A multiscale analysis of the distribution of Common Eiders *Somateria mollissima* preying on shellfish in the Dutch Wadden Sea

Bruno J. Ens, Romke K.H. Kats, Tammo Bult, Martin de Jong, Elze Dijkman, Mardik F. Leopold

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Abstract

For the winters of 1994-2004, we correlated the distribution of the Common Eiders counted from airplanes in the Dutch Wadden Sea with the distribution of important shellfish prey (littoral cockles, sublittoral cockles, littoral mussels, sublittoral wild mussels and mussels on sublittoral culture plots) at different scales, using grid cells with a size of 750 m, 1500 m, 3000 m, 5000 m and 10000 m respectively. The smallest grid cell size corresponds to the accuracy with which flocks of Common Eiders can be located.

Log-linear models linking the distribution of Common Eiders to the shellfish stocks explained more deviance with increasing scale. We think this is partly due to the reduction of sampling error associated with large grid cells and to the fact that Eiders select for profitable mussel culture plots that are distributed in larger clusters over the western part of the Dutch Wadden Sea.

Irrespective of scale, sublittoral mussels, especially on culture plots, seemed to be the most important factor in determining the distribution of Eiders in the Dutch Wadden Sea as a whole. However, sublittoral mussels are virtually restricted to the western part of the Dutch Wadden Sea where most Eiders are present in winter. When focussing on the eastern part of the Wadden Sea, the distribution of Eiders seemed to be largely driven by littoral mussels.

Cockles were not found to be of great importance relative to the sublittoral mussel stocks as few analyses showed any significant contribution of either sublittoral or littoral cockle stocks to the distribution of Eiders.

These findings corroborate previous results that the stocks of sublittoral mussels are of paramount importance to the survival of the Common Eiders that winter in the Dutch Wadden Sea. However, these findings should not be taken as evidence that mussel culture benefits Common Eiders.
Introduction

Quantitative knowledge on diet composition of Common Eiders (Somateria mollisima) is important to better gauge the ecological role of this important bird predator in the food web of the international Wadden Sea ecosystem and to increase our understanding of the interaction between Common Eiders and shellfish fisheries.

Common Eiders are a key component in the food chain of the international Wadden Sea as they are the most important carnivorous birds in the Wadden Sea in terms of biomass consumed. Different authors have estimated the annual biomass consumption of the various carnivorous bird species in the Dutch Wadden Sea (Hulscher 1975, Swennen 1976b, Smit & Wolff 1981). Their estimates vary between 3.7 and 4.3 g AFDM per m² per year and 28% of this consumption is due to Common Eiders (Smit & Wolff 1981). For the Sylt-Rømø tidal inlet in the Danish-German Wadden Sea, the annual consumption by birds was estimated at 3.4 g AFDM per m² per year and Common Eiders were responsible for an estimated 37% of this consumption (Scheiffarth & Nehls 1997).

Common Eiders feed predominantly on molluscs and to a lesser extent on crustaceans and other benthic animals (Simmons et al. 1977). On the basis of faecal analysis, Swennen (1976a) concluded that the diet in the Dutch Wadden Sea consisted of 40% mussels Mytilus edulis, 40% cockles Cerastoderma edule, 6.5% shore-crab Carcinus maenas and only a few per cent of other prey, like starfish Asterias rubens and periwinkles Littorina littorea. However, more recent studies in the Wadden Sea have made it clear that the diet can vary widely, sometimes consisting almost entirely of mussels, or cockles, or other prey, depending on availability, year and the location (van Buuren 1983, Nehls 1989, Asferg 1990, Nehls 1995, Hilgerloh 1999, Scheiffarth & Frank 2006). Large numbers of Eiders occurring in the North Sea coastal zone since the early 1990s feed predominantly on the cut through shell Spisula subtruncata (Camphuysen et al. 2002). Thus, the diet is much more variable than originally envisaged by Swennen (1976a). In addition, the estimates of Swennen (1976a) may be biased. It is known that faecal analyses contain many biases, including the fact that faeces can only be collected from birds that spend time resting on land. However, large wintering flocks of Eiders occur in the sublittoral parts of the western Dutch Wadden Sea, where they never leave the water. An alternative approach to obtain an estimate of the diet of the population as a whole is to relate the distribution of the birds to the distribution of the food stocks.

Mass mortalities and changes in the distribution of Common Eiders in the winters of 1991 (Swennen 1991b), 2000 (Camphuysen et al. 2002) and 2002 (Ens et al. 2002) have been explained as the result of the negative impact of shellfish fishery on the shellfish stocks available to the Common Eiders. According to Camphuysen et al. (2002) both mechanized fishing for cockles, mussel fishery and
suction dredging of *Spisula* contributed to the food shortage. More recent analyses by Kats *et al.* (2007a) confirmed that low stocks of mussels and *Spisula* contributed to mass mortality, but they were unable to demonstrate a relationship between low cockle stocks and high mortality of Common Eiders. Other authors have argued that high mortality was not due to food shortages, but instead to Common Eiders falling victim to intestinal parasites (Smaal *et al.* 2001).

Various lines of evidence suggest that the stocks of sublittoral mussels are of paramount importance to Common Eiders wintering in the Dutch Wadden Sea. Compared to other shellfish, sublittoral mussels have the most flesh per unit shell mass (Ens & Kats 2004). As a result, they are the most profitable prey for Eiders, since these birds swallow their prey whole (Bustnes 1998, Bustnes & Erikstad 1990, Ens & Kats 2004). Large stocks of sublittoral mussels are found in the western part of the Dutch Wadden Sea and this is also the area where, in general, the largest numbers of wintering Eiders are found (Swennen *et al.* 1989, Koffijberg *et al.* 2001). Recently, there have been several years with low numbers in this area and these have coincided with low stocks of sublittoral mussels (Koffijberg *et al.* 2001, Camphuysen *et al.* 2002, Ens & Kats 2004). Finally, as already mentioned, shortage of sublittoral mussels is the best predictor of the occurrence of mass mortality among wintering Common Eiders (Kats *et al.* 2007a).

