DDT, caused dramatic decreases in the number of top predators, like birds of prey. When usage of DDT was prohibited during the 1970s, the number of natural predators started to increase again and this increase has not stopped. Risk of predation may no longer be negligible, as it probably was during the 1960s. Locally, there is evidence that risk of predation may be substantial (Cresswell & Whitfield, 1994; Whitfield, 2003). High risk of predation may cause birds to move elsewhere (Ydenberg et al., 2004). Thus, we predict that an increase in the number of birds of prey will lead to a decline in the number of waterbirds, especially in those species that run a high risk of predation. To assess predation risk the diet of the birds of prey must be known. To test this hypothesis we need information on the numbers of raptors in each region and their diet.

2.2.4.2 Infection

Waterbirds may die from infection with a disease, be it a virus, a bacteria or a multi-cellular parasite. Theoretically one can imagine that the risk of infection has increased in certain areas and decreased in other areas and that this has led to changing numbers. The problem with this hypothetical possibility is that to date there is no evidence that the possibility is more than hypothetical. Mass mortality of common eider in the Dutch and German Wadden Sea (Camphuysen et al., 2002) has been attributed to infection with parasites (Smaal et al., 2001). However, the available evidence makes it much more likely that food shortage was the primary determinant of the mass mortality (Ens et al., 2002; Kats, 2007; Thieltges et al., 2006). The first step in testing this hypothesis would be to investigate if there are regional differences in the risk of infection for various diseases. Lack of data will make it impossible to take this first step. However, a study of potential changes in the metazoan endoparasite fauna in the northern Wadden Sea during the past 4 decades suggested little change during this period (Thieltges et al., 2008). Thus, we feel that this hypothesis is not a likely candidate to explain contrasting trends of waterbirds in the Wadden Sea.

2.2.4.3 Invasion of exotic species

Man has introduced many new species into the Wadden Sea, both voluntarily and involuntarily (Wolff, 2005). Some of these species have increased, or are increasing, exponentially. A prime example is the Pacific oyster, which was introduced in 1978 on Texel (Wim Wolff, pers. comm.), in 1986 on the island of Sylt and is now found throughout the Wadden Sea, but is still increasing its coverage/density (Nehls & Büttger, 2007). Since the Pacific oyster preferentially settles on mussel beds, we would expect that an increase in oyster beds would occur at the expense of mussel beds, but this has been hard to prove in e.g. Germany, where the climate seems the prime determinant of the current decline in mussels (Nehls et al., 2006). However, once Pacific oysters have taken over, mussels are relegated to an "understory suspensions feeder", both less abundant and less available to birds.

In the Quality Status Report, six species are singled out because they are having, or are expected to have, a strong effect on the ecosystem of the Wadden Sea (Essink et al., 2005). These species are: common cord-grass (Spartina anglica), Japanese seaweed (Sargassum muticum), the North American polychaete Marenzelleria cf. wireni, American razor clam (Ensis directus), American slipper limpet (Crepidula fornicata) and Pacific oyster (Crassostrea gigas). Some of these introduced species are expected to be beneficial for specific species of birds, whereas others may have a negative impact. For the Pacific oyster, it has been established that there was a clear change in abundance during the study period, i.e. the period for which we analyzed data, and that initially the species only occurred in the northern and western parts of the Wadden Sea, but not in the central part. Thus, invading exotic species may contribute to explaining contrasting trends of waterbirds in the Wadden Sea. There is no need to include all known introduced exotic species in the analysis, but only the species that seem to have an impact on the ecosystem functioning. At present, the ecological impact of Japanese seaweed and American slipper limpet seems minimal. In contrast, the available evidence indicates that the Pacific oyster may strongly reduce the foraging opportunities of some shellfish-eating bird species (Scheiffarth et al., 2007).

2.2.5 Externally mediated population changes

Due to events outside the Wadden Sea, the total population of birds using the Wadden Sea may either increase or decrease. Since there are regional differences in the suitability of an area for a particular bird species, we may expect a redistribution of birds, which will appear as differences in trends between different areas. Under the buffer hypothesis, we expect that the best areas fill up first and poorer areas will only be filled up once the best areas are "full" (Kluyver & Tinbergen, 1953). Such processes may operate both on a small scale (Fretwell & Lucas, Jr., 1970; Sutherland, 1983), and on a large scale (Gill et al., 2001). Making precise predictions is difficult, as these depend on the details of the process (Bernstein et al., 1988; van der Meer & Ens, 1997). Our general expectation is that when populations decline, these declines will be especially apparent in "poor" areas. When populations increase, we expect this increase to mainly take place in the "poor" areas.

In the following, the word "region" refers to the respective Wadden Sea "country", i.e. The Netherlands, Lower Saxony, Schleswig-Holstein and Denmark. Ultimately, we would like to use smaller and more spatial units, but for the present exploratory analysis this proved not feasible.

Tidal flats
(Photo: A. Szczesinski)

3.1 Selection of study species

Data on trends of migratory waterbirds in the period 1987/88-2005/06 are derived from the 'Joint Monitoring Program of Migratory Birds in the Wadden Sea'. This program, consisting of international synchronous counts, spring-tide counts and aerial counts (only common shelduck and common eider), has been carried out by all Wadden Sea countries since 1992 (Blew et al., 2007). Some differences between the countries' programs exist, due to different national approaches and older existing counting programs, but these do not hamper the overall goal for calculating trends. Because many usable counting data before 1992 exist as well, it has been decided to include counts back to the season 1987/1988 in the recent trend analyses. For details on study area and counting effort we refer to Blew et al. (2007). For our analyses, we used data on 26 common migratory waterbirds (Table 3). These are all species which use the Wadden Sea as a staging, roosting or wintering area during one part of their yearly cycle with their entire flyway population or large parts of their flyway population. Species which only occur in low numbers or species which cannot be adequately counted have been excluded from the analyses, after consulting with the JMMB.

3.2 Data on testing variables

From the list of hypotheses, a long list of testing variables was derived. For each of these testing variables we assessed the importance to this study and we present some crude information on the availability on data for this variable in each of the countries (Table 4).

Euring	Species	Preferred food	Preferred habitat
720	Great cormorant	Fish	Open water
1440	Eurasian spoonbill	Fish/shrimp	Intertidal flats
1680	Brent goose	Grass	Saltmarsh
1670	Barnacle goose	Grass	Saltmarsh
1730	Common shelduck	Molluscs	Intertidal flats
1790	Eurasian wigeon	Grass	Saltmarsh
1840	Common teal	Seeds	Saltmarsh, low salinity tidal flats
1860	Mallard	Seeds/benthos	Saltmarsh, intertidal flats
1890	Northern pintail	Seeds/benthos	Saltmarsh, intertidal flats
2060	Common eider	Shellfish	Open water
4500	Eurasian oystercatcher	Shellfish	Intertidal flats
4560	Pied avocet	Benthos	Intertidal flats
4700	Great ringed plover*	Benthos	Intertidal flats
4860	Grey plover	Benthos	Intertidal flats
4690	Red knot*	Benthos/shellfish	Intertidal flats
4970	Sanderling	Benthos	Intertidal flats
5120	Dunlin	Benthos	Intertidal flats
5340	Bar-tailed godwit*	Benthos	Intertidal flats
5410	Eurasian curlew	Benthos	Intertidal flats
5450	Spotted redshank	Benthos/fish/shrimp	Intertidal flats
5460	Common redshank*	Benthos	Intertidal flats
5480	Common greenshank	Benthos/fish/shrimp	Intertidal flats
5610	Ruddy turnstone*	Benthos	Intertidal flats
5820	Common black-headed gull	Benthos/fish/shrimp	Intertidal flats
5900	Common gull	Benthos	Intertidal flats
5920	Herring gull	Benthos/shellfish	Intertidal flats

Table 3. List of the 26 species for which sufficient data were available to warrant inclusion in the study on contrasting trends of waterbirds in the international Wadden Sea. Species marked with a * consist of different sub-populations, but no distinction was attempted in this study.

