WADDEN SEA ECOSYSTEM No. 20

Shellfish-Eating Birds in the Wadden Sea - What Can We Learn from Current Monitoring Programs?

Gregor Scheiffarth
Dietrich Frank

2005
Common Wadden Sea Secretariat
Trilateral Monitoring and Assessment Group
Joint Monitoring Group of Migratory Birds in the Wadden Sea

Contents

Summaries 187
- Summary 187
- Sammenfatning 187
- Zusammenfassung 188
- Samenvatting 188

1. Introduction 189

2. Methods 190
- 2.1 Available monitoring data 190
- 2.2 Assessment of mussel and cockle stocks 190
- 2.3 Bird numbers 190
- 2.4 Calculation of consumption 191
- 2.5 Correlations 192

3. Results 193
- 3.1 Shellfish landings 193
- 3.2 Consumption 194
- 3.3 Wintering Common Eiders 195

4. Discussion 196
- 4.1 Shellfish as a food source 196
- 4.2 Consumption by shellfish-eating birds 196
- 4.3 Wintering Common Eider in the Wadden Sea 197
- 4.4 What do we learn from the current monitoring programs ? 197

5. References 199

Summaries

Summary

The Trilateral Wadden Sea Monitoring revealed a strong decline during the 1990s of the European Oystercatcher (*Haematopus ostralegus*), a probable decline of the Herring Gull (*Larus argentatus*) and since winter 1996 a decline of the Common Eider (*Somateria mollissima*). All three species feed on large shellfish species (*Mytilus edulis, Cerastoderma edule*), which are also commercially exploited by fisheries.

In this contribution we investigate the different fishing regimes in the four Wadden Sea regions in relation to the conflict of shellfish eating birds vs. fisheries. We calculate biomass consumption for the three bird species and relate those to the landings of mussels and cockles. Additionally, we investigate the numbers and spatial variation of wintering Common Eiders. Of the three bird species, the Common Eider is the most important predator, with regional differences in its importance.

In all countries but Denmark, biomass consumption by Oystercatchers declined strongly between 1993 and 1999. There was a negative correlation between mussel landings and the consumption by Common Eider and Oystercatcher for the entire Wadden Sea, which could indicate an existing conflict between fisheries and birds. The numbers of wintering Common Eiders in the Wadden Sea averaged around 280,000 birds for the years 1985–2000. However, between countries and Wadden Sea regions numbers fluctuated independently, indicating an opportunistic choice of the wintering site. Birds seem to shift between areas and showed highest fluctuations where they had to rely on one single food source. Due to food shortage a large drop in numbers together with a high mortality occurred after 2000.

The trilateral Wadden Sea monitoring has delivered highly valuable data about the decline of shellfish-eating birds. However, the level of sustainable fishing cannot be determined on the basis of this data. To answer this complex ecological topic a combination of the monitoring with a modeling approach, based on sound studies of the foraging ecology for each species is needed.

Sammenfatning

Det trilaterale overvågningsprogram for Vadehavet afslørede en stærk nedgang i 1990´erne i antallet af Strandskader (*Haematopus ostralegus*), en sandsynlig nedgang i antallet af Sølvmåger (*Haematopus ostralegus*), og siden vinteren 1996, en nedgang i antallet af Ederfugle (*Somateria mollissima*). Alle tre arter fouragerer på større skaldyr (*Mytilus edulis, Cerastoderma edule*), som også udnyttes kommercielt.

I det foreliggende bidrag undersøger vi de forskellige fiskerireguleringer i de fire Vadehavsregioner i relation til konflikten mellem på den ene side de fugle, som fouragerer på skaldyr og på den anden side fiskeriet. Vi beregner biomasse føden for de tre arter, og relaterer det til landingerne af blå- og hjertemuslinger. Derudover undersøger vi antallet og den geografiske fordeling af overvintrende Ederfugle. Ederfuglen er med regionale forskelle i forekomsten den vigtigste predator af de tre nævnte arter.

Med undtagelse af Danmark var der en stærk nedgang i biomasse føden for Strandskade mellem 1993 og 1999. Der var en negativ korrelation mellem landinger af blåmuslinger og fødeoptag af Ederfugle og Strandskader i hele Vadehavet, hvilket kan indikere en eksisterende konflikt mellem blåmuslingefiskeriet og fuglene. Antallet af overvintrende Ederfugle lå gennemsnitligt på omkring 280.000 for 1985-2000. Antallet svingede dog mellem landene og de enkelte Vadehavsregioner, hvilket indikerer et opportunisk valg af overvintrings lokaliteter. Fuglene synes at skifte mellem de forskellige områder. Største udsving forekom, hvor de var afhængige af én enkelt fødekilde. Et stort fald i antal sammen med en høj dødelighed forekom efter 2000 p.g.a. fødemangel.

Det trilaterale moniteringsprogram har givet særdeles værdifulde data omkring faldet i de arter, der fouragerer på skaldyr. Niveauet for et bæredygtigt fiskeri kan dog ikke fastlægges på grundlag af disse data. For at kunne besvare dette komplekse økologiske spørgsmål er det nødvendigt at kombinere overvågningen med modeller, som er baseret på solide studier af fourageringsøkologien for hver af de omtalte arter.

Zusammenfassung

Das trilaterale Wattenmeermonitoring zeigte für die 1990er Jahre einen starken Rückgang des Europäischen Austernfischers (*Haematopus ostralegus*), einen wahrscheinlichen Rückgang der Silbermöwe (*Larus argentatus*) und seit 1996 einen Rückgang der Überwinterungspopulation der Eiderente (*Somateria mollissima*). Alle drei Vogelarten ernähren sich hauptsächlich von großen Muschelarten (*Mytilus edulis*, *Cerastoderma edule*), die gleichzeitig durch kommerzielle Fischerei genutzt werden.

In diesem Beitrag untersuchen wir die unterschiedlichen Fischereiregulierungen der vier Wattenmeerregionen in Bezug zum Konflikt zwischen muschelfressenden Vögeln und der Fischerei. Dazu berechneten wir die Biomassekonsumtion der drei Vogelarten und setzten sie in Bezug zu den Mies- und Herzmuschelanlandungen durch die Fischerei. Zusätzlich untersuchten wir die Variation der Anzahlen und der räumlich Verteilung der Eiderente. Von den drei untersuchten Vogelarten ist die Eiderente, mit regionalen Unterschieden, der wichtigste Biomassekonsument.

In allen Ländern, außer Dänemark, nahm die Biomassekonsumtion durch Austernfischer zwischen 1993 und 1999 stark ab. Für das gesamte Wattenmeer gab es eine negative Korrelation zwischen den Muschelanlandungen und der Konsumtion durch Eiderente und Austernfischer, was auf einen Konflikt zwischen Fischerei und Vögel hindeutet. Die Anzahl der im gesamten Wattenmeer überwinternden Eiderenten schwankte in den Jahren 1985-2000 um 280.000 Enten. Jedoch fluktuierten die Winterzahlen in den einzelnen Wattenmeerregionen unabhängig voneinander, was auf eine opportunistische Wahl des Überwinterungsgebietes hindeutet. Die Enten schienen zwischen den Gebieten zu wechseln und zeigten die höchsten Fluktuationen in Gebieten, in denen sie von einer einzelnen Nahrungsressource abhängig waren. Aufgrund einer Nahrungsverknappung trat ab dem Jahr 2000 ein starker Rückgang der Eiderentenzahlen, verbunden mit einer hohen Mortalität auf.

Das trilaterale Wattenmeermonitoring konnte wertvolle Daten über den Rückgang muschelfressender Vögel liefern. Jedoch kann das Niveau einer nachhaltigen Muschelfischerei nicht allein auf der Basis der Monitoringdaten bestimmt werden. Zur Beantwortung dieser komplexen ökologischen Frage ist eine Kombination des Monitorings mit Modellierungsansätzen, basierend auf fundierten nahrungsökologischen Studien der einzelnen Arten, notwendig.