While stocks of sublittoral mussels are undoubtedly of great importance to the wintering Common Eiders, it is unlikely that other food stocks play no role. For instance, there are no significant stocks of sublittoral mussels in the eastern part of the Dutch Wadden Sea, so the 5.000 – 25.000 Eiders wintering there (Arts & Berrevoets 2006, Kats *et al.* 2007a) must feed on other prey. In addition, since the introduction of mussel culture in the Dutch Wadden Sea in 1951 (Dijkema 1997, Smaal & Lucas 2000) a substantial amount of the sublittoral mussels occurs on the commercial culture lots instead of on wild beds (Bult *et al.* 2004b, Ens *et al.* 2004). According to Swennen *et al.* (1989) the overall distribution of Common Eiders in the international Wadden Sea is not clearly related to the presence or absence of mussel culture plots, but the birds use these plots to some extent. However, Swennen *et al.* (1989) also present data that in January 1987 52% of the more than 130.000 Common Eiders in the western Dutch Wadden Sea occurred on or near mussel cultures. To increase our understanding of the impact of mussel fishery and mussel culture on Common Eiders, we need to know whether Eiders prefer sublittoral mussels on wild beds over sublittoral mussels on culture lots or *vice versa*.

Considering the above, our primary aim in this paper is to quantify the relative importance of various shellfish stocks to the Common Eiders that winter in the Dutch Wadden Sea. To this end we will relate the distribution of the Eiders to the distribution of the food stocks using a multi-scale approach, as recommended by Schneider (1994).
Methods

Our study focuses on analyzing the distribution of the large numbers of Eiders that spend the winter in the Dutch Wadden Sea, i.e. we exclude the North Sea coastal zone from our analysis. The majority of these birds breed in the Baltic area (Swennen et al. 1989, Desholm et al. 2002). They arrive in autumn until November and depart in March. We therefore defined the winter period as running from November to March the next year. Throughout this paper we will refer to the winter of year $t/t+1$ as the winter of $t+1$. Thus, the “winter” of 2000 is the winter that started 1 November 1999 and ended on 1 March 2000.

Eiders have been counted from boats and from the air, but only aerial counts have covered the entire Dutch Wadden Sea. Thus, we only used aerial counts. Many aerial counts were conducted in the period 1960-1990 (Swennen et al. 1989), but these data could not be used, because of lack of quantitative surveys of the available shellfish stocks. Since the early 1990s shellfish stocks in the Dutch Wadden Sea are surveyed on an annual basis. Usually, these surveys are not timed to the middle of winter, so a decision is necessary how to link the prey survey to the aerial counts. Our decision will be motivated when we describe each survey in more detail.

Aerial counts of the Common Eiders

Since 1993 aerial counts of Common Eiders are performed in a standard fashion by RIKZ (Berrevoets & Arts 2003) and Alterra (de Jong et al. 2005) and we refer to these publications for a detailed description of the methodology. Here, we provide a short summary. The Dutch Wadden Sea and the North Sea coastal zone to the north of the Wadden Sea islands and to the west of the province of Holland are systematically searched for birds by flying along previously defined transects, separated by 1.5 km from each other. Counters are positioned at both sides of the plane (a Cessna 172P with wings above the hull) and each counts an area with a width of 750 m. Flight altitude is 150 m and ground speed varies between 140 and 190 km per hour, depending on wind speed and wind direction. During the flight, the geographical location is determined with a Global Positioning System (GPS: Garmin 12XL or Garmin 76) every 5 seconds.

The location of counted groups of Common Eiders was determined as follows:
1. For each group, we determined the last GPS point before and the first GPS point after the group was encountered.
2. The distance between the two locations was calculated and the fraction of that distance that was covered when the group was encountered, allowing the determination of the exact location of the plane.
3. Depending on whether the group was spotted left or right of the plane, a standard distance of 250 m left or right was added to arrive at the best estimate of the location of the group.
Subsequently the data were stored in a database and GIS was used to link the numbers of birds counted to data on shellfish stocks in grids of different sizes.

RIKZ has counted during high tide, whereas Alterra has counted during low tide. Counts were averaged per winter, but also per counting type. The latter allowed us to analyze whether the distribution during high tide correlated to the distribution during low tide and at which scale, for winters where both types of counts were conducted.

Food stocks
Food stocks were expressed in two ways. First, as surface area of a grid cell covered by a cockle bed, a wild mussel bed, or a culture plot with mussels on it. Second, as total biomass (in that grid cell) of a given year class (or size class) of mussels (or cockles). Biomass was measured in gram fresh weight, which includes the weight of the shell, the enclosed water and the flesh of a live animal. To obtain the biomass estimate, we first multiplied each biomass density estimate with the area for which it was thought to be representative and then added all samples in a given grid cell.

Cockles Cerastoderma edule in littoral and sublittoral areas
In the 1980s and 1990s, fishermen walked the littoral mud flats during low tide in early spring in March and April, to map the cockle beds. These maps were subsequently digitized as polygons as part of the EVA II research project (Ens et al. 2004) and electronically available from the CD accompanying the report by Zwarts et al. (2004). We assigned these spring surveys to the preceding winter. This means that cockle beds that disappeared during winter are not included (see discussion). The variable that we used was the surface of the grid cell covered with cockle bed. The maps of the fishermen were used by Wageningen IMARES (formerly known as RIVO) to design a stratified sampling of the cockle beds in April/May. The first cockle survey was conducted in 1990 and a detailed description of the sampling scheme is provided by Bult et al. (2004a). The cockles were categorized according to age (0, 1, 2 and more than 2 years) and their number and biomass (gram fresh weight) was recorded. Almost certainly, the cockles aged 0 were misidentified individuals with age 1. We therefore lumped them with cockles of age 1. We assigned the results of the spring survey to the preceding winter and distinguished between cockles sampled in the littoral zone and cockles sampled in the sublittoral zone.

For obvious reasons the mapping of the fishermen was restricted to the littoral zone. Thus, we can only compare the area estimate with the biomass estimate for this littoral zone. The area covered by cockle beds closely correlated with the biomass estimate, especially when grid cells were large and when data were averaged over winters, thereby reducing sampling error (Table 8.1). Thus, the two variables could not be treated as independent in the statistical analysis and we decided to
use the biomass of littoral cockles in the majority of analyses. However, for important results we checked if replacing the area of littoral cockle beds with the biomass of littoral cockles affected the results.