Table 4 does not list "benthic food stocks in general" as a testing variable, but only specific components like mussel beds and cockle stocks. It is clear that when benthic food stocks increase we expect more birds. However, benthic food stocks may increase or decrease for many different reasons. As a result, the very fact that total benthic food stocks have increased does not allow us to discriminate between climate change, eutrophication or a specific human activity. For this reason, "benthic food stocks in general" was not listed as a testing variable in Table 4. Yet we did obtain

Table 4: List of testing variables and the availability of information on these testing variables for each of the four Wadden Sea "countries". For each country and testing variable, it is indicated what parameter is actually measured. A small x indicates that local time series are available and a capital X indicates that data are available for the entire area. With the symbols -, + and ++ it is indicated whether compiling information on that variable has no priority (-), little priority (+) or high priority (++) for the purpose of our study.

Testing variable		NL	LS	SH	DK
Climate change					
Hypsometric curve	-	X	X	X	X
Ambient temperature	++	x	X	X	X
Frequency severe winters	++	x	x	x	X
Wind direction	+	x	X	X	X
Storm frequency	+	x	x	x	X
Exposure time tidal flats	+	x	x	x	X
Phenological data	++	x	x	x	X
Declining eutrophication					
Nutrient inputs (N, P)	++	x	x	x	X
Primary production [1]	+	x	x	x	X
Human activities and impacts					
Hunting bags	++		X	X	X[2]
Hunting policy	++	X	X	X	X
Landings of shrimp	+	X	X	X	X
Closed areas for shrimp fishery	+	X	X	X	X
Mussel landings	++	X	X	X	X
Area and biomass of mussel beds	++	X	x	X	X
Closed areas for mussel fishery	++	X	X	X	X
Cockle landings	++	X	X	X	X
Cockle stocks	++	X			x[3]
Quality of cockles	++	x			
Sediment composition	+	X			x
Closed areas for cockle fishery	++	X	X	X	X
"Recent" area lost to reclamation	++	X	X	X	X
Hypsometric curve (2)	+	X	X	X	x
Sediment composition(2)	+	X			x
Turbidity	++	x			x
Dredging activity	++	X	X	X	x
Saltmarsh management	++		X	X	
Saltmarsh vegetation	++	x	X	X	x
Hypsometric curve (3)	-	X	x	x	
Recreation activity	++	x	x	x	x
Recreation management	++	x	x	x	x
Military exercises	++	X	X	X	X
Artificial night lighting	++				
Area of SPA or protection levels	+	X	X	X	X
Levels of pollutants	++	x	x	x	x
Changes in the biological community					
Populations natural predators	++	X	x	x	
Prey choice predators	++	x	x	x	x
Intensity of infection	+				
Occurrence exotic benthic species	++	X	x	x	x
Total numbers using Wadden Sea	++	X	x	x	X

[1] The only data on primary production that is available, is data on the production of phytoplankton. There is no data on the production by benthic algae.

[2] Information from a larger region than the Wadden Sea.

[3] Only information for some years.

different data sets on benthic food stocks and we did investigate whether these could be related to changes in bird numbers.

In most cases, it proved to be rather difficult and time consuming to assemble appropriate data sets for the testing variables. We had to make a selection even among the testing variables classified as having high priority. Below is the description of data sets obtained and which information was used in the analysis.

3.2.1 Winter severity

Data on ambient temperature are available from the European Climate Assessment & Dataset (ECA&D) project http://eca.knmi.nl/. Daily values for daily minimum, daily maximum and daily mean temperature are available for the weather stations depicted in Figure 2. We downloaded data for the weather stations of De Kooij (127), Leeuwarden (544), Eelde (129), Helgoland (413), Schleswig (415) and List (414). We used "blended data", which means that the gaps in a daily series are filled in with observations from nearby stations, provided that they are within 25km distance and that height differences are less than 50m. We extracted daily minimum and maximum temperatures and calculated the following numbers for each winter:

1. V = number of frost days
   (minimum temperature < 0° C)
2. Y = number of ice days
   (maximum temperature < 0° C)
3. Z = number of very cold days
   (minimum temperature < -10° C)

This allowed us to calculate the IJnsen index (IJnsen, 1988), which is an index of winter severity often used in ecological studies:

IJnsen index = 0.00275*V2 + 0.667*Y + 1.111*Z

From the winter of 1952/1953 (which we indicate as winter 1953) onwards data were available for all six weather stations, allowing us to compare the various indices. Clearly, cold winters are cold everywhere and this does not depend on the index chosen. In Figure 3 we have depicted the IJnsen index, but similar patterns are evident for the number of frost days, the number of ice days and the number of very cold days. It is also clear that cold winters have become less frequent. However, when we study the data in more detail it becomes clear that the weather stations located inland, tend to be colder than the weather stations direct-

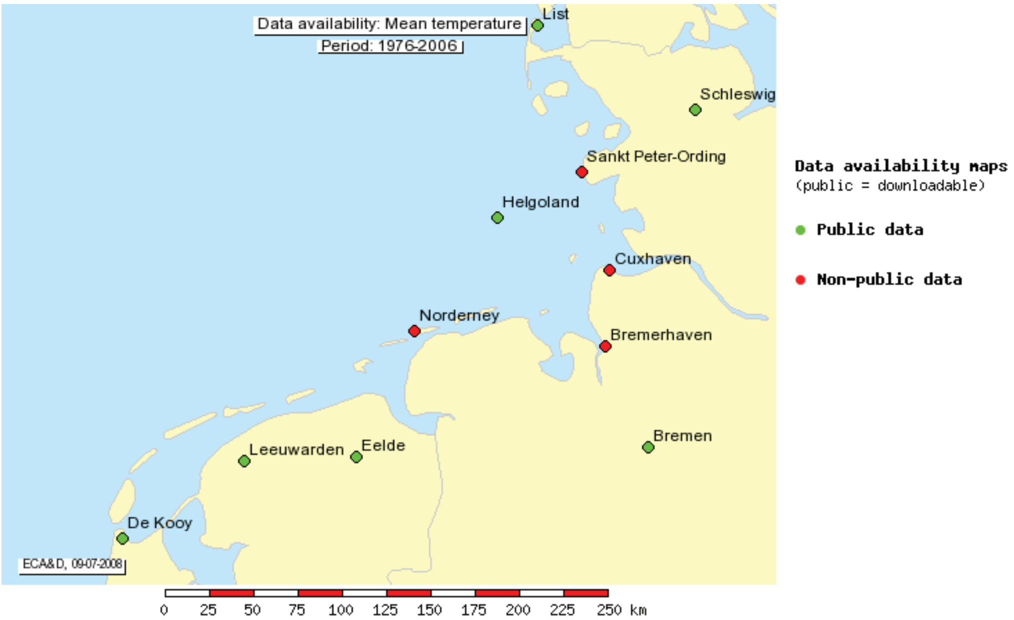


Figure 2:
Map of weather stations around the international Wadden Sea for which daily temperature data are available in the database of the European Climate Assessment & Dataset (ECA&D) project. In a selected number of cases the data can be freely downloaded (indicated with green dots as public data).