Samenvatting

Resultaten van de trilaterale monitoring in de Waddenzee wijzen er op dat in de jaren negentig van de vorige eeuw een sterke afname plaatsvond van Scholekster (*Haematopus ostralegus*), Eider (*Somateria mollissima*) (sinds 1996) en waarschijnlijk ook van Zilvermeeuw (*Larus argentatus*). Alle drie de soorten hebben gemeen dat ze voor een belangrijk deel van hun voedsel afhankelijk zijn van schelpdieren, met name Mosselen *Mytilus edulis* en Kokkels *Cerastoderma edule.*

Voor beide prooien concurreren de vogels met de commerciële visserij. Het mogelijke conflict tussen vogels en visserij werd onderzocht aan de hand van de visserijregimes in de vier verschillende Waddenregios (Nederland, Nedersaksen, Sleeswijk-Holstein, Denemarken). Consumptie door de drie soorten werd vergeleken met gegevens over de hoeveelheden opgeviste Mosselen en Kokkels. Daarnaast werd de verspreiding van Eiders geanalyseerd. Van de drie vogelsoorten is de Eider de belangrijkste schelpdier-consument, zij het wel met regionale verschillen.

Met uitzondering van Denemarken nam de consumptie van scheldieren door Scholeksters sterk af tussen 1993 en 1999. Bovendien werd een negatief verband gevonden tussen de hoeveelheid opgeviste schelpdieren en de aantallen Eiders en Scholeksters in de internationale Waddenzee, wat wijst op een mogelijk conflict tussen vogels en visserij. Het aantal overwinterende Eiders in de internationale Waddenzee bedroeg gemiddeld zo'n 280.000 vogels in de periode 1985-2000. Tussen de vier regio's bestaan echter grote verschillen in trends, wat er op wijst dat geen sprake is van vaste overwinteringsplaatsen. Er is veelvuldig sprake van verplaatsingen, en gebieden met grote fluctuaties worden gekenmerkt doordat ze slechts één voedselbron herbergen. Door voedselschaarste en daaropvolgende sterfte vond een sterke afname van Eiders plaats vanaf 2000.

Dankzij de trilaterale monitoring kunnen de aantalsveranderingen van de scheldiereters (en andere soorten) nu goed worden gedocumenteerd. Echter, het zal niet mogelijk zijn op grond van de hier gepresenteerde uitwerking tot een duurzaam concept voor schelpdier-visserij te komen. Hiervoor zijn meer modelstudies, alsmede meer kennis omtrent de voedselecologie van de vogels noodzakelijk.

1. Introduction

The Joint Monitoring Project for Migratory Bird in the Wadden Sea (JMMB) was set up within the framework of the Trilateral Wadden Sea Monitoring (TMAP) to observe changes in peak numbers, changes in spatial and temporal patterns, and intensity of usage by migratory bird species in the European Wadden Sea (Rösner *et al.*, 1994). This monitoring provides a good overview of bird numbers utilizing the Wadden Sea at different stages of the annual cycle. One result of the recent data analysis, underlining the importance of the monitoring program, was a substantial overall decrease of Oystercatcher (*Haematopus ostralegus*) numbers plus indications for an overall decrease of Herring Gulls (*Larus argentatus*) 1992-2000; for the Common Eider (*Somateria mollissima*) winter numbers decreased from 1996 onwards (Blew *et al.*, 2005).

Bivalves form a major part of the biomass in the Wadden Sea. In particular the Blue Mussel (*Mytilus edulis*) and the Edible Cockle (*Cerastoderma edule*) can dominate intertidal benthic communities in terms of biomass and production. Several bird species have specialized in exploiting this prominent food resource. Major predators of these bivalve species in the Wadden Sea are the Common Eider, the European Oystercatcher, and the Herring Gull. Together they contribute 50% of the annual consumption by carnivorous birds in the Wadden Sea (Scheiffarth and Nehls, 1997). On natural mussel beds these species can consume a substantial part of the annual production (Nehls *et al.*, 1997). The contribution of different prey species in the diet of these species varies depending on the natural fluctuations in the bivalve stocks (Zwarts *et al.*, 1996).

Shellfish fisheries have a long tradition in the Wadden Sea (Buschbaum and Nehls 2003). However, since the intensification of this economic activity in the 1950s, conflicts between fishermen and conservationists have arisen, in particular in years when mussel and cockle stocks were low. To protect bivalve stocks, as well as their natural predators, different management regimes have been set up in the Wadden Sea countries (CWSS, 2002 b). Nonetheless, overfishing of cockles and mussels has occurred, resulting in food shortages and consequently elevated mortality in bivalve feeders in the Wadden Sea (*e.g.* Smit *et al.*, 1998; Camphuysen *et al.*, 2002) and elsewhere in Europe (Atkinson *et al.*, 2003; Goss-Custard *et al.*, 2004).

In this contribution we evaluate whether data obtained within the framework of the trilateral Wadden Sea monitoring TMAP is sufficient to answer complex ecological questions as a basis for management decisions. We try to elucidate whether we can investigate the influence of shellfish fisheries on shellfish eating birds with the data available within the trilateral monitoring program. The role of the most important avian predators in the Wadden Sea ecosystem is examined by estimating the food consumption on the basis of bird numbers and the specific energy demands for each species considered. Landings of marketable mussels and cockles are used as parameters reflecting the spatial and temporal patterns of bivalve stocks in the area. Additionally, we try to estimate in how far fluctuating food stocks are responsible for shifts in the spatial distribution of wintering Common Eiders, the most important consumer of bivalves in the Wadden Sea.

2. Methods

2.1 Available monitoring data

Monitoring responsibilities differ between countries bordering the Wadden Sea. In The Netherlands and Denmark, monitoring is carried out by national organizations. Within the federal German system the federal states are responsible for monitoring the Wadden Sea, namely Niedersachsen, Hamburg, and Schleswig-Holstein. To account for this distinct administrative organization, the different areas are termed here Wadden Sea *regions*.

For the present analysis data from different monitoring projects was available. Within TMAP, area and density of intertidal mussel beds are estimated. Numbers of coastal breeding birds are estimated every 5 years for the entire Wadden Sea, supplemented by annual surveys on some 80 sample plots (Rasmussen *et al.*, 2000). Migratory birds are synchronously counted each January in the entire Wadden Sea area with additional counts in other months. Additionally, each spring tide non-breeding birds are counted in selected sample areas (Blew *et al.*, this report). Since Common Eiders are not well covered by land based counts, aerial counts are conducted at least once per winter. Further details of the data will be given in each part introducing the data.

2.2 Assessment of mussel and cockle stocks

During the last 10 years monitoring of intertidal Blue Mussels has been carried out in the course of national programs and as a contribution to TMAP in all countries (cf. CWSS, 2002 b; CWSS 2002, c). However, data about biomass and the area covered by mussel beds was not available for all regions for the time period 1993 - 2000, so this data could not be used for analysis. Later on, large scale data about subtidal mussels and cockles is only available for The Netherlands. As no comparable long term data about the shellfish stock which covers the entire Wadden Sea area adequately is available, yearly landings of mussels and cockles were used as an indicator of the food stocks. Since shellfish landings depend on many more factors than natural circumstances, they form only a very rough estimate of shellfish stocks (Smit *et al.* ,1989). In addition, in The Netherlands mussel seed is brought from the Wadden Sea to culture lots outside the Wadden Sea in Zeeland, so that the Mussel production and extraction by fisheries in the Dutch Wadden Sea is much higher than landings suggest. A comprehensive summary of shellfish fishing policies for the 1990s in the different Wadden Sea regions is given in CWSS (2002 b). Data about shellfish landings was provided by the CWSS (CWSS, 2002; TMAP).

2.3 Bird numbers

Three key-species of birds use the stock of larger shellfish in the Wadden Sea on a large scale as a food source: The Common Eider, the European Oystercatcher and the Herring Gull. Eiders and Oystercatchers may shift their diet between Mussels, Cockles and other shellfish (Zwarts et al. 1996) depending on the availability of food resources. The Herring Gull uses a broad variety of food resources, but is an important predator on young Mussel beds (Hilgerloh et al. 1997).

For a calculation of the total numbers of the target bird species, numbers of breeding, migratory and wintering birds had to be combined. For calculating spatial variation in consumption by birds, the total number of birds for each species, month and country was estimated; complete data for this exercise was only available for 1993 to 2000.

Numbers of non-breeding Oystercatchers and Herring Gulls were taken from synchronous counts with imputed numbers to account for missing data (Blew *et al.*, this report). Over the entire period no counts were available for July in Denmark. To compensate for this, the relation in numbers between July and August was calculated from the spring-tide counts in Denmark. Using this relation, July numbers in Denmark were calculated from the available August numbers.