**Mussels *Mytilus edulis* in the littoral areas**

The contours of littoral mussel beds have been mapped by Wageningen IMARES since 1994 (Steenbergen *et al.* 2003). Contours are obtained by walking with a GPS around a mussel bed according to a fixed protocol (Brinkman *et al.* 2003). Not all beds are always visited making it necessary to reconstruct areas, usually from observations in the following years – if an old bed is present in year t, it must have been present in year t-1 as well (Steenbergen *et al.* 2003, Steenbergen *et al.* 2005). If possible, beds were categorized as seed beds, beds with half-grown mussels, or beds with consumption-sized mussels. Seed mussels are less than 1 year old. Half-grown mussels are more than 1 year old and have a maximum length of 45 mm. Consumption-sized mussels are all mussels exceeding 45 mm in length (van Stralen *et al.* 2006). Surveys were carried out in autumn and spring. The autumn survey was assigned to the following winter and the spring survey to the preceding winter. However, the autumn surface data preceding the winter were highly correlated to the spring data following the winter (Table 8.2). This was especially true for large grid cells and when data was averaged per grid cell, i.e. when sampling error was reduced. Thus, the two variables could not be treated as independent in the statistical analysis. We decided to average the two values to obtain a single value for each winter.

No precise measurements are available for the years preceding 1994, but it is known that virtually all littoral mussel beds disappeared in 1990 and that the first major spatfall was in the autumn of 1994 (Dankers *et al.* 2003). Thus, we felt it safe to assume that the area of littoral beds was 0 in the years 1991-1993, as did Ens *et al.* (2004). In this study, this assumption only affected the data for the winter of 1994.

### Table 8.1

The correlation between the area in a grid cell covered by littoral cockle *Cerastoderma edule* beds in spring and the biomass estimated that same spring for grid cells of different sizes in the Dutch Wadden Sea. Winters were either kept separate or averaged. All correlations were highly significant (P < 0.01).

<table>
<thead>
<tr>
<th>Grid size (m)</th>
<th>Winters kept separate</th>
<th>Winters averaged per grid cell</th>
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<tbody>
<tr>
<td></td>
<td>Pearson r</td>
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</tr>
<tr>
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</tr>
<tr>
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<td>1692</td>
</tr>
<tr>
<td>10000</td>
<td>0.62</td>
<td>516</td>
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</table>
The maps of the mussel beds were used by Wageningen IMARES to design a stratified sampling of the mussel beds in April/May. A detailed description of the sampling scheme is provided by Bult et al. (2004a). Mussels were categorized as seed mussels, half-grown mussels and consumption-sized mussels and their number and biomass (gram fresh weight) was recorded. We assigned the results of the spring survey to the preceding winter.

Wild Mussels *Mytilus edulis* in the sublittoral areas

Wild sublittoral mussel beds are not mapped, but their general occurrence is known from experience and pilot samplings in early spring by fishery inspectors. This allows Wageningen IMARES to design a stratified sampling scheme which takes place in March/April. A detailed description of the sampling scheme is provided by Bult et al. (2004a). Mussels were categorized as seed mussels, half-grown mussels and consumption-sized mussels (see above) and their number and biomass (gram fresh weight) was recorded. We assigned the results of the spring survey to the preceding winter.

Mussels *Mytilus edulis* on (sublittoral) culture plots

Within our study area, culture plots only occur in sublittoral areas in the western part of the Dutch Wadden Sea. Although estimates are available of the total biomass of mussels on all culture plots together (Bult et al. 2004b), we lack data on the distribution of biomass for our study period: the winter of 2005 was the first time that a quantitative sampling of mussels on the culture plots was effectuated (Kamermans et al. 2005). What is available are estimates from fishery inspector Nico Laros (pers. comm.) for the winters of 1994 to 2004 whether a particular culture plot was empty or seeded with seed mussels, half-grown mussels or consumption-sized mussels. The estimates are based on a combination of a sampling program of the fisheries inspectors that takes place between October and March, with

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### Table 8.2

The correlation between the area in a grid cell covered by littoral mussel *Mytilus edulis* beds in the autumn preceding the winter and the spring following the winter for grid cells of different sizes in the Dutch Wadden Sea. Winters were either kept separate or averaged. All correlations were highly significant (P < 0.01).

<table>
<thead>
<tr>
<th>Grid size (m)</th>
<th>Winters kept separate</th>
<th>Winters averaged per grid cell</th>
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<tr>
<td>10000</td>
<td>0.85</td>
<td>516</td>
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</table>
The general picture of mass-mortality among Common Eiders in the Netherlands during the winters of 1999/2000 and 2001/02: top a dead, and bottom a dying Common Eider along the coastline of the Wadden Sea  (Photos: Ingrid van der Spoel)
information on landings of mussels from the culture plots during this period. We also knew the exact location of each culture plot as well as the area suitable for culturing mussels. From this, we could calculate for each grid cell the area covered with seed mussels, half-grown mussels and consumption-sized mussels on culture plots.

**Statistical analysis**

The distribution of Eiders was analyzed relative to shellfish distributions to obtain an impression of:

- **The scales at which Eiders are selecting for food**: Do Eiders select for small-scale profitable patches of shellfish or for larger areas where profitable patches are more common? What scales are most relevant for efficient modelling; i.e. at what scales are eider distributions best described from shellfish distributions?
- **The relative importance of different shellfish food sources** to the distribution of Eiders, including sublittoral and littoral cockles and mussels, in the wild and on mussel culture plots.

For this, we used a multi-scale analysis by aggregating data over increasingly larger spatial scale, i.e. we varied the size of the grid cells where we compared estimates of the food stock to estimates of the number of Eiders from 750x750 m to 10x10 km. With increasing grid cell sizes, an increasing proportion of grid cells includes areas outside the littoral and sublittoral areas of the Wadden Sea (Figure 8.1). We did not consider this a problem, since our analysis seeks to link the total number of Eiders in a grid cell to the total area of that grid cell covered by shellfish beds or the total biomass of shellfish, i.e. we did not use densities. For the winter of 1993, we lacked data on mussels on culture plots. Thus, we restricted the analysis to the winters of 1994-2004.