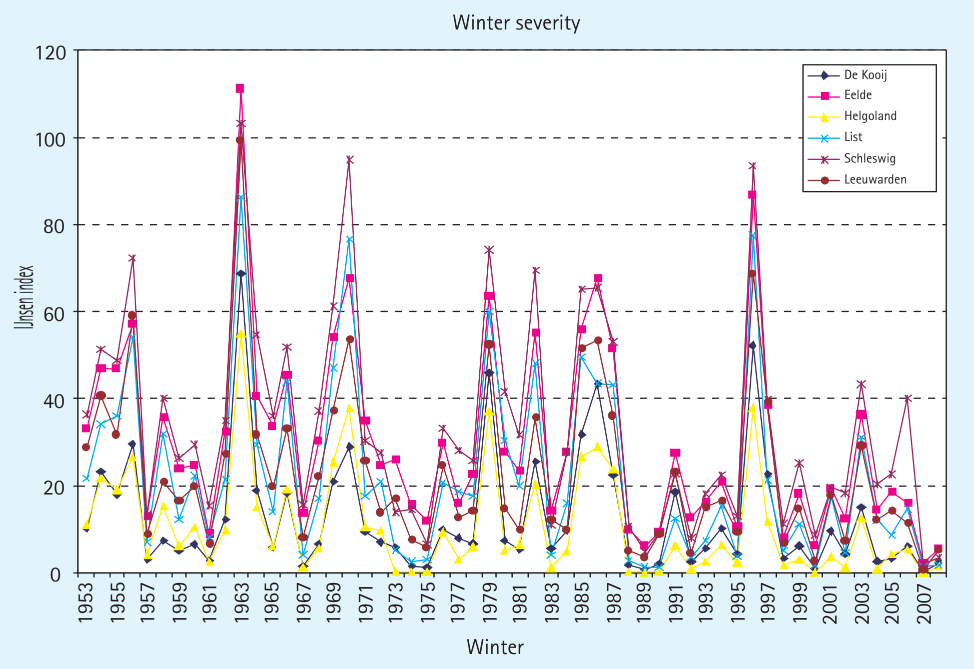


Figure 3: IJnsen index for winter severity for the winters 1953-2008 comparing data from six weather stations in or near to the international Wadden Sea.

ly adjacent to the Wadden Sea and these Wadden Sea locations are colder than Helgoland, located far out in the North Sea. This is also clear from the average values listed in Table 5. Among the terrestrial weather stations, Schleswig is colder than Eelde and Eelde is colder than Leeuwarden. Among the Wadden Sea weather stations, List is colder than De Kooij.

The fact that winters on Helgoland and Schleswig differ more from each other than winters on De Kooij in the far west of the Wadden Sea and List in the far north-east of the Wadden Sea, implies that our current selection of weather stations cannot be used to characterize the weather in the various parts of the Wadden Sea. Probably, the situation would be improved if data could be obtained from Sankt-Peter Ording, Cuxhaven and Norderney. However, these data are not freely available.

For the analysis, we used the data listed in Table 6. In the period 1953-2008, there is a clear tendency for winters to become less severe, despite large variations in winter severity between years (Figure 3). However, in the period 1987-2005, the period of our data analysis, the most severe winter occurs halfway in 1996 (Table 6). This explains why there is no clear trend in winter severity for the two countries for which we have adequate data.

Table 5: Average values for various indices of winter severity of six different weather stations for the winters 1953-2008. The weather stations are ordered on the basis of the IJnsen index.

Weather station		Number of frost days		Number of ice days		Number of very cold days		IJnsen index of winter severity	
		mean	SD	mean	SD	mean	SD	mean	SD
413	Helgoland	32.3	22.0	9.3	11.0	0.1	0.4	10.4	12.0
127	De Kooij	39.9	19.1	8.9	10.2	1.2	2.7	12.6	14.1
414	List	54.2	27.9	15.8	14.4	1.3	3.1	22.2	20.7
544	Leeuwarden	61.1	21.6	10.7	10.6	3.8	5.7	22.8	19.1
129	Eelde	71.5	21.1	13.8	12.0	5.0	6.6	30.1	21.8
415	Schleswig	74.0	24.0	19.4	15.3	3.9	5.0	33.9	24.1

Year	NL	LS	SH	DK
1987	22.46			43.20
1988	1.66			2.82
1989	0.70			1.29
1990	1.88			1.29
1991	18.46			12.40
1992	2.43			3.46
1993	5.57			7.29
1994	10.19			15.16
1995	4.23			3.72
1996	52.12			77.48
1997	22.62			21.30
1998	3.21			4.98
1999	6.18			11.16
2000	0.79			1.66
2001	9.52			17.26
2002	4.16			4.53
2003	15.01			31.15
2004	2.53			12.11
2005	3.18			8.64

Table 6: Data on winter severity, expressed as the IJnsen index, used in the analysis. We used temperature data from De Kooij to calculate the IJnsen index for NL, and data from List to calculate the IJnsen index for DK. Data for LS and SH had to be assigned as missing.

3.2.2 Eutrophication

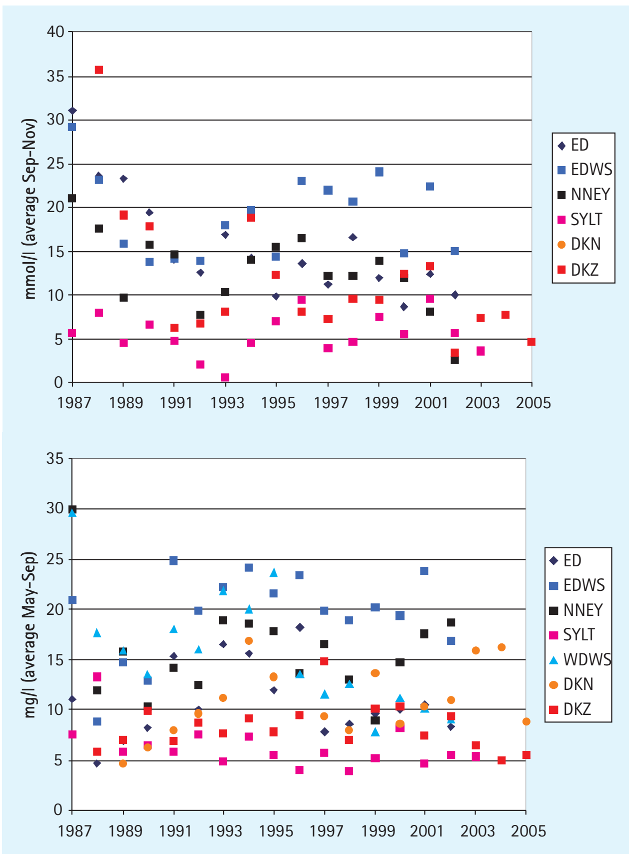
There is discussion among experts which data to use to characterize the eutrophication status of different parts of the Wadden Sea. On the basis of calculations with an ecosystem model, Brinkman & Smaal (2004) conclude that total phosphate is currently limiting the carrying capacity for filter feeders in the western Dutch Wadden Sea. A similar conclusion was reached by Philippart *et al.* (2007) when analysing time series on nutrients, primary production, benthos and birds for the same area. However, according to the analyses by Justus van Beusekom (*pers. comm.*) for the Quality Status Report 2004, summer chlorophyll and autumn NH_4^+ and NO_2 values are good indicators of the eutrophication status (Essink *et al.*, 2005). Summer chlorophyll seems to be the best indicator working for all long-term data sets available for that report (Western Dutch Wadden Sea, Norderney, Sylt). Summer chlorophyll-a does not work in the Eastern Dutch Wadden Sea, presumably because of high turbidity. We do not want to take sides in this scientific debate, but for pragmatic reasons (easily accessible data) decided to follow the criteria adopted in the Quality Status Report. Justus van Beusekom provided the monthly data for the eastern Dutch Wadden Sea, the western Dutch Wadden Sea, Norderney and Sylt for the years 1987-2002 (2003) that were also used in the Quality Status Report. Jacob Carstensen agreed to use the data from the Danish National Aquatic Monitoring and Assessment Program (DNAMAP). To obtain summer chlorophyll-a for the Danish data, we averaged values for May, June, July, August and September. To obtain autumn NH_4^+ and NO_2, we averaged values for September, October and November. We averaged stations in Grådyb, Juvre Dyb and Knude Dyb, to obtain values for the northern Danish Wadden Sea (DK1), whereas stations in Lister Dyb were averaged to obtain values for the southern Danish Wadden Sea (DK2). The resulting data set is listed in Table 7.

NH_4^+ and NO_2 concentrations have decreased in all countries except Schleswig-Holstein (data from Sylt). Chlorophyll a concentrations have decreased in most countries, but apparently not in parts of the Danish (DKN) and Dutch Wadden Sea (EDWS).NH_4^+ and NO_2 concentrations have decreased in all countries, except Schleswig-Holstein (data from Sylt). Chlorophyll a concentrations have decreased in most countries, but apparently not in parts of the Danish (DKN) and Dutch Wadden Sea (EDWS).