The numbers of Common Eiders were calculated on the basis of aerial counts, since this species uses mainly remote areas which are often impossible to count from the ground. Between the four regions the seasonal counting coverage varied strongly, with aerial counts in The Netherlands only available for the months of January and February (Figure 1). For the Danish part, seasonal coverage was quite complete. Apart from July, any missing data was imputed (Blew *et al.*, this report). For Schleswig-Holstein and Niedersachsen the phenologies derived from the results of all aerial counts in each region in the years 1986–2003 were used as a pattern to estimate the Eider numbers in months when no aerial counts were carried out. In The Netherlands Eider numbers were calculated on the basis of the counting results in January or February according to the phenology observed in Niedersachsen. The seasonal pattern given by Swennen *et al.* (1989) for the year 1987 confirms the assumption that the overall seasonal pattern for the Dutch Wadden Sea and the adjacent North Sea coast follows the phenology observed in Niedersachsen.

The number of breeding pairs for each species was given for Germany by Hälterlein and Steinhardt (1993), Hälterlein and Südbeck (1996; 1998), Knief *et al.* (1996; 1998; 1999), Südbeck and Hälterlein (1994; 1997; 1999), for The Netherlands by Dijksen and Koks (2001) and for Denmark by Laursen (pers. comm.). Additionally, the complete survey from 1996 and the analysis of colony breeding birds by Rasmussen *et al.* (2000) were used. In Schleswig-Holstein and Niedersachsen breeding pair numbers were available for all years considered. In contrast to this, for Denmark and The Netherlands breeding pair numbers of Common Eiders and Oystercatchers were available for 1996 only and therefore this data was applied for all years from 1993 to 1999. For Herring Gull breeding pair data was available for 1993 to 1996 and was used for the calculations. To estimate the total number of birds, the number of breeding birds was added to the number of non-breeding birds from April to June for the Common Eider and the Oystercatcher, from May to July for the Herring Gull.

2.4 Calculation of consumption

Calculation of biomass consumption allows a comparison of species with different body sizes on an ecosystem level since it forms a universal currency. In addition, it is a standard measure for biomass extraction and mass flow through ecosystems (*e.g.* Asmus *et al.*, 1998). Calculation of consumption by birds follows the approach described by Smit (1981), Meire *et al.* (1994), and Scheiffarth and Nehls (1997). The number of birds in each month multiplied by the numbers of days of the respective month resulted in bird-days per month and region for each month of the years from 1993 to 1999. On the basis of these parameters, monthly consumption and total consumption for each year were calculated.

For the Common Eider the seasonal pattern of daily food requirements is known from a detailed foraging study by Nehls (1995). Daily biomass intake per bird for this species varies between 130 g AFDM in summer and 180 g AFDM in winter. Monthly bird days were multiplied by daily biomass intake to yield monthly food consumption.

For the Oystercatcher and the Herring Gull until now no field studies of daily food requirements are available. Therefore, seasonally differentiated values for food intake were calculated by the following allometric equation relating metabolic rate to body mass (see Scheiffarth and Nehls, 1997):

C = D * 3 * BMR * (1/Q)/E (equation 1), where:

C = monthly biomass consumption per species [g AFDM];

D = number of bird days per month;

BMR = basal metabolic rate, estimated by mass dependent scaling equations:

BMR [Watt] = 5.06 * $W^{0.729}$ for the Oystercatcher (Kersten and Piersma, 1987; equation 2);

BMR [Watt] = 3.56 * $W^{0.734}$ for the Herring Gull (Aschoff and Pohl, 1970; equation 3);

W [kg] = body mass of the target species; for each month the actual mass was used to retain a seasonal pattern.

BMR values were transformed into KJ day^{-1};

Q = assimilation efficiency (80 %; mean value of different sources; Kersten and Piersma, 1987; Castro *et al.*, 1989; Zwarts and Blomert, 1990);

E = 22 KJ g $AFDW^{-1}$; mean energy content of marine benthic animals in the Wadden Sea (Zwarts and Wanink, 1993)

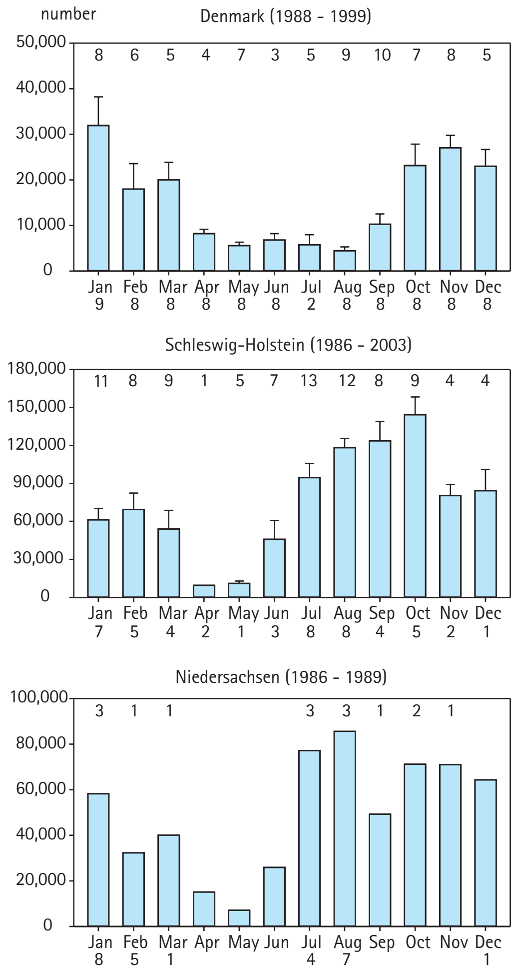


Figure 1: Phenologies of Common Eider (*Somateria mollissima)* in different regions of the Wadden Sea (mean + SE) as obtained from aerial surveys. Figures above bars denote number of years in which birds were counted; figures below months indicate number of years of respective months used for the calculation of consumption. These numbers are sometimes higher than numbers above bars since for the calculation of consumption different years or months with a high proportion of imputed values were used which were discarded for the calculation of the phenology (see text). Phenology for Niedersachsen was taken from Nehls (1989).

According to the right-hand side of equation (1), for individual Oystercatchers daily consumption varied between 43.58 in May and 52.04 g AFDM d^{-1} $bird^{-1}$ in December. For the Herring Gull only a constant value of 52.62 g AFDM d^{-1} $bird^{-1}$ could be calculated since no seasonal pattern of body mass from the Wadden Sea is available. This value falls well within the range of other studies which estimated food consumption of Herring Gulls (Hilgerloh *et al.*, 1997; Nehls *et al.*, 1998).

We did not convert consumption estimates to fresh mass as this would add a large error to the consumption estimates. For relating patterns of bird consumption to patterns of shellfish landings, this step is unnecessary since the relationship is scale-independent. Nor did we 'guesstimate' the proportion of cockles and mussels in the diet, since the contribution of these prey species to the energy intake of the birds ranges from 0% to 100% and varies between years and locations.

2.5 Correlations

Patterns of annual consumption estimates and shellfish landings were analyzed for each Wadden Sea region separately. As no linear relationship between these data series can be assumed, a Spearman rank correlation was performed. Two types of correlations were tested: a) the relation between shellfish landings and food consumption in the same year and b) shellfish landings and food consumption in the preceding year. Correlation b) was assumed to be particularly important, as shellfish landed for marketing has partly grown out of the size range profitably harvestable by birds but available to them the year before. Apart from in Denmark, mussels attractive to birds are transferred to mussel cultures at least one year before they are marketed (Figure 2). Particularly if these mussels are fished in the intertidal, they are removed as a food source for Oystercatchers and Herring Gulls.