Analyses were done using analyses of variance and analyses of deviance in SAS. The deviance analyses were done using a log-link function and assuming a Poisson distribution of residuals. The scale factor was estimated within the procedure (PROC GENMOD) to minimize effects of possible overdispersion.

As such, models were made of the following general structure:

\[
Eiders = e^{(a + b*MSw + c*MSp + d*ML + e*CS + f*CL)}
\]

These models were estimated at various spatial scales. For this, rectangular grid patterns were used with sides of 750 m, 1500 m, 3 km, 5 km and 10 km. Within the individual cells of these grids the stocks of Eiders, mussels and cockles were estimated for the winters of 1994-2004 separately, using the following indices (1994 = winter 1993-1994):

- Eiders: total number of Eiders, from aerial survey counts (#)
- EiderHT: total number of Eiders, from aerial survey counts at high tide (#; winters of 2000, 2001, 2003 only)
EiderLT: total number of Eiders, from aerial survey counts at low tide (#; winters of 2000, 2001, 2003 only)
MSw: total biomass of sublittoral wild mussels (g)
MSP: total area of culture plots that are actively used for the culture of sublittoral mussels (m²)
ML: total area of littoral mussel beds (m²)
CS: total biomass of sublittoral cockles (g)
CL: total biomass of littoral cockles (g)
CA: area of cockle beds (ha)

A p-value of 0.05 was used as a selection criterion to separate “significant” from “non-significant” effects.

In these analyses a three-step approach was used:
1. Relevant scales to behaviours and modelling. First the scales that were most appropriate to Eider behaviour and model building were determined from scale analyses and the aggregation routines mentioned above.
2. Relative importance of food sources. Next, detailed models were made at the relevant scales from the first step, to look at the relative importance of the 5 different shellfish food sources mentioned previously.

The analyses of these steps were of an exploratory nature, i.e. not taking into account possible effects of differences in Eider behaviours at different densities of Eiders or shellfish stocks. Obviously, such an approach is only warranted, if it does not compromise the general conclusions regarding relevant scales and relative importance of food items.
Dissection of dead eiders collected in the Wadden Sea area with from left to right Mardik Leopold, Cees Camphuysen, Piet Duiven, Fred Borgsteede and Romke Kats (Photo: Alterra)

Horror in the Wadden Sea. Scalped Eiders were frequently reported (alive and dead) since the end of the 1990’s, but sightings and recoveries were restricted to in the western part of the Wadden Sea. (Photo: Alterra)
Several lines of evidence suggest that Ensis is an alternative food source to Mussels and Spisula, but selection is size-limited. Dead Common Eider with too large Ensis in the oesophagus, which has also been reported by Swennen & Duiven (1989). (Photo: Alterra)
3. Because of this, additional analyses were performed in order to obtain an impression of the robustness of the general conclusions.

   Ad 1. The scales that were most appropriate to Eider behaviour and model building were determined by correlating the number of Eiders in the cells of the grid patterns at high tide with the number of Eiders at low tide. We hypothesized that Eiders select for larger areas and from this, we expected the correlation to be higher at larger spatial scales. In addition, models were made that described the Eider distribution relative to their food sources at various spatial scales. We expected the descriptive powers of these models, estimated from the % of deviance explained by the model, to increase with spatial scale as Eiders were expected to select for larger scale areas with a bigger availability of food, instead of small-scale food patches.

   Ad 2. In order to determine the relative importance of the various shellfish stocks, first a backward stepwise regression approach was used to exclude all non-significant variables. Next, the relative contribution of the (significant) explanatory variables to the overall descriptive powers of the model was estimated by looking at the % deviance explained of the variables separately.

   Ad 3. The analyses above did not take into account the fact that Eider populations and their food sources varied among winters and that the distribution of Eiders may be density dependent. In addition, the various food sources may not be independent in their effect on the distribution of Eiders. From this, additional analyses were done that included the effect of “winter” as a class variable and interaction terms between explanatory variables. We stress that these analyses were not meant to look for e.g. possible density-dependent distribution of Eiders. Instead, these analyses were meant to determine if such processes, when present, prevented us to draw valid general conclusions from the first two steps.

In addition to the aggregation or grouping routine described above, we performed several multiscale analyses based on a lagging procedure (distance method). These analyses were aimed at obtaining a better understanding of the effects of small-scale sampling variation. Thus, we varied “scale” in our analysis by (1) aggregating data on Eiders and shellfish at increasingly larger cells covering the Dutch Wadden Sea (checkerboard with varying cell sizes) and (2) by correlating shellfish and Eider numbers from the 750*750 m cell data over increasingly larger distance slots, cf. Sokal & Oden (1978).

Both procedures accomplish the same thing, i.e. changes in attention by zoom rescaling, despite differences in presentation and execution (Schneider 1994). However, the methods differ with respect to the effects of small-scale sampling variation on results. Larger cells will contain more samples on Eiders and shellfish, resulting in a reduction of the variation in mean densities among cells at larger cell sizes. Larger cells occur especially at the larger scales within the grouping procedure. From this, we expected that small-scale sampling variation would have a different effect on the results when using a lagging (2) versus a grouping (1) routine. We will return to this topic in the discussion.
Results

Distribution of Common Eiders
Eiders tended to be more common in the western part of the Dutch Wadden Sea than in the eastern part, but this large-scale pattern was not very obvious when small grid cell sizes were used (Figure 8.2). It was most apparent for grid cells with a large size.