Table 7:
Data on eutrophication status used in this study. We used two measures: Chlorophyll a and NH_4^+ and NO_2. We obtained time series for the following areas: NL1 = eastern Dutch Wadden Sea, NL2 = western Dutch Wadden Sea, DK1 = norther Danish Wadden Sea, DK2 = southern Danish Wadden Sea. For LS we used the data from Norderney and for SH we used the data for Sylt. Values for NH_4^+ and NO_2 for DK1 are missing.

	Chlorophyl a (µg/l)						NH_4^+ and NO_2 (µM/l)				
Year	NL1	NL2	LS	SH	DK1	DK2	NL1	NL2	LS	SH	DK2
1987	20.99	29.67	29.99	7.61			29.08	24.79	21.05	5.63	35.71
1988	8.80	17.69	11.93	13.24		5.80	23.09	15.43	17.57	7.92	19.12
1989	14.70	15.90	15.69	5.83	4.67	6.99	15.89	14.48	9.73	4.49	17.70
1990	12.87	13.53	10.32	6.49	6.29	9.84	13.74	8.77	15.70	6.53	6.21
1991	24.83	18.08	14.15	5.84	7.90	6.95	14.16	13.43	14.66	4.74	6.65
1992	19.86	15.97	12.48	7.56	9.60	8.75	13.92	13.71	7.83	2.12	8.05
1993	22.28	21.90	18.84	4.77	11.20	7.66	17.95	12.24	10.35	0.62	18.86
1994	24.20	20.01	18.64	7.24	16.97	9.17	19.75	15.03	14.10	4.42	12.25
1995	21.59	23.70	17.76	5.47	13.32	7.85	14.28	12.42	15.48	7.04	8.02
1996	23.46	13.52	13.64	4.03	9.43	9.52	22.91	10.51	16.36	9.40	7.09
1997	19.88	11.62	16.52	5.68	9.43	14.88	21.88	11.12	12.16	3.82	9.61
1998	18.92	12.57	12.96	3.96	7.89	7.07	20.59	10.45	12.11	4.70	9.48
1999	20.23	7.83	8.98	5.21	13.60	10.21	24.01	11.87	13.82	7.50	12.34
2000	19.36	11.21	14.67	8.24	8.56	10.26	14.84	7.11	11.97	5.55	13.25
2001	23.75	10.20	17.55	4.66	10.28	7.47	22.33	10.89	8.02	9.59	3.42
2002	16.87	9.06	18.78	5.46	10.87	9.38	14.87	8.12	2.53	5.62	7.29
2003				5.30	15.92	6.57				3.60	7.82
2004					16.25	4.88					4.59
2005					8.89	5.52					5.61

Figure 4:
Trends in 1) sum of autumn NH_4^+ and NO_2 concentrations (top) and 2) summer chlorophyll-a concentrations (bottom) in different areas in the Netherlands (blue dots), Niedersachsen (black), Schleswig-Holstein (purple) and Denmark (red).



3.2.3 Cockle fishery

Data on cockle landings were obtained from the Common Wadden Sea Secretariat (CWSS), which assembled the data from different sources (DTU Aqua, Fischerblatt, Wagenigen IMARES (formerly RIVO), PVIS) as part of the preparations for the next Quality Status Report. The data are listed in Table 8 (Figure 5).

3.2.4 Mussel landings and mussel stocks

Data on mussel landings were obtained from own requests and from the secretariat (CWSS), which derived their data from the Trilateral Workshop on Blue Mussel Fishery Management 2008.

Mussel landings (Figure 6, Table 9) fluctuated less markedly compared to cockle landings (Figure 5). As for cockles, landings were on average highest from The Netherlands. However, the differences between countries were not as marked as for cockle landings. In the period 1987-2005 landings have declined in all countries. The available data suggest that trends in the stocks of littoral mussels are quite different between countries (Figure 7, Table 9). There are many missing data and for Denmark, the figure includes data on sublittoral stocks. Nonetheless, there is a clear difference between The Netherlands, where stocks have increased during the last decade, and the other countries, where stocks have declined.

Table 8: Annual landings of cockles (in tons fresh weight) in the four different countries. Fresh weight refers to the weight of live cockles, including the shell.

Year	NL	LS	SH	DK
1987	8,000	4,747	337	0
1988	55,333	987	418	1,189
1989	42,667	2,633	269	4,454
1990	36,953	4,960	0	3,010
1991	0	3,487	0	321
1992	16,667	0	0	2,423
1993	31,500	0	0	543
1994	15,880	0	0	31
1995	24,880	0	0	0
1996	0	0	0	5
1997	9,633	0	0	2,603
1998	62,253	0	0	1,993
1999	52,000	53	0	246
2000	19,333	0	0	2,089
2001	12,667	0	0	2,392
2002	12,000	0	0	78
2003	1,913	0	0	258

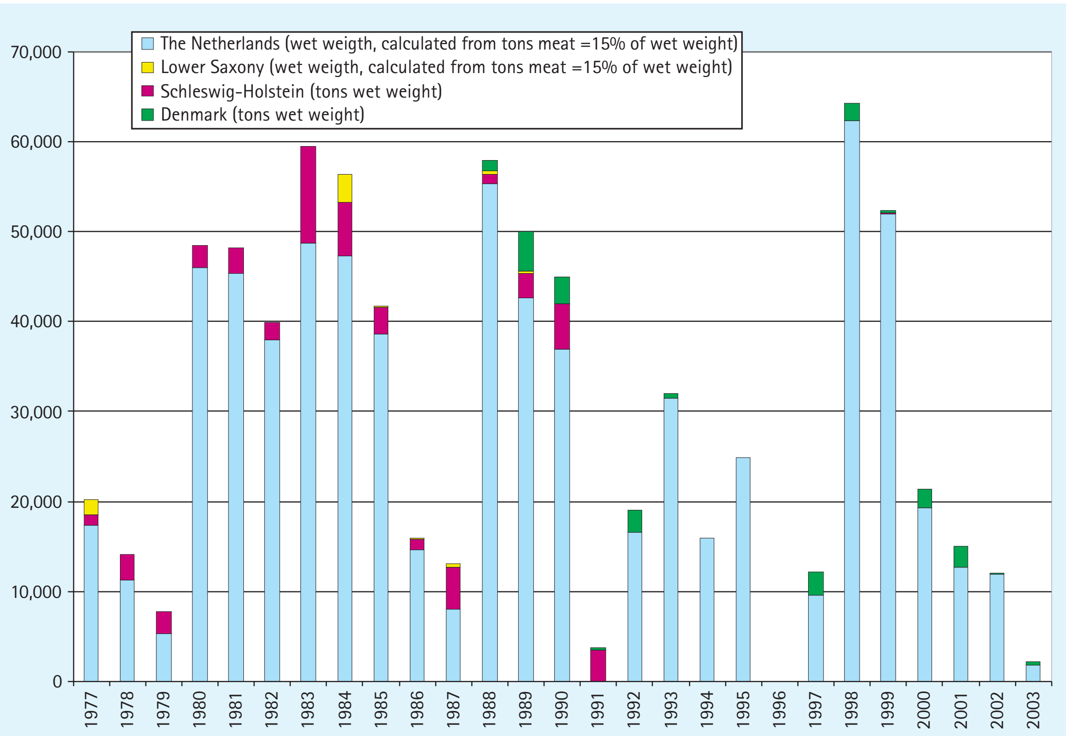


Figure 5: Annual landings of cockles in the four different countries in tons fresh weight (this is the weight of the live cockle, including the shell).

Table 9:
Data on mussel landings and mussel stocks (tons fresh weight, which includes the weight of the shell) for the four different Wadden Sea countries. Data on mussel stocks refer to stocks in the eulittoral zone, except for Denmark (DK), where figures for sublittoral mussel stocks are included with the eulittoral stocks.