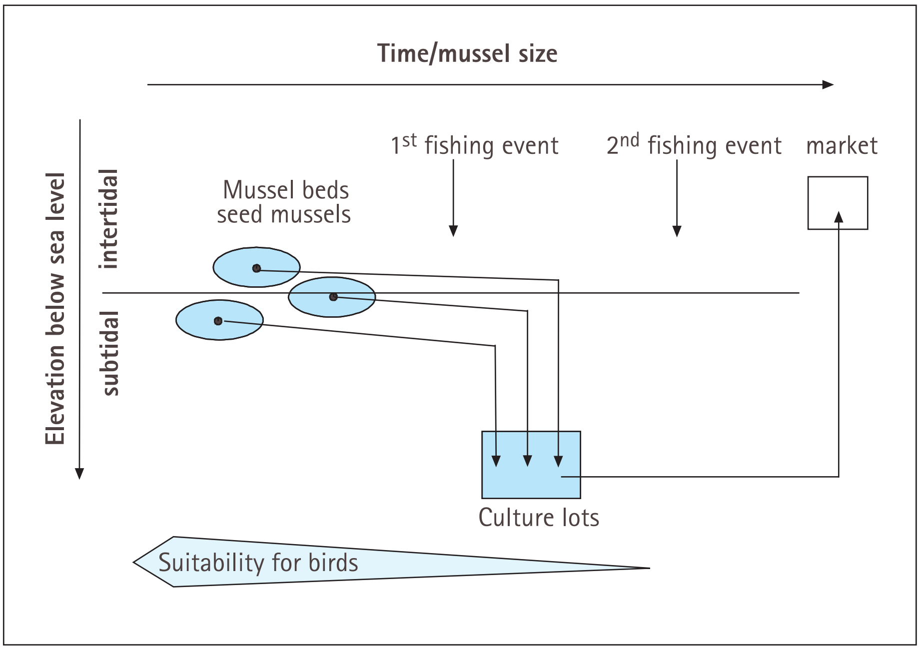


Figure 2: Schematic representation of space and time for commercially exploited mussels (*Mytilus edulis*) in the Wadden Sea. Mussels are fished twice. Most important is the first fishing event that removes mussels from the intertidal and makes them unavailable for non-diving birds. Note that fishing for seed mussels in the intertidal is not allowed in Schleswig-Holstein.

3. Results

3.1 Shellfish landings

Shellfish landings showed considerable fluctuations in the period 1993-1999 and varied from 60,476 t (wet mass) Blue Mussels in The Netherlands in 1998 to 262 t in 1997 Denmark (Figure 3). Annual average of mussel landings for the period 1991–2000 was highest, at 37,712 t a^{-1} in The Netherlands, resulting in a fishing intensity of 0.15 t a^{-1} ha^{-1} total area (subtidal and intertidal, data from CWSS, 2002 b). At 20,837 t a^{-1}, annual mussel landings were second highest for Schleswig-Holstein, which also resulted in the second highest fishing intensity of 0.09 t a^{-1} ha^{-1}. The lowest average amount of mussels was landed in Denmark, at 4,152 t a^{-1}, resulting in a fishing intensity of 0.06 t a^{-1} ha^{-1}. In Niedersachsen, annual mussel landings amounted to 7,332 t a^{-1}, resulting in the lowest fishing intensity with 0.04 t a^{-1} ha^{-1}. The amount of mussels landed in The Netherlands and in Niedersachsen the following year was positively correlated ($r_s = 0.943$; $p < 0.01$, $n = 6$). The same correlation was found between landings in Niedersachsen and Schleswig-Holstein in the following year ($r_s = 0.829$; $p < 0.05$, $n = 6$).

In Niedersachsen, apart from few exceptions, and in Schleswig-Holstein, cockle fishing is not allowed. On average, in The Netherlands 23,215 t (wet mass, 1991-2000) and in Denmark 7,000 t (1990–1999) were landed annually. In Niedersachsen, only 53 t were harvested in 1999 (CWSS, 2002 b). Cockle landings in the various parts of the Wadden Sea were not correlated to one another or to the yields in the preceding years. Also no relations between the cockle and mussel landings could be established. For the entire Wadden Sea both mussel and cockle landings increased during the period 1993–1999 (Figure 4).

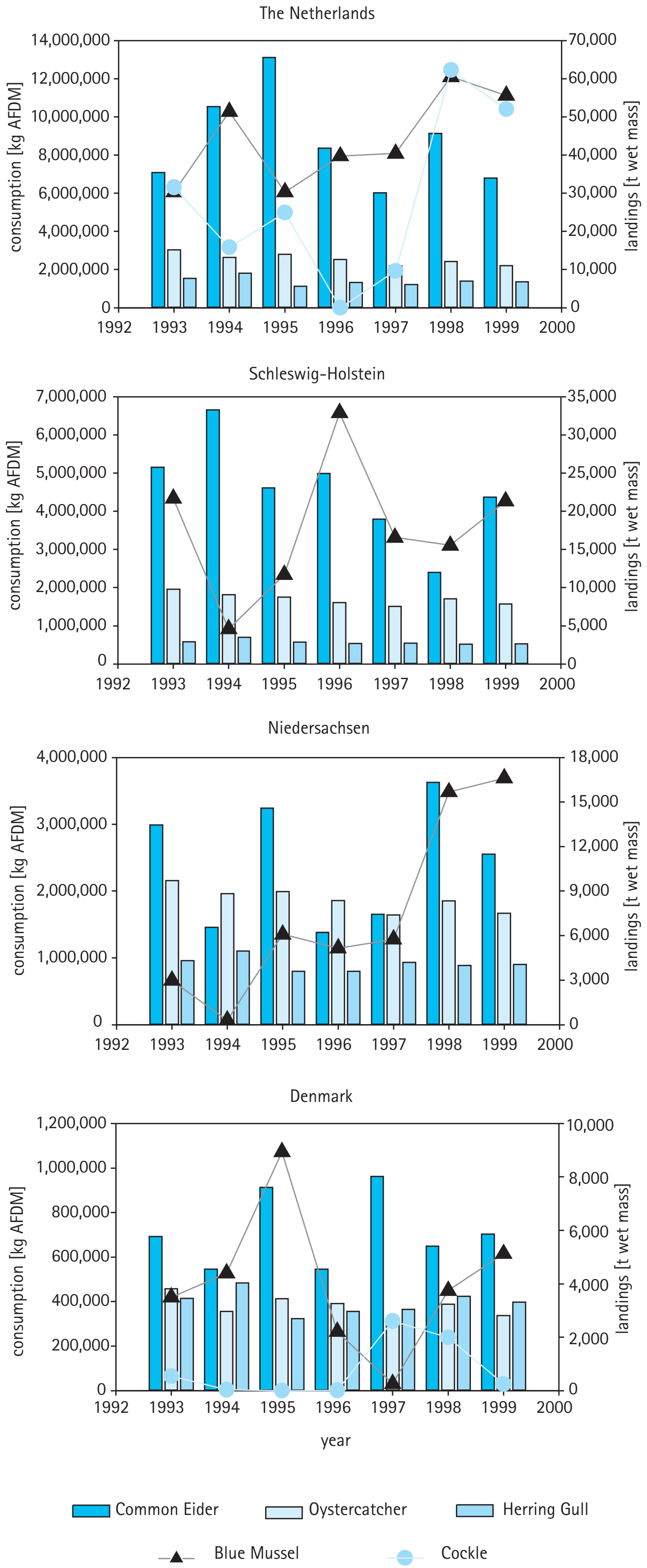
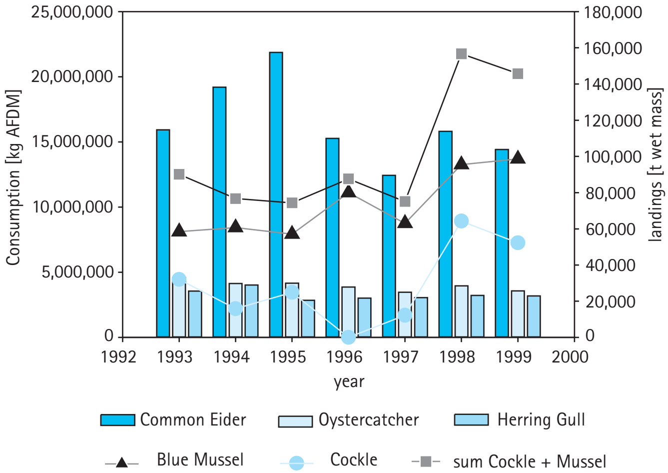


Figure 3: Consumption by major shellfish-eating birds and landings of mussels and cockles in different Wadden Sea regions. Please note the different scales on the axes.

Figure 4: Consumption by the three major shellfish-eating birds and landings of cockles and mussels for the entire Wadden Sea.