Distribution of the food stocks
Each food stock had a well defined distribution in the Wadden Sea, which clearly differed from the distribution of other food stocks (Figure 8.3–8.5). These patterns were especially clear at small spatial scales. Visual inspection of the distribution

![Maps showing distribution of Common Eiders](image)

**Figure 8.2** Average distribution of Common Eiders *Somateria mollissima* in the Dutch Wadden Sea for the winters 1994-2004 at different spatial scales, i.e. grid cells of different size: (A) 750 m, (B) 1500 m, (C) 3000 m, (D) 5000 m, (E) 10000 m.
Chapter 8

The remainings of Shore Crabs *Carcinus maenas*, which is the intermediate host of *Profilicollis botulus*, in the faeces of Common Eiders. (Photo: Alterra)

The plane (PH-TXL) and crew of the aerial surveys of Common Eiders in safety outfit at airport De Kooy, south of Den Helder, with from left to right Piet Duiven, Simon IJspeert (pilot) and Mardik Leopold. (Photo: Martin de Jong)
Aerial view of tidal musselbeds in the eastern part of the Wadden Sea around low tide (top), and cockle feeding Common Eiders (dabbling) around low tide using tidal currents creating dark patterns of released mud from the tidal flats in the water (bottom). (Photos: Alterra)
patterns of the Common Eiders (Figure 8.2) and the distribution patterns of the shellfish stocks (Figure 8.3–8.5) allows a first assessment of the correlation between Eiders and shellfish. During the study period, littoral cockle beds were especially common near the edges of the Wadden Sea, whereas large flocks of Eiders were more likely to be found in the central parts of the Wadden Sea. Littoral mussel beds were especially common in the eastern part of the Wadden Sea, whereas the majority of the Eiders occurred in the western part of the Wadden Sea. Sublittoral wild mussel beds were especially common in the southern part of the western Wadden Sea and the sublittoral culture plots are found along a diagonal in the western Wadden Sea from the south to the north east. Eiders are common in these
areas. Thus, on the basis of this visual inspection we expect that sublittoral mussels will be the best predictor of the number of wintering Common Eiders.

Comparing counts during high tide to counts during low tide
For the winters of 2000, 2001 and 2003, counts of the Common Eiders during both low tide and during high tide were available, allowing us to investigate if the distribution during high tide matched the distribution during low tide.

To this end we correlated the number of Eiders counted during low tide with the number of Eiders counted during high tide (Figure 8.6). Apart from performing the analysis on untransformed data, we also ln-transformed the counts (in which case
Direct access to fresh water in the vicinity of the high density breeding area of Common Eiders in the colony on Vlieland, i.e. the Kroons Polders. (Photo: Martin de Jong)

Male and female Common Eider near the breeding colony on Vlieland. (Photo: Jeroen Reneerkens)

Nest with eggs and down of breeding Common Eider in the colony of Vlieland. (Photo: Martin de Jong)
Resting Common Eiders in the Wadden Sea on sand bank with seals at low tide. (Photo: Bram Fey)

The Pacific Oyster *Crassostrea gigas* has invaded the Wadden Sea area. (Photo: Alterra).
we added 1 to all counts to avoid taking the logarithm of 0). The results are displayed in Table 8.3. In all cases, there was a positive correlation between the number of Eiders counted during high tide and the number of Eiders counted during low tide. However, the magnitude of the correlation was higher for the transformed counts and strongly increased when the size of the grid cells was increased.

**Table 8.3** Results of correlations between the number of Common Eiders *Somateria mollissima* counted during low tide and the number of Eiders counted during high tide in the Dutch Wadden Sea, for both untransformed and ln-transformed counts at different grid cell sizes. All correlations were highly significant (P<0.01).

<table>
<thead>
<tr>
<th>Grid size (m)</th>
<th>N</th>
<th>Pearson r (untransformed counts)</th>
<th>Pearson r (transformed counts)</th>
</tr>
</thead>
<tbody>
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**Figure 8.5** Average distribution in the Dutch Wadden Sea over the winters 1994-2004 of (A) biomass littoral mussel *Mytilus edulis* beds in spring and (B) biomass wild sublittoral mussel stocks in spring. Graphs on the left indicate the average distribution using a grid cell size of 750 m by 750 m and the graphs on the right indicate the average distribution using a grid cell size of 10 km by 10 km. See text for details.
Distribution of Eiders and shellfish varies with scale

The potential to describe Eider distributions from shellfish data was estimated using the % deviance explained by model (1) described above in the methods section. These models were fitted at various spatial scales, including all explanatory variables, regardless if the contribution of these variables to this model was “significant” or not. Error! Reference source not found. (solid line) shows that % deviance explained of these models increases with spatial scale.

Additional analyses revealed that the mussels on culture plots were largely responsible for these patterns and that cockles and wild mussels were of minor importance. This is illustrated in Figure 8.7 (grey line) that shows that roughly 70% of the deviance explained by model (1) could be achieved using a model based on MSp alone:

\[
Eiders = e^{(a+b\times MSw)}
\]  

(2)

The above analyses apply to the 11 winters in the period 1994-2004. When repeating these analyses for Low Tide situations in the winters of 2000, 2001 and 2003, similar results were found (Figure 8.8) in that the % deviance explained...
Figure 8.7 Common Eider *Somateria mollissima* distributions from shellfish information at various spatial scales (0.75, 1.5, 3, 5, 10 km) in the Dutch Wadden Sea. % deviance explained by the models “Full:” *Eiders* = $e^{(a+b^{*}MSw+c^{*}MSp+d^{*}ML+e^{*}CS+f^{*}CL)}$ and “MSp only (= culture plots only)” *Eiders* = $e^{(a+b^{*}MSp)}$; winters of 1994-2004.

Figure 8.8 Common Eider *Somateria mollissima* distributions from shellfish information at various spatial scales (0.75, 1.5, 3, 5, 10 km) in the Dutch Wadden Sea. % deviance explained by the models “Full:” *Eiders* = $e^{(a+b^{*}MSw+c^{*}MSp+d^{*}ML+e^{*}CS+f^{*}CL)}$ and “MSp only (= culture plots only)” *Eiders* = $e^{(a+b^{*}MSp)}$; winters of 2000, 2001, 2003 during low tide and high tide.

Figure 8.9 Non-ergodic correlogram of Common Eider *Somateria mollissima* distributions in the Dutch Wadden Sea at multiple space-time scales. Period 1994-2004.
increased with spatial scale and that roughly $\frac{3}{4}$ of the deviance explained by the “full” model could be achieved using a model based on MSp alone (model (2)). The % deviance explained was higher however, regardless of spatial scale.