	Mussel landings (tons fresh weight)				Mussel stocks (tons fresh weight)			
Year	NL	LS	SH	DK	NL	LS	SH	DK
1987	63,443	5,467	20,000	17,384				26,950
1988	36,788	9,842	19,800	1,161			53,000	15,400
1989	72,889	9,024	9,525	1,403			61,000	27,720
1990	74,511	4,613	15,625	1,759	41,628		27,000	40,040
1991	11,917	580	29,397	5,539	1,704		21,000	27,540
1992	25,854	8,256	42,539	5,041	1,044		36,000	61,600
1993	30,256	2,971	21,695	3,498	1,335		35,000	90,090
1994	51,358	285	4,583	4,397	2,494			117,000
1995	30,330	6,089	11,693	8,931	12,428			66,000
1996	39,703	5,154	32,874	2,212	5,194	1,000		47,000
1997	40,414	5,761	16,569	262	25,463	27,000		11,800
1998	60,476	15,678	15,535	3,745	16,178		31,742	66,225
1999	55,555	16,601	21,311	5,121	10,810	110,000	39,718	66,200
2000	31,253	11,944	12,177	2,718	16,543	70,000	24,666	49,100
2001	16,231	6,643	4,996	4,993	18,085	55,000	27,534	
2002	30,628	642	7,377	2,428	49,905	25,000	15,450	16,600
2003	35,376	3,988	24,561	263	64,155	14,000	12,920	
2004		2,669	12,473		73,531	15,000	12,604	5,840
2005		3,792			50,156	9,000	5,357	

Figure 6:
Annual mussel landings (in tons fresh weight, including the weight of the shell) for the four Wadden Sea countries for the period 1965-2003.

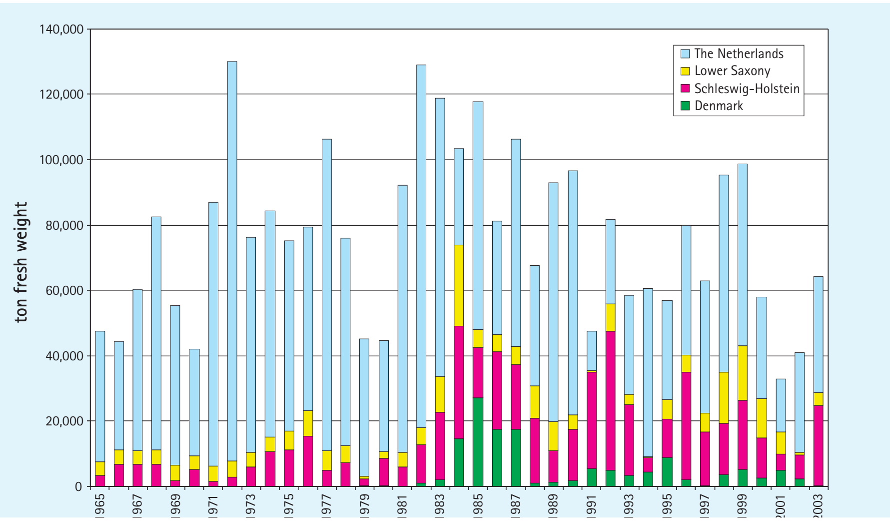
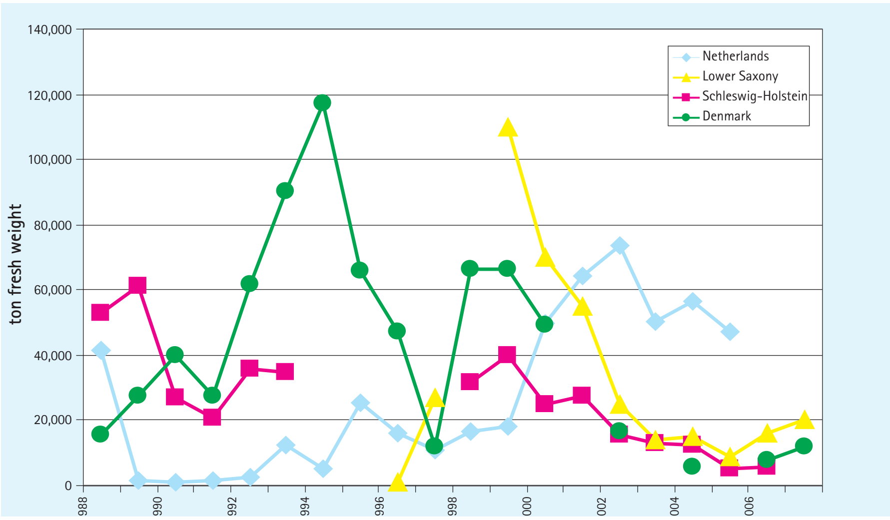


Figure 7:
Stocks of littoral mussels (tons fresh weight, including the weight of the shell). For Denmark, the figures include data on sublittoral mussel stocks as well.



3.2.5 Macrozoobenthos

According to data from Essink *et al.* (2006) the biomass of polychaetes increased in all Wadden Sea countries. Data from Drent (*pers. comm.*), which are from different regions within a country, are in agreement with his findings, but indicate declining polychaetes biomasses in several parts of the Dutch Wadden Sea (Table 10).

Data from Essink *et al.* (2006) and Drent (*pers. comm.*) (Table 11) indicate increasing bivalve biomasses in most parts of the Dutch Wadden Sea, Lower Saxony and Schleswig-Holstein, but decreases in Denmark (Table 12).

Year	NL (BZ)	NL (WS)	NL (PS)	NL (GW)	NL (DD)	LS (NN)	SH
1987	9.044					19.844	
1988	12.607		19.033	20.640	7.867	13.693	1.667
1989	10.321		16.834	30.820	12.933	23.084	1.772
1990	12.195	3.968	14.267	24.780	13.910	17.487	678
1991	7.629	3.568	5.617	14.740	13.332	23.657	6.433
1992	12.654	2.400	14.787	23.100	13.591	21.970	5.593
1993	10.038	1.285	16.581	31.300	11.608	17.559	6.057
1994	10.410	611	8.166	26.860	9.536	14.142	4.792
1995	11.050	834	7.651	22.440	5.636	21.629	1.872
1996	8.859	4.411	9.476	20.320	1.980	17.693	1.945
1997	9.655	6.590	7.651	16.284	3.749	10.648	1.449
1998	11.481	6.469	9.891	21.108	2.767	16.330	5.889
1999	14.966	3.537	17.932	26.147	3.371	22.406	3.147
2000	17.367	10.178	18.260	29.842	3.662	36.413	2.718
2001	14.798	13.770	10.116	13.630	3.329	24.522	2.688
2002	14.576	18.230	9.194	15.281	3.382	23.105	2.660
2003	17.869	16.160	11.293	21.121	2.603	16.138	3.028
2004	15.874	3.332	13.639	25.050	3.012	22.053	3.902
2005	13.516	3.307	14.906	20.943	2.851	21.420	4.288

Table 10: Data on biomass of polychaetes (g/m^2 AFDW) for different parts of the Wadden Sea obtained from Drent (*pers. comm.*).

(Photo: A. Szczesinski)

Table 11:
Data on biomass of bivalves (g/m^2 AFDW, selection of species suitable as wader food) for different parts of the Wadden Sea. Data obtained from Drent (pers. comm.)