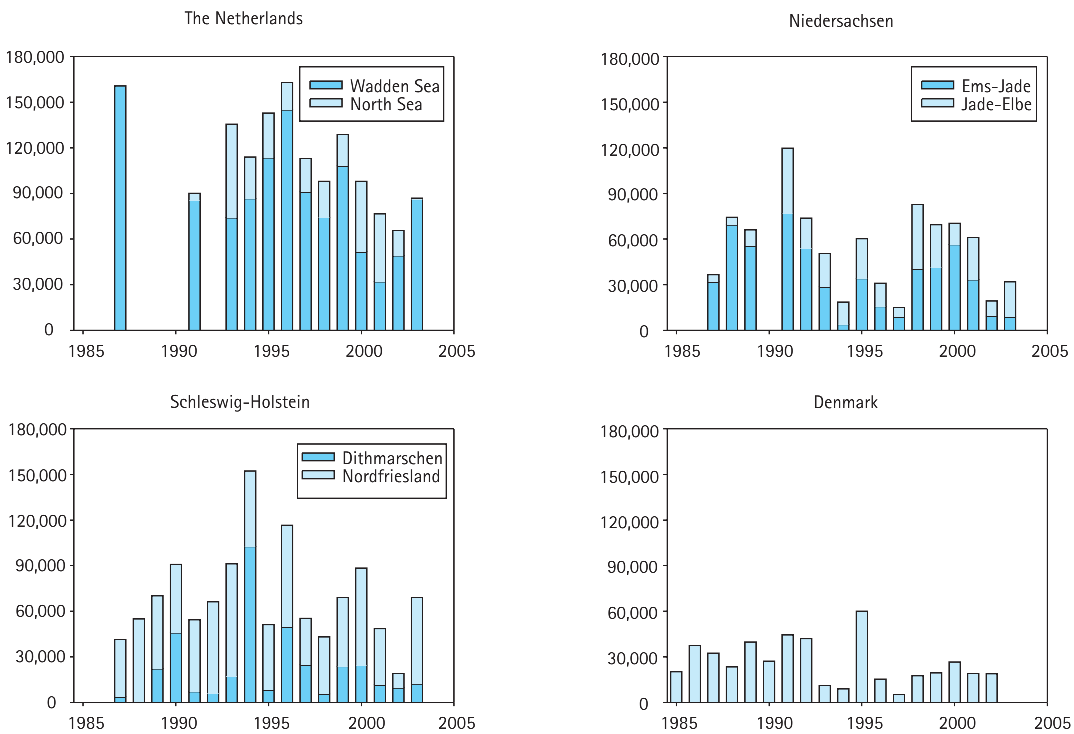


3.2 Consumption

Total consumption by the three target species, Common Eider, Oystercatcher, and Herring Gull, in the entire Wadden Sea varied between 19,000 t AFDM a^{-1} and 29,000 t AFDM a^{-1} (Figure 4). With on average 69%, the Common Eider took the largest share. For the period considered, consumption by Common Eider and Oystercatcher varied synchronously (r_s = 0.893, $p < 0.01$, n = 7). In all regions a significant positive correlation between the consumption by Eiders and the overall consumption was found, indicating the prominent status of the Common Eider in terms of biomass consumption in all regions. However, the importance of the Common Eider as a predator varied between regions, with on average 68% of the total consumption of the three species in The Netherlands, 45% in Niedersachsen, 65% in Schleswig-Holstein, and 47 % in Denmark.

In all countries apart from Denmark consumption by Oystercatchers declined significantly in the period 1993–1999 (Figure 3; The Netherlands r_s = -0.857, p = 0.014, n = 7; Niedersachsen r_s = -0.857, p = 0.014, n = 7; Schleswig-Holstein r_s = -0.821 p = 0.023, n = 7). Overall, only few correlations between shellfish landings and consumption by the three target bird species were found. Common Eider and Oystercatcher showed a weak negative

Figure 5: Winter numbers of Common Eider in different Wadden Sea regions. For The Netherlands 'Wadden Sea' denotes the area between the islands and the mainland coast and 'North Sea' the area north of the islands. Niedersachsen and Schleswig-Holstein were subdivided in two parts. The areas Jade-Elbe and Dithmarschen are unsheltered inner parts of the German Bight whereas the Wadden Sea of the areas Ems-Jade and Nordfriesland are protected by islands and high sands against the North Sea. In years with missing bars no counting data was available.



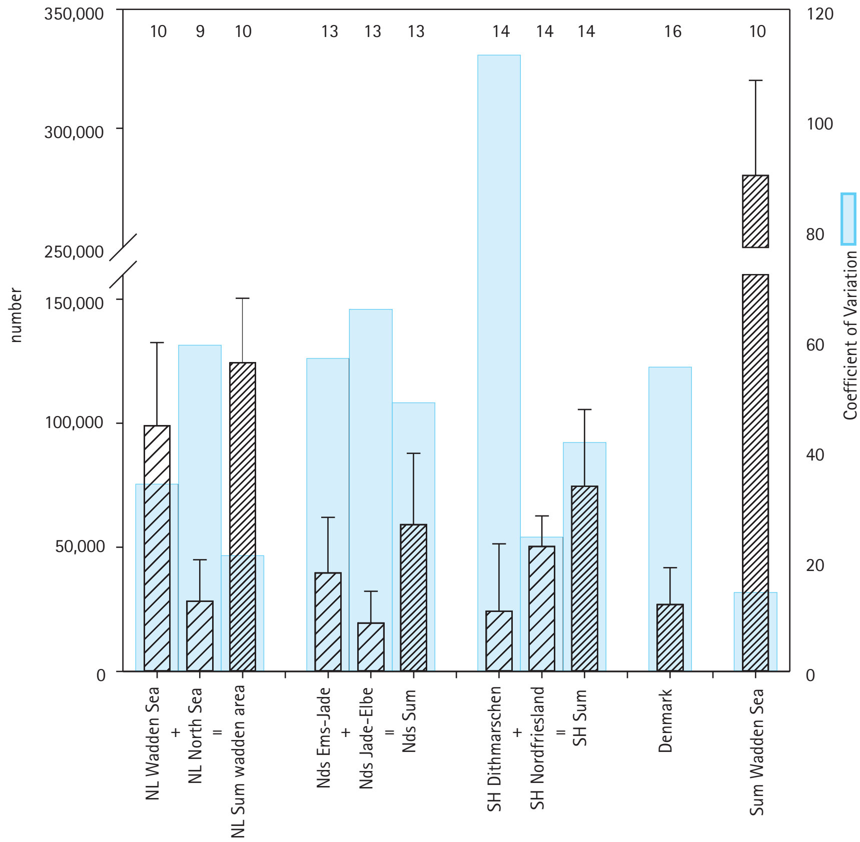


Figure 6: Numbers of wintering Common Eider in different regions of the Wadden Sea (mean + SD), based on data from Figure 5 from 1985 - 2000. Please note that if the regions were subdivided, numbers in these sub-regions, as well as the sum of the regions are presented. The blue bars show the coefficient of variation. Figures above the bars show the number of years. NL = The Netherlands, NL Wadden area = entire area between islands and mainland and North Sea adjacent to islands, Nds = Niedersachsen, SH = Schleswig-Holstein.

correlation with the total mussel landings for the entire Wadden Sea (r_s = -0.714, p = 0.071, n = 7, Figure 4). In Niedersachsen, mussel landings were negatively correlated to the consumption by Oystercatchers in preceding years (r_s = -0.886, $p < 0.05$, n = 6), which might indicate that in this region Oystercatchers and fishermen compete for the same resource of half-grown mussels in the intertidal. For The Netherlands a similar negative correlation was found for Common Eider and Blue Mussel landings in the following year (r_s = -0.771, p =0.072, n = 6).

3.3 Wintering Common Eiders

The Common Eider is the major consumer of shellfish in the Wadden Sea. This species is not only sensitive to fluctuations in the total stock of shellfish but also, because of its foraging ecology, to food quality (Nehls, 2001) which becomes particularly obvious in winter. Food quality is represented by the relationship of flesh mass to shell mass: the more flesh in relation to shell, the better and the higher the net energetic gain per food item for the birds. The total number of Common Eider wintering in the Wadden Sea area 1985-2000 varied around 280,000 individuals with numbers fluctuating independently of each other in different regions (Figure 5). The coefficient of variation in the total Wadden Sea was not higher than 14% (Figure 6). Fluctuations within the different regions of the Wadden Sea also remained comparatively small, whereas numbers counted in the sub-regions showed higher variations. A significantly positive correlation was found between the total number of wintering Eiders in The Netherlands and Schleswig-Holstein (r_s = 0.673, $p < 0.05$, n = 11), especially the northern part of Schleswig-Holstein (SH Nordfriesland, r_s = 0.618, $p < 0.05$, n = 11), which might indicate similar processes controlling Eider numbers in these two areas. The numbers counted in the southern part of Schleswig-Holstein (SH Dithmarschen) are significantly negatively correlated to the numbers in Niedersachsen (r_s = -0.571, $p < 0.05$, n = 15), which might indicate that birds shift between the two regions.