Similar analyses for High Tide situations in the years 2000, 2001 and 2003 revealed a somewhat different pattern in that MSp contributed much less to % deviance explained of the full model (15-40% of total % deviance explained instead of $\frac{3}{4}$). The Eider distribution at high tide at a 10 km scale was significantly correlated with ML, MSp and MSw. The % deviance explained by these variables separately was 0.5, 9 and 14 respectively and 24 when combined (n=129; % deviance explained of full model = 25%).

**Distribution of Eiders and shellfish at the scale of 10 km**
The previous analyses suggested that Eiders select for larger scale areas, and that models are most effective at larger spatial scales. Because of this the following analyses concentrated on the largest scale (10 km).

As shown above, Eiders were significantly correlated with MSp and MSw at the 10 km scale. The % deviance explained by these variables separately was 11 and 4 respectively, and 15 when combined (n=473; % deviance explained of full model = 15%). The contributions of CL, CS and ML were not significant.

As all mussel culture plots are found in the western part of the Wadden Sea, our next step was to perform the analyses separately for the eastern and western part of the Wadden Sea. We defined the western part as RIKZ areas 1 and 2, and the eastern part as RIKZ areas 3 and 4 (Arts & Berrevoets 2006).

In the western part, Eiders were significantly correlated with MSp and MSw, as before. The % deviance explained by these variables separately was 8 and 3 respectively and 10 when combined (n=297; % deviance explained of full model = 11%). The contributions of CL, CS and ML were not significant.

In the eastern part, Eiders were significantly correlated with ML and MSw. The % deviance explained by these variables separately was 21 and 2 respectively and 10 when combined (n=176; % deviance explained of full model = 23%). The contributions of CL, CS were not significant. MSp did not contribute as no culture plots were present in this area.

Next, we attempted to build a model that included all possible interaction terms, provided their contribution to the overall model was significant. To a degree these models were difficult to fit as the estimation routines did not converge in some of the steps of the stepwise approach. Nevertheless, the end model did converge, suggesting a significant “winter” effect and a positive effect of MSp. All other variables or interaction terms were excluded. The % deviance explained by these two variables separately was 6 and 11 respectively and 16 when combined (n=473).

Because of the significant winter effect, we repeated the analysis for each winter separately. The results are summarized in Table 8.4 and indicate that MSp is
significantly related to the Eider distributions in 9 of 11 winters. In 1999 Eider distributions were not related to any of the explanatory variables. MSw was significantly related to the Eider distributions in 5 winters, ML and CS in two, and CL in only one. Again, these analyses show that sublittoral mussels, especially the ones on sublittoral culture plots, are important to Eider distributions. Cockles were clearly much less important.

It is possible that our conclusion that CL had little effect on Eider numbers at large spatial scales was due to our decision to express CL in kg fresh weight on the basis of the sampling surveys, instead of ha from contour data. We therefore repeated the analyses summarized in Table 8.4, but now with CL quantified in terms of ha from the available contour data, i.e. using CA. The general outcome of these analyses was in line with Table 8.4, in terms of the variables included in the model.

Another possible explanation for our failure to demonstrate an effect of CL in the majority of winters could be the fact that we did not distinguish between age classes of cockles. Young and small cockles have a more favourable shell/flesh ratio (Ens & Kats 2004) and are preferred by the Eiders (Swennen 1976a, Ens & Kats 2004). We therefore repeated the analysis mentioned above, that included all pos-

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**Table 8.4** Overview of variables that significantly (p=0.05) contributed to a description of the Common Eider *Somateria mollissima* distribution in the Dutch Wadden Sea using a grid size of 10 km by 10 km, for each of the winters in the period 1994-2004; the significance of the variables is indicated for each variable-winter combination. For a description of the model, the variables and the model fitting procedure: see text. Also indicated is the percentage of the deviance explained by the model. All significant explanatory variables were positively related to the Eider distribution. The final column (n) indicates the number of years in which the variable was included in the model.

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sible interaction terms and winter as a class variable, but now separating CL and CS into two size/age classes (1 year old cockles versus older individuals). Again, the results from this analysis were in line with the previous analysis that showed that only “winter” and MSp significantly contributed to an explanation of Eider distributions. In short, we did not find any evidence to suggest that the relative importance of sublittoral mussels on culture plots over the other variables in explaining Eider numbers was the result of the units we chose to quantify cockles.

**Table 8.5 Overview of variables that significantly (p=0.05) contributed to a description of the Common Eider *Somateria mollissima* distribution in the Dutch Wadden Sea, using a grid size of 750 m by 750 m for each of the winters in the period 1994-2004; the significance of the variables is indicated for each variable-winter combination. For a description of the model, the variables and the model fitting procedure: see text. Also indicated is the percentage of the deviance explained by the model. All significant explanatory variables were positively related to the Eider distribution. The final column (n) indicates the number of years in which the variable was included in the model.**

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**Multiscale distribution in relation to shellfish stocks**

Finally, we repeated the analysis presented in Table 8.4, for the smallest possible grid size (Table 8.5). As before, MSp significantly affected the distribution of Eiders in the largest number of winters (10 winters compared to 9 winters in the previous analysis). However, MSw remained the same with 5 winters, but ML changed from 2 to 7 winters with a significant impact, CL from 1 to 6 and CS from 2 to 4. Usually, prey-winter combinations that were significant at a scale of 10 km, were also significant at a scale of 750 m, but this was not always the case. Even though many models contained three of four prey variables, the total deviance that could be explained was usually only a few percent.
Multi scale analysis using distance measures

Two additional scaling analyses were done using a lag procedure instead of a grouping procedure. First, we analysed the patchiness of Eider distributions by calculating autocorrelation functions (non-ergodic correlograms) for Eider distributions using the calculations procedures described in Rossi et al. (1992) (Figure 8.9). Next, we correlated Eider distributions and sublittoral culture mussels over various scales using the (non ergodic cross-) correlation routines described by Rossi et al. (1992) (Figure 8.10).