Year	NL (BZ)	NL (WS)	NL (PS)	NL (GW)	NL (DD)	LS (NN)	SH
1987	18.438					6.618	
1988	21.408		16.900	27.640	2.766	12.880	2.313
1989	17.305		15.934	19.000	1.534	17.697	2.192
1990	18.080	10.062	6.700	22.260	991	41.244	1.552
1991	4.990	6.211	4.830	6.780	1.550	47.116	5.780
1992	13.344	5.713	7.550	23.180	2.230	26.438	2.568
1993	26.184	11.053	8.570	34.660	2.516	14.065	4.093
1994	28.754	7.933	17.042	33.920	3.513	10.787	6.144
1995	26.762	16.327	17.537	63.840	3.330	6.824	7.398
1996	18.149	20.221	5.093	24.220	955	1.151	3.854
1997	16.973	32.021	8.401	44.952	2.298	3.448	1.171
1998	22.608	21.680	24.843	79.563	1.121	16.942	3.403
1999	25.945	18.941	21.982	39.832	1.141	32.712	2.433
2000	24.703	32.888	13.579	55.905	1.558	24.270	4.641
2001	18.774	52.190	17.384	34.810	1.924	40.624	9.458
2002	19.159	68.463	12.802	32.241	2.332	36.054	6.577
2003	13.850	53.746	12.118	35.155	2.314	25.906	10.144
2004	20.835	79.885	18.373	41.291	2.108	22.109	6.354
2005	27.009	46.655	10.727	55.386	1.536	16.263	5.803

3.2.6 Salt marsh vegetation

Detailed trilaterally harmonized geographical information on salt marsh vegetation is available in TMAP. However, we could not use this data for several reasons. First, all data was of recent origin; the oldest digitally available geographical data (GIS shape files) date from 1995. Second, for some countries the data are from a single period, so that it is not possible to calculate a trend line. We therefore decided to take the data on salt marsh vegetation from the Quality Status Report (Essink *et al.*, 2005). From Fig. 7.6 in the QSR 2004 we obtained the total area of salt marsh in different parts of the Wadden Sea. From Fig. 7.7 in the QSR 2004 we obtained the percentage land use of these salt marshes in 1987 and more recently, 1999/2002. From this, we could calculate for each country, the area that was intensively grazed, moderately grazed and not grazed in both periods (Table 12). Although it is mentioned in the QSR that different methods were used in these two periods, we decided to calculate a trend nonetheless, since these trends represent the best estimates of changes in salt marsh management available for our analysis.

The area of intensively grazed salt marsh decreased in all countries, the strongest in Lower Saxony and The Netherlands (Table 12, Figure 8). The area of moderately grazed salt marsh increased, especially in The Netherlands and Schleswig-Holstein. The area of ungrazed salt marsh strongly increased, especially in Schleswig-Holstein and Denmark.

Table 12:
Area of saltmarsh (ha) for each country that was intensively grazed, moderately grazed and not grazed in 1987 and in 1999/2002. See text for origin of these data.

	intensively grazed				moderately grazed				not grazed			
Year	NL	LS	SH	DK	NL	NS	SH	DK	NL	LS	SH	DK
1987	3,855	3,616	9,468	2,853	1,792	1,822	1,263	2,714	3,441	4,619	803	435
recent	1,786	1,277	5,156	1,985	3,544	2,423	2,203	2,868	3,720	6,350	4,176	1,143

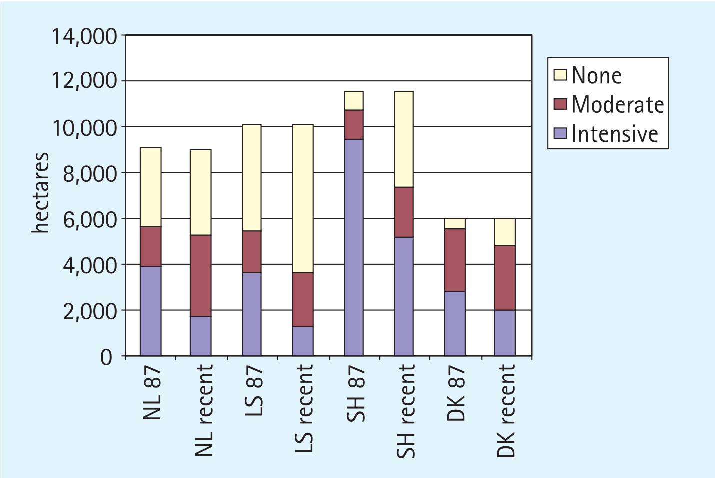


Figure 8: Trends in area of intensively grazed, moderately grazed and ungrazed saltmarshes in the Netherlands, Lower Saxony, Schleswig-Holstein and Denmark.

3.3 Data analysis

3.3.1 Calculating bird trends

To calculate year indices, waterbird counting data per site, per month, and per year were analysed with UINDEX. The program UINDEX is able to take site-, year- and month-factors and thus the phenology and the trend into account to impute missing values in the dataset (Underhill & Prys-Jones 1994). Sites are grouped in four regional strata representing the four different 'countries' (Netherlands, Lower Saxony, Schleswig-Holstein and Denmark). The imputed monthly counts are added to yearly estimates for the respective 'bird-years' covering the period from July to June in the following year.

Thereafter, we used loglinear Poisson regression in Genstat 9 to retrieve linear trends for the period 1987/88-2005/06 (similar approach as implemented in the TRIM package). Linear trends are expressed as a single estimate (including a standard error) representing the average annual increase or decrease in numbers. We did not calculate smoothed trends with TrendSpotter, as has been conducted for the migratory bird reports, because the aim of this study is to identify the possible causes of contrasting trends between the Wadden Sea countries on the long-term, and we want to relate linear trends in bird numbers to trends in environmental variables.

3.3.2 Calculating trends in testing variables

We gathered data on 13 testing variables from a variety of sources (Table 13). The testing variables can be classified into five main categories:

1. Eutrophication: sum of autumn NH_4 and NO_2 concentrations, summer chlorophyll-a concentrations.
2. Climate: index of winter severity according to the IJnsen classification.
3. Salt marsh management: area of intensively grazed, moderately grazed and ungrazed salt marsh.
4. Impact of shellfish fishery: cockle landings, blue mussel landings and blue mussel stocks.
5. Availability of benthos: biomass of polychaetes and bivalves on the basis of data from J. Drent (pers. comm.) currently analyzed for the Quality Status Report 2009 and from Essink et al. (2006).

For several testing variables, more than one time series per 'country' is available (different transects or areas). Since we only use national trends in bird numbers, we had to 'upscale' the testing variables from transects or areas within a country to national trends. We decided not to take average values from all transects within a country, because of large differences in observed trends between transects. We had no information on the representativeness of each transect or area for larger parts of the region or indeed, the entire country. Instead, we carried out the correlations between testing variables and bird trends using several alternatives for every testing variable, by taking a different transect in each alternative as the representative for the whole country. For the 13 variables we used in total 19 alternatives.

As for the bird trends, we used loglinear Poisson regression to retrieve linear trends for the period 1987/88-2005/06. Linear trends in testing variables are also expressed as a single estimate representing the average annual increase or decrease in concentration, biomass or area.

3.3.3 Analysis

Contrasting trends in bird numbers between Wadden Sea countries are presented by grouping species in five feeding guilds: herbivores (6 species), piscivores (2 species), bivalve feeders (4 species), polychaete feeders (6 species) and mixed benthos feeders (8 species).

Next, possible causes for contrasting trends were explored using ordination techniques. We used Principal Component Analysis (PCA; indirect gradient analysis) in Canoco 4.5 for Windows of a dataset containing 26 species, 19 testing variables and 4 samples (representing the four Wadden Sea regions). In a PCA the variation in the dataset is maximized, using 'theoretical' ordination axes. These axes thus correspond to the directions of the greatest variability in individual species trends. The environmental variables are correlated with the ordination axes in a second-step analysis (Leps & Smilauer, 1999). The result is an ordination diagram in which the samples (countries) are displayed by points, the species and environmental variables by arrows (the direction refers to an increase of trends). The larger the distance between the locations of the samples in the diagram, the larger the differences in species trends in these samples.

Table 13: The 13 testing variables covered in this study, including abbreviations of the several alternatives used.