The shellfish landings were in only a few cases correlated to the number of wintering Eiders. In Denmark, the total landings of Blue Mussels and cockles were positively correlated to the number of wintering Eiders (r_s = 0.810, $p < 0.05$, n = 8).

4. Discussion

4.1 Shellfish as a food source

The shellfish landings were set in relation to the consumption by shellfish-eating birds. However, it is not clear how far these landings represent the actual food stock. At least in The Netherlands and Schleswig-Holstein mussel landings from the Wadden Sea represent the stock on subtidal culture lots out of reach of Oystercatchers and Herring Gulls (Ens *et al.*, 2002). For cockles in The Netherlands, patterns of landings and stock show some similarities, however, the percentage of the stock harvested by fishermen each year shows large variations ranging from 3% up to 38% (Smit *et al.*, 1998).

Shellfish landings have to be seen against the background of different legal regulations on the shellfish fisheries in the regions. In The Netherlands since 1991 no fishing has been practiced on intertidal mussel beds with the exception of minor fisheries in autumn 1994. In Niedersachsen, fishery of wild mussels for consumption is not allowed in the intertidal, whereas seed fishing is carried out in both the intertidal and subtidal. In Schleswig-Holstein, no mussel fishery on tidal flats and no fishery of wild mussels for consumption in the subtidal area is allowed. Seed mussels for culture lots are fished in the subtidal (CWSS, 2002 b). In Denmark no mussel cultures are allowed, so fishing is restricted to wild natural beds (CWSS, 2002 b).

Information about cockle stocks is scarce, with the exception of The Netherlands, where yearly cockle surveys are made by the RIVO-DLO. Some information is also available for Denmark (*e.g.* Kristensen, 1997). As no cockle fishery is practiced in Niedersachsen or Schleswig-Holstein, no information about the live-stock of cockles in these areas is available.

The high mortality of mussels and cockles due to severe winters and storms causes strong variations in the shellfish stock (Beukema *et al.*, 1993; Nehls and Thiel, 1993), which are reflected in the mussel and cockle landings. Although cockle and mussel landings did not correlate with each other, the influence of the hard winter 1995/1996 could be seen in both data series. At least the increase in landings the following years could be related to an increased recruitment after a cold winter. Nonetheless, only if mussel and cockle stocks fluctuate independently can they serve as an alternative food for birds (see also Zwarts *et al.*, 1996).

4.2 Consumption by shellfish-eating birds

The estimates of the consumption are constrained by several uncertainties (Scheiffarth and Nehls, 1997) with error sources occurring in two steps. First, we had to estimate the total number of birds for each country and each month. Due to a considerable shortage of data, this can only be a rough estimate of the birds actually present. Second, consumption was calculated from an allometric equation for the Oystercatcher and Herring Gull, which cannot take into account annual differences in energy demands such as varying winter temperatures. Additionally, the contribution of cockles and mussels to the diet of Common Eider, Oystercatcher, and Herring Gull is highly variable (*e.g.* Leopold *et al.*, 2001 for Common Eider).

Consumption by Herring Gull showed no relation to shellfish landings nor to the consumption by other shellfish-eating birds. This reflects the opportunistic and highly variable foraging ecology of Herring Gulls which allows easy swapping between different food sources, in contrast to Common Eider and Oystercatcher. Consumption by Common Eider and Oystercatcher correlated with each other at the level of the entire Wadden Sea. This might indicate that numbers of these species are driven by the same large-scale processes in the entire Wadden Sea. Since these patterns were not found on the regional level, regional conditions influencing numbers might differ for the two species. Considering the entire Wadden Sea, consumption by Common Eider was negatively correlated with Mussel landings, an effect which again was not found on national levels. Thus, considering the entire Wadden Sea area seems to be important, since birds can move between different localities depending on the suitability of the food supply (Scheiffarth *et al.*, 2001), as indicated by the 'wave' of mussel landings from The Netherlands to Schleswig-Holstein. For the negative correlation between mussel landings and consumption by Common Eiders different hypotheses can be formulated:

1. Mussels were concentrated on mussel cultures before being brought to market. Because of social interactions between birds, fewer birds can be supported by the same biomass.
2. In the year mussels are marketed they have grown out of the profitable size range for the Common Eider.
3. Because of a large spatfall in 1996, bird numbers could not react to the same extent as the increase in food supply. Therefore this spatfall was exploited only by fishermen and not by birds.

Distinct studies are needed to test these hypotheses, which go far beyond the current calculations.

4.3 Wintering Common Eider in the Wadden Sea

Common Eiders, mainly breeding in the Baltic, utilize the Wadden Sea area as a moulting and wintering area. The central parts of the German Wadden Sea are used as a moulting area predominantly, whereas the more peripheral parts in The Netherlands and Denmark mainly serve as wintering grounds (Swennen *et al.*, 1989). Whereas the seasonal pattern of utilization remained more or less constant, the geographical pattern of distribution changed during the 1990s. Especially the number of Eiders wintering in Denmark was comparatively low in the middle of this decade.

The case of the high fluctuations in Dithmarschen/Schleswig-Holstein demonstrates the consequences for shellfish-consuming birds relying mainly on one food species. Since almost no mussel beds exist in this part of the Wadden Sea (Nehls pers. comm.), Common Eiders have to rely entirely on cockles (Nehls, 1991). It is most likely that birds exploit this highly variable food source in years with high availability. In years with low cockle availability they have to leave the area, since no alternative food is present.

With the exception of the drop of numbers after 1996, the overall total number of Common Eider wintering in the Wadden Sea was quite stable until 2000. Higher variation within the regions and few correlations between different regions show that birds decided opportunistically where to spend the winter in the Wadden Sea.

The Baltic/Wadden Sea population underwent a strong decline in the 1990s (Desholm *et al.*, 2002) which was until recently not seen in the Wadden Sea wintering numbers. Nevertheless, a continued decrease has taken place since 2000 and in January 2002 numbers in the German Wadden Sea were the lowest ever counted. Additionally, in the winter 1999/2000 and subsequent winters large numbers of Common Eiders died due to a lack of profitably harvestable mussels or cockles (Camphuysen *et al.*, 2002; Scheiffarth, 2001), demonstrating that these bird may face a bottleneck when wintering in the Wadden Sea. Therefore, large international concern exists over the state of the Baltic/Wadden Sea Common Eider population (Desholm *et al.*, 2002).

4.4 What do we learn from the current monitoring programs?

Results of the current Wadden Sea monitoring schemes have clearly shown that shellfish-eating birds came under threat in the 1990s. There was a continuous decline in Oystercatcher numbers which led to a decrease in consumption by this species. In the winter 1999/2000 and following years a large mortality of Common Eider was observed, on top of a decline in the Baltic/Wadden Sea population of 36% from 1990 – 2000 (Desholm *et al.*, 2002). Additional evidence for potential shellfish overexploitation is given by strong declines of cockle and *Macoma balthica* feeding Knots (*Calidris canutus*) in areas with high fishing activity (Piersma and Koolhaas, 1997), which can be attributed to long-term indirect effects of cockle dredging (Piersma *et al.*, 2001).

Monitoring data has already been able to show a direct negative relationship between fishing activity and bird numbers when fishing activities have removed almost all intertidal mussel beds, resulting in drastic effects such as distribution shifts and high bird mortalities (Smit *et al.*, 1998, Camphuysen *et al.*, 2002). An earlier study in a situation with a much lower fishing pressure came to the conclusion that Common Eider and mussel fishery did not influence each other (Nehls and Ruth, 1994). The question we have to ask is not whether fishing activity in general has a negative impact, but what level of fishing is sustainable without negative effects on bird populations (*cf.* Stillman *et al.*, 2003). Simple correlations as used in this study are never a valid scientific proof. With monitoring data we can try to build models if we know the underlying processes behind changes in bird numbers (*e.g.* Rappolt *et al.*, 2003). In relation to shellfish fisheries this has been a successful approach for the Oystercatcher population of the Wash, England (Stillman *et al.*, 2003). Current monitoring schemes can serve as a basis on which additional specific studies can then disentangle the relationships between birds and their benthic food resources. While the foraging ecology of the Oystercatcher is well studied, data and results on this topic for Common Eider and Herring Gull are still very basic.