Figure 8.9 suggests that Eider distributions occur in patches of 2-3 km, and that the distribution of Eiders in a certain year is not informative for the distributions in the previous or next year. In other words, the patch distribution varies independently from one year to the next. In addition, “r” is low, suggesting that the autocorrelation is not very strong, possibly the result of small scale sampling variation.

Figure 8.10 suggests that in most years Eiders select for small-scale patches of mussels on mussel culture plots, as r increases at small scales. These small-scale patches could in fact be individual culture plots. The culture plots of individual mussel farmers are aggregated in large clusters, which may be more than 5 km long and several 100 m wide.
Discussion

Sublittoral mussels, especially on culture plots, seemed to be the most important factor in determining the distribution of Eiders wintering in the Dutch Wadden Sea as a whole during the study period. These sublittoral mussels are virtually restricted to the western part of the Dutch Wadden Sea where most Eiders are present in winter. When focusing on the eastern part of the Wadden Sea, the distribution of Eiders seemed to be largely driven by littoral mussels.

The problem of scale

Correlations between Eiders and sublittoral mussels on culture plots were higher at larger spatial scales when using a grouping routine in the scaling analyses. When using a lagging routine, correlations were higher at smaller spatial scales.

At first sight, these results contrast (cf. Figure 8.7 and 8.8). However, we feel that the results of these analyses are quite in line with the hypothesis that Eiders select for small-scale profitable patches of mussels on mussel culture plots, that these small-scale mussel patches are distributed within larger clusters of mussel culture plots, and that our estimates of mussel densities on mussel culture plots and especially our estimate of Eider numbers are very crude at small spatial scales. The profitable patches may correspond to plots of individual mussel farmers, which each have their own stocking regime. The individual culture plots occur in clusters, which may be more than 5 km long and several 100 m wide.

When aggregating information at larger scales, some of the (random) noise and variance associated with sampling are reduced. This may result in better models at larger scales, not because the distribution behaviour of Eiders is operating at larger scales, but because the estimates of densities of Eiders and shellfish are better at larger spatial scales as more samples are used for the individual estimates. In addition, by aggregating data at very large scales, the number of observations that are available for model building are reduced whereas the number of parameters in the models is rather similar or stays the same, especially when variables are not excluded based on some criterion for significance. Because of this the models may be over parameterized and % deviance explained will increase with scale.

In short, the scale dependent patterns may be a result of (1) real Eider duck behaviour, (2) sampling error and precision of estimates, (3) possible over parameterization. Especially when interested in the distribution behaviour of Eiders, a clear separation of #1 versus #2 and #3 is needed. For this, additional data that allow for precise estimates at small scales and independent data for model validation are needed. Such data were not available.

Sampling variance certainly affected our results, but did not invalidate our general conclusion that sublittoral mussels on culture plots (MSp) were the prime determinant of the distribution of Common Eiders. Similarly, there are good arguments that our results are not an artefact of over parameterization. The reason for
this is that the models that only included “significant” variables, thereby reducing
the possible effects of over parameterization, nearly always included sublittoral
mussels as the most important variable.

Thus, in order to describe the Eider distributions from MSp a larger scale
approach using larger grid cells is most effective (Eider density best explained from
shellfish densities, % deviance explained highest), despite that Eiders may select
for small scale profitable patches of sublittoral mussel plots (see Figure 8.10).
Under this hypothesis, the small scale behaviours of Eiders can be extrapolated to
larger scales from an understanding of the distribution of small-scale individual
culture plots over larger areas and clusters of mussel culture plots.

Additional analyses on artificial data confirmed that the correlation between
Eiders and MSp may decrease with increasing spatial scales in a lagging procedure
(distance method) and may increase with scale using an aggregation routine based
on the very same data, provided that the sampling variance is large enough. In
these analyses, small- scale Eider distributions were created from small-scale MSp
distributions (Eider = MSp), with MSp distributions organized in a nested struc-
ture of larger and smaller scale clusters. Next, we varied the degree of sampling
error and compared the results from correlation analyses based on aggregation and
lagging routines.

Similar scale-dependent results were found in other studies on bird distribu-
tions and their prey. For instance Schneider & Piatt (1986) observed that the pat-
tern in change in density of Murres (Uria spp.) along a transect in the northwest
Atlantic was almost exactly the same as the pattern of change in fish density at a
resolution of 2000 m, whereas this match was not quite as good at lower resolu-
tions and at a resolution of 200 m the match was weak. Obviously, these results
underline the fact that the choice for any particular scale may have a large effect
on whether or not correlations are found. From this, multiscale analyses may pre-
vent that relevant scales are overlooked, especially when we do not have prior
information the relevance of various measurement scales. Similar examples on bird
distributions can be found in a growing list of papers (Schneider & Duffy 1985,
Schneider 1989, Piatt 1990, Schneider 1990, Schneider 1993, Horne &

On a more general note, animal distributions are generally the result of process-
es that operate at multiple space and time scales. The distributions we observe at
any one particular scale may be the result of processes that operate at scales that
are very different from the scale of our observations. From this, extrapolation of
inferences on animal distributions across scales requires knowledge on the relative
importance of processes at different scales (Horne & Schneider 1994, Schneider et
al. 1999, Robinson et al. 2002, Robinson et al. 2004) and suitable extrapolation
routines (Levin 1992). Such knowledge can only be obtained from multi scale
approaches, instead of a single scale approach settled on by a combination of logis-
tical constraints, habitual field operations and expert judgment. Multi-scale analy-
ses of bird distributions are more cumbersome, however, and relatively rare. Examples include studies mentioned above, which underline the importance of a multiscale approach to understand bird distributions, to determine effective measurement scales and to extrapolate observations and inferences from one scale to the other.