Category	Testing variable	Name of variable during analyses
Eutrophication	NH_4+ NO_2	nh4no2-1, nh4no2-1
	Chlorophyll-a	chl-1, chl-2
Climate	Ijnsen-index	ijnsen
Saltmarsh	Intensively grazed	grazint
	Moderately grazed	grazmod
	Not grazed	graznot
Shellfish fishery	Cockle landings	cockle
	Mussel landings	musland
	Mussel stocks	musstock
Benthos	Biomass polychaetes (data Essink)	polyes-1, polyes-2
	Biomass polychaetes (data Drent)	polydr-1, polydr-2
	Biomass bivalves (data Essink)	bives-1, bives-2
	Biomass bivalves (data Drent)	bivdr-1, bivdr-2

Island of Amrum (Photo: J. Enemark)

4.1 Species trends

In Figure 9 trends of migratory water birds in four Wadden Sea 'countries' in the period 1987/88-2005/06 are presented, by grouping species in feeding guilds. Piscivores (spoonbill and cormorant) are strongly increasing in all countries. Other feeding guilds are on average either rather stable or increasing in Denmark, but decreasing in Niedersachsen and (especially) Schleswig-Holstein. In The Netherlands the situation is intermediate, with all feeding guilds on average either stable or increasing except for the bivalve-eaters (common eider, oystercatcher, red knot, herring gull). In a statistical analysis, linear trends of individual species appear to significantly depend on feeding guild (t-test; $p<0.001$) and, as an added effect, on country ($p=0.025$). The interaction term between these two variables, which answers the question if the effect of feeding guild on trends differs between countries (in other words, if feeding guilds behave differently in the four countries), is only near-significant ($p=0.086$). Leaving out the two strongly increasing piscivore species in the analysis, only a near-significant effect of the remaining four feeding guilds on species trends remains ($p=0.098$). However, as an added effect, the effect of country is still highly significant ($p<0.001$). The interaction term between feeding guild and country is now far from significant ($p=0.575$). This will be partly caused by the large differences in trends within feeding guilds in individual countries. While individual species trends may strongly contrast between countries (e.g. grey plover, dunlin, bar-tailed godwit, curlew, redshank, common gull), it appears difficult to upscale this pattern to the main feeding guilds involved. This is illustrated by the trends of worm-eaters ('polychaete feeders') in Schleswig-Holstein: whereas dunlin and bar-tailed godwit are declining, grey plover seems stable and ringed plover shows increasing numbers.

In conclusion, the situation regarding migratory water bird trends is most similar in Lower Saxony and Schleswig-Holstein on the one hand, and The Netherlands and Denmark on the other hand. Trends of individual species differ between feeding guilds and countries, but there is little evidence that feeding guilds on average show contrasting trends between different countries. Since trends of species differ strongly within functional groups, it will be difficult to identify the processes causing these patterns.

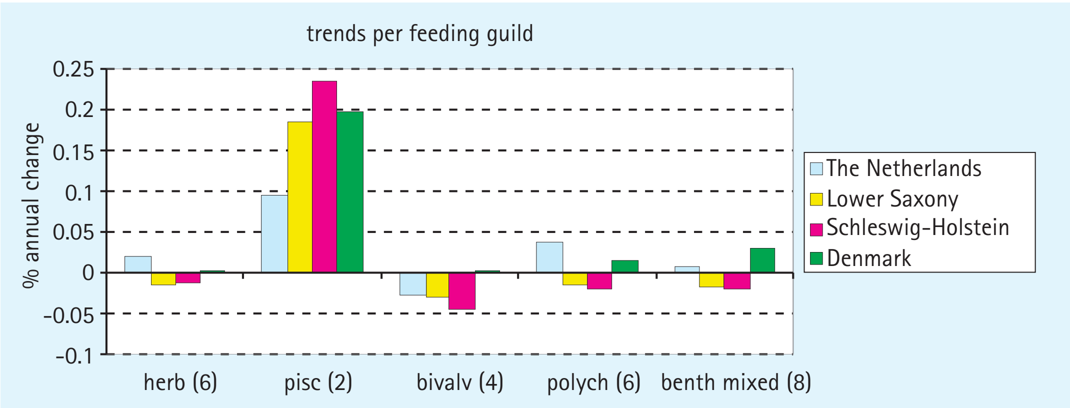


Figure 9: Average trends of migratory water birds in four Wadden Sea countries (NL, LS, SH, DK) per feeding guild. Number of species per feeding guild is given between brackets.

4.2 Possible causes for contrasting trends

To explore the possible causes of contrasting bird trends between the four Wadden Sea countries, we related linear trends in 26 common migratory water bird species to linear trends in 19 environmental variables, using PCA. The resulting ordination diagram is shown in Figure 10 to Figure 12.

The position of the countries in the diagram (Figure 10) generally confirms the results of the feeding guild analysis. Bird trends are most similar in Lower Saxony and Schleswig-Holstein and differ strongly with bird trends in the other two countries. However, in contrast to the feeding guild analysis, bird trends in The Netherlands and Denmark differ strongly from each other. This will be caused by the large variation of individual species trends within feeding guilds.

The position of the species in the diagram

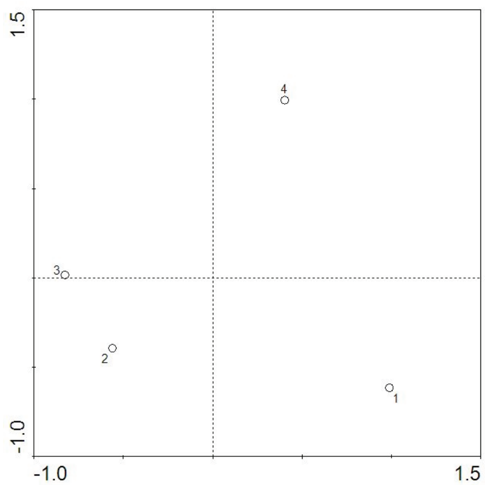


Figure 10: PCA diagram showing the position of the different samples (1=Netherlands, 2=Lower Saxony, 3=Schleswig-Holstein, 4=Denmark).

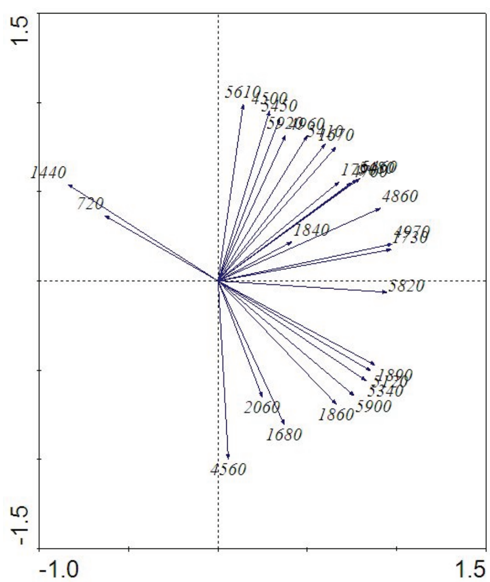


Figure 11 (right): PCA diagram showing the position of the different species (for explanation of Euring codes see Table 5.1).

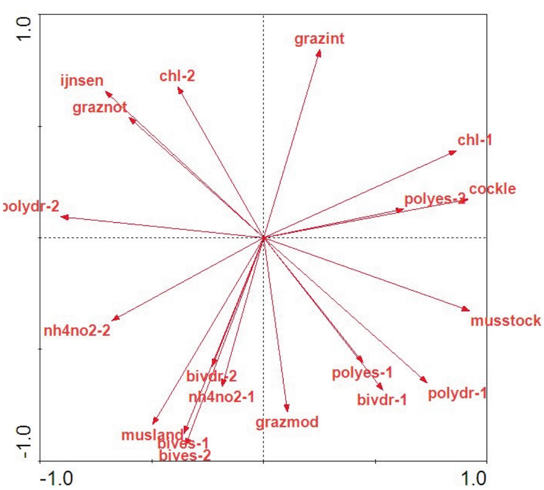


Figure 12: PCA diagram showing the position of the different environmental variables (for explanation of abbreviations see Table 4). The length of the arrows corresponds to their importance in explaining the differences in species trends.

shows some clear patterns (Figure 11). The strongly increasing piscivores (spoonbill and cormorant) are on the far left hand side of the diagram. Other increasing species are generally positioned above the x-axis (e.g. barnacle goose, ringed plover), decreasing species below the x-axis (e.g. brent goose, common eider, pied avocet). Three species of bivalve feeders (oystercatcher, herring gull, red knot) however are positioned at the top end of the diagram. They decrease in all countries, except for Denmark. The remaining bivalve feeder, common eider, is at the bottom end of the diagram because it decreases in all four countries. The position of species within the groups of herbivores, polychaete feeders and mixed benthos feeders is rather scattered, which again indicates that trends of species within feeding guilds can be quite different.