In addition to studies which relate prey choice to prey quality (*e.g.* Nehls, 1995; Laursen and Christensen, in prep.), we have to consider effects which affect the condition and in the long run mortality of the birds, for example, by measuring blood parameters (Verhulst *et al.*, 2004). Such parameters could also serve as an early warning system since it reacts much more quickly to environmental changes than population sizes. These additional studies in combination with models are urgently needed if we want to understand the processes behind changes in bird numbers identified by the current monitoring programs.

As shown in the present study, complex ecological questions cannot be adequately solved by the present monitoring scheme alone. However, it serves as a basis on which accompanying research can resolve specific questions. In the case of shellfish-eating birds, monitoring of birds which can be counted from land delivers valuable data. On the contrary, the data for Common Eider is not sufficient for the entire area during the annual cycle. In particular for the Dutch Wadden Sea only wintering numbers are known.

To resolve questions related to foraging ecology, parameters describing the food stock are indispensable. Unfortunately, monitoring of intertidal mussel beds did not run long enough for the results to be incorporated in this study. At least for the Oystercatcher this would provide a good index of availability of one important prey species. Once this mussel monitoring data series is long enough we should be able to show how far Oystercatcher numbers are influenced by the intertidal mussel stock. In order to cope with environmental changes, birds depend on more than one prey species. For Oystercatcher and Common Eider one additional food source is the cockle. However, apart from in The Netherlands, almost nothing is known about the cockle population in the Wadden Sea. For an explanation of the variation in numbers of shellfish-eating bird species, information about the cockle stocks and cockle population dynamics on a large scale is essential.

Acknowledgements

Many people contributed to this study. First of all we would like to thank all the people who went out to the mudflats to count birds, sometimes in adverse weather conditions. Peter Südbeck initiated this study, was always willing to discuss various aspects, and commented on several drafts. Also Petra Potel was always ready to discuss matters, commented on the text, and helped with information we might not have otherwise obtained. Jan Blew processed and analyzed most of the data in the framework of JMMB and commented on the text as well. We would like to thank Karsten Laursen for further comments. For data supply we would like to thank SOVON, NERI, the Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, the Nationalparkverwaltung Niedersächsisches Wattenmeer and the Staatliche Vogelschutzwarte Niedersachsen.

5. References

Aschoff, J. and Pohl, H., 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. J. Ornithol. 111: 38-47.

Asmus, H., Lackschewitz, D., Asmus, R., Scheiffarth, G., Nehls, G. and Herrmann, J.-P., 1998. Transporte im Nahrungsnetz eulitoraler Wattflächen des Sylt-Rømø Wattenmeeres. In: Gätje, C. and Reise, K. (eds.), Ökosystem Wattenmeer - Austausch-, Transport- und Stoffumwandlungsprozesse. Springer-Verlag, Berlin, Heidelberg pp 393-420.

Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J., Clark, J. A. and Ireland, P. L., 2003. Changes in commercially fished shellfish stocks and shorebird populations in the Wash, England. Biol. Conserv. 114: 127-141.

Beukema, J. J., Essink, K., Michaelis, H. and Zwarts, L., 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? Neth. J. Sea Res. 31: 319-330.

Blew, J., Günther K., Laursen, K., van Roomen, M., Südbeck, P., Eskildsen, K., Potel, P. and Rösner, H.U., 2005. Overview of Numbers and Trends of Migratory Waterbirds in the Wadden Sea 1980-2000. Wadden Sea Ecosystem No. 20, Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Joint Monitoring Group of Migratory Birds in the Wadden Sea, Wilhelmshaven, FRG.

Buschbaum, C. and Nehls, G., 2003. Effekte der Miesmuschel- und Garnelenfischerei. In: Lozán, J.L., Rachor, E., Reise, K., Sündermann, J. and von Westernhagen, H. (eds), Warnsignale aus Nordsee und Wattenmeer. Eine aktuelle Umweltbilanz, Wissenschaftliche Auswertungen, Hamburg, pp. 250-255.

Camphuysen, C.J., Berrevoets, C.M., Cremers, H.J.W.M., Dekinga, A., Dekker, R., Ens, B.J., van der Have, T.M., Kats, R.K.H., Kiuken, T., Leopold, M.F., van der Meer, J. and Piersma, T., 2002. Mass mortality of Common Eiders (Somateria mollissima) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biol. Cons. 106: 303-317.

Castro, G., Stoyan, N. and Myers, J.P., 1989. Assimilation efficiency in birds: a function of taxon or food type? Comp. Biochem. Physiol. 92A: 271-278.

CWSS, 2002. Final Draft Mussel Fisheries Report, document TWG 02/1/-3.2, version 18 April 2002.

CWSS, 2002 b. Shellfish Fisheries. An Overview of Policies for Shellfish Fishing in the Wadden Sea. Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

CWSS, 2002 c. Report of the second TMAP Blue Mussel workshop, Ameland, 8 – 10 April 2002. Common Wadden Sea secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven.

Desholm, M., Christensen, T. K., Scheiffarth, G., Hario, M., Andersson, Å., Ens, B. J., Camphuysen, C. J., Nilsson, L., Waltho, C. M., Lorentsen, S.-H., Kuresoo, A., Kats, R. K. H., Fleet, D. M. and Fox, A. D., 2002. Status of the Baltic/Wadden Sea population of the Common Eider Somateria m. mollissima. Wildfowl 53: 167-203.

Dijksen L.J. and Koks B.J., 2001. Broedvogelmonitoring in het Nederlandse Waddengebied in 2000. SOVON-monitoringrapport 2001/09. SOVON-Vogelonderzoek Nederland, Beek-Ubbergen.

Ens, B. J., Borgstede, F. H. M., Camphuysen, C. J., Dorrestein, G. M., Kats, R. K. H. and Leopold, M. F., 2002. Eidereendensterfte in de winter 2001/2002. Alterra-report 521, Wageningen, Alterra, Green Wrold Research.

Goss-Custard, J. D., Stillman, R. A., West, A. D., Caldow, R. W. G., Triplet, P., dit Durell, S. E. A. le V. and Mcgrorty, S., 2004. When enough is not enough: shorebirds and shellfishing. Proc. R.Soc.Lond.B 271: 233-237.

Hälterlein, B. and Steinhardt, B., 1993. Brutvogelbestände an der deutschen Nordseeküste im Jahr 1991 - fünfte Erfassung durch die Arbeitsgemeinschaft „Seevogelschutz". Seevögel 14: 1 - 5.

Hälterlein, B. and Südbeck, P., 1996. Brutvogelbestände an der deutschen Nordseeküste im Jahr 1994. Achte Erfassung durch die Arbeitsgemeinschaft „Seevogelschutz". Seevögel 17: 5 - 11.

Hälterlein, B. and Südbeck, P., 1998. Brutbestandsmonitoring von Küstenvögeln an der deutschen Nordseeküste im Jahre 1996. Zehnte Erfassung durch die Arbeitsgemeinschaft „Seevogelschutz". Seevögel 19: 73 -79.

Hälterlein, B. Südbeck, P., Knief, W. and Köppen, U., 2000. Brutbestandsentwicklung der Küstenvögel an Nord- und Ostsee unter besonderer Berücksichtigung der 1990er Jahre. Vogelwelt 121: 241 – 267.

Hilgerloh, G., Herlyn, M. and Michaelis, H., 1997. The influence of predation by Herring Gulls Larus argentatus and Oystercatchers Haematopus ostralegus on a newly established mussel Mytilus edulis bed in autumn and winter. Helgoländer Meeresunters., 51, 173-189.

Kersten, M. and Piersma, T., 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. Ardea 75: 175-187.

Knief, W., Berndt, R.K. and Schwennesen, W., 1996. Entwicklung der Küstenvogelbrutbestände in den Naturschutzgebieten an der schleswig-holsteinischen Ostseeküste von 1984 bis 1995. Seevögel 13: 82-93.