In our study, the multiscale analyses did enable us to identify “effective” scales in that the distributions of Eiders was better explained from shellfish distributions at particular scales. However, the contrasting results of the multiscale analyses using grouping and lagging routines underlie that care should be taken when interpreting these results in terms of processes, e.g. the scales at which behaviours operate, without direct behavioural observations. The grouping exercise might have enticed us to conclude that Eiders select for larger scale profitable areas where sublittoral culture mussels are more abundant, as correlations peaked at larger scales; the lagging routine might have enticed us to conclude that Eiders select for small scale profitable mussel culture plots, as correlations peaked at smaller scales. Thus, the results did not clearly indicate the scales of these behaviours, but did allow us to devise a hypothesis of Eider behaviours that explicitly addresses some seemingly relevant scales: small-scale selection behaviours (of individual selecting culture plots stocked with profitable mussels) and larger scale distributions of clusters of culture plots within the Wadden Sea. Further research should reveal how to extrapolate small scale behaviours to larger scale distributions of Eiders.

Within a winter, the distribution of Eiders counted during high tide correlated better with the distribution counted during low tide with increasing scale. We think that this can be explained by the fact that wintering Common Eiders often occur in large flocks. The likelihood that flocks move between grid cells between counts increases with decreasing size of the grid cells. It is the day-to-day movement of flocks of Common Eiders that requires study.

**How important are cockles as a food source?**

Although Common Eiders regularly feed on cockles (Swennen 1976a, Hilgerloh 1999, Scheiffarth & Frank 2006), cockles did not contribute to models of Eider distribution when all data were lumped. When winters were analyzed separately using large grid cells, there was only one winter (1997) in which we observed a significant correlation between the number of Eiders and the stock of littoral cockles and there were only two winters (1997 and 1998) in which we observed a significant correlation between the number of Eiders and the stock of sublittoral cockles. During the January count in the winter of 1997, large parts of the Wadden Sea were covered with ice, and this may have influenced the distribution of the birds (Arts & Berrevoets 2006). That winter, there were few birds in the vicinity of the mussel culture plots, but the birds had moved to nearby sublittoral areas and not to littoral areas. Thus, the correlation with littoral cockle beds may have been an artefact of the ice. Using the area of cockle beds, instead of biomass, or distin-
guishing between different year classes of cockles did not change the general conclusion on the “unimportance” of cockles.

A potential problem is that Eiders were counted in winter and cockles were sampled in spring. We assigned the results of the spring survey of the cockles to the distribution of the Eiders counted in the preceding winter. This means that cockle beds that disappeared during winter are not included in the analysis. This problem may have affected the results for the winters of 1996 and 1997. Both winters were severe with extensive periods where the Wadden Sea was covered with ice, leading to mass mortality of cockles. Following the severe winter of 1996, there was a good spatfall of cockles in the summer of 1996, but the majority of these young cockles were killed in the severe winter of 1997. Because the frost period started in December and the Eiders were counted 9 and 10 January, the cockles most probably died before the count took place. Yet, 1997 was the only winter in which we observed a significant correlation between the distribution of Eiders and the distribution of littoral cockles at large spatial scales. Thus, it seems unlikely that the difference in timing between counts and sampling is responsible for the “unimportance” of cockles.

When we repeated the analysis using small grid sizes (750 m by 750 m), sublittoral mussels on culture plots (MSp) was again the most important variable, but we found more winters with a significant relationship between Eider numbers and both littoral and sublittoral cockle stocks. However, these models explained very little deviance. It is possible that our analyses are sensitive to the relative importance of mussels versus cockles to Eider distributions. Cockles may still be an important part of the diet of Eiders, but the importance of sublittoral mussels on mussel culture plots is so much larger when compared to cockles, that MSp is the determining explanatory variable and CL or CS are seldom included in the models.

The most likely explanation for the attractiveness of sublittoral mussels compared to cockles and littoral mussels are their thin shell and the high flesh content (Bustnes & Erikstad 1990, Bustnes 1998, Ens & Kats 2004). Due to the attractiveness of sublittoral mussels, densities of wintering Eiders are low in the eastern part of the Dutch Wadden Sea, despite large stocks and locally high densities of littoral cockles and littoral mussels. According to our analyses, the relatively small number of Eiders that winters in the eastern part of the Dutch Wadden Sea is primarily found near littoral mussel beds. A possible explanation is that the shell/flesh ratio of littoral mussels compares favourably to the shell/flesh ratio of littoral cockles (Ens & Kats 2004). However, a much more thorough investigation of the actual energetic benefits of feeding on cockles or littoral mussels indicates that there is not much difference between these two prey on average (Scheiffarth & Frank 2006). The study of Scheiffarth & Frank (2006) also demonstrates large differences in flesh content of mussels on different beds. On some beds the mussels are of such poor quality that it is impossible for the Eiders to maintain a positive ener-
gy balance. It seems likely that better models of Eider distribution will only be possible when information on the prey would also include the quality of the shellfish.

Sublittoral mussels on wild beds versus culture plots
Mussels on culture plots, which are only found in the western part of the Dutch Wadden Sea, seemed to be the most important factor, relative to wild mussels or cockles, to the distribution of Eiders. This finding corroborates previous results that the stocks of sublittoral mussels are of paramount importance to the survival of the wintering Common Eiders in the Dutch Wadden Sea (Camphuysen et al. 2002, Ens et al. 2002, Ens & Kats 2004, Kats et al. 2007a). During the study period nearly all mussel seed used to stock the culture plots was fished from wild mussel beds in the sublittoral of the western Dutch Wadden Sea (Bult et al. 2004b). These wild sublittoral mussels also significantly affected the distribution of Common Eiders, but in fewer winters than the mussels on the culture plots. In most analyses mussels on culture plots explained more deviance than wild sublittoral mussels, but in one analysis this was reversed. Thus, mussels on wild sublittoral beds were important to Eiders, but perhaps mussels on culture plots were even more important during the study period. If so, this could be due to mussels on culture plots being larger and more profitable than wild mussels. Even if true, that does not necessarily imply that mussel culture benefits Common Eiders. During the study period mussel seed fishery in the sublittoral was so intense that most mussels on wild beds were fished before they could grow to a large size (Bult et al. 2004b). Culture plots are located in different areas than the wild beds, and one might argue that Eiders simply moved with the mussels as they were transported from the wild beds to the culture plots. Thus, the fact that Eiders are attracted to culture plots does not prove that mussel culture benefits Eiders.

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