The position of the testing variables in the diagram is far from clear (Figure 12). Nearly all variables appear equally important in explaining differences in species trends between countries. Some variables, for which similar positions might be expected, are positioned at relatively large distance from each other. Examples are the two alternatives of chlorophyll-a concentrations (chl-1, chl-2), the four alternatives of polychaete biomass (polyes-1, polyes-2, polydr-1, polydr-2), and some alternatives of bivalve biomass (musstock, cockle and bives). This is caused by the different trends of these variables, which are apparently not representative for the general situation in a country. This severely hampers the interpretation of the results from the PCA.

5 Discussion

Time and budget limitations only allowed us to assemble information on a limited number of variables and our statistical analysis was necessarily of a preliminary and exploratory nature. Nonetheless, we do think that our project was an important step forward in gaining a better understanding of the causes for the differences in waterbird trends between Wadden Sea countries. As a result of the project we also have a better grasp of the most profitable next steps to be taken and these next steps are discussed at the end of the report.

This study succeeded in identifying many possible causes for differences in trends between migratory waterbird species between the four Wadden Sea regions. We are also quite confident that our list of hypotheses includes all reasonable alternatives. As such and considering the details given for their potential relevance for migratory bird species, it can serve as a checklist for future studies seeking to explain contrasting trends of waterbirds.

We were aware that our study might only be of an exploratory nature. Nonetheless, it was unexpected and in a way disappointing that none of these hypotheses or a combination of these explains the observed contrasting trends. While expert judgement may point at the most likely causes for differences in trends, PCA results indicate that no statistics will support this expert judgement. Below we will investigate the likely reasons and causes of this result.

This study was inspired by the observation that the trends of various species of waterbirds differed between the four Wadden Sea regions. This starting point naturally led us to collect data on testing variables for those four regions. While this is the most effective approach for variables driven by national management schemes / legislation (e.g. fisheries, salt marsh management), for others a different and / or finer spatial resolution would be more suitable. One expert suggested dividing the area into a mixture of ecological and political regions. This would be the western Dutch Wadden Sea, the Eastern Dutch Wadden Sea, the East-Frisian Wadden Sea (maybe up to the River Weser), the Weser-Elbe region, the Dithmarschen region (Elbe-Eider), the North-Frisian Wadden Sea and the Danish Wadden Sea. Another expert suggested that the data be grouped into southern, central and northern Wadden Sea, which might be more in accordance to morphological-ecological subdivisions. This could also help to single out effects linked to oceanographic, riverine or some biotic variables such as seagrass cover. In fact, it turns out that a considerable drawback is statistical in origin. Having only four sample units (the four Wadden Sea regions) but 19 testing variables (all related to clear functional hypotheses) strongly restricted the potential of the statistical analysis.

In fact, during the preparation of this report it became clear that trends in individual species numbers and in individual testing variables often strongly differ between regions within a country (e.g. bar-tailed godwit in Western and Eastern part of the Dutch Wadden Sea, salt marsh management on islands and mainland of Schleswig-Holstein). This intra-country variation could not be taken into account, but may be very important in explaining the processes behind the contrasting trends. For a part of the species and testing variables the differences in trends within countries may be even larger than the differences between countries, indicating that the spatial scale of the analysis is inappropriate. Thus, both from a statistical and an empirical perspective, it would have been better if we had used bird numbers in smaller areas as the dependent variable.

Although the trends in bird numbers reflect the situation in the entire country (total population counts), many testing variables consist of data from separate transects or areas within a country. For instance, the majority of the transects sampled for macrozoobenthos in the Dutch Wadden Sea are located on the Balgzand. The problem is that it is not known if the Balgzand area is representative for the Dutch Wadden Sea as a whole. One possible solution is to analyze bird trends per counting area, in relation to trends in testing variables representing the same counting areas.

However, while bird data could potentially be provided for smaller scales, it is less likely that data on testing variables are available on a smaller spatial scale; in fact, some of them lack both the desired spatial and temporal resolution. Data on testing variables also often contained missing values, for which it is not yet possible to account. Climate data show that it is not always necessary to increase the number of sampling stations to obtain good estimates of weather data on a small spatial scale. There are only a handful of weather stations in the Wadden Sea (Figure 2). Using smart interpolation techniques, the weather is reconstructed on a fine grid covering Europe and with a fine temporal resolution. However, these so-called reanalysis data are not freely available from ECWMF, the European Centre for Medium-Range Weather Forecasts http://www.ecmwf.int/. For other testing variables, it is quite clear though that the number of sampling stations needs to be increased.

This study focused on causes of long-term trends in bird numbers, and therefore we used linear trends in both bird numbers and testing variables. However, trends are often far from linear, and smoothed trends may give a better description of the actual trends. Dealing with non-linear trends requires adopting complicated statistical techniques to correlate birds with testing variables, which was beyond the scope of this exploratory study.

Trends of individual species do differ between feeding guilds and countries, but this study presents little evidence that it is also the case that feeding guilds show contrasting trends between different countries. Since trends of species apparently strongly differ within functional groups, it will be difficult to identify the processes causing these patterns. Another classification of guilds, not referring to main diet, may be worthwhile exploring.

During the project we became aware that, by focussing on contrasting trends, we may have missed out on hypotheses explaining a general increase or a general decrease in the number of waterbirds using the international Wadden Sea In a follow-on project, these hypotheses should be addressed as well and it might be useful to compare developments in the international Wadden Sea to developments in other intertidal areas in western Europe, especially the many estuaries in the United Kingdom, which have been surveyed even longer than the Wadden Sea.

Kentish Plover
(Photo: L. Dijksen)

6 Recommendations

Relating trends in bird numbers to trends in testing variables proved to be a tall order; one could even say that it proved "a bridge too far". However, the exercise provided us with many suggestions for alternative approaches that might yield important insights.

Independent of the type of analysis, new analyses of the bird data should use smaller spatial units as this has many statistical advantages. Data on bird trends are already available on smaller spatial scales, i.e. for 29 sub-areas.

If the analysis focuses on explaining the distribution of the various shorebird species throughout the Wadden Sea, there is no need for a very high temporal resolution of the explanatory or testing variables. One good data point per geographical area suffices. It would be very valuable to obtain a better insight in why particular birds prefer particular areas of the Wadden Sea. If this exercise proves successful, the next step could be to relate trends in bird numbers to values (not trends) for the testing variables.

Alternatively, it is possible to restrict the analysis to the bird counting data only. Cluster analysis could be employed to seek answers to the following questions:

- Which species of birds show similar trends across different areas of the Wadden Sea?
- Which parts of the Wadden Sea have bird populations that vary in a similar way?

Ultimately, it would be valuable to repeat and extend this study on the relationship between bird numbers and testing variables. This requires that good data on the testing variables is available. For several variables, such data is currently not being collected. We recommend to make an inventory of what it would take to initiate the necessary monitoring.

More generally, we note that the monitoring of the Wadden Sea as part of TMAP has two main objectives:

- To provide a scientific assessment of the status and development of the Wadden Sea ecosystem
- To assess the status of implementation of the trilateral targets of the Wadden Sea Plan

Thus, the monitoring is not specifically designed to facilitate the explanation of trends in bird numbers or acquire a deeper understanding of the functioning of the Wadden Sea ecosystem in general. To achieve a deeper understanding, including causal explanations for trends in bird numbers, we suggest establishing several long-term ecological research (LTER) sites throughout the international Wadden Sea. Monitoring of abiotic and biotic parameters in these LTER sites should be designed in such a way that different hypotheses on the functioning of the Wadden Sea ecosystem can be tested.

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