Knief, W., Schennesen, W. and Berndt, R.K., 1998. Ergebnisse der Brutbestandserfassung in den Naturschutzgebieten an der schleswig-holsteinischen Ostseeküste 1996. Seevögel 19: 17-18.

Knief, W., Schwennesen, W. and Berndt, R.K., 1999. Ergebnisse der Brutbestandserfassung in den Naturschutzgebieten an der schleswig-holsteinischen Ostseeküste 1997. Seevögel 20: 41-42.

Kristensen, P.S., 1997. Hjertemuslinger (Cerastoderma edule) på fiskebankerne omkring Grådyb i Vadehavet. DFU rapport nr. 37-97.

Laursen, K. and Kristensen, P.S. (in prep.) Carrying capacity of Blue Mussel Mytilus edulis for Eiders Somateria mollissima and Oystercatcher Haematopus ostralegus in the Danish Wadden Sea.

Leopold, M.F., Kats, R.K.H. and Ens, B.J., 2001. Diet (preferences) of Common Eiders Somateria mollissima. Wadden Sea Newsletter 2001-1: 25-31.

Meire, P.M., Schekkermann, H. and Meininger, P.L., 1994. Consumption of benthic invertebrates by waterbirds in the Oosterschelde estuary, SW Netherlands. Hydrobiologia, 282/283: 525-546.

Nehls, G., 1989. Eiderenten im Nationalpark Niedersächsisches Wattenmeer. Hannover, Niedersächsisches Landesverwaltungsamt.

Nehls, G., 1991. Bestand, Jahresrhythmus und Nahrungsökologie der Eiderente, Somateria mollissima, L. 1758, im Schleswig-Holsteinischen Wattenmeer. Corax 14: 146-209.

Nehls, G., 1995. Strategien der Ernährung und ihre Bedeutung für Energiehaushalt und Ökologie der Eiderente (Somateria mollissima (L. 1758)). Berichte, Forsch.- u. Technologiezentrum Westküste d. Univ. Kiel 10: 1-177.

Nehls, G., 2001. Food selection by Eiders – Why quality matters. Wadden Sea Newsletter 2001-1: 39-41

Nehls, G. and Ruth, M., 1994. Eiders, Mussels, and fisheries in the Wadden Sea - continuous conflicts or relaxed relations? Ophelia Suppl. 6: 263-278.

Nehls, G. and Thiel, M., 1993. Large-scale distribution patterns of the Mussel Mytilus edulis in the Wadden Sea of Schleswig-Holstein: Do storms structure the ecosystem? Neth. J. Sea Res. 31: 181-187.

Nehls, G., Hertzler, I. and Scheiffarth, G., 1997. Stable mussel Mytilus edulis beds in the Wadden Sea - They're just for the birds. Helgoländer Meeresunters. 51: 361-372.

Piersma, T. and Koolhaas, A., 1997. Shorebirds, shellfish(eries) and sediments around Griend, Western Wadden Sea, 1988-1996. NIOZ-Rapport 1997-7, Netherlands Institute for Sea Research, Texel.

Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J. J., Dekker, R. and Essink, K., 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. Journal of Applied Ecology 38: 976-990.

Rappoldt, C., Ens, B. J., Bult, T. P. and Dijkman, E. M., 2003. Scholeksters en hun voedsel in de Waddenzee; Rapport voor deelproject B1 van EVA II, de tweede fase van het evaluatieonderzoek naar de effecten van schelpdiervisserij op natuurwaarden in de Waddenzee en Oosterschelde 1999-2003. Alterra-Rapport 882, Wageningen.

Rasmussen, L.M. , Fleet, D.M. Hälterlein, B. Koks, B.J., Potel, P. and Südbeck, P., 2000. Breeding Birds in the Wadden Sea in 1996. Results of a Total survey in 1996 and of numbers of colony breeding species between 1991 and 1996. Wadden Sea Ecosystem No. 10. Common Wadden Sea Secretariat, Wilhelmshaven.

Rösner, H.-U., Roomen, M., Südbeck, P. and Rasmussen, L. M., 1994. Migratory waterbirds in the Wadden Sea 1992/1993. Wadden Sea Ecosystem No. 2, Common Wadden Sea Secretariat and Trilateral Monitoring and Assessment Group, Wilhelmshaven.

Scheiffarth, G. and Nehls, G., 1997. Consumption of benthic macrofauna by carnivorous birds in the Wadden Sea. Helgoländer Meeresunters. 51: 373-387.

Scheiffarth, G., 2001. Eiderentensterben im niedersächsischen Wattenmeer: der Einfluß der Nahrungsqualität auf Bestand und Kondition der Eiderente. Progress report, Institut für Vogelforschung, Wilhelmshaven.

Scheiffarth, G., Kempf, N. and Potel, P., 2001. Numbers and distribution of Eider Ducks (*Somateria mollissima*) in the German Wadden Sea in winter 1999/2000: Fleeing the fate of death. Wadden Sea Newsletter 2001-1: 14-15.

Smaal, A.C., Craeymeersch, J.A. , Kamermans, P. Kesteloo, J.J. and Schuiling, E., 2000. Schelpdieren en krabben in het Waddengebiet in de periode 1994 – 2000 als mogelijk voedsel voor Eiderenten. RIVO Rapport C029/00.

Smit, C.J., 1981. Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea area. In: Smit C.J. and Wolff W.J. (eds). Birds of the Wadden Sea: 290-301. Report no. 6, Final report of the section Birds of the Wadden Sea Working Group, Balkema, Rotterdam.

Smit, C. J., Dankers, N., Ens, B. J. and Meijboom, A., 1998. Birds, Mussels, Cockles and Shellfish fishery in the Dutch Wadden Sea: How to deal with low food stocks for Eiders and Oystercatchers. Senckenbergiana marit. 29: 141-153.

Stillman, R. A., West, A. D., Goss-Custard, J. D., Caldow, R. W. G., Mcgrorty, S., Durell, S. E. A. I. V., Yates, M. G., Atkinson, P. W., Clark, N. A., Bell, M. C., Dare, P. J. and Mander, M., 2003. An individual behaviour-based model can predict shorebird mortality using routinely collected shellfishery data. Journal of Applied Ecology 40: 1090-1101.

Südbeck, P. and B. Hälterlein, 1994. Brutvogelbestände an der deutschen Nordseeküste im Jahre 1992. Elfte Erfassung durch die Arbeitsgemeinschaft „Seevogelschutz". Seevögel 14:11 - 15.

Südbeck, P. and B. Hälterlein, 1997. Brutvogelbestände an der deutschen Nordseeküste im Jahre 1995. Neunte Erfassung durch die Arbeitsgemeinschaft „Seevogelschutz". Seevögel 18: 11 - 19.

Südbeck, P. and B. Hälterlein, 1999. Brutvogelbestände an der deutschen Nordseeküste im Jahre 1997. Elfte Erfassung durch die Arbeitsgemeinschaft „Seevogelschutz". Seevögel 20: 9 - 16.

Swennen C., 1976. Populatiestructuur en voedsel van de Eidereend Somateria mollissima in de Nederlandse Waddenzee. Ardea 64: 311-371.

Swennen C., Nehls G. and Laursen K., 1989. Numbers and distribution of Eiders Somateria mollissima in the Wadden Sea. Neth. J. Sea Res. 24: 83-92.

Verhulst, S., Oosterbeek, K., Rutten, A. L. and Ens, B. J., 2004. Shellfish fishery severely reduces condition and survival of Oystercatchers despite creation of large marine protected areas. Ecology and Society 9: 17, URL: http://www.ecologyandsociety.org/vol9/iss1/art17.

Zwarts, L. and Blomert, A.-M., 1990. Selectivity of Whimbrels feeding on Fiddler Crabs explained by component specific digestibilities. Ardea 78: 193-208.

Zwarts, L. and Wanink, J. H., 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. 31: 441-476.

Zwarts, L., Wanink, J. H. and Ens, B. J., 1996. Predicting seasonal and annual fluctuations in the local exploitation of different prey by Oystercatchers Haematopus ostralegus: A ten-year study in the Wadden Sea. Ardea 84A: 401-440.

Authors

Gregor Scheiffarth
Wehlens 5
D - 26388 Wilhelmshaven
Germany
g.scheiffarth@t-online.de

Dietrich Frank
Kreuzweg 132
D - 26419 Schortens
Germany
dietrich_frank@t-online